



The Hardy Orchid Society Committee

President: Prof. Richard Bateman, Jodrell Laboratory, Royal Botanic Gardens

Kew, Richmond, Surrey, TW9 3DS

Chairman: Colin Scrutton, 14 Trafalgar Road, Tewkesbury, Gloucestershire,

GL20 5FN Colin.Scrutton@dunelm.org.uk

Vice-Chairman: Carol Armstrong, 18 Flaxfield Way, Kirkham, Preston,

Lancashire, PR4 2AY <u>carol.armstrong75@yahoo.com</u>

Treasurer: Colin Rainbow, The Old Post Office, Somerton Road, North Aston,

Bicester, Oxfordshire, OX25 6HX car.northaston@btopenworld.com

Secretary: Angela Scrutton, 14 Trafalgar Road, Tewkesbury, Gloucestershire,

GL20 5FN angelascrutton@btinternet.com

Membership Secretary: Moira Tarrant, Bumbys, Fox Road, Mashbury,

Chelmsford, CM1 4TJ moira.tarrant@outlook.com

Plant Show Secretary: Colin Rainbow, The Old Post Office, Somerton Road, North Aston, Bicester, Oxfordshire, OX25 6HX car.northaston@btopenworld.com

Photographic Competition Secretary: Neil Evans, 48 Friars Avenue, Peacehaven,

Sussex, BN10 8SB neilfevans@btinternet.com

Journal Editor and Website: Mike Gasson, Moor End Cottage, Moor End,

Stibbard, Norfolk, NR21 0EJ moorend@globalnet.co.uk

Speakers Secretary: Celia Wright, The Windmill, Vennington, Westbury,

Shrewsbury, Shropshire, SY5 9RG celia.wright@windmill.me.uk

Southern Meetings Organiser: Simon Tarrant, Bumbys, Fox Road, Mashbury,

Chelmsford, CM1 4TJ tarrant.simon@outlook.com

Northern Meeting Organiser: Alan Gendle, Strathmore, Grayrigg, Kendal,

Cumbria, LA8 9BU alan@gendle.plus.com

Publicity & Outreach Officer: Sue Parker, Bwlchgwyn, Rhydlewis, Llandysul,

SA44 5RE, Wales sue@first-nature.com

Seed Bank Manager: Alan Leck, 1 Stoodley Terrace, Oakfield Road, Frome,

Somerset, BA11 4FF <u>alanleck@alanleck.plus.com</u>

Journal Distributor: Nigel Johnson, Cassandene, Station Road, Soberton,

Hampshire, S032 3QU cassandene@waitrose.com

Conservation Officer: Bill Temple, Primrose Cottage, Hanney Road, Steventon,

Oxon., OX13 6AP <u>bill@billtemple.f9.co.uk</u>

Field Meetings Co-ordinator: Richard Kulczycki, 206 Blythe Road, London,

W14 0HH richardkulczycki@gmail.com

Front Cover Photograph

Close-up of *Ophrys insectifera*, a species that featured in the HOS field trip to Cumbria Wildlife Trust's Waitby Greenriggs Reserve. See Alan Gendle's report on page 137.

Photo by Mike Gasson

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

This time we have another authoritative and informative article from our President Richard Bateman. Here he has again addressed the tricky *Dactylorhiza* genus with an update on evolutionary relationships informed by recent results from modern high throughput DNA sequencing techniques. In addition, we have a very timely and up to date piece from Sue Parker on this year's discovery of Irish Lady's Tresses in Wales. I should also take the opportunity to draw attention to all the work that Sue has contributed to the HOS website in recent months by resurrecting my stalled attempt to rejuvenate the orchid identification photo section. Individual species pages are now all live and accessible from the "photographs" link on the home page. I hope to add the outstanding galleries shortly. Elsewhere I have included some of this year's field trip reports with the remainder ready to go out in the January *JHOS*. We are running low on submitted articles now with space currently available in January, so please do think about making contributions – your journal needs them!

Chairman's Note Colin Scrutton

At the end of July – beginning of August, Angela and I spent a week in Ireland with the intention of photographing Irish Lady's-tresses (*Spiranthes romanzoffiana*) in its nominal heartland. We had some likely locality details from friends and colleagues and we began our hunt on the shores of Lough Corrib just north of Oughterard.

There, the single specimen that we found had been strimmed, along with the rest of the immediate foreshore, by an enthusiastic local! We did find a single good specimen on the Dooros Peninsula and two rather nondescript specimens on the shore of Lough Conn. However we hit the jackpot on the shore of Lough Cullin with an impressive display of 23 perfect specimens, fully out. They made a magnificent sight. Then as soon as we got home, we heard of the new sighting on the mid-Wales coast! Perhaps we could have saved ourselves a trip across the Irish Sea. However, we did enjoy exploring the lovely scenery of Connacht and particularly the spectacular twelve pins of Connemara, although the dearth of footpaths was disappointing.



Going back to the new Welsh locality, publicity of the site on Facebook led to the recruitment of several new members for HOS. Hard work for Moira Tarrant, our excellent Membership Secretary, but always welcome for the Society. I hope to meet them at future meetings.

We've just returned from the northern meeting at Leeds. Over 60 members and friends had signed up for the meeting, a record for St Chads. They were treated to an excellent and varied programme plus 3 videos on widely differing topics. The winning video demonstrated the awful problem of trying to photograph Australian Spider Orchids on a windy day. I'm sure most of us would have given up long before this persistent photographer! We will show the video again at the November meeting when the Tony Hughes trophy will be presented to the winner.

This year, John & Shelagh Temporal organised the sound system for the Leeds meeting for the last time. Hopefully we will have access to a new sound system at St Chads sometime in the future, although it is not yet clear when it will be installed. If

it is not ready for next September, Charlie Philpotts, who has generously offered to run sound at St Chads for us, may be able to use equipment owned by another group that uses the venue. We are very grateful to Charlie for his offer to take on sound at future Leeds meetings and look forward to seeing how whatever system is then available performs next year.

John & Shelagh will run the sound system for a Kidlington meeting for the last time next April. Thus we still do need a member, or members, to come forward to organise sound for the Kidlington November meeting next year and hopefully for meetings there for the next few years. We had originally hoped to recruit someone who could cover sound at all our meetings, Leeds included. However, with Charlie's generous offer to look after sound at St Chad's, we can manage with someone who could take on the sound system for Kidlington meetings only. I hope that a member or members will come forward to at least consider whether or not they could fill this post, as future southern meetings will be much less attractive, and indeed of little interest to some members with hearing difficulties, in the absence of enhanced sound. So I strongly urge that anyone interested please get in touch with me or John Temporal (john.temporal@btinternet.com) to explore what is involved and whether or not they could take on sound for the Kidlington meetings.



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Next-Generation Dactylorchids Richard Bateman

My recent article in *JHOS* on *Ophrys* systematics (Bateman 2018) laid considerable emphasis on the results, generated at the University of Vienna, of a comparatively new genetic technique termed restriction-site associated sequencing (RAD). RAD is one form of a new category of DNA-based genetic techniques known as next-generation sequencing (or high-throughput sequencing). Although RAD is technically challenging, both to generate results in the laboratory and to analyse the data through complex filtration techniques, it brings the considerable advantage of revealing several thousand genetic differences carried on the chromosomes of even closely related plants, thereby strengthening interpretations of their relationships compared with earlier "candidate gene" techniques.

In my previous JHOS article, I promised that our pioneering paper on the genus Ophrys (Bateman et al. 2018a) would be followed by similar studies of other genera of European orchids. I'm pleased to state that, at the time of writing, further RAD studies are about to be published on Epipactis section Epipactis (Sramkó et al. 2019), Gymnadenia subgenus Nigritella (Brandrud et al. 2019b) and Dactylorhiza (Brandrud et al. 2019a). Although each of these studies has considerably improved understanding, I have chosen here to focus on the Dactylorhiza study, thereby updating my previous JHOS article on the genus (Bateman 2011b). Why choose Dactylorhiza? Well, the RAD results offer a welcome opportunity to construct bettersupported evolutionary trees (termed phylogenomics) and to adjudicate between classifications that recognise six species of *Dactylorhiza* (Sundermann 1980) from those that recognise at least 60 (Averyanov 1990; Delforge 2016). But more valuably, they offer fascinating insights into the evolutionary processes that have generated such spectacularly head-scratching diversity, asking of each tetraploid taxon questions such as Who were your ancestors?; Who was your mum and who was your dad?; and When and where were you born?

Why dactylorchids excite scientists

Particularly since the turn of the century, it has become increasingly clear that the evolutionary history of plants has been strongly – possibly even dominantly – driven by a process termed whole-genome duplication. Put simply, this involves an "error" in duplicating the nuclear chromosomes during reproduction that allows the descendants of that reproductive event to inherit twice the number of chromosomes and thus twice the number of copies of the genes that they carry. This does not mean that the descendants gain any extra kinds of genes – they simply acquire twice as many copies of each ancestral gene. Nonetheless, the consequences of genome doubling can be profound. An analogy would be duplicating the white pieces in a chess set such that one was obliged to play with two queens, four knights, and

an embarrassingly large number of pawns. The rules of the game itself would not immediately change, but the game would become infinitely more difficult to play. Among other consequences, whole-genome duplication generates twice as many targets for mutation, thereby offering innumerable new opportunities for particular genes to change in their genetic composition and/or to change the way that they interact with each other to construct a new plant. The ancestors are termed diploids and the descendants, containing twice as many chromosomes, are termed tetraploids (Box 1).

Box 1: Glossary of terms routinely used when discussing genome size

Diploid: Two sets of chromosomes present in most cells of the organism.

Tetraploid: Four sets of chromosomes present in most cells of the organism (typically reflecting duplication in a diploid ancestor).

Polyploid: (Three–)four or more sets of chromosomes present in most cells.

Autopolyploid: Duplicated set(s) of chromosomes derived from a single ancestral species.

Allopolyploid: Duplicated set(s) of chromosomes derived from two ancestral species via hybridisation.

Phylogenetics: Inference of evolutionary histories through comparison of one to several selected genes.

Phylogenomics: Inference of evolutionary histories through comparison of (almost) entire genomes.

Epigenetics: Study of changes across generations that are heritable but do not require alteration to the identity or linear order of bases (A, G, C, T) within strands of DNA.

What I have just described constitutes a process called autopolyploidy, and was responsible for the origin of *D. maculata* from an ancestor that probably closely resembled *D. fuchsii* or *D. saccifera*. But more pervasive among dactylorchids is a process called allopolyploidy, when the whole-genome duplication event occurs within a primary hybrid of *Dactylorhiza*, most commonly a hybrid between a member of the *D. fuchsii* group and a member of the *D. incarnata* group. Earlier chromosomal and DNA evidence (e.g. Heslop-Harrison 1954; Pillon *et al.* 2007; Hedrén *et al.* 2011) had demonstrated that allopolyploidy had occurred several times between these two groups, generating several subtly different allopolyploid lineages that are now the cause of much of the taxonomic confusion and associated identification problems posed by the dactylorchids. Effectively, we have duplicated all of the white chess pieces but also all of the black ones to yield a single player's set of pieces that would include two white plus two black knights and eight white plus eight black pawns. Given such complexity, even a super-computer would struggle to play such a chess set effectively.

This challenging situation is further exacerbated by the ability of the resulting, supposedly independent, allopolyploid lineages (which in the British Isles consist of *D. purpurella*, *D. praetermissa*, *D. kerryensis* and *D. traunsteinerioides*) to hybridise among themselves and to back-cross with their parents through the far more commonplace process of hybridisation without genome duplication. I doubt that there exists a single reader of this article who has not become enmeshed in the ensuing identification problems when out orchid hunting; dactylorchids are feared for good reason.

Armed with a generous grant, courtesy of the Austrian Science Fund, awarded to team leader Ovidiu Paun, we (i.e., Brandrud *et al.* 2019a) used the RAD technique to analyse 28 named dactylorchids: 11 diploid, one autotetraploid and 16 allotetraploids. Our study included all of the major taxa that occur within the British Isles and employed samples collected across Europe and Asia Minor. We generated vast amounts of genetic data for each plant studied and used those data to build statistically robust trees, employing two contrasting mathematical approaches and using the diploid potential ancestors as a framework within which the more problematic tetraploids could more readily be interpreted. Which all sounds very grand. But what did we learn? (and, indeed, what did we not?).

Relationships among the diploid parents

Here, I have chosen to reproduce modified versions of two of our RAD-based trees. Figure 1 is a straightforward rooted tree of the kind now familiar to most readers of JHOS, except that it is based on vastly more DNA data per analysed plant than were previous trees. It provides the latest in a long line of estimates of relationships among supposed dactylorchid species (the results of which are often contradictory: reviewed by Bateman et al. 2018b), though the new tree omits all of the allotetraploids because they arose through hybridisation rather than through the simple dichotomous splitting of evolutionary lineages represented by this diagram. Despite the vast amount of underpinning data, some key relationships implied by the tree still lack strong statistical support. Dactylorhiza viridis is more likely to have originated before D. iberica, but this is not certain; in any case, their evident closeness of relationship should (but probably won't!) be sufficient to finally persuade sceptics that viridis is better treated as a dactylorchid than as a separate genus, Coeloglossum. Both D. viridis and D. iberica originated before D. sambucina and its close relatives. The incarnata group and fuchsii group, which together provided the parents of all of the allotetraploid taxa, are separated by the intriguing, under-researched East Asian-Alaskan endemic D aristata.

Relationships within the *incarnata* group are resolved as expected; within Asia Minor, *D. euxina* originated before not only the similarly distributed *D. umbrosa* (which includes the supposed species *osmanica*) but also the more widespread Eurasian

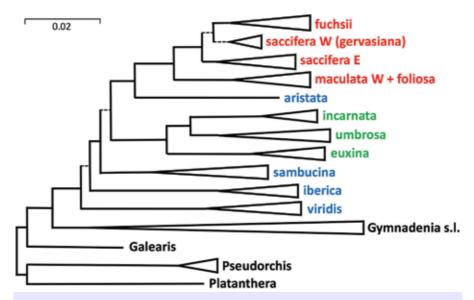


Figure 1: 'Rooted' evolutionary tree based on DNA RAD-seq data, summarising the relationships among diploid dactylorchids. Spotted-orchids are highlighted in red, diploid marsh-orchids in green. Dashed branches received less statistical support. Redrafted after Figure 3 of Brandrud *et al.* (2019a).

species *D. incarnata*. It is within the *fuchsii* group that the greatest ambiguities persist among the diploid taxa, despite the vast amount of DNA data now accumulated. Both the diploid *D. saccifera* and the autotetraploid *D. maculata* segregate into eastern and western clusters, while the distinctive Madeiran endemic *D. foliosa* is placed within the tetraploid Western *D. maculata* group, despite being diploid (it evidently never learned that tetraploids are supposed to evolve *from* diploids!). Also placed within the western portion of *D. maculata* are several named taxa (e.g. *ericetorum*, *islandica*, *caramulensis*, *savogiensis*) some or all of which have been treated as species by most previous authorities (e.g. Delforge 2016).

The present results controversially suggest that the distinct DNAs of the Western *sacciferas* should cause them to be viewed as a separate species, *D. gervasiana*, despite the fact that my unpublished morphometric analyses suggest that these two taxa cannot readily be separated on the basis of their morphology. In addition, we still cannot determine with confidence whether the closest relative of *D. fuchsii* – the one and only spotted-orchid whose status as a species is comparatively unproblematic – is *D. gervasiana* or *D. maculata* plus *D. foliosa*. Overall, for the spotted-orchids at least, RAD data have created as many problems as they have solved.

Relationships among their allopolyploid descendants

However, the more significant progress achieved by Brandrud *et al.* (2019a) is not represented by the rooted tree of diploid taxa (Fig. 1) but rather by the unrooted tree that includes the allotetraploids – species that originated through hybridisation plus chromosome doubling (Fig. 2). We finally have a means of not only (a) optimally circumscribing species within this problematic allopolyploid complex but also (b) determining which species provided the 'mother' and 'father' of each named tetraploid and (c) inferring approximately how long ago those tetraploid species originated. Here I have summarised that information as Table 1. The combination of Figure 2 and Table 1 is sufficiently powerful to finally end some of the most important long-standing controversies surrounding the allopolyploid dactylorchids, provided that opinions based on science are finally allowed to trump opinions that are not.

Beginning with circumscription, we can readily see from Figure 2 that the most genetically distinct allotetraploids are those from the southwest (*D. elata* s.l.) and southeast (*D. urvilleana*, *D. armeniaca*, *D. cordigera*). In the southwest, *D. kalopissii* and (somewhat to my surprise) *D. pythagorae* also appear to form discrete taxa. The exclusively Irish *D. kerryensis* is placed as sister to the exclusively Continental *D. sphagnicola*, within the group of three similar but nonetheless separable species that had *D. maculata* as their 'mother'. Among the north-western allopolyploid progeny of *D. fuchsii* and *D. incarnata*, *D. majalis*, *D. praetermissa*, *D. purpurella* and *D. traunsteineri* all merit species status, together with the typical north-eastern allotetraploid *D. baltica*. It is less clear whether *elatior* (syn. *osiliensis*) is a *bona fide* species or would be better incorporated back into *baltica*, but we can at least refute previous suggestions that it belongs within *D. praetermissa*. Other narrow endemics included in the analysis – *nieschalkiorum* (north-west Turkey) and *brennensis* (central France) – present less convincing cases for species status.

For me, the most reassuring feature of Figure 2 is that British and Irish narrow-leaved marsh-orchids can finally be seen to be distinct from those in the Alps and (to a large degree) Scandinavia – in other words, *D. traunsteinerioides* clearly is not *D. traunsteineri* (I'll return to this topic a little later). Indeed, the circumscription of the British and Irish dactylorchids indicated by these latest analyses is broadly consistent with the situation as I summarised it several years ago, based on a combination of much smaller quantities of DNA data supplemented with morphometric data (Bateman 2011a, 2011b; Bateman & Denholm 2012). We have in the UK flora seven *bona fide Dactylorhiza* species. The diploid spotted-orchid *D. fuchsii*, the autotetraploid marsh-orchid *D. maculata* and the diploid marsh-orchid *D. incarnata* are all geographically widespread and maintain habitat-restrictive ecotypes that vary in degrees of distinctiveness. In addition, descended from these three parental lineages we have four allotetraploid marsh-orchid species: *D. praetermissa* in the

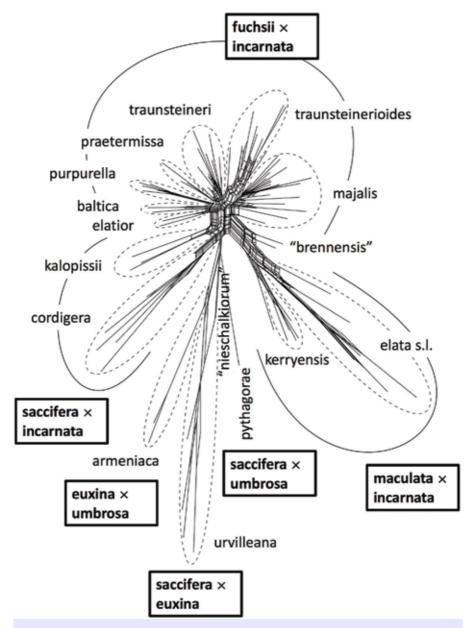


Figure 2: 'Unrooted' evolutionary tree based on DNA RAD-seq data showing the relationships of tetraploid dactylorchids among each other and to their parental diploid species (boxed: 'mother given before 'father'). Modified after a preliminary version of Supplementary Figure S3 of Brandrud *et al.* (2019a).

south, *D. purpurella* in the north, *D. traunsteinerioides* in the north and west, and *D. kerryensis* confined to Ireland. Unlike the other three allotetraploids present, *D. kerryensis* has as its 'mother' *D. maculata* rather than *D. fuchsii* (Table 1).

Ovule parent ('mother')	Pollen parent ('father')	Allopolyploid species generated	Geographic distribution of allopolyploid	Relative age
fuchsii	incarnata	majalis praetermissa purpurella traunsteineri traunsteinerioides ?baltica [inc. ruthei] ?elatior (= osiliensis)	W+C Europe W Europe NW British Isles, S Scand, Alps, Scandinavia NW British Isles Baltic, Russia Baltic	Medium Young V Young Medium Young V Young Young
maculata	incarnata	kerryensis sphagnicola elata [part?]	Ireland Benelux, S Scandinavia SW Europe, NW Africa	Young Medium Old
saccifera s.l.	incarnata	cordigera kalopissii [inc. maced.]	SE Europe NW Greece	Old Medium
saccifera	euxina	urvilleana	NE Turkey, Caucasus	?
urvilleana	euxina	armeniaca	(NE Turkey), Caucasus	?
saccifera	urvilleana	pythagorae	Dodecanese (Samos)	?

Table 1: Evolutionary origins, parentage, geographic distributions and relative ages of allotetraploid dactylorchid species in Europe and Asia Minor, summarising the conclusions of Brandrud *et al.* (2019a).

The latest DNA data also confirm several deductions that have developed gradually through the past 70 years regarding the tetraploids. We know for certain that the evolutionary process of allopolyploidy has been rife among European dactylorchids for several million years. We know that, with one exception, all of the allopolyploid species had as their 'mother' one of the species of spotted-orchid: either the diploid fuchsii in Europe or the diploid saccifera in Asia Minor and the Caucasus or, more extraordinarily, the autotetraploid maculata in the western seaboard of Europe. We know that the allopolyploids had as their 'father' one of the species of diploid marsh-orchid: either incarnata in Europe or its close relative euxina in Asia Minor. More perplexingly, we learn that autotetraploids (maculata) and even allotetraploids (urvilleana) have acted as 'mother' to at least one further allopolyploid species. Given such evolutionary complexity, it is small wonder that dactylorchids can be so problematic to identify, irrespective of whether morphology or genomes are under scrutiny.

Origins of the allopolyploids in space and time

Using DNA to determine the point in time and space at which a species originated is fraught with difficulties that are too technical to adequately explore in this article. But if we acknowledge these uncertainties and so treat Brandrud *et al.*'s (2019a) results as indicative rather than conclusive, the oldest surviving dactylorchid species is probably *D. viridis*, an estimated 12 million years old. *Dactylorhiza foliosa* is estimated to have originated about 4 million years ago, a figure that satisfies logic because the island of Madeira (to which it is confined today) has only existed above sea level for the last 5 million years or so. By counting the number of DNA markers unique to the allopolyploids we can also estimate their ages, at least relative to each other (Table 1). Obviously, they cannot be older than their youngest parental species. All are likely to be less than 2 million years old, and all but the oldest (*D. cordigera* and *D. elata*) may post-date the most recent period of periglacial landscapes in Europe, which ended a mere 11,500 years ago.

It seems likely that diploid species resembling *D. saccifera* and *D. euxina* originated in western Asia and migrated westward into south-eastern Europe before spreading out across the Continent and speciating to form fellow diploids *D. fuchsii* and *D. incarnata*, respectively. They have since generated an impressive array of allotetraploids across Europe whose geographic origin is less readily inferred. However, it seems logical to speculate that the centres of their current distributions are probably close to their points of origin. Thus, the older allotetraploid species would have originated in southerly latitudes – for example, *D. elata* possibly originating in Morocco and *D. urvilleana* in Iran or Turkey. In contrast, the most recently formed allotetraploids occupy terrains that were glaciated comparatively recently – *D. traunsteinerioides* and *D. purpurella* in the British Isles, *D. baltica* to the east of the Baltic Sea.

Future research is likely to further elucidate these issues. For now, I find it exciting to contemplate the likelihood that at least two members of the impoverished, largely post-glacial flora of the British Isles are, along with *Gymnadenia borealis* (Bateman *et al.* 2018b), genuinely largely endemic and evolved *in situ*. But is this figure actually an under-estimate; could there be other British and/or Irish dactylorchids that merit the status of endemic species? A question that returns us yet again to the knotty topic of the "Hebridean Marsh-orchid."

The Hebridean Marsh-orchid (yet again)

In his recent article in *JHOS*, Pikner (2019) introduced us to the Late Victorian 'Baltic School' of taxonomy. This should not be confused with other 'schools' of orchid systematics operating around the Baltic, particularly that led by Henrik Pedersen in Denmark and the highly productive research group of Mikael Hedrén in Sweden. Pikner described the distinguishing features of the Baltic School as voluntarily

discarding the rank of subspecies (typically elevating its former occupants to species rather than demoting them to varieties, such that the dune ecotype of *D. incarnata* becomes "*D. coccinea*") and then considering flower colour to be relevant almost exclusively at the levels of variety and forma (surely a cogent argument for demoting the red-flowered *D. incarnata* subsp. *coccinea* to a variety in the sense of the Baltic School, rather than promoting it to a species?).

Despite my repeated attempts to drive a stake through the heart of a monster that I was partly responsible for creating (Bateman 2011a, 2011b; Bateman et al. 2012), Pikner (2019) has made yet another valiant attempt to resurrect "D. ebudensis" from the living dead, thereby condemning it to haunt the desolate dune slacks of the Hebridean islands of North Uist and Berneray as an orchidological zombie. We learn that ebudensis consists of a handful of clusters of up to ten plants that are marooned in a sea of "D. coccinea" and D. purpurella, and that it is best identified by its heavily marked leaves and purple-magenta flowers with comparatively broad, somewhat deltoid lips. We are also told that the epigenetic data of Paun et al. (2010) show that ebudensis formed in situ no more than 2,500 years ago, and that its core population of approximately 60 plants are intermixed with a similar number of hybrids with D. purpurella. Thus, it is claimed to be a "very rare endemic" species that "needs proper protection measures because we do not have thousands of specimens but only hundreds or even tens" (Pikner 2019, p. 67).

I will begin my critique by re-examining the argument that Paun *et al.*'s (2010) epigenetic results support the views of Pikner and Delforge that *ebudensis* is an exceptionally rare but genuine species. I have reproduced here as Figure 3 the crucial diagram of Paun *et al.* (2010) that summarises our epigenetic results, but here I have labeled it even more explicitly with the current names and geographic origins of the samples analysed. As you would predict, given the results of our recent RAD analyses, the first (horizontal) axis of the diagram separates the British *D. traunsteinerioides* to the left from the Continental *D. traunsteineri* and *D. majalis* to the right. The even weaker second (vertical) axis separates plants from two populations of *D. traunsteinerioides* subsp. *traunsteinerioides* (North York Moors) from three populations of *D. traunsteinerioides* subsp. *francis-drucei*, two of which are located 35 km apart on the western seaboard of Scotland and the third of which occurs 85 km distant on the Hebridean island of North Uist (i.e. *ebudensis*).

These three populations evidently show roughly equal differences from each other in DNA methylation (the epigenetic property that was assessed by Paun *et al.* 2010), a pattern consistent with their being three populations of a single subspecies of a single species. Concurrent analyses of two distinct kinds of genome (plastid haplotypes and nuclear microsatellites), published less than a year later (Hedrén *et al.* 2011), showed similar patterns. Indeed, during the last quarter-century I have

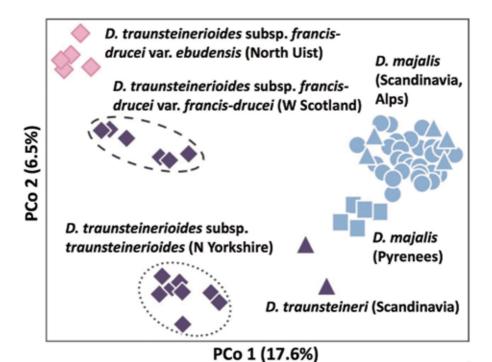


Figure 3: Principal coordinates plot summarising epigenetic patterns detected in *Dactylorhiza majalis* s.s., *D. traunsteineri* and three geographically constrained infraspecific taxa of *D. traunsteinerioides*. Modified after Figure 1B of Paun *et al.* (2010).

been involved in projects that studied the morphometrics, proteins, nuclear genes, plastid genes, epigenetics and phylogenomics of *ebudensis*, and frankly, I'm running out of ideas for what other aspects of these accursed plants I might study! All these analyses except one (Pillon *et al.* 2007) told the same story; there are no meaningful differences between *ebudensis* and other populations of *D. traunsteinerioides* in the British Isles. Sadly, there is nothing special or fundamentally different about var. *ebudensis* (Bateman & Denholm 2012).

DNA-based research that I and my colleagues have performed through the last 25 years has taught me that, unlike Pikner (2019), I am unable to identify with confidence hybrids of *ebudensis* with intermixed *D. purpurella* without first gathering detailed genetic information. Indeed, it was probably one such hybrid that misled our research group and caused me to mistakenly promote *ebudensis* to species level in 2006 (as detailed in Bateman 2011a, 2011b; Bateman & Denholm 2012). But by the same token, our DNA work has shown that some plants of *traunsteinerioides*



(i.e. *ebudensis* sensu lato) at the site have unmarked leaves and a range of flower colours (compare Figs. 8 and 9). However much we might wish it were otherwise, confident identification of hybrids between such morphologically and molecularly similar species as *D. traunsteinerioides* and *D. purpurella* requires science rather than wizardry.

Rather than reflecting the epigenetic data they had collected in the laboratory, the suggestion by Paun $et\ al.\ (2010)$ that ebudensis arose at its current location within the last 2,500 years was based on geomorphological evidence that the seaside strand that supports the plant today did not exist earlier in time due to earlier fluctuations in sea-level. Indeed, one surprising result of the Brandrud $et\ al.\ (2019a)$ analysis is that $D.\ traunsteinerioides$ apparently arose significantly longer ago than $D.\ purpurella$ (Table 1) – a species that possesses a similar distribution but is more ecologically tolerant and therefore more frequent.

Also, given that Pikner and I do at least agree than genes are actively being exchanged between *D. purpurella* and *ebudensis*, it seems unlikely that *ebudensis* would be able to remain recognisable for 2,500 years rather than be assimilated rapidly into the larger local population of *D. purpurella*. If we take an overview of the taxonomy of British and Irish dactylorchids, what credible argument can be made for elevating hyperchromic plants of *D. traunsteineroides* (Fig. 9) to species level while hyperchromic plants of, for example, *D. purpurella* (Fig. 7) and *D. fuchsii* (Fig. 5) languish in the annals as mere varieties or formae? In summary, although I support Pikner's (2019) plea for conservation of the North Uist locality, I do so because of its overall botanical value, rather than invoking the presence of a mythical orchid species of unparalleled rarity.

Unanswered questions

Inevitably, there remain several important aspects of the dactylorchids to perplex us. With regard to relationships among the diploid species, could the under-researched East Asian/North American species *D. aristata* resemble the ancestor of the European spotted-orchids, perhaps having migrated eastward from central Asia while the ancestor(s) of *D. fuchsii* and *D. saccifera* migrated westward? And with regard to the origins of the allotetraploid species, it seems remarkable that in almost all cases the

Figures 4–9: 'Normally' pigmented (left) and hyperchromic (right) plants of *Dactylorhiza fuchsii* (Figs. 4 and 5), *D. purpurella* (Figs. 6 and 7), and *D. traunsteinerioides* subsp. *francis-drucei* (Figs. 8 and 9). Surely it makes most taxonomic sense to treat all three hyperchromic taxa as varieties or formae rather than single out var. *ebudensis* (Fig. 9) as a supposed species?

Photos by Richard Bateman.

spotted-orchid parent is the 'mother' of the allotetraploid whereas the marsh-orchid is always the father. Is it relevant that, as demonstrated yet again by Brandrud *et al.* (2019a), genetic diversity is comparatively (and, so far, inexplicably) low within plants and populations of *D. incarnata*?

And what is the likely taxonomic status of the numerous named taxa that escaped analysis by Brandrud et al.? The majority of the remaining taxa, especially supposed local endemics, are unlikely to survive future analysis as full species, though the apparent distinctiveness of D. pythagorae on the Aegean island of Samos offers them at least a little hope of retaining credibility. Far more attention should be given to determining whether supposed local endemics are simply hybrid swarms that, unlike the allotetraploids, have not benefited from the partial reproductive isolation conferred by genome duplication. It is essential that slightly morphologically divergent populations of dactylorchids are not named as local endemic species until they have been subjected to intensive research to demonstrate that they have the right to receive such exalted status. Having said that, a few additional bona fide species may still be circumscribed in due course. Although many examples of taxonomic 'oversplitting' in various groups are evident within the genus Dactylorhiza, Brandrud et al.'s trees may have identified at least one case of taxonomic 'under-splitting'; Figure 2 tentatively suggests that D. elata s.l. could encompass two or three species, and the group certainly merits its own more detailed study.

Further research is also needed to verify supposed occurrences in the near-Continent of species predominantly native to (and probably originating in) the British Isles: *D. purpurella* in the Low Countries and Scandinavia, including the Faroe Islands, and in Norway *D. traunsteinerioides* (also *Gymnadenia borealis*). The RAD study even offers slight hope to those among us who have speculated that *D. traunsteinerioides* may once have occurred in Norfolk (still within the influence of the ice sheets) but recently have been hybridised into obscurity by *D. praetermissa*.

From a conceptual viewpoint, the more scientifically inclined students of the genus have, until now, used monophyly of clusters of samples as a key element in circumscribing species, but this does not end the debates. For example, I have argued that each group of allopolyploids with a single evolutionary origin constitutes a single species, whereas my colleague Mikael Hedrén effectively treats as single species all taxa that originate from the same parental pairing. Thus, for me, *D. purpurella*, *D. praetermissa*, *D. traunsteinerioides* and *D. kerryensis* are separate species, whereas for Hedrén, all allotetraploids originating from hybridisation between *D. fuchsii* and *D. incarnata* are subspecies of a single species, *D. majalis*. Even *D. kerryensis* (*D. maculata* × *D. incarnata*) is included by him in *D. majalis*, because Hedrén views *D. fuchsii* as a subspecies of *D. maculata*, despite the fact that *D. fuchsii* is a diploid and *D. maculata* is an autotetraploid. Both positions are scientifically justifiable based

on present evidence, while recognising that perceptions are likely to change as more data are brought to bear on these problems.

More difficult to defend are treatments that ignore or misunderstand the scientific evidence and/or that voluntarily constrain our ability to recognise an evolutionary hierarchy; the great majority of such classifications are open to criticism. Many authors find little or no use for the rank of subspecies (e.g. Averyanov 1990; Delforge 2016; Pikner 2019), whereas others produce equally egalitarian classifications that emphasise subspecies at the expense of species. For example, Kühn *et al.* (2019) recently recognised no less than 17 subspecies (including all four of the British and Irish allotetraploids) within an exceptionally broadly circumscribed *D. majalis*. In my opinion, such 'flat' classifications, whether focused at the species or subspecies level, are classifications of despair – they are attractive because of their simplicity rather than their logic or their scientific accuracy. Current, hard-won scientific knowledge should allow us to better represent the natural hierarchy of evolution within the (all too often artificial) hierarchy of taxonomy.

Current evidence would place the number of species of *Dactylorhiza* (including *D. viridis*) at about 30 – more than the six of Sundermann (1980) or 13 of Kühn *et al.* (2019) but less than the 62 of Delforge (2016) or 75 of Averyanov (1990). This may prove to be a less traumatic conclusion for readers of *JHOS* than is the radical idea of the genus *Ophrys* encompassing only nine defensible species (Bateman *et al.* 2018a)? However, the more important conclusions of recent DNA-based research on dactylorchids relate not to classification but rather to the remarkable story of how these species originated – a story that, as it becomes more firmly rooted in facts rather than speculation, develops in ever more intriguing directions.

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Welsh Lady's-tresses? Sue Parker

To discover one of Britain's rarest orchids in a country where it had never before been recorded must be great, but to do so a mere four hours before leaving to go on holiday is *not* ideal. This is just what happened to Justin Lyons, Senior Officer, Land Management, based at Wales's Dyfi National Nature Reserve. The orchids popped up on a part of Cors Fochno (Borth Bog) modified by drainage and agricultural use but which has now reverted to boggy grassland following three decades of low intensity grazing and drain blocking. Although the drainage scheme failed, largely due to the unfavourable climatic conditions in Wales, parts of the bog were partially drained, including the field in question.



One of the eight *Spiranthes romanzoffiana* plants found in Borth Bog. Photos by Mike Bailey

It was during a last minute pre-holiday check of the grazing animals that Justin literally stumbled over the orchids. He knew immediately that this was not an outpost of the small colony of Autumn Lady's-tresses *Spiranthes spiralis* that grow in the sand dune section of the NNR at Ynyslas, some 2km away. These plants were so much larger



One of the miniscule *Spiranthes spiralis* (which grow in the dune system). This one was around 4cm tall and very difficult to spot.

Photo by Sue Parker

and more robust than the orchids at Ynyslas, which are truly minute. Dashing back to his office, Justin consulted his field guide and was convinced that, no matter how unlikely, he had found Irish Lady's-tresses Spiranthes romanzoffiana. This was soon confirmed by Arthur Chater, one of Wales's top botanists, who abandoned a planned trip to another site and instead hastened to the Bog to see the new orchids. Spiranthes romanzoffiana, one of our rarest and most enigmatic wild orchids, has been the subject of much speculation and debate, little of which seems to have added much to our understanding of the curious geographical distribution of this species. Relatively common and widespread in North America, where it is known as Hooded Ladies-tresses, this orchid has a socalled amphi-Atlantic distribution, and there are various suggestions as to how it crossed the Atlantic to its second best known location of Ireland. Was the seed wind blown? Were viable parts of plants carried across the ocean by birds and then deposited in places where they just happened to survive and grow?

Who can say for sure? Either of these options might better explain how Irish Lady's -tresses travelled the much shorter distance from Ireland to Britain.

The development and growth of Irish Lady's-tresses is also perplexing. Perhaps spending as long as five years developing below ground before leaves appear, the plant grows from a cluster of fleshy roots. Between July and October a bud develops from which leaves appear the following spring. This is followed, in June, by the appearance of a flower stem. Dormancy below ground can be up to six years between flowering seasons.

Ynyslas sand dunes, at Borth, are well known to lovers of wild orchids. Many of us make annual pilgrimages to see the wonderful displays of *Dactylorhiza* species (and many confusing hybrids) as well as Marsh Helleborines *Epipactis palustris* that carpet the dune slacks. The 'bog' part of the nature reserve is less visited - in part due to the difficult and potentially dangerous nature of the terrain - but it is in fact home to some of the most impressive colonies of Heath Spotted-orchid *Dactylohriza maculata* that I have ever seen. There are also increasing numbers of

Lesser Butterfly-orchids *Platanthera bifolia* and Early Marsh-orchid *Dactylorhiza incarnata* subspecies *pulchella* – testament to the management of the nature reserve since its initial acquisition by the Nature Conservancy Council in the 1970s and 80s, and further expansion by its successor bodies.



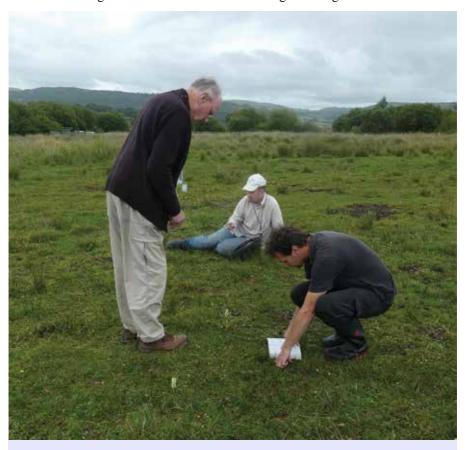
Marsh orchids in the dune system at Dyfi National Nature Reserve.

Photo by Sue Parker

The field in which the eight *Spiranthes romanzoffiana* plants have appeared is dominated by Purple Moor-grass *Molinia caerulea* interspersed with patches of shorter turf. The orchids were growing in one of the drier close-cropped areas together with Common Yellow-sedge *Carex viridula* subspecies *oedocarpa* (syn. *Carex demissa*), Velvet Bent *Agrostis canina*, Tormentil *Potentilla erecta*, Marsh Pennywort *Hydrocotyle vulgaris*, Lousewort *Pedicularis sylvatica* and sporadic tufts of Sharp-flowered Rush *Juncus acutiflorus*. Other plants in the vicinity of the orchids include Devil's-bit Scabious *Succisa pratensis*, Ling *Calluna vulgaris* and Round-leaved and Intermediate Sundews *Drosera rotundifolia* and *D. intermedia* – all typical species of wet acidic grassland.

Two years ago the part of the field where the Irish Lady's-tresses have appeared was subjected to late season mowing and litter removal in order to encourage the grazing livestock to better maintain a short sward. This changed management regime may well have promoted the sudden appearance of these orchids, which are often associated with heavily grazed wet grassland habitats.

For those of us who are fascinated by orchids, discoveries such as this provide more questions than answers. Why did these plants spring up in a place where they had never before been recorded? Are there more plants in the vicinity simply waiting to be discovered? Have Irish Lady's-tresses flowered there in previous years and simply not been noticed, or have they been grazed-off before having a chance to flower? Or were subtle changes in habitat due to the new management regime the crucial factor?



Justin Lyons (right) confirming the identity of *Spiranthes romanzoffiana*. Photo by Justin Lyons

For Justin, and for his colleague Mike Bailey who has spent years observing and managing the habitats at Borth Bog, these are important questions as they strive to ensure that conditions remain suitable for the survival of their 'new' orchid, a task that might even conflict with the major conservation objective of active raised bog restoration in which they are currently involved.

Habitat management may be the least of the problems raised by the sensational appearance of *Spiranthes romanzoffiana* at Borth Bog. This find has created a real buzz in the orchid world. For some people, the discovery of a rare species in such a remote location is not something to be celebrated from afar. Visitor numbers to Borth Bog in 2020 could increase exponentially and will have to be managed. Some form of protection against damage by unintentional trampling will be necessary, of course, but equally crucial is the need for security.

All this underlines the vital importance of government's continued investment in our National Nature Reserves. Land management work by staff at Natural Resources Wales delivers key outcomes for our international obligations towards stemming the tide of biodiversity loss. But there are also substantial economic benefits to local communities from the additional tourism prompted by the wonderful spring and summer wildflowers, and particularly wild orchids, at Dyfi NNR and other sanddune sites around Britain's coast. Always assuming that the Irish Lady's-tresses at Borth Bog decide to bloom next year, we intend to arrange a HOS visit – and in any case there will *definitely* be lots of other interesting plant species to see in this NNR.

A Fine Example of Hybrid Vigour Gordon James

Having recently joined the Hardy Orchid Society and reading in the April Journal about various hybrids, I thought the following notes on some plants that we know in southern France might be interesting. We have a small village house in southern France, situated at around 700m altitude on the very southern edge of the great limestone plateau known as the Causse du Larzac. The surrounding countryside provides wonderful walking and has a very rich flora including in excess of fifty distinct species of orchid, with all but a few growing within walking distance of the house.

Most species of orchid grow in such abundance that they hybridise freely, forming hybrid swarms, and when looking at a particular plant it is sometimes quite difficult to determine exactly what species it belongs to; this is particularly true of plants in the genera *Orchis* and *Ophrys*. In early June 2016, whilst driving along a narrow road several kilometres from the village we saw a nice cluster of *Orchis simia* and *Orchis*

anthropophora growing on the road verge. There was nothing particularly special about this as both species are quite abundant throughout our region but we stopped to take some photographs. The plants of both *O. simia* and *O. anthropophora* were of average height, which is around 25 to 35 cm.

Looking across the road we were attracted by several clumps of exceptionally tall, dark coloured orchids that turned out to be the hybrid between the two species, named in our flora of Aveyron as ×Orchis bergonii and described as being rare, occurring in less than five locations in the department. Many of the individual spikes were over a metre tall, with more than one hundred flowers on each spike. Individual flowers were much darker in colour than either the typical O. simia or O. anthropophora, with the 'leg' and 'arm' sections of the labellum long, as in O. simia, but with the 'body' section unspotted as in O. anthropophora, also the hood tends to droop somewhat and is closer in shape to the typical O. anthropophora. Anyone who may be unsure about the existence of 'hybrid-vigour' should stand one side of the road and look at both parents and then cross to see their off-spring.



Figure 1 (above): Orchis simia and Orchis anthropophora on the road verge.

Figure 2: Spike of the hybrid ×Orchis bergonii.

Figure 3: Close-up of Orchis anthropophora spike.

Figure 4: Spike of Orchis simia.

Photos by Gordon James





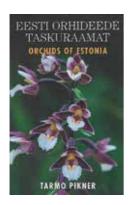


We returned to the site a year later in late May 2017 and the colony was still there; but 2017 had been a very strange year for orchids in our region of southern Aveyron, due mainly we suspect to an exceptionally hot and dry early spring followed by wet, cold weather. Not only were most orchid plants very much shorter than usual, others, notably members of the genus *Ophrys*, were virtually non-existent. However, our *O. simia* × *anthropophora* hybrids were still standing tall, but not nearly as tall as a year before.

Figure 5: Clump of hybrid ×*Orchiaceras*bergonii plants.

Photo by Gordon James

Book Review: *Eeesti Orhideede – Orchids of Estonia* Richard Kulczycki



Eeesti Orhideede – Orchids of Estonia by Tarmo Pikner Published 2019; ISBN 978-9949-669-15-8; 122 pages. Available at: https://kirjastus.postimees.ee/eesti-orhideedetaskuraamat/ Also shows stock levels at Estonian booksellers.

This is the third book on Estonian orchids reviewed here in recent years, but it may be that there are still members who have not been there! Tarmo Pikner's complete guide was reviewed by Simon Tarrant in July 2013. In this handy short pocket book (only 16×10.5cm) each of the 37 species is described on the left-hand page in Estonian

with a shorter English text below. The right-hand page has a photograph of the full orchid. The book also has one page distribution and flowering time guides – useful overviews when planning trips. There is a short English introduction which focuses on the Estonian endemics – *Dactylorhiza vironii* and *Dactylorhiza osiliensis*.

Estonia has many rich and easily accessible orchid sites. For the British visitor, the Dactylorhizas, similar to but different from our flowers, and the large numbers of Cypripediums (growing free!) will be particularly interesting.

Field Trip to Waitby Greenriggs Reserve and South Stainmore Alan Gendle

On 23rd June a group of 20 members visited Cumbria Wildlife Trust's Waitby Greenriggs Reserve. Entering the reserve and wandering along the old railway track bed we found examples of hybridisation between *Dactylorhiza purpurella* and *Dactylorhiza fuchsii*. Both parent species were also present. Many *Ophrys insectifera* were seen on the banksides as the group progressed through the reserve. Some robust *Platanthera bifolia* attracted the attention of the photographers in the southern end of the reserve. In an area of low grassland sward an interesting *Gymnadenia borealis* was seen. The labellum was white, the petals and sepals were pink. *Gymnadenia densiflora* was also present in the area. Lots of *Epipactis palustris* that would normally have been in flower were seen in bud. Spikes of *Neottia ovata* were seen all over the reserve.



Interesting bi-coloured *Gymnadenia borealis* (left) and a robust *Platanthera bifolia* (right) on Cumbria Wildlife Trust's Waitby Greenriggs reserve

Photos by Alan Gendle

After lunch the members visited a hay meadow high in the Pennines on private land with an interesting orchid population including *Dactylorhiza purpurella* and the *alpina* variant of *Dactylorhiza fuchsii*. *Gymnadenia borealis* was just starting to flower. There were some *Orchis mascula* with a few flowers still on the spike reflecting the high-level nature of the site.

Thanks to the members who contributed to the funds of the Cumbria Wildlife Trust.

Field Trip to Teesmouth NNR County Durham Alan Gendle

On Saturday 22nd June a group of 20 set off to try to find *Dactylorhiza purpurella* var. *atrata* on its only site in the UK. It had been suggested that the heavy metal ground pollution from a nearby zinc works, which shut down in 1946, was being diluted by rain water. Low numbers of plants had been regularly reported but were the numbers really just in twos & threes? Phil Smith had been on the site last year and located 15 plants so we followed Phil's lead down to the southern end of the site. We located five plants but the area we wanted to access appeared to be closed off to the public with 'Danger notices' posted on the fence. We noticed an access point to the north which appeared to give unrestricted access. As we made our way there, we passed through an area where I had found plants years ago and we found five plants and also recorded *Dactylorhiza praetermissa* and the first *Ophrys apifera* and *Anacamptis pyramidalis* plants. Entering safely into the fenced off area we began to see lots of *Dactylorhiza purpurella* var. *atrata* plants. Some of the plants had heavy spotting on their leaves, others had none and yet had the characteristic purple staining on the labellum.

Plastic garden plant labels were laid out by the members by each plant to aid an accurate count. We had a final total of 52 spikes of *D. purpurella* var. *atrata*. Historically in 1976 over 100 spikes were recorded. Without the help of the HOS members we would never have achieved the totals we did – thanks to all attendees.

After a lunch break, we explored the east side of the site and found two spikes of *Dactylorhiza incarnata* ssp. *incarnata*, many more *Ophrys apifera*, *Anacamptis pyramidalis* and *Neottia ovata*. Details of the orchids and locations have been passed onto the VC county recorder.

Figure 1: Very pink-coloured *Dactylorhiza praetermissa*, possibly due to heavy-metal ground pollution.

Figures 2-4: Dactylorhiza purpurella var. atrata.

Photos by Alan Gendle



Field Trip to Bedfordshire and Buckinghamshire Richard & Geraldine Hogg

The field-trip on the 8th June attracted eight HOS members. In the morning there was some rain, but by the afternoon it was dry and sunny. Four sites were explored starting with Cowslip Meadow (CWS), Luton. This is a large area of grassland by the A6, and is surrounded on two sides by houses. Orchids can be found scattered over much of the site, but an area called 'The Scrape' which some years gets flooded in the Winter, has less vegetation and contains an interesting chalk flora. Commonspotted Orchids (*Dactylorhiza fuchsii*), Southern Marsh Orchids (*Dactylorhiza praetermissa*), and many hybrids (×*Dactylorhiza grandis*), some richly coloured, were seen here, along with a few Bee Orchids (*Ophrys apifera*). This year Cowslip Meadow has been relatively dry, but the orchids were doing well.

The second site visited was Sharpenhoe Clappers (NT). This is a large reserve with meadows, woodland, and downland. The wild-flower rich grassland close to the road was explored and produced Common Spotted-orchids, Common Twayblades (*Neottia ovata*), Bee Orchids, and Pyramidal Orchids (*Anacamptis pyramidalis*) which were just coming into flower. A white flowered Common Spotted-orchid was found (var. *albiflora*). At lunchtime, on our way to the next site, there was a short break at a local garden centre.

In the afternoon Totternhoe Nature Reserve (BCN Wildlife Trust) was visited. This is an old chalk quarry where many orchids were in evidence, including Common Spotted-orchids, Bee, Pyramidal, Common Twayblades and Man Orchids (*Orchis anthropophora*). The latter were flowering well this year. Two Common Spotted-orchids of the variety *rhodochila* were found on one of the slopes. The Musk and Frog Orchids were not yet in flower.

By the time we had finished at Totternhoe, it was mid-afternoon, and we then offered the field-trippers another excursion to Aston Clinton Ragpits (BBOWT), which all but two of them accepted. After refreshments at College Lake Reserve (BBOWT) we went on to the Ragpits where a number of orchid species were in flower. The Greater Butterfly-orchids (*Platanthera chlorantha*) were flowering very well this year, and there were a few White Helleborines (*Cephalanthera damasonium*) still in flower.

Figures 1 & 2: Common Spotted-orchid variety *rhodochila* at Totternhoe, Bedfordshire.

Figure 3: Many of the Man Orchids at Totternhoe are protected by fences. Other Man Orchids could be found just outside the fence, and also scattered across the site.

Photos by Richard Hogg





Many other orchids, including Common Spotted, Common Twayblades, and Chalk Fragrant (*Gymnadenia conopsea*) were in flower. There were thousands of the latter species, but they were not quite at their peak. A number of Broad-leaved Helleborines (*Epipactis helleborine*) were seen in leaf, some with the start of the flower stalk. Two intergeneric hybrids were found of Chalk Fragrant-orchid × Common Spotted-orchid (×*Dactylodenia st-quintinii*).

During the trip, a total of £32 in donations was collected and was forwarded on to the BCN Wildlife Trust.

Field Trip to Minera Quarry: Sunday Roast! Sue Parker

I'm delighted to say that everybody on the 1st July 2018 walk at this wonderful 'new' North Wales Wildlife Trust (NWWT) reserve found the site location, and all 15 of us were ready to set off on time with our two excellent NWWT guides, Simon Mills and 'Kipper' Davies. It was roasting hot – already 22 degrees at 10.30 and 28 degrees when we finished at around 14.00. The walk was taxing in parts due to the underlying



HOS Field Trip to Minera Quarry Photo by Sue Parker

limestone scree, but there were plenty of gallant helpers to give assistance at stiles and a couple of low fences. Despite my worst fears about a lack of orchids due to the intense heat of the past few weeks, we found most of species known to occur in the quarry – and in quantities I could not believe given the conditions. These included a few Frog Orchids, which our guides knew were tucked away in a shady section of the reserve and therefore still in flower when plants in more open locations had definitely croaked several days earlier. Species found were Chalk Fragant-orchid *Gymnadenia conopsea*, Common Spotted-orchid *Dactylorhiza fuchsii*, Northern Marsh-orchid *Dactylorhiza purpurella*, Frog Orchid *Dactylorhiza viridis* and Broadleaved Helleborine *Epipactis helleborine*. Bee Orchid *Ophrys apifera* had already gone over.

Minera Quarry is already an outstanding orchid-rich nature reserve and we eagerly anticipate developments as NWWT get their management programme underway. In the few months since they acquired the site huge strides have already been made in improving various parts of the reserve and the numbers (and possibly the diversity) of plants can only increase under the new stewardship.

Many thanks to Simon Mills and 'Kipper' Davies of NWWT and to those HOS members who came along and 'stuck with the programme' despite the extreme heat.





A selection of our botanical tours

Autumn Flora of the Peloponnese

Crete in Autumn

Drakensberg in South Africa

Cyprus in Spring

Orchids of Rhodes

Italy: The Gargano

Greece: Peloponnese in Spring

Lesvos at Leisure

Greek Macedonia

Kent: Orchid Garden of England

Eastern French Pyrenees

France: The Vercors

Bulgaria: Flowers & Butterflies

Italy: The Dolomites

Turkey: The Kackars

20 - 27 Oct

27 Oct - 3 Nov

24 Jan - 7 Feb

2 - 10 Mar

4 - 11 Apr

11 - 18 Apr

11 - 18 Apr

26 Apr - 3 May

3 - 10 May

16, 17 & 18 May

17 - 24 May

25 Jun - 2 Jul

25 Jun - 3 Jul

3 - 10 Jul

11 - 19 Jul

Private and bespoke tours also available on request

Led by knowledgable & experienced guides, including Dr Yiannis Christofides, Jon Dunn & Dr Paul Harcourt Davies