# A study of some Dactylorhiza populations in Greater Manchester

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### ABSTRACT

A biometric study was made of selected morphological characters of a series of populations of *Dactylorhiza* growing on artificial substrates in the Bolton and Wigan districts of S. Lancs., v.c. 59.

The results suggest that: a) most populations can be readily referred either to *D. majalis* subsp. *purpurella* (T. & T. A. Stephenson) D. Moresby Moore & Soó or to *D. majalis* subsp. *praetermissa* (Druce) D. Moresby Moore & Soó; b) the two subspecies generally do not occupy the same sites; c) populations appear to be genetically isolated from one another and distinct local variants exist; d) populations probably owe their origins to site-specific means of introduction.

However, there remains the possibility that hybridization between these two closely related taxa may have played a major part in determining the present characters of at least one of the seven populations studied.

#### INTRODUCTION

The colonization of suitable artificial habitats by orchids of various genera including Dactylorhiza is now a widespread and well-known occurrence in many parts of England and Wales. Greenwood & Gemmell (1978) have documented many instances of the colonization by Dactylorhiza species of calcareous substrates left by past and present industrial activity in north-western England. Naturally occurring calcareous soils are almost absent in and around the conurbations of the region, and indeed very localized in S. Lancs., v.c. 59, as a whole. Although there are records (Travis 1917) for marsh-orchids (i.e. Dactylorhiza excluding D. fuchsii and D. maculata) dating back to the time that Orchis praetermissa Druce was first described in 1914, these relate almost entirely to the coast, and to the dune-slacks in particular. Grindon (1859) included records for "Orchis latifolia" from the . Mersey Valley west of Manchester, but the populations concerned seem to have become extinct. With the exception of a single record for D. incarnata (L.) Soó from railway land near St Helens in 1915, there are no further records for these species from the south or south-east of the vice-county until about the time of the last war. Since that time, and more especially in the last two decades, species of *Dactylorhiza* and other orchid genera have colonized new sites scattered widely inland, almost always on man-made habitats not in agricultural use (Savidge et al. 1963, Greenwood & Gemmell 1978).

This paper is primarily concerned with the study of plants (as populations) resembling *D. majalis* subsp. *praetermissa* (Druce) D. Moresby Moore & Soó and *D. majalis* subsp. *purpurella* (T. & T. A. Stephenson) D. Moresby Moore & Soó. These were known until recently as *D. praetermissa* (Druce) Soó and *D. purpurella* (T. & T. A. Stephenson) Soó respectively. The two taxa have generally been regarded as geographical vicariants (Summerhayes 1951) and, although S. Lancs. is not unique in

this respect, the apparent presence of both taxa in the same area is relatively unusual and of particular interest. Most populations of these very variable marsh-orchids in S. Lancs. can be referred to one or another of these subspecies, or to hybrids between each of them and other members of the genus, without much difficulty. However, it has emerged that a few populations of marsh-orchids exist there whose identity has never been satisfactorily resolved. In particular, a large proportion of plants from certain sites have appeared in the past to be intermediate, at least in some respects, between *D. majalis* subsp. *praetermissa* and subsp. *purpurella*, and this has given rise locally to reports of hybrid swarms. Despite the fact that hybrids between these two subspecies are cited in the literature (e.g. Summerhayes 1951, Roberts 1975), it appears that authenticated examples of this hybrid are not numerous (Roberts 1966, pers. comm. 1977). We also suspect that the existing names of these subspecies have not always been applied consistently, even within the British Isles.

It was against this background that the authors set out to make a preliminary biometric examination of some of the taxonomic characters of a series of populations of *D. majalis* in the Bolton and Wigan districts in S. Lancs., v.c. 59. Measurements were made over a period from 1977 to 1979, whilst supporting observations dated from 1976 to 1979. The study attempted to relate these characters to those given in existing published accounts (Clapham 1962, Summerhayes 1951) and also to reveal something of the pattern of variation within and between the populations in this area.



FIGURE 1. Location of *Dactylorhiza* populations included in the present study, together with an indication of other orchid species present.

### THE POPULATION SITES

The location of the seven sites is shown in Fig. 1.

1. Nob End, Farnworth, GR 34/748.063

The site occupied by a small chemical works which manufactured soda by the Leblanc process between 1850 and 1880. A flat-topped tip of alkali waste was left alongside a canal disused since 1930. Most of the surface material is believed to have weathered more or less undisturbed for up to 90 years, yielding a substrate rich in calcium carbonate with low levels of major plant nutrients. The area has a rich calcicole flora which was first recorded over 25 years ago (Hind 1956). This includes typical plants of *D. majalis* subsp. *purpurella*, of which more than a 1000 individuals are present, although the colony has latterly been reduced in size owing to erosion of the sparse vegetation cover by motor cycles. Other orchids include *D. incarnata* (L.) Soó, *D. fuchsii* (Druce) Soó, *Gymnadenia conopsea* (L.) R. Br., *Orchis morio* L. and *Listera ovata* (L.) R.Br., although the last two are rare. Putative hybrids between *D. majalis* subsp. *purpurella* and *D. fuchsii* and, more rarely, between *D. fuchsii* and *G. conopsea* are present.

2. Hart Common, Westhoughton, GR 34/636.055

A former colliery including the site of associated railway sidings, last worked about 50 years ago. A small colony of up to about 50 individuals of *D. majalis* subsp. *purpurella* in a marshy area now being invaded by *Salix* spp. has been known since about 1972. Also present are *D. fuchsii* and, a short distance away on the same site, *D. incarnata* subsp. *incarnata*.

3. Kirkless, Higher Ince, GR 34/608.065

The site of a large ironworks last operated in the 1930s. Small colonies of orchids were found scattered over a large area in the mid 1970s. Apart from *D. incarnata*, most of the marsh-orchids present are apparently referable to *D. majalis* subsp. *purpurella*, although there are usually a few individuals which seem closer to subsp. *praetermissa*. It is difficult to estimate the size of such a scattered population, but it is probably of the order of 100. *D. fuchsii* and, at one extremity of the site, *Epipactis palustris* (L.) Crantz are also present.

4. Leverhulme Park, Darcy Lever, GR 34/734.086

A small but probably long-established marsh at the edge of an overgrown stream (formerly a mill pond). The vegetation is unusual in that, although herbaceous, it is relatively tall and forms a virtually closed community. A compact colony of 300-400 marsh-orchids was discovered in the mid 1970s; they are apparently *D. majalis* subsp. *praetermissa*, although differing in detail from populations of this subspecies in the Wigan area. There are a few putative hybrids of *D. majalis* subsp. *praetermissa*×*D. fuchsii*, but *D. fuchsii* is not present in the immediate vicinity.

5. Amberswood Common, Ince, GR 34/608.047

A relatively recently developed open marsh lying over poorly draining restored open-cast coal workings. *D. majalis* subsp. *praetermissa* and *D. fuchsii* are the most widespread species, with *D. incarnata* occurring locally but absent from the immediate vicinity from which the sample was taken. The orchids were first observed in the early 1970s.

6. Westwood Power Station, Wigan, GR 34/580.043

A colliery subsidence flash in and around which pulverized fuel ash was tipped in the early 1950s. Orchids were first recorded here in the early 1960s; they include *D. majalis* subsp. *praetermissa*, *D. fuchsii*, *D. incarnata* subsp. *coccinea* (Pugsley) Soó and *Epipactis palustris*, each in populations of several hundreds of plants. The hybrid *D. majalis* subsp. *praetermissa*×*D. fuchsii* appears to be common.

7. Bedford Moss, nr Leigh, GR 33/693.974

An area of drained but uncultivated peat occupying the north-western corner of Chat Moss, the largest of the former raised bogs or mosses of S. Lancs. The present vegetation is generally poor in plant species, most areas carrying *Molinia caerulea* with patches of birch scrub. However, the site itself appears to have been the subject of experimental reclamation for agriculture at the end of the 1939–45 war, and is believed to have been heavily limed at that time, and lime was stored nearby. Efforts to cultivate the area ceased at the end of the war but the surface peat is still markedly alkaline and it was on this unusual site that orchids were first reported in 1974. The growth of birch and sallow scrub has been checked by burning the site, which has apparently occurred each winter in recent years. However, much of the site was destroyed in the spring of 1980 when peat, to a depth of several inches, was burnt to an alkaline ash during a prolonged fire.

In addition to *D. fuchsii* and *D. incarnata* a very large population of *D. majalis* was established, until the fire of 1980. Observations prior to 1978 had suggested an unusually complex population with a long overall flowering period from late May to mid July. Moreover, different variants appeared to predominate at different times during the flowering period in any single year. The population was therefore sampled on four separate occasions in 1978; in addition, two separate samples were recorded on each of the last two visits as there appeared to be two distinct variants present on each of these occasions. Six samples were therefore recorded in all, as follows:

BM1-25.5.78

BM2-5.6.78

BM3A-Large plants 13.6.78

BM3B-Small plants 13.6.78

BM4A-Northern side of site 10.7.78

BM4B-Southern side of site 10.7.78

Hybrids between these orchids and *D. fuchsii* appeared to be common, and some hybrids with *D. incarnata* may have been present.

Marsh-orchids of uncertain identity were found approximately  $1\frac{1}{2}$  miles to the north-east at Astley Green Colliery in the early 1950s, and it is possible that this could be the origin of the Bedford Moss population. Marsh-orchids have been rediscovered at Astley Green Colliery, although the number of individuals available for examination at the time of the field work was too small for inclusion in this study.



FIGURE 2. Polygraphs from three populations of *Dactylorhiza majalis* subsp. *purpurella* (top row) and three populations of subsp. *praetermissa* (bottom row). Polygraphs in dashed lines refer to 1977; polygraphs in continuous lines refer to 1978. For key to axes see p. 385.

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#### METHODS

Individual plants within visually more or less homogeneous populations were sampled at random in the field, except in the case of the smallest populations, where every flowering individual may have been included. Putative hybrids between marsh-orchids and *D. fuchsii* can be recognized readily in terms of their intermediate characters and often also by their exceptional vigour. Hybrids between *D. incarnata* and other marsh-orchids may also occur at a few sites. All plants showing visible suggestions of hybridity with either *D. fuchsii* or *D. incarnata* were deliberately excluded from the samples.

Some of the characters relating, for example, to floral morphology that have been used to differentiate between *D. majalis* subsp. *praetermissa* and subsp. *purpurella* are not amenable to simple measurements, or have been previously demonstrated to show much variability within a single subspecies (e.g. Roberts 1961). This is not to say that such characters may not, in conjunction with others, be useful ones. Partly for these reasons, and partly in the interests of obtaining results which could be compared with those from a wider geographical area, the characters measured here are those used by Roberts (1966) to compare populations of *D. majalis* subsp. *purpurella* and subsp. *occidentalis* (Pugsley) P. D. Sell in North Wales. The same parameters have also been used by Roberts (unpublished) to characterize one Welsh population of *D. majalis* subsp. *praetermissa*.

Sample means for the following characters were calculated for each population sampled and are represented on five 'polygraph' axes, as shown in Figs. 2 and 3 (see Roberts 1966):



FIGURE 3. Polygraphs from Bedford Moss population samples, 1978. For key to axes see p. 385.



FIGURE 4. Diagram showing mean spur dimensions for all populations.



FIGURE 5. Histograms of labellum index (left) and number of non-sheathing leaves (right) for all population samples.

Site	N	Tota mean	l no. le s.e.m.	eaves s.d.	No. n mean	on-shea leaves s.e.m.	athing s.d.	% non- sheathing leaves mean	Leaf mean	length s.e.m.	(cm) s.d.	Leaf mean	width s.e.m.	(cm) s.d.	Leaf index (length/ width) mean	
Hart Common	21	5.62	0.16	0.80	1.33	0.13	0.65	23.22	10.3	0.29	1.48	1.8	0.07	0.34	5.86	
Nob End	30	5.90	0.11	0.71	1.40	0.09	0.56	22.84	6.7	0.23	1.50	1.9	0.05	0.36	3.61	
Kirkless	25	5.52	0.11	0.65	1.12	0.10	0.60	19.76	10.3	0.48	2.75	1.8	0.05	0.31	5.82	
Leverhulme Park	20	7.75	0.20	1.02	2.30	0.10	0.57	29.70	12.4	0.40	2.90	2.4	0.10	0.52	5.37	
Amberswood	20	7.60	0.16	0.82	2.80	0.20	0.62	36.74	11.93	0.42	3.25	2.6	0.02	0.61	4.61	
Westwood	20	7.15	0.26	1.31	2.15	0.15	0.74	29.60	9.85	0.16	0.79	2.6	0.14	0.68	3.93	
Bedford Moss																
BM1	18	6.50	0.16	0.62	2.44	0.15	0.70	37.14	8.77	0.29	1.39	2.5	0.13	0.43	3.65	
BM2	14	6.30	0.20	0.68	1.86	0.13	0.54	31.80	8.60	0.27	1.07	2.19	0.12	0.50	3.85	
BM3A	15	6.20	0.22	0.94	1.87	0.15	0.64	29.50	11.80	0.28	1.21	2.93	0.18	0.77	4.57	
BM3B	15	4.87	0.18	0.74	1.20	0.09	0.41	24.30	9.95	0.23	0.95	1.69	0.08	0.34	6.07	
BM4A	15	5.67	0.12	0.49	1.60	0.12	0.51	28.40	11.27	0.44	1.86	2.12	0.09	0.39	5.42	
BM4B	15	5.53	0.15	0.64	1.26	0.11	0.46	22.60	10.30	0.28	1.19	1.96	0.13	0.53	5.53	
	Labellum length (cn						dth (cm)	Labellum index	Spur length (cm)				ır width	n (cm)	Spur length/ width	Spur length ×width
Site	Ν	mean	s.e.m.	s.d.	mean	s.e.m.	s.d.	mean	mean	s.e.m.	s.d.	mean	s.e.m.	s.d.	mean	mean
Hart Common	†19	0.68	0.008	0.04	0.76	0.01	0.06	0.53	0.61	0.017	0.06	0.22	0.01	0.04	2.87	0.13
Nob End	†29	0.65	0.009	0.06	0.83	0.01	0.07	0.54	0.74	0.017	0.06	0.23	0.01	0.05	3.27	0.16
Kirkless	†23	0.71	0.014	0.07	0.87	0.02	0.11	0.62	0.61	0.022	0.11	0.24	0.01	0.05	2.59	0.14
Leverhulme Park	†18	0.79	0.007	0.03	0.88	0.01	0.07	0.70	0.64	0.012	0.05	0.30	0.02	0.09	2.12	0.19
Ambserswood	20	0.81	0.015	0.08	1.08	0.02	0.10	0.88	0.69	0.016	0.08	0.30	0.01	0.06	2.36	0.21
Westwood	20	0.84	0.011	0.06	1.08	0.02	0.12	0.91	0.60	0.010	0.06	0.31	0.01	0.04	2.11	0.20
Bedford Moss																
BM1	*22	0.69	0.011	0.06	0.76	0.05	0.28	0.56	0.77	0.01	0.05	0.28	0.01	0.05	2.76	0.22
BM2	*65	0.76	0.006	0.08	0.94	0.007	0.10	0.72	0.77	0.01	0.09	0.30	0.003	0.03	2.55	0.21
BM3A	15	0.86	0.016	0.07	1.01	0.03	0.12	0.87	0.86	0.016	0.06	0.31	0.01	0.02	2.77	0.27
BM3B	15	0.75	0.019	0.08	0.85	0.02	0.10	0.65	0.77	0.03	0.10	0.29	0.01	0.02	2.70	0.22
BM4A	15	0.83	0.019	0.08	0.77	0.013	0.06	0.64	0.67	0.01	0.04	0.25	0.01	0.04	2.99	0.17
BM4B	15	0.76	0.013	0.06	0.69	0.009	0.24	0.52	0.60	0.02	0.08	0.23	0.01	0.03	2.58	0.14

# TABLE 1. POPULATION SAMPLE MEANS FROM ALL SEVEN SITES

\* Flowers were collected from a larger random sample from these populations than were measured for vegetative characters. † Smaller sample sizes resulted from damage to specimens in mounting.

Axis A. Non-sheathing leaves\* as a percentage of total number of leaves.

Axis B. Flower labellum index, i.e. length  $(cm) \times$  width (cm).

Axis C. Total number of leaves.

Axis D. Number of non-sheathing leaves.\*

Axis E. Leaf index, i.e. length/width of first fully extended leaf.

\*Non-sheathing leaves are those immediately below the inflorescence (i.e. without axillary flowers) whose bases do not completely surround the stem.

In addition measurements were made of the length and width of the flower spur; a visual comparison of population means for these spur characters is shown separately in Fig. 4. Field observations were also made on labellum shape, flower colour, leaf spotting and plant stature. Leaf characters were measured in the field, and one flower was collected from each plant sampled; the labellum and spur were removed and mounted under transparent adhesive film. Measurements made on the flower parts were taken as soon as possible after mounting.

### RESULTS

Table 1 shows the sample means, together with the standard error of each mean and the standard deviation of each sample, from all seven sites. The histograms (Fig. 5) show how the members of each population sample are distributed in relation to two of these characters, labellum index and the number of non-sheathing leaves.

Fig. 2 shows the polygraphs obtained for all sites except Bedford Moss, while Fig. 3 shows polygraphs obtained for the populations studied at Bedford Moss. Visual inspection of the polygraphs in Figs. 2 and 3 and evidence from other characters would suggest that the majority of the samples other than those from Bedford Moss can be readily assigned to one of two groups.

Plants from Hart Common, Nob End and Kirkless have a low total number of leaves, 5 or 6 being most common; they also tend to be of low stature, and have a low number and low proportion of non-sheathing leaves, with mean values less than 1.5 and 25% respectively. Fig. 5 shows the majority of these plants to have only one non-sheathing leaf, whilst about 10% of the plants at Hart Common and Kirkless have none at all. Small solid leaf spots about the size of a pin-head are also a feature, although this is more constant in the Nob End than the Hart Common or Kirkless populations. Comparatively short leaves in relation to their width is a peculiar character at Nob End. Small, relatively narrow labella are characteristic at Nob End and Hart Common, and of most individuals at Kirkless. (The Kirkless histogram for labellum index shows a double peak suggesting the presence of more than one taxon in the sample). Whilst this group of populations generally has rather small, narrow spurs, that from Nob End is again peculiar in its particularly long spurs. Distinct dark blotches or paired loops on either side of the labellum centre on a deep purple background are highly characteristic of all three samples. A small proportion of plants with larger, paler labella occurs at Kirkless (see above). The actual shape of the labellum varies considerably with each sample (Fig. 6), but it is commonly fringed along the lower edge, and often shows distinctive lateral incisions. The relative uniformity within each of the Hart Common and Nob End samples is notable. A comparison of the polygraphs from these three sites with those from a pure population of D. majalis subsp. *purpurella* from North Wales (Roberts 1966) serves to confirm that the former three populations can be referred to that subspecies. Their flowering period is from mid June to early July.

The second well-defined group of populations comprises those from Amberswood and Westwood. Plants from both are relatively tall (although also more variable in this respect), and have a relatively high total number of leaves, with median values of 7 and 8 respectively. The Westwood population is rather variable generally and individuals with up to 12 leaves are recorded. Both have mean values for non-sheathing leaves of greater than 2, median values being 3 (Amberswood) and 2 (Westwood). Plants with fewer than two non-sheathing leaves are recorded only from Westwood, where individuals with up to five are also present. The mean proportion of non-sheathing leaves in relation to total leaf number, around 30%, is also significantly higher than that from the population of *D. majalis* subsp. *purpurella* group. Leaf spots are absent. High values for labellum index are characteristic of plants from Westwood and Amberswood, although again the former are very variable. The broad saucer-shaped labellum is 9–12 mm wide and characteristically marked lightly



FIGURE 6. Typical labellum outlines from four selected populations.

with dots or occasionally fine lines on a magenta or pale magenta background. Spurs are stout but shorter in relation to flower size than in the first group (Fig. 4). The close resemblance of polygraphs for these marsh-orchids (Fig. 2 bottom row) and that for *D. majalis* subsp. *praetermissa* made by Roberts from a Merioneth population (Fig. 7A) can be seen. These two populations can therefore be identified as subsp. *praetermissa*, although a significant proportion of plants in both had the labellum less than 10 mm wide, thus falling outside the range given for this character by Soó (1980). The flowering period is from late May to late June.

In most respects the Leverhulme Park sample resembles this second group. It shows the highest mean total leaf number of any population sample in the study, despite the rather low stature, and all individuals in the sample had two or more non-sheathing leaves. Although the mean labellum index value is intermediate between the two taxa, the flowers otherwise resemble those of *D. majalis* subsp. *praetermissa*, except that those of many individuals are of a somewhat deeper purple colour.

On the basis of a general comparison of the polygraphs shown in Figs 2 and 3, Bedford Moss samples BM1, BM2 and BM3A appear to be closely related to *D. majalis* subsp. *praetermissa*. The BM1 sample (the first plants to flower at Bedford Moss) is, in detail however, unlike any other as a result of the combination of low labellum index, low stature, and a very high proportion of non-sheathing leaves. Like most of the plants which follow it in flower at this site, a distinctive white ridge occupies the centre of the labellum. BM1 is considered to be a diminutive variant of *D. majalis* subsp. *praetermissa*, resembling that subspecies in most respects. Although the number of non-sheathing leaves is lower in BM2 and BM3A than in Amberswood, Westwood or Leverhulme Park samples, the proportion of the total number of leaves which are non-sheathing is closely similar to the Westwood sample mean.



FIGURE 7. Dactylorhiza majalis polygraphs from North Wales (by kind permission of R. H. Roberts): A) subsp. *praetermissa* from Harlech Dunes, Merioneth, v.c. 48; B) subsp. *purpurella* (population P7 from Roberts (1961)) from Malltraeth Marsh, Anglesey, v.c. 52, selected to show how extreme forms of this subspecies can tend towards subsp. *praetermissa*. For key to axes see p. 385.

Of all the Bedford Moss samples, only BM3A approaches Amberswood and Westwood in terms of the labellum index, but this is due to the very long pointed labellum which is highly characteristic of this sub-population of conspicuously large plants. Labella that are longer than they are wide are in fact a peculiarity of the later flowering Bedford Moss groups (BM3A, 3B, 4A and 4B). BM1, 2, 3A and 3B also show higher mean values for spur length than any other samples in the survey (Fig. 4).

BM4A is probably the most consistently intermediate between *D. majalis* subsp. *purpurella* and subsp. *praetermissa* in terms of measured characters, although even this is close to the subsp. *praetermissa* group in its proportion of non-sheathing leaves.

Two of the later-flowering samples, BM3B and BM4B would seem to show some possible affinity with *D. majalis* subsp. *purpurella*. In particular, plants of BM4B, amongst the last of the plants to flower (in mid-July), resemble the three populations of subsp. *purpurella* in mean values for labellum index, number and proportion of non-sheathing leaves, but have flowers which are paler and labellum markings which are less distinct. A few individuals from BM4B show a little leaf spotting, all other samples being unspotted. Individuals which resemble subsp. *purpurella* in all characters cited for the Nob End, Hart Common and Kirkless populations have not been observed at Bedford Moss.

#### DISCUSSION

The majority of populations of marsh-orchids studied can be referred either to *D. majalis* subsp. *praetermissa* or to *D. majalis* subsp. *purpurella*, at least on the basis of a combination of characters. Particularly useful characters to differentiate between the two taxa in S. Lancs. appear to be flower colour, the form of labellum markings, labellum size and morphology, and the number of

non-sheathing leaves, both as an absolute value and in relation to the total leaf number. This last character, used by Roberts (1961, 1966) in his studies in Wales, does not seem previously to have been suggested as of value in distinguishing these two subspecies. It would be of interest to survey marsh-orchids in other areas for this character.

It is important, however, to note that such is the variability of some of these populations that individual plants, and sometimes populations, may not be identified satisfactorily using any single character difference. Whilst relative morphological uniformity tends to be a feature of the populations of D. majalis subsp. purpurella in this study, a comparison of our data obtained for subsp. *praetermissa* populations in S. Lancs. with those for subsp. *purpurella* populations in North Wales (Roberts 1961 and Fig. 7B) shows that, over a wider geographical area, the two taxa can show continuous or overlapping ranges of variation in respect of each of the quantified characters. The Nob End, Hart Common and Kirkless populations of D. majalis subsp. purpurella do conform reasonably well with the descriptions of D. purpurella in Summerhayes (1951) and Clapham (1962), although each of these populations showed minor morphological peculiarities which persisted throughout the three years during which measurements were made. The long spur and low leaf index characteristic of Nob End plants is a good example. This population has probably existed for at least 40 years, as has a population of D. majalis subsp. purpurella at Penwortham, near Preston, which is the earliest authenticated record of either subspecies in an 'industrial' habitat in S. Lancs. (Savidge et al. 1963). Whilst the populations at Hart Common and Kirkless have only been known for about a decade, both sites are believed to have lain essentially undisturbed for some 40 years. Nevertheless the Penwortham record is the earliest of any for this subspecies cited by Savidge *et al.*; in fact it does not seem to have been recorded in any semi-natural habitats in S. Lancs. and may not be native there.

On the other hand, the very large variable populations which have developed in recent years on artificial sites at Westwood, Amberswood and a number of other localities outside the Bolton and Wigan Districts in S. Lancs. (Greenwood & Gemmell 1978) must be referred to *D. majalis* subsp. *praetermissa* (and its hybrid with *D. fuchsii*). This would seem to be a more recent phenomenon, for records in Savidge *et al.* (1963) for this subspecies are predominantly from coastal, semi-natural habitats. Thus, this subspecies would seem more likely to be a native of S. Lancs. at least on the coastal fringe. Whether the recent inland populations are derived from native stock is a question awaiting further study. The removal of sand from the Lancashire coast for industrial uses inland may have contributed to the spread of this orchid. The distribution of *Epipactis palustris* on coastal dune-slacks in S. Lancs. and W. Lancs. and on the Westwood and Kirkless sites near Wigan would support this possibility.

The identity of the complex series of populations at Bedford Moss remains speculative, not least because several of the plants present are markedly different from those on any other sites known to the authors. There remain the following possible explanations:

i) Populations are referable to *D. majalis* subsp. *praetermissa*, which is exhibiting a wide range of its variability at this site;

ii) Populations are referable to *D. majalis* subsp. *praetermissa*, into which introgression of subsp. *purpurella* has occurred following hybridization of the two subspecies and the loss of typical subsp. *purpurella*. In view of the difficulty apparently encountered with the identification of the earlier population of Astley Green Colliery (see above), if such hybridization has occurred it may have done so over a considerable period of time at Astley Green Colliery before the orchids spread to nearby Bedford Moss.

iii) Certain of the sampled populations contain hybrids with one or more subspecies of the diploid *D. incarnata*. Since *D. majalis* subsp. *praetermissa* and subsp. *purpurella* are both tetraploids (2n=80), cytological studies should assist in assessing the extent to which variation can be attributed to hybridization with *D. incarnata*. Certain unsampled sub-populations at Bedford Moss are thought on morphological grounds to comprise this hybrid. Whilst the latter may represent an F<sub>1</sub> cross, back-crossing with subsp. *praetermissa*, if it occurs, may produce plants which are difficult to recognize morphologically.

There seems no reason to suppose that these alternative explanations are mutually exclusive.

The problem of the identity of the Bedford Moss populations is compounded by the difficulty of locating examples or detailed descriptions of *bona fide* hybrids between *D. majalis* subsp. *praetermissa* and subsp. *purpurella* outside the study area. The fact that there are no known sites

within the study area on which typical examples of both subspecies occur, and the apparent variability of 'pure' populations of subsp. *praetermissa*, tends to reduce the chance of recognizing a hybrid. The results at Bedford Moss up to the present do not seem to provide good evidence for hybridization between two clear-cut taxa. Controlled breeding experiments seem the most fruitful means of establishing the characters of the hybrid, if it exists, and work has started towards this.

Fig. 1 shows that, in the area of study, the populations of both *D. majalis* subsp. *purpurella* and subsp. *praetermissa* are accompanied by both *D. incarnata* (except at Leverhulme Park) and *D. fuchsii*, but not by one another. Other sites are known which support either *D. incarnata* or *D. fuchsii* (not both), but are then unaccompanied by any other member of the genus. These associations of species are not easy to explain. There would appear to be no obvious ecological explanation for the observation that either *D. majalis* subsp. *purpurella* or subsp. *praetermissa* occurs on a wide variety of essentially artificial sites not very far from one another, but in general not in mixed populations. The substrates concerned are all relatively base rich and in general support a rather open vegetation cover, suggesting low nutrient levels. Otherwise, they differ widely from one another in physical characteristics, water regimes and composition of the vegetation.

Overall, these observations seem to suggest, firstly, that many populations of marsh-orchids in this area owe their origin to some site-specific means of introduction, and, secondly, that gene exchange between populations is a rare event. It may be significant that the sample sites are adjacent to a railway or a canal or could reasonably be expected to be descended from a nearby colony which was thus located. At the same time, Victorian industrial sites were of course located close to the canal or railway network, so the correlation may not be meaningful to the means of colonization. Whilst it is unlikely that wind-blown seed from the Lancashire coast is the origin of most of these populations, there is some evidence that orchid species will spread locally in this way from their original sites of introduction.

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