Journal of the HARDY ORCHID SOCIETY

Vol. 11 No. 3 (73) July 2014

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 website <u>www.hardyorchidsociety.org.uk</u>, January 2004 Journal, Members' Handbook 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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Cover Photographs

Front Page: Fen Orchid (*Liparis loeselii* subsp. *loeselii*) in Norfolk Back Page: *Ophrys apifera* var. *chlorantha* in Norfolk See report of HOS field trip on page 103 Photos by Mike Gasson

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Editorial Note

Richard Bateman has contributed another of his informative articles to this issue of *JHOS*. This time he addresses an important and sometimes overlooked aspect of orchid biology, namely their intimate and critical association with fungi.

During May this year I was asked by the RSPB if HOS members would be interested in visiting a normally closed site to see and photograph the Fen Orchid in Norfolk. As described in a separate report, this proved to be a popular and successful extra field trip. I am sorry if the use of the Discussion Forum to organise this event missed some members but it was deemed to be the only way to publicise it as we were between journals. There may be another opportunity next year, hopefully integrated with the main field trip programme. Related to this, there is a serious conservation issue associated with agricultural abstraction of water near to these orchid sites. Please take a moment to read the panel on page 105 and do all you can to support RSPB in protecting these sites. There is a petition to sign and you can make personal support statements via the RSPB and Environment Agency websites. There is another website to investigate if you have an interest in a co-ordinated search for the Ghost Orchid at its former UK sites. For this, take a look at Sean Cole's article on page 106.

Chairman's Note Celia Wright

Greetings to you all. I hope you're all enjoying this year's hardy orchid season, especially those who have been on one or more HOS field trips. Iain and I enjoyed an excellent walk in Surrey with lots to see and have vowed to try to attend more field trips next year. Volunteers to lead these are always welcome, especially to new areas: please contact Alan Bousfield. Along with all our committee members, you'll find his contact details inside the front cover of this Journal.

I hope to see many of you at one or both of our autumn meetings – Leeds on Saturday 6th September and Kidlington on Sunday 16th November. The booking forms (with programmes on the reverse) are enclosed with this issue of the Journal. I'd also like to remind you that a few places are still available at the seed sowing workshop on Sunday August 17th. Contact Alan Leck, our Seed Bank Manager, if you'd like more details.

Our committee has changed following the AGM with all roles filled for now. We have a Treasurer elect for 2015 onwards, but will need a new Secretary and Vice Chairman then, so there are still opportunities for you to volunteer.

Looking ahead to our 2015 Plant Show at Kidlington on April 19th, we will have a new trophy. For many years, the Banksian Medal has been awarded to the most successful exhibitor, but when an individual has won this, they cannot win again for 3 years, quite often leaving a member without recognition of their recurrent achievement. For this reason, and to mark the end of my 5 years as HOS Chairman, I have decided to donate a trophy for the exhibitor gaining the highest number of points overall in the Show in that year. We have also agreed to have a new class for plants grown from seed by the exhibiting member. Full details of this new class will appear on the website later in the year.

As we move into 2015, The European Orchid Congress returns to London on $9^{th} - 12^{th}$ April, and will include a hardy orchid symposium. The British Orchid Council plans to have a display stand with plants from various orchid societies. Because of the emphasis on hardy orchids, I hope HOS will be able to contribute to this and also supply our society information to all the delegates. More information is available at <u>http://www.rhs.org.uk/shows-events/rhs-london-shows/european-orchid-show-and-conference-2015</u>

My best wishes to you all.

Results of HOS Plant Show 2014

Class 2: Three pots native European (not native to Britain) orchids, distinct varieties

1st Barry Tattersall: Ophrys bertolonii; Ophrys bombyliflora; Ophrys vernixa

Class 3: Three pots non-European hardy orchids, distinct varieties

- 1st Barry Tattersall: Diuris orientalis; Serapias carica; Ophrys regis-ferdinandii
- 2nd Mike Powell: Ophrys fusca; Ophrys garganica; Ophrys iricolor

Class 4: Three pots hardy orchids, distinct varieties, any country of origin

- 1st Barry Tattersall: Serapias neglecta × Anacamptis morio; Ophrys speculum; Anacamptis longicornu Miles Bernelli, Orchis maringiclis; Orchis and henry Orchisiti
- 2nd Mike Powell: Orchis provincialis; Orchis anthropophora; Orchis italica

Class 5: One pot native British orchid

- 1st Neil Hubbard: Anacamptis morio
- 2nd Mike Powell: Anacamptis morio

Class 6: One pot native European (not native to Britain) orchid

- 1st Mike Powell: Gennaria diphylla
- 2nd Barry Tattersall: Ophrys speculum
- 3rd Andrew Bannister: Orchis italica

Class 7: One pot non-European orchid

1st Malcolm Brownsword: *Pleione* Dr. Mo. Weatherhead

Class 8: One pot Dactylorhiza

1st Barry Tattersall: Dactylorhiza romana

Class 9: One pot Orchis, Anacamptis or Neotinea

- 1st Barry Tattersall: Orchis ichnusae
- 2nd Malcolm Brownsword: Anacamptis morio × Anacamptis longicornu
- 3rd Neil Evans: Anacamptis papilionacea

Class 10: One pot Ophrys

- 1st Barry Tattersall: Ophrys tenthredinifera
- 2nd Mike Powell: Ophrys tenthredinifera
- 3rd Neil Evans: Ophrys kotschyi subsp. ariadne



Class 11: One pot Serapias

- 1st Barry Tattersall: Serapias neglecta × Serapias lingua
- 2nd Neil Evans: Serapias vomeracea

Class 12: One pot Cypripedium

- 1st Malcolm Brownsword: Cypripedium formosanum
- 2nd Andrew Bannister: Cypripedium formosanum
- 3rd Mike Powell: Cypripedium formosanum

Class 13: One pot Calanthe

- 1st Jeff Hutchings: Calanthe brevicornu
- 2nd Jeff Hutchings: Calanthe Kozu Brown

Class 14: One pot *Pleione*

1st Malcolm Brownsword: Pleione Masaya

There were no further entries in classes where only 1st or 1st & 2nd places are recorded There were no entries in Class 1 and Class 15.

Winner of Best in Show Trophy - Barry Tattersall for Diuris orientalis in Class 3

Winner of RHS Banksian Medal - Mike Powell

Banksian Medal Points:

Barry Tattersall - 29 points; Mike Powell - 16 points; Malcolm Brownsword - 11 points; Neil Evans - 3 points; Neil Hubbard - 3 points; Jeff Hutchings - 3 points

Barry Tattersall had most points (29) but won the medal in 2012; the RHS rules preclude winning it again this year, hence the medal was awarded to Mike Powell (16 points).

Thanks to Brian Walker for judging the Plant Show

More 2014 Plant Show Winners

Numbers indicate the class for first place winning plants. Fig. 2: Ophrys bertolonii Fig. 3: Diuris orientalis (Best in Show) Fig. 10: Ophrys tenthredinifera Fig.11: Serapias neglecta × Serapias lingua Plants by Barry Tattersall Photos by Mike Gasson



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Visit our new web site <u>www.lanesidehardyorchids.com</u> for full details of plants available for sale on line, 2014 shows and events, cultural information and nursery opening.

A wide range of different hardy orchids are stocked including pleiones for the first time

Contact: Jeff Hutchings, 74 Croston Road, Garstang, Preston PR3 1HR 01995 605537 jcrhutch@aol.com 07946659661



Plumbing the Depths: A Review of Recent Research on Terrestrial Orchid Mycorrhizae Richard Bateman

The recent study of speciation among the Azorean Butterfly-orchids – first unveiled at the HOS's spring 2012 Kidlington meeting – is the first of my research projects to have involved gathering data from the mycorrhizal fungi associated with the roots of my beloved orchids. Writing up the fruits of this three-year project recently encouraged me to read through the rapidly growing body of relevant literature more widely and more carefully than I have done before. Having consequently become even more impressed and/or intrigued by the content of some of the papers published during the 'DNA Era', I decided to prepare a brief summary of potential interest to HOS members. Given my own interests, I have inevitably focused more on ecology and evolution than on horticulture, though growers should nonetheless be able to find something of value within this (admittedly term-laden) article.

Perhaps surprisingly, non-horticultural studies of orchid mycorrhizae have focused more on temperate terrestrial species than on tropical epiphytic species. Fortunately for us, European species have been especially popular models. The scientific interest of orchid mycorrhizae resides in four main questions relating to the fungal symbionts:

(1) What are the taxonomic identities of the mycorrhizae associated with particular orchids?

(2) What are the taxonomic diversity and evolutionary breadth of the fungi? (ideally estimated at different levels – individual, population and species – within the relevant orchid species).

(3) What is the net contribution (if any) of the fungi to the nutrition of the orchid, particularly in nitrogen- and carbon-based compounds? (hereafter abbreviated to N and C; ideally tracked from seed to senescent adult and across all phases of the orchid's annual growth cycle, and assessed using isotopic ratios).

(4) Where did that net fungal contribution of N and/or C originate?

Admittedly, by no means all of the relevant questions have yet been answered and, as always in science, each question answered prompts further questions.

Where do the orchids and fungi obtain their nutrients?

I suppose it was inevitable that the 'obligate mycoheterotrophs' (those orchids formerly known, less jaw-crackingly, as 'saprophytes') would generate the earliest relevant data-sets, as for a typical mycologist they are the sexiest of all fungal host-plants (Fig. 1). Early expectations that these orchids were merely using their fungal partners as conduits to extract nutrients from rotting vegetation were rudely overturned when it became clear that the orchids were actually using the mycorrhizae

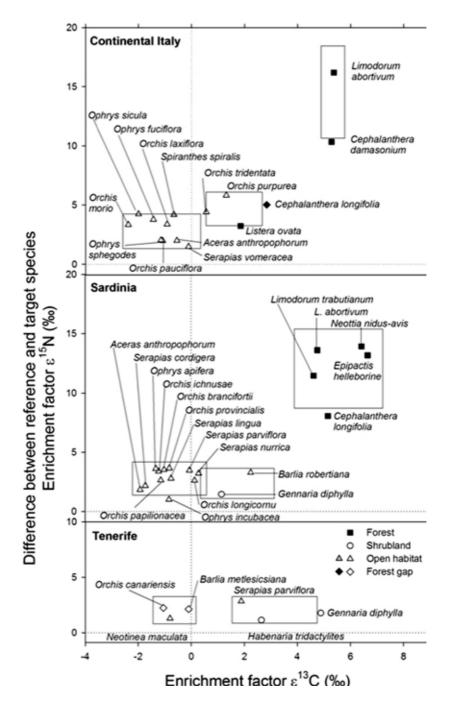
as plumbing systems to connect them to the roots of living trees (Selosse *et al.* 2002; Bidartondo *et al.* 2004). An innocent-looking Bird's-nest Orchid (*Neottia nidus-avis*) projecting from leaf litter in the middle of a sparsely populated beechwood takes on a far more sinister aspect when you realise that it is not genuinely saprophytic but rather parasitic, sucking the life blood out of the trees that also provide their muchneeded shade (admittedly, I may be over-dramatising a little here). And mycorrhizal networks can become sufficiently extensive that the orchid could be tapping into not one but several adjacent trees, drawing heavily on both N and C nutrients (Fig. 2). To use a rather dubious analogy, the orchid can be viewed as a light bulb that draws energy from solar-powered photosynthetic trees via mycorrhizal cabling.



Figure 1 (above) Morphological comparison of (a) autotroph *Orchis militaris*, (b) mixotroph *Neottia* (*Listera*) *ovata*, and (c) obligate mycoheterotroph *Neottia ni- dus-avis*.

Photos by Richard Bateman

Figure 2 (right) Mycorrhizally-mediated enrichment of C and N, assessed via isotopic signatures, for several woodland and grassland orchid species studied in northern Italy, Sardinia and the Macaronesian island of Tenerife. Figure 1 of Liebel *et al.* (2010), who used traditional rather than modern orchid names.



When mycologists later turned their attention to orchids of unshaded habitats, the results were both less spectacular and more ambiguous. Studies of individual species often yielded apparently contradictory results. For example, one investigation of *Platanthera bifolia* in southern France suggested that it drew at least some C and N from its fungal partners (Gebauer & Meyer 2003), whereas a study of a conspecific population in Estonia (Tedersoo *et al.* 2007) indicated that the orchids were actually losing a small amount of their home-produced nutrients to the fungus – in other words, the fungi were lightly parasitising the orchids rather than vice versa! It has been suggested (notably by Girlanda *et al.* 2011) that Orchideae that do not produce leaf rosettes until the spring (e.g. most species of *Orchis s.s.*) may require more input from mycorrhizae than those that produce rosettes in autumn. These wintergreen genera, which include *Anacamptis s.l.*, *Ophrys* and *Serapias* (Fig. 3), have a longer cumulative period of photosynthetic activity. However, this inference is not supported by data generated during the few studies that compared the mycorrhizal performance of several grassland orchid species (e.g. Liebel *et al.* 2010).

In truth, the distinction between obligate mycoheterotrophs such as Bird's-nest Orchid that are constantly dependent upon their fungal symbionts for nutrition versus grassland orchids such as anthropomorphic *Orchis* species that apparently gain far less benefit from their fungal cohabitants (at least as mature plants) is less clearcut than might first appear (Fig. 2). Strategically placed between the two seemingly discrete categories is a poorly-defined group of orchids known collectively as mixotrophs (e.g. Gebauer & Meyer 2003). These orchids gather nutrition from both their leaves through photosynthesis (an approach termed autotrophy) and from their fungal partners through what is effectively parasitism (mycoheterorophy). Within particular species, the relative contributions of the two sources of C differ from population to population and, within populations, from juvenile to mature plants. Also, within each of these categories of maturity, plants differ between contrasting phases of the annual growth cycle, especially spring versus summer (e.g. Roy *et al.* 2013).

Studies of such mixotrophs have focused on species that have been shown, through DNA-based reconstructions of evolutionary trees, to be closely related to obligate mycoheterotrophs. A good example is the Common Twayblade, *Neottia* (formerly *Listera*) *ovata*, which is closely related to, and a potential ancestor of, *Neottia nidus-avis*. Another example of a mixotroph is the Japanese Butterfly-orchid, *Platanthera minor*. Mixotrophic orchids obtain variable amounts (typically less than half) of their N and C from fungal associates, the amount generally increasing through the growing season. Biologists are especially interested in inferring how such a mixed-economy plant may successfully evolve into an obligate mycoheterotroph. One fruitful approach has been to study, within mixotrophic species such as *Cephalanthera damasonium* and *Epipactis purpurata*, individuals that have at least temporarily

switched to an obligately mycoheterotrophic lifestyle. Such plants take on a spectral appearance – they are translucent white in the case of *C. damasonium* and translucent pink in the case of *E. purpurata*. By definition, once they have lost the functional green chloroplasts essential for photosynthesis, these plants must rely entirely on mycorrhizae to supply their energy needs (e.g. Roy *et al.* 2013), yet – as has been noted previously in the pages of *JHOS* – such individuals often flower for several successive years. They do not appear to be overly handicapped by their happenstance 'misfortune'.

What kind of fungi form relationships with orchids?

One of the more startling discoveries achieved through early DNA-based investigations was that fungi are more closely related to animals than they are to plants. The relatively simple morphology of fungal hyphae, combined with the reluctance of many mycorrhizal fungi to reproduce sexually, has caused determining the taxonomic affinity of mycorrhizal fungi to become almost entirely the preserve of DNA studies. Indeed, the most popular gene for studying the identity of, and relationships among, mycorrhizae is that also favoured for studying their 'host' orchids, namely ITS. Because species concepts are far less well-developed for mycorrhizal fungi than for their orchid hosts, a particular fungal species is more likely to be 'named' using a number rather than a Linnean binomial. And even when a Linnean binomial is used (e.g. arguably the most common mycorrhizal associate of European grassland orchids is *Tulasnella calospora*), the name is likely to encompass several species of fungus that have not yet been adequately distinguished through applying a battery of analytical techniques.

Woodland-dwelling neottioid orchids tend to associate with particular basidiomycetes (the major group of fungi that produce toadstools) whose survival requires them to form mycorrhizal relationships with plants (obligate mycorrhizae: e.g. Selosse *et al.* 2002; Bidartondo *et al.* 2004; Girlanda *et al.* 2006). Fungi associated with *Cephalanthera, Epipactis* and *Neottia* include *Inocybe, Sebacina* and *Tomentella*, occasionally with the non-obligate mycorrhiza *Ceratobasidium*, the ascomycete *Wilcoxina* and most memorably, the truffle *Tuber. Limodorum* reliably associates with *Russula*. Moving on to consider obligate mycoheterotrophic orchids other than neottioids, *Corallorhiza* similarly associates with *Russula* and close relatives, whereas *Epipogium* favours *Inocybe*.

The taxonomic affinities of fungi extracted from the grassland orchids have proven to be remarkably consistent at family level. Although the heliotalean ascomycete *Leptodontidium orchidicola* has been shown to be the most common fungal associate of *Gymnadenia conopsea s.s.* in some German populations, almost all grassland orchid mycorrhizae are basidiomycetes. A pattern of dominant Tulasnellaceae and subordinate Ceratobasidiaceae – fungal families within the basidiomycete order Cantharellales that form optional rather than obligate relationships with their orchid hosts – has emerged from almost all studies of European Orchideae genera (e.g. Bidartondo et al. 2004; Liebel et al. 2010; Girlanda et al. 2011; Jacquemyn et al. 2011, 2012a, 2012b; Bailarote et al. 2012; Kohout et al. 2013; Tesitelova et al. 2013): Dactylorhiza, Gymnadenia, Platanthera, Pseudorchis, Orchis s.s., Anacamptis s.l., Serapias and Ophrys. Occasionally, orchid populations are found that are dominantly associated with Ceratobasidiaceae rather than Tulasnellaceae; for example, single populations of *Himantoglossum s.l.* on Sardinia, and of *Habenaria* and *Neotinea* s.l. on Tenerife (Liebel et al. 2010). Another Tenerifean orchid population, of the comparatively 'primitive' Orchideae Gennaria, proved to be associated with Russulaceae and Sebacinaceae (Liebel et al. 2010) – mycorrhizae more typical of neottioid orchids pursuing mixotrophic or obligately mycoheterotrophic life histories (cf. Girlanda et al. 2006; Bidartondo & Read 2008; Roy et al. 2013). This fact may explain why, among the six Tenerifean orchid genera analysed by Liebel et al., Gennaria was the only genus to show substantial gains in C comparable with those achieved by neottioid orchids in mainland Europe (Fig. 2).

How specfic are mycorrhizal partners?

Recent mycorrhizal studies have tended to address more profound questions than simply identifying the mycorrhizae found within a particular population of orchids. They go on to ask how many species of fungi can be found within a single orchid plant, within a single population, and among populations across part or all of the geographic range of the orchid species. Also, if multiple fungal species are associated with a particular orchid species, it is helpful to know whether those fungal species are closely or more distantly related to each other. When an orchid forms relationships with a few closely related partners it indicates what is known as high specificity (e.g. Bailarote *et al.* 2012) – this implies an intimate, long-term relationship between fungus and orchid that could in theory reflect co-evolution. In contrast, an orchid that develops relationships with a larger number of less closely related fungi could indicate the formation of loose and perhaps transient 'marriages (affairs?) of convenience' – in other words, the orchid seed reaches a congenial habitat and then becomes infected with whichever vaguely compatible partner is most readily available in the underlying soil.

Obviously, the distinction between high and low specificity is of importance well beyond the boundaries of evolutionary biology. Certainly, it has profound implications for attempts to conserve declining orchid species or to predict the likely impact on orchids of climate change. However, anyone seeking to extract generalised statements from the data currently available on mycorrhizal associations is facing an uphill struggle. Some studies suggest the potential for exceptional specificity. For example, a recent study of ten populations of *Gymnadenia conopsea* in Czechoslovakia (Tesitelova *et al.* 2013) showed that, within the spectrum of

Tulasnellaceae fungi typical of grassland orchids, plants of different ploidy levels (i.e. possessing different chromosome numbers) form relationships with different *Tulasnella* speces. Moreover, this statement appears to apply irrespective of spatial scale. Population-level rather than species-level specificity characterizes mycorrhizae of North American *Corallorhizas* and Belgian *Dactylorhizas* (Jacquemyn *et al.* 2012a). Within *Dactylorhiza*, even individual orchids often prove to have multiple fungal partners (Jacquemyn *et al.* 2012a).

Bailarote *et al.* (2012) compared the mycorrhizae of five populations each of the successful, resilient *Dactylorhiza fuchsii* and rapidly declining *Anacamptis morio* in Belgium, anticipating that the degree of mycorrhizal specialisation would be greater in the less ecologically successful orchid – in other words, that *A. morio* was being penalised ecologically for having formed close relationships with few fungi rather than transient relationships with many. In fact, *D. fuchsii* proved to be associated with a smaller number of more closely related mycorrhizal species. Having found a similar degree of conservatism among mycorrhizae associated with *Orchis s.s.* species across Europe, Jacquemyn *et al.* (2011) speculated that orchid species with lower mycorrhizal diversity tend to form relationships with more geographically and/or ecologically widespread generalist fungal partners, making these orchids comparatively independent of the distributions of their mycorrhizae – wherever their seeds land there is a reasonable chance that they will encounter at least one acceptable fungal partner.

An additional complicating factor is provided by the high probability that a particular orchid plant will form relationships with different suites of fungi as it matures. It has long been known that an orchid tends to require different spectra of mycorrhizae to initiate germination in its minute, resource-deficient 'dust-seeds' than it does to maintain its mature tuber or rhizome (e.g. Bidartondo & Read 2008; Jacquemyn *et al.* 2012b). However, more recent studies suggest that mycorrhizal specialisation is greater in seedlings than in either germinating seeds or adult plants (e.g. Bidartondo & Read, 2008; Jacquemyn *et al.* 2012a, 2012b). Expressed another way, providing adequate nutrients to the developing seedlings may be the most crucial stage in the growth of an orchid, constituting a potential ecological bottleneck during which the effects of natural selection are likely to be felt most severely ... but only if the mycorrhizal association is indeed crucial to the well-being of the orchid. All too often, the existence of this co-dependence is assumed rather than truly demonstrated.

The many challenges posed by the all-important specificity question are epitomised by the recent, exceptionally thorough study of the fungal associates of *Pseudorchis* conducted by Kohout *et al.* (2013). They subjected 17 plants, sampled twice (June and September) within five Czech populations of *Ps. albida*, to three contrasting approaches designed to assess the range of fungal species associated with the roots.

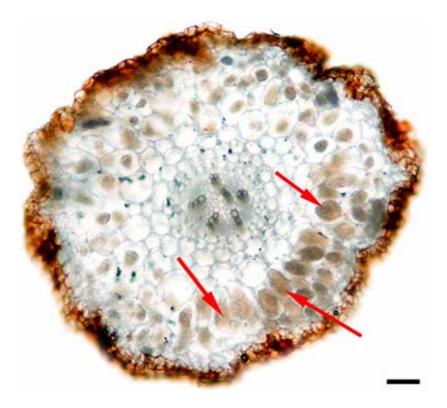


Figure 3. Pelotons of mycorrhizal hyphae (arrowed) filling the intracellular spaces of cortical cells of a Serapias vomeracea root. Scale = $50 \mu m$. Figure 1 of Girlanda *et al.* (2011)

Taken together, the three approaches detected exceptional diversity, totalling 66 presumed species of fungi (similar fungal diversity was detected by other authors in the threatened North American endemic *Platanthera leucophaea*). However, only 15% overlap was identified between the spectra of fungal genetic lineages obtained in June and September. Simply screening any fungi associated with the roots of the orchids yielded an estimated 42 species. Narrowing sampling to fungi found within root sections yielded 26 species (20 in June and 12 in September). Constraining sampling still further to only fungi that formed spaghetti-like pelotons within the cells of the orchid roots (Fig. 3) revealed only eight species.

But the most remarkable observation of Kohout *et al.* was that individual orchids sampled for pelotons in June yielded one or more of three species of *Tulasnella*, whereas this near-ubiquitous fungal genus was not detected in the September sampling; rather, two species of the heliotalean ascomycete *Varicosporium* dominated.

The authors understandably inferred that *Tulasnella* is a *bona fide* mycorrhiza, whereas *Varicosporium* has merely invaded the senescing roots that remain attached to the superannuated tuber through the autumn. Viewed with hindsight, this novel observation makes perfect sense.

What insights may the future hold?

So, where do all of these insights (and attendant complications) leave the attempt by my research collaborators and I to interpret the significance (if any) of the mycorrhizae associated with the Azorean *Platanthera* species? One of the more interesting papers of recent years (Waterman *et al.* 2011) contrasted the importance for both speciation and ecological success of inter-species relationships at both ends of the orchids – in this case, in the South African temperate terrestrials of the *Disperis* group (Diseae: Coryciinae). They concluded that speciation in this group of orchids is driven primarily by pollinator specificity (expressed in terms of both the identity of the pollinating insect and the preferred location for placement of the orchid's pollinaria on the body of that insect). In contrast, mycorrhizae act largely as what Waterman *et al.* termed 'habitat filters', the orchids shifting only rarely (but then often radically, and hence significantly) between groups of fungal partners in what is otherwise a highly conserved below-ground symbiotic relationship.

Our Azorean data suggest a somewhat different scenario (Bateman *et al.* 2014). Admittedly, thus far, no-one has observed the pollination of any of the three endemic *Platanthera* species (Fig. 4); we assume that the pollinators are night-flying moths. But the mycorrhizal spectra of the three species are strongly suggestive of a drive towards increased specialisation. All three species have formed relationships with the classic mycorrhizal partners of European orchids, Tulasnellaceae and Ceratobasidiaceae. But the most widespread Azorean *Platanthera*, *P. pollostantha*, has demonstrably formed relationships with six fungal species, whereas the two rarer species each have a single preferred partner – *P. azorica* shares its partner with a few plants of the widespread *P. pollostantha*, whereas *P. micrantha* has a mycorrhizal partner that has not been found in any *P. pollostantha* plant but has been found in some mainland populations of the *P. bifolia–chlorantha* aggregate – the group that undoubtedly contains the mainland ancestor of the Azorean species (Bateman *et al.* 2014). Given these data, it is difficult to believe that mycorrhizae have not played a significant role in these speciation events.

Returning to my overview of the literature on mycorrhizae, this suggested that obligate mycoheterotrophs and mixotrophs (a) belong to the orchid subfamily Epidendroideae (most in tribe Neottieae), (b) typically occur in deep shade in forests, (c) typically form mycorrhizal relationships of varying degrees of specificity with obligate mycorrhizae of families such as Inocybaceae, Tuberaceae, Sebacinaceae and Russulaceae, and (d) rely heavily on their mycorrhizae to supply both C and N



throughout their annual growth cycle – particularly the relatively large proportion of species in tribe Neottieae that are obligate mycoheterotrophs (e.g. Gebauer & Meyer 2003; Bidartondo *et al.* 2004; Roy *et al.* 2013). In contrast, most dominantly autotrophic species (a) belong to subfamily Orchidoideae (most in tribe Orchideae), (b) typically occur in open and/or semi-shaded habitats, (c) typically form mycorrhizal relationships of varying degrees of specificity with facultative mycorrhizae of Tulasnellaceae and/or Ceratobasidiaceae, and (d) rely on mycorrhizae for at most modest injections of N early in the growing season. However, this apparent nutritional distinction between mycoheterotrophs and autotrophs cannot be viewed as definitive, because attempts to quantify transfer of N and C rely on isotopic ratios, and these are prone to fractionation – preferential accumulation and/or utilisation of one isotope over the other isotope by the host plant.

Also, it is even less clear how these four factors (a–d, above) are interrelated. Considering the evolutionary origin of the mycoheterotrophs and mixotrophs, the most likely explanation is that the neottioid lineage first formed a relationship with one or more lineages of fungi that had already entered into mycorrhizal relationships with various tree species. The resulting influx of C and/or N generated by photosynthesis in the trees and then channeled through the conduit of the fungi allowed the orchids to move into deeper shade, where there was less competition from non-orchid herbs for both nutrients and pollinators. Finally, several neottioid lineages underwent the transition from being partially photosynthetic (mixotrophic) to becoming largely or wholly reliant on energy supplied by the surrounding trees.

The considerable number of times when orchid lineages have made this transition from autotrophy to obligate mycoheterotrophy suggests that it is relatively easily achieved (e.g. Bateman *et al.* 2005). On the other hand, the fact that neottioids repeatedly made this transition and orchidoids did not implies that inherited genes may also play a key role. Availability of opportunities to form mycorrhizal relationships may also be crucial; one interesting comment made by Liebel *et al.* (2010) is that neottioids could have failed to invade any of the Macaronesian archipelagos because suitably aggressive mycorrhizae may be absent from the islands' soils.

The present definitions of a fungal species (e.g. greater than 97% similarity in ITS sequences) are far less sophisticated than the species definitions that can now be applied to the orchids (cf. Bateman 2012). Nonetheless, it is clear that the fungal diversity associated with an orchid throughout its life-span is far greater than most of us ever suspected. Consequently, it remains a serious challenge to identify the

Figure 4. Mycorrhizal generalist (a) and specialists (b, c) among Azorean orchids, illustrated using flowers of (a) *Platanthera pollostantha*, (b) *P. micrantha* and (c) *P. azorica*.

Photos by Richard Bateman

precise physiological relationship between the orchid and any particular fungal species (e.g. Waterman *et al.* 2011), particularly as both the identity and contribution of the fungal associates can apparently change through a single growing season. Indeed, our methods of identifying both fungi and their nutritional contributions remain relatively crude and unreliable. We have evidently learned much about the relationships between terrestrial orchids and their mycorrhizal associates, but equally, much of importance still eludes us.

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Some Observations on *Dactylorhiza fuchsii* × *Gymnadenia conopsea* hybrids found in the Chilterns Richard Hogg

In the Chiltern Hills there are many sites where the Common Spotted-orchid (*Dactylorhiza fuchsii*) and the Chalk Fragrant-orchid (*Gymnadenia conopsea*) occur together in large numbers. So the possibility of the inter-generic hybrids of the two (*xDactylodenia st-quintinii*) occurring is high, especially as the two genera are closely related. Encouraged by Alan Gendle's article on "Identifying Hybrid Orchids" in 2012, my wife and I carried out initial searches for *xDactylodenia* hybrids at Grangelands/Pulpit Hill, Buckinghamshire, and at Aston Clinton Ragpits (BBOWT), Buckinghamshire, in June 2013. At that time, the two species were in full flower at both sites. Looking for hybrids in the large populations of orchids is very time consuming, and only one possible hybrid was found at each location. Even then the identification of each as a hybrid was not certain.

Then in early July, one definite \times *Dactylodenia* hybrid was found by myself on the downland on the east side of Sharpenhoe Clappers, Bedfordshire. At this National Trust site, most of the Chalk Fragrant-orchids had finished flowering, and some of the Common Spotted-orchids still had a few flowers, but most were more or less finished. It was during a search for Bee orchids (which are scattered across the downland) that the hybrid was found. The plant was 29cm high and in full flower. The inflorescence was long, similar to many Chalk Fragrant-orchids, but from a distance the plant as a whole looked like a Common Spotted-orchid. The leaves were faintly spotted, the spurs were longer and thinner than those on Common Spotted-orchids, the flowers had a strong fragrance, and the labellum was marked similarly to Common Spotted orchids.



Inflorescence (left) and flower close-up (right) of the *Dactylorhiza fuchsii* × *Gymadenia conopsea* hybrid at Sharpenhoe Clappers, Bedfordshire. Photos by Richard Hogg

Later in July, a return visit was made to Aston Clinton Ragpits to search for whiteflowered Pyramidal orchids (of which one was found). Most orchids had finished flowering, but the Pyramidal Orchids were in full flower, as were a few shaded Common Spotted-orchids. Amongst the remaining flowering orchids, we spotted four definite ×*Dactylodenia* hybrids and all were in an open position. From a distance they all had the appearance of being Chalk Fragrant-orchids, but closer inspection showed Common Spotted-orchid characteristics. The first three described in the following list were very close to each other and the fourth was in another part of the reserve: **Hybrid 1:** Leaves faintly spotted, 38cm high with inflorescence of 10cm, fragrant and with Common Spotted-orchid markings on the labellum.

Hybrid 2: Leaves unspotted, 22cm high with inflorescence of 4.5cm, fragrant, with Common Spotted-orchid markings on the labellum, and long spurs.

Hybrid 3: Leaves spotted, 37.5cm high with inflorescence of 14cm, fragrant and with Common Spotted-orchid markings on the labellum.

Hybrid 4: Leaves spotted, 47cm high with inflorescence of 18cm, fragrant and with Common Spotted-orchid markings on the labellum. The flowers were almost finished - the top ones had long curved spurs.



Inflorescence of a *Dactylorhiza fuchsii* × *Gymadenia conopsea* hybrid at Aston Clinton Ragpits, Buckinghamshire, showing very long spurs. Photo by Richard Hogg

Another scented plant, in full flower, was found in the open. This was a tall plant, 60cm high, with pure white flowers and short spurs, but no markings. It had faintly spotted leaves and looked like a Common Spottedorchid. From later research at home (Harrap & Harrap 2009, and Foley & Clarke 2005) it appears that Common Spotted-orchids can be scented. So from the plants' characteristics it was concluded that this was probably a fragrant late-flowering Common Spotted-orchid, and not a hybrid.

From this brief study a number of observations and points can be made:

i) The hybrids were a lot more common than we expected. The only problem seems to be finding them in large populations.

ii) The hybrids described here from Bedfordshire and Buckinghamshire are assumed to be all *×Dactylodenia*

st-quintinii, as the two parent plants are found in large numbers at the same sites.

iii) The hybrids seem to flower later, or perhaps longer, than the parent plants, making them easier to spot at a later date.

iv) The leaves may be spotted or unspotted. The flowers have markings like Common Spotted-orchids and the spurs are longer than those on Common Spotted-orchids.

v) The hybrids that we found all had a strong scent, but it is important to note that fragrance is not just a characteristic of Fragrant-orchids and their descendants, as Common Spotted-orchids and other orchids can also be scented.

vi) The hybrids from the two sites were certainly different in appearance. Could this be the result of different seed-parents? Some could be produced from seeds of Common Spotted-orchids and others from Chalk Fragrant-orchid seeds.

Next year we shall continue to look for more hybrids and we hope to find out more about them, and perhaps answer some of the following unresolved questions:

i) Can both species be the seed-parent of this hybrid?

ii) At the Aston Clinton Ragpits orchid count in June (Townsend, 2013) it was reported that 5837 Fragrant-orchids and 1210 Common Spotted-orchids were found, whereas at Sharpenhoe Clappers there are many Common Spotted-orchids and fewer Fragrant-orchids. So is it possible that, if there are more individuals of one species at a site, then the probability of that species being the seed-parent of a hybrid is increased? Or is it the case that one of the seed-parent species is more likely to produce viable seed?

iii) Are seeds produced by back-crosses possible, and if so, are they viable? Seed capsules certainly do form on the hybrids.

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Variations of the genus *Cephalanthera* on Estonian Island of Saaremaa Tarmo Pikner

Taxonomy and distribution of the genera Cephalanthera

This article is based on more than ten years' observations of several populations of *Cephalanthera* on the Estonian Island of Saaremaa and describes a number of interesting variations. *Cephalanthera* have a mainly Eurasian distribution and include at least 15 species (Delforge 2005). Three species, *Cephalanthera damasonium, C. longifolia* and *C. rubra*, are found in most of the European regions where wild orchids are present.

C. damasonium prefers mid-shade to shade on calcareous to slightly acidic substrates in beechwoods, pine forests or mixed forests. *C. longifolia* grows in mid-shade on calcareous substrates in open pine forests, mixed forests, in clearings of broad-leaved woodlands; sometimes even in open grassland. *C. rubra* likes mid-shade to shade on calcareous to slightly acidic substrates in pine forests, beechwoods or woodland edges. All of these three species need a habitat with dry soil, although *C. longifolia* is more dependent on moisture than the two others.

Surprisingly, *C. damasonium* is absent in Estonia and the closest distribution area is on the Island of Gotland (Sweden), some two hundred kilometers from the Estonian Island of Saaremaa. The ecological preconditions for appearance of similar taxa exist on both Baltic Sea islands but for some reason *C. damasonium* did not reach Estonia during the recolonisation process after the last glaciation (Pikner 2012). In contrast, *C. longifolia* is comparatively widespread in Saaremaa, especially in the wooded western part of the island. However, on the mainland of Estonia *C. longifolia* is rare, having just a few populations in the western littoral. *C. rubra* is sparsely distributed in Saaremaa and rarely found on the mainland of Estonia (Kuusk 1984; Schmeidt 1996; Kull & Tuulik 2002; Pikner 2013).

Double-spike Helleborine

Cephalanthera species are rhizomatous geophytes having underground, creeping, short rhizomes and deep roots reaching up to a half metre. Every year new buds appear underground, facilitating vegetative multiplication starting from the rhizome and providing an alternative method of multiplication to seed reproduction.

Sometimes, during monitoring of populations of *Cephalanthera longifolia* in Saaremaa, clusters of plants consisting of 5-9 individuals have been discovered. Often the plants grow very close to each other such that they appear to be shooting from the same source (see Fig. 1). In extreme situations a phenomenon of 'grown together stem' appears. The author has observed different variations of the phenomenon. Firstly there is a case where one stem comes out from the ground but very soon, at a height of 3-4 cm, it branches into two stems. The plant looks like a normal *C. longifolia* having just two branches but both have an inflorescence (see Fig. 2). The spikes and the other features of the two-branched stem form of *C. longifolia* are the same as normal individuals.

Another similar variation discovered by the author is where the plant has a double inflorescence (see Fig. 3). It should be noticed that the stem of the plant is not twice as thick and a presumptive division-line between two stems is not visible. The two inflorescences are in every respect as in normal individuals and the plant looks just like an orchid with two inflorescences. Earlier reports of similar plants of *Cephalanthera* have been published such as that named as f. *bispicata* Schulze and f. *trispicata* Camus (P. Delforge in litt.).

In June 2002 the author discovered another double individual. In this case it was very robust with a thick stem where a division-line of two stems is slightly visible. The sturdy plant ended with a very dense inflorescence of 59 flowers (see Fig. 4). The flowers are not half-closed as in normal individuals but rather opened, which makes the plant's appearance very different from the ordinary *Cephalanthera longifolia*.

Yellow Helleborine: Cephalanthera longifolia f. ochroleuca

On 15th June 2005 during monitoring of early flowering orchids in Undva (western littoral of Saaremaa) an extraordinary sight caught the author's eye. About 15 metres beside the walking path, three yellow-flowered plants stood out among some white flowered *C. longifolia*. The yellow flowers could not belong to *Cephalanthera* because such a colored taxon simply doesn't exist. But getting closer to the plants it turned out that a Yellow Helleborine does indeed exist. In 2010 nine yellow-flowered *C. longifolia* were found in Kõruse and another was found in Kiljatu during 2012, all in the western littoral of Saaremaa. In all the following years these yellow-flowered plants continued to flower, accompanied by several normal white flowered individuals of *C. longifolia* (see Fig. 5 and Fig. 6).

The habitat where Yellow Helleborine grows is as for the normal *C. longifolia*. The plants grow in calcareous soil in open pine-wood edges. The morphological features do not differ from the white-flowered individuals; their height varies from 15 to 36 cm with similar leaves as in white-flowered plants. Flowers are more than half open and the pale yellow colour is homogeneous, not washed as for example in the flowers of *Dactylorhiza incarnata* subsp. *ochroleuca*.

There is information on the discovery of yellow-flowered *C. longifolia* on the Swedish island of Gotland, the neighbour of Saaremaa (Presser 2002). In earlier literature there have been similar descriptions of Yellow Helleborine e.g. f. *citrina* Aschers. & Graebn,; var. *citrina* Camus, Bergon & Camus; f. *ochroleuca* Rupp. (P. Delforge in litt.).

Fig. 1: Cluster of *Cephalanthera longifolia* (11th June 2012 at Kuusnõmme, Saaremaa)
Fig. 2: Two-branched stem form of *Cephalanthera longifolia* (11th June 2009 at Kuusnõmme, Saaremaa)
Fig. 3: Double-spike *Cephalanthera longifolia* (12th June 2009 at Kuusnõmme, Saaremaa)
Fig. 4: Inflorescence of *Cephalanthera longifolia* with 59 flowers (20th June 2002 at Kuusnõmme, Saaremaa)
Photos by Tarmo Pikner



Bell-flowered Cephalanthera longifolia

In addition to the extraordinary double-spike variations described above, other variant forms have been found, particularly in the appearance of flowers. Sometimes in the deep shade of a pine-forest plants of *C. longifolia* appear with completely opened flowers in which sepals and petals are longer than in normal individuals and curved outwards to create bell-like flowers, more similar to the flowers of *C. rubra* (see Fig. 7). The length of the lateral sepals of these bell-flowers of *C. longifolia* can reach 28 mm.

A whiter shade of pale: Cephalanthera longifolia f. albiflora

In some orchids the photosynthetic ability can be lost, leading to pale albino plants. This can occur in species of *Cephalanthera*. Several reports have come from western Saaremaa on the discovery of completely pale plants of *C. longifolia* where chlorophyll is missing. Existence of albino plants without chlorophyll is possible only where there is a mycorrhizal symbiosis. The author discovered a completely pale-beige plant in Kuusnõmme. Another case of a defective biosynthetic process is when the plant cannot produce a particular colour. An example is the plants of *C. longifolia* with entirely white flowers discovered by the author, in Kuusnõmme and in Undva. While in normal *C. longifolia* the epichile of the flowers is decorated with five to seven orange-yellow coloured ridges this colour is completely missing in the 'whiter shade of pale' variant, *Cephalanthera longifolia* f. *albiflora* (see Fig. 8).

White Red Helleborine: Cephalanthera rubra f. albiflora

It is a well-known fact that sometimes among red-pink-purple flowered orchids variants appear that lack the ability to synthesize anthocyanins, the pigment responsible for conferring these colours. As a result, albino forms appear and they are well known in *Orchis* and *Dactylorhiza*. Rarely, albino-forms of *C. rubra* have appeared in Saaremaa. There have been two such plants in the past ten years in Hindi, northern Saaremaa. Surprisingly, seven albino-forms of *C. rubra* were discovered in Papissaare in July 2012, and they flowered again in 2013. The forms with white flowers were growing within a population of normal Red Helleborine plants, being in every other respect similar to those with heights between 25 and 50 cm (see Fig. 9).

Fig. 5: Young plant of *Cephalanthera longifolia* f. *ochroleuca* (11th June 2012 at Kõruse, Saaremaa)
Fig. 6: Inflorescences of *Cephalanthera longifolia* f. *ochroleuca* of two plants. In the background there is shining a white-flowered individual (10th June 2013 at Kõruse, Saaremaa)
Fig. 7: Bell-flowered form of *Cephalanthera longifolia* (20th June 2005 at Kuusnõmme, Saaremaa)
Fig. 8: A whiter shade of pale: *Cephalanthera longifolia* f. *albiflora* (14th June 2006 at Kuusnõmme, Saaremaa)

Photos by Tarmo Pikner





Fig. 9 (left): White Red Helleborine: Cephalanthera rubra f. albiflora (3rd July 2013 at Papissaare, Saaremaa)

Fig.10 (right): Inflorescence of Cephalanthera rubra (3rd July 2013 at Papissaare, Saaremaa)

Photos by Tarmo Pikner

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HOS Field Trip for Norfolk Fen Orchids Mike Gasson

During the late spring, an unexpected opportunity arose for an additional HOS field trip. The RSPB offered the society a rare chance to visit their normally closed Sutton Fen site to see and photograph Fen Orchids. This is one of the very few remaining extant sites for the species in East Anglia in an unspoilt fenland habitat. As we were between journals, the visit was publicised and organised via the HOS Discussion Forum. Whilst this will have undoubtedly missed many members, we still managed a healthy group of 38 people for the event on 15th June. The Fen Orchid enjoys a very wet habitat and whilst wellingtons were essential footwear the organisers had taken care to provide some temporary access mats making it more comfortable and drier to photograph some of the orchid plants. An excellent insight was provided by the site warden Richard Mason, RSPB's area manager Ian Robinson and Plantlife's Tim Pankhurst, who painstakingly monitors the Fen Orchid populations.

As well as the Fen Orchids, there was a range of *Dactylorhiza*, most of which were well past their best. Interestingly, they included some very robust plants that may well match old descriptions of a *gemmana* variant of *D. incarnata* on this site (Heslop-Harrison, 1956). We were promised swallowtail butterflies but it turned out to be a dry but overcast day that suited orchid photography rather better than butterfly watching. Nonetheless, as soon as the sun made its brief appearances Papilio machaon was on the wing, albeit for a short time.

Many visitors had made a long trip and several stayed over, providing additional opportunities to visit other sites. This included detours south to see the ochroleuca subspecies of *D. incarnata* or the *chlorantha* variant of *Ophrys apifera* and detours north for *D. incarnata* subsp. *coccinea* or a fascinating population of *Dactylorhiza maculata* featuring very rare white variants. Details of the latter were provided by Ian Denholm who highlighted the fact that white mutant forms are inherently rare in all tetraploid *Dactylorhiza* species. An additional group visit was arranged for early folk, who moved on to Upton Fen for the afternoon. Upton is one the quieter and in my view more attractive fenland reserves owned by Norfolk Wildlife Trust. Again, a

knowledgeable local warden, Mark Amiss, was on hand to introduce visitors to the site and its treasures.



Left: RSPB's Ian Robinson who invited HOS members to visit Sutton Fen with Sean Cole and friends in the background.

Right: One of Ian's Fen Orchid photos showing how hard they can be to spot.

The good news for anyone who missed out on this rather hastily arranged visit is that in all probability RSPB will open the Sutton site for another event next year. Hopefully, we will be able to include it in the list of HOS field trips that are featured in the January issue of JHOS. There is however a serious side to East Anglian Fen Orchids in that the sites holding 99% of its plants are under collective threat from water abstraction. HOS is supporting a campaign by RSPB to publicise the problem and raise objection to the Environment Agency continuing to grant of licences for massive amounts of agricultural water abstraction in the immediate locality of the nature reserves. Please take a look at the accompanying panel that explains this in more detail and do give your support to RSPB if you want our Fen Orchids to have a future.

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Fen Orchids Endangered by Water Abstraction

As reported on page 103, the RSPB hosted a visit to Norfolk this June and enabled HOS members to see one of the country's largest Fen Orchid colonies at Sutton Fen, in the Ant valley. As well as these orchids, RSPB manage another very large Fen Orchid colony at Catfield Fen, just to the south of Sutton Fen. Between them, the two sites hold over 99% of the UK population of Liparis loeselii subsp. loeselii. These sites are the hub of ongoing ecological studies to increase our understanding of this sensitive species and to inform future re-introduction projects in East Anglia. At this time, both sites are under serious threat from local water abstraction. At Catfield Fen habitat changes are occuring and indicate negative consequences of drying and acidification. Already, this has caused loss of suitable Fen Orchid habitat and this is highly likely to lead to a reduction in Fen Orchid plants in future years. At Sutton Fen, this change has not been detected yet, but there is great concern that hydrological changes are occurring gradually and that they may threaten this orchid colony in the longer term.

At this time, there is a critical decision being taken by the Environment Agency with respect to the renewal of licences for water abstraction at Catfield. The Hardy Orchid Society is supporting RSPB and other conservation organisations in opposing the licence renewal application. Individual members of HOS can help by signing a petition organised by RSPB and by writing as individuals to the Environment Agency with personal concerns (see the Environment Agency website link below). Much more detail is available at the following websites:

> Petition and information collated by RSPB is at www.rspb.org.uk/catfieldfen

Environment Agency information here https://www.gov.uk/government/publications/catfield-norfolk-abstraction -licences/catfield-fen-norfolk-abstraction-licences

More detailed background material (need to register) https://www.gov.uk/government/publications/catfield-norfolk-abstraction -licences



Ghost Orchid Project 2014 Sean Cole

Currently, I am preparing a major article for *JHOS* on the occurrence of Ghost Orchid in England. This year, together with like-minded enthusiasts Mike Waller and Stephanie Leese, we are organising a co-ordinated search for Ghost Orchid at its historically known locations during the 2014 season. Searchers are being asked to spend as much or as little time searching as they can spare. Location information will be provided, along with hints on where and how to look. Negative search information is valuable, although a positive search result would be preferred! If you would like to help more details are available at:

www.ghostorchidproject.co.uk

There is also a Facebook page and a Twitter account which can be accessed via the website. All participants will be kept informed of progress, and when search data is published, will be fully acknowledged. If you are out searching for other species and want to spend some time helping out, please get in touch.



Ghost Orchid in Sweden from the Ghost Orchid Project website Photos by Oscar Stahle

Frogs and Twayblades Mike Gasson

The field trip reports in the April *JHOS* included two photographs taken at Whitegates in Shropshire but their incorrect identities and captions managed to elude two photographers as well as half a dozen people involved in putting together and proof



reading the journal article. In both cases, the orchids were of course Common Twayblades that ended up being incorrectly labelled as Frog Orchids.

This is an easy mistake to make and one that is easily missed once the little green fellows are embedded in article format. Thanks are due to Sean Cole for spotting the error first and to Alan Bousefield for providing comparison images. Both of these were photographed during the Whitegates field trip. The Frog Orchid is on the left and the Twayblade on the right!

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