

THE MARSH ORCHIDS IN HAMPSHIRE AND DORSET: SOME RECENT RESEARCH

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ABSTRACT

The recent history of the study of the tetraploid marsh orchids (Dactylorhiza majalis ssp.) presents a picture of controversy and confusion. The reasons for this are explored, with an account of recent developments. Some populations in Hampshire and Dorset are compared with others elsewhere in the country, by means of multivariate analysis of morphometric data. Some potential solutions to the problems, and avenues for further investigation are explored. The problems and relevance of hybrids are discussed.

INTRODUCTION

The orchid group known collectively as the Dactylorchids (*Dactylorhiza* Soó spp.) causes more problems of identification than any other, both to amateur botanist and expert orchidologist alike. It consists of two main subgroups, the spotted orchids and the marsh orchids. Whilst the spotted orchids and the members of the Early Marsh Orchid group, the diploid marsh orchids (*D. incarnata* (L.) Soó ssp.), are fairly readily distinguished, few botanists (including many orchid specialists) are able confidently and accurately to identify all subspecies and varieties of the tetraploid marsh orchid group (*D. majalis* (Reichenbach) P F Hunt & Summerhayes). Even the few recognised experts disagree with alarming consistency. It is this subgroup therefore which forms the principal subject matter of this paper.

I shall summarise the difficulties caused by the group, attempt to account for them, and outline some of the recent research which has attempted to resolve them. They are not yet fully resolved, by any means, and research continues into various problematical aspects of the biology of this difficult group.

My own particular area of research is taxo-

nomy in relation to morphology ie nomenclatural classification on the basis of distinctive floral and vegetative characteristics of the various recognised members of the *D. majalis* group (and indeed some which are not). In common with several other workers, I have been actively involved in such research for several years, and it may be that a helpful schematic resolution of the group is beginning to emerge, as detailed knowledge of these orchids increases: opinion however remains divided. It must be stressed that such research is continuing, and is likely to do so for many years. In the meantime, it may be helpful for me to outline my own research, to examine the results to date (subject to the proviso that it is as yet incomplete), and to attempt to offer some conclusions and avenues for future enquiry.

THE PROBLEMS

The degree of taxonomic confusion in this group is caused by two main factors peculiarly characteristic of the tetraploid marsh orchids, to some extent compounded by the nature of some past research and attitudes of some workers.

The main difficulty is in assessing the current taxonomic status of the marsh orchids, when it is apparent from all the available evidence that the group is in an extremely fluid state of active evolution. This process is most apparent in the tetraploid group.

It has been suggested that *D. majalis* may be a comparatively young species in the process of stabilisation; on the other hand, it has also been proposed that it may be an old species being progressively altered by the continuous influence of hybrids (Summerhayes 1951, *et al*). My own view, to some extent supported by

hybrid evidence that I shall outline later in this paper, is that it is a very young species indeed. Unfortunately, what little evidence is available is capable of use in a cyclic argument that can support either point of view: as yet there is no conclusive proof either way, and indeed may never be. Whatever the correct view may be, I have noticed that over a period of years, significant changes can occur in the morphology of plants in some populations. Whilst in most populations such changes are slight (and perhaps attributable to ecological change), in some they are quite marked – to the extent that I have altered my opinion on identification of some plants in the same population over a period of twenty years or so. The reasons for such changes are difficult to determine, but those populations which show the most marked changes are geographically isolated from others, and also contain more than one species of *Dactylorhiza*: the progressive influence of hybrids is therefore a legitimate assumption. It is hybridisation, of course, which is the second major factor contributing to the problems posed by the marsh orchids.

The exceptional propensity of *Dactylorhiza* spp. to hybridise with each other is well known amongst orchid enthusiasts: I have even heard them described by one as 'an incestuous little lot!' The welter of forms to be found in the average mixed colony has to be seen to be believed. Identification of the individual plants concerned can at best be putative, and at worst is sometimes impossible. Whereas many plant hybrids are infertile, that is not true of *Dactylorhiza* hybrids: most of the F1 hybrids produced from initial crossings of two species are themselves fertile, and hence capable of further hybridisation, both with each other, and with the original parent plants (introgression). What is more, it is my belief, based on what I have observed in certain populations in the New Forest (see p 247 below), that even these further hybrids retain a high degree of fertility. The marsh orchids hybridise particularly frequently with the spotted orchids: the resultant forms are usually robust vigorous plants, apparently capable of considerable resistance to

ecological change, and therefore of outliving the less adaptable parent plants in sites undergoing progressive change, and also of perpetuating themselves with consistent inbreeding.

Attempts to resolve the problems posed by apparent evolution and hybridisation amongst *Dactylorhiza*, and to produce an acceptable taxonomic organisation of the group, have to an extent suffered from the limitations of both the research itself and of the workers involved in the research. Many workers have tended to concentrate their attention on a comparatively small number of distinguishing characteristics in order to determine the taxonomic status of particular groups of *Dactylorhiza*. For example, great emphasis has always been placed on differences in labellum shape and markings: examination of Figure 3 in this paper will show at once how unreliable it is to place too much emphasis on those features alone. The extent of labellum variation within subspecies of *D. majalis* is such that individual plants within a population of one subspecies will often show the characteristic features of another subspecies. Other characters such as number, length and breadth of leaves, type and degree of leaf markings, level of anthocyanin staining of stems and floral bracts, and colour of flowers have all assumed considerable importance in the determination of taxa: examination of the majority of floras and flower keys, and even many specialist papers, will show that they tend to concentrate on a small number of features such as these, and ascribe 'diagnostic' significance to alleged differences between taxa in these features. Recent research however (Bateman & Denholm 1983) has shown that the diagnostic status of some of these much-used character-states is not supported by the morphometric evidence. I shall also show that my own studies have revealed certain potentially diagnostic features that have never before been considered, and have also considerably weakened certain characters as potentially diagnostic. *Dactylorhiza* groups have thus, it would appear, been subdivided into species, subspecies and varieties on the basis of a small number of rather minor differences: the examination of a much wider range

of floral and vegetative characteristics, and of the range of variation apparent in a large number of different marsh orchid populations from a wide area, presents a rather different picture.

Thus the parochial nature of some research work must have a considerably more limited application than that claimed for it by the workers concerned. What one worker has described as 'taxonomic chauvinism' is a feature of much past research: the status acquired in botanical circles by the claiming of a new, perhaps rare taxon for the local county flora, or the naming of a hitherto undiscovered taxon, has tended to militate against taking the wider over-view. More pragmatically, the expenditure of time, money and effort that is required in order to make adequate comparisons of a large number of samples from a wide geographical range must inhibit much valuable work. In Europe, for example, there are wide differences in the assessment and distinction of taxa from those prevailing in the British Isles: the two spotted orchids, *D. fuchsii* and *D. maculata*, regarded as separate species in Britain, are treated on the Continent as conspecific (Sundermann 1980, Buttler 1986) – and in fact the range of variation present in Continental populations is such that there is morphological overlap between the two that justifies such a taxonomic decision. Conversely, most authorities in Europe regard the Narrow-Leaved Marsh Orchid as a separate species (*D. traunsteineri* (Sauter) Soó), whereas some recent research (Bateman & Denholm 1983) in Britain has indicated that the range of variation present in the British Isles is such that there is morphological overlap with *D. majalis*, and that it should therefore be regarded as a subspecies of *D. majalis* (see below). Opinion in this country, however, remains divided on this point: some recent work (Roberts 1988, Foley 1990) has also attempted to maintain its separate status.

One solution must be to make detailed analyses of a much wider range of morphological characteristics, in order to determine objectively what characteristics, if any, may in fact be regarded as 'diagnostic' of the different

taxa. Furthermore, widening the scope of such analysis, to sample populations from as wide an area as possible of not only the British Isles, but also of Continental Europe, would vastly enhance the validity of taxonomic decisions, and perhaps ultimately arrive at a more satisfactory schematic resolution of this difficult group of orchids.

I make no such ambitious pretensions for this paper, however: that is for the future. I shall simply compare some marsh orchid populations in Hampshire, Dorset, Oxfordshire, Gwynedd, Dyfed and Yorkshire, in order to give the reader some idea of the problems we face, and perhaps give some useful clues as to the likely eventual resolution of those problems.

THE TETRAPLOID MARSH ORCHIDS: RECENT HISTORY

Until comparatively recently, it was widely accepted that there were five full species of marsh orchid present in the British Isles, as follows:

1. Early Marsh Orchid (*D. incarnata* (L.) Soó, and subspecies);
2. Southern Marsh Orchid (*D. praetermissa* (Druce) Soó);
3. Northern Marsh Orchid (*D. purpurella* (T & T A Stephenson) Soó);
4. Broad-Leaved, Irish or Western Marsh Orchid (*D. majalis* (Reichenbach) P F Hunt & Summerhayes ssp. *occidentalis* (Pugsley) P D Sell); and
5. Narrow-Leaved, Wicklow or Pugsley's Marsh Orchid (*D. traunsteineri* (Sauter) Soó). (Ettliger 1976 *et al.*)

It had been felt for some years, however, by many experts, that the Southern, Northern and Broad-Leaved Marsh Orchids were more closely related to each other than their taxonomic labels indicated: thus the Southern and Northern Marsh Orchids were relegated to subspecies of *D. majalis* (Tutin *et al* 1980, Davies *et al* 1983). This left only the Narrow-Leaved Marsh Orchid to be regarded as a distinct species within the tetraploid group.

Many botanists even now adhere to the former classification, and as a result even some of the most recent treatments still show the tetraploid marsh orchids as four distinct species (Buttler 1986, Lang 1989).

In 1983, however, Bateman and Denholm went a stage further: they sought by means of biometric study of the marsh orchids (ie the careful measurement of a large number of floral and vegetative characteristics) to resolve amongst other things some of the long-standing anomalies in the taxonomy of this group. Their survey results were processed on a computer by means of multivariate analysis, ie the reduction of all the available data to two co-ordinates capable of being plotted on a graph, thereby reducing each plant to a single point on the plot, capable of direct comparison with other plants on the same plot. Because the plotted areas of plants from different taxa were found to overlap, it was concluded that no 'zones of discontinuity' (or clear dissimilarities) in the morphology of these orchids were present between the four plant groups under study: it was argued that such zones of discontinuity should be present in order to justify the separation of plant groups into distinct species on morphological grounds. It was therefore proposed that all four of the tetraploid marsh orchids (ie including *D. traunsteineri*) should henceforward be regarded as subspecies of *D. majalis*, and the Narrow-Leaved Marsh Orchid was therefore reclassified as *D. majalis* ssp. *traunsteinerioides* (Pugsley) Bateman & Denholm, at least insofar as the taxon related to plants in British populations. The relationship between such plants and Continental plants classified as *D. traunsteineri* is the subject of continuing research which is as yet unresolved. Initial superficial indications are that the morphology of British and Continental plants is so similar as to render them almost indistinguishable: if that is in fact found to be the case, they should all then be classified as *D. majalis* ssp. *traunsteineri* (Sauter) Sundermann (Sundermann 1980, R M Bateman pers comm 1987, Bateman & Denholm 1989b).

More recently still, further attempts have been made to reinstate the Narrow-Leaved

Marsh Orchid as a full British species (Roberts 1988 & 1989, Foley 1990) on the basis of comparison of data from British plants with data obtained by another worker (Reinhard 1985) from Continental plants. In my view, however, these treatments fail to achieve their primary objective for a number of reasons:

- (a) the use of a small number of allegedly 'diagnostic' characteristics, unsupported by evidence of their validity as such;
- (b) the use of data obtained by different workers, with no supporting evidence of the compatibility of such data; and
- (c) the failure to take into account morphologically peripheral (ie intermediate) populations, and the apparent dismissal of the available evidence of morphological overlap between the groups under study.

Foley uses data from one unrepresentative Swedish population, thus accepting in principle the possible existence of morphological intermediates, but restricts his British sampling to 'classic' or well-determined sites. Most of the Continental data used by both him and Roberts is obtained from Reinhard: Bateman & Denholm have said (1989b) that 'internal consistency is likely within any one project but that, in the absence of detailed consultation, the comparison of data collected by different workers is fraught with hazard'.

Other workers continue to research other areas of potential significance in the biological make-up of these difficult orchids, some of which, such as karyotyping (the study of chromosomes) and the study of isoenzymes, may well prove fruitful, particularly if taken in conjunction with morphological studies. The study of isoenzymes has already revealed some unexpected relationships between the different plant groups (M R Lowe pers comm 1990), and close co-operation between workers in different fields of study may be the way forward for the future.

LOCAL DEVELOPMENTS

In the early 1980s I was studying several colonies of marsh orchids in Hampshire and

Dorset which contained a number of plants intermediate in morphology between *D. majalis* ssp. *praetermissa* and *D. traunsteineri*, as it was then called. All of these plants displayed some features described by various authorities (Summerhayes 1951, Ettliger 1976, Lang 1980, and Davies *et al* 1983) as 'typical' or 'diagnostic' of both taxa. None of the plants showed all of the requisite characteristics, and thus could not be satisfactorily assigned firmly to either taxon. A similar population near Southampton, the only site in Southern England for the Northern Marsh Orchid (*D. majalis* ssp. *purpurella*), also supported a number of plants intermediate in morphology between ssp. *praetermissa* and ssp. *purpurella*. At all these difficult sites, hybrids were numerous: there was however no evidence to suggest that these intermediate plants were of hybrid origin. They were merely extreme variants of one or the other subspecies, whose morphological characteristics took them outside the normal accepted range of variation for one subspecies, and well towards that of the other.

The presence of such confusing intermediates in populations in this area appeared to add weight to the taxonomic proposals of Bateman and Denholm, and I drew their attention to these plants. It was as a result of the ensuing discussion that I embarked on the extensive survey work carried out during the following years (1986–9), the results of which are published and discussed in this paper.

THE POPULATIONS SURVEYED

The survey work encompassed a total of eight sites for ssp. *traunsteinerioides*, three for ssp. *praetermissa*, four for ssp. *praetermissa* var. *junialis* (the so-called 'Leopard' Marsh Orchid, widely considered to be a leaf-marked form of the Southern Marsh Orchid), five for ssp. *purpurella*, three for ssp. *occidentalis* var. *cambrensis* (the Welsh form of the Broad-Leaved Marsh Orchid) and four populations of intermediate plants (all *praetermissa* approaching *traunsteinerioides*, as the Southampton population referred to above, of *purpurella*-*praetermissa*

intermediates, died out in 1986 as a result of destruction of the habitat by motorway construction). Details of the twenty-seven populations surveyed are shown on Table 1. Some explanatory notes on them, however, are felt to be necessary.

Ssp. *traunsteinerioides*:

1. A previously unknown site for the subspecies, this is a very young site created some 30 years ago by the clearance of a strip of woodland for the installation of a pipeline. It is unusual not only for the rapid development on the site of a rich orchid population, but also for the distinctive form of ssp. *traunsteinerioides* that grows there, for which a new variety (var. *bowmanii*) will be proposed in a forthcoming paper.

2. Supporting a population of plants very similar to those at Exbury, this site is an area of acid grassland with bracken, damp in places, but mostly consisting of a thin layer of dry peat over sand. It thus dramatically extends the known ecological range of the subspecies, which to date has only been recorded from fens and basic flushes.

3. A well-known Yorkshire site, this population has also been the subject of earlier research (Foley 1990).

4. This site, a tiny relict area of fen near Basingstoke, has been the subject of some controversy in recent years (R P Bowman pers comm 1984) regarding the status of the marsh orchids: this research confirms ssp. *traunsteinerioides* at the site.

5–8. All well-known sites for the subspecies, the populations of ssp. *traunsteinerioides* have all featured in previous research (Heslop-Harrison 1953, Roberts 1966, 1988, Bateman & Denholm 1983) and as such are regarded as 'classic' sites for the subspecies. They therefore fulfil a legitimate function in this research as 'control samples'.

Ssp. *praetermissa*:

1. Concentrated in a damp hollow in close proximity to the second population of ssp.

Table 1: Study Populations

Taxon/Location:	Grid Reference	Habitat	Approx no plants	Accomp <i>Dactylorhiza</i> plants
<i>Ssp. traunsteinerioides</i> :				
1. Exbury, S Hants. VC11	SU 4.0..	Neutral flush	>200	Dmpr, Df, hybrids
2. Avon Forest, S Hants VC11	SU 1.0..	Acid grassland	<50	Dmpr, Df, Dm
3. Wharfedale, M W Yorks VC64	SD 9.6..	Basic flush	>200	Dii, Df, Dm, hybrids
4. Basingstoke, N Hants VC12	SU 6.5..	Fen	<100	Dmpr, Df, hybrids
5. Cothill, Berks VC22	SU 4.9..	Fen	<10	Df
6. Cothill, Berks VC22	SU 4.9..	Fen	<50	Dmpr, Df, hybrids
7. Rhos-y-Gad, Anglesey VC52	SH 5.7..	Fen	>200	Dp, Dip, Dic, Df, Dm, hybrids
8. Cors Erddreiniog, Anglesey VC52	SH 4.8..	Fen	>1000	As (7) above
<i>Ssp. praetermissa</i> :				
1. Avon Forest, S Hants VC11	SU 1.0..	Acid/neutral marsh	>100	Dmt, Df, Dm
2. Avon Forest, S Hants VC11	SU 1.0..	Damp acid meadow	>100	Dm, Df, hybrids
3. Pamphill, Dorset VC9	ST 9.0..	Basic flush	>500	Df, hybrids
<i>Ssp. praetermissa var. junialis</i> :				
1. Axmouth, S Devon VC3	SY 2.8..	Shale landslip	>500	Dmpr
2. Bisterne, S Hants VC11	SU 1.0..	Calcareous watermeadow	<50	Dmpr, Dii
3. Winkton, S Hants VC11	SZ 1.9..	Calcareous watermeadow	>200	Dmpr, Dii, Dip, hybrids, intermeds.
4. Winchester, S Hants VC11	SU 5.3..	Calcareous watermeadow	<50	Dmpr
<i>Ssp. purpurella</i> :				
1. Pately Bridge, M W Yorks VC64	SE 1.6..	Neutral marsh	<50	None
2. Pately Bridge, M W Yorks VC64	SE 1.6..	Damp meadow	>500	Df, hybrids
3. Malham Tarn, M W Yorks VC64	SD 8.6..	Acid bog	<20	Dip
4. Cors Geirch, Caerns VC49	SH 3.3..	Fen	<20	Dmt, Dii, Dip, Dm, hybrids
5. Newborough Warren, Anglesey VC52	SH 4.6..	Dune slack	>1000	Dic, Dm
<i>Ssp. occidentalis var. cambrensis</i> :				
1. Portmadoc, Merions VC48	SH 5.4..	Watermeadow	>20	None (but Df & Dii recorded) (R M Bateman pers comm 1986)
2. Aberystwyth, Cards VC46	SN 6.9..	Neutral marsh	>100	None (but Dm recorded - Roberts 1961b)
3. Aberystwyth, Cards VC46	SN 6.9..	Dune slack	>1000	Dmpr, Dp, Dic, Df
Intermediates <i>praetermissa/traunsteinerioides</i> :				
1. Winkton, S Hants VC11	SZ 1.9..	Calcareous watermeadow	>100	Dmpr, Dii, Dip, hybrids
2. Avon Forest, S Hants VC11	SU 1.0..	Neutral flush	>50	Dmpr, Df, hybrids
3. Stapehill, Dorset VC9	SU 0.0..	Damp neutral grassland	>100	Dmpr, Df, hybrids
4. Frilford, Berks VC22	SU 4.9..	Basic flush	>100	Dmpr, Df

Key to accomp *Dactylorhiza*: Dmt = *traunsteinerioides*, Dmpr = *praetermissa*, Dp = *purpurella*, Dii = *incarnata*, Dic = *coccinea*, Dip = *pulchella*, Df = *fuchsii*, Dm = *maculata*.

traunsteinerioides var. *bowmanii* described above, it is nevertheless clearly distinct from it. It is an atypical population of the subspecies, in that the plants have an unusually lax inflorescence, with flowers showing an exceptionally long, narrow labellum with a markedly elongated central lobe, and leaves that are distinctly narrower than the typical form. It may be referable to the rare and enigmatic var. *macrantha* (Sipkes) Bateman & Denholm (Vermeulen 1949, Bateman & Denholm 1983).

2. Scattered throughout a wide area of damp meadow and acid grassland in the vicinity of population (1) above, these plants are more 'typical' of the subspecies, and are clearly distinct in appearance from (1) above.

3. Well-known locally, this large population of the subspecies in a damp meadow near Wimborne is representative of the form most commonly encountered throughout Southern England.

Ssp. praetermissa var. *junialis*:

1. The 'Leopard' Marsh Orchid is well-known from the many calcareous flushes along the shale landslips between Seaton and Lyme Regis, and this population is representative of those referred to by Summerhayes (1951, and pers comm 1964).

2-3. Adjacent populations in calcareous watermeadows about two miles apart along the Avon Valley on the Hampshire/Dorset border, they are both part of much larger mixed colonies of *Dactylorhiza*, and show a wide range of variation.

4. A small population in a watermeadow east of Winchester, the plants are distinctive in a number of respects: they are unusually dark, both in base colour and in intensity of lip markings, labella are unusually frequently entire (ie three-lobing is absent), and the leaves are often very heavily marked with dark confluent rings and blotches, that produce a very distinctive marbled effect. These plants are thus intermediate in many respects between typical var. *junialis* and *ssp. occidentalis* var. *cambrensis* as it occurs in populations in North Wales. This Winchester population may well

also be that referred to by Roberts (1961) and Nelson (1976) (after Wilmott and Hall) as var. *pardalinoides*.

Ssp. purpurella:

1-2. Two adjacent populations of the subspecies in wet meadows and marshland near Duck Street, Pately Bridge, the plants show a high degree of uniformity in morphology, and can reasonably be described as 'typical' *ssp. purpurella*.

3. Recognised at once as atypical of the subspecies, the plants at Malham Tarn have many features (marked three-lobing of the lip, intense anthocyanin-staining of stem and bracts, and few narrow leaves) more typical of *ssp. traunsteinerioides*, and should more accurately be classified as intermediate between these two subspecies. Only four plants however were measured, so the analyses, although interesting, cannot be ascribed great significance, until such time as a larger sample is available for analysis.

4. A peculiar feature of the plants at this site (a damp riverside bank at the edge of the fen proper) is that the floral bracts of every plant are spotted with numerous fine pinpoint solid dots, supposedly a 'diagnostic' feature of *ssp. purpurella* var. *majaliformis* (Lang 1989, ex M R Lowe), which has a restricted distribution in north and north-west Scotland. Other features, however, do not accord with the description of var. *majaliformis*, and are indeed true to type for normal *ssp. purpurella*.

5. *Ssp. purpurella* is characteristically typical of damp dune slacks throughout the north-west, in a diminutive form with a characteristic 'inverted kite'-shaped labellum. The subspecies is abundant (many 1000s) throughout the Newborough Warren dune system, showing a consistently similar morphology. The plants for this sample were all measured in one slack in the centre of this famous National Nature Reserve.

Ssp. occidentalis var. *cambrensis*:

Only a handful of sites is recorded for this rare taxon: all were visited in 1986 and 1989. A fine

population near Penrhyndeudraeth was measured on a 30-variate database in 1986, but no plants were found at this site in 1989, after two successive very dry summers. However, a similar site to the north of Portmadoc was surveyed in 1989, using the current database: those measurements have been used for the analyses presented here. At the *locus classicus* on Newborough Warren only one plant was found that could reasonably be ascribed to this taxon, the site now being swamped with hybrids between *ssp.purpurella* and *D.fuchsii* in a bewildering array of forms. No plants were found in 1986 or 1989 at a site near Malltraeth, and it is probably extinct there. The two sites near Aberystwyth are adjacent marsh and coastal dune slacks, where it is numerous. There is a distinct morphological difference between the plants at the North Wales and mid-west Wales sites, which is very apparent in the field, and is clearly reflected in the multivariate analysis (Fig 1). This distinction is mentioned, but rather glossed over in earlier research (Roberts 1961b), but cannot be ignored in the light of the results published here.

Intermediates praetermissa/traunsteinerioides:

1. A vast mixed colony of *Dactylorhiza* in a riverside water-meadow, including population (3) of *var.junialis* measured; the intermediates are small plants which in most respects could be regarded as miniature *ssp.praetermissa*, with few leaves, short lax flower-spikes, and a markedly three-lobed lip.
2. Similar in many respects to (1) above, the plants differ in that they are deeper in colour, with more marked anthocyanin-staining of the upper stem and bracts. They are accompanied by plants of *ssp.praetermissa* which are relatively 'typical' of the subspecies except that they are unusually short and stocky. As the site is relatively dry, however, this is undoubtedly an environmental response rather than a genetic character.
3. The plants selected for measurement from this population are not clearly distinct from the many more typical plants of *ssp.praetermissa* at the site, but are merely taken from the extreme end of a morphological continuum

encompassing an unusually wide range of variation. Some plants, however, show an unusually narrow, elongated lip.

4. *Ssp.traunsteinerioides* has been recorded from this site (Bowen 1968), which is a marshy hollow by a stream running across a golf course, and only a couple of miles away from the two adjacent famous Cothill sites. I have treated the plants as intermediate because they show a high percentage of entire, broadly rounded, saucer-shaped labella, totally atypical of *ssp.traunsteinerioides*, but sometimes found in *ssp.praetermissa*. In all other morphological characteristics, however, these plants are closer to *ssp.traunsteinerioides*, and this is reflected in their plotted area on the multivariate analysis (Fig 1).

There are many populations of intermediate plants, particularly in Dorset, that could have been used for this research: each has its own distinctive characteristics. There are fine populations in the marshland south of Poole Harbour, near Corfe Castle, near Wimborne St Giles, and near Beaulieu in Hampshire. There are also scattered individuals in many colonies throughout the area, particularly in the Avon Valley. The selected populations were felt, however, to be reasonably representative of the range of variation which may be encountered. If more such populations were to be analysed in this way, the evidence of a morphological continuum encompassing *ssp.praetermissa* and *ssp.traunsteinerioides* would be overwhelming.

Botanical vice-counties are used for locations in Table 1, although political boundary changes have resulted in the following populations being in current administrative counties as follows:

Cothill and Frilford – Oxfordshire;
Winkton and Avon Forest – Dorset;
all North Wales sites – Gwynedd; and
mid-west Wales sites – Dyfed.

Because many of the sites are on private land, support populations of scarce or threatened species, or are in some other respect environmentally sensitive, only 10 km square grid references are given in Table 1. Full details are available from the author to *bona fide* researchers with appropriate references.

THE DATABASE

Bateman and Denholm's 1983 research study of the tetraploid marsh orchids involved the measurement and assessment of 51 morphological characters, or variates (by far the longest database ever used by any researchers up to that time), which were then analysed on a computer by means of multivariate analysis (see Recent History above). As facilities for certain laboratory work were not at that time available to me, I initially used a much simpler database, consisting of 30 variates easily recorded on site: that database was used for 1986-7 survey work. Subsequently however a much longer database, consisting of 59 variates, was developed and used for all 1988-9 survey work (and will continue to be used for all future work). Because the shorter database is not compatible with the new longer one, all analysis results presented in this paper are based entirely on the 1988 and 1989 surveys. The following characters are used:

Stem and Inflorescence (7 variates):

1. Plant height in cm, measured from ground level to the tip of the inflorescence.
2. Inflorescence length in cm, measured from the junction of the lowest floral bract with the stem.
3. Inflorescence, greatest width in cm.
4. Stem diameter in mm, at lowest unshathed point on stem (usually immediately above lowest sheathing leaf).
5. Degree of anthocyanin staining of upper stem below inflorescence (0 = none, 1 = faint, 2 = medium, 3 = intense).
6. Colour of stem in parts unaffected by anthocyanin staining (1 = yellow-green, 2 = light green, 3 = dark green).
7. Number of flowers.

Leaves (13 variates):

8. Number of sheathing leaves.
9. Number of non-sheathing leaves.
10. Number of basal sheaths.
11. Length of longest leaf in cm, measured from upper limb of sheath on opposite side of stem from open leaf blade.
12. Maximum width of longest leaf in cm.
13. Position of maximum width in relation to long-

est axis (1 = nearer to stem, 2 = \pm at middle, 3 = nearer to leaf-tip).

14. Numerical position of longest leaf, counted from bottom of stem, excluding basal sheath (1 = lowest fully-expanded sheathing leaf . . . etc).
15. Length of widest leaf in cm.
16. Width of widest leaf in cm.
17. Position of maximum width.
18. Numerical position of widest leaf.
19. Leaf colour (1 = yellow-green, 2 = light green, 3 = grey-green, 4 = dull or mid-green, 5 = dark green).
20. Shape of leaf-tip (1 = subacute, 2 = acute, 3 = hooded).

Leaf markings (5 variates):

21. Frequency (0 = absent, 1 = light, 2 = medium, 3 = heavy, 4 = intense, 5 = marbled or solid blotch).
22. Annular (0 = no, 1 = yes) (majority of markings on largest leaves).
23. Approximate mean size in mm of markings on largest leaves.
24. Distribution (0 = absent, 1 = sparse at leaf-tips, 2 = sparse but widespread, 3 = average, 4 = many, close-spaced, 5 = dense all over, including leaf edges, 6 = marked on under-side).
25. Type (0 = absent, 1 = fine pinpoint dots, 2 = \pm round spots, 3 = transversely elongated spots/bars, 4 = irregular blotches, 5 = mixed).

Bracts (5 variates):

26. Length of lowest floral bract in mm.
27. Maximum width of lowest floral bract in mm.
28. Bract markings (0 = absent, 1 = faint or small dots, 2 = well-marked but not annular, 3 = annular).
29. Degree of anthocyanin staining (see 5 above for scale).
30. Mean length in μm of 20-90 peripheral cells, measured by counting number of cells across microscope field of known diameter, at three points (base, middle and tip) along each bract.

Ovary (2 variates):

31. Length of lowest ovary in mm.
32. Diameter of lowest ovary in mm.

Spur (5 variates):

33. Length in mm of flattened mounted spur, excised immediately behind column at junction with ovary.
34. Width at entrance in mm of flattened mounted spur.

35. Horizontal internal diameter in mm, measured in the field, of unpressed spur at its entrance.
 36. Shape in outline (1 = sac-like, 2 = cylindrical, 3 = conical/tapering).
 37. Curvature (1 = upcurved, 2 = straight, 3 = downcurved).

Labellum (13 variates):

38. Length in mm from spur entrance to tip of central lobe.
 39. Greatest width in mm.
 40. Position of greatest width (1 = above middle, 2 = \pm at middle, 3 = below middle).
 41. Length of central lobe in mm, measured from base of deepest sinus, where present.
 42. Depth of right sinus in mm, measured from tip of lateral lobe. (Characters 38–42 measured from excised labella, flattened and mounted according to British school – see Bateman & Denholm 1983 and 1989b).
 43. Reflexion of lateral lobes (1 = deflexed, 2 = \pm flat, 3 = slightly reflexed, 4 = markedly reflexed, 5 = completely reflexed, with lateral lobes touching at back).
 44. Number of indentations on right lateral lobe.
 45. Shape (1 = entire, 2 = diamond-shaped, 3 = inverted kite, 4 = slightly three-lobed, 5 = markedly three-lobed).
 46. Base colour (0 = white, 1 = pale, 2 = medium, 3 = dark).
 47. Markings colour/contrast (0 = markings absent, 1 = faint or ill-defined, 2 = medium/fairly well-defined, 3 = dark, strongly or intensely marked).
 48. Markings type (0 = absent, 1 = dots, 2 = dashes, 3 = lines, 4 = solid loops/lines, 5 = mixed blotches, blurred lines, dots/solid loops etc).
 49. Markings distribution (0 = absent, 1 = peripheral, 2 = central, 3 = extensive coverage).

Perianth Segments (8 variates): excised and mounted:

50. Length of dorsal outer perianth segment (sepal) in mm.
 51. Width of dorsal OPS in mm.
 52. Length of right lateral OPS in mm.
 53. Width of right lateral OPS in mm.
 54. Length of right inner perianth segment (petal) in mm.
 55. Width of right IPS in mm.
 56. Lateral OPS markings (0 = absent, 1 = faint, 2 = well-defined, 3 = annular).
 57. Position of lateral OPS (1 = horizontal, 2 =

slightly raised, 3 = 45° or more, 4 = \pm vertical, 5 = vertical and folded back, touching at back).

Column (2 variates):

58. Length of column in mm, measured from junction with ovary to apex.
 59. Width of column in mm, measured across widest part of mouth of spur, exterior–exterior.

A random sample of ten plants (whenever available) of each target taxon was measured, such plants being necessarily subject to a *priori* 'identification' based on accepted ranges of variation published by earlier authorities, coupled with my own experience of *Dactylorhiza* over a period of nearly thirty years study. All characters were measured or assessed at peak flowering. It is accepted that a ten-plant sample from each population is small, and that a larger sample would be desirable. It is prohibitive, however, in terms of the expenditure of the limited time available to an amateur (particularly using such a long database), and the ten-plant sample is recognised as the minimum required for valid statistical comparison (Bateman & Denholm 1989b). It is considered more important to measure a large number of character-states from as many populations as possible. Where samples of fewer than ten plants have been available (*ssp.junialis* at Bisterne (9), *ssp.traunsteinerioides* at Cothill'A' (5), and *ssp.purpurella* at Malham Tarn (4)), it is accepted that any comparisons made using the data have only limited value until more data are available.

Much data obtained by other workers were available for use in this research, including in particular a 1986 survey by R M Bateman of the Exbury population of *ssp.traunsteinerioides* var. *bowmanii*. However, in order to compare data compiled by other workers, standards of assessment and methods of measurement of characters must be subjected to the closest scrutiny to ensure total compatibility of data (Bateman & Denholm 1989b – see also p. 228 above). As such compatibility cannot be guaranteed other than within the bounds of the personal research of any one worker, I have used only my own data for this study.

THE MULTIVARIATE ANALYSIS

The method of analysis used is known as Canonical Discriminant Analysis, using the SPSS-X package, which is a statistical package used for determining the best possible within-group and between-group separation of statistical data using a large number of variables. It then determines within-group means, and analyses the range of variation within each group around that mean. It also analyses the extent to which each variate contributes to the degree of separation achieved: this is a valuable function enabling the identification of the most significant (and thus potentially diagnostic) morphological characters which separate, and thus allow determination of taxa (see Table 2).

In order to compare different groups of data (in this case, morphometric data from different *Dactylorhiza* taxa) it determines a series of Canonical Discriminant Functions, or numerical co-efficients, which best separate

the groups compared. Selection of the first two (ie the best two) functions then enables them to be plotted against each other on a scatterplot which represents each individual plant measured as a single point on the plot, in effect a composite representation of all the data analysed. A direct comparison of the morphology of the taxa surveyed is thus obtained in graph form (Fig 1).

It should be stressed, however, that this is a two-dimensional representation of what is in effect a multi-dimensional figure: the computer views the aggregate of plotted points from all angles until it finds a point at which it obtains the best possible visible two-dimensional representation of maximum separation of all groups compared.

RESULTS

It will be seen from Figure 1 that there is apparently a degree of separation between

Table 2: List of Top 20 Most Significant Variables, Arranged in Order of Level of Contribution to Functions.

Function 1		Function 2	
Variate/Description	Coefficient	Variate/Description	Coefficient
45 Labellum shape	0.68	23 Leaf marking size	0.52
7 Number of flowers	0.44	16 Width widest leaf	0.44
28 Bract markings	-0.42	22 Annular leaf markings	0.40
46 Labellum base colour	-0.40	12 Width longest leaf	-0.40
26 Length floral bract	0.38	48 Labellum markings type	0.38
29 Bract anthocyanin	0.36	2 Inflorescence length	-0.36
15 Length widest leaf	-0.31	30 Bract cell length	-0.32
56 Lateral OPS marks	-0.31	1 Plant height	0.32
5 Stem anthocyanin	0.29	46 Labellum base colour	-0.31
8 No of sheathing leaves	-0.28	3 Inflorescence width	0.28
16 Width widest leaf	-0.28	6 Stem colour	0.28
54 Length right IPS	0.27	49 Labellum marks distribution	-0.27
33 Spur length	0.27	31 Ovary length	0.21
59 Column width	-0.26	27 Floral bract width	-0.19
25 Leaf marks type	0.24	19 Leaf colour	-0.19
3 Inflorescence width	-0.24	32 Ovary width	-0.19
31 Ovary length	-0.23	56 Lateral OPS marks	0.19
39 Labellum width	0.22	34 Spur width (pressed)	-0.17
27 Floral bract width	-0.21	41 Length central lobe	0.16
58 Length of column	0.20	57 Position lateral OPS	-0.16

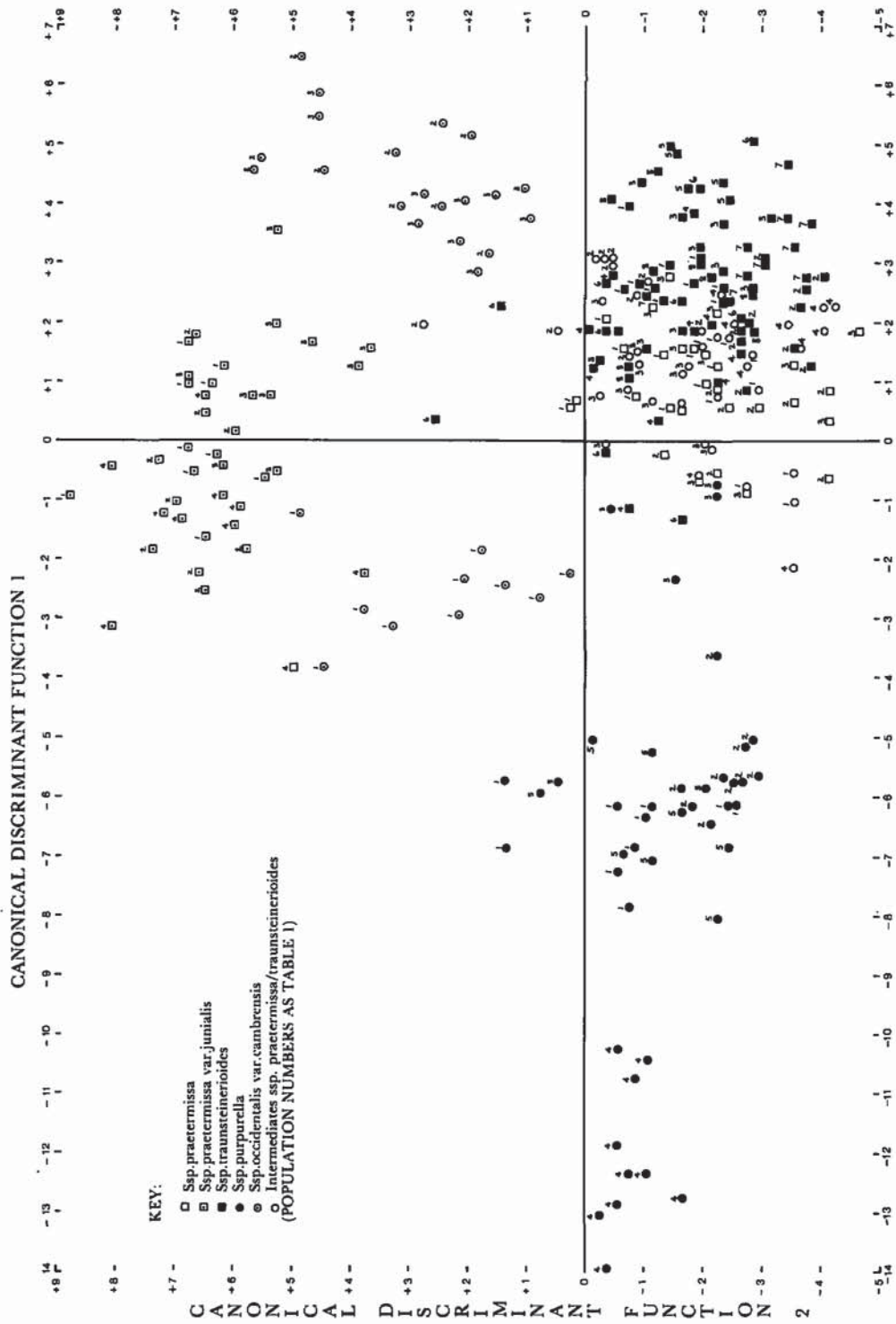


Fig 1. Canonical discriminant analysis: SPSS-X. All-groups scatterplot: *Dactylorhiza majalis* subspecies

three broad groups ie the *ssp.purpurella* group (lower left of plot), the *var.cambrensis/ var.junialis* group (upper centre-right), and the *ssp.praetermissa/intermediates/ssp. traunsteinerioides* group (lower right), although even between these broad groups there is some overlap.

Notable features of this analysis are as follows:

(a) *Ssp.praetermissa* (lower centre) is widely separated from *ssp.praetermissa var.junialis* (upper centre), to which it is supposedly closely related.

(b) *Ssp.occidentalis var.cambrensis* from the Portmadoc population (upper left centre) is clearly separated from the two Aberystwyth populations (upper right), and indeed the plotted area for all populations of *var.junialis* measured is interposed between the two *var.cambrensis* groups. There is also some overlap between *ssp.junialis* and both groups of *var.cambrensis*.

(c) Overlap between *ssp.praetermissa*, *ssp.traunsteinerioides* and those populations identified as intermediate between the two is complete. The picture presented by these groups on the all-groups analysis is so confusing, in fact, that a separate analysis was felt to be necessary in order to attempt to establish more clearly the relationship between them. The result of that analysis is presented at Fig 2.

This to a large extent resolves the confusion of the all-groups analysis. It will be seen that:

(a) *Ssp.praetermissa* at Avon Forest (lower right) is clearly distinct from both the intermediates (largely upper centre) and *ssp.traunsteinerioides* (lower centre-left).

(b) Interestingly, however, the population of 'typical' *ssp.praetermissa* at Pamphill (upper centre right) shows some overlap with both *ssp.traunsteinerioides* and intermediates, with a particularly close affinity with *ssp.traunsteinerioides* at Basingstoke (Population 4).

(c) The population of 'intermediates' at Frilford, in spite of the entire labella displayed by many plants (see p 232 above, and Fig 3), shows a close affinity to the populations of *ssp.traunsteinerioides* at the two Cothill sites (lower centre of plot).

On the basis of this second analysis, it seems likely that more extensive survey work on *ssp.praetermissa* would largely fill in the gap between the Avon Forest populations and that at Pamphill, thus completing a broadly triangular plot which clearly indicates a morphological continuum encompassing *ssp.praetermissa* and *ssp.traunsteinerioides*.

It has been suggested (R M Bateman pers comm 1989) that some of the distinctions apparently revealed by the multivariate analysis (particularly between *ssp.praetermissa* and *var.junialis* in Fig 1) may not be true distinctions, in that they may be largely due to the predominance of certain types of morphological variate in the two Functions used for the plot, ie that CDF 1 is principally a vigour co-ordinate, and CDF 2 is determined primarily by pigmentation, and that the relative positions on the plot of *ssp.praetermissa* and *var.junialis* are thus accounted for largely by the presence of heavy annular leaf-markings in *var.junialis*.

An examination of Table 2, however, shows that this is not in fact the case: there is a roughly equal proportion of vigour and pigmentation variates contributing significantly to both Functions. Furthermore the presence of the small taxa surveyed at opposite ends of the so-called 'vigour co-ordinate' (*ssp.purpurella* far left, and *ssp.traunsteinerioides* far right) tends to re-inforce my view that this analysis presents a morphologically broadly-based picture of the relationships between groups, using statistically viable criteria, and that valid conclusions may thus be drawn from it.

AFFINITIES BETWEEN GROUPS

A useful further by-product of the multivariate analysis is an assessment by the computer of the 'highest probability group' (HPG) and 'second highest probability group' (2HPG) to which each individual plant belongs. As one could reasonably expect, in the vast majority of cases the HPG for each plant is the group being surveyed, ie the population of which it is a member. In some cases, however, that is not

in fact the case, ie the computer considers that the particular plant concerned is actually more akin morphologically to those of another group altogether. Those cases, together with the 2HPG of all plants, are charted in Table 3. Numbers in the left-hand column denote population numbers as per Table 1, the %age figures show the proportion of plants in each group for which the computer considers the HPG is that of the population being surveyed, and the remaining columns show the 2HPG by number of plants for each population surveyed. Those numbers marked with an asterisk (*) indicate plants where the HPG is a group other than the population being surveyed.

Table 3 thus reveals the closest affinities morphometrically between groups, and some interesting relationships are indicated:

(a) All plants of *ssp.traunsteinerioides* show closest affinities either with other groups of the same subspecies, or with one or other of the 'intermediate' populations;

(b) *Ssp.praetermissa* at Avon Forest shows predictable affinities with other Avon Forest populations, except for six plants at Avon Forest 2 (not shown on chart) whose closest affinity is with a hybrid plant from a New Forest population included in the multivariate analysis, but not plotted on Fig 1. Perhaps significantly, that hybrid is probably *D.fuchsii* x *D.maculata* backcrossed with *D.incarnata* var. *pulchella* - which may be a possible clue to the evolutionary origin of *ssp.praetermissa* (see later in this paper, discussion on HYBRIDS). Pamp-hill plants show some affinity to *ssp.traunsteinerioides* both at Avon Forest and Basingstoke.

(c) The affinities of *var.junialis* lie largely within its own group, with the exception of one plant at Winkton whose closest correspondence is with *var.cambrensis* at Aberystwyth.

(d) *Ssp.purpurella* at Malham Tarn not unexpectedly shows a close affinity to populations of *ssp.traunsteinerioides* at Cothill 'B' and Cors Erddreiniog. *Ssp.purpurella* at Cors Geirch, however, shows a closest affinity to *var.cambrensis* at Portmadoc (7 plants) and to *ssp.purpurella* at Pately Bridge 'B' (3 plants).

(e) *Var.cambrensis* at Portmadoc shows affinities

with *ssp.purpurella* at Malham Tarn and Cors Geirch, and also interestingly with *var.junialis* at Winkton. The two Aberystwyth populations, however, show a close correspondence with each other, apart from two plants close to *ssp.traunsteinerioides* at Exbury and to the intermediates on Avon Forest respectively. The absence of any apparent close affinity between the Portmadoc and Aberystwyth populations is significant.

(f) The intermediates occasionally reveal some unexpected correspondences: the Avon Forest population has one plant whose closest resemblance is to *var.junialis* at Axmouth, and one whose closest affinity is with *var.cambrensis* at Aberystwyth. Frilford intermediates on the other hand confirm their position on the multivariate scatter-plot with a close affinity to *ssp.traunsteinerioides* at Basingstoke.

In fact, broadly speaking the affinities outlined above are reflected in the scatterplot by the relative positions of the outlying plants of each group to their nearest neighbours in other groups.

RANGES OF VARIATION

A major difficulty in the identification of *Dactylorhiza* has been the lack of consistency between the various authorities in the published descriptions of acceptable ranges of variation, or diagnostic character-states most commonly used to determine taxa. In the course of this research, detailed comparisons of maximum and minimum values for all the characters measured or assessed have been made between all populations surveyed. In addition, population means, with standard deviations, have been calculated for all variates. The resulting table of figures is a considerable document in itself, and space does not permit its publication here. It is available, however, to any interested party who cares to write to the author. Table 4, however, is a summary of the ranges of variation of population means for the twenty most significant variables contributing to Function 1 in the multivariate analysis. The following points are worthy of note:

Ssp. traunsteinerioides:



(a) Rhos-y-Gad, Anglesey



(b) Var. *bowmanii*, Exbury

Ssp. praetermissa



(c) 'Typical' form, Christchurch



(d) (?) Var. *macrantha*, Avon Forest

Ssp. praetermissa var. *junialis*:



(a) Bisterne



(b) Winchester

Ssp. occidentalis var. *cambrensis*:



(c) Portmadoc



(d) Aberystwyth

Ssp. purpurella:

Dactylorhiza majalis: variations

PLATE 3



(a) Southampton



(b) Pateley Bridge

Intermediates:



(c) *cambrensis/purpurella*, Portmadoc.



(d) *cambrensis/traunsteinerioides*, Aberystwyth

Intermediates:

Dactylorhiza majalis: variations

PLATE 4



(a) *purpurella/traunsteinerioides*, Malham Tarn



(b) *purpurella/praetermissa*, Southampton



(c) *praetermissa/traunsteinerioides*, Winkton



(d) *praetermissa/traunsteinerioides*, Avon Forest

Labellum shape: only *ssp.purpurella* has a high proportion of entire labella – all other taxa have a high proportion of three-lobed labella. Number of flowers: this feature only clearly separates *ssp.praetermissa* (over 20) from *ssp.traunsteinerioides* (under 20). All other groups overlap with each other. Note, however, that *var.junialis* has fewer flowers than *ssp.praetermissa*.

Length of floral bracts: *var.junialis* has consistently shorter bracts than *ssp.praetermissa*, and is in fact closer in this character to *ssp.purpurella*.

Bract anthocyanin: this feature largely distinguishes *ssp.praetermissa* and *var.junialis* (low) from *ssp.traunsteinerioides*, but all other groups overlap with *ssp.traunsteinerioides*.

Length of widest leaf: *var.junialis* has consistently shorter leaves than *ssp.praetermissa*.

Lateral OPS markings: the presence of strong markings broadly distinguishes *var.junialis* and *ssp.purpurella* from all other groups except *var.cambrensis* with which there is slight overlap.

Number of sheathing leaves: *var.junialis* has a consistently lower leaf-count than *ssp.praetermissa*, but overlaps with all other groups except *ssp.traunsteinerioides*, which has fewer leaves than all other groups.

Width of widest leaf: *var.junialis* has consistently narrower leaves than *ssp.praetermissa* – only *ssp.praetermissa* may occasionally have leaves broader than 3 cm. Only *ssp.traunsteinerioides* may occasionally have leaves narrower than 1 cm.

Length of right IPS: only *ssp.praetermissa* has petals regularly longer than 8 mm, whereas *var.junialis* is usually less than 7 mm, and overlaps with all other groups.

Table 4: Ranges of Variation of Population Means of Twenty Most Significant Variables in Function 1

Var no/Character	Dmt	Dm \bar{p} r	Dm \bar{p} rj	Dm \bar{p}	Dmoc	Int
45 Labellum shape	3.8–5.0	4.4–5.0	3.3–4.3	1.0–4.0	4.0–5.0	3.1–5.0
7 Number of flowers	8.0–19.1	26.5–42.5	15.4–22.8	13.2–17.0	16.9–32.1	10.3–13.9
28 Bract marks	None	None	0.1–0.3	0.0–1.7	0.0–0.3	None
46 Labellum base colour	1.7–3.0	1.1–2.0	1.4–2.3	2.5–3.0	1.9–2.0	1.7–2.2
26 Length floral bracts	18.7–25.9	18.6–27.0	17.2–20.7	15.8–21.7	19.1–25.3	18.6–19.9
29 Bract anthocyanin	2.4–3.0	1.1–1.6	1.4–2.2	1.0–3.0	1.2–3.0	2.4–2.9
15 Length widest leaf†	6.3–11.9	12.3–13.2	10.4–12.2	6.2–12.7	8.1–11.3	7.1–8.0
56 Lateral OPS marks	0.4–1.6	0.5–1.0	2.0–3.0	2.0–3.0	1.0–2.3	0.3–1.1
5 Stem anthocyanin	1.3–3.0	0.0–0.6	0.3–1.5	0.6–2.5	0.6–2.6	1.2–2.2
8 Number sheathing leaves †	2.2–3.5	4.2–4.8	3.6–3.9	3.3–4.5	3.5–4.5	2.8–4.0
16 Width widest leaf†	0.9–2.3	2.0–3.3	1.8–2.2	1.7–2.2	1.7–2.3	1.2–1.6
54 Length RIPS*	5.9–7.7	7.9–8.9	6.6–7.1	5.4–6.6	6.1–6.8	6.6–7.2
33 Spur length	6.7–8.3	7.1–8.1	6.6–7.8	5.7–8.8	7.1–7.6	6.3–7.6
59 Column width*	2.6–3.1	3.2–3.4	3.1–3.2	2.9–3.3	2.7–3.2	2.7–2.9
25 Leaf marks type	0.0–1.2	None	4.7–5.0	0.0–1.0	2.0–3.9	0.0–0.5
3 Inflorescence width	2.5–3.1	3.3–3.9	2.9–3.0	2.5–3.1	3.0–3.2	2.3–2.7
31 Ovary length*	9.6–12.7	11.2–12.7	9.5–12.0	10.8–12.5	10.4–12.1	9.5–10.6
39 Labellum width	9.3–10.6	10.1–12.4	9.6–10.2	7.9–9.5	9.0–9.9	6.6–9.8
27 Width floral bract*	3.8–5.4	4.4–5.9	3.6–4.6	4.0–5.0	4.3–4.8	3.7–4.6
58 Column length*	4.6–5.7	5.0–5.6	4.7–5.0	4.3–4.7	4.7–4.9	4.3–4.9

* Character not measured by any other published researcher.

† Similar characters measured in different ways by other workers (eg many workers only measure width of second or longest leaf, count total number of leaves, or place emphasis on numbers of non-sheathing leaves – all characters measured in surveys, but not found to be of highest significance).

Column width: *ssp.praetermissa* regularly has a broader column (more than 3.2 mm) than all other groups including *var.junialis*.

Inflorescence width: *ssp.praetermissa* regularly has a substantially broader inflorescence (more than 3.3 cm) than all other groups, including *var.junialis* (less than 3.0 cm).

Labellum width: *ssp.purpurella* usually has a narrower labellum than all other groups. *Ssp.praetermissa* is often broader than *var.junialis*.

Width of floral bracts: these are broader in *ssp.praetermissa* than in *var.junialis*, which overlaps with all other groups.

Length of column: *ssp.praetermissa* (more than 5 mm) regularly has a longer column than *var.junialis* (less than 5 mm). *Ssp.traunsteinerioides* shows the widest inter-population variation in this feature.

Characters significant by their absence from the list of the top twenty variates in Function 1 are as follows:

	Coefficient	Position
4 Stem thickness	0.18292	26th
9 Number of non-sheathing leaves	0.14652	30th
1 Plant height	0.13104	31st
11 Length of longest leaf	0.10798	34th
47 Colour of labellum markings	-0.08152	39th
48 Type of labellum markings	0.07693	41st
30 Mean length of bract cells	-0.05279	49th
2 Length of inflorescence	-0.04708	50th
41 Length of central lobe	-0.04029	53rd
43 Reflection of lateral lobes	-0.03152	54th

All the above characters have assumed over the years a degree of importance in the descriptions of taxa by many workers. It may be, however, that reliance upon them as diagnostic to determine *Dactylorhiza* taxa should be regarded with some caution: this would appear to have potential for giving rise to considerable

confusion, and possibly even erroneous records.

Furthermore, it will be seen from Table 4 that no fewer than five characters have never before been measured in published research, and a further three are significant in a different way from other workers. It is therefore apparent that a complete re-appraisal of diagnostic character-states, or combinations of character-states which taken together may be diagnostic, is necessary in order substantially to reduce the level of confusion that has bedevilled identification of *Dactylorhiza* for so long, particularly for the non-specialist botanist.

'SUBJECTIVE IDENTIFICATION'

An essential ingredient of any morphometric research is the *a priori* 'identification' of the target taxa required for examination. That is necessarily largely a visual analytical process founded on (a) knowledge of recorded locations of taxa, (b) knowledge of acceptable parameters of variation and (c) many years of experience in the particular field of study. It could be described as a more or less 'subjective' process, except that the human brain is nothing if not an extremely efficient computer, capable of very rapid conscious and unconscious analysis. Given that the right data, ie acquired knowledge, is input, there is no reason to suppose that the brain's response to visual stimuli is anything other than efficient. However, that unfortunately is not sufficiently scientific for research purposes: morphometrics is an attempt scientifically to quantify all available data which may be capable of contributing to an identification, in a form which another sort of computer is capable of absorbing and subjecting to analysis.

It must be accepted, however, that the dominant factors in a visual 'subjective' identification are the more obvious visual features, consisting usually of such characters as plant size, leaf size and number, and size, shape, colouring and markings of flowers – in fact, those features which have largely dominated taxonomic decisions based on morphology in the past.

Visual recording is therefore an important feature of any research of this type, if only to enable the reader to relate current discussion to his or her own experience in the field, or to preconceived ideas culled from past reading. To that end, a comprehensive series of photographs has been taken, as a permanent record, of most of the plants surveyed. That practice also serves another purpose, of course: it enables other workers to make independent decisions as to the accuracy or validity of the taxonomic decisions on which the current work is based.

Some of the photographs are reproduced at Plates 1-4, as a small but hopefully representative sample of 'typical' plants of the populations surveyed. As the cost of reproduction of colour transparencies is so high, however, a helpful visual supplement is available in the form of the excised and mounted labella used for the detailed measurements of floral parts. A sample of those has been reproduced in Fig 3: drawings have been made at approximately 3x enlargement of a few of the labella from most of the populations surveyed, covering as far as possible the range of variation encountered in each population.

A cursory glance at Fig 3 will be sufficient to demonstrate that placing too great an emphasis on labellum shape and markings for the purpose of identification is fraught with hazard (see also page 226 above). The extent of similarities immediately apparent that cross existing taxonomic divisions is such that no further comment or explanation is necessary.

HYBRIDS

Hybrids are an important aspect of any serious examination of *Dactylorhiza* as a group: they are very common, to the extent that they sometimes outnumber parent plants in some colonies, and were present to a greater or lesser extent in all the populations studied in the course of this research.

A combination of the features of both 'pure' parent plants is usually a clue to hybridity, coupled typically with hybrid vigour: first

generation (F1) hybrids are usually fairly easy to identify. *Dactylorhiza* hybrids, however, unlike many other hybrids, are highly fertile, and F1 hybrids are capable of further hybridisation, both with one or other of the original parents (introgression) and with other hybrids (F2 etc). With each further hybrid stage, identifiable features attributable to the original parent plants become progressively more obscure. The resultant intermediate plants can be virtually impossible to identify morphologically with any certainty, even by experienced orchid specialists, and may at best be described as 'putative' hybrids of (taxon A x taxon B) x (taxon A x taxon C) or similar.

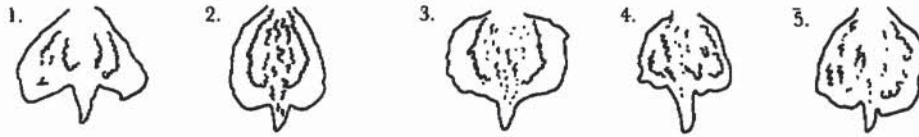
If one represents the range of variation of *Dactylorhiza* taxa by means of diagrammatic circles, those representing the marsh and spotted orchids respectively will overlap to a small extent with the other marsh or spotted orchid group, but there will be no overlap between the marsh orchid group and the spotted orchid group. The area of hybridisation morphology however may then be represented diagrammatically as a roughly cruciform area of cross-hatching (see Fig 4 below - after R M Bate-man, pers comm 1986).

It will readily be seen that any hybrid between the two species of marsh orchid, or between the two species of spotted orchid, will be virtually impossible to distinguish from any robust intermediate form, unless chromosome examination is carried out. As orchid chromosomes are extremely small, it is notoriously difficult to carry out chromosome counts. Hybrids between either of the marsh orchids and either of the spotted orchids, however, are readily identified as such in broad terms, although it may sometimes be much more difficult to determine which particular species of marsh or spotted orchid is actually involved on morphological grounds alone, as almost any such hybrid will overlap morphologically to some extent with other hybrids between the other two species. In practice, many are determined mainly by reference to the co-existing putative parents ie it is unlikely that a hybrid *D.incarnata* x *D.maculata* will occur in a colony consisting solely of *D.majalis* ssp.*praetermissa*

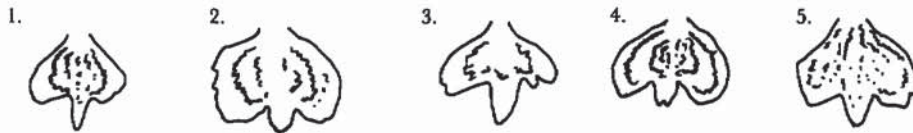
Fig 3. Labellum variation in *Dactylorhiza majalis*.
Ssp. traunsteinerioides, Exbury (1-3) and Avon Forest (4 & 5)



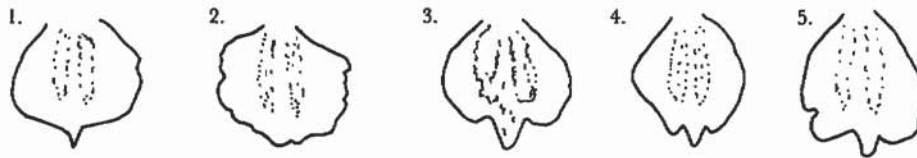
Ssp. traunsteinerioides, Basingstoke (1 & 2) and Cothill (3-5)



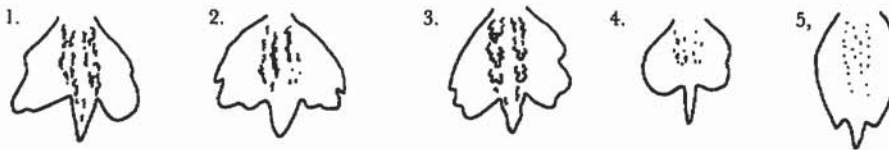
Ssp. traunsteinerioides, Wharfedale (1 & 2) and Anglesey (3-5)



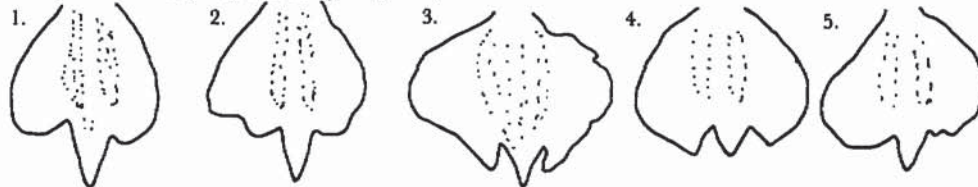
Intermediates, Frilford (1 & 2) and Winkton (3-5)



Intermediates, Avon Forest (1-3) and Stapehill (4-5)



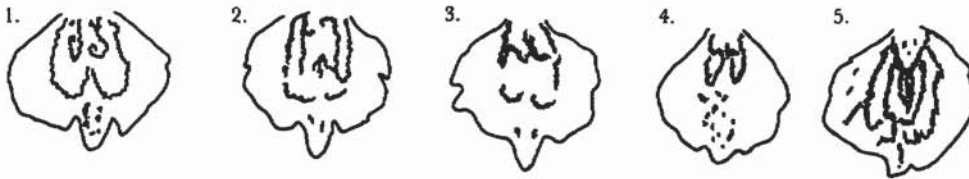
Ssp. praetermissa, Avon Forest (1-3) and Pamphill (4 & 5)



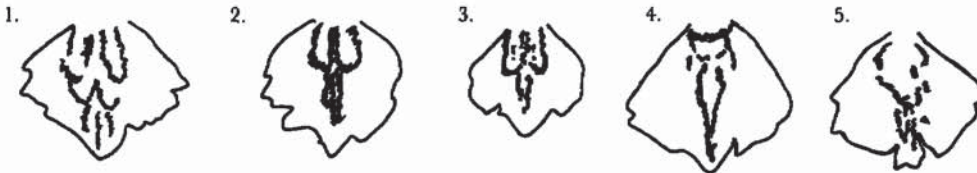
Var. junialis, Bisterne (1 & 2) and Winkton (3-5)



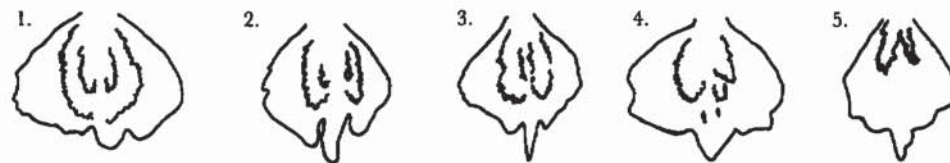
Var. junialis, Axmouth (1-3) and Winchester (4 & 5)



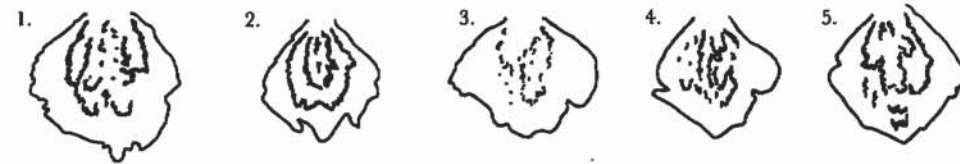
Var. cambrensis, Portmadoc



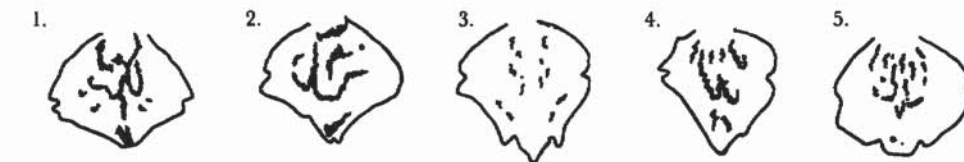
Var. cambrensis, Aberystwyth



Ssp. purpurella, Malham Tarn (1 & 2), and Pately Bridge (3-5)



Ssp. purpurella, Cors Geirch (1 & 2) and Newborough Warren (3-5)



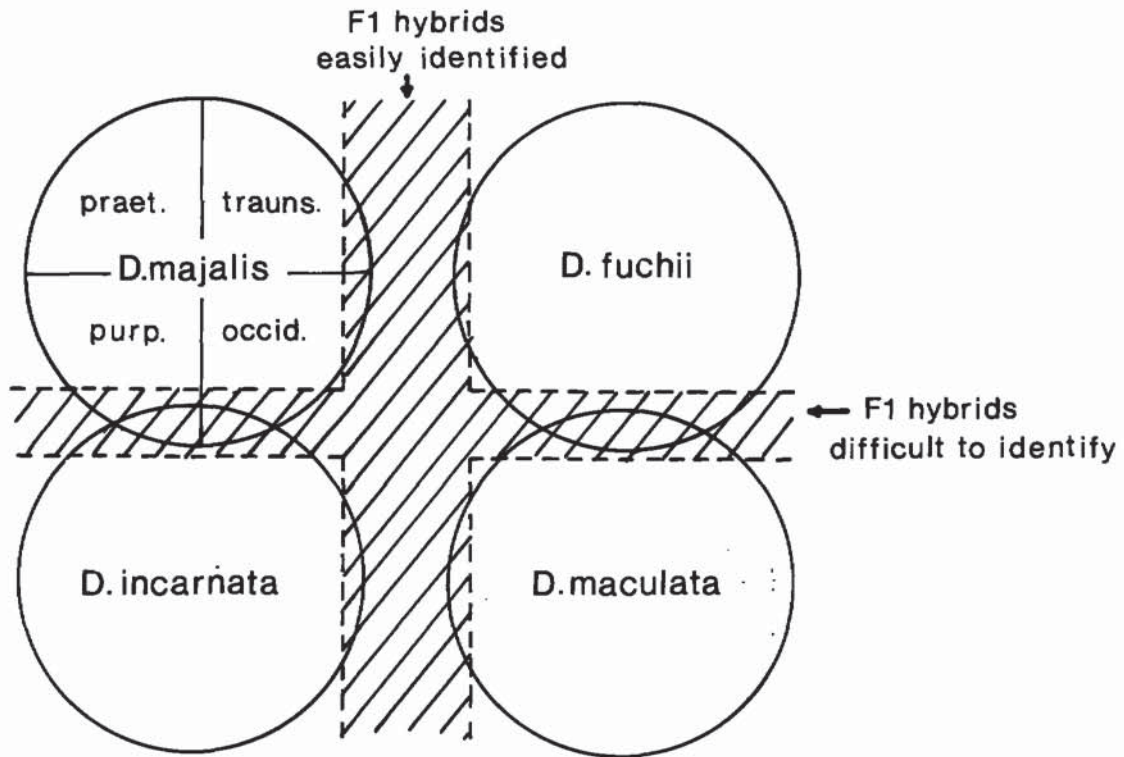


Fig 4. Hybridisation Morphology.

and *D. fuchsii*. Problems do sometimes occur, however, when more than two taxa co-exist in the same colony!

The most commonly encountered hybrids are those between one or other of the marsh orchids and one of the spotted orchids: understandably, for the reasons outlined above, hybrids between the two marsh orchids are rarely recorded, although I am fairly certain that I have seen some in a few of the colonies studied in the course of this research. Hybrids between the two spotted orchids are decidedly uncommon, but I have seen them in those rather unusual intermediate habitats where both

species occur together: in practice, they are not so difficult to determine as those between the two marsh orchids, as they are almost invariably exceptionally robust – up to three or four times the size of either parent.

Having observed, however, in the preceding sections of this paper, that there is substantial morphological overlap between the subordinate taxa of the *D. majalis* group, it will be recognised at once that the existence of hybrids between any but the most extreme members of the group cannot possibly be determined with any certainty. What I describe in this paper as 'intermediate' plants

would be virtually indistinguishable from any putative hybrid between the two subspecies concerned. Indeed, many such intermediate forms, particularly leaf-marked plants, could well have arisen originally from hybrids. Possibly the only clue to such hybrids would be unusual vigour: one plant in the Exbury population of *ssp.traunsteinerioides* var. *bowmanii* in 1987 showed all the floral characteristics of *ssp.traunsteinerioides*, but the vegetative characteristics of *ssp.praetermissa*. How does one interpret such a plant? It may well have been a hybrid, but could also accurately be described as a robust intermediate. Similarly the population of *ssp.traunsteinerioides* at Avon Forest, with rather more robust vegetative features than the Exbury population, is open to alternative interpretation.

If most 'experts' were truly honest with themselves, with each other, and with their unsuspecting public, they would have to admit that some field identifications of such plants are based on a combination of scientific comparative morphology, informed guess-work based on years of experience, and pure blind instinct!

It will by now be abundantly clear that *Dactylorhiza* hybrids present us with some enormous problems: equally if we are to be able to sort out the difficulties of the group as a whole, we must grasp the nettle and confront the problems posed by hybrids. It is particularly helpful to be able to study those populations where one can at least be reasonably confident not only of the parent taxa involved, but also of the degree of hybridisation and the progressive development of the hybrid forms that are present. There is one such population in the New Forest.

AN IMPORTANT NEW FOREST HYBRID COLONY

A narrow perimeter strip around a recent inclosure on the eastern border of the New Forest supports an impressive display of orchids. The whole area was dry heathland until the early 1960s: a 1951 botanical survey

of the area recorded no orchids (R P Bowman pers comm 1985). In the early 1960s, however, a commercial crop of conifers was planted, and the perimeter strip was rotavated, limed and reseeded to provide a firebreak and forage for ponies. This interference with the ecology of the strip has substantially altered the nature and fertility of the soil, and has raised the normally markedly acid pH value of heathland podzol and peat to just below the neutral level (pH 5.0–5.7). Liming of the strip will have been the principal cause of this, but rotavating may also have broken up the 'iron-pan' of leached minerals below the surface, releasing mineral nutrients at a higher level in the soil. The whole process was intended as 'agricultural improvement' that in terms of the purpose for which it was intended actually failed (Edwards *et al*, 1982). For local botanists, however, it was a resounding success: the strip now supports, amongst other scarce plants, a remarkable heterogeneous population of orchids, which has developed in no more than 25 years, an extremely short time (in orchid terms) for some of the hybrids at the site to have acquired their current morphology.

Parent species at the site consist of the Common Spotted Orchid (*D.fuchsii*) in small numbers scattered along the strip, the Heath Spotted Orchid (*D.maculata*) in abundance, and showing considerable variation, and the Early Marsh Orchid (*D.incarnata* ssp. *pulchella*) in a few small groups. The latter species occurs both in its typical acid-soil deeply-coloured form, and also in its creamy-white anthocyanin-free form, although these lovely plants do not appear to have been reproduced in any of the hybrids present.

The main interest of the site is the range of hybrids that have developed in such a remarkably short space of time. F1 hybrids between all three parent plants are present in fairly small well-defined areas, generally in the immediate vicinity of the greatest concentrations of the respective parents. More significant, however, is what appears to be a series of second and subsequent generation backcrosses, mostly of the respective F1 hybrids with *D.incarnata*.

The principal clue to this progression is in the leaf-spotting: the heavy leaf-spotting apparent in the obvious F1 hybrids becomes gradually more attenuated in succeeding groups of plants. Remarkably, most of these putative backcrosses form small homogeneous groups separated by a few metres from preceding and succeeding generations: in other words, they appear to have stabilised to the extent that they are propagating themselves with a degree of consistency, albeit within a very small area. This curious feature of the site enables one to walk from one end of the long narrow strip to the other, a distance of about a kilometre, and follow the progress of hybrid development, which I believe may represent a microcosm of *Dactylorhiza* evolution.

Particularly interesting products of this series of hybrids are forms in three distinct areas which bear remarkable resemblances to three different subspecies of *D. majalis*:

(1) Near the main population of *D. fuchsii* is a small group of tiny unspotted plants, with dark but virtually unmarked deeply three-lobed labella: these bear more than a passing resemblance to *D. majalis* ssp. *traunsteinerioides*. My assessment of these plants is that they are the result of successive backcrosses of the hybrid *D. fuchsii* x *D. incarnata* with pure *D. incarnata*.

(2) Further west along the strip, there is a large group of plants, of medium size, with lightly spotted or unspotted leaves, and paler flowers, with lightly marked, broadly rounded and shallowly three-lobed labella, which have several features in common with ssp. *praetermissa*. These plants I assess as the product of backcrossing of the hybrid *D. maculata* x *D. incarnata* with pure *D. incarnata*, and also in some instances of a second generation cross between two of the F1 hybrids.

(3) At the far north-western end of the strip, there is a small population of remarkably consistent plants, of medium size, with unspotted leaves very similar to those of *D. incarnata*, but with a broad, deeply three-lobed, dark-coloured and heavily marked labellum very similar to that of ssp. *occidentalis* – the overall appearance of these plants recalls descriptions of the paler, unspotted form of

that taxon, var. *kerryensis*. The hybrid *D. fuchsii* x *D. maculata* occurs in the vicinity, as do backcrosses with *D. incarnata*, which have much less heavily spotted leaves: it may therefore be logical to assign these unusual unspotted plants to subsequent backcrosses with *D. incarnata*, where the leaf-spotting has been eventually eliminated.

Morphometric surveys of hybrid plants have limited value, because of the confusing combinations of morphological characteristics emanating from the various parent taxa. As a matter of curiosity, however, this last population has been surveyed and subjected to multivariate analysis. The result is intriguing, albeit impossible to gauge its significance: these plants plot in an area intermediate between the ssp. *praetermissa*/ssp. *traunsteinerioides* group and the var. *junialis*/var. *cambrensis* group on Fig 1, in the upper centre of the plot.

It will immediately be apparent that the implications of such remarkable hybrid development are of potentially enormous significance in the context of *Dactylorhiza* research, particularly with regard to evolutionary theory and discussion. What is also clear, however, is that a great deal more research and critical study of these hybrid plants is essential before any definitive statements can be made. Amongst other things, exhaustive studies of the chromosome complements both of the hybrid plants and of their putative parents must be undertaken, if only to establish, if at all possible, the degree of hybridity of these plants. That research has commenced, but is likely to take many years to complete. It may even be that the results of that research will prove to be unhelpful, as will become apparent from the following section, a very brief summary of the salient points of chromosome studies in *Dactylorhiza*.

THE IMPORTANCE OF CHROMOSOMES

All living cells propagate by division: they pass on their hereditary characteristics by means of their chromosomes, each of which divides into two (mitosis) in order to pass on a complete

complement of chromosomes to each new cell. The only exception to this rule is in the creation of reproductive cells: in their case the complement of chromosomes is halved, in order that when egg and pollen fuse to create a new generation, the number of chromosomes remains the same as that of the parents. The reduction division of reproductive cells is known as meiosis.

Most life-forms have a regular number of chromosomes peculiar to each species – a specific 'fingerprint'. Within that complement of chromosomes, a certain number each carry their own individual genetic characteristics: this subordinate complement of unduplicated chromosomes may be duplicated several times. *Dactylorhiza* have a complement of twenty unduplicated chromosomes: these are usually (though not always) repeated twice in *D. incarnata* and *D. fuchsii* (the diploid species) and four times in *D. majalis* and *D. maculata* (the tetraploid species).

In chromosome counts, n is the complement of chromosomes passed to each new generative cell at meiosis: the full number of chromosomes in normal cells is therefore expressed as $2n$. The somatic chromosome count for the diploid species of *Dactylorhiza* is therefore $2n = 40$, and that of the tetraploids is $2n = 80$.

One would naturally expect the hybrid offspring of diploid and tetraploid parents to be triploid ($2n = 60$), and the offspring of subsequent generations of hybrid parents to be aneuploid (ie $2n =$ more than 40 and less than 80, but not triploid). That is in fact normally the case, but unfortunately is not always true (Lord & Richards 1977). There are certain well-documented vagaries in the mechanism of cell division that make it occasionally possible for first and subsequent generation hybrids of diploid and tetraploid parents to be themselves tetraploid (Stace 1980).

There seems to be some logical force in the supposition that chromosome complements of 40 and 80 are likely to produce the most genetically stable and consistent populations of *Dactylorhiza*: hence the evolution, establishment and continuing viability of the four recognised species. It seems at least theoretic-

cally possible, therefore, that if by one of the various quirks of genetic mechanism hybrids with a tetraploid chromosome count became established, they would have the potential to be relatively stable, genetically viable, and therefore self-perpetuating, providing only that there existed some sort of barrier, whether physical, temporal or genetic, to inhibit contamination of the newly-stabilised type by further hybridisation.

If the three distinctive groups of hybrid plants on the New Forest perimeter strip described above were found to be tetraploid, could we perhaps have the germ of a potentially fruitful avenue of research, which could even lead to some hard evidence as to the past course of evolutionary development of the orchids of the *D. majalis* group? On morphology alone, it is tempting to consider the case almost proven: the flaw in that argument of course is the probable absence of any barrier preventing further hybridisation of these groups of plants, as bumble-bees pollinate all species of *Dactylorhiza* indiscriminately. It is therefore difficult to account for the apparent stabilisation of these small discontinuous but closely adjacent groups of plants.

It has been suggested (Summerhayes 1951, amongst others) that all the various subspecies and varieties of the *D. majalis* group have evolved from a series of stabilised hybrid forms resulting from cross-fertilisation between the two spotted orchids and the various subspecies and colour forms of the Early Marsh Orchid. The idea has arisen largely from morphological study of *Dactylorhiza* species and hybrids, reinforced by the geographically and ecologically localised nature of the different forms of *D. incarnata* in relation to similarly localised forms of *D. majalis*. It is an attractive theory, but has to date been unprovable – comparative morphology, whilst helpful, is too imprecise to amount to anything approaching proof of parentage in hybrid plants.

It is therefore apparent that comprehensive study of the chromosomes of the interesting series of hybrids in the New Forest colony is absolutely essential. Such study would be time-consuming and expensive, requiring

specialist skills, and the results could be equivocal and inconclusive: the vagaries of chromosome division in hybrids could produce a preponderance of aneuploid counts – which would prove nothing! The attempt, however, would seem to be amply justified by the potential for resolving one of the major questions in orchidology that has perplexed botanists for many years.

CONCLUSIONS

Perhaps the most important firm conclusion that may be drawn from this research merely re-inforces Bateman and Denholm's (1983) conclusions as to the conspecificity of the four tetraploid marsh orchids under study. There is overwhelming evidence of morphological overlap between all four groups, and particularly of a morphological continuum encompassing *ssp.traunsteinerioides*, a series of intermediate forms, and *ssp.praetermissa*. Continued separation of British '*D.traunsteineri*' from the *D.majalis* group cannot therefore be justified.

Differences, however, between *ssp.praetermissa* in its unspotted form, and its so-called variety, the leaf-marked *var.junialis*, tend to indicate that these two taxa should be separated. It is accepted that further survey work on more populations of both taxa is desirable, accompanied by multivariate analysis omitting leaf- and labellum-marking variates, in order to determine whether or not there is a clear distinction between them on morphological grounds other than leaf/labellum markings. Initial indications, however, from this study, are that such differences do exist. Distinction of these taxa has traditionally been restricted to leaf- and labellum-markings, with other morphological characteristics commonly held to be indistinguishable (eg Bateman & Denholm 1983). My studies, however, tend to show that *var.junialis* usually has fewer, narrower leaves, shorter and narrower floral bracts, a narrower, laxer inflorescence with fewer flowers, which have shorter petals, a narrower labellum and a shorter, narrower column. These differences are only those evi-

dent from Table 4, and there may be others revealed by further study of the data, and more extensive survey work.

Overlap between *var.junialis* and *ssp.occidentalis var.cambrensis* which is revealed by this study suggests that it may be appropriate to amalgamate these taxa, perhaps as *D.majalis ssp.junialis* (as the epithet *junialis* has historic precedence over *occidentalis* in nomenclatural terms). In addition, it appears that the two main areas of distribution of '*var.cambrensis*' in Wales support populations of plants which differ so widely from each other that continued treatment of them both as a single variety may well not be justified. I reserve judgement on these decisions, however, until current studies are completed: a detailed study of all the heavily leaf-marked tetraploid taxa, including *D.lapponica* (Laest.ex Hartman) Soó in Scotland, *D.majalis ssp.occidentalis* in Ireland, and *D.majalis ssp.majalis* in France is progressing, and should provide definitive data sufficient for a full reappraisal of these taxa. One of the omissions of the extensive survey work conducted by Bateman and Denholm (1983) was that *var.junialis* was not surveyed as a separate entity. It was dealt with as a very small percentage of some (not all) of the populations of *ssp.praetermissa* studied. It may be that the apparent distinction of *var.junialis* did not become apparent for that reason. Furthermore, they did not survey *var.cambrensis* from any of the Aberystwyth populations, relying entirely on the population north of Portmadoc used for this study.

Further survey work is also required on *D.majalis ssp.traunsteinerioides* in Scotland and Ireland, and on *D.traunsteineri* in continental Europe, in order to determine the correct nomenclature for these apparently closely related taxonomic groups. The relationship between them remains unproven to date, because of inherent weaknesses in the survey work published to date, and the incompatibility of data proffered as evidence of their conspecificity.

One of the major problems highlighted by this study is the inadequacy of current criteria for determining taxa: several of the morphological

characteristics traditionally regarded as diagnostic are shown to be invalidated by the extent of overlap of their ranges of variation across taxonomic boundaries, and the assessment by the computer of the relative insignificance of their contribution to the separation of the groups analysed in this study. A fundamental review of potentially diagnostic characteristics is therefore required in order to provide an authoritative and universally acceptable schematic resolution of taxonomic divisions, delimited by readily identifiable criteria which can be applied satisfactorily by non-specialist botanists and general naturalists.

It may be that there is no solution as such to the problems presented by the *Dactylorhiza* group. My studies to date at the perimeter strip in the New Forest, and at other populations elsewhere, tend to indicate an astonishing rate of evolutionary development achieved by these orchids, when prevailing conditions allow hybrid influence to become significant. It may be that their state of evolutionary flux is such that the biological and morphological characteristics of these plants may not remain sufficiently static during the foreseeable future to permit any totally satisfactory schematic resolution of their taxonomy.

Whilst recognising that such a dismal prospect is a possibility, the need to persevere with the avenues of research available to us is compelling: *Dactylorhiza* have presented such problems to botanists for so long that even a partial resolution of a few of the problems would be preferable to the level of utter confusion that has prevailed for so many years. Co-operation between different disciplines in the field may well prove to be one of the most potentially fruitful avenues for the future.

Finally, an important by-product of this research has been the authoritative determination of three populations of *ssp. traunsteinerioides* for the Hampshire flora, two of which (Exbury and Avon Forest) are of what appears to be a form sufficiently distinct to merit varietal status, to be proposed as *var. bowmanii* Jenkinson, named in honour of the BSBI recorder for VC11, who first drew these plants to my attention (R P Bowman pers

comm 1985). These two populations are also significant insofar as they considerably extend the traditional view of the subspecies, both in terms of range of morphological variation, and of its ecological range.

Whilst I do not suggest that this paper will have dispelled any of the major areas of confusion that exist in relation to this enigmatic group of orchids, it may be that a fuller appreciation of the problems faced by *Dactylorhiza* specialists, and of some of the steps currently being taken in an effort to resolve them, will be found to be helpful. Much work remains to be done, but the prospect is full of fascination for the botanists attempting to deal with these challenges.

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Further Reading

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