

## THE 'HEBRIDEAN MARSH-ORCHID': NOMENCLATURAL AND CONCEPTUAL CLARIFICATION OF A BIOLOGICAL ENIGMA

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The 'Hebridean Marsh-orchid' is a controversial dactylorchid taxon currently regarded as endemic to the island of North Uist in the Scottish Hebrides. Re-evaluation of past taxonomic treatments reveals that none of its three names – *Dactylorhiza majalis* (Reichenbach f.) P. F. Hunt & Summerhayes subsp. *scotica* Nelson (1976, 1979), *D. majalis* subsp. *occidentalis* (Pugsley) Soó var. *ebudensis* Wiefelspütz (in Landwehr, 1977), and *D. majalis* subsp. *occidentalis* var. *scotica* (Nelson) R. M. Bateman & Denholm (1983) – has been validly published. We herein legitimize *D. majalis* subsp. *occidentalis* var. *ebudensis* Wiefelspütz ex R. M. Bateman & Denholm, presenting for the first time full details of its lectotype. However, we also note that this nomenclatural clarification has no relevance to determining the most appropriate rank for, and biological significance of, this taxon, which is one of many doubtfully distinct 'critical' taxa of dactylorchids that occur in western and northern regions of the British Isles. Taxonomic opinions expressed on these populations to date have been based on sparse, qualitative, and often contradictory data, and most lacked an explicit conceptual framework. We outline a more rigorous analytical protocol.

### INTRODUCTION

Unusually intense taxonomic scrutiny of the temperate terrestrial orchid genus *Dactylorhiza* Necker ex Nevski has generated many nomenclatural controversies and assured widespread recognition of the dactylorchids as a 'critical group'. Differences of opinion over the delimitation of taxa and their most appropriate ranks have produced a plethora of formal epithets. These in turn have caused many nomenclatural problems related to priority and synonymy, which often reflect ignorance of the existence of relevant epithets, an inevitable consequence of the rapidly inflating taxonomic literature. Such ambiguities are often further compounded by failure to provide all of the obligatory details of type and/or basionym prescribed by the International Code of Botanical Nomenclature (ICBN).

We have attempted to resolve some of the taxonomic controversies surrounding the British and Irish dactylorchids by applying multivariate morphometric methods within an explicit conceptual framework (Bateman & Denholm, 1983, 1985, 1989a–c). Unfortunately, in the first part of our numerical monograph, which assessed the tetraploid marsh-orchid *D. majalis* (Reichenbach f.) P. F. Hunt & Summerhayes (Bateman & Denholm, 1983), we inadvertently propagated one such

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nomenclatural error (D. M. T. Ettlenger, pers. comm., 1986). The problem in question, which usefully illustrates several of the pitfalls commonly encountered in critical group taxonomy, centres on a few early flowering, anthocyanin-rich marsh-orchid populations that occur in coastal habitats of north-west Scotland. They were well described and illustrated in a recent popular monograph of Scottish native orchids (Allan et al., 1993: v, 19, 104–5).

### NOMENCLATURAL HISTORY

Although these controversial populations were discussed informally by Campbell (1936: 551) and Heslop-Harrison (1948, 1954), Nelson's detailed monograph on *Dactylorhiza* contained the first formal description; the plants were assigned to a new subspecies, *D. majalis* subsp. *scotica* (Nelson, 1976: 90). Nelson illustrated the new subspecies using two individuals from the Outer Hebridean island of North Uist (plate 61a–b) and one distinctly different morphotype from the Scottish mainland (plate 61c) but, as noted by several critics, he failed to designate a holotype or specify a type locality. Earlier in the same year, Wiefelspütz (1976: 49) published a field-based report on British and Irish dactylorchids that he had presented orally at the Wuppertal dactylorchid conference in November 1975. He mentioned by name subsp. *scotica* but explicitly deferred its formal description to Nelson. The following year, Landwehr (1977) simultaneously clarified and complicated the taxonomy of these populations. He redrafted as plate 85.3 of his monograph of European orchids one of Nelson's (1976: plate 61a) illustrations of subsp. *scotica*, which was in turn based on a photograph provided by Wiefelspütz (very similar plants, probably from the same locality, were photographically illustrated more recently by Allan et al., 1993: 19, 105). Although aware of Nelson's epithet, Landwehr gave this by now pivotal plant a new epithet, var. *ebudensis*. Using a diagnosis provided by Wiefelspütz, Landwehr (1977: 557) typified this new variety as *D. majalis* subsp. *occidentalis* var. *ebudensis* Wiefelspütz; no synonyms were listed in the diagnosis to acknowledge the existence of the epithet *scotica*. Two years later, Nelson attempted to validate several illegitimate names first used in his 1976 monograph, including *D. majalis* subsp. *scotica* (Nelson, 1979: 593). Ostensibly, the correct epithets for these controversial Scottish marsh-orchid populations then became *scotica* Nelson at subspecific level and *ebudensis* Wiefelspütz at varietal level, creating scientifically unnecessary but nomenclaturally legitimate duplication of epithets.

We then made our own erroneous contribution to this nomenclatural quagmire. Although our three-part revision of the British and Irish dactylorchids (Bateman & Denholm, 1983, 1985, 1989a) entailed re-ranking 17 taxa, in every case this was achieved by recombination of pre-existing epithets; we regard the coining of new epithets for dactylorchid taxa as undesirable in most circumstances. Hence, unaware of the existence of the epithet *ebudensis*, we recombined Nelson's (1979) *D. majalis* subsp. *scotica* as *D. majalis* subsp. *occidentalis* var. *scotica* (Nelson) R. M. Bateman & Denholm (1983: 368).

Unfortunately, both Wiefelspütz in Landwehr (1977) and Nelson (1979) still failed to provide sufficiently detailed accounts of the type to allow valid publication, thereby also invalidating our own new combination via the inadequate basionym (R. K. Brummitt, pers. comm., 1994). Both authors merely referred to the private herbarium of Wiefelspütz and the very generalized locality of North Uist; Nelson (1979) added oblique references to the key specimen illustrated as plate 61a of his 1976 monograph and to 12 mounted flowers of different unspecified individuals shown in his plate 86.8. Thus, neither author provided a specific holotype or type locality, thereby contravening Articles 9.1 and 37.3 of the ICBN.

W. Wiefelspütz (pers. comm., 1994a) kindly provided us with a photocopy of the relevant herbarium sheet. It bore the 12 mounted flowers illustrated by Nelson (1976), together with seven whole plants; all were collected at Lingay Strand, North Uist in June 1974. The specimens were unnumbered, and none was identified as the holotype. In January 1994, at our behest, Dr Wiefelspütz removed from the sheet the whole plant that was illustrated by Nelson (1976, plate 61a) and Landwehr (1977, plate 85.3) and deposited it as holotype (HEID DM 37) in the Heidelberg Botanical Institute (W. Wiefelspütz, pers. comm., 1994b). Thus, after four false attempts, the way is now clear for valid description of the Hebridean Marsh-orchid as a variety of *D. majalis*:

***Dactylorhiza majalis*** (Reichenbach f.) P. F. Hunt & Summerhayes subsp. ***occidentalis*** (Pugsley) Soó var. ***ebudensis*** Wiefelspütz ex R. M. Bateman & Denholm.

Original diagnosis: W. Wiefelspütz in J. Landwehr, 1977, *Wilde Orchideeën van Europa*, p. 557.

Lectotype (chosen here): Scotland, North Uist, Lingay Strand, in dunes near Newton Hotel, 4 vi 1974, *W. Wiefelspütz* DM 37 (HEID). Figs: E. Nelson, 1976, *Monographie und Ikonographie der Orchidaceen-Gattung Dactylorhiza*, plate 61a; J. Landwehr, 1977, *Wilde Orchideeën van Europa*, plate 85.3 (p. 195). Iso.: Private herbarium of W. Wiefelspütz; six whole plants and 12 dissected flowers, mounted together on a single sheet.

Etymology: Derived from the Latin *ebudes*; Hebridean islands.

Invalid names: *D. majalis* subsp. *scotica* Nelson (1976, *Monographie und Ikonographie der Orchidaceen-Gattung Dactylorhiza*: 90 and plates 61a–c, 86.8); *D. majalis* subsp. *occidentalis* var. *ebudensis* Wiefelspütz in Landwehr (1977, *Wilde Orchideeën van Europa*: 557 and plate 85.3); *D. majalis* subsp. *scotica* Nelson (1979, *Taxon* 28: 593); *D. majalis* subsp. *occidentalis* var. *scotica* (Nelson) R. M. Bateman & Denholm (1983, *Watsonia* 14: 368).

We have preferred *ebudensis* to *scotica* because the epithet (1) was the earlier to be applied at varietal rank, (2) more accurately describes the distribution of the Hebridean Marsh-orchid as currently perceived, and (3) is favoured by W. Wiefelspütz, the photographer and collector of the type specimen that was the

TABLE 1. Comparison of quantitative characters presented in the diagnoses of *D. majalis* subsp. '*scotica*' (Nelson, 1976: 90–91) and *D. majalis* subsp. *occidentalis* var. *ebudensis* (Wiefelspütz in Landwehr, 1977: 557). Note that both descriptions are based on the same field population (ND=data not provided; all measurements are in mm).

Character	<i>scotica</i>	<i>ebudensis</i>
<i>Vegetative</i>		
Stem height	(60–)90–110(–140)	60–100
Total number of leaves	3–4(–5)	4(–5)
Leaf width	10–14	ND
Inflorescence length	ND	60
Inflorescence width	ND	30
<i>Floral</i>		
Labellum length	6–7(–8)	6
Labellum width	8–10(–11)	10
Spur length	7–8(–10)	ND
Spur width	3	ND

basis of both epithets. At subspecific rank, *scotica* would be the earlier and hence perhaps more appropriate epithet for the Hebridean Marsh-orchid, though of course it would require validation in the same manner as var. *ebudensis*.

### TAXONOMIC AND BIOLOGICAL IMPLICATIONS

We are satisfied that the epithets *ebudensis* and *scotica* are based on the same type specimen, collected by Wiefelspütz from an inter-dune depression in North Uist and illustrated, without sight of living material, in the monographs of Nelson (1976) and Landwehr (1977). This taxonomic parallelism makes comparison of the characters put forward to delimit *ebudensis* and *scotica* particularly interesting, as the numerous contrasts and ambiguities can only reflect different perceptions of the same reality: (1) many characters are mentioned in only one of the two diagnoses; (2) most of the characters mentioned in *both* diagnoses are described qualitatively rather than quantitatively, with the two authors drawing descriptive terms from substantially different vocabularies; (3) Nelson (1976) provided data for seven quantitative characters and Landwehr (1977) for six, but only four – stem height, total leaf number, labellum length and labellum width – are common to both descriptions and thus can be compared (Table 1); (4) even these figures can only be compared in ignorance of the sample sizes or methods of measurement used; (5) although values for these four parameters are broadly similar in the two publications, none coincides precisely (Table 1). Together, these observations underscore the need for further detailed morphometric study of these problematic populations.

In short, unravelling the legalistic aspects of this nomenclatural problem has little bearing on deeper, more biological ramifications of the controversies surrounding these plants. All of the above taxonomic statements (including our own) were made

without detailed scientific investigation of the populations in question, driven by the commonly held desire to include and classify all relevant taxa within a monographic treatment. Even when hard data are available, the comparability of different types of data is weak and even that of similar data acquired by different researchers is questionable (cf. Bateman & Denholm, 1989b; Roberts, 1989; Jenkinson, 1992). Also, different authors often express contrasting opinions of the appropriate definitions for different taxonomic ranks (e.g. Hamilton & Reichard, 1992). More frequently, and more worryingly, authors express no opinion at all on these key conceptual issues (e.g. Lowe et al., 1986; Kenneth et al., 1988; Foley, 1990; Allan et al., 1993).

### MORPHOMETRIC AND GENETIC CONCEPTS OF INFRASPECIFIC TAXA

We advocate a large-scale census approach to acquisition of both morphological (e.g. Bateman & Denholm, 1983, 1985, 1989a–c) and molecular (e.g. Nybom & Schaal, 1990; Davis & Manos, 1991; Davis & Nixon, 1992) data for delimiting species and infraspecific taxa. We define morphological species as aggregates of populations whose individual members are reliably distinguishable from members of all other comparable populations; such morphospecies are separated by morphological discontinuities on multivariate ordinations. We also define subspecific and varietal ranks primarily through morphometric comparison of populations using individuals as the basic analytical entities, but within species these lesser ranks show morphological overlap. The two infraspecific ranks are similar concepts but differ in the greater degree of overlap and the lesser predictivity of distinguishing characters in the variety relative to the subspecies (Bateman & Denholm, 1989a, c; see also Stuessy, 1990: 189). By contrast, we perceive the forma as qualitatively different from the variety, assigning to this rank individuals that are readily distinguished by a few prominent characters from other individuals occurring in *the same* geographically and ecologically restricted population (ecotopodeme sensu Gilmour & Heslop-Harrison, 1954). Notable examples among the dactylorchids include extreme states of certain pigmentation characters, such as anthocyanin-lacking albinos on the one hand and anthocyanin-rich plants on the other.

Many other workers ignore the rank of forma, preferring to apply concepts analogous to those underlying our forma in the delimitation of varieties, including the anthocyanin-high modes of *D. fuchsii* (Druce) Soó and *D. majalis* subsp. *purpurella* (T. & T. A. Stephenson) D. M. Moore & Soó informally described by Bateman & Denholm (1989a) and formally diagnosed as varieties by Ettliger (1991). Such conceptual disagreements are unavoidable in systematics and, provided they are carefully explained, cause little damage at infraspecific levels. Rather, most of the many controversies in dactylorchid taxonomy stem from the failure to consider such conceptual foundations and/or from unwarranted reliance on 'specialist's intuition' as a basis for alpha-taxonomy.

This point is well illustrated by the recent histories of *D. majalis* subsp. *occidentalis* var. *ebudensis* and its dominantly Welsh analogue *D. majalis* subsp. *occidentalis* var. *cambrensis* (R. H. Roberts) Bateman & Denholm (Roberts, 1961, 1966; Bateman & Denholm, 1983). *Dactylorhiza majalis* subsp. *occidentalis* was reported from widely scattered localities in western and northern Scotland by Summerhayes (1968), Perring & Walters (1976) and Lang (1980), but in the recent monograph by Allan et al. (1993) it has retreated to North Uist, the type locality of var. *ebudensis* ("*D. majalis* subsp. *scotica*" of Allan et al.). Rather than indicating a recent catastrophic decline in geographic distribution, this actually reflects taxonomic re-assignment of most of these populations to *D. majalis* subsp. *occidentalis* var. *cambrensis* (arguably "*D. purpurella* subsp. *majaliformis* Nelson" of Allan et al.) and *D. majalis* subsp. *lapponica* (Laest. ex Hartman) Sundermann ("*D. lapponica* (Laest. ex Hartman) Soó" of Allan et al.). We regard these controversial taxonomic depredations as justified; indeed, they were advocated many years earlier by Wiefelspütz (1976). The residuum that remains assigned to "*D. majalis* subsp. *scotica*" by Allan et al. (1993) is confined to perhaps three dune systems on the Hebridean island of North Uist (cf. Pankhurst & Mullin, 1991). Can subspecific recognition of such a geographically and ecologically restricted taxon be justified?

The few ecotopodemes that comprise var. *ebudensis* are characterized in the literature as vegetatively compact and anthocyanin-rich. Flowers are dark purple-violet; bracts and stems are suffused with anthocyanins, which tend to coalesce into large, apically concentrated blotches on the adaxial surfaces of the leaves. Flowering occurs in late May and early June, somewhat earlier than the co-existing *D. majalis* subsp. *purpurella*.

Such vegetative reduction characterizes all dactylorchid taxa that grow in these exposed machair habitats, including co-occurring populations of *D. majalis* subsp. *purpurella* and *D. incarnata* (L.) Soó subsp. *coccinea* (Pugsley) Soó; it is probably at least partly caused by ecophenotypic dwarfing. In our opinion, the characters reflecting anthocyanin richness could justify varietal status if distributed reasonably homogeneously throughout the populations – that is, if the anthocyanin-rich individuals figured by Nelson (1976), Landwehr (1977) and Allan et al. (1993) are typical. However, in our experience, type specimens of dactylorchids rarely correspond to the median morphology of the source population; morphological extremes are collected in preference as they appear more distinct. It could be argued that the widespread occurrence of less anthocyanin-rich individuals of *D. majalis* subsp. *occidentalis* on North Uist (P. S. Lusby, pers. comm., 1993) justifies the relegation of *ebudensis* to forma, analogous to the anthocyanin-rich morphs that occur sporadically in populations of many other dactylorchid species and subspecies (cf. Nelson, 1976; Landwehr, 1977; Bateman & Denholm, 1989a; Ettliger, 1991).

Certainly, a broader comparative viewpoint allows a more balanced taxonomic treatment. All four dactylorchid species native to the British Isles (*D. fuchsii* (Druce) Soó, *D. maculata* (L.) Soó, *D. incarnata*, *D. majalis*) include 'boreal' morphological 'facies' that have disjunct westerly and/or northerly distributions, and only those of

*D. maculata* have largely escaped formal description (Bateman & Denholm, 1983, 1985, 1989a). The most likely explanation for the origin of these facies lies in neo-Darwinian microevolution, reflecting adaptive responses to local selection pressures (e.g. Dawkins, 1986; Ridley, 1993). Each such taxon is probably polytopic, having evolved independently in many localities (rather than once in a single locality, followed by widespread dispersal from the point of origin). The isolation of local ecotopodemes within these facies allows further diversification, perhaps slowly by random genetic drift (e.g. Kimura, 1983) or more rapidly by shifting balance (e.g. Wright, 1968; Levin, 1993). Both processes would be aided by small population sizes such as those of var. *ebudensis* in the dune machair of North Uist. A continuum of form within such facies is inevitable, and is well reflected in the reports of Allan et al. (1993) of intermediates among "*D. majalis* subsp. *scotica*", "*D. purpurella* subsp. *purpurella*" and "*D. purpurella* subsp. *majaliformis*". 'Subsp. *majaliformis*' has in turn already been recognized as morphologically overlapping both subsp. *occidentalis* and subsp. *purpurella* (Bateman & Denholm, 1983). Alternatively, polytopic origins of putatively tetraploid dactylorchid taxa such as var. *ebudensis* could represent iterative saltational origins by polyploidy (e.g. Bateman & DiMichele, 1994). In summary, we believe that such limited genetic differentiation should not be over-inflated taxonomically.

However, we conclude by noting that any objectivity inherent in such taxonomic decisions could be compromised by the fact that taxa of rank lower than subspecies do not qualify for national conservation protection in Britain (cf. Perring & Farrell, 1983). Thus, the future existence of the 'Hebridean Marsh-orchid' could in theory depend on whether it is referred to *D. majalis* subsp. *scotica* (which remains invalid) or *D. majalis* subsp. *occidentalis* var. *ebudensis* (validated herein).

## CONCLUSIONS

Future taxonomic treatments of dactylorchids (and many other critical groups) would benefit from closer adherence to the following general principles:

(1) Taxonomic descriptions (and revisions) should be based on comparison of individuals and populations using large-scale, census-style databases.

(2) The criteria used to define each taxonomic rank used should be explicitly stated, preferably encompassing not only the observed phenotypic variation of the taxon but also its underlying genetic cause(s).

(3) Wherever possible, existing epithets should be recycled when re-ranking and/or re-diagnosing taxa, to avoid burdening the literature with superfluous new epithets.

(4) As has long been recognized, only arduous searches for existing epithets and careful diagnosis within the stringent legal constraints of the ICBN can minimize convoluted nomenclatural histories such as that of *D. majalis* subsp. *occidentalis* var. *ebudensis*. As this study demonstrates, compound errors can be very difficult to unravel.

(5) In a situation where coining a new epithet *can* be justified, the chosen holotype should represent the median morphology of the individuals in the ecotopodeme

rather than being atypically distinctive. Conservation interests permitting, the holotype should be supported by several paratypes that illustrate the range of phenotypic variation present in the type population. However, even large numbers of dried pressed specimens are no substitute for a rigorous morphometric database, supported by fixed-magnification colour photographs.

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