An assessment of populations of *Dactylorhiza traunsteineri* (Sauter) Soó in the British Isles and a comparison with others from Continental Europe

M. J. Y. FOLEY

87 Ribchester Road, Clayton-le-Dale, Blackburn, Lancs., BB1 9HT

ABSTRACT

The acceptance of *Dactylorhiza traunsteineri* (Sauter) Soó (Orchidaceae) as a British and Irish species has frequently been questioned. Twelve populations of dactylorchids from widely separate parts of the British Isles which have traditionally or recently been referred to this taxon, have been the subject of a critical morphometric evaluation. An inter-population comparison of the mean values of the key diagnostic characters indicated a degree of uniformity through the twelve populations although some geographical trends were identified. The data obtained were compared to, and found to be closely similar to those for populations of *D. traunsteineri* from the alpine region of Europe, including the type locality, and from Scandinavia, and this is offered as additional evidence for the inclusion of the species in the British and Irish floras. For *D. traunsteineri* in the British Isles, a comparison has been made with other dactylorchid taxa and their differences highlighted. The principal diagnostic characters of *D. traunsteineri* are summarised and a provisional distribution map is given.

INTRODUCTION

In a footnote to his *Flora* and under the name *Orchis Traunsteineri*, Reichenbach gave what was the first brief description of a species of marsh orchid from Kitzbühl, Austria, quoting Sauter as the authority (Reichenbach 1831). Shortly afterwards, Sauter himself provided a more detailed diagnosis of *O. traunsteineri* based upon similar Austrian specimens (Sauter 1837); in current nomenclature this is known as *Dactylorhiza traunsteineri* (Sauter) Soó.

Plants with characters corresponding to the description of continental *D. traunsteineri* were known in the British Isles as long ago as the last century, but were only first considered as such relatively recently (Heslop-Harrison 1953). Before and since then, however, their exact taxonomic status has been the subject of much speculation and various re-classifications have been attempted with treatments at varietal (Godfery 1933), subspecific (Pugsley 1936; Bateman & Denholm 1983) and specific level (in the latter case as *Orchis Traunsteinerioides* (Pugsley) Pugsley 1940). These treatments have been summarised by Roberts & Gilbert (1963), Tennant (1979), and Roberts (1988), and these workers along with others (Pugsley 1936; Heslop-Harrison 1953; Lacey 1955; Lacey & Roberts 1958) have also listed localities for similar dactylorchids. Morphometric studies of this taxon aimed at clarifying the situation have, in the British Isles, been restricted to the well-known Welsh populations (Cors Geirch, v.c. 49, and Cors Bodeilio, Rhos-y-gad, and Cors Erddreiniog (all v.c. 52)) (Lacey 1955; Lacey & Roberts 1958; Roberts 1966, 1988; Bateman & Denholm 1983), to one in Berkshire, v.c. 22 (Cothill), and also to three in Ireland, v.cc. H19, H20 and H23 (Heslop-Harrison 1953), and two small Yorkshire populations, v.cc. 62 and 64 (Roberts & Gilbert 1963) both of which are now almost extinct. Each of these independent studies has therefore covered only a very limited geographical range. Also, in addition to these differing views on taxonomic status, controversy has also arisen (Bateman & Denholm 1989; Roberts 1989) over the merits of the morphometric techniques employed, the interpretation of the data, and possible associated errors.

Within recent years, further populations referred to this taxon have been located in the British Isles, including several in Yorkshire, v.cc. 62 and 65 (Tennant *et al.* 1983; Foley 1986, 1989; Bolton & Horsman 1987; Tennant 1987), Norfolk, v.cc. 27 and 28 (Petch & Swann 1968; Swann 1975; F. Rose, pers. comm. 1988), Ireland, v.cc. H4, H5, H9 H16, H17, H18, H22, H26 and H29 (Scannell

1973; Webb & Scannell 1983; Curtis & McGough 1988; M. Keane, pers. comm. 1989), northern Wales, v.c. 49 (Roberts & Ward 1978), and scattered localities in southern England, v.cc. 6 and 12 (Rose 1975; Hedley 1987). Only very recently however, has it been confirmed from Scotland; Cunningham & Kenneth (1979) first tentatively identified as *D. traunsteineri*, a population of marsh-orchids from Kintyre, v.c. 101, but this was later refuted (Tennant & Kenneth 1983) when the plants were reassigned to *D. majalis* (Reichenb.) P. F. Hunt & Summerhayes subsp. *occidentalis* (Pugsl.) Sell. It was not until the discovery of a population very similar to *Orchis francis-drucei* Wilmott in W. Ross, v.c. 105, and its subsequent identification as *D. traunsteineri* (Lowe *et al.* 1986) that it was finally recognised from Scotland, although its presence there had been suspected for many years. Since then other populations have come to light (Kenneth *et al.* 1988), mostly very small and including some in Kintyre, but one larger Scottish population from W. Ross is known and is included in this study.

In a recent morphometric evaluation of British and Irish tetraploid marsh-orchids, which included two populations of this taxon from Anglesey, Bateman & Denholm (1983) assigned such plants to the new combination *D. majalis* subsp. *traunsteinerioides* (Pugsley) Bateman & Denholm. Roberts (1988), however, has shown that morphological data from one of these Anglesey populations compare well with those obtained by Reinhard (1985) for *D. traunsteineri* from the alpine region of continental Europe, and that separation of the Anglesey plants from these on the basis suggested by Bateman & Denholm (1983) cannot be justified. The present study, independently instigated, was already in progress prior to the publication of the work of Roberts (1988) and was undertaken in order to assess the degree of similarity or otherwise of various populations representing the full geographical range of the taxon in the British Isles. A morphometric examination of randomly selected plants has been made for each population, and data obtained compared with those for *D. traunsteineri* from the alpine region of Europe including the type locality. Comparisons have also been made with plants from Scandinavia, and with other British and Irish dactylorchids. This study therefore addresses two independent questions: (i) are British and Irish populations conspecific with continental *D. traunsteineri*, and (ii) should this taxon be considered at specific level or as a subspecies of some other dactylorchid, for example *D. majalis*?

POPULATIONS SAMPLED

A provisional map indicating the distribution of *D. traunsteineri* in the British Isles is given in Fig. 1. For the present study, evaluated populations have been selected as representative of the known range. Many of these have been discovered or identified only quite recently and have not been previously assessed morphometrically.

Details of the twelve British and Irish populations studied are given in Table 1. Other than at Booton (F) and Killinaboy (K), where the number of plants is small (approx 50), all are relatively strong populations often comprising several hundred flowering plants. This is significant particularly in the case of the Yorkshire sites, since the only previous morphometric study (Roberts & Gilbert 1963) carried out on similar plants from this area, was on colonies of total size nine and 22 plants respectively. Populations examined also include three which have previously been studied morphometrically (Heslop-Harrison 1953; Roberts 1966, 1988; Bateman & Denholm 1983). These are in Berks (v.c. 22) at Cothill (G), and in Anglesey (v.c. 52) at Cors Erddreiniog (H) and at Rhos-y-gad (I), and again all comprise a relatively large number of plants.

These twelve populations which are the subject of this study each occur in eutrophic, base-rich fens or flushes, some of which are quite small in area and are isolated. *Schoenus nigricans* L. is invariably present and grows in close association with these dactylorchids, whilst *Valeriana dioica* L., and where their distributional ranges allow, *Pinguicula vulgaris* L. and *Primula farinosa* L., are usually present also. Other associates can include *Carex lepidocarpa* Tausch, *Menyanthes trifoliata* L., *Epipactis palustris* (L.) Crantz, *Listera ovata* (L.) R. Br., and in Anglesey and Ireland, *Ophrys insectifera* L. Other dactylorchids are quite often absent, but *Dactylorhiza incarnata* (L.) Soó subsp. *incarnata* and subsp. *pulchella* (Druce) Soó sometimes occur nearby but not usually in direct association or intermixed with *D. traunsteineri*. *D. majalis* subsp. *purpurella* (T. & T. A. Steph.) Moore & Soó is a rarer associate, but subsp. *praetermissa* (Druce) Moore & Soó occurs at sites in southern and eastern England, whilst *D. fuchsii* (Druce) Soó and *D. maculata* (L.) Soó also occur

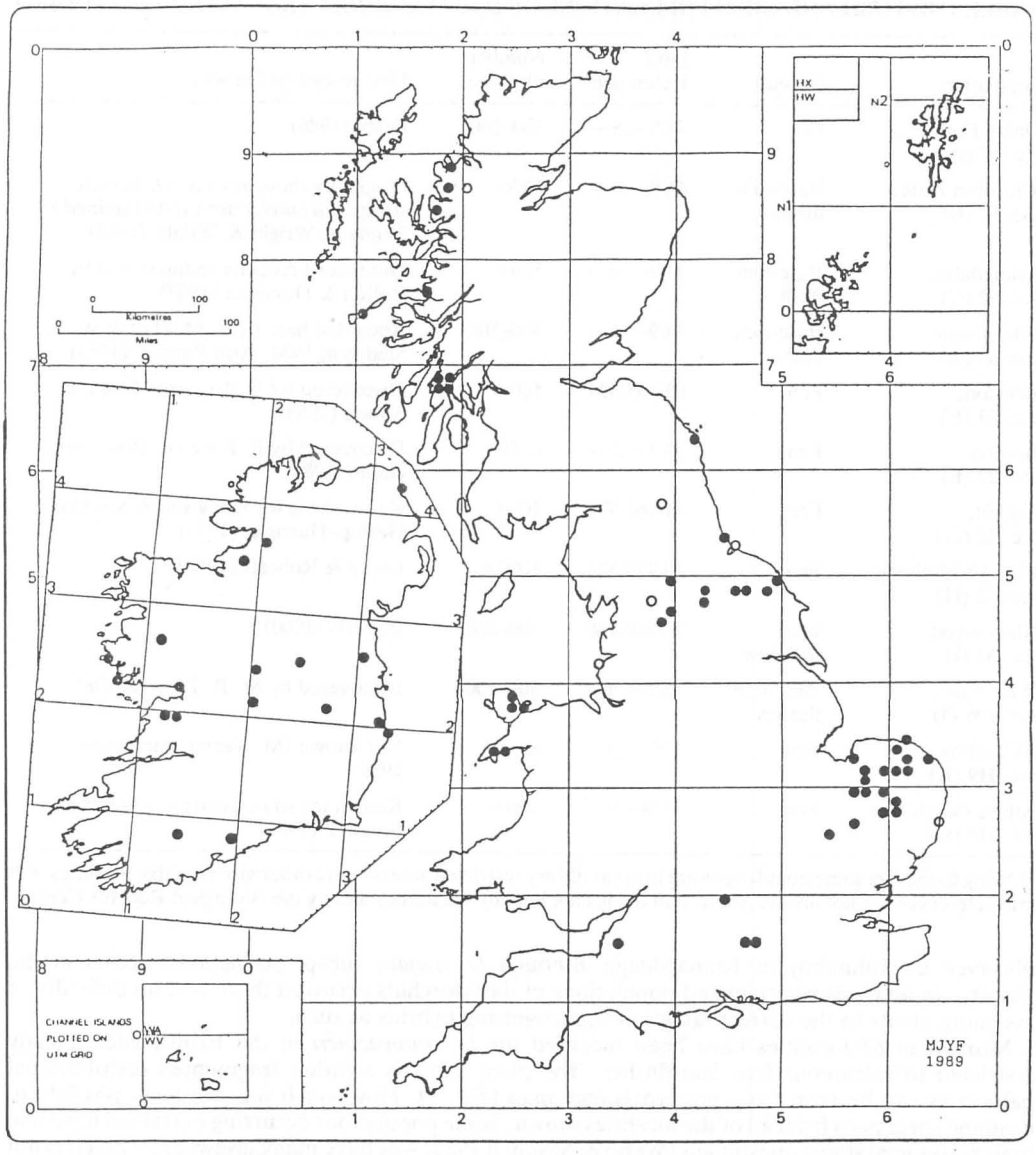

FIGURE 1. The distribution of *Dactylorhiza traunsteineri* in the British Isles plotted on a 10-km square basis (provisional). ● recorded sites; ○ doubtful or unconfirmed records.

within the general vicinity of most populations. Hybrids with other dactylorchids have been recorded by the author and others at several of the sites studied; the hybrid with *D. maculata* is known at Thornton Dale, Dalby Forest (Foley 1986), Cors Erddreiniog and Rhos-y-gad; that with *D. fuchsii* at the two Anglesey colonies; with *D. incarnata* at Wharfedale and again at the two Anglesey colonies; and with *D. majalis* subsp. *praetermissa* at the three sites in southern and eastern England. In all cases they are relatively infrequent and often very rare. No hybrids were found at Fylingdales although that with *D. fuchsii* may have been recorded here recently (Horsman 1989). In addition hybrids with the spotted orchids are suspected to occur at W. Ross, but no hybrids were

TABLE 1. BRITISH AND IRISH POPULATIONS OF *DACTYLORHIZA TRAUNSTEINERI* STUDIED

Population	Habitat	Grid Reference[a]	Number of plants	First record (if known)
Dalby Forest, v.c. 62 (A)	Fen	44/8—.8—	100–200	Foley (1986)
Thornton Dale, v.c. 62 (B)	Base-rich flushes	44/8—.8—	1000+	Originally thought to be *D. majalis* subsp. *purpurella* until redetermined by Tennant, Wright & Wright (1983)
Fylingdales, v.c. 62 (C)	Base-rich flush	44/9—.9—	500+	Old record recently rediscovered by Bolton & Horsman (1987)
Wharfedale, v.c. 64 (D)	Base-rich flush	34/9—.6—	300–500	Recorded here by P. M. Hall & W. A. Sledge in 1934. Also Pugsley (1935)
Beeston, v.c. 27 (E)	Fen	63/165.424	500+	Discovered by F. Rose, see Petch & Swann (1968)
Booton, v.c. 27 (F)	Fen	63/1—.2—	c. 50	Discovered by F. Rose (F. Rose, pers. comm. 1988)
Cothill, v.c. 22 (G)	Fen	41/461.998	100+	Known here for many years. See also Heslop–Harrison (1953)
Cors Erddreiniog, v.c. 52 (H)	Fen	23/475.821	1000+	Lacey & Roberts (1958)
Rhos-y-gad, v.c. 52 (I)	Fen/ meadow	23/510.788	100–200	Roberts (1960)
West Ross, v.c. 105 (J)	Base-rich flushes	18/7—.4—	500–1000	Discovered by M. R. Lowe in 1985
Killinaboy, v.c. H9 (K)	Fen	11/2—.9—	c. 50	Not known (M. Keane, pers. comm. 1989)
Kilmacduagh, v.c. H9 (L)	Fen	11/3—.9—	100+	Known for some years; see Webb & Scannell (1983)

[a] Owing to the fact some populations are in areas of very restricted access or are otherwise sensitive localities, full grid references are not always given. Full details are held by the author and by the Biological Records Centre.

observed at Killinaboy or Kilmacduagh although *D. majalis* subsp. *occidentalis* occurs in the vicinity. In all cases where mixed populations of dactylorchids occurred there was no difficulty in assigning plants to the correct taxon, or in recognising hybrids as such.

More than 85 localities have been recorded for *D. traunsteineri* in the British Isles, mostly restricted to calcareous fens and flushes. The plant exhibits a rather fragmented distributional pattern as can be seen from the provisional map (Fig. 1). However it has not been possible to examine specimens from all of the localities shown. Some populations occurring in Ireland have had their taxonomic status questioned (Webb & Scannell 1983) – as have many elsewhere – and it is not too clear how many Irish localities are still extant (Curtis & McGough 1988).

In the British Isles plants are normally in full flower in late May in western localities including Anglesey, and by early/mid-June inland, at higher altitudes, and to the north.

METHODS

Morphological characters were recorded from ten randomly selected plants in each population. The characters selected (and method of measurement), were in accord with those of other workers (Bateman & Denholm 1983; Roberts & Gilbert 1963; Roberts 1966, 1988), namely, plant height, total number of all developed and developing leaves (excluding the basal scale-like leaf which often decays), length of fully open inflorescence (from apex to the junction of the lowest flower with the

stem), the number of flowers in the inflorescence, and the maximum dimensions of the second leaf above the stem base (which is also usually the largest leaf). These characters were all measured on field material. At the same time the degree of leaf spotting was assessed (0 = absent, 1 = present) and the extent/distribution and size of the spots noted; an estimate was also made of the degree of anthocyanin staining of the upper stem and floral bracts (0 = absent, 1 = light, 2 = heavy). A single flower was removed from below the mid-point of each inflorescence, and from it, the maximum labellum width, the labellum length from the apex of the central lobe to the spur opening, the depth of the deeper inter-lobe sinus (if different) measured parallel to the vertical axis through the labellum from the base of the sinus to a point level with the apex of the adjacent lateral lobe, and the spur length from its tip to the junction with the labellum as well as the spur width at this point (with spur detached), were all obtained from flattened specimens which had been pressed within 48 hours of sampling. The shape of the labellum and the type and distribution of markings upon it were noted on similarly flattened specimens and also in the field.

The peripheral cells of a floral bract selected from below the mid-point of the inflorescence were also assessed for shape in profile and measured under microscopic examination (×100). In order to overcome any variation in shape and size of individual cells within and between bracts from the same and different plants, the total length of ten contiguous peripheral cells was measured at a point approximating to the mid-length on five separate bracts each from different plants within the population. The mean length and range of the cell lengths was calculated and any characteristic cell shapes noted. Any other distinct differences between populations which were readily apparent in the field, were also recorded, and at some localities, pH measurements were made on samples of surface water taken from within the immediate vicinity of the plants.

Results for most of the characters studied are recorded as population mean values, and where appropriate the standard error has also been calculated.

From the above measurements two further characters, floral density (number of flowers/cm of inflorescence length), and mean leaf index (second leaf from the base of the stem, mean length/mean (maximum) width) were calculated. All the data were obtained during the period 1985–1989.

RESULTS AND DISCUSSION

The main diagnostic characters of *D. traunsteineri* were given in some detail by Sauter (1837), viz: long narrow leaves, a lax, few-flowered inflorescence with relatively large flowers, each having a tri-lobed labellum. In addition other continental plants of *D. traunsteineri* have been described or illustrated as being typically slender, possessing relatively few, spotted or unspotted leaves, which are well-spaced along the stem, and with relatively broad labella (e.g. Landwehr 1977; Reinhard 1985; Kalteisen & Reinhard 1986; H. R. Reinhard, pers. comm. 1988).

VARIATION WITHIN THE BRITISH AND IRISH POPULATIONS STUDIED

For the populations studied, Table 2 lists data for the above-mentioned distinctive features. The mean length and shape of the peripheral cells of the floral bracts (character 19) are included in Table 3.

The average of the character means and the range which encompass the twelve British and Irish populations examined have been extracted from these data and are also given in Table 2 where it can be seen that there is close inter-population agreement in many key characters namely:–

(a) *Mean number of flowers per plant (character 3).* There is close agreement between most populations, falling within a narrow range 7·0–9·0; the slightly higher values for some populations (E–L), especially those from Ireland (K and L), reflects the presence of more robust plants at these sites.

(b) *Mean floral density (character 4).* Again there is good agreement throughout with little regional trend indicated. Inflorescences are variable in shape or very roughly cylindrical/tapering.

(c) *Mean total leaves per plant (character 5).* No significant regional trends were apparent, with good inter-population agreement. The mean number of non-sheathing leaves (character 6) is often considered to be a partially diagnostic character of *D. traunsteineri* (range 0–1) since the value for other British dactylorchids is much higher. Here, where known, the range is 0·6–1·0. In all cases it

TABLE 2. MEAN CHARACTER MEASUREMENTS AND STANDARD ERRORS (IN PARENTHESES) FOR TEN RANDOMLY SELECTED PLANTS IN EACH OF TWELVE POPULATIONS OF *DACTYLORHIZA TRAUNSTEINERI*

Character	A. Dalby Forest	B. Thornton Dale	C. Fyllingdales	D. Wharfedale	E. Beeston	F. Booton	G. Cothill	H. Cor Erddreiniog	I. Rhos-y-gad	J. West Ross	K. Killinaboy	L. Kilmacduagh	Overall mean and range
1. Mean plant height (cm)	14·9 (1·04)	18·5 (1·28)	14·5 (0·62)	12·7 (0·63)	18·9 (1·06)	23·6 (1·47)	20·5 (2·05)	15·6 (0·41)	15·1 (1·09)	12·2 (0·56)	30·0 (1·41)	30·5 (1·45)	18·9 (12·2–30·5)
2. Mean length of inflorescence (cm)	3·4 (0·19)	3·4 (0·20)	3·4 (0·15)	3·4 (0·18)	4·0 (0·21)	4·93 (0·29)	4·2 (0·34)	3·9 (0·20)	4·0 (0·27)	3·4 (0·17)	4·6 (0·40)	5·5 (0·48)	4·0 (3·4–5·5)
3. Mean number of flowers	7·0 (0·53)	7·7 (0·45)	8·6 (0·89)	9·0 (0·37)	9·6 (0·85)	10·2 (1·07)	11·3 (1·30)	11·4 (0·99)	9·3 (0·74)	7·7 (0·74)	12·2 (1·45)	12·4 (1·76)	9·7 (7·0–12·4)
4. Floral density[a]	2·06 (—)	2·26 (—)	2·53 (—)	2·65 (—)	2·40 (—)	2·07 (—)	2·69 (—)	2·92 (—)	2·33 (—)	2·30 (—)	2·65 (—)	2·25 (—)	2·43 (2·06–2·92)
5. Mean total no. of leaves	3·3 (0·15)	3·5 (0·16)	3·8 (0·13)	3·9 (0·22)	4·0 (0·14)	3·5 (0·16)	3·7 (0·15)	3·4 (0·15)	3·7 (0·15)	3·5 (0·18)	3·3 (0·15)	3·7 (0·15)	3·6 (3·3–4·0)
6. Mean no. of non-sheathing leaves	0·9 (0·09)	0·6 (0·15)	0·7 (0·15)	0·8 (0·13)	0·9 (0·09)	0·7 (0·15)	1·0 (0·00)	0·9 (0·09)	0·6 (0·15)	0·8 (0·12)	0·9 (0·09)	0·8 (0·13)	0·8 (0·6–1·0)
7. Mean length of second leaf (cm)	7·60 (0·46)	8·35 (0·30)	7·55 (0·30)	5·70 (0·18)	9·84 (0·56)	10·00 (0·71)	9·13 (0·68)	8·10 (0·48)	7·97 (0·49)	5·00 (0·40)	13·95 (0·63)	14·37 (0·77)	8·96 (5·00–14·37)
8. Mean max. width of second leaf (cm)	1·04 (0·03)	1·10 (0·07)	0·83 (0·03)	1·03 (0·06)	0·93 (0·03)	1·01 (0·06)	1·00 (0·05)	1·10 (0·05)	1·03 (0·05)	0·91 (0·04)	1·09 (0·08)	1·14 (0·08)	1·02 (0·83–1·14)
9. Mean leaf index[b]	7·31 (—)	7·59 (—)	9·10 (—)	5·53 (—)	10·58 (—)	9·90 (—)	9·13 (—)	7·36 (—)	7·74 (—)	5·49 (—)	12·80 (—)	12·60 (—)	8·76 ((5·49)7·31–12·80)
10. Degree of leaf spotting[c]	0·3 (—)	0·1 (—)	0·0 (—)	0·5 (—)	0·0 (—)	0·0 (—)	0·1 (—)	0·0 (—)	0·0 (—)	0·0 (—)	0·1 (—)	0·8 (—)	0·2 (0·0–0·8)

TABLE 2 *cont'd*

Character	A. Dalby Forest	B. Thornton Dale	C. Fyldingales	D. Wharfedale	E. Beeston	F. Booton	G. Cothill	H. Cor Erddreiniog	I. Rhos-y-gad	J. West Ross	K. Killinaboy	L. Kilmacduagh	Overall mean and range
11. Upper stem – anthocyanin staining[d]	0·5 (—)	1·5 (—)	1·0 (—)	1·5 (—)	0·7 (—)	0·2 (—)	0·8 (—)	1·0 (—)	0·8 (—)	1·0 (—)	0·2 (—)	0·6 (—)	0·8 (0·2–1·5)
12. Bracts – anthocyanin staining[d]	1·0 (—)	2·0 (—)	1·5 (—)	2·0 (—)	1·3 (—)	1·0 (—)	1·4 (—)	1·0 (—)	1·4 (—)	1·5 (—)	0·6 (—)	0·8 (—)	1·3 (0·6–2·0)
13. Mean labellum width (cm)	1·07 (0·04)	1·06 (0·02)	0·95 (0·02)	0·94 (0·04)	1·07 (0·03)	0·96 (0·04)	0·94 (0·03)	1·09 (0·05)	0·94 (0·03)	0·97 (0·03)	0·90 (0·02)	1·12 (0·06)	1·00 (0·90–1·12)
14. Mean labellum length (cm)	0·87 (0·03)	0·80 (0·02)	0·73 (0·02)	0·79 (0·02)	0·87 (0·03)	0·79 (0·03)	0·81 (0·03)	0·77 (0·04)	0·80 (0·03)	0·72 (0·02)	0·77 (0·01)	0·82 (0·04)	0·80 (0·72–0·87)
15. Mean spur width (cm)	0·36 (0·01)	0·32 (0·02)	0·34 (0·01)	0·32 (0·01)	0·31 (0·01)	0·30 (0·01)	0·31 (0·01)	0·33 (0·02)	0·32 (0·02)	0·29 (0·01)	0·28 (0·01)	0·31 (0·01)	0·32 (0·28–0·36)
16. Mean spur length (cm)	0·79 (0·02)	0·87 (0·02)	0·75 (0·01)	0·72 (0·03)	0·86 (0·03)	0·80 (0·03)	0·77 (0·03)	0·82 (0·04)	0·85 (0·02)	0·75 (0·04)	0·84 (0·02)	0·90 (0·03)	0·81 (0·72–0·90)
17. Mean sinus depth (mm)	0·36 (0·16)	0·89 (0·16)	0·85 (0·20)	0·78 (0·11)	0·70 (0·18)	0·47 (0·09)	0·32 (0·13)	1·10 (0·20)	0·92 (0·15)	1·17 (0·17)	0·27 (0·07)	0·77 (0·10)	0·72 (0·27–1·17)
18. Trilobed nature of labellum (or otherwise)	trilobed	distinctly trilobed	trilobed	distinctly trilobed	trilobed	trilobed to sub-rhomboidal	trilobed/sub-rhomboidal (very prominent central lobe)	distinctly trilobed	distinctly trilobed	distinctly trilobed (very prominent central lobe)	trilobed	trilobed	—

[a] Floral density = Character 3/Character 2.
[b] Mean leaf index = Character 7/Character 8.
[c] Degree of leaf spotting (always very light and about 1 mm diameter when present); 0 = absent, 1 = present.
[d] Degree of anthocyanin staining; 0 = absent, 1 = light, 2 = heavy.

TABLE 3. VARIATION IN BRACT PERIPHERAL CELLS OF *DACTYLORHIZA TRAUNSTEINERI* AND RELATED TAXA

Mean cell length and typical cell shape based upon ten contiguous peripheral cells from at least five bracts from separate plants in each population.

Species and population	Population mean cell length (μm), and range of means for individual bracts in parentheses		Typical cell shape in profile
D. traunsteineri (Britain and Ireland)			
A. Dalby Forest	98	(80–115)	elongated subacute to serrate
B. Thornton Dale	83	(80– 90)	,,
C. Fylingdales	85	(73–100)	,,
D. Wharfedale	74	(63– 80)	,,
E. Beeston	77	(65– 88)	,,
F. Booton	83	(70–108)	,,
G. Cothill	78	(65– 93)	,,
H. Cors Erddreiniog	93	(85–105)	,,
I. Rhos-y-gad	85	(68–100)	,,
J. W. Ross	88	(78–108)	,,
K. Killinaboy	85	(70– 98)	,,
L. Kilmacduagh	89	(78–100)	,,
D. traunsteineri (Continental Europe)			
Schwarzsee, Kitzbühl (Austria)	89	(80–112)	elongated subacute to serrate
Schmerikon, St. Gallen (Switzerland)	89	(78–103)	,,
Njurunda (Sweden)	76	(68–88)	,,
Visby (Sweden)	84	(70–103)	,,
D. incarnata subsp. *cruenta* (Ireland)			
Knockaunroe, v.c. H9	46	(40– 53)	rounded-crenate
D. incarnata subsp. *pulchella* (Cumbria)			
Milnthorpe, v.c. 69	56	(50– 58)	rounded-crenate
Sunbiggin Tarn, v.c. 69	46	(43– 50)	,,
D. majalis subsp. *purpurella* (Cumbria)			
Beckfoot, v.c. 70	69	(60– 80)	rounded-obtuse
Sandscale Haws, v.c. 69	68	(58– 78)	,,
Sunbiggin Tarn, v.c. 69	69	(55– 83)	,,
D. majalis subsp. *praetermissa* (England and Wales)			
Sandwich, v.c. 15	66	(58– 78)	rounded-obtuse
Elstead, v.c. 17	67	(58– 75)	,,
Kenfig, v.c. 41	57	(50– 65)	,,
D. majalis subsp. *occidentalis* (Ireland)			
Ballynaleckan, v.c. H9	78	(70– 85)	rounded-obtuse

was noted that leaves were well spaced along the stem and not crowded towards the base as is the case in some species of dactylorchid.

(d) *Mean leaf index of second leaf (character 9, incorporating characters 7 and 8).* The mean leaf index (length/maximum width of second leaf from stem base) showed some inter-population variation with the Wharfedale (D) population particularly low. Conversely the East Anglian populations (E and F) possessed relatively high values and the Irish (K and L) the highest of all, a character which is quite noticeable in the field. The Fylingdales plants (C) had the narrowest leaves (character 8) and showed little variation in width – this again was noticeable in the field. The mean maximum leaf width varied between 0·83–1·14 cm in the populations studied.

(e) *Degree of leaf spotting (character 10).* Leaf spots, when they occurred, were always small in size, about 1 mm diameter, solid, never densely distributed, and often spread over most of the upper surface of the leaf. In many plants in all populations spotting was absent, and in the samples examined, was not recorded from the Yorkshire population (C), nor from either of the East Anglian populations (E and F), nor those from Anglesey (H and I) (although recorded in a small proportion

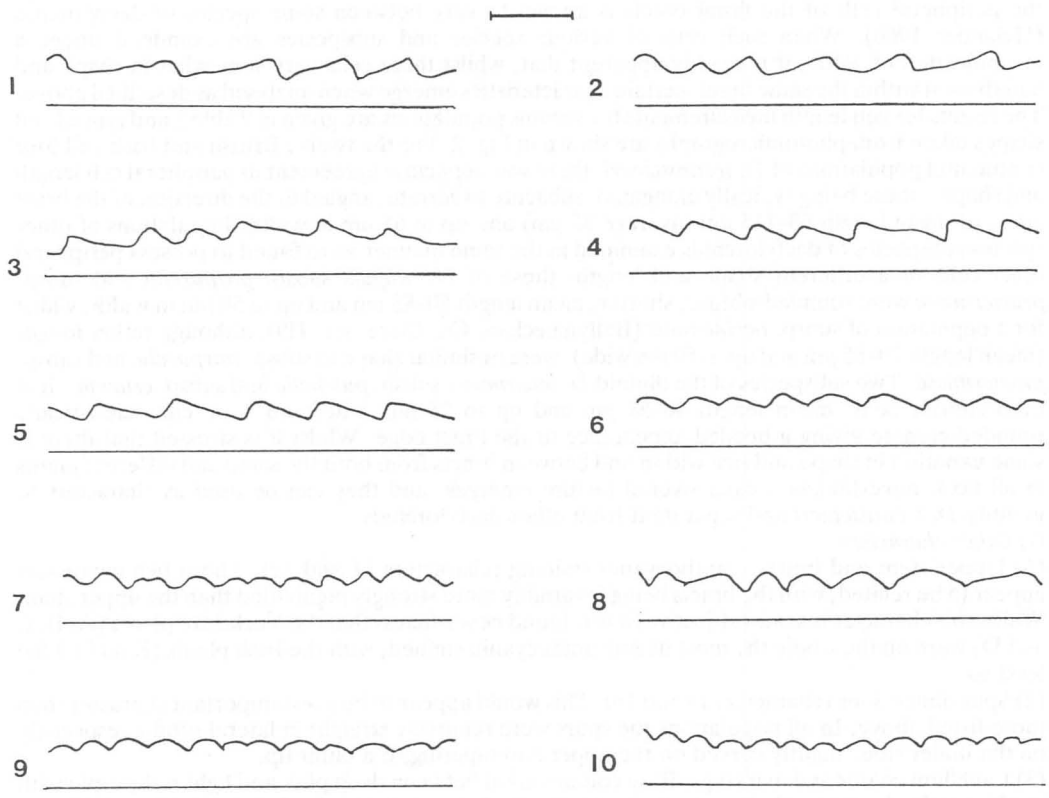

FIGURE 2. Profiles of peripheral cells of floral bracts (scale bar = 100 μm). 1. *D. traunsteineri* (Schmerikon, St. Gallen, Switzerland), 2. *D. traunsteineri* (Schwarzsee, Kitzbühl, Austria), 3. *D. traunsteineri* (Visby, Sweden), 4. *D. traunsteineri* (Thornton Dale, v.c. 62), 5. *D. traunsteineri* (Dalby Forest, v.c. 62), 6. *D. majalis* subsp. *purpurella* (Beckfoot, v.c. 70), 7. *D. majalis* subsp. *praetermissa* (Elstead, v.c. 17), 8. *D. majalis* subsp. *occidentalis* (Ballynaleckan, v.c. H9), 9. *D. incarnata* subsp. *pulchella* (Milnthorpe, v.c. 69), 10. *D. incarnata* subsp. *cruenta* (Knockaunroe, v.c. H9).

of the plants at colony I (Roberts 1960)), nor that from Scotland (J). In contrast, two Yorkshire colonies (A and D) were extensively leaf-spotted as was one of the Irish populations (L).

(f) *Mean labellum width (character 13) and mean labellum length (character 14).* Taken together these two characters showed no significant inter-population trend although five, Dalby Forest (A), Thornton Dale (B), Beeston (E), Cors Erddreiniog (H), and Kilmacduagh (L), had the greatest mean labellum widths. In all cases labella were slightly to semi-reflexed along the vertical axis.

(g) *Mean depths of sinuses and trilobed nature of labellum (characters 17 and 18).* This composite character was partly assessed subjectively on flattened specimens of labella from the plants sampled, together with measurements of inter-lobe sinus depths. The Anglesey populations (H and I) and that from W. Ross (J) could be separated from the others in being the most distinctly trilobed and possessing deeper inter-lobe sinuses (mean depth 0·92–1·17 mm), whereas the southern England populations (E, F and G) were trilobed/sub-rhomboidal with generally much less prominent sinuses (0·32–0·70 mm) and with the Cothill (G) and W. Ross (J) plants, especially, displaying very prominent central lobes. The Yorkshire populations had on average rather more pronounced sinuses (0·36–0·89 mm) than the southern plants. The Irish plants were somewhat variable and intermediate in this respect.

(h) *Bract peripheral cells – mean length and shape (character 19).* The shape in profile and length of

the peripheral cells of the floral bracts is known to vary between some species of dactylorchid (Hylander 1966). When such cells of various species and subspecies are examined under a magnification of ×100, it is readily apparent that, whilst these cells vary somewhat in shape and length even within the same bract, certain characteristics emerge when analysed as described above. The results for cell length measurements for various populations are given in Table 3 and typical cell shapes taken from photomicrographs are shown in Fig. 2. For the twelve British and Irish and four continental populations of *D. traunsteineri*, there was very close agreement in peripheral cell length and shape – these being typically elongated, subacute to serrate, angled in the direction of the bract apex, of mean length 63–115 μm (average 85 μm) and up to 65 μm in width. Populations of other species/subspecies of dactylorchids examined in the same manner were found to possess peripheral bract cells of a different shape and length; those of *D. majalis* subsp. *purpurella* and subsp. *praetermissa* were rounded-obtuse, shorter, mean length 50–83 μm and up to 50 μm in width, whilst for a population of subsp. *occidentalis* (Ballynaleckan, Co. Clare, v.c. H9), although rather longer (mean length 70–85 μm and up to 50 μm wide), were of similar shape to subsp. *purpurella* and subsp. *praetermissa*. Two subspecies of the diploid *D. incarnata* – subsp. *pulchella* and subsp. *cruenta* – had even shorter cells, mean length 40–58 μm and up to 35 μm wide, and were characteristically rounded-crenate giving a beaded appearance to the bract edge. Whilst it is stressed that there is some variation in shape and size within and between bracts from both the same and different plants in all taxa, nevertheless a clear overall picture emerges, and they can be used as characters to identify *D. traunsteineri* and separate it from other dactylorchids.

(i) *Other characters*

(1) Upper stem and bracts – anthocyanin staining (characters 11 and 12). These two characters appear to be related, with the bracts being invariably more strongly pigmented than the upper stem. Whilst this character is semi-subjective, it was found nevertheless that the Yorkshire plants (A, B, C and D) were on the whole the most deeply anthocyanin stained, with the Irish plants (K and L) the least so.

(2) Spur dimensions (characters 15 and 16). This would appear to be a less important character than those listed above. In all populations the spurs were relatively straight in lateral profile, especially on the under side, slightly curved on the upper and tapering to a blunt tip.

(3) Labellum colour and markings. Base colour varied between deep pink and light red-purple with markings of a similar much deeper colour. All the Yorkshire colonies (and especially C and D) were generally noticeably deeper in base colour than the others and marked overall by many small spots and flecks. On the other hand the Anglesey plants (H and I) were much lighter in base colour yet marked with much more contrasting heavier semi-continuous lines and blotches, and the Irish plants (K and L) possessed a very characteristic lilac-pink base colour. The remaining populations (E, F and G) were similar in base colour to the Anglesey plants but much more lightly and less contrastingly marked.

The degree of variation in all major characters between the populations studied is relatively small and throughout there is good agreement between the results presented here and those for the same populations studied by previous workers, e.g. Roberts (1988).

Regional differences may be summarised as follows:–

The Yorkshire plants (A, B, C and D) have fewer flowers of a deeper base colour with labella relatively finely marked, and with a proportion of plants with lightly spotted leaves. The upper stem and bracts are invariably strongly stained with anthocyanin. Other populations of similar plants have been given varietal status by Godfery (1933) as *Orchis latifolia* var. *eborensis*, and more recently as *D. majalis* subsp. *traunsteinerioides* var. *eborensis* by Bateman & Denholm (1983). The latter imply that such plants are always leaf marked, such marks more often than not being annular in shape, that inflorescences have often more than eight flowers, and that labella rarely exceed more than 7·5 × 9·5 mm, often more or less as broad as long and with a base colour only occasionally dark. Such diagnostic characters for the Yorkshire plants are not upheld in this study, and although there is some regional variation as outlined above, this appears to be within acceptable limits, and suggests that a separate varietal status may not be justified. Furthermore as Roberts & Gilbert (1963) acknowledge, in the two very small and isolated Yorkshire populations which they studied, there may have been appreciable genetic deviation from the norm, and the results now obtained seem to confirm this.

The southern England populations (E, F and G) have longer narrow leaves (high leaf index), with

labella trilobed to sub-rhomboidal, and relatively lightly coloured but not heavily spotted or loop marked.

Plants from the Anglesey populations (H and I) have much more lightly coloured flowers which are more heavily and contrastingly marked on the labella, these being distinctly trilobed, with relatively deep inter-lobe sinuses.

The Scottish population (J) comprises plants of small stature with relatively short leaves, and flowers which are markedly trilobed, with deep sinuses and a prominent central lobe.

Plants in both Irish populations (K and L) are relatively robust with a somewhat larger number of flowers in the inflorescence, these being a distinctive lilac-pink colour. They possess the highest leaf index of the populations examined and also have the longest leaves, and one population (L) has a high incidence of leaf-spotted plants; spurs are somewhat down-curved. Some of these characters agree closely with those possessed by plants in a population of *D. traunsteineri* from Njurunda, Sweden which is discussed in more detail below, and is thought to show some affinity to *D. russowii* (Klinge) J. Holub.

From examination of the above data, it is apparent that plants from the twelve populations included in this study, because of their relative geographical isolation from other populations of this taxon, understandably exhibit some inter-populational differences. Nevertheless, the populations show good agreement in the key diagnostic characters and it is therefore concluded that they should be treated as a single species, possibly with varietal status accorded to some Irish populations.

COMPARISON OF THE BRITISH AND IRISH POPULATIONS WITH DATA FOR *D. TRAUNSTEINERI* AT CONTINENTAL SITES

The average and range of the mean character measurements obtained for the twelve British and Irish populations taken together are included in Table 4. These are compared with data supplied by H. R. Reinhard of Zürich (pers. comm. 1989) for *D. traunsteineri* at the type locality, Schwarzsee, Kitzbühl, and with other composite data obtained by Reinhard for populations in Austria and Switzerland (Reinhard 1985) (note – data given by Kalteisen & Reinhard (1986) and described as "*locus classicus*" differ slightly from the Kitzbühl data since they also include plants from Zell am See, Salzburg). My observations and measurements on bract peripheral cells for *D. traunsteineri* populations from the British Isles and continental Europe are given in Table 3.

When the diagnostic characters 3, 4, 5, 8, 9, 13, 14, 18 and 19, are examined for British, Irish and continental European populations (Table 4), very close agreement is obtained in each case. In addition Reinhard (pers. comm. 1988) states that in plants from Austria and Switzerland the leaves can be either spotted or unspotted. The only significant difference lies in spur length which is found to be appreciably lower in this study (0·81 cm) than that found by Reinhard (1·11 cm and 1·09 cm). This is not a diagnostic character, but it is still surprising in view of the fact that Reinhard's data (Reinhard 1985) for spur length of *D. lapponica* (Laest. ex Hartman) Soó (0·78–0·96 cm), a taxon closely related to *D. traunsteineri*, are consistently lower and in close agreement with the present results. This difference from Reinhard's spur length data is also displayed in the results of Roberts (1988) and earlier workers. Nevertheless, the overall good agreement in the principal diagnostic characters supports the view of Roberts (1988) when concluding that the Rhos-y-gad plants (I) are indeed *D. traunsteineri*; similarly, the conclusion is now drawn that the British and Irish populations covered in this study are also conspecific with *D. traunsteineri*. However, if further work shows that British and Irish populations differ in some small respect from continental ones (e.g. as in spur length above), then the former should be placed as a subspecies of *D. traunsteineri*.

Tables 3 and 4 also include the author's data for a dactylorchid population from Njurunda, Sweden. This, whilst acceptably complying with the diagnostic characters for *D. traunsteineri*, nevertheless possesses some features applicable to the relatively elusive and rather vaguely described *D. russowii*, recorded for the Baltic area of Scandinavia and north-eastern Europe. This latter is a robust plant with a relatively long, rather dense-flowered inflorescence with a large number of flowers, each with comparatively small labellum dimensions, somewhat down-curved spurs, and with leaves quite heavily spotted and blotched. The Njurunda population occurs in neutral to slightly calcareous conditions (pH 6·9) growing with *Epipactis palustris*, the only locality for the latter in northern Sweden (R. Lidberg, pers. comm. 1989). Again most characters of the British populations agree well, and those from Ireland, (mean number of flowers, floral density, spur shape) especially so. Further work might show that *D. russowii* itself warrants consideration

only as a variety or subspecies of *D. traunsteineri*, possibly intergrading with the type, with the Njurunda population representing an intermediate variant. Morphometric data have also been obtained for a further population of *D. traunsteineri* from Visby, Gotland, Sweden which shares some similar characters with the Njurunda plants (inflorescence length, number of flowers). In the Visby plants, labella are slightly trilobed to sub-rhomboidal often with a prominent central lobe; the mean dimensions (n = 10) for labella are 0·96 cm (wide) × 0·79 cm, and for flattened spurs, 0·30 cm (wide) × 0·88 cm, with the floral bracts appreciably anthocyanin-stained (mean value 1·5). These data again agree closely with those for British and Irish populations, and fall well within the range of their appropriate character means.

As already commented, *D. traunsteineri* in the British Isles is usually restricted to calcareous fens and flushes with an approximate pH range 7·0–7·5, although it can occur in slightly acidic conditions as at Fylingdales (pH 6·5). Its existence in calcareous habitats is also the case at many sites in the alpine region of continental Europe and in Scandinavia where its associates can include calcicoles such as *Eriophorum latifolium* Hoppe and *Schoenus ferrungineus* L. (Simonsson & Lindström 1977; Jonsell 1982; Devillers-Terschuren & Devillers 1986). *D. traunsteineri* is also recorded from calcareous fens in the Haute-Marne area of north-eastern France growing with *Schoenus nigricans*, *S. ferrugineus*, and *Epipactis palustris* (Tyteca 1981), and from calcareous coastal fens in Pas-de-Calais (F. Rose, pers. comm. 1989). Records for *D. traunsteineri* from somewhat acidic habitats in continental Europe suggest a tolerance to such, possibly as a specialised ecotype of the species. Other records from distinctly acidic localities may be a result of confusion with a similarly described, taller, relatively narrow-leaved but more dense-flowered taxon accorded specific status as *D. sphagnicola* (Höppner) Soó. This latter has been recognised within the geographical range of *D. traunsteineri*, and has been recorded for West Germany (Rube 1972), for Belgium and north-eastern France (Tyteca 1986), for Sweden (Birkedal & Danielson 1981; Ericsson 1982), and is also claimed to occur along with the taxon described as *D. traunsteineri* subsp. *curvifolia* (Nyl.) Soó in eastern Finland (Räsänen & Saari 1987). It is known to inhabit acidic habitats as shown by such associates as *Juncus acutiflorus* Ehrh. ex Hoffm., *Drosera rotundifolia* L., and *Erica tetralix* L. (Landwehr 1977; Tyteca 1981).

Illustrations of continental *D. traunsteineri* closely similar to plants encountered in this study are given by Landwehr (1977) (see p. 159, nos. 1–5), as well as others in the same work from Ireland (p. 166, nos. 1–2). However those shown by him as *D. traunsteinerioides* (Pugsl.) Landw. (p. 166, nos. 3–5) from the same Irish locality are not typical of British and Irish plants, being much more dense-flowered and robust and are possibly of hybrid origin. A series of colour photographs of examples of *D. traunsteineri* from various sites in Switzerland and in Austria have been provided by H. R. Reinhard, and all show a very close similarity to plants from British and Irish populations. In addition, Reinhard has examined detailed colour photographs of typical plants from the British and Irish populations studied and has confirmed that all agree very well with *D. traunsteineri* from Kitzbühl – "Alle Ihne Bilder stimmen recht gut mit *D. traunsteineri* von Kitzbühel überein".

COMPARISON OF THE BRITISH AND IRISH POPULATIONS OF *D. TRAUNSTEINERI* WITH OTHER DACTYLORCHIDS

In Britain and Ireland, dactylorchids which may occasionally bear a superficial similarity to *D. traunsteineri* are the various subspecies of *D. majalis*:– subsp. *occidentalis*, subsp. *purpurella*, and sometimes subsp. *praetermissa*, and also and in particular, *D. incarnata* subsp. *pulchella*. Occasionally *D. incarnata* subsp. *cruenta* can exist in a form somewhat similar to *D. traunsteineri*.

Comparative mean characters for *D. majalis* subsp. *purpurella* from populations in Cumbria (v.cc. 69 and 70) and for subsp. *praetermissa* from S. Lancs (v.c. 59), are included in Table 5, and can be seen to differ from the principal diagnostic characters of *D. traunsteineri* which are indicated in column 2. (It should be emphasised that not all the characters shown in Table 5 are useful in separating *D. traunsteineri* from the various subspecies of *D. majalis*.) *D. majalis* subsp. *occidentalis*, as observed in western Ireland, also differs noticeably from *D. traunsteineri* particularly with respect to flower density, leaf number and shape, and in having significantly greater maximum leaf width; it also differs in spur shape, and all three subspecies of *D. majalis* differ from *D. traunsteineri* in that they possess leaves which are relatively crowded towards the base of the stem. Bract peripheral cell data (Table 3) also help separate *D. traunsteineri* from these taxa.

D. incarnata subsp. *pulchella* is readily separated from *D. traunsteineri* by its denser inflorescence

TABLE 4. COMPARISON OF DATA FOR THE TWELVE POPULATIONS (BRITISH ISLES) OF *DACTYLORHIZA TRAUNSTEINERI* STUDIED HERE WITH THOSE FROM EUROPEAN LOCALITIES

For each character, means are given together with either the standard error or range in parentheses.

Character	Twelve populations (A–L) from the British Isles	Schwarzsee, Kitzbühl, Austria (*locus classicus*) n = 13 (data ex Reinhard, pers. comm. 1989)	Composite data from eight separate European populations n = 75 (data ex Reinhard 1985)	Måckelmyra, Njurunda, Sweden n = 10 (author's data)
1. Mean plant height (cm)	18·9 (12·2–30·5)	22·4 (0·96)	24·7 (0·53)	25·7 (1·07)
2. Mean length of inflorescence (cm)	4·0 (3·4–5·5)	4·7 (0·23)	4·7 (0·13)	5·0 (0·22)
3. Mean number of flowers	9·7 (7·0–12·4)	8·3 (0·35)	8·4 (0·27)	13·5 (0·83)
4. Floral density[a]	2·43 (2·06–2·92)	1·77 (—)	1·78 (—)	2·68 (—)
5. Mean total no. of leaves	3·6 (3·3–4·0)	4·1 (0·20)	4·0 (0·07)	3·7 (0·14)
6. Mean no. of non-sheathing leaves	0·8 (0·6–1·0)	nd	nd	0·7 (0·14)
7. Mean length of second leaf (cm)	8·96 (5·0–14·37)	10·20 (0·29)	9·03 (0·24)	10·33 (0·38)
8. Mean max. width of second leaf (cm)	1·02 (0·83–1·14)	0·77 (0·02)	1·00 (0·03)	1·06 (0·07)
9. Mean leaf index[a]	8·76 ((5·49)7·31–12·80)	13·25 (—)	9·01 (—)	9·75 (—)
10. Degree of leaf spotting[a]	0·2 (0·0–0·8)	0·54 (0·14)	nd	1·0 (0·00)
11. Upper stem – anthocyanin staining[a]	0·8 (0·2–1·5)	nd	nd	0·6 (0·12)
12. Bracts – anthocyanin staining[a]	1·3 (0·6–2·0)	nd	nd	1·1 (0·11)
13. Mean labellum width (cm)	1·00 (0·90–1·12)	1·00 (0·04)	1·06 (0·01)	0·90[b] (0·02)
14. Mean labellum length (cm)	0·80 (0·72–0·87)	0·76 (0·02)	0·77 (0·01)	0·68[b] (0·02)
15. Mean spur width (cm)	0·32 (0·28–0·36)	0·27[d] (0·01)	0·26[d] (0·00)	0·25[c] (0·01)
16. Mean spur length (cm)	0·81 (0·72–0·90)	1·11 (0·03)	1·09 (0·01)	0·80[b] (0·04)
17. Mean sinus depth (mm) from tip of lateral lobe (where available)	0·72 (0·27–1·17)	nd	nd	0·50[b] (0·13)
18. Trilobed nature of labellum (or otherwise)	usually distinctly trilobed, occasionally approaching sub-rhomboidal, dotted lined or flecked	distinctly trilobed with lines, flecks and loops	distinctly trilobed with sinuses, occasionally sub-rhomboidal, with lines, flecks and loops	more or less trilobed

[a] See Table 2 for an explanation of these characters.
[b] n = 19.
[c] n = 17.
[d] True diameter (not flattened).
nd = No data available.

TABLE 5. COMPARISON OF TWELVE POPULATIONS (BRITISH ISLES) OF *DACTYLORHIZA TRAUNSTEINERI* WITH BRITISH POPULATIONS OF *D. MAJALIS* SUBSP. *PURPURELLA* AND SUBSP. *PRAETERMISSA*

For each character, means are given together with either the standard error or range in parentheses.

Character	Character importance[a]	*D. traunsteineri* Twelve populations (A–L)	*D. majalis* subsp. *purpurella* Beckfoot, v.c. 70 (35/0.5)	*D. majalis* subsp. *purpurella* Sunbiggin Tarn, v.c. 69 (35/6.0)	*D. majalis* subsp. *purpurella* Sandscale Haws, v.c. 69 (34/1.7)	*D. majalis* subsp. *praetermissa* Longton, v.c. 59 (34/4.2)
1. Mean plant height (cm)	–	18·9 (12·2–30·5)	13·7 (0·55)	17·1 (0·75)	9·4 (0·49)	40·1 (2·66)
2. Mean length of inflorescence (cm)	–	4·0 (3·4–5·5)	5·2 (0·24)	4·6 (0·29)	3·9 (0·17)	8·5 (0·53)
3. Mean number of flowers	+	9·7 (7·0–12·4)	>30[c] (—)	>25[c] (—)	>20[c] (—)	>40[c] (—)
4. Floral density[b]	+	2·43 (2·06–2·92)	>5·77 (—)	>5·43 (—)	>5·12 (—)	>4·73 (—)
5. Mean total no. of leaves	+	3·6 (3·3–4·0)	5·8 (0·19)	5·8 (0·19)	6·3 (0·20)	7·2 (0·28)
6. Mean no. of non-sheathing leaves	+	0·8 (0·6–1·0)	1·0 (0·00)	1·8 (0·19)	1·1 (0·09)	2·4 (0·29)
7. Mean length of second leaf (cm)	–	8·96 (5·00–14·37)	8·31 (0·27)	7·90 (0·25)	5·97 (0·30)	14·35 (0·67)
8. Mean max. width of second leaf (cm)	+	1·02 (0·83–1·14)	2·34 (0·10)	1·71 (0·06)	1·69 (0·10)	3·97 (0·17)
9. Mean leaf index[b]	+	8·76 ((5·49)7·31–12·80)	3·55 (—)	4·62 (—)	3·53 (—)	3·61 (—)

TABLE 5 *cont'd*

Character	Character importance[a]	*D. traunsteineri* Twelve populations (A–L)	*D. majalis* subsp. *purpurella* Beckfoot, v.c. 70 (35/0.5)	*D. majalis* subsp. *purpurella* Sunbiggin Tarn, v.c. 69 (35/6.0)	*D. majalis* subsp. *purpurella* Sandscale Haws, v.c. 69 (34/1.7)	*D. majalis* subsp. *praetermissa* Longton, v.c. 59 (34/4.2)
10. Degree of leaf spotting[b]	–	0·2 (0·0–0·8)	1·0 (—)	0·0 (—)	0·3 (—)	0·1 (—)
11. Upper stem – anthocyanin staining[b]	+/–	0·8 (0·2–1·5)	0·5 (—)	0·6 (—)	0·6 (—)	<0·5 (—)
12. Bracts – anthocyanin staining[b]	+/–	1·3 (0·6–2·0)	0·5 (—)	1·0 (—)	1·0 (—)	<0·5 (—)
13. Mean labellum width (cm)	+/–	1·00 (0·90–1·12)	0·86 (0·03)	0·84 (0·03)	0·81 (0·02)	1·27 (0·03)
14. Mean labellum length (cm)	–	0·80 (0·72–0·87)	0·64 (0·02)	0·66 (0·02)	0·62 (0·02)	0·86 (0·02)
15. Mean spur width (cm)	–	0·32 (0·28–0·36)	0·34 (0·01)	0·32 (0·01)	0·28 (0·01)	0·32 (0·02)
16. Mean spur length (cm)	–	0·81 (0·72–0·90)	0·81 (0·01)	0·80 (0·03)	0·69 (0·02)	0·92 (0·02)
18. Trilobed nature of labellum (or otherwise)	+/–	usually distinctly trilobed, occasionally approaching sub-rhomboidal, dotted, lined or flecked	more or less rhomboidal, sometimes slightly trilobed	more or less rhomboidal, sometimes slightly trilobed	more or less rhomboidal, sometimes slightly trilobed	rhomboidal/ trilobed

[a] The usefulness of characters in separating *D. traunsteineri* from the taxa listed in Table 6; + = useful, +/– = partially useful, – = not useful.
[b] See Table 2 for an explanation of these characters.
[c] Difficult to determine precisely without destroying the inflorescence.

TABLE 6. CHARACTERS OF *DACTYLORHIZA TRAUNSTEINERI* COMPARED WITH OTHER BRITISH AND IRISH *DACTYLORHIZA* TAXA
Although individual plants may sometimes lie outside the limits given, the mean values for an analysis of 10+ randomly selected plants in any colony should conform to most of these criteria; + = agrees with description, +/− = borderline for description, − = disagrees with description.
All data based upon the author's field measurements and observations except where shown.

		Dactylorhiza traunsteineri					*D. majalis* subsp. *occidentalis*	*D. majalis* subsp. *purpurella*	*D. majalis* subsp. *praetermissa*	*D. incarnata* subsp. *pulchella*	*D. incarnata* subsp. *cruenta*
Character	Description	All British & Irish populations examined (A–L)	Kitzbühl (*locus classicus*)[a]	Alpine localities (European) – eight populations[a]	Måckelmyra, Njurunda, Sweden[b]	Visby, Gotland, Sweden	Ballynaleckan v.c. H9	Sunbiggin Tarn v.c. 69	Longton v.c. 59	Milnthorpe v.c. 69	Knockaunroe v.c. H9
No. of flowers	Few-flowered – from 7 to maximum of 14 per inflorescence	+	+	+	+	+	+/−	−	−	+/−	+/−
Floral density	Lax inflorescence – less than 3 flowers (mean) per cm of inflorescence length	+	+	+	+	+	−	−	−	−	−
No. of leaves	Leaves well-spaced along stem, total maximum of 4	+	+	+	+	+	−	−	−	+/−	−
Leaf width	Maximum width largest leaf 1·20 cm	+	+	+	+	+	−	−	−	−	−
Leaf shape/ spotting	Leaves unspotted or lightly spotted, linear-lanceolate, largest leaf at least 5·5× longer than wide (usually 7×–14×)	+	+	+	+[c]	+	−	−	−	+/−	−[d]

TABLE 6 *cont'd*

		Dactylorhiza traunsteineri					*D. majalis* subsp. *occidentalis*	*D. majalis* subsp. *purpurella*	*D. majalis* subsp. *praetermissa*	*D. incarnata* subsp. *pulchella*	*D. incarnata* subsp. *cruenta*
Character	Description	All British & Irish populations examined (A–L)	Kitzbühl (*locus classicus*)[a]	Alpine localities (European) – eight populations[a]	Måckelmyra, Njurunda, Sweden[b]	Visby, Gotland, Sweden	Ballynaleckan v.c. H9	Sunbiggin Tarn v.c. 69	Longton v.c. 59	Milnthorpe v.c. 69	Knockaunroe v.c. H9
Bract colouration	Bracts often noticeably anthocyanin-stained	+	+	+	+	+	–	+	–	+	–[e]
Labellum width	Labellum at least 0·90 cm wide	+	+	+	+	+	+	–	+	–	–
Labellum shape	Labellum usually trilobed, often with prominent, elongated central lobe, and noticeable sinuses	+	+	+	+	+/–	+	–	–	–	–
Spur shape	Spur thick, robust and more or less horizontal, and only slightly tapering	+	+	+	–	+	–	–	+/–	–	–
Bract cells	Bract peripheral cells elongated sub-acute to serrate (typical mean length 60–115 μm, average 85 μm)	+	+	+	+	+	–	–	–	–	–

[a] Details for populations in Switzerland and Austria are ex Reinhard (1985), and H. R. Reinhard, pers. comms. 1988, 1989. Some live material supplied by H. R. Reinhard and F. Wischmann.
[b] Affinity to *D. russowii*.
[c] Leaves often heavily spotted.
[d] All leaves heavily spotted on both surfaces.
[e] Bracts spotted but not typically stained.

(often 20 or more flowers per plant and floral density >5 flowers/cm of inflorescence), its relatively small, strongly reflexed, and not noticeably trilobed labella (mean 0·67 cm wide × 0·56 cm long (details from Milnthorpe, v.c. 69)), relatively broad leaves, and again and most characteristically, by the rounded-crenate and consistently shorter peripheral cells of the floral bracts (Table 3). This latter character is an effective method of separating all subspecies of *D. incarnata* from *D. traunsteineri*. *D. incarnata* subsp. *cruenta* is also readily separated on characters similar to those which separate subsp. *pulchella* from *D. traunsteineri*.

In Table 6, based mainly upon data obtained by the author, the key characters useful in identifying British and Irish *D. traunsteineri* are applied to various other dactylorchids as well as to *D. traunsteineri*. From this, the latter is clearly shown to be separate from the other dactylorchids.

CONCLUSIONS

The mean values for the principal characters of the twelve British and Irish populations examined were found to be similar, although some regional trends could be detected. Whilst individuals within any population may deviate appreciably from the typical variant, generally populations exhibit a uniformity in diagnostic characters, particularly the characters of floral density, leaf index, maximum leaf width and labellum width. The data obtained for all populations were very close to those recorded for continental *D. traunsteineri*, including plants at the type locality. Also, when these data were compared to those for populations of other dactylorchid taxa, clear differences were found. It is therefore concluded that plants from the British Isles are conspecific with *D. traunsteineri* from the classic localities of continental Europe, and should be retained at specific rank and not placed under *D. majalis* as suggested by Bateman & Denholm (1983).

SYNONYMY

Dactylorhiza traunsteineri (Sauter) Soó, *Nom. nov. gen. Dactylorhiza* 6 (1962). *Orchis Traunsteineri* Sauter ap Reichenbach, *Flora Germ. Exc.* (1831). *Orchis latifolia* L. var. *eborensis* Godfery, *Mon. Icon. Br. nat. Orchidaceae* 219 (1933). *O. majalis* Reichenbach subsp. *Traunsteinerioides* Pugsley in *Proc. Linn. Soc. Lond.* **148**: 124 (1936). *O. Francis-Drucei* Wilmott in *Proc. Linn. Soc. Lond.* **148**: 128 (1936). *O. majalis* Reichenbach subsp. *traunsteinerioides* Pugsley var. *eborensis* (Godfery) Pugsley in *J. Bot., Lond.* **77**: 54 (1939). *O. traunsteinerioides* (Pugsley) Pugsley in *J. Bot., Lond.* **78**: 179 (1940). *Dactylorchis traunsteineri* (Sauter) Vermeulen, *Stud. Dactyl.* 66 (1947). *Dactylorchis traunsteinerioides* (Pugsley) Vermeulen, *Stud. Dactyl.* 66 (1947). *Dactylorhiza traunsteineri* (Sauter) Soó subsp. *traunsteinerioides* (Pugsley) Soó, *Nom. nov. gen. Dactylorhiza* 6 (1962). *D. traunsteineri* (Sauter) Soó subsp. *francis-drucei* (Wilmott) Soó, *Nom. nov. gen. Dactylorhiza* 6 (1962). *D. traunsteinerioides* (Pugsley) Landwehr in *Orchideeën* **37**: 80 (1975). *D. traunsteineri* (Sauter) Soó subsp. *hibernica* Landwehr in *Orchideeën* **37**: 79 (1975). *D. majalis* (Reichenbach) P. F. Hunt & Summerhayes subsp. *traunsteinerioides* (Pugsley) Bateman & Denholm in *Watsonia* **14**: 372 (1983). *D. majalis* subsp. *traunsteinerioides* var. *traunsteinerioides* Bateman & Denholm in *Watsonia* **14**: 373 (1983). *D. majalis* subsp. *traunsteinerioides* var. *eborensis* Bateman & Denholm in *Watsonia* **14**: 373 (1983). *D. majalis* subsp. *traunsteinerioides* var. *francis-drucei* Bateman & Denholm in *Watsonia* **14**: 373 (1983).

DESCRIPTION

The principal diagnostic features of populations of *D. traunsteineri* in the British Isles are summarised as:–

Variable in height (12–30 cm tall), distinctly slender in appearance, often with flexuous stems. Leaves few (usually 3–4 including 0–1 non-sheathing leaf), narrow, linear-lanceolate, strict to occasionally subarcuate, usually more than 7× as long as broad, (second lowest (usually also largest) leaf 8–12 mm at maximum width), well-spaced out along the stem, unspotted or lightly spotted (spots solid, c. 1 mm diameter). The inflorescence is often rather variable in shape or roughly cylindrical/tapering, often subsecund, few-flowered (usually 7–12) and distinctly lax, the flowers coloured deep pink/red-purple, relatively large with ± semi-reflexed, broad (c. 10 mm) labella which are flecked and loop-marked in a similar but much deeper colour, usually distinctly trilobed, sometimes with a pronounced central lobe. The floral bracts and upper stem are often

stained red-brown with anthocyanin, and the peripheral cells of these bracts are characteristically elongated, sub-acute to serrate, 60–115 μm in mean length. Plants are in full flower from late May to mid-June, and are usually found in calcareous fens and flushes.

A provisional distribution map of *D. traunsteineri* in the British Isles (Fig. 1) is included, but it is very likely that further field work will lead to a consolidation of its distributional pattern. Colour photographs of plants, samples of pressed and mounted labella, spurs and bracts of the plants examined, photomicrographs of bract peripheral cells, and site details of the populations studied, are all retained by the author.

ACKNOWLEDGMENTS

I am very grateful to R. H. Roberts for his helpful comments and advice whilst drafting this paper and to L. Blainey, M. Keane, M. R. Lowe, A. J. Richards, R. H. Roberts, F. Rose, W. A. Sledge, B. G. Tattersall and D. A. Webb for contributing information relating to the location of populations of this taxon. I am also very grateful to H. R. Reinhard for commenting on photographs of the populations studied and for providing information on European *D. traunsteineri* and for data relating to the type locality, to B. G. Johannsson and R. Lidberg for help with Swedish populations, to M. S. Porter and B. G. Tattersall for assistance in the field, and to G. Halliday (University of Lancaster) for providing herbarium facilities.

REFERENCES

Bateman, R. M. & Denholm, I. (1983). A reappraisal of the British and Irish Dactylorchids, 1. The tetraploid marsh-orchids. *Watsonia* **14**: 347–376.

Bateman, R. M. & Denholm, I. (1989). Morphometric procedure, taxonomic objectivity and marsh-orchid systematics. *Watsonia* **17**: 449–455.

Birkedal, S. & Danielson, J. (1981). Första fyndet av Mossnycklar (*Dactylorhiza sphagnicola*) i Skåne. *Svensk bot. Tidskr.* **75**: 313–314.

Bolton, J. H. & Horsman, F. (1987). Botanical records for 1985. *Naturalist, Hull* **112**: (No. 980) 25.

Cunningham, M. H. & Kenneth, A. G., eds. (1979). *The flora of Kintyre.* Wakefield.

Curtis, T. G. F. & McGough, H. N. (1988). *The Irish red data book. 1. Vascular plants*. Dublin.

Devillers-Terschuren, J. & Devillers, P. (1986). Distribution et systématique du genre *Dactylorhiza* en Belgique et dans les régions limitrophes. *Naturalistes belg.* **67**: 143–155.

Ericsson, B. C. (1982). Mossnycklar och skogsfru växter på Öland. *Svensk bot. Tidskr.* **76**: 1–4.

Foley, M. J. Y. (1986). *Dactylorhiza maculata* (L.) Soó × *D. traunsteineri* (Sauter) Soó in N. E. Yorks. *Watsonia* **16**: 175–176.

Foley, M. J. Y. (1989). *Dactylorhiza traunsteineri* (Sauter) Soó: variants in north-east Yorkshire. *Watsonia* **17**: 355–356.

Godfery, M. J. (1933). *Monograph and iconograph of native British Orchidaceae*. Cambridge.

Hedley, S. (1987). Plant records. *Watsonia* **16**: 450.

Heslop-Harrison, J. (1953). Studies in *Orchis* L., II. *Orchis traunsteineri* Saut. in the British Isles. *Watsonia* **2**: 371–391.

Horsman, F. (1989). Botanical Report for 1987. *Naturalist, Hull* **114**: 51.

Hylander, N. (1966). *Nordisk Kärlväxtflora* **2**: vii. Stockholm.

Jonsell, B. (1982). Ångsnycklar och sumpnycklar i nordligaste Uppland. *Svensk bot. Tidskr.* **76**: 103–111.

Kalteisen, M. & Reinhard, H. R. (1986). Orchideen in zentralen italienischen Südalpenraum. *Mitt. bl. Arbeitskr.-Heim. Orch., Baden-Württ.* **18**: 1–136.

Kenneth, A. G., Lowe, M. R. & Tennant, D. J. (1988). *Dactylorhiza lapponica* (Laest. ex Hartman) Soó in Scotland. *Watsonia* **17**: 37–41.

Lacey, W. S. (1955). *Orchis traunsteineri* Saut. in Wales. *Proc. bot. Soc. Br. Isl.* **1**: 297–300.

Lacey, W. S. & Roberts, R. H. (1958). Further notes on *Dactylorchis traunsteineri* (Saut.) Vermeul. in Wales. *Proc. bot. Soc. Br. Isl.* **3**: 22–27.

Landwehr, J. (1975). Het geslacht *Dactylorhiza. Orchideeën* **37**: 76–80.

Landwehr, J. (1977). *Wilde orchideeën van Europa*. Vol. 1. Amsterdam.

Lowe, M. R., Tennant, D. J. & Kenneth, A. G. (1986). The status of *Orchis francis-drucei* Wilmott. *Watsonia* **16**: 178–180.

Petch, C. P. & Swann, E. L. (1968). *Flora of Norfolk*. Norwich.

PUGSLEY, H. W. (1935). On some marsh orchids. *Bot. J. Linn. Soc.* **49**: 553–592.
PUGSLEY, H. W. (1936). New British marsh orchids. *Proc. Linn. Soc. Lond.* **148**: 121–125.
PUGSLEY, H. W. (1939). Recent work on dactylorchids. *J. Bot., Lond.* **77**: 50–56.
PUGSLEY, H. W. (1940). Further notes on British dactylorchids. *J. Bot., Lond.* **78**: 177–181.
RÄSÄNEN, J. & SAARI, H. (1987). Kaitakämmekän (*Dactylorhiza traunsteineri*) muuntelusta Pohjois-Karjalassa. *Lutukka* **3**: 35–39.
REICHENBACH, H. G. L. (1831). *Flora Germanica Excursoria*, p. 140. Lipsiae.
REINHARD, H. R. (1985). Skandinavische und Alpine *Dactylorhiza*-Arten (*Orchidaceae*). *Mitt. Bl. Arbeitskr.-Heim. Orch., Baden-Württ.* **17**: 321–416.
ROBERTS, R. H. (1960). The Wicklow marsh orchid in Anglesey. *Nature Wales* **6**: 14–17.
ROBERTS, R. H. (1966). Studies on Welsh orchids. III. The coexistence of some tetraploid species of marsh orchids. *Watsonia* **6**: 260–267.
ROBERTS, R. H. (1988). The occurrence of *Dactylorhiza traunsteineri* (Sauter) Soó in Britain and Ireland. *Watsonia* **17**: 43–47.
ROBERTS, R. H. (1989). Errors and misconceptions in the study of marsh-orchids. *Watsonia* **17**: 455–462.
ROBERTS, R. H. & GILBERT, O. L. (1963). The status of *Orchis latifolia* var. *eborensis* Godfery in Yorkshire. *Watsonia* **5**: 287–293.
ROBERTS, R. H. & WARD, S. D. (1978). Plant records. *Watsonia* **12**: 177.
ROSE, F. (1975). Plant records. *Watsonia* **10**: 433.
RUBE, G. (1972). *Dactylorhiza sphagnicola* (Höppner) Soó in der Lüneburger Heide. *J. ber. naturw. Ver. Wuppertal.* **25**: 138–139.
SAUTER, J. (1837). *Flora* **20**: Beilbl. 3.
SCANNELL, M. J. P. (1973). *Dactylorhiza traunsteineri* (Sauter) Soó in east Cork, mid Cork, Offaly, Meath, Leitrim and east Mayo. *Ir. Nat. J.* **17**: 426.
SIMONSSON, P. & LINDSTRÖM, B. M. (1977). Myrar i västra Ramsele, Ångermanland. *Svensk bot. Tidskr.* **71**: 419–428.
SWANN, E. L. (1975). *Supplement to the Flora of Norfolk*. Norwich.
TENNANT, D. J. (1979). *Dactylorhiza traunsteineri* in Yorkshire. *Naturalist, Hull* **104**: 9–13.
TENNANT, D. J. (1987). Plant records. *Watsonia* **16**: 450.
TENNANT, D. J. & KENNETH, A. G. (1983). The Scottish records of *Dactylorhiza traunsteineri* (Sauter) Soó. *Watsonia* **14**: 415–417.
TENNANT, D. J., WRIGHT, B. & WRIGHT, A. (1983). Plant records. *Watsonia* **14**: 431.
TYTECA, D. (1981). Observations sur quelques *Dactylorhiza* de Belgique et du nord de la France. *Bull. Soc. r. Bot. Belg.* **114**: 15–30.
TYTECA, D. (1986). Observations orchidologiques en Belgique et dans les territoires voisins: bilan 1981–1985. *Dumortiera* **34–35**: 107–111.
VERMEULEN, P. (1947). *Studies on dactylorchids*. Utrecht.
WEBB, D. A. & SCANNELL, M. J. P. (1983). *Flora of Connemara and the Burren*. Cambridge.
WILMOTT, A. J. (1936). New British marsh orchids. *Proc. Linn. Soc. Lond.* **148**, 126–130.

(*Accepted November 1989*)