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Cover Photographs

Front Cover: Malcolm Brownsword’s *Calanthe tsoogiana,* winner in Class 13 of the HOS Plant Show 2018, photographed by Jon Evans. See full Plant Show report on page 77.
Back Cover: John Haggar’s photograph of a Sutton Fen Marsh-orchid. See article on page 85.

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The Hardy Orchid Society

Our aim is to promote interest in the study of Native European Orchids and those from similar temperate climates throughout the world. We cover such varied aspects as field study, cultivation and propagation, photography, taxonomy and systematics, and practical conservation. We welcome articles relating to any of these subjects, which will be considered for publication by the editorial committee. Please send your submissions to the Editor, and please structure your text according to the "Advice to Authors" (see Members' Handbook, website www.hardyorchidsociety.org.uk, or contact the Editor). Views expressed in journal articles are those of their author(s) and may not reflect those of HOS.

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Editorial Note

Mike Gasson

Slightly unusual issue this time in that it is dominated by results from the 2018 Plant Show and a major article on Marsh-orchids. The plant show winners this year were photographed by our photographic competition judge Jon Evans and with such a lovely set of image files it seemed worthwhile to include a good number of them here.

It was also an opportunity to give some space to the orchid cultivation side of the society that sometimes can get a bit neglected in *JHOS*. John Haggar was a major contributor when I started as Editor and contributed a series of authoritative articles describing his experiences of, and insights into, the Early Marsh-orchid. Also, some members, taking advantage of earlier HOS field trips, will have experienced the confusing population of *Dactylorhiza* plants that share the Fen Orchid habitat at Norfolk's Sutton Fen. Hence it is good to have John's detailed article that includes his analysis of these plants. It is unusual to have someone with the experience of this group in the field in diverse geographical areas and also first hand knowledge of the results of inter-species crosses. Although John's older articles can be found amongst the pdf journals on the HOS website I will aim to extract the individual articles as a collection so that they can be accessed with greater ease on the website.

Chairman's Note
Colin Scrutton

The 25th Anniversary meeting on April 15th was a great success. We had an excellent and varied series of presentations and our President, Richard Bateman's Anniversary Keynote Lecture provided much food for thought. It seems that we must radically rethink species definitions in the genus *Ophrys* and I await the publication of the relevant paper with very great interest.

There was also a fine range of orchids displayed in the Plant Show. Photographs of the winning exhibits can be found elsewhere in this journal. Before judging began, Barry Tattersall kindly presented the Society with a new Best in Show trophy – and promptly won it! The old trophy had run out of room for the winners' names to be engraved and as Barry's had featured prominently, the Committee had decided that the old trophy should be presented to him to keep in perpetuity.

A trend has arisen for members to book quite late for our meetings, both at Kidlington and Leeds. This can create difficulties for the meeting organisers. Clearly we do not wish to discourage members from attending the meetings and in some cases there may be a very good reason for a late booking. But please remember that the organisers are amateur orchid enthusiasts who volunteer their time for the benefit of the Society so please do your best to help them by submitting your booking form well in advance of the closing date. And if you do have to leave it to the last minute, don't expect a lunch to be available!

We need members to come forward to serve on the Committee. There are a number of posts which will become vacant in the near future, including Plant Show Secretary, Kidlington Meetings Organiser and, slightly further ahead, Organiser of the sound system at meetings, electrical safety checks and Leeds Meetings Organiser. Further details of what is involved in each case can be found by contacting the present post holder. Any member with an interest in taking on one of these important posts please let me know by email (Colin.Scrutton@dunelm.org.uk).

I am writing this as the domestic orchid season is just beginning, delayed by the spell of unusually cold weather earlier in the year. In addition, some of the sites we have visited so far have a much sparser flowering than in previous years. Whether this will be rectified in time remains to be seen. By the time you read this, there will be not much more than a month left for our domestic orchids.

We do have a very short and concentrated flowering season in the UK. We'll miss a good chunk of it this year with a longish trip to Australia, where we hope to photograph some of their late winter flowering orchids. Around 150 species flower there during June and July, including many Greenhoods and several Helmet Orchids, in which we are particularly interested.

Meanwhile, I hope those of you with an interest in video are preparing short video clips suitable for the Video Competition to be held at the Leeds meeting in September. Steve Pickersgill, the Competition Organiser, included a box in the last journal with details of the competition and the deadline for entries (*JHOS* 15, 2, p.48). I look forward to a good turnout at Leeds and some excellent orchid videos for the audience to admire and vote on to decide the winner of the Tony Hughes trophy.

Results of HOS Plant Show 2018

Class 2: Three pots native European (not native to Britain) orchids, distinct varieties
1st Barry Tattersall: *Ophrys balearica* (Fig. 5); *Neotinea lactea* (Figs. 16 & 17); *Ophrys sitiaca*

Class 3: Three pots non-European hardy orchids, distinct varieties
1st Mike Powell: *Pleione grandiflora* (Fig. 11); *Cymbidium goeringii* (Fig. 9) *Cypripedium formosanum* (Fig. 12)
2nd Malcom Brownsword: *Pleione* Dr Mo Weatherhead; *Pleione grandiflora* “cream”; Pleione Masaya

Class 4: Three pots hardy orchids, distinct varieties, any country of origin
1st Barry Tattersall: *Serapias neglecta* × *lingua* (Figs. 14 & 15); *Anacamptis boryi*; *Ophrys vernixia* (Fig. 6)

Class 5: One pot native British orchid
1st Barry Tattersall: *Anacamptis laxiflora*

Class 6: One pot native European (not native to Britain) orchid
1st Barry Tattersall: *Orchis brancifortii* (Figs. 1 & 2)

Class 7: One pot non-European orchid
1st Malcolm Brownsword: *Calanthe lamellose* × *yuana* (Figs. 3 & 4)
2nd Barry Tattersall: *Anacamptis morio* ssp. *caucasica*

Class 8: One pot *Dactylorhiza*
1st Barry Tattersall: *Dactylorhiza romana*

Class 9: One pot *Orchis*, *Anacamptis* or *Neotinea*
1st Barry Tattersall: *Orchis italica* (Fig. 10)
2nd Malcolm Brownsword: *Anacamptis morio* × *longicornu*

Class 10: One pot *Ophrys*
1st Barry Tattersall: *Ophrys bombyliflora* (Fig. 8)

Class 11: One pot *Serapias*
1st Mike Powell: *Serapias neglecta* × *orientalis* × *neglecta* (Fig. 13)
2nd Barry Tattersall: *Serapias bergonii*

Class 12: One pot *Cypripedium*
1st Mike Powell: *Cypripedium formosanum*

Class 13: One pot Calanthe
1st Malcolm Brownsword: *Calanthe tsoogiana*

Class 14: One pot Pleione
1st Malcolm Brownsword: *Pleione grandiflora* "cream" (Fig. 18)

Class 15: One plant or pan of plants raised from seed by the grower
1st John Haggar: *Ophrys fusca* × *reinholdii* (Fig: 7)
2nd John Haggar: *Ophrys tenthredinifera* × *reinholdii*

Winner of Best in Show Trophy:
Barry Tattersall for *Orchis brancifortii* in Class 6

Winner of Chairman's Trophy:
John Haggar for *Ophrys fusca* × *reinholdii*

Most Points & Winner of RHS Banksian Medal:
Barry Tattersall

Thanks to Nick Fry for judging the Plant Show

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Fig. 18: *Pleione grandiflora* "cream" (Malcolm Brownsword in Class 14)

Photos by Jon Evans

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The Early Marsh-Orchid in Northern Europe: One Decade On

John Haggar

Introduction

Between 2003 and 2007, I published a personal view of the Early Marsh-orchid, *Dactylorhiza incarnata,* in *JHOS* (Haggar, 2003a; 2003b; 2004a; 2004b; 2005a; 2005b; 2007). The series of articles was based on an extensive literature search, cultivation experiments and my own observation of the species both here in the British Isles and on the other side of the North Sea in Scandinavia, particularly in southern Sweden and the Baltic Islands of Öland and Gotland. Öland, in particular, figured largely in Linnaeus's original description of the Early Marsh-orchid, initially as *Dactylorhiza (Orchis) latifolia*, and later as *Dactylorhiza* (*Orchis*) *incarnata*.

The last published article, which focussed on flesh pink-flowered morphs, was originally meant to be my penultimate offering but due to circumstances beyond my control the series ended precipitously in 2007, leaving unanswered many questions that I had earlier posed. I like to think that my contribution hitherto though, is in part the reason that many knowledgeable botanists now have decided to refer to the former subspecies of the Early marsh-orchid as varieties and to acknowledge that this varietal status infers no genetic integrity to the described "types" but is often based largely on their predominant flower colour.

I am disappointed, however, at the decision of many of the British botanists to retain the variety *pulchella* to describe all the British and Irish purple-flowered *D. incarnata* with unmarked leaves, especially when many of these plants, particularly those found in fen habitats in East Anglia and Ireland share their morphology in most other respects than flower colour with plants that could otherwise be termed var. *incarnata*. Indeed, in Scandinavia from which the species was first formally described by Linnaeus, this is the recognised nomenclature. According to Swedish botanists, var. *incarnata* is usually purple-flowered, sometimes lilac and more rarely pink. It was Heslop-Harrison who in 1956 assembled all British and Irish Early Marsh-orchids with purple flowers and unmarked leaves (except inconsistently for purple-flowered specimens of his var. *gemmana*) into the subspecies *pulchella* for reasons of "expediency", even though he clearly acknowledged at the time that "the assemblage is homogenous in relation to no other phenotypic feature of those which have been studied" (Heslop-Harrison, 1956). I agree with Bateman and Denholm's assessment of the Early Marsh-orchid in that all purple-flowered individuals contain purple and red anthocyanin pigments and probably also yellow anthoxanthin (Bateman & Denholm, 1985).

It is indicative to me that the violet-purple flower colour bestowed by this combination of pigments expressed in high concentration is a primitive state for *D. incarnata* and that the other flower colours seen are derived from it, either by dilution or exclusion of one, two or all of these pigment classes. The fact that Heslop-Harrison found such a high degree of morphological variation in his purple-flowered cohort supports this hypothesis. In addition, it has been shown that on Gotland it is the purple-flowered plants with unblotched (i.e. non-cruenta) leaves that span the entire spectrum of genetic diversity seen in all the other morphs combined (Hedrén & Nordström, 2009). Although it should be accepted that the species is evidently potentially highly polymorphic for flower colour in general, I hope to be able to offer some explanations regarding why, in certain circumstances and situations, flower colours other than purple appear to come to predominate. I also hope to be able to demonstrate reasons why the dichotomy in nomenclature on either side of the North Sea has persisted. Furthermore, I shall be discussing and adding some more detail to propagation experiments that I carried out with *Dactylorhiza* hybrids more than ten years ago, some of the results of which were presented as a lecture to the Hardy Orchid Society in 2006 and formally reported in part some years later (Haggar & Malmgren, 2012). In addition, some novel observations and results will be included.

Pollinator preferences in food-deceptive *Dactylorhiza* species

The Marsh-orchids of the genus *Dactylorhiza* have non-rewarding, nectar-less flowers which attract their pollinators, mainly bumblebees, by deception. It is generally thought that early flowering temperate orchids are typically pollinated by naïve, newly-emerged bumble bees attracted mainly by the conspicuous flower colour of the orchids, before they have learned that the blooms offer no nectar reward. In addition, it may be that in the case of later flowering species (such as the midsummer flowering *Dactylorhiza incarnata* in Sweden), older bees are additionally duped into visiting *Dactylorhiza* flowers by the orchid exhibiting a floral resemblance to nearby nectar-rich flowers that they have previously and recently visited. Such a situation has been seen in the case of *Anacamptis morio* in Sweden where the orchid is pollinated more successfully when it grows in the presence of the similarly coloured but highly nectar-rewarding *Allium schoenoprasum* (Johnson *et al.*, 2003). Nearly all dactylorchids appear to be unscented (*Dactylorhiza umbrosa* does have a weak, *Gymnadenia*-like scent but its comparatively long spur is probably an indication that its most common pollinators are not actually bees), so the smell of the flowers is unlikely to play an important role. Furthermore, the colour violet-purple, which in various states of dilution or concentration is the flower colour of most *Dactylorhiza* species, is the colour for which bumblebees have been shown to have the greatest innate preference (wavelengths 400 - 420nm) (Gumbert, 2000). In southern Germany, and most likely elsewhere, violet-purple flowers are more nectariferous than those of other colours, possibly explaining why this flower colour should be favoured by food deceptive orchids, like *Dactylorhiza* Marsh-orchids (Raine and Chittka, 2007).

Foraging bumblebees demonstrate a high degree of constancy for protracted periods of many minutes as far as the colour of the blooms that they visit is concerned (Gegear

& Laverty, 2005). In an experimental model using naïve bees and specimens of the mainly dimorphic (for flower colour) *Dactylorhiza sambucina*, it has been shown that repeated fruitless visits to flowers of a more favoured colour (yellow) will cause the pollinators to shift to a less favoured one (red). Innate colour preferences are believed to be the most important driving force in naïve, inexperienced bumblebees. The frequency of the shifts was shown to depend on the proportions of each colour morph in any particular population. Thus, the rarer the less common red form, the greater the chance that a red flowered morph will be visited by a naïve bee. This "negative frequency-dependent selection" is the reason that populations of *D. sambucina* tend to stabilise throughout the Continental distribution of the species at about 70% yellow flowered and 30% red (Gigord et al., 2001). A similar phenomenon is likely to be working in polymorphic populations of *D. incarnata*, but in the case of this species, dark violet-purple is the most favoured innate pollinator flower colour so proportions would be expected to differ from those seen in the Elder-flowered Orchid and purple would be expected to be the commonest flower colour. Unlike the case of *D. sambucina*, however, proportions of different colour forms of Early Marsh-orchid in northern and western Europe are extremely geographically variable and some undetermined factors other than "negative frequency-dependent selection" must be acting additionally upon them.

What evolutionary pressures, though, would cause whole populations of predominately purple-flowered dactylorchids to abandon the preferred flower colour of the genus and successfully evolve into plants with a seemingly much less attractive flower colour (to bumblebees) such as ivory (*D. incarnata* var. *ochroleuca*), crimson-red (*D. incarnata* var. *coccinea*) or pale pink (*D. incarnata* var. *incarnata* in the English sense)? I have already suggested in a past article that *D. incarnata* var. *ochroleuca* may have adopted a novel pollinator, possibly a crepuscular lepidopteran, by virtue of its yellowish-white flowers which are more visible in the half-light of dawn and dusk than are other *D. incarnata* varieties (Haggar, 2005b). Certainly, var. *ochroleuca* in parts of Scandinavia does appear to maintain a certain genetic integrity separate from other varieties, suggesting that it does not cross as freely with other coloured flowers as it does with its own kind (Hedrén & Nordström, 2009).

Red, however, is a colour that has been reported to be invisible to some bumblebee species, although in reality inconspicuous is probably a better description (Chittka & Waser, 1997). It is also important to accept that some flowers that appear red to us may also reflect light in the UV part of the spectrum; this is visible to bees and so the flowers appear quite different to them than they would to human eyes. In many tropical plant species, though, red flower colour is heavily associated with pollination by birds, not bees, such is the degree of avoidance demonstrated by the latter to the colour. What is the advantage in being a *Dactylorhiza incarnata* population with entirely red or pale red (flesh-pink) flowers? The red flower colour of some *D. sambucina* individuals has already been discussed and has been shown to persist by virtue of the rewardless state of the mainly yellow flowers and the naïvety of the pollinators, but the proportion of red-flowered plants is always much lower than that of the yellow ones. Red is apparently more visible to bumblebees in less heavily foliated environments, possibly partially explaining why the colour is present in the spring-flowering *D. sambucina* and in British/Irish dune forms of *D. incarnata* (both situations in which surrounding vegetation is low), but what might the evolutionary pressures be that caused the latter to arise in the dune systems of northern Britain and Ireland but not in similar environments on the near continent and Scandinavia (Rivest *et al*., 2017)?

Why is it that in southern England pale pink forms of the Early Marsh-orchid flower somewhat earlier and in completely different environments than supposedly more attractive (to pollinators) purple forms? Why do these pink-flowered plants grow as whole populations, rather than just as occasional individuals in a polymorphic population as they do in the Baltic Islands? Can it be explained, moreover, why many British sites for *D. incarnata* outside southern England contain contemporaneously blooming pink and purple individuals in proportions that appear to contradict the “most favoured for pollinators” state of the purple flowers? A Nordic study into pale (pink) and dark (purple) morphs of *Dactylorhiza maculata* identified a clear bumblebee preference for the darker coloured flowers although each colour form exhibited equal reproductive success, causing the authors to postulate the existence of an alternative, balancing, possibly night-time pollinator (Kolvisto *et al*., 2008). Perhaps this phenomenon occurs in pink-flowered morphs of *D. incarnata* too, but I know of no other evidence to support such an idea. Naïve bees are more likely to pollinate the first flowers to open, but surely such a trend could not explain the emergence of entire populations of early blooming, pink-flowered plants at the expense of purple ones in the fens of southern England and the near continent (Tremblay, 2005).

It is my contention that pure populations of red- and pink-flowered Early Marsh-orchids have evolved as a positive result of not being attractive to the bees that are foraging purple-flowered plants. Their evolutionary strategy is not to look red or pink but rather to avoid looking purple.

Crossing experiments with marsh orchids and the polymorphic population at Sutton Fen

As alluded to at the end of my 2007 article (Haggar, 2007), I have long believed that ongoing interactions between *Dactylorhiza incarnata* and various species of *incarnata*-containing allotetraploid marsh-orchids have a profound effect on the former species. My suspicion that this may be the case arose when I first started cultivating *Dactylorhiza* species from seed and growing the plants in a greenhouse

Fig. 1: Bumblebee visiting a cultivated specimen of *D. majalis* in the glasshouse. Pollinia are visible on the bee's head.
Photo by John Haggar

setting in the 1990s. On many occasions I witnessed bumblebees quite promiscuously visiting species after species in the glasshouse. A mixture of (purple-flowered) *D. incarnata*, *D. majalis* and *D praetermissa*, plus hybrids between them and *D. fuchsii* were flowering together and the pollinators quite happily visited plant after plant with no regard to species. Pollen bundles were frequently removed and the bumblebees often would fly away carrying pollinaria detached from several species and hybrids. I now grow my *Dactylorhiza* plants outside in large plunge beds and I have frequently witnessed the same bumblebee behaviour in this setting too. I have long since ceased to grow any seed set naturally from my collection as it never seems to develop true to the mother plant! The pollinating insects do not appear to make any distinction between different species in my cultivated setting and my strong suspicion is that this is the case in wild situations too. Several studies have shown that bee pollinators switch much more readily between plant species with similarly coloured flowers than they do between flowers of similar structure but different colour (Goulson, 2012, p.120). Indeed, it appears that in most cases the decision by a bumblebee to visit a particular *Dactylorhiza* flower is based on flower colour alone; the pollinators appear to be blind to the slight differences in floral morphology between species and hybrids.

If inability to distinguish between orchid species is the general rule in dactylorchid pollinators and they are primarily attracted by purple flower colours, then it seems eminently reasonable to postulate that random and frequent pollinator interactions would occur between diploids and tetraploids that are of similar (purple) flower colour and that have at least partially overlapping flowering periods.

Considering that cross-pollination between a diploid and a tetraploid *Dactylorhiza* invariably produces seed that is fully fertile according to my own experimental crosses, and if pollinator promiscuity is real in the field, one is tempted to ask why hybrid plants are not more commonly reported in mixed populations. In one such East Anglian population that I have had the good fortune to be able to visit for the last few summers on the south side of Sutton Fen in Norfolk, pink- and purple-flowered Early


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Marsh-orchids (both of which I would personally call var. *incarnata* in view of their identical morphology apart from flower colour) bloom in the company of what are probably mainly Southern Marsh-orchids. Although standard Early Marsh-orchids are the commonest and most easily identified component in this fen community, the population as a whole is highly polymorphic and many atypical forms can be found. Still extant here are some robust pink-flowered *D. incarnata* with a somewhat *praetermissa*-like labellar shape and patterning - the so-called var. *gemmana*, which were described in pink- and purple-flowered morphs from the north side of the same fen by Heslop-Harrison (1956). Chromosome counts made at the time clearly identified these unusual plants as diploid *D. incarnata*. On my first visit to the site, I also found a few tall, dark purple-flowered individuals with *praetermissa*-like flowers but with foliage that was typical of *D. incarnata*. Extended floral bracts and long, slender, erect leaves reaching up as far as the base of the flower spike with markedly hooded leaf tips are clearly a feature of *D. incarnata*, not *D. praetermissa*. Might these plants be hybrids or did they represent, perhaps, a remnant of Heslop-Harrison's purple-flowered var. *gemmana*? If the latter, their stature, morphology and flower colour would surely make them prime candidates to be hybridised with co-flowering *D. praetermissa* by a promiscuous bumble bee. Robust *D. incarnata* varieties are well known elsewhere in the area of distribution of the species; below I have pictured a rather pale-coloured specimen of Swedish *D. incarnata* var. *latissima* from Gotland (Fig. 6) and opposite for the sake of comparison typical *D. incarnata* var. *incarnata* and possible *D. incarnata* var. *gemmana* from Sutton Fen (Figs. 2-5). These robust forms all appear to share labellar markings that could be described loosely as "exploded" loops and lines.

Fig. 2: A typical pink-flowered specimen of *D. incarnata* var. *incarnata* at Sutton Fen.
Fig. 3: A typical purple-flowered specimen of *D. incarnata* var. *incarnata* at Sutton Fen.
Fig. 4: Possible pink-flowered *D. incarnata* var. *gemmana* at Sutton Fen.
Fig. 5: Possible purple-flowered *D. incarnata* var. *gemmana* at Sutton Fen.
Fig. 6: *D. incarnata* var. *latissimia* at Gotland, Sweden.

Photos by John Haggar

Dactylorhiza ×*wintoni* is the name given to the hybrid between *D. praetermissa* and *D. incarnata*. I have grown this hybrid from seed on several occasions, once using a pink-flowered *D. incarnata* var. *coccinea* (I would prefer to call it var. *dunensis*) as the mother plant and *D. praetermissa* as the pollen donor. On another occasion, the seed parent was *D. praetermissa* and pollen from Scandinavian specimens of *D. incarnata* forma *cruenta* and *D. incarnata* var. *ochroleuca* were used to fertilise the flowers. The plants were grown to flowering size and in all cases the orchids bore foliage typical of *D. praetermissa* rather than *D incarnata*. The hybrids had relatively broad, spreading leaves with the basal leaves failing to rise up to the base of the flower spike. None of the plants bore typically *incarnata*-like foliage. (Interestingly, a proportion of the *D. praetermissa* × *incarnata* forma *cruenta* specimens had leaves blotched on both sides, perhaps suggesting that there are unexpressed genes for bilateral leaf blotching buried somewhere in the *D. praetermissa* genome.) A minority of the flowers exhibited the loop and line patterns characteristic of *D. incarnata* to a greater or lesser extent. The rest were almost perfect copies of standard *D. praetermissa* and despite the fact that their floral bracts were sometimes longer than those of their *D. praetermissa* parent, they would be indistinguishable from "genuine" *D. praetermissa* in the wild. In this respect, *D.* ×*wintoni* is quite unlike *D.* ×*grandis* (the hybrid of *D. praetermissa* and *D. fuchsii*) which is clearly identifiable as being intermediate between the two parents and often exhibits more marked hybrid vigour. So the main reason that *D.* ×*wintoni* is not more commonly identified in mixed populations is that it is largely indistinguishable from the Southern Marsh-orchid.

Close examination of the *D. praetermissa* population at Sutton Fen reveals that there are indeed orchids that might casually be assumed to be Southern Marsh-orchids but that do exhibit *incarnata*-type floral patterns and could really be specimens of *D.* ×*wintoni*. If so, my experiments would indicate that for each plant with such an appearance there is likely to be at least one more plant of *D.* ×*wintoni* that is completely indistinguishable from *D. praetermissa*. My failure to produce any hybrids with *incarnata*-type leaves leads me to think that these are not robust diploids. Plants with *praetermissa*-like flowers and clearly *incarnata*-like foliage, however, could well be purple-flowered diploid var. *gemmana*. Marginal bract-cell shape and size could offer a (weak) test of this hypothesis. Another feature of the *D. praetermissa* population

Fig. 7: *D. incarnata* parent of the *D.* ×*wintoni* hybrid in Figs. 8 & 9.
Fig. 8: Cultivated *D.* ×*wintoni* from *D. incarnata* var. *coccinea*/*dunensis* (seed parent) × praetermissa (pollen parent). This specimen exhibits a *praetermissa*-like labellar patterning.
Fig. 9: Another example of the same hybrid but exhibiting an *incarnata*-like pattern.
Fig. 10: Cultivated *D.* ×*wintoni* from *D. praetermissa* (seed parent) × *D. incarnata* forma *cruenta* (pollen parent). This hybrid had bilaterally blotched leaves.

Photos by John Haggar

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here is that their flowers are frequently of a very much darker purple hue than might be expected of *D. praetermissa* in general and I have little doubt that the reason is introgression from the dark violet-purple *D. incarnata* with which they grow – but more on that topic another time.

If we accept the premise that *D. praetermissa* crosses more easily and more frequently with purple-flowered *D. incarnata* than pink in polymorphic mixed populations like Sutton Fen, can we make any theoretical deductions about the dynamics of such populations? *Dactylorhiza ×wintoni* is probably in nearly all cases a triploid entity and has demonstrably very low fertility. Although I have more thoroughly tested the fertility of *D. ×grandis* than I have *D. ×wintoni*, I can say that naturally and artificially pollinated flowers of the latter hybrid produce deceptively normal looking seed capsules but on maturation seed is sparse and defective; most seeds lack embryos and so are sterile. Virtually all the seed produced by the hybrid represents an evolutionary dead-end; a conclusion that also can be extended to the ovules and pollen of the *D. incarnata* and *D. praetermissa* plants that gave rise to the hybrid in the first place. Thus, if cross pollination between purple-flowered *D. incarnata* and *D. praetermissa* is more common than that between *D. praetermissa* and other colour morphs of *D. incarnata* there must through time be a greater proportional loss of purple-flowered *D. incarnata* germ cells relative to their pink equivalents. Over generations, this would necessarily lead to a reduction in the proportion of purple-flowered *D. incarnata* in the population as a whole and if true could be a major reason

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Figs. 11 & 12 plus back cover: Sutton Fen Marsh-orchids that could be *D. praetermissa*, *D. incarnata* or *Dactylorhiza ×wintoni*

Photos by John Haggar

why many Early Marsh-orchids that share habitats with Southern Marsh-orchids are predominantly pink-flowered.

Bumblebee foraging flights tend to be maintained at an approximately uniform distance from the ground, increasing the likelihood of interactions between plants of similar height (Goulson, 1999). Such pollinator behaviour would lead to those purple-flowered *D. incarnata* plants that are of a similar stature to that of *D. praetermissa* and that flower at the same time to disappear first. Larger diploids akin to the type specimen of *D. latifolia* and to Heslop-Harrison's purple flowered var. *gemmana* would be expected to be early casualties of their own reproductive failure. By filtering out the progeny of the purple-flowered plants as infertile hybrids evolution would be expected to select for pink (or other non-purple colour) flowers and such pressures could also result in plants of smaller stature and/or for those with a different peak flowering time. This is, of course, exactly what we see in much of southern England: Early Marsh-orchids that usually have a peak flowering time somewhat earlier than that of the Southern Marsh-orchid, that generally bear pink flowers and that are smaller than *D. praetermissa*. Contrast this with the extremely polymorphic but mainly purple-flowered and temporally extended populations of Early Marsh-orchid on Öland in Sweden that grow in comparative isolation and almost exclusively in the absence of allotetraploid competition. It is interesting to further compare the nearby island of Gotland where the allotetraploid *D. lapponica* (formerly called *D. traunsteineri*) and hybrid forms are common. Perhaps as a consequence, a majority of the Early Marsh-orchids here bear "pale red" (i.e. pink) flowers, rather than purple as they do on Öland (Rosvall & Pettersen, 1951, pp 42, 46 & 49) .

A major problem with this theory as it stands is the question regarding the loss of the allotetraploid's germ cells into the *D. ×wintoni* hybrids. Why does the described deleterious effect on the purple-flowered *D. incarnata* population not also and equally affect the Southern Marsh-orchids? Why do we not end up with exclusively pink-flowered *D. incarnata* colonies with no purple plants at all because they have been hybridised out of existence? Why might the balance be tipped in favour of *D. praetermissa* rather than purple-flowered *D. incarnata*?

It may be that it is the hybrid vigour associated with the allotetraploid state that causes *D. praetermissa* spikes to be larger and more floriferous than those of most *D. incarnata* specimens. Bee pollinators almost invariably work their way up the flower spike from the base so it could be that the grander, taller and more floriferous spikes of *D. praetermissa* increase the chances of a *praetermissa-praetermissa* pollinator interaction over that of a *praetermissa-incarnata* or an *incarnata-incarnata* one, and perhaps the seed yield per capsule is greater in *D. praetermissa* than it is in *D. incarnata*, causing hybridisation to have differential effects on each species (Goulson, 2012, p.104).

The most significant reason, however, is that Early Marsh-orchids appear to take at least a year longer and often more, to reach flowering size from seed than do Southern Marsh-orchids. Experimentally in cultivation, most dactylorchids can be expected to flower for the first time three or more usually four years after seed sowing. This is the case irrespective of whether the seed is grown symbiotically with fungus on oats medium or asymbiotically on nutrient agar. This is true of *D. fuchsii*, *D. praetermissa*, *D. purpurella* and *D. ×wintoni*. In my experience, however, *Dactylorhiza incarnata* will not flower for the first time until it is four, more often five and frequently six years old. A large proportion of the young, freshly weaned seedlings of the species undergo very weak growth or none at all during their first year on soil and require vernalisation for another one or sometimes two winters before they suddenly appear to burst into proper growth comparable with that of other taxa. This prolonged "pseudo-dormancy" often results in much higher seedling losses soon after weaning *ex vitro* than it does with species and hybrids that grow vigorously after just a single period (symbiotic protocorms) or two periods (asymbiotic seedlings) of pre-weaning refrigeration. These heavy early losses are likely to be paralleled in nature, in my opinion, and there would consequently be a reduced survival rate of *D. incarnata* seedlings when compared with those of *D. praetermissa* or of *D. ×wintoni*. This effect has been noted with *D. incarnata* seedlings grown from Scandinavian seed, British seed, French seed and Hungarian seed, so it appears to be an innate characteristic of the species, perhaps indicating an evolutionary history spent in a colder climate than today when the winters were longer and the summers more unpredictable. It is always difficult to extrapolate conditions from cultivation to natural conditions but it seems likely that these observed differences between *D. incarnata* and other marsh orchids are reflected in the wild. Perhaps the Early Marsh-orchid is a plant better adapted to cooler conditions than the balmier modern times that might better favour allotetraploids such as *D. praetermissa*. One result of the longer growth period would be that average generation turnover time in *D. incarnata* would be expected to be significantly slower than in *D. praetermissa* (and probably other allotetraploid marsh orchids as well) and clearly this would make any negative effect caused by hybridisation very much more significant on the former species than the latter.

In summary, the lower flower production, poorer seed production, increased early seedling death and significantly longer generation turnover time of *D. incarnata* will cause any deleterious effect of hybridisation into *D. ×wintoni* to be more profound on purple-flowered *D. incarnata* than on *D. praetermissa* in mixed populations. One could imagine that once an allotetraploid has arisen within or entered a polymorphic and largely purple-flowered *D. incarnata* population, the effect of hybridisation on the population would intensify as the tetraploid proportion of the population increases and that of the *D. incarnata* population decreases. A stable situation may be reached when the hybridisation reduces to a low or negligible rate. This, of course, is dependent on the pollinators coming to regard the *D. incarnata* and *D.*

praetermissa individuals as different and ceasing to interact as significantly between the two species. I would suggest that this why *D. incarnata* is pink-flowered and early blooming in most of southern Britain and the near continent – the process has already reached a steady state in these locations because the two species have co-existed for longer than they have in sites where marked polymorphism persists. Such a situation would cause genetic diversity to be lost from the *D. incarnata* component of any mixed population and introgression from *D. incarnata* to the tetraploids (see below) could increase theirs. This phenomenon too could progressively increase the reproductive success of the allotetraploids as their numbers and genetic richness increase at the expense of the diploids.

The theory of allotetraploid predation and its implications for Marsh-orchid classification

It is thought that both *D. praetermissa* and *D. majalis* (*sensu stricto*) are old allotetraploids, having arisen in unglaciated parts of northern Europe prior to the last Ice Age. In contrast, species like *D. traunsteinerioides*, *D. purpurella* and *D. kerryensis* are believed to have arisen more recently in regions that until 12,000 to 16,000 years ago were buried under ice sheets (Bateman, 2011). For this reason, it might be expected that the older species have had much longer to influence the *D. incarnata* with which they grow and from which they may have arisen. Polymorphic populations of *D. incarnata* are commoner in Britain in more recently glaciated areas suggesting that interaction with allotetraploids in these places is a more recent event. Perhaps polymorphic *D. incarnata* populations that re-entered Britain after the last Ice Age did so well in advance of *D. praetermissa* or perhaps moved across the marshy Doggerland from the east, whereas *D. praetermissa* moved up from the south to meet them. In any event, it would be expected that *D. praetermissa* is a more recent arrival in the northernmost part of its current range, most distant from its centre of distribution, than elsewhere. Recent identification of the species from Denmark in 1977 (Pedersen & Faurholdt, 2010) and from Sweden in 1980 (S. Malmgren personal communication 2018) and the presence of many specimens attributable to F1 and F2 generations of *D.* ×*insignis* (*D. praetermissa* × *purpurella*) at sites around its northern British limit suggests that *D. praetermissa* is still extending its postglacial range.

In essence, my theory of “allotetraploid predation” says that genes, particularly those coding for purple anthocyanin and their neighbouring chromosomal elements, are being lost from diploid marsh-orchid populations and becoming incorporated into allotetraploids via introgression from hybrid forms. The effect is mediated by pollinator preferences. The theory also provides potential theoretical explanations for other long-standing questions that have previously seemed insoluble regarding marsh-orchid populations elsewhere in northern Europe.

As one example, the theory neatly explains the confinement of (later flowering) purple-flowered Early Marsh-orchids to acidic bog habitats in the south of England. This type of habitat would clearly be regarded as marginal for the species as a whole in pan-European terms but because it is a habitat that is currently unfavourable to *D. praetermissa*, the ancestral flower colour of the Early Marsh-orchids is maintained and the plants have become relatively isolated within their distinct habitat. It is worth noting that pale pink and also *ochrantha* forms of var. *pulchella* in this strict sense are not infrequently found, supporting the notion that polymorphism for flower colour really is a primitive characteristic of this deceptive species. Should a bog-adapted form of *D. praetermissa*, similar to *D. sphagnicola* for example, become common in England then I would expect exactly the same process to affect southern English var. *pulchella* as, I maintain, has occurred in the local fens. *Dactylorhiza incarnata* var. *pulchella* (*sensu stricto* i.e. following my circumscription) has also been described from northern France where it grows in similar waterlogged habitats, but within the distributional range of the Southern Marsh-orchid and outside the range of *D. sphagnicola* (Aymonin & Bournerias, 1998). In my opinion, being found within the range of *D. praetermissa* should be a defining characteristic of the bog-adapted, purple-flowered variety of Early Marsh-orchid and it alone should be called var. *pulchella*. Elsewhere and in atypical habitats, purple-flowered diploid Marsh-orchids should be called by other varietal names, including var. *incarnata*, as they are elsewhere in northern Europe. It is time to move on from Heslop-Harrison's concept of "expediency".

Using a similar argument, Early Marsh-orchids that bear red flowers and grow in the sand dune systems of northern Britain and Ireland are almost exclusively found within the area of distribution of *Dactylorhiza purpurella*, with which they have co-evolved and in whose proximity they frequently grow. The coccineal red flower colour so typical of the British dune variety (but dune forms are not exclusively red-flowered; paler flowered morphs are not uncommon) and which is really an intensification of flesh-pink (dilute red), may well be a product of thousands of years of hybridisation between the two species. Now, the colour difference could serve to prevent cross-pollination between them. Red-coloured diploid marsh-orchids are not infrequently found as minor components in some of the East Anglian and Anglesey polymorphic fen populations (e.g. Wicken Fen and Cors Goch, respectively), but by growing in the distributional range of the Northern Marsh-orchid and in a very specific sand dune habitat the flower colour appears to have been positively selected for. There is also some evidence that certain aspects of the environment itself, particularly the moisture content of the dune slacks, can intensify or dilute the red flower colour of the flowers but the mechanism is not known. As mentioned earlier, red may be a better flower colour than the pink of Continental dune forms of *D. incarnata* at "blinding" bumblebees foraging for the deep violet-purple flowers of *D. purpurella*.

Inland populations of Early Marsh-orchid in northern England and Scotland are much more likely to be polymorphic for flower colour than those of southernmost England, and mixed pink and purple flowers are often the norm rather than the exception here. It is likely that a significantly earlier peak flowering time and consequently reduced opportunity to interact with the more recently evolved and later flowering *Dactylorhiza purpurella* in such regions is the reason that the colonies remain of mixed colour.

Large Early Marsh-orchid populations also occur in the west of Ireland. Here, their flower colour is almost exclusively purple and many have marked *cruenta*-style leaves. Although many of the orchids can be found in somewhat acidic suboptimal habitats, the plants are at their most numerous beside limestone lochs in areas like the Burren in County Clare. Here they share their often intermittently peaty "mosaic" habitats with *D. fuchsii*, *D. maculata* and the more recently evolved *D. traunsteinerioides* and *D. kerryensis*. In some sites a most bewildering array of forms and hybrids can be found indicating a population of marsh-orchids that is still very actively changing and has yet to find a stable state.

In the Low Countries, *D. incarnata* is almost exclusively an early flowering orchid with flesh-pink flowers and this is also the case with the dune slack variety (here called var. *lobelii*) found around the coasts (Kreutz & Dekker, 2000). A late-flowering purple-flowered form that may be analogous to var. *pulchella* is recorded from just a few sites. In this part of Europe, the Early Marsh-orchid has long had to grow within the area of distribution of two competing allotetraploid species, the early flowering *D. majalis* (*s.s.*) as well as the later flowering *D. praetermissa*. This dual selection pressure has probably caused the species here to favour a flowering time sandwiched between the two allotetraploids and to grow wherever possible in sites that do not host them. *Dactylorhiza incarnata* in the Low Countries is very likely to have become genetically depauperate – the tell-tale sign, perhaps, being the virtually exclusive presence of pale flowers lacking in purple anthocyanin.

Further east, southern Sweden is home to the northernmost population of Broad-leaved Marsh-orchid, *D. majalis* (*s.s.*). Here, particularly in the province of Scania, it is the only common native allotetraploid that might share its habitat with *D. incarnata*. The May-flowering *D. majalis* is not found further north and within this allotetraploid's area of distribution in Sweden, the Early Marsh-orchid has similarly developed its own local characteristics. Here the peak flowering time of *D. incarnata* is mid-summer, about a month later than the pink-flowered plants from the south of England and the flower colour, although variable, is usually pale lilac. This is quite different from more northern sites in Sweden where the more usual flower colour is a darker purple. The reason for the difference may well be past interactions between the two species that have resulted in pushing the Early Marsh-orchid to a later flowering time and resulting in a different, paler, lilac flower colour. In the south of Sweden, *D. incarnata* is known as the Meadow Orchid. It is *D. majalis* that is the early flowering marsh-orchid here. (Weimarck, H & Weimarck, G, 1985).

If my arguments are sound and my conclusions are valid, it may be that mixed tetraploid and diploid marsh-orchid populations would be better looked upon as a single community that shares and transfers at least some of its genetic material, rather than as several clearly delineated species. Certainly, a future and more accurate classification of the Early Marsh-orchid should take into account not only habitat, geographic distribution, form and flower colour but also the presence and potential influence of co-existing allotetraploids. My next article will describe the results of some hybridisation experiments between *Dactylorhiza* species and hybrids and discuss possible mechanisms by which introgression may occur.

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Achlorophyllous Narrow-lipped Helleborine

Richard Mielcarek

On 18th June 2017 Alan Smith found a curious, ghostly pale *Epipactis* in the Cotswolds amongst a small colony of Narrow-lipped Helleborines (*E. leptochila*); although in bud the stem was bent right over and flattened but he suspected it was probably also *E. leptochila*. He returned the next day to stake and water the plant, hoping it would survive. On 29th June the first flower bud opened and he was able to confirm the identification. On 1st July there were four open flowers but the stem, where it had been bent over, was noticeably stressed and starting to brown. Eventually eight flowers opened but by 9th July they had all faded and the stressed section of the stem was completely brown. It seems that Narrow-lipped Helleborines lacking chlorophyll are almost unknown, the only other record I could find is mentioned in Young (1962), a plant in VC11 in 1954 that persisted until 1957 and even this was probably not fully lacking in chlorophyll as the leaves are described as 'a pale greenish-yellow'. Lewis (2015) mentions achlorophyllous forms for various *Epipactis*, ten different species in total, but not for *E. leptochila*.

Figs. 1 & 2: Narrow-lipped Helleborines (*E. leptochila*) lacking chlorophyll on 30th June 2017 (Fig. 1) and 5th July 2017 (Fig. 2).

Photos by Richard Mielcarek

My thanks to Alan Smith for finding and resurrecting the plant and alerting others to its presence.

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HOS Photographic Competition 2018

Entry details for the competition at Kidlington, November 18th 2018

E-mail digital entries by 15th October 2018 to Neil Evans at neilevans@hardyorchidsociety.org. E-mail notification of entries for print classes to Neil by 5th November 2018. For entrants who are unable to attend the meeting Neil will accept postal entries by the same date, SAE if return of pictures is required. Please email Neil for the address for postal entries. Note: The Schedule of Classes and Rules has been amended and can be found on the website: http://www.hardyorchidsociety.org.uk/HOS%201012/PhotoCompIntro.html

HOS Scientific Show

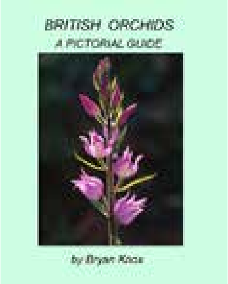
The show will be a non-competitive event and members are encouraged to bring up to three separate displays. Contributions must be contained within an area equal to A2 and ideally should be mounted on a board, up to A2 size. Each contribution may consist of one, or more, photographs and up to 200 words of description/explanation. The text should be large enough for people to read easily but not so large that it dominates the display. Contributions will be displayed on boards in the main hall so they can be viewed throughout the day. The display format will be finalised when the number of contributions is known. Please let Neil Evans know, by 5th November 2018, how many contributions you intend to bring. The contributions should be of a scientific nature and examples of such images may include, but are not restricted to:

- An ultra-close image showing features not readily seen by the human eye
- A pollinator visiting a flower
- A predator consuming a pollinator
- A herbivore consuming a plant
- Mycorrhizal fungi infecting orchid roots
- Seeds and seedlings; germinating pollen
- Anatomical sections
- Stained chromosomes

If you wish to contribute to the show but are unable to attend the meeting at Kidlington please contact Neil Evans to discuss ways of getting your contribution to the meeting.

Book Review: *British Orchids: a Pictorial Guide*

Simon Tarrant



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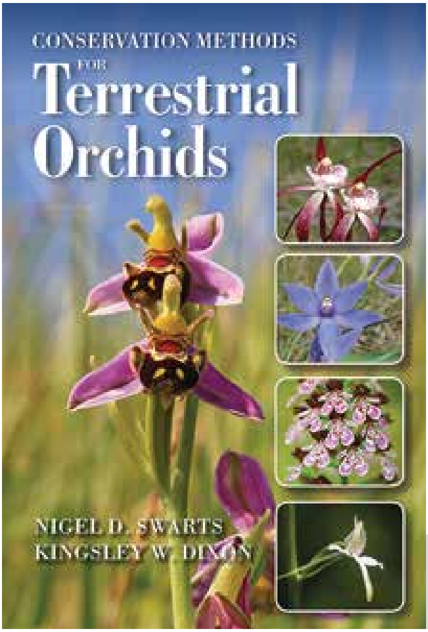
This is a coffee-table book and a labour of love. The author, a skilled wildlife photographer, has over a period of several decades set out to record almost all of the British native orchids in their natural habitats. He has had to admit defeat with the Ghost Orchid, travelling to Germany to photograph it.

You would want this book for the photographs, the text is kept to a minimum. Genera are arranged in a recognisable sequence starting with *Cypripedium* and concluding with *Ophrys*. Curiously, Frog Orchid is still called *Coeloglossum*, but otherwise modern naming conventions are followed. Each taxon has a range of photographs (only two for *Goodyera repens* but fourteen for *Dactylorhiza fuchsii*), with some excellent habitat shots as well as close-ups of flower spikes. Inevitably a collection of photographs taken over a period of fifty years or so shows some inconsistency of quality, and a few pictures have that 'flat' look which I have sometimes found when I have scanned my own older slides.

The sub-title is 'A Pictorial Guide to British Orchids and some of their variations, hybridizations and other oddities', and that is a pretty accurate description of what it achieves. It is a very pleasant book, albeit quite pricey. The e-book version is very cheap, but for me this is the sort of book to browse through on a winter's evening in the comfort of an armchair.



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