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A reappraisal of the British and Irish dactylorchids, 2. The diploid marsh-orchids

R. M. BATEMAN

Geology Department, Royal Holloway College, Egham, Surrey, TW20 0FX

and

I. DENHOLM

Rothamsted Experimental Station, Harpenden, Herts., AL5 2JQ

ABSTRACT

52 morphological characters were recorded for 169 individuals from 17 British and Irish populations of diploid marsh-orchids. Multivariate analysis suggested that they should be referred to a single species, *Dactylorhiza incarnata* (L.) Soó. Five infraspecific taxa are best treated at subspecific rank: subsp. *incarnata* (L.) Soó, subsp. *coccinea* (Pugsley) Soó, subsp. *cruenta* (O. F. Müller) P. D. Sell, subsp. *pulchella* (Druce) Soó and subsp. *ochroleuca* (Wüstnei ex Boll) Heslop-Harrison f. A new combination, **D. incarnata** subsp. **incarnata** f. **punctata** (Vermeulen) Bateman & Denholm, **comb. nov.**, is proposed. These subspecies showed differing amounts of morphological overlap, which increased considerably when floral pigmentation characters were excluded from the analysis; only *D. incarnata* subsp. *ochroleuca* remained distinct. The other subspecies show only partial morphological differentiation and ecological specialization. A pigmentation scheme is presented to account for the remarkable variation in flower colour. Several supposedly diagnostic characters of *D. incarnata* or its subspecies were found to be unsatisfactory. Possible mechanisms responsible for maintaining the extensive morphological variation within *D. incarnata* are discussed. Principal coordinates provided the basis for revised diagnostic descriptions of *D. incarnata* and its British and Irish subspecies. These are compared with descriptions of Continental plants in an attempt to resolve several taxonomic and nomenclatural controversies. Suitable areas for further research are outlined.

INTRODUCTION AND TAXONOMIC HISTORY

British and Irish diploid marsh-orchids are now generally assigned to a single species, *Dactylorhiza incarnata* (L.) Soó (Early Marsh-orchid). The exceptional variation shown by the diploid marsh-orchids has resulted in the recognition of several morphologically and ecologically differentiated taxa. Table 1 compares 15 previous taxonomic treatments with our classification, and lists authorities for each taxon. *D. incarnata* subspp. *incarnata, coccinea, pulchella* and *ochroleuca* (or synonymous taxa) were treated at varietal rank by early workers (Camus & Camus 1929; Pugsley 1935) but were elevated to subspecies in most subsequent classifications. *D. incarnata* subsp. *gemmana* was given subspecific status only by Heslop-Harrison (1954, 1956), and was omitted from several classifications. *D. incarnata* subsp. *cruenta* was regarded as a full species by most orchidologists, but was relegated to a subspecies of *D. incarnata* by Heslop-Harrison (1954, 1956) and more recently by Sundermann (1980) and Soó (1980).

Most of these classifications were based on a qualitative examination of live or herbarium specimens and were therefore too subjective. Only Heslop-Harrison (1956) attempted to resolve the problem biometrically, but he measured relatively few characters and compared only population means. This method does not take proper account of the extensive variation present within dactylorchid populations;[1] apparently significant differences in population means for

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[1] We regard both 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. COMPARISON OF OUR CLASSIFICATION WITH 14 OTHER TAXONOMIC TREATMENTS OF THE DIPLOID MARSH-ORCHIDS

	British authors				Continental authors						
TAXA (AND SYNONYMS)	Pugsley (1935)	Clapham (1952)	Summerhayes (1951) Hunt & Summerhayes (1965)	Heslop-Harrison (1954, 1956) Clapham (1962) Davies *et al.* (1983)	Camus & Camus (1929)	Soó (1962)	Senghas (1968)	Nelson (1976)	Landwehr (1977)	Sundermann (1980)	Soó (1980)
D. incarnata											
subsp. *incarnata* (L.) Soó (*lanceata, strictifolia*)	var.[2]	subsp.	subsp.	subsp.	var.[2]	subsp.	subsp.	subsp.	subsp.	subsp.	subsp.
'subsp. *gemmana* (Pugsley) Heslop-Harrison f.'[1] (*latissima, macrophylla*)	var.	—		subsp.	—	var.	var.	—	var.	—	—
subsp. *ochroleuca* (Wüstnei ex Boll) P. F. Hunt & Summerhayes (*straminea*)	var.	—	subsp.	subsp.	var.	var.	subsp.	subsp.	subsp.	var.	subsp.[3]
subsp. *coccinea* (Pugsley) Soó (*dunensis*)	var.	subsp.	subsp.	subsp.	var.	subsp.	subsp.	subsp.	subsp.	subsp.	subsp.
subsp. *pulchella* (Druce) Soó (*cambrica*)	var.	var.	subsp.	subsp.	var.	subsp.	subsp.	var.[3]	var.	var.	subsp.
subsp. *cruenta* (O. F. Müller) P. D. Sell	sp.	sp.	sp.	subsp.	sp.	sp.	sp.	sp.	sp.	subsp.	subsp.

[1] Status uncertain.

[2] Type variety not formally described.

[3] Discussed at this taxonomic rank but not formally described.

characters conceal important intra-population variation (Bateman & Denholm 1983a). To overcome this difficulty we measured many morphological characters in representative samples of several diploid marsh-orchid populations and used principal coordinates to analyze data for individual plants. The results provide an objective assessment of the phenetic similarities of individuals, and the amount of separation or overlap of groups of individuals on principal coordinates plots provides a quantitative basis for assessing their taxonomic status (Bateman & Denholm 1983a).

The classification suggested by the results of the present study (shown in the left-hand column of Table 1) is used throughout the paper.

MATERIALS AND METHODS

17 diploid marsh-orchid populations were sampled during 1981 and 1982, including populations of five of the six taxa listed in Table 1 (*D. incarnata* subsp. *gemmana* was not examined). Details of these populations and the sample localities are presented in Table 2.

Morphological characters were recorded for each of ten flowering plants per population, which were chosen randomly in the 11 colonies that contained only one colour variant of *D. incarnata* (Table 2). At five of the six remaining localities, random sampling was performed only within areas where a particular colour variant formed pure stands, and at Wicken nine yellow-flowered plants growing alongside abundant pink- and purple-flowered *D. incarnata* were deliberately selected. 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 up the inflorescence. Destructive studies of tuberoids and stem cavities were not attempted. The 52 quantitative and qualitative (scaled) characters that were recorded largely follow Bateman & Denholm (1983a). However, character 30a (ovary length) replaces character 30 (inflorescence width) and there is an additional character (=39a, position of longest leaf along stem). Fig. 1 illustrates many of the following characters:

A. *Labellum* (14 characters).

All except character 7 were taken from flattened mounted labella. Labellum colour was measured immediately after mounting as it subsequently deepened rapidly. The base colour of the lower part of each labellum was matched to the nearest colour block of the Royal Horticultural Society Colour Chart (Anon. 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 white at the centre of the triangle. The corners correspond to pure blue, pure green and pure red (Fig. 2). Density of pigment is measured by a third coordinate (reflectivity, 'Y'), which decreases in value from the centre of the triangle outwards and is represented on Fig. 2 by dashed contours.

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).

TABLE 2. DETAILS OF SAMPLE LOCALITIES AND STUDY POPULATIONS

Subspecies	Habitat and locality	Grid reference	Altitude (m O.D.)	Soil parent materials	Soil pH (in H_2O)	Approx. no. of plants	Peak flowering period[1]	Presence (and frequency) of other dactylorchids[2]
incarnata	Meadow, BLAGROVE Common, Sandon, Herts., v.c. 20	52/326.337	135	Till	6·3–7·5	4000	5/4–6/1	FF(c) FF×MPr(o) MPr(f) MPr×II(vr) FF×II(r)
	Marsh, Rushy Meadow, TRING Rural, Herts., v.c. 20	42/907.127	105	Peat & alluvium/ chalk	7·6	16	6/1	MPr(o) FF×MPr(vr)
	Marsh, W. LLYN RHOS-DDU, Newborough, Anglesey, v.c. 52	23/420.645	10	Peat/Precambrian schist & gneiss	—	15	5/4–6/1	MP(o)
coccinea	Marshy meadow, RHOS-Y-GAD, Pentraeth, Anglesey, v.c. 52	23/510.788	35	Peat/till	6·8	50	6/1	IP(vr) MP(o) FF(o) MT(f) McE(o) McE×MP(vr) FF×MP(vr)
	Dune slack, NEWBOROUGH Warren, Anglesey, v.c. 52	23/424.621	10	Blown sand/Precambrian schist & gneiss	7·6	5000	5/4	MP(o) FF×MP(vr)
	Marshy meadow by Cob Pool, MALLTRAETH, Anglesey, v.c. 52	23/410.680	1	Peat and blown sand/ coal measures	7·2	70	6/1	MP(f) FF×MP(vr)
	Dune slack, AINSDALE, S. Lancs., v.c. 59	34/296.120	3	Blown sand/Keuper marl	8·1	1000	6/2	MPr(vr)
	Dune slack, HOLME, W. Norfolk, v.c. 28	53/709.448	2	Blown sand	7·2	1000	7/1	II(o)
cruenta	Fen, S.W. LOUGH CARRA, Ballinrobe, W. Mayo, v.c. H27	02/164.684	25	Carboniferous limestone	7·8	150	6/1–6/2	FF(r)
	Pavement, S. LOUGH GELAIN, Corrofin, Co. Clare, v.c. H9	11/314.944	35	Carboniferous limestone	7·3	100	6/2	FF(o)
	Fen, E. LOUGH BUNNY, Gort, Co. Clare, v.c. H9	11/382.975	20	Peat/Carboniferous limestone	7·7	150	6/2	FF(f)
pulchella	Marsh, EAST WALTON Common, W. Norfolk, v.c. 28	53/735.165	15	Peat/marine clay & sand/chalk	6.0[3]	35	6/1–2	II(vr) FF(o) MPr(vr)
	Bog, THURSLEY Common, Surrey, v.c. 17	41/904.416	55	Peat/Lower greensand	6·0[3]	1000	6/2	McE(r)
	Bog, N. of STEPHILL BOTTOM, Beaulieu, S. Hants., v.c. 11	41/360.061	20	Peat/Barton sand	4·5[3]	100	6/1	McE(r)
	Bog, BAGSHOT Moor, east Boldre, S. Hants., v.c. 11	41/368.000	35	Peat/Plateau gravel	4·9[3]	100	6/2–3	McE(vr)
	WICKEN Fen, Cambs., v.c. 29	52/556.701	6	Peat/Gault clay	7·6[3]	9	6/2	II(f) IP(f)
ochroleuca	CHIPPENHAM Fen, Cambs., v.c. 29	52/6—.6—	12	Peat/chalk	7·7	50	6/1	II(vr) MPr(f)

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 infloresence).
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. Length of peripheral cells (mean of 10–30 cells).
27. Mean shape of peripheral cells, on a scale 1–3 (1=rounded, often barrel-shaped; 2=subangular; 3=angular).

E. *Stem and inflorescence* (6 characters).

28. Stature.
29. Inflorescence length.
30a. Ovary length.
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* (12 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 summarised as characters 37–42.

FOOTNOTES TO TABLE 2

[1] The number before the oblique denotes the month, number(s) after the weeks of that month. Observations were made in 1981 (subsp. *cruenta*) and 1982 (all other subspecies), both particularly early seasons.

[2] FF=*D. fuchsii* subsp. *fuchsii*
McE=*D. maculata* subsp. *ericetorum*
II=*D. incarnata* subsp. *incarnata*
IP=*D. incarnata* subsp. *pulchella*
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.

[3] Value approximate due to very large amount of organic matter in sample.

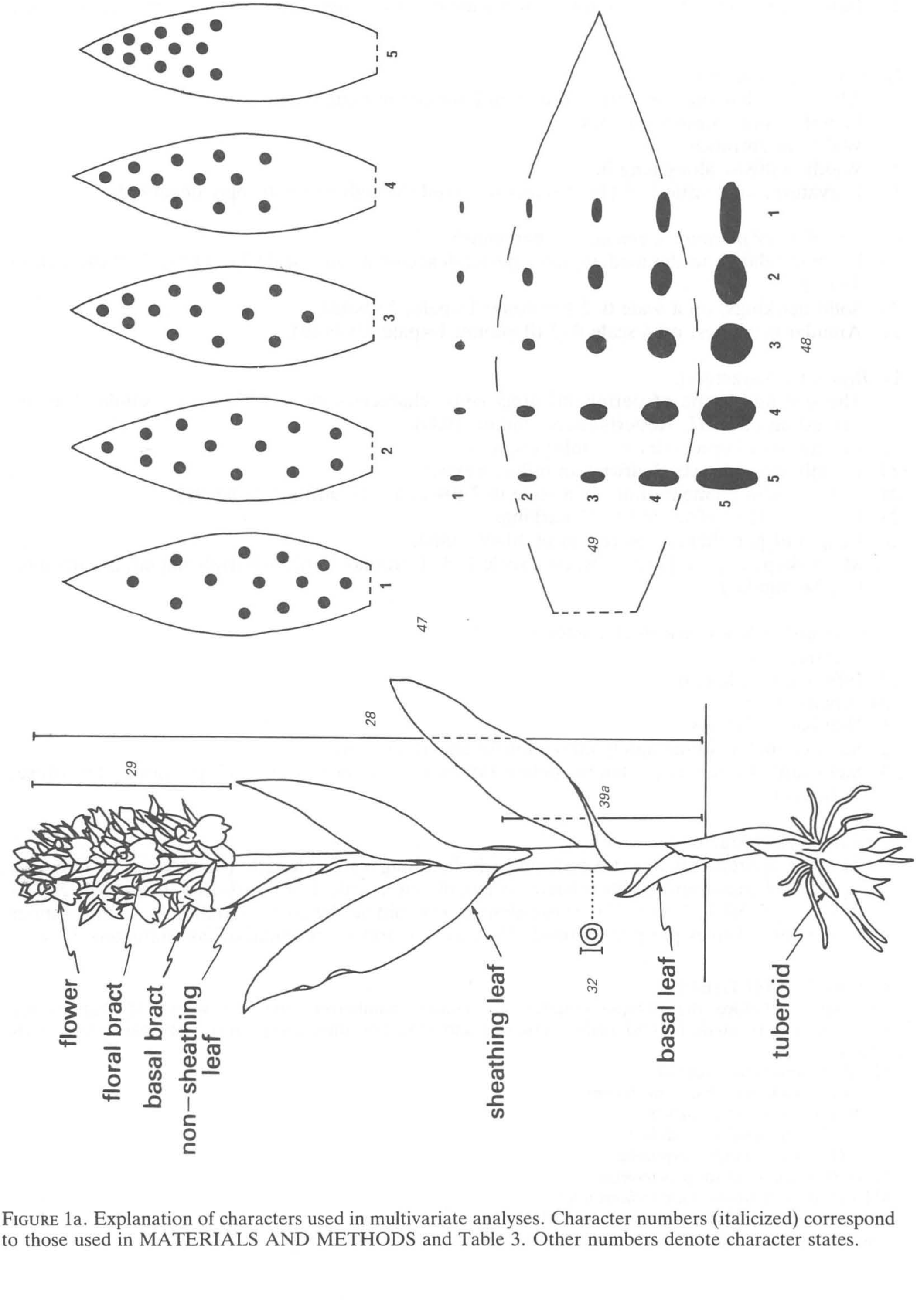

FIGURE 1a. Explanation of characters used in multivariate analyses. Character numbers (italicized) correspond to those used in MATERIALS AND METHODS and Table 3. Other numbers denote character states.

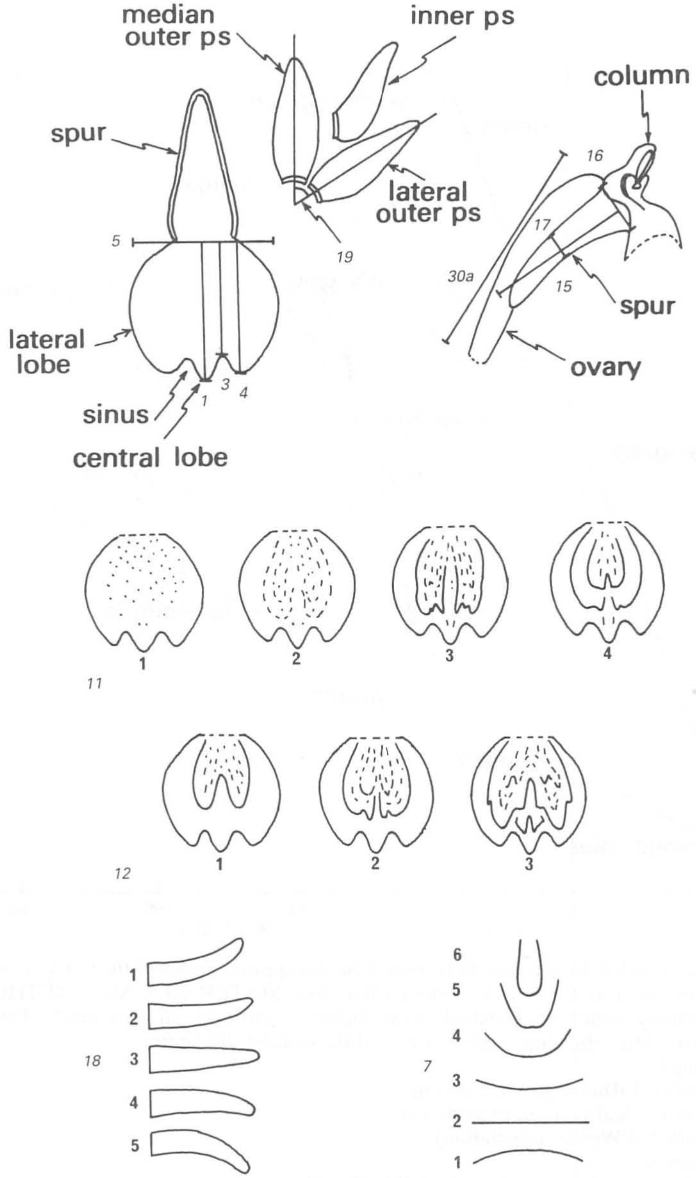

FIGURE 1b. Explanation of characters used in multivariate analyses. Character numbers (italicized) correspond to those used in MATERIALS AND METHODS and Table 3. Other numbers denote character states. ps=perianth segment.

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 (width of longest leaf was also recorded if it was not the widest).

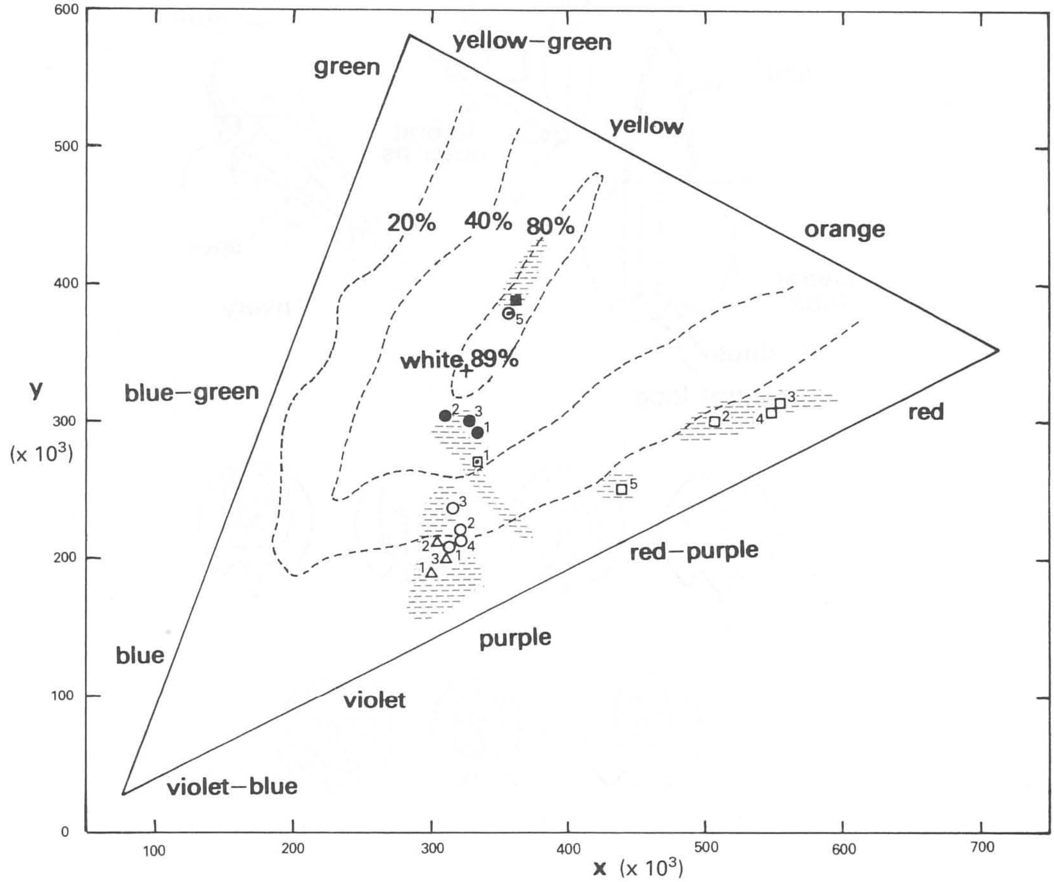

FIGURE 2. Variation of labellum colour in *D. incarnata*. An approximation of the C.I.E. colour triangle, derived from coordinates given in the R.H.S. Colour Chart (see MATERIALS AND METHODS). Dashed lines represent reflectivity contours. Hatched areas include points for all individual plants, symbols denote population means. The following symbols are used throughout the figures:
● subsp. *incarnata*
□ subsp. *coccinea* (⊡ Rhos-y-gad population)
△ subsp. *cruenta* (◬ leaf-marked individuals)
○ subsp. *pulchella* (⊙ Wicken population)
■ subsp. *ochroleuca*
Superscripts denote populations (shown in full in Fig. 5).

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).
39a. Height of base of longest leaf above ground level.
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.* 1mm; 2=*c.* 1·5mm; 3=*c.* 2·5mm; 4=*c.* 4mm; 5=*c.* 6mm).
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 ten indices, which summarise 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. Width of longest 1f/(width of longest 1f+C37).
h. Percentage of stem below base of longest leaf. 100×C39a/C28.
i. Ovary length as a percentage of floral bract length. 100×C30a/C23.
j. Spur length as a percentage of ovary length. 100×C15/C30a.

Data were analyzed by multivariate methods using the 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). The 44 remaining characters were used to compute two symmetrical matrices of indices that quantified the similarities of pairs of data sets using Gower's (1971) coefficient of similarity:

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

where S_{ij} 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 then linked by maximum similarities to yield a minimum spanning tree expressing their 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 incorporating positively or negatively correlated characters that are most variable and therefore of potential diagnostic value. The first two principal coordinates (PC1, PC2) were plotted together to assess the degree of morphological separation of taxa in these dimensions.

VARIATION IN SINGLE CHARACTERS

Population means for all recorded characters are listed in Table 3, with sample standard deviations where applicable.

TABLE 3. POPULATION MEANS (AND SAMPLE STANDARD DEVIATIONS IN PARENTHESES WHERE APPROPRIATE) OF RECORDED CHARACTERS

Character:	Labellum													
Population	1 mm	2	(3)[1] mm	(4) mm	5 mm	6	7	8 C.I.E. units	9	10 %	11	12	13	14
BLAGROVE	7·09 (0·54)	0·9	5·51 (0·52)	5·96 (0·65)	8·25 (0·47)	2·0	4·5	332·9 (5·1)	292·5 (11·7)	59·0 (7·9)	2·0	2·0	1·2	0
TRING	5·75 (0·64)	0·2	4·50 (0·57)	4·85 (0·49)	6·09 (0·63)	2·2	5·2	310·2 (3·8)	303·1 (3·5)	75·9 (3·5)	2·9	2·0	1·6	0·1
LLYN RHOS-DDU	5·79 (0·43)	0·9	4·58 (0·29)	5·06 (0·38)	7·11 (0·91)	1·8	5·5	328·2 (6·7)	299·4 (3·4)	64·0 (4·2)	3·0	1·2	1·6	0·4
RHOS-Y-GAD	5·36 (0·49)	0·6	4·25 (0·33)	4·68 (0·45)	6·27 (0·67)	2·0	4·8	333·8 (16·7)	267·4 (28·2)	46·8 (16·1)	3·4	2·0	2·1	0·2
NEWBOROUGH	4·93 (0·23)	0·7	3·96 (0·25)	4·26 (0·23)	5·51 (0·38)	2·3	5·3	508·5 (8·5)	300·4 (3·4)	12·8 (2·5)	3·0	2·0	1·8	0·4
MALLTRAETH	5·68 (0·42)	1·0	4·53 (0·44)	4·80 (0·44)	6·80 (0·46)	2·0	5·8	552·1 (12·1)	313·3 (5·9)	10·3 (2·4)	3·0	1·9	1·6	0·9
AINSDALE	6·09 (0·38)	0·7	5·01 (0·61)	5·53 (0·45)	7·92 (1·03)	2·2	4·7	542·3 (37·3)	310·9 (12·7)	13·3 (3·9)	3·1	2·1	2·0	0·7
HOLME	6·07 (0·34)	1·0	4·80 (0·36)	5·28 (0·33)	6·72 (0·45)	2·5	5·1	439·4 (5·1)	250·3 (0·9)	9·5 (1·6)	3·0	1·8	2·0	0·7
LOUGH CARRA	6·15 (0·40)	1·0	4·92 (0·53)	5·28 (0·74)	7·31 (0·90)	1·9	3·6	300·5 (13·6)	188·0 (24·1)	14·6 (5·2)	4·0	3·0	2·8	0·7
LOUGH GELAIN	6·96 (0·75)	0·8	5·63 (0·95)	5·91 (1·02)	8·00 (1·59)	1·9	3·5	306·5 (11·4)	213·4 (25·6)	20·3 (7·6)	3·5	2·6	1·9	0·3
LOUGH BUNNY	6·37 (0·58)	0·9	5·11 (1·03)	5·44 (0·94)	7·66 (1·14)	2·0	4·1	312·4 (12·0)	203·1 (23·3)	16·9 (6·1)	3·3	2·4	2·7	0·6
EAST WALTON	6·48 (0·29)	0·7	5·59 (0·27)	5·87 (0·28)	7·86 (0·34)	2·1	4·5	309·2 (1·0)	207·6 (16·0)	17·2 (3·6)	3·0	1·0	2·0	0·1
THURSLEY	5·75 (0·37)	0·4	4·70 (0·62)	4·95 (0·68)	6·45 (0·75)	2·3	5·4	318·6 (9·2)	223·0 (25·1)	22·2 (7·0)	3·3	2·0	2·4	0·5
STEPHILL	6·19 (0·76)	0·9	5·20 (0·83)	5·47 (0·82)	7·47 (1·10)	2·3	5·4	315·1 (2·8)	238·4 (42·7)	27·3 (11·4)	3·1	1·8	2·1	0·2
BAGSHOT	6·28 (0·41)	0·6	5·10 (0·51)	5·50 (0·49)	7·26 (0·42)	2·4	5·0	318·9 (9·0)	217·7 (44·5)	22·0 (12·8)	3·1	2·1	2·0	0·3
WICKEN	6·72 (0·61)	0·7	5·22 (0·44)	5·43 (0·43)	8·77 (0·63)	2·2	5·6	352·0 (0)	381·0 (0)	85·0 (0)	0	0	0	0·2
CHIPPENHAM	7·09 (1·00)	1·0	4·60 (0·93)	5·15 (0·96)	8·98 (0·81)	1·7	5·1	352·0 (0)	381·0 (0)	85·0 (0)	0	0	0	1·0

[1] Characters in parentheses were not used in multivariate analyses.

TABLE 3 (cont.) POPULATION MEANS (AND SAMPLE STANDARD DEVIATIONS IN PARENTHESES WHERE APPROPRIATE) OF RECORDED CHARACTERS

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
BLAGROVE	6·47 (0·59)	3·84 (0·20)	3·21 (0·16)	4·0	4·9	0·9	0	31·8 (4·5)	20·5 (2·7)	0	0	44·0 (5·8)	1·0
TRING	6·19 (0·40)	2·68 (0·30)	2·12 (0·15)	4·3	4·3	1·0	0·1	26·8 (7·1)	14·7 (3·1)	0	0	53·1 (5·7)	1·0
LLYN RHOS-DDU	7·16 (0·41)	3·34 (0·35)	2·46 (0·23)	4·5	4·8	1·1	0	21·7 (2·0)	14·9 (1·3)	0·4	0	48·8 (6·3)	1·1
RHOS-Y-GAD	6·44 (0·68)	2·60 (0·39)	1·97 (0·21)	4·4	4·7	1·1	0·9	15·3 (2·9)	11·3 (2·3)	1·5	0	46·4 (3·9)	1·1
NEWBOROUGH	6·10 (0·49)	3·08 (0·14)	2·73 (0·16)	4·4	4·9	0·8	0	14·3 (2·5)	10·6 (2·0)	1·8	0	46·1 (2·5)	1·5
MALLTRAETH	6·35 (0·44)	3·02 (0·25)	2·42 (0·20)	4·5	4·2	1·0	0	16·6 (2·1)	13·4 (1·3)	0·8	0	47·5 (7·2)	1·1
AINSDALE	6·92 (0·85)	3·70 (0·56)	2·85 (0·27)	4·7	5·0	0·7	0	18·6 (4·8)	13·7 (3·0)	1·6	0	46·9 (4·3)	1·7
HOLME	6·65 (0·63)	3·13 (0·25)	2·29 (0·24)	3·5	4·9	0·6	0·1	19·1 (2·3)	13·8 (2·4)	1·9	0	44·0 (6·9)	1·3
LOUGH CARRA	6·68 (0·69)	3·07 (0·48)	2·52 (0·27)	3·9	3·0	0·5	1·7	20·3 (3·2)	15·1 (1·9)	1·6	0·1	53·0 (8·4)	1·2
LOUGH GELAIN	6·74 (0·57)	3·28 (0·34)	2·71 (0·27)	4·2	2·4	1·2	1·2	21·7 (4·9)	15·7 (2·6)	1·5	0·3	52·2 (6·0)	1·1
LOUGH BUNNY	7·07 (0·70)	3·29 (0·37)	2·58 (0·35)	4·0	4·0	1·5	1·1	21·5 (2·9)	15·5 (1·7)	1·6	0	45·5 (3·1)	1·4
EAST WALTON	6·81 (0·26)	3·23 (0·18)	2·61 (0·17)	4·2	4·0	1·0	0	24·7 (1·3)	15·8 (1·6)	1·5	0	52·0 (6·6)	1·1
THURSLEY	5·88 (0·42)	3·12 (0·34)	2·47 (0·28)	4·5	3·1	1·7	1·9	19·3 (3·5)	13·1 (1·8)	0·6	0	58·7 (20·9)	1·1
STEPHILL	6·41 (0·98)	3·48 (0·54)	2·72 (0·50)	4·2	3·9	1·4	0·3	21·7 (4·7)	11·6 (3·1)	0·3	0	50·9 (6·5)	1·3
BAGSHOT	6·75 (0·78)	3·56 (0·28)	3·06 (0·12)	4·2	2·9	1·3	0·4	19·5 (3·7)	12·7 (2·3)	0·6	0	58·1 (7·0)	1·8
WICKEN	7·58 (0·36)	3·16 (0·26)	2·63 (0·27)	3·4	4·4	0	0	19·8 (3·3)	14·4 (1·8)	0	0	53·3 (7·1)	2·0
CHIPPENHAM	5·09 (1·89)	3·90 (0·71)	3·05 (0·13)	3·1	3·3	0	0	39·5 (8·3)	22·8 (4·5)	0	0	49·8 (5·9)	1·7

TABLE 3 (cont.) POPULATION MEANS (AND SAMPLE STANDARD DEVIATIONS IN PARENTHESES WHERE APPROPRIATE) OF RECORDED CHARACTERS

Character:	Stem and inflorescence						Leaves											
Population	28 cm	29 mm	30a mm	31	32 mm	33	34	35	36	37 mm	38 mm	39	39a cm	40	41	42	43	44
BLAGROVE	25·5 (5·5)	62·7 (20·4)	13·3 (1·5)	32·2 (10·0)	8·14 (1·23)	0	3·9	1·1	1·0	119·5 (14·0)	25·0 (4·6)	1·8	7·4	1·7	2·0	2·8	1·6	1·0
TRING	25·1 (9·6)	61·0 (19·2)	9·8 (1·8)	29·2 (9·5)	7·23 (1·00)	0	4·4	1·1	1·0	123·5 (19·5)	22·7 (2·3)	1·7	4·5	1·8	2·0	2·6	1·3	2·0
LLYN RHOS-DDU	31·2 (3·8)	71·4 (10·3)	10·3 (1·2)	27·6 (5·9)	6·58 (0·57)	0	4·3	1·5	0·9	102·3 (16·1)	26·5 (3·4)	1·6	6·6	1·7	2·2	2·7	1·2	1·9
RHOS-Y-GAD	18·2 (5·5)	32·9 (8·1)	9·0 (0·9)	13·1 (4·4)	3·84 (0·57)	1·1	3·9	0·7	0·3	75·7 (14·4)	12·3 (2·5)	2·1	3·6	1·4	2·1	2·8	1·4	1·2
NEWBOROUGH	9·9 (2·5)	35·9 (11·8)	9·8 (0·9)	11·7 (4·3)	3·13 (0·33)	0·6	3·6	0·5	1·0	47·1 (9·3)	12·4 (2·4)	1·8	0·5	1·7	2·1	2·4	1·2	1·0
MALLTRAETH	13·9 (2·1)	38·4 (5·7)	11·1 (0·9)	17·3 (5·4)	4·17 (0·85)	0·4	4·0	1·7	1·0	87·5 (12·2)	16·3 (3·2)	1·7	3·1	2·3	2·7	3·0	1·2	1·5
AINSDALE	10·7 (2·9)	47·6 (13·5)	11·3 (2·6)	28·2 (14·5)	5·29 (2·19)	0·4	4·0	1·1	1·0	73·9 (13·4)	19·7 (7·3)	1·7	1·2	1·8	2·1	2·6	0·9	1·4
HOLME	16·5 (7·4)	37·3 (8·5)	8·7 (1·3)	17·1 (6·7)	4·22 (0·78)	1·5	3·3	1·6	1·0	101·7 (24·0)	14·5 (2·1)	1·8	4·3	2·4	3·0	3·1	0·8	2·1
LOUGH CARRA	15·0 (2·5)	42·3 (7·2)	9·5 (1·0)	21·3 (6·0)	4·53 (0·92)	1·5	3·3	1·1	1·0	70·9 (24·2)	14·7 (3·8)	2·0	—	2·2	2·1	1·9	1·9	1·4
LOUGH GELAIN	15·9 (3·2)	37·6 (7·4)	10·0 (1·1)	13·8 (4·0)	4·02 (0·70)	1·1	3·6	1·0	1·0	93·0 (24·8)	12·5 (2·6)	2·0	—	1·9	1·7	1·9	1·7	1·5
LOUGH BUNNY	21·6 (4·0)	42·0 (5·3)	9·5 (0·8)	17·3 (2·5)	4·32 (0·70)	0·8	3·5	0·9	1·0	79·8 (12·5)	13·2 (3·0)	2·0	—	1·7	2·2	2·2	1·9	1·4
EAST WALTON	30·7 (5·1)	45·4 (9·1)	10·6 (1·0)	25·8 (6·5)	5·09 (0·76)	0·1	3·7	1·2	0·9	130·9 (19·4)	14·4 (2·3)	1·9	11·3	1·4	1·9	2·2	1·9	1·2
THURSLEY	23·5 (6·4)	49·0 (12·4)	9·5 (1·0)	23·3 (10·1)	5·05 (1·27)	0	2·9	0·8	0·4	105·0 (22·8)	13·3 (2·7)	1·9	6·6	1·7	2·0	2·6	1·1	1·7
STEPHILL	19·2 (4·0)	43·4 (15·5)	8·9 (1·9)	21·2 (10·0)	4·64 (2·10)	0	3·0	1·1	0·8	83·8 (24·0)	14·4 (3·8)	1·9	5·0	2·1	2·7	3·0	1·0	2·0
BAGSHOT	19·1 (3·2)	46·3 (10·0)	9·6 (1·1)	33·4 (6·4)	5·07 (0·91)	0	2·9	0·9	1·0	86·4 (9·4)	16·9 (2·3)	1·9	4·3	1·7	2·5	2·8	1·1	1·8
WICKEN	12·1 (3·7)	32·8 (8·5)	9·6 (1·6)	13·3 (3·1)	4·88 (1·12)	0	3·3	0·9	1·0	118·3 (18·4)	20·4 (3·2)	1·7	3·9	2·0	2·6	2·8	1·0	1·3
CHIPPENHAM	34·8 (9·6)	67·4 (20·0)	11·3 (1·7)	33·0 (13·0)	9·97 (2·01)	0	3·5	1·1	1·0	109·8 (14·8)	29·1 (4·1)	2·0	12·1	1·4	2·2	2·5	1·6	1·5

TABLE 3 (cont.) POPULATION MEANS (AND SAMPLE STANDARD DEVIATIONS IN PARENTHESES WHERE APPROPRIATE) OF RECORDED CHARACTERS

Character:	Leaf markings							Indices									
Population	45	(46)[1] %	(47)	(48)	(49)	(50)	51 %	(a)	(b)	(c) mm	(d)	(e) %	(f) fls/cm	(g)	(h) %	(i) %	(j) %
BLAGROVE	0	0	0	0	0	0	0	0·462	1·25	0·44	0·453	24·7	5·2	0·171	38·3	65·5	50·2
TRING	0	0	0	0	0	0	0	0·478	1·17	0·60	0·442	24·9	4·8	0·156	21·5	68·5	64·8
LLYN RHOS-DDU	0	0	0	0	0	0	0	0·451	1·21	0·76	0·425	23·0	4·0	0·203	27·7	69·7	70·5
RHOS-Y-GAD	0	0	0	0	0	0	0	0·461	1·14	0·42	0·433	18·7	4·0	0·139	22·9	82·5	72·0
NEWBOROUGH	0	0	0	0	0	0	0	0·423	1·21	0·70	0·469	35·8	3·3	0·207	6·7	94·5	62·8
MALLTRAETH	0	0	0	0	0	0	0	0·455	1·22	0·27	0·446	28·1	4·5	0·154	29·4	83·5	57·4
AINSDALE	0	0	0	0	0	0	0	0·436	1·18	0·59	0·431	45·2	5·7	0·207	16·2	84·4	62·9
HOLME	0	0	0	0	0	0	0	0·472	1·21	0·79	0·424	25·8	4·5	0·125	30·8	63·7	64·1
LOUGH CARRA	0·4	14·3	3·5	3·5	1·8	0	15·0	0·458	1·22	0·77	0·453	28·6	5·0	0·176	—	63·5	70·7
LOUGH GELAIN	0·3	8·3	3·0	3·0	2·3	0	10·0	0·469	1·24	1·16	0·451	23·5	3·7	0·121	—	62·2	74·6
LOUGH BUNNY	0·2	11·0	1·0	2·5	1·0	0	0	0·456	1·25	0·96	0·440	19·8	4·2	0·143	—	65·0	71·1
EAST WALTON	0	0	0	0	0	0	0	0·452	1·13	0·29	0·449	15·3	5·7	0·099	42·2	67·8	64·7
THURSLEY	0	0	0	0	0	0	0	0·473	1·21	0·83	0·443	21·7	4·6	0·115	36·0	74·0	62·4
STEPHILL	0	0	0	0	0	0	0	0·453	1·17	0·76	0·438	24·0	4·8	0·150	33·0	79·5	70·7
BAGSHOT	0	0	0	0	0	0	0	0·463	1·19	0·80	0·464	24·7	7·3	0·160	28·3	76·6	70·9
WICKEN	0	0	0	0	0	0	0	0·434	1·22	1·03	0·454	28·7	4·1	0·146	46·6	67·3	80·6
CHIPPENHAM	0	0	0	0	0	0	0	0·438	1·48	1·94	0·425	20·2	4·9	0·210	43·8	51·5	44·1

[1] Characters in parentheses were not used in multivariate analyses.

TABLE 4. FLORAL PIGMENTATION SCHEMES FOR THE SUBSPECIES OF *D. INCARNATA*
a) Scheme suggested by observations of Heslop-Harrison (1956).
b) Scheme suggested by observations of Uphoff (1979, 1982) and the present authors.

a)	Purple anthocyanin		Yellow anthoxanthin
Subspecies	Intense	Dilute	(acting as co-pigment)
pulchella	+	−	−
cruenta	+	−	−?
coccinea	+	−	+
incarnata	−	+	+
ochroleuca	−	−	+

b) Subspecies	red anthocyanins[1]	Violet anthocyanin[2]	Yellow anthoxanthin	Combined density of pigments (measured as % reflectivity)
pulchella	+	+	+	dark/moderate
cruenta	+	+	+	dark/moderate
coccinea	+	−	+	dark/moderate/(pale)
incarnata	+	−	+	pale
ochroleuca	−	−	+	very pale

[1] Cyanin (no co-pigment) and Orchicyanin II (cyanin with a non-bathochromic co-pigment).
[2] Orchicyanin I (cyanin with a bathochromic co-pigment).

PIGMENTATION CHARACTERS

The characters showing most variation between subspecies of *D. incarnata* are those determined by the presence and distribution of floral pigments. Consequently, flower colour is the major diagnostic character of the subspecies given in *Flora Europaea* (Soó 1980), and is the only criterion used to distinguish the subspecies in some other treatments. Fig. 2 illustrates the variation in flower colour found in each of the subspecies examined during the present study. Yellow-flowered plants formed a cohesive group, which occurred within the 80% reflectivity contour but was distinct from the maximum (89%) reflectivity point that represents pure white. This group comprised the Chippenham population of *D. incarnata* subsp. *ochroleuca*, the Wicken sample (thought to be anthocyanin-less subsp. *pulchella*), and six pale yellow-flowered plants that were included in samples of subsp. *pulchella* from Thursley, Stephill and Bagshot.

D. incarnata subsp. *incarnata* formed a cohesive group between the 40% and 80% reflectivity contours. The exceptionally variable Rhos-y-gad population of *D. incarnata* subsp. *coccinea* spanned both the 20% and 40% reflectivity contours and overlapped with subsp. *incarnata* on the colour triangle. Flowers of plants from Rhos-y-gad also had an appreciable purple-violet component, and were consequently separated from the other dark (reflectivity <20%), predominantly red-flowered populations of subsp. *coccinea*. We have examined populations of *D. incarnata* subsp. *coccinea* that are intermediate in flower colour to the red-purple-flowered Rhos-y-gad population and the main groups of red-flowered populations in Fig. 2. However, although the Rhos-y-gad population was atypical in flower colour, it resembled the other populations of *D. incarnata* subsp. *coccinea* in most characters (Table 3).

D. incarnata subsp. *cruenta* and subsp. *pulchella* both occupied the violet-purple colour zone and showed almost complete overlap in Fig. 2. These subspecies had flower colours that were either dark (reflectivity <20%) or, less frequently, moderate (20%–40%).

Labellum colours of diploid marsh-orchids can thus be resolved into three groups: red/red-purple (*D. incarnata* subsp. *incarnata* and subsp. *coccinea*), purple/purple-violet (subsp. *cruenta* and subsp. *pulchella*), and yellow (subsp. *ochroleuca* and anthocyanin-less variants of other subspecies). Heslop-Harrison (1956) also recognized these three groups and devised a pigmentation scheme to account for them (Table 4a). He postulated that all the subspecies of *D. incarnata* except subsp. *ochroleuca* contain a purple anthocyanin, which is modified to red in subsp. *incarnata* and subsp. *coccinea* by a yellow anthoxanthin that acts as a co-pigment. Flowers of *D. incarnata* subsp. *ochroleuca* contain only the yellow anthoxanthin, which is masked by anthocyanin in other subspecies and evident only in anthocyanin-less variants (often incorrectly described as albinos). Anthocyanin-less plants of *D. incarnata* subsp. *incarnata* and subsp. *coccinea* should therefore be yellow and those of subsp. *pulchella* and subsp. *cruenta* should be white (i.e. true albinos, lacking all floral pigments) if Heslop-Harrison's scheme is correct.

Flowers of anthocyanin-less plants of *D. incarnata* subsp. *incarnata* and subsp. *coccinea* are indeed yellow (Clarke 1882; Heslop-Harrison 1956), but so are those of subsp. *pulchella* and subsp. *cruenta*. Anthocyanin-less individuals of *D. incarnata* subsp. *pulchella* occurred in four of the five populations that we examined (Stephill, 50% of the population; Bagshot, 30%; Wicken, 5%; Thursley, 1%), but their flowers were without exception suffused with yellow anthoxanthin. We have seen several pale yellow-flowered individuals of *D. incarnata* subsp. *cruenta* at Lough Carra, and Landwehr (1977) illustrated a yellow-flowered individual of this subspecies from Europe. True albinos of *D. incarnata*, presumably the result of non-expression of genes coding for both anthocyanins and anthoxanthins, appear to be very rare. Yellow anthoxanthin is evidently ubiquitous in *D. incarnata*, and therefore cannot be the cause of the red flower colour of subsp. *incarnata* and subsp. *coccinea*.

Chromatographic investigations by Uphoff (1979, 1982) suggest a more probable pigmentation scheme for *D. incarnata* (Table 4b). Flowers of *D. fuchsii* (Druce) Soó, *D. maculata* (L.) Soó, *D. majalis* (Reichenbach) P. F. Hunt & Summerhayes and *D. sambucina* (L.) Soó contain *c.* 10% red Cyanin, 25% red Orchicyanin II (Cyanin plus a non-bathochromic co-pigment) and 65% violet Orchicyanin I (Cyanin plus a bathochromic co-pigment). The synthesis of the co-pigment occurs during anthesis, causing a bathochromic shift in maximum absorbance that is expressed as a change in flower colour from red to purple-violet (Uphoff 1982). Similar colour changes occur during anthesis in flowers of *D. incarnata* subsp. *cruenta* and subsp. *pulchella*, which probably contain Orchicyanin I. The red flowers of *D. incarnata* subsp. *coccinea* and subsp. *incarnata* presumably contain only Cyanin and Orchicyanin II, though some Orchicyanin I may be present in the red-purple-flowered populations of subsp. *coccinea* at Holme and, especially, Rhos-y-gad.

Uphoff (1979) also demonstrated large differences in the total amount of anthocyanins both within and between species of *Dactylorhiza*. We measured density of pigment indirectly, using percentage reflectivity to define four categories: dark, reflectivity 8–20%; moderate, 20–40%; pale, 41–80%; very pale, 81–89%. Flowers of *D. incarnata* subspp. *cruenta, pulchella* and *coccinea* are predominantly dark, though flowers of subsp. *cruenta* and subsp. *pulchella* are occasionally moderate and those of subsp. *coccinea* are rarely moderate or pale (Fig. 2, Table 4b). Flowers of *D. incarnata* subsp. *incarnata* are pale (reflectivity <55% in all the plants that we examined), and those of subsp. *ochroleuca* and anthocyanin-less variants of other subspecies are very pale. *D. incarnata* subsp. *incarnata* and subsp. *coccinea* probably contain the same combination of anthocyanins, though they are much more concentrated in most individuals of subsp. *coccinea*.

The presence and distribution of anthocyanins also determine characters that describe markings on labella, lateral outer perianth segments, leaves and bracts, and also diffuse bract and stem pigmentation, so these characters are not expressed by *D. incarnata* subsp. *ochroleuca*. *D. incarnata* subsp. *cruenta* is characterized by bold, broad labellum markings that are deficient in dashes and often cover most of the labellum. *D. incarnata* subspp. *pulchella, coccinea* and *incarnata* usually have less distinct loop markings that enclose dashes and cover less than two-thirds of the labellum.

Lateral outer perianth segment markings are usually solid in *D. incarnata* subsp. *incarnata* and subsp. *coccinea*, but are occasionally annular in subsp. *pulchella* and often annular in subsp. *cruenta*. *D. incarnata* subspp. *coccinea*, *cruenta* and *pulchella* frequently have anthocyanin pigmentation on the bracts, which often extends to the upper part of the stem in subsp. *cruenta* and subsp. *coccinea*. Vegetative anthocyanins are reddish-brown in *D. incarnata* subsp. *coccinea* but purplish-brown in subsp. *cruenta* and subsp. *pulchella*. Leaf and bract markings are virtually restricted to some individuals of *D. incarnata* subsp. *cruenta*, and occur independently of variation in other pigmentation characters such as density (i.e. reflectivity) of flower colour and boldness of labellum markings.

TABLE 5. VARIATES CONTRIBUTING APPRECIABLY TO THE FIRST TWO PRINCIPAL COORDINATES, LISTED IN ORDER OF DECREASING IMPORTANCE. ANALYSIS INCLUDES FLORAL PIGMENTATION CHARACTERS

Principal coordinate	PC1			PC2		
Percentage of variance accounted for	23·9%			10·7%		
Taxonomic significance of coordinate[1]	*ochroleuca*+anthocyanin-less *pulchella*: *incarnata*: *coccinea*+*pulchella*. *cruenta*			anthocyanin-less *pulchella*: *ochroleuca*, also *coccinea*: 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 more conspicuous labellum markings tend to occur towards the right side of PC1 on Fig. 3, whereas plants with pale-coloured labella tend to occur towards the left side).	11	Labellum markings, type	+	8	Labellum colour, 'x'	−
	10	Labellum colour, reflectivity (Y)	−	39a	Position of longest leaf up stem	+
	13	Labellum markings, contrast	+	19	L.o.p.s., position	−
	9	Labellum colour, 'y'	−	21	L.o.p.s., annular markings	+
	24	Bract anthocyanin	+	23	Length of floral bracts	+
	12	Labellum markings, distribution	+	28	Plant height	+
	38	Width of widest leaf	−	22	Length of basal bracts	+
	32	Stem diameter	−	43	Hooding of leaf tips	+
	33	Stem anthocyanin	+	7	Labellum lateral lobe reflexion	−
	22	Length of basal bracts	−	1	Labellum, length to central lobe	+
	21	L.o.p.s.[2], annular markings	+			
	37	Length of longest leaf	−			
	23	Length of floral bracts	+			
	20	L.o.p.s., solid markings	−			

[1] Stop indicates partial separation, colon indicates more-or-less complete separation.

[2] L.o.p.s.=lateral outer perianth segments.

TABLE 6. VARIATES CONTRIBUTING APPRECIABLY TO THE FIRST TWO PRINCIPAL COORDINATES, LISTED IN ORDER OF DECREASING IMPORTANCE. ANALYSIS EXCLUDES FLORAL PIGMENTATION CHARACTERS

Principal coordinate		PC1			PC2	
Percentage of variance accounted for		18·4%			12·5%	
Taxonomic significance of coordinate[1]		*ochroleuca*: anthocyanin-less *pulchella*. *incarnata*. *coccinea*+*pulchella*. *cruenta*			*ochroleuca*+*cruenta*. remainder	
Variate number, variate name, and direction of increase in value of variate in relation to increase in value of vector (see Table 5).	24	Bract anthocyanin	+	2	Presence of labellum sinuses	−
	32	Stem diameter	−	5	Labellum, width	+
	38	Width of widest leaf	−	39a	Position of longest leaf up stem	+
	22	Length of basal bracts	−	7	Labellum lateral lobe reflexion	−
	33	Stem anthocyanin	+	18	Spur curvature	−
	29	Inflorescence length	−	1	Labellum, length to central lobe	+
	31	Number of flowers	−	23	Length of floral bracts	+
	23	Length of floral bracts	−	33	Stem anthocyanin	+
	37	Length of longest leaf	−			
	28	Plant height	−			

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[1] Stop indicates partial separation, colon indicates more-or-less complete separation.

OTHER CHARACTERS

D. incarnata is said to have entire or sub-entire labella (Summerhayes 1951; Clapham 1962; Soó 1980), but most plants in the majority of populations that we studied possessed labellum sinuses (Table 3). Furthermore, the strong reflexion of the lateral lobes that is said to characterize labella of *D. incarnata* is not always evident, particularly in subsp. *cruenta*, and the supposedly upright lateral outer perianth segments are often nearer horizontal in subspp. *cruenta*, *pulchella* and *ochroleuca*. Spurs of *D. incarnata* are usually broad and fairly long. Soó's (1980) statement that the spur is less than half the length of the ovary was true of only 7% of the plants that we examined. Sundermann (1975) used spur length/ovary length (our index 'j') to differentiate subspecies of *D. incarnata*, but our populations showed little variation in this ratio (Table 3).

Leaves of *D. incarnata* are fairly constant in number but variable in size and shape. *D. incarnata* subsp. *incarnata* and subsp. *ochroleuca* have relatively tall, broad stems, long many-flowered inflorescences and are generally the most vigorous subspecies. They also have large bracts; even the floral bracts of subsp. *ochroleuca* often considerably exceed the flowers. Their leaves are large and particularly broad (index 'g' values >0·2, Table 3), suggesting that leaf width is a useful diagnostic character for *D. incarnata* subsp. *incarnata* and subsp. *ochroleuca*, though Heslop-Harrison (1956) obtained narrower mean leaf widths for populations of these subspecies. Only 50% of all the plants that we measured had yellow-green leaves and only 41% had leaves with strongly hooded (cucculate) tips, features that supposedly characterize *D. incarnata* (Summerhayes 1951; Clapham 1962; Soó 1980). The peripheral bract cells of all subspecies of *D. incarnata* are small and generally rounded.

MULTIVARIATE ANALYSES AND TAXONOMIC STATUS

33 of the 44 characters used for multivariate analyses contributed appreciably to the first two principal coordinates (Table 5). The first principal coordinate (PC1 on Fig. 3) accounted for 23·9% of the total variance, and partially separated individuals into four groups comprising subsp. *incarnata*, subspp. *coccinea* and *pulchella*, subsp. *cruenta*, and plants lacking anthocyanins. Although PC2 was weaker, accounting for only 10·7% of the variance, it partially separated *D. incarnata* subsp. *ochroleuca* from other plants lacking anthocyanins, and subsp. *coccinea* from subsp. *pulchella*. PC1 and PC2 together resolved individuals into six groups (Fig. 3); five corresponded to subspecies recognized by Heslop-Harrison (1954, 1956), the sixth comprised anthocyanin-less plants that showed only minimal overlap with *D. incarnata* subsp. *ochroleuca*. There was a marked discontinuity between plants with anthocyanins and those without.

The six characters contributing most to PC1 and two of the four most important contributors to PC2 were determined by the presence and/or density of anthocyanins (Table 5). This resulted in the scattered distribution on Fig. 3 of Rhos-y-gad plants of *D. incarnata* subsp. *coccinea*, which were unusually variable in flower colour. When anthocyanin-dependent floral characters (nos. 8–13, 20–21) were omitted from principal coordinates analyses, the six groups evident in Fig. 3 were much less cohesive and their overlap increased considerably (Fig. 4), illustrating the importance of these characters for separating subspecies of *D. incarnata*. Much of the remaining separation reflected variation in characters describing vegetative anthocyanins, plant size and vigour, and the depth of labellum sinuses (Table 6). The Chippenham population of *D. incarnata* subsp. *ochroleuca* persisted as a separate cohesive group because of its vegetative vigour and large, deeply three-lobed labella, but other anthocyanin-less plants were separated from subsp. *ochroleuca* and occurred in the zone of overlap of subsp. *incarnata* and subsp. *pulchella*. The close affinity of Rhos-y-gad to other populations of *D. incarnata* subsp. *coccinea* is more apparent on this second plot (Fig. 4).

Minimum spanning trees of population means supported these taxonomic relationships (Fig. 5). In the tree incorporating floral pigmentation characters (Fig. 5a), the weakest links (i.e. lowest maximum similarities) occurred between the Chippenham population of *D. incarnata* subsp. *ochroleuca* and subsp. *incarnata*, and between subsp. *incarnata* and subsp. *pulchella*. The sample of anthocyanin-less plants from Wicken was loosely attached to the Stephill population of *D. incarnata* subsp. *pulchella* and had a very low similarity (78·8%) to the Chippenham population of

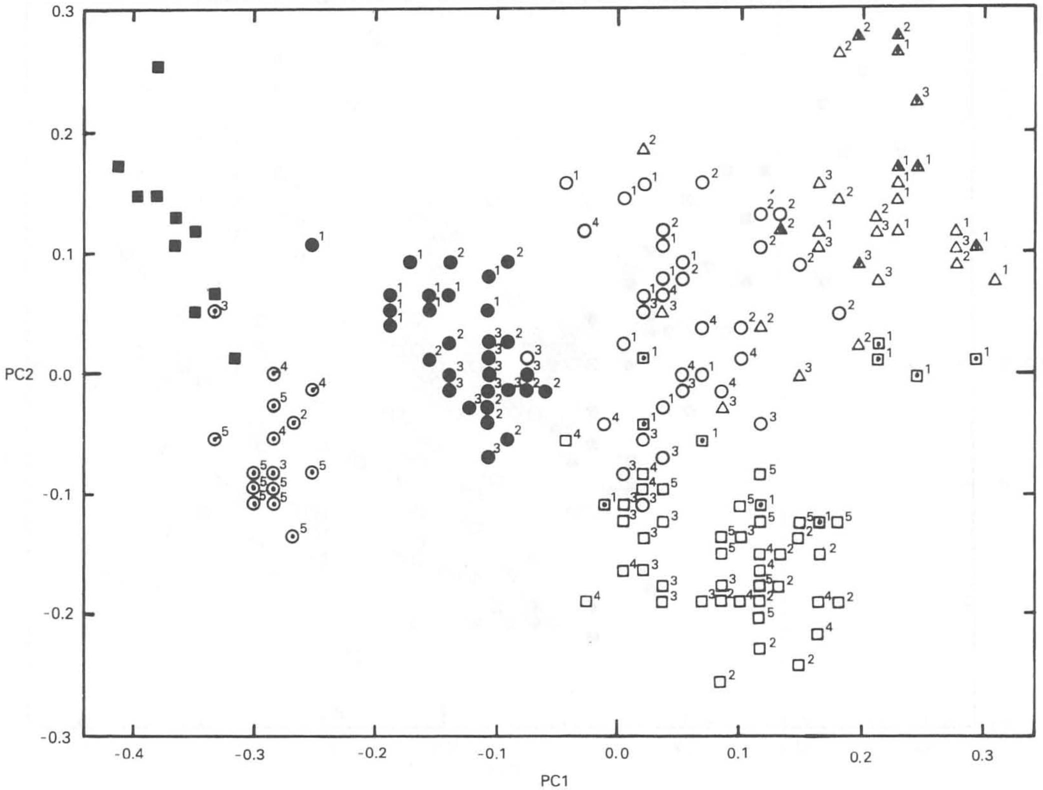

FIGURE 3. Principal Coordinates plot of PC1:PC2 for individual plants. Analysis includes floral pigmentation characters.
See Fig. 2 for explanation of symbols.

subsp. *ochroleuca*. The very cohesive group of *D. incarnata* subsp. *cruenta* populations surprisingly also included the East Walton population of subsp. *pulchella*, showing that the maximum similarities of populations of different subspecies can be greater than those of populations of the same subspecies. In the tree excluding anthocyanin-dependent floral characters (Fig. 5b), subsp. *incarnata* was loosely connected to subsp.*coccinea* (including the Rhos-y-gad population) rather than subsp. *pulchella*. The link between the sample of anthocyanin-less plants from Wicken and subsp. *pulchella* was strengthened, suggesting that the Wicken plants should be referred to this taxon rather than to subsp. *ochroleuca*.

We argued in an earlier paper (Bateman & Denholm 1983a) that the four British and Irish tetraploid marsh-orchid taxa formerly regarded as species merited only subspecific status because they showed mutual and approximately equal overlap on principal coordinates plots. The amount of separation of the diploid marsh-orchids was less consistent (Figs 3 & 4); the subspecies showed varying degrees of overlap on the plots. However, the discontinuities evident between some subspecies in Fig. 3 were largely due to variations in floral pigmentation characters, which must be interpreted with caution since they may reflect plëiotropism of few genes. Nevertheless, we consider that these colour differences, the partial morphological differentiation apparent even when pigmentation characters were excluded (Fig. 4), and some ecological specialization (see 'Evolutionary Aspects'), together justify the retention of these taxa as subspecies, though they are recognizable primarily by differences in population means for only a few characters. Other published data (Heslop-Harrison 1956) show that some of the subspecies are more variable than our results suggest and are unlikely to be separated by morphological discontinuities. The purple-

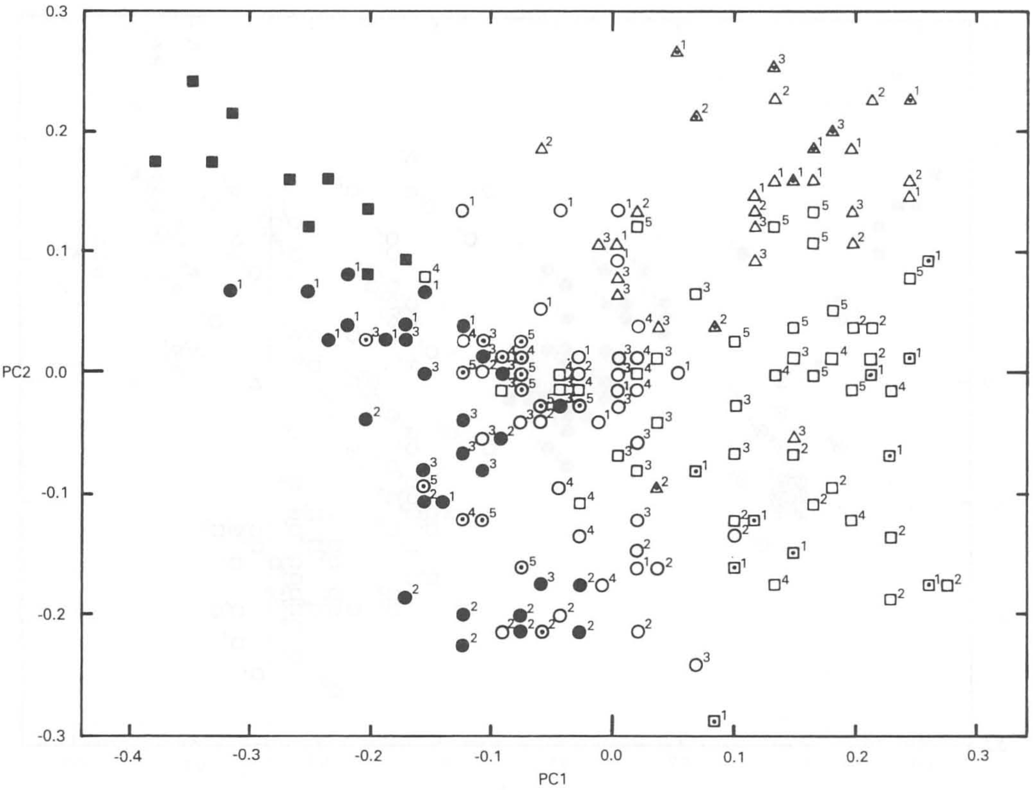

FIGURE 4. Principal Coordinates plot of PC1:PC2 for individual plants. Analysis excludes floral pigmentation characters.
See Fig. 2 for explanation of symbols.

flowered *D. incarnata* subsp. *pulchella* and subsp. *cruenta* pose the greatest taxonomic problems; they share the same range of purple/purple-violet flower colour (Fig. 2) and overlap considerably on the principal coordinates plots. Consequently, the identity of some populations, particularly in western Ireland, has been controversial (see 'Classification').

Our analyses suggest that *ochroleuca* is the most distinct subspecies of *D. incarnata*; further study may show that it merits specific rank. Unfortunately, it has become so rare in Britain that such work will need to be performed on Continental material.

EVOLUTIONARY ASPECTS OF VARIATION IN *D. INCARNATA*

The causes of the extensive variation within and between populations of *D. incarnata* are poorly understood. Small-scale experiments using different cultivation regimes showed that many floral characters of this species are probably under direct genetic control (Heslop-Harrison 1956). However, vegetative characters, which are generally more subsceptible than floral characters to environmental modification (Clausen *et al.* 1940; Heslop-Harrison 1953; Cook 1968; Jones & Luchsinger 1979), have not been examined in this way. Until more is known of the relative contributions of genotype and environment to this variation, both the extent of evolutionary divergence of the subspecies and the adaptive significance of the differences between them must remain speculative. Any genetic differentiation that does exist could only be maintained if one or more possible barriers to gene flow between subspecies prevents (or restricts) their hybridization. Most of the potential barriers to gene exchange listed by Stace (1975) are considered below.

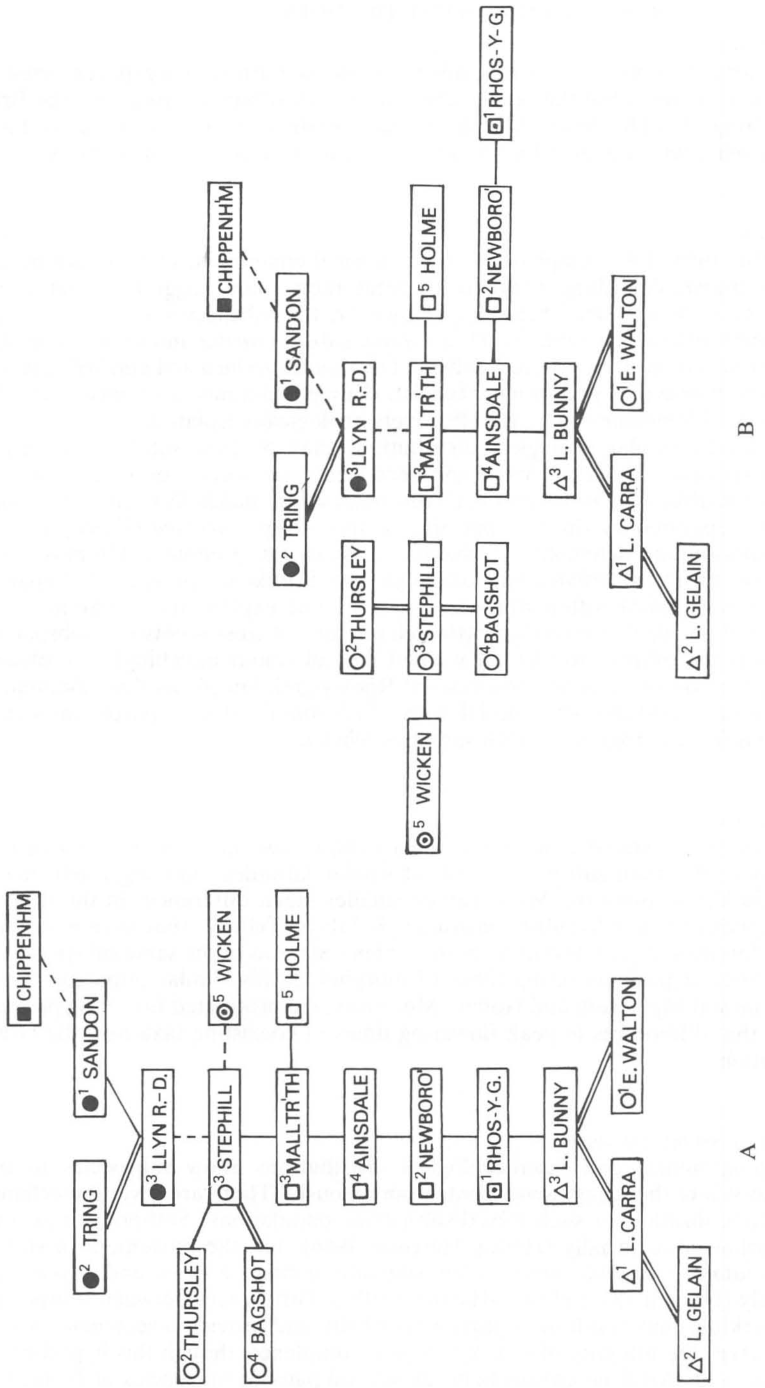

FIGURE 5. Minimum spanning trees expressing the maximum similarities of populations.
A – Based on population means for 44 characters, including floral pigmentation characters.
B – Based on population means for 36 characters, excluding floral pigmentation characters.
Double line, maximum similarity >93%; single line, 90–93%; dashed line, <90%.
See Fig. 2 for explanation of symbols.

GEOGRAPHICAL SEPARATION

The ranges of *D. incarnata* subsp. *cruenta* and subsp. *ochroleuca* are sufficiently restricted and disjunct to prevent interbreeding, but the other subspecies are distributed throughout the British Isles (Table 7) (Perring & Sell 1968). Morphological variation of *D. incarnata* is largely independent of geography, which is therefore an unlikely cause of reproductive isolation.

ECOLOGICAL SEPARATION

Heslop-Harrison (1954, 1956, 1968) emphasised the ecological component of variation between subspecies of *D. incarnata*, describing them as "habitat races" and suggesting that each is physiologically superior in its preferred habitat(s). However, the subspecies differ only in their relative ranges of habitat tolerance (Table 7). *D. incarnata* subsp. *cruenta* and subsp. *ochroleuca* are almost confined to calcareous fens, whereas subspp. *incarnata*, *coccinea* and *pulchella* grow in a wider range of habitats, where they occasionally coexist. Only populations of *D. incarnata* subsp. *pulchella* in extensive acid *Sphagnum* bogs are effectively ecologically isolated.

However, these broadly similar ecological distributions may obscure subtle differences in microecological requirements, which are most apparent where subspecies occur together. For instance, in a field near Rathkeale, Co. Limerick, *D. incarnata* subsp. *pulchella* occupied a series of depressions that were separated by ridges supporting mainly subsp. *coccinea* (Heslop-Harrison 1956). However, separation into definable microhabitats is much less pronounced in most mixed-subspecies populations of *D. incarnata*, and although the Rathkeale population apparently demonstrated some physiological differentiation, this does not explain the apparent lack of hybridization of red- and purple-flowered plants (though progeny of crosses between subspecies of different flower colours are difficult to identify without careful colour matching). We observed some microhabitat specialization of these subspecies at Rhos-y-gad, but plants that resembled *D. incarnata* subsp. *coccinea* in most characters had flowers which contained some purple anthocyanin that may have resulted from introgression with subsp. *pulchella*.

PHENOLOGICAL SEPARATION

Heslop-Harrison (1954, 1956) stated that *D. incarnata* subspp. *coccinea*, *cruenta* and *pulchella* often flower 7–14 days later than subsp. *incarnata* at similar latitudes, and suggested that this results in partial phenological isolation. We observed smaller mean differences in the flowering periods of these subspecies relative to subsp. *incarnata* (4–7 days, Table 2) that were insignificant compared to large differences in peak flowering periods of populations of the same subspecies, e.g. the four week difference in peak flowering times of morphologically similar populations of *D. incarnata* subsp. *coccinea* at Malltraeth and Holme. Moreover, the protracted flowering periods of dactylorchids means that differences in peak flowering times of coexisting taxa must be large to prevent cross-pollination.

OTHER POTENTIAL ISOLATING MECHANISMS

Their overlapping geographical and macroecological distributions allow subspecies to occur together at many sites where they may flower contemporaneously. There are several mechanisms that could prevent hybridization in such mixed-subspecies populations. Self-pollination of *D. incarnata* has been achieved artificially (Heslop-Harrison 1956), but the movement of stalks of removed pollinia to attain a suitable position for stigmatic contact is slow and makes cross-pollination more likely (Darwin 1877; Heslop-Harrison 1956). Differences between subspecies in flower colour and markings may result in pollinator specificity and provide a secondary isolating mechanism that preserves the integrity of coadapted gene complexes, though this hypothesis has not been tested in the field. Artificial crosses between several pairs of subspecies of *D. incarnata* were invariably successful (Heslop-Harrison 1956), so pollen germination and gametic fusion must have been unimpaired. Furthermore, extensive introgression of *D. fuchsii* and *D. majalis* subsp. *purpurella* (T. & T. A. Stephenson) D. Moresby Moore & Soó (Lord & Richards 1976) suggests that the more closely related subspecies of *D. incarnata* are unlikely to be separated by intrinsic barriers to either cross-pollination or the development of fertile progeny.

TABLE 7. GEOGRAPHICAL AND ECOLOGICAL DISTRIBUTIONS AND FLOWERING PERIODS OF THE SUBSPECIES OF *D. INCARNATA* IN THE BRITISH ISLES

Subspecies	Geographical distribution	Ecological distribution	pH range	Flowering periods, relative to subsp. *incarnata*
incarnata	Throughout the British Isles	Fens, marshes, dune marshes, water meadows, less frequently dune slacks	(6–)6·5–8	Late May to late June (to early July)
coccinea	Throughout the British Isles, mainly coastal	Dune slacks, less frequently dune marshes and inland meadows (especially in Ireland)	(6–)7–8	Contemporaneous (e.g. in Ireland) to 14 days later (e.g. in the Hebrides)
cruenta	W. Ireland (Co. Galway, Co Mayo, Co. Clare), also W. Scotland	*Schoenus*/*Cladium* fens, mostly at lough-sides	(7–)7·5–8+	Variable, from contemporaneous to 14 days later
pulchella	Throughout the British Isles	*Schoenus*/*Cladium* fens, *Carex*/*Phragmites* 'poor' fens, *Sphagnum* bogs.	4·5–7·5(–8)	Variable, from contemporaneous (e.g. in Ireland) to 14+ days later (e.g. in Dorset/Hampshire)
ochroleuca	East Anglia, possibly also W. Ireland and S. Wales	*Schoenus*/*Cladium*/*Phragmites* fens	(7–)7·5–8	Contemporaneous

Data from several sources and modified according to the authors' observations.

CLASSIFICATION

The classification and diagnostic descriptions that follow are based on our principal coordinates (Figs. 3 & 4, Tables 5 & 6), minimum spanning trees (Fig. 5) and population means (Table 3). Data published by Heslop-Harrison (1948, 1956) and unpublished data of N. R. Campbell (pers. comm. 1981) 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 subspecies. Some terms used in the descriptions are qualitative but are derived from quantitative measurements:

Leaf distribution: strongly crowded towards the base, index 'h' value=0–20%; slightly crowded towards the base, h=21–40%; more-or-less evenly distributed along stem, h=41–60%.

Leaf shape: narrow, index 'g' value less than 0·15.

Density of labellum pigments: dark, reflectivity=8–20%; moderate, reflectivity=21–40%; pale, reflectivity=41–80%; very pale, reflectivity=81–89%.

Depth of labellum sinuses: deep, index 'b' value greater than 1·3.

Prominence of central labellum lobe: prominent, index 'c' value equal to or greater than 1 mm.

Reflexion of lateral labellum lobes: strongly reflexed, lobes subtend an angle of less than 40° (character states 5 or 6 in Fig. 1).

Soil pH: acid, <6; neutral, 6–7; alkaline, >7.

The taxonomy of diploid marsh-orchids is complicated by extensive synonymy (listed for all taxa) and by ambiguous original descriptions for *D. incarnata* subspp. *incarnata*, *cruenta* and *ochroleuca* (nomenclatural problems concerning these subspecies are discussed after their detailed descriptions). Several of the many varieties and forms of *D. incarnata* described by Continental workers (cf. Vermeulen (1949) and Landwehr (1977) for *D. incarnata* as a whole and Neuman (1909) for subsp. *cruenta*) occur in the British Isles, but they have been omitted from this classification because they are barely distinguishable.

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

1. *DACTYLORHIZA INCARNATA* (L.) Soó, *Nom. nov. gen.* Dactylorhiza 3 (1962).

Orchis incarnata L., *Fl. Suecica*, 2nd. ed., 312 (1755); *O. mixta* Retzius var. *incarnata* (L.) Retzius, *Fl. Scand. Prodr.* 167 (1779); *O. latifolia* L. var. *incarnata* (L.) Cosson & Germain, *Fl. Paris*, 2nd ed., 684 (1861); *Dactylorchis incarnata* (L.) Vermeulen, *Stud. Dactyl.* 65 (1947).
Orchis impudica Crantz, *Stirpes Austriacae* 497 (1769).
Orchis divaricata Richard in Mérat, *Fl. Paris.* 345 (1812).
Orchis strictifolia Opiz, in *Naturalientausch*, **10**: 217 (1825).
Orchis angustifolia Wimmer & Grabowski, *Fl. Silesiae* 252 (1829); *O. latifolia* L. var. *angustifolia* (Wimmer & Grabowski) Babington, *Manual Br. Bot.* 291 (1843).
Orchis lanceata Dietrich, *Fl. Konigreichs* 11 (1833).
Orchis latifolia L. var. *longibracteata* Neilreich, *Fl. Wien* 129 (1846).
Orchis latifolia auct., sic Pugsley, in *Bot. J. Linn. Soc.*, **49**: 577 (1935).

Stem (8–)10–35(–45) cm, 3–9(–12) mm in diameter, often lacking anthocyanins. Basal lf or sheath (0–)1, broadest at middle or somewhat below middle; sheathing lvs (2–)3–4(–5), ±evenly distributed along stem to strongly crowded towards the base, upright or recurved, narrowly to broadly lanceolate, usually broadest above the base, longest lf usually also widest, 4–15 cm long, widest lf 1–3·5 cm wide, width/length ratio of lvs decreasing up stem (often±constant in subsp. *cruenta*), yellowish-green to bright green, hooding of tips poorly- or less frequently well-developed; non-sheathing lvs (0–)1(–2), narrow, broadest at base; lvs unmarked (solid markings on both surfaces or less frequently on upper surface only in some individuals of subsp. *cruenta*). Inflorescence usually 2·5–8 cm, 15–50% of stem length, fls usually 8–40, fairly lax to dense (3–7·5 fls/cm). Basal bracts greatly exceeding ovaries (and usually flowers), floral bracts 1–2(–4) times the length of the ovaries, often suffused with anthocyanins (rarely spotted in subsp. *cruenta*); peripheral bract cells 40–70 μm long, barrel-shaped to sub-triangular. Labellum width exceeding or less frequently ± equalling length, 4·5–8×5–9 mm, usually broadest ± at middle, rarely above (obtriangular) or below (deltoid), base colour varying densities (reflectivity 8–85%) of purple-violet, purple, red-purple, red, or yellow (very rarely white); markings pale to bold dashes and/or loops (absent from subsp. *ochroleuca* and anthocyanin-less individuals of other subspecies), often covering about two-thirds of the labellum, occasionally covering most of the labellum or concentrated at its centre; sinuses present (labellum three-lobed) or less frequently absent (labellum entire), only occasionally deep (especially subsp. *ochroleuca*); central lobe equalling or exceeding lateral lobes; lateral lobes often entire, moderately to strongly reflexed; lateral outer perianth segments slightly above horizontal to near-vertical, often with solid or less frequently annular markings (absent from subsp. *ochroleuca* and anthocyanin-less individuals of other subspecies); median outer perianth segment and inner perianth segments connivent; spur slightly to moderately decurved (rarely straight), 5·5–8×2·5–5·4 mm at entrance, 2–3·5 mm halfway along (when flattened), slightly tapering, half as long to nearly as long as the ovary. $2n=40$. Flowering late May to early July (rarely later in the north). Locally frequent throughout the British Isles.

There has been considerable controversy concerning the correct specific epithet for the plant presently known as *D. incarnata*. Pugsley's (1935) detailed argument for the use of *Orchis latifolia* L. (Linnaeus 1745) prevailed in Britain, but Continental workers such as Mansfeld (1938) and Vermeulen (1947a,b) stated that *O. latifolia* should be discarded as a *nomen ambiguum*. Mansfeld advocated the use of *O. strictifolia* Opiz (Opiz 1825), but Vermeulen preferred *Orchis incarnata* L. (Linnaeus 1755), which he renamed *Dactylorchis incarnata* (L.) Vermeulen. *D. incarnata* was subsequently used by most British and Continental botanists, though *O. strictifolia* was favoured by many Scandinavian botanists and by Clapham (1952). The relative merits of *O. incarnata* and *O. latifolia* were debated in three papers published simultaneously by Vermeulen (1947b), Pugsley (1947) and Wilmott (1947). These papers contained some intriguing theories, exemplified by Wilmott's assertion that "There is no doubt that . . . the specimen representing *Orchis latifolia* in the Linnaean Herbarium . . . is *O. incarnata* auct. of the form met with when a cow-pat has been dropped upon the plant"!

The use of *O. latifolia* declined thereafter, and it was eventually declared a *nomen rejiciendum* by the 1975 Leningrad Botanical Congress. The compelling reasons for its rejection were summarized by Vermeulen (1976). However, Pugsley's (1935, 1947) arguments against *incarnata* as a specific epithet are also persuasive; the morphology intended by Linnaeus (1755) for the typification of *O. incarnata* is unclear (he apparently changed his mind at least twice). Nevertheless, we cannot recommend the rejection of *Dactylorhiza incarnata* now that it has finally gained general acceptance among European botanists.

a. Subsp. *INCARNATA*

Orchis incarnata L., *Fl. Suecica*, 2nd. ed., 312 (1755); *Dactylorchis incarnata* (L.) Vermeulen subsp. *lanceata* (Dietrich) Vermeulen, *Stud. Dactyl.* 108 (1947).

Orchis incarnata L. var. *lanceata* Reichenbach f., *Icon. Fl. Germ.* 51 (1851); *O. incarnatus* L. subsp. *lanceatus* (Reichenb. f.) Blytt & Dahl, *Handb. Norges Fl.* 227 (1906).

Orchis strictifolia Opiz subsp. *strictifolia* sensu Clapham in Clapham *et al., Fl. Br. Isl.* 1318 (1952).

Stem usually >20 cm, *usually >6 mm in diameter*, usually lacking anthocyanins. Sheathing lvs usually more than 3 (occasionally 5), usually moderately to strongly crowded towards the base of the stem, longest lf usually >9 cm long, rarely narrow, *widest lf usually >2 cm wide*, lower lvs usually broadest well above the base; lf markings absent (present in f. *punctata*). *Inflorescence usually >5 cm*, usually <30% of stem length, *fls usually more than 25*. Basal bracts often >25 mm, floral bracts often <18 mm, usually less than twice the length of the ovaries, usually lacking anthocyanins. Labellum often less than 6·5×8 mm; *base colour pale, dilute red-purple or red* (i.e. pink: x=305–345, y=285–305); markings usually including several dashes, rarely bold, often concentrated in the centre of the labellum; sinuses usually shallow or absent; central lobe rarely prominent; lateral lobes usually entire, often strongly reflexed; lateral outer perianth segments usually nearer vertical than horizontal, annular markings absent; spur often <3·5 mm wide at entrance, <2·8 mm halfway along. Distributed throughout the British Isles, most frequent in England and Wales. Alkaline or neutral soils.

Our data suggest that *D. incarnata* subsp. *incarnata* is characteristically vegetatively robust (stems and leaves broad, inflorescences large), though most of the populations of subsp. *incarnata* measured by Heslop-Harrison (1956) had narrower leaves and longer spurs than our study populations. Plants at Sandon had unusually large labella, often with the normally solid pair of loop markings broken into dashes, and are thus intermediate in floral characters between *D. incarnata* subsp. *incarnata* and subsp. *gemmana* as described by Heslop-Harrison (1954, 1956).

Six of the seven plants of *D. incarnata* subsp. *incarnata* illustrated by Nelson (1976) were purple-flowered, and Landwehr (1977) also attributed several of the purple-flowered specimens he illustrated to subsp. *incarnata*. The inclusion of purple-flowered plants in *D. incarnata* subsp. *incarnata* by many Continental orchidologists reflects their apparent lack of understanding of *D. incarnata* subsp. *pulchella* (see discussion of subsp. *pulchella*).

i. f. **punctata** (Vermeulen) Bateman & Denholm, **comb. nov.**
Basionym: *Dactylorchis incarnata* (L.) Vermeulen f. *punctata* Vermeulen, *Ned. kruidk. Archf.*, **56**: 209 (1949).

Sheathing lvs with a few small dots on upper surface, usually concentrated towards the lf tips.

This form has been recorded from Coll, Outer Hebrides (Heslop-Harrison 1948) and from Malham, Yorkshire (R. H. Roberts pers. comm. 1982). Most of the other 18 varieties and forms of *D. incarnata* described by Vermeulen (1949) are referable to subsp. *incarnata* and many occur in the British Isles, but they are insufficiently distinct to justify continued recognition.

b. Subsp. *COCCINEA* (Pugsley) Soó, *Nom. nov. gen.* Dactylorhiza 4 (1962).
Orchis latifolia L. var. *coccinea* Pugsley, in *Bot. J. Linn. Soc.*, **49**: 579 (1935); *O. strictifolia* Opiz subsp. *coccinea* (Pugsley) Clapham, *Fl. Br. Isl.* 1319 (1952); *Dactylorchis incarnata* (L.) Vermeulen subsp. *coccinea* (Pugsley) Heslop-Harrison f., in *Ber. geobot. Forsch. Inst. Rübel*, **1953**: 54 (1954).
Orchis incarnata L. var. *dunensis* Druce, in *Rep. botl Soc. Exch. Club Br. Isl.*, **4**: 212 (1916); *Dactylorchis incarnata* (L.) Vermeulen var. *dunensis* (Druce) Vermeulen, in *Ned. kruidk. Archf.*, **56**: 207 (1949); *Dactylorhiza incarnata* (L.) Soó var. *dunensis* (Druce) Landwehr, in *Orchidëen*, **37**: 80 (1975).
Orchis incarnata L. f. *atriruba* Godfery, *Mon. Icon. Br. nat. Orchidaceae* 187 (1933).

Stem usually <20 cm (occasionally <10 cm), usually <6 mm in diameter, *often suffused with anthocynanins*. Sheathing lvs often more than 3, often strongly crowded towards the base of the stem, longest lf often <9 cm, occasionally narrow, widest lf usually <2 cm wide, lower lvs usually broadest well above the base; lf markings absent. Inflorescence often <5 cm, often >30% of stem length, fls usually less than 25. Basal bracts usually <25 mm, floral bracts usually <18 mm, less than twice the length of the ovaries (occasionally shorter than the ovaries), *usually suffused with anthocyanins*. Labellum usually less than 6·5×8 mm; *base colour dark or less frequently moderate, red or red-purple* (x=430–580, y=250–325); markings usually including several dashes, rarely bold, rarely concentrated in the centre of the labellum; sinuses usually shallow or absent; central lobe rarely prominent; lateral lobes often indented, usually strongly reflexed; lateral outer perianth segments usually nearer vertical than horizontal, annular markings usually absent; spur often <3·5 mm wide at entrance, <2·8 mm halfway along. Distributed throughout the British Isles, most frequent along the west coasts. Alkaline or neutral soils.

Previous literature contains several conflicting statements concerning characters that separate *D. incarnata* subsp. *coccinea* from subsp. *incarnata*; leaves of subsp. *coccinea* are said to be fewer (Wiefelspütz 1976a) and darker green (Heslop-Harrison 1948; Wiefelspütz 1976a; Lang 1980), labella are said to be smaller (Clapham 1952), less reflexed and less boldly marked (Pugsley 1935). Soó (1980) stated that *D. incarnata* subsp. *coccinea* has erect leaves, whereas most previous authors (Godfery 1933; Pugsley 1935; Heslop-Harrison 1956) had emphasised the value of its spreading, frequently recurved leaves as a diagnostic character. Although Heslop-Harrison (1948, 1954) and Sundermann (1980) stated that *D. incarnata* subsp. *coccinea* flowers two weeks later than subsp. *incarnata*, this was only observed at Holme where *D. incarnata* subsp. *coccinea* flowers especially late; subsp. *coccinea* and subsp. *incarnata* were contemporaneous at Newborough and Ainsdale.

Populations of *D. incarnata* subsp. *coccinea* growing in exposed dune slacks, e.g. Newborough and Ainsdale, tend to be shorter (*c.* 10 cm, so that the inflorescence forms a greater proportion of the length of the stem) and have leaves that are often recurved, shorter, broadest closer to their bases and more crowded towards the base of the stem than the leaves of subsp. *coccinea* growing in less exposed dune slacks (e.g. Holme) or stabilized 'dune meadows' (e.g. Malltraeth).

The population of *D. incarnata* at Rhos-y-gad is one of many variable populations of this species that occur in dune systems and inland in the north and west, and are particularly abundant on Anglesey (Summerhayes 1951; Perring & Sell 1968). Rhos-y-gad plants have the reddish-brown bract and stem anthocyanins that characterize *D. incarnata* subsp. *coccinea*, and their mean values for vegetative characters are similar to the Holme and Malltraeth populations (Table 3); they therefore occur with other individuals of *D. incarnata* subsp. *coccinea* in Fig. 4. However, they differ from the other populations of *D. incarnata* subsp. *coccinea* in a few characters; they have narrower spurs, annular outer perianth segment markings and red-purple (often described as rose-red) flowers. These presumably contain both red and violet-purple anthocyanins (see 'Variation in Single Characters'), the violet-purple component possibly being derived from *D. incarnata* subsp. *pulchella* at Rhos-y-gad, and their reflectivities range from pale to dark (Fig. 2). Consequently, they occur throughout the zone of overlap of *D. incarnata* subsp. *coccinea* with subsp. *pulchella* and subsp. *cruenta* on the principal coordinates plot that includes floral pigmentation characters (Fig. 3). Landwehr (1977) illustrated comparable Continental plants and named them *D. incarnata* f. *dunensis*, and Druce's (1916) description of its basionym, *Orchis incarnata* var. *dunensis*, also specified rose-red flower colour rather than the maroon that is more typical of *D. incarnata* subsp. *coccinea*. However, this subtle colour difference is insufficient to justify separating populations such as the one at Rhos-y-gad from subsp. *coccinea* to form an additional taxon.

c. Subsp. *CRUENTA* (O. F. Müller) P. D. Sell, in *Watsonia*, **6**: 317 (1967).

Orchis cruenta O. F. Müller, *Fl. Danica*, 15: 4, t.876 (1782); *O. latifolia* L. var. *cruenta* (O. F. Müller) Lindley, *Gen. et spec. Orchid*. 260 (1835); *O. incarnatus* L. var. *cruentus* (O. F. Müller) Blytt & Dahl, *Handb. Norges Fl.* 227 (1906); *O. incarnatus* L. subsp. *cruentus* (O. F. Müller) Ascherson & Graebner, *Synop. Mitteleurop. Fl.* 720 (1907); *Dactylorchis cruenta* (O. F. Müller) Vermeulen, *Stud. Dactyl.* 66 (1947); *D. incarnata* (L.) Vermeulen subsp. *cruenta* (O. F. Müller) Heslop-Harrison f., in *Ber. geobot. Forsch. Inst. Rübel*, **1953**: 54 (1954); *Dactylorhiza cruenta* (O. F. Müller) Soó, *Nom. nov. gen.* Dactylorhiza 4 (1962).

Orchis haematodes Reichenbach, *Fl. Germ. Excurs.* 126 (1830); *O. cruenta* O. F. Müller var. *haematodes* (Reichenbach) Neuman, in *Bot. Notiser*, **1909**: 157 (1909); *Dactylorhiza incarnata* (L.) Soó var. *haematodes* (Reichenbach) Soó, *Nom. nov. gen.* Dactylorhiza 4 (1962).

Orchis incarnata L. var. *rhombeilabia cruenta* Reichenbach f., *Icon. Fl. Germ.* 53 (1851).

Orchis matodes Reichenbach f., *Icon. Fl. Germ.* 56, t.46 (1851).

Orchis latifolia L. var. *brevifolia* Reichenbach f., *Icon. Fl. Germ.* t.51 (1851); *O. cruenta* O. F. Müller f. *brevifolia* (Reichenbach f.) Neuman, *Sveriges Fl.* 631 (1901); *O. cruenta* O. F. Müller var. *brevifolia* (Reichenbach f.) Neuman, in *Bot. Notiser*, **1909**: 157 (1909).

Orchis incarnatus L. var. *haematodes* Schulze in Ascherson & Graebner, *Synop. Mitteleurop. Fl.* 717 (1907); *Dactylorchis incarnata* (L.) Vermeulen var. *haematodes* (Schulze) Vermeulen, *Stud. Dactyl.* 117 (1947).

Orchis cruentiformis Neuman, in *Bot. Notiser*, **1909**: 243 (1909).

Orchis cruenta O. F. Müller var. *lanceolata* Neuman, in *Bot. Notiser*, **1909**: 157 (1909); *Dactylorhiza incarnata* (L.) Soó subsp. *cruenta* (O. F. Müller) P. D. Sell var. *lanceolata* (Neuman) Landwehr, in *Orchideën*, **37**: 80 (1975).

Orchis incarnata L. var. *hyphaematodes* Neuman, in *Bot. Notiser*, **1909**: 244 (1909); *Dactylorhiza incarnata* (L.) Soó var. *hyphaematodes* (Neuman) Landwehr, in *Orchideën*, **37**: 80 (1975).

Stem often <20 cm, usually <6 mm in diameter, *usually suffused with anthocyanins*. Sheathing lvs often 3 or less, often slightly crowded towards the base of the stem, longest lf often <9 cm long, often narrow, widest lf usually <2 cm wide, lower lvs usually broader fairly close to (but not at) the base; lf markings occasionally present on both surfaces or much less frequently on upper surface only, solid, transversely to longitudinally elongated, usually small (<2 mm in diameter), ± evenly distributed on lvs or somewhat concentrated towards the tips. Inflorescence usually <5 cm, often <30% of stem length, fls usually less than 25. Basal bracts usually <25 mm, floral bracts usually <18 mm, usually less than twice the length of the ovaries, *suffused with anthocyanins*, rarely spotted. Labellum often less than 6·5×8 mm; *base colour intense or less frequently moderate, purple-violet/purple* (x=285–325, y=165–240); *markings often loops enclosing few if any dashes*, often bold, *often covering most of the labellum*; sinuses often shallow or absent; central lobe often prominent; lateral lobes often indented, only occasionally strongly reflexed; lateral outer perianth segments often nearer horizontal than vertical, *annular markings usually present*; spur often <3·5 mm wide at entrance, <2·8 mm halfway along. Locally frequent in western central Ireland, rare in Scotland (Continental distribution: Alps, Scandinavia and U.S.S.R.). Alkaline or, less frequently, neutral soils.

D. incarnata subsp. *cruenta* was originally described from Denmark (Müller 1782) and is now known to be widespread in Scandinavia. It was later found by H. W. Pugsley in the Alps (Gsell 1935; Pugsley 1935; Senay 1937; Wilmott 1938) and by J. Heslop-Harrison in western Ireland, where it is frequent in the lough-side fens of Co. Galway and Co. Mayo and the Burren region of Co. Clare (Heslop-Harrison 1949, 1950a, 1950b, 1952, 1954, 1956; Gough & Teacher 1950; D. M. Turner Ettlinger pers. comm. 1983). Early records for *D. incarnata* subsp. *cruenta* from Britain (Goss 1899) were attributed to *D. majalis* (Reichenbach) P. F. Hunt & Summerhayes subsp. *purpurella* (T. & T. A. Stephenson) D. M. Moore & Soó by later workers (Heslop-Harrison 1950b), but a small July-flowering population of subsp. *cruenta* has since been found in Ross (Kenneth & Tennant 1984) and further discoveries in Scotland are likely. Kenneth & Tennant (1984) listed several morphological differences between Scottish and Irish plants, but comparison of their description of Scottish plants with our data from Irish plants revealed only two apparently significant differences: Scottish plants have inflorescences of similar length but fewer flowers so they are more lax, and their labella may be more reflexed. However, the Scottish population occurred in acid hillside flushes, an unusual habitat for subsp. *cruenta*.

Floral characters of Irish and Scottish *D. incarnata* subsp. *cruenta* are consistent with descriptions of Scandinavian and Alpine plants (Müller 1782; Reichenbach 1830; Reichenbach 1851; Klinge 1898; Ascherson & Graebner 1907; Neuman 1909; Camus & Camus 1929; Pugsley 1935; Gsell 1935; Senay 1937; Wilmott 1938; Vermeulen 1947a; Heslop-Harrison 1950a, 1956; Summerhayes 1951, 1968; Senghas 1968; Beisenherz 1973; Sundermann 1975, 1980; Wiefelspütz 1976a; Nelson 1976; Landwehr 1977); labella are sub-rounded or cordate, shallowly three-lobed or less frequently entire, purple or purple-violet with bold solid loop markings enclosing few if any dashes, and the lateral lobes are usually only moderately reflexed. However, the labella of most Irish plants are larger (6–7·5×6·5–9 mm) than the labella of Continental plants (usually described as *c.* 6×6 mm). Anthocyanins occur on the upper part of the stem and on the bracts (Gsell 1935; Vermeulen 1947a; Heslop-Harrison 1950b, 1956; Summerhayes 1951; Beisenherz 1973; Kenneth & Tennant 1984). Rare anthocyanin-less individuals, such as those that we observed at Lough Carra, have pale yellow flowers.

The leaf markings of *D. incarnata* subsp. *cruenta* are usually described as small, abundant, sometimes longitudinally elongated and often merging into diffuse fields. Vermeulen (1947a) argued that markings on both leaf surfaces were always present in *D. incarnata* subsp. *cruenta*, and most authors have emphasized their importance. Heslop-Harrison (1950a, 1956) stated that *D.*

incarnata subsp. *cruenta* at Lough Carra "falls well within the total range of variation encompassed by the populations placed under subsp. *pulchella*" and that "the principal distinction lies . . . in the quite unique pigmentation of the vegetative parts of some 65% of the individuals of the colony". Furthermore, "populations of *Orchis cruenta* always contain a high proportion of individuals in which the characteristic marking is present on both sides of the foliage leaves". Elsewhere, "small numbers of leaf-marked individuals appear in similar habitats among populations otherwise simply referable to subsp. *pulchella*". Heslop-Harrison apparently believed that leaf-marked individuals should predominate in populations of *D. incarnata* subsp. *cruenta*; he therefore assigned the Lough Carra population to subsp. *cruenta* and the Lough Bunny population, which contains a smaller proportion of leaf-marked individuals, to subsp. *pulchella*.

However, leaf-marked individuals did not predominate in any of our study populations (including Lough Carra) and comprised only 30% of the total number of individuals measured.[2] Similar estimates of the frequency of leaf markings in Irish populations of *D. incarnata* subsp. *cruenta* were made by Wiefelspütz (1976a) and by D. M. Turner Ettlinger (pers. comm. 1983), who noted that leaf-marked plants predominated in only one of twelve populations examined and were absent from one. The single recorded Scottish population of *D. incarnata* subsp. *cruenta* contained unmarked individuals (Kenneth & Tennant 1984), and populations of this subspecies containing only a minority of leaf-marked individuals occur in Scandinavia (Neuman 1909) and the Alps (Gsell 1943; Heidemann 1971). Furthermore, leaf markings on both surfaces were not included in the original diagnosis of *Orchis cruenta* (Müller 1782) and were ignored by subsequent workers until Klinge (1898), suggesting that plants without leaf markings were acceptable as *D. incarnata* subsp. *cruenta* ('*O. cruenta*') if they conformed to the other morphological criteria. However, Vermeulen (1947a) reached different conclusions concerning the taxonomy of leaf-marked *D. incarnata*, *viz*:

Dactylorchis incarnata (excluding var. *haematodes* (Reichenbach) Soó and var. *hyphaematodes* (Neuman) Landwehr): sheathing lvs unspotted.

D. incarnata var. *haematodes*: sheathing lvs spotted only on upper surface (spreading according to Reichenbach (1830) but erect according to Neuman (1909)).

D. incarnata var. *hyphaematodes*: sheathing lvs spotted on both surfaces, longer than one third of the stem length, erect (erect or spreading according to Neuman (1909)).

D. cruenta: sheathing lvs spotted on both surfaces, sometimes shorter than one third of the stem length, spreading (although Vermeulen argued that *cruenta* was best treated as a subspecies of *D. incarnata*, he nevertheless retained it as a full species).

23% of the Irish plants that we examined had leaves marked on both surfaces (13% also had spotted bracts), 7% had leaves marked on the upper surface only and 70% were unmarked. Their sheathing leaves were longer than one-third of the stem length and erect or suberect. Since Vermeulen (1947a) considered that *D. incarnata* subsp. *cruenta* must have spreading leaves marked on both surfaces he would not have assigned the Irish plants to this taxon. Following his classification, the unspotted plants should be assigned to *D. incarnata* (?typical variety), those spotted only on the upper surface to *D. incarnata* var. *haematodes*, and those spotted on both surfaces to *D. incarnata* var. *hyphaematodes*. However, Heslop-Harrison (1950b) compared Irish and Swedish leaf-marked populations of *D. incarnata* and concluded that both resembled *D. cruenta* var. *lanceolata* Neuman. Although the leaves of Irish and Scottish plants agree with the original description of *D. cruenta* var. *lanceolata* in size and shape, they lack the spreading posture noted by Neuman (1909) and Vermeulen (1947a).

We do not accept that there is a fundamental distinction between plants of *D. incarnata* with erect leaves and those with spreading leaves, and we recommend the inclusion of vars. *haematodes* and *hyphaematodes* in *D. incarnata* subsp. *cruenta*. We also believe that too much emphasis has been placed on the importance of leaf markings as a diagnostic character of *D. incarnata* subsp. *cruenta*, probably because this is a visually striking character. Leaf markings were infrequent in Irish populations of *D. incarnata* subsp. *cruenta* and were not correlated with variation in floral

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[2] In Ireland *D. incarnata* subsp. *cruenta* has a prolonged flowering period from early June to mid-July. During this period the proportion of the population with leaf markings is almost constant but the mean density of vegetative anthocyanin on the leaf-marked plants increases. The heavily marked plants also show some ecological specialization, being concentrated towards the margins of large water bodies.

characters or the presence of bract and stem anthocyanins that separated subsp. *cruenta* from the other subspecies of *D. incarnata* on the principal coordinates plot (Fig. 3, Table 5).

Examination of previous literature on leaf-marked *D. incarnata* suggests an important division into a narrow-leaved group and a broad-leaved group. The narrow-leaved group has longest sheathing leaves <1·5 cm wide with index 'g' values <0·2 and comprises *D. incarnata* var. *haematodes, D. incarnata* var. *hyphaematodes, D. incarnata* subsp. *cruenta* var. *lanceolata* and var. *brevifolia* Neuman. This group occurs in Ireland and Scandinavia. The broad-leaved group (longest sheathing leaves >1·5 cm wide, index 'g' values > 0·2, leaves generally more spreading, less keeled and less hooded) comprises *D. incarnata* subsp. *cruenta* var. *subelliptica* Neuman and var. *subtriangularis* Neuman and occurs in the Alps and Scandinavia. A biometric investigation of Continental plants is needed to confirm the validity of these two apparent groups. The similarity between *D. incarnata* subsp. *cruenta* and *D. pseudocordigera* (Neuman) Soó should also be assessed.

d. Subsp. *PULCHELLA* (Druce) Soó, *Nom. nov. gen.* Dactylorhiza 4 (1962).

Orchis incarnata L. var. *pulchella* Druce, in *Rep. botl Soc. Exch. Club Br. Isl.*, **5**: 167 (1918); *O. latifolia* L. var. *pulchella* (Druce) Pugsley, in *Bot. J. Linn. Soc.*, **49**: 578 (1935); *O. strictifolia* Opiz var. *pulchella* (Druce) Clapham in Clapham *et al.*, *Fl. Br. Isl.* 1319 (1952); *Dactylorchis incarnata* (L.) Vermeulen subsp. *pulchella* (Druce) Heslop-Harrison f., in *Ber. geobot. Forsch. Inst. Rübel*, **1953**: 55 (1954).

Orchis traunsteineri Sauter var. *serotina* Haussknecht, in *Mitt. geogr. Ges. Thüringen*, **2**: 220 (1884); *O. incarnata* L. var. *serotina* (Haussknecht) Haussknecht in Schultze, M., *Orchid. Deutsch.* 19 (1894); *O. serotinus* (Haussknecht) Schwarz, *Fl. Nürnb. Erlangen* 765 (1901); *Dactylorchis incarnata* (L.) Vermeulen var. *serotina* (Haussknecht) Vermeulen, *Stud. Dactyl.* 162 (1947); *Dactylorhiza incarnata* (L.) Soó subsp. *serotina* (Haussknecht). D. M. Moore & Soó, in *Bot. J. Linn. Soc.*, **76**: 367 (1978).

Orchis angustifolia Wimmer & Grabowski var. *haussknechtii* Klinge, *Rev.* Orchis cordigera, O. angustifolia 70 (1893).

Orchis incarnata L. var. *borealis* Neuman, in *Bot. Notiser*, **1909**: 229 (1909).

Orchis incarnata L. var. *pulchriora* Druce, in *Rep. botl Soc. Exch. Club Br. Isl.*, **7**: 419 (1927).

Orchis latifolia L. var. *cambrica* Pugsley, in *Bot. J. Linn. Soc.*, **49**: 579 (1935).

Stem often >20 cm, often <6 mm in diameter, usually lacking anthocyanins. Sheathing leaves often 3 or less, usually ± evenly distributed up the stem or slightly crowded towards its base, longest leaf often >9 cm long, often narrow, widest 1f usually <2 cm wide, lower 1vs usually broadest well above the base; 1f markings absent. Inflorescence often <5 cm, often <30% of stem length, fls often less than 25. Basal bracts often <25 mm, floral bracts usually <18 mm, less than twice the length of the ovaries, *often suffused with anthocyanins*. Labellum often less than 6·5×8 mm; *base colour dark or less frequently moderate, purple or purple-violet* (x=310−330, y=175−280); markings usually including several dashes, occasionally bold, occasionally concentrated in the centre of the labellum; sinuses usually shallow or absent; central lobe occasionally prominent; lateral lobes often entire, usually strongly reflexed; lateral outer perianth segments often nearer vertical than horizontal, annular markings often absent; spur often <3·5 mm wide at entrance, <2·8 mm halfway along. Distributed throughout the British Isles. Acid to alkaline soils.

This is the least distinct subspecies of *D. incarnata*, characterized only by purple/purple-violet flowers and the presence of bract anthocyanins. Its labella have been described as entire or subentire (Summerhayes 1951; Clapham 1962; Sundermann 1980), slightly laterally reflexed (Pugsley 1935; Clapham 1962; Sundermann 1980) and relatively large, *c.* 8 mm long (Pugsley 1935; Heslop-Harrison 1950a, 1953; Clapham 1962; Sundermann 1980). However, most of the plants that we examined had shallowly three-lobed labella (though entire labella predominated at Thursley) that were strongly laterally reflexed and *c.* 6 mm long. East Walton plants had unusually tall stems and long leaves, and labella that had short central lobes and centrally-concentrated markings. They also possessed dense bract anthocyanins and moderately reflexed labella, characters that are more typical of *D. incarnata* subsp. *cruenta*. The East Walton population is consequently connected to populations of subsp. *cruenta* on the minimum spanning trees (Fig. 5).

The habitat of *D. incarnata* subsp. *pulchella* is often described simply as acid *Sphagnum* bogs. However, it also grows with other subspecies in neutral or even moderately alkaline soils. Heslop-Harrison (1956) observed a positive correlation between the stature, leaf and labellum dimensions of *D. incarnata* subsp. *pulchella* and the pH of its rhizosphere. Although our data support these correlations for all characters except leaf width, there are exceptions for each character, e.g. plants at Thursley have the smallest labella but occur in a habitat that gave only a mildly acidic pH. The overall reduction in the sizes of structures that accompany reductions in pH are small and were only evident when population means are compared.

Many populations of *D. incarnata* subsp. *pulchella* contain anthocyanin-less individuals, which are frequent in some populations, e.g. Bagshot. Although several workers (Druce 1915; Stephenson & Stephenson 1923; Nannfeldt 1944; Summerhayes 1951; Heslop-Harrison 1956) stated that the flowers of anthocyanin-less *D. incarnata* subsp. *pulchella* are white, we have seen many such plants in eight populations and they all had pale creamy yellow flowers (Bateman & Denholm 1983b). They can be confused with *D. incarnata* subsp. *ochroleuca*, especially if they occur in neutral or alkaline fens that could support subsp. *ochroleuca*. The yellow-flowered plants that we measured at Wicken had previously been referred to *D. incarnata* subsp. *ochroleuca* (Perring *et al*. 1964) but they lacked most of the diagnostic characters of subsp. *ochroleuca*, were attached to subsp. *pulchella* on the minimum spanning trees (Fig. 5), and occurred with subsp. *pulchella* on the principal coordinates plot lacking anthocyanin-dependent floral characters (Fig. 4). This evidence strongly suggests that they are anthocyanin-less *D. incarnata* subsp. *pulchella*. The purple hue typical of *D. incarnata* subsp. *pulchella* is less obvious in flowers of only moderate reflectivity, which may superficially resemble flowers of subsp. *incarnata*. The Bagshot population of *D. incarnata* subsp. *pulchella* contained approximately equal proportions of plants with dark purple, moderate purple and very pale yellow flowers; consequently, some botanists acquainted with the site believed that these were *D. incarnata* subsp. *pulchella*, subsp. *incarnata* and subsp. *ochroleuca* respectively.

Continental workers have consistently misunderstood the nature of *D. incarnata* subsp. *pulchella*. Nelson (1976) illustrated a very atypical plant with more or less flat labella of an unusual moderate reddish-purple intermediate to *D. incarnata* subsp. *pulchella* and subsp. *coccinea*. Landwehr (1977) depicted a similarly coloured plant with a very large inflorescence, and his second illustration, a line drawing, appears to be *D. majalis* subsp. *purpurella*. Landwehr named both plants *D. purpurella* var. *pulchella*, suggesting that he confused *D. incarnata* subsp. *pulchella* with *D. majalis* subsp. *purpurella* var. *pulchella* (Druce) Bateman & Denholm. Several purple-flowered *D. incarnata* illustrated by Nelson (1976) and Landwehr (1977) as subsp. *incarnata* would be assigned to subsp. *pulchella* by most British orchidologists. Surprisingly, most Continental workers also state that *D. incarnata* subsp. *pulchella* is endemic to the British Isles (Soó 1980). They assign purple-flowered *D. incarnata* without leaf markings to either subsp. *incarnata* or subsp. *serotina* (Haussknecht) D. Moresby Moore & Soó, which is said to differ from subsp. *pulchella* by its fewer-flowered inflorescence, narrower stem and fewer (3–4), narrower (1–1·5 cm) leaves (Soó 1980) that are broadest about 2 cm above their base (Wiefelspütz 1976a). However, these characters are common in *D. incarnata* subsp. *pulchella* (Table 3), indicating that Heslop-Harrison (1956) was correct to suggest that subsp. *serotina* and subsp. *pulchella* are synonymous.

e. Subsp. *OCHROLEUCA* (Wüstnei ex Boll) P. F. Hunt & Summerhayes, in *Watsonia*, **6**: 130 (1965).

Orchis incarnata L. var. *ochroleuca* Wüstnei ex Boll, in *Arch. Ver. Freunde Naturg. Mecklenb*. **14**: 307 (1860); *O. ochroleuca* (Wüstnei ex Boll) Schur, *Enum. Plant. Transsilvaniae* 641 (1866); *O. incarnatus* race *ochroleucus* (Wüstnei ex Boll) Ascherson & Graebner, *Synop. Mitteleurop. Fl.* 719 (1907); *O. latifolia* L. var. *ochroleuca* (Wüstnei ex Boll) Pugsley, in *Bot. J. Linn. Soc.*, **49**: 578 (1935); *O. strictifolia* Opiz var. *ochroleuca* (Wüstnei ex Boll) Hylander, in *Bot. Notiser,* **1942**: 228 (1942); *O. incarnata* L. subsp. *ochroleuca* (Wüstnei ex Boll) Schwarz, in *Mitt. Thuringen bot. Ges.*, **1**: 94 (1949); *Dactylorchis incarnata* (L.) Vermeulen subsp. *ochroleuca* (Wüstnei ex Boll) Heslop-Harrison f., in *Ber. geobot. Forsch. Inst. Rübel*, **1953**: 55 (1954).

O. incarnata L. var. *straminea* Reichenbach f., *Icon. Fl. Germ.* 183 (1851); *Dactylorhiza incarnata* (L.) Soó var. *straminea* (Reichenbach f.) Soó, *Nom. nov. gen.* Dactylorhiza 3 (1962).

Stem usually >20 cm, *usually >6 mm in diameter*, anthocyanins absent. Sheathing lvs often more than 3, usually ± evenly distributed along the stem, longest lf usually >9 cm long, rarely narrow, *widest lf usually >2 cm wide*, lower lvs usually broadest well above the base; lf markings absent. *Inflorescence usually >5 cm*, usually <30% of stem length, *fls usually more than 25*. Basal bracts usually >25 mm, *floral bracts usually greater than 18 mm*, often greater than twice the length of the ovary, anthocyanins absent. Labellum usually less than 6·5×8 mm; *base colour very pale, yellow* (x=c. 350, y=c. 380) deepening towards the spur entrance; markings absent; *sinuses usually deep*; central lobe prominent; *lateral lobes often deeply indented*, usually strongly reflexed; lateral outer perianth segments often nearer horizontal than vertical, unmarked; spur usually >3.5 mm wide at entrance, >2.8 mm halfway along, often straight. Possibly confined to East Anglia. Alkaline or less frequently neutral soils.

D. incarnata subsp. *ochroleuca* is characterized by a tall, broad stem, large leaves and bracts (Pugsley 1935, 1939; Heslop-Harrison 1953, 1956; Rajchel 1964; Lundqvist 1967; Nelson 1976; Davies *et al*. 1983; Bateman & Denholm 1983b). Labella are large (usually *c*. 7×9 mm in Britain), pale yellow (though darkening towards the spur entrance), and deeply three-lobed (Pugsley 1939; Nannfeldt 1944; Summerhayes 1951; Heslop-Harrison 1953, 1956; Clapham 1962; Rajchel 1964; Lundqvist 1967; Hunt & Summerhayes 1967; Nelson 1976; Bateman & Denholm 1983b), often with notched lateral lobes (Heslop-Harrison 1956; Clapham 1962; Bateman & Denholm 1983b); they resemble labella of *D. fuchsii* in shape when mounted. The Chippenham plants conformed to all these criteria (Table 3) and occurred in an alkaline fen, the typical habitat of *D. incarnata* subsp. *ochroleuca*. A larger population of *D. incarnata* subsp. *ochroleuca* that formerly occurred at Blo Norton Fen, Norfolk resembled the Chippenham plants in most characters but had on average longer, narrower leaves and longer spurs (Heslop-Harrison 1956). Some Chippenham plants had abnormally short spurs.

Authors who have identified *D. incarnata* subsp. *ochroleuca* by its flower colour alone (Perring & Sell 1968; Sundermann 1975, 1980; Soó 1980) have often confused this subspecies with yellow-flowered anthocyanin-less individuals of other subspecies, especially subsp. *pulchella* (Pugsley 1939; Lundqvist 1967; Wiefelspütz 1976b; Bateman & Denholm 1983b). This has resulted in the publication of some erroneous records, e.g. for the pale yellow-flowered plants at Wicken and Thursley (see discussion of subsp. *pulchella*). Lundqvist (1967) even argued that yellow flowers are not obligatory for *D. incarnata* subsp. *ochroleuca*, basing his argument on a population of robust *D. incarnata* near Öland, Denmark, with unmarked three-lobed labella that were either pale yellow or deep violet.

Possibly the earliest British record for *D. incarnata* subsp. *ochroleuca* was from Kidwelly, Dyfed (Stephenson & Stephenson 1923). The plants were robust and the labella were pale yellow and deeply three-lobed, but the labella were also small (*c*. 6×6 mm) and marked with a faint but discernable pattern. Recent attempts to rediscover this population have been unsuccessful (D. M. Turner Ettlinger pers. comm. 1983). The few subsequent bona fide British records for *D. incarnata* subsp. *ochroleuca* were from East Anglian fens, where it was first found in 1936 by J. E. Lousley (Lang 1980) and one or two years later by H. W. Pugsley (Pugsley 1939). The largest populations occurred in fens in the Waveney Valley, but since these are progressively drying out as the water table falls, *D. incarnata* subsp. *ochroleuca* is now endangered in Britain.

The epithet *ochroleuca* was first used by Boll (1860: 307) to describe *D. incarnata* with yellow flowers and broad but short stems found by Wüstnei (1854) in northern East Germany (Ascherson 1907). Wüstnei (1854) stated that the plants occurred in peat bogs and alder swamps with red-(?purple-)flowered *D. incarnata*, suggesting that they may have been anthocyanin-less individuals of *D. incarnata* subsp. *pulchella* (='subsp. *serotina*'). Thus the nature of the plants that provided the basis for *Orchis incarnata* var. *ochroleuca* Wüstnei ex Boll is uncertain. Some authors (e.g. Sundermann 1980) treated *D. incarnata* subsp. *ochroleuca* as a variety, but *straminea* Reichenbach (Reichenbach 1851) has precedence at this taxonomic rank, although it was unaccompanied by written or pictorial description. Moreover, the name *straminea*, which means straw-coloured, describes *D. incarnata* subsp. *ochroleuca* and other anthocyanin-less variants of *D. incarnata* equally well. *D. incarnata* var. *straminea* should therefore be considered a *nomen ambiguum*. Landwehr (1977) argued that *D. incarnata* subsp. *ochroleuca* has bright greenish-yellow flowers and is confined to eastern Europe. He assigned paler yellow-flowered plants from western Europe to *D. incarnata* f. *ochrantha* Landwehr. We doubt the validity of this distinction; Rajchel's (1964) description of Polish *D. incarnata* subsp. *ochroleuca* (stem tall, leaves and bracts large, labella three-lobed and yellow, outer perianth segments *pale* yellow) diverges considerably from Landwehr's concept of subsp. *ochroleuca* but corresponds precisely to East Anglian populations such as that at Chippenham. Landwehr's description and illustration of *D. incarnata* f. *ochrantha*, together with its type locality (Lisdoonvarna, Co. Clare), suggest that it is anthocyanin-less *D. incarnata* subsp. *incarnata* or subsp. *pulchella*.

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