

A photograph of a yellow orchid flower growing in a forest floor covered with brown leaves. The flower is the central focus, with a long, slender stem and a cluster of small, pale yellow blossoms at the top. The background is a dense forest floor covered in fallen, brown leaves, with tree trunks visible in the distance.

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The Hardy Orchid Society

Our aim is to promote interest in the study of Native European Orchids and those from similar temperate climates throughout the world. We cover such varied aspects as field study, cultivation and propagation, photography, taxonomy and systematics, and practical conservation. We welcome articles relating to any of these subjects, which will be considered for publication by the editorial committee. Please send your submissions to the Editor, and please structure your text according to the "Advice to Authors" (see website www.hardyorchidsociety.org.uk, 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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Front Cover Photograph

Albino Bird's -nest Orchid, *Neottia nidus-avis* var. *pallida*
photographed by Rosemary Webb, see article on page 114

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Editorial Note

Three big articles in this *JHOS* are headed up by Rosemary Webb's account of orchid hunting in Hampshire and her encounter with a white Bird's-nest Orchid. It is good to have this in print as it was featured at a meeting talk a while back and deserves wider exposure. Many will relate to the excitement on finding a special orchid that Rosemary has captured in her article. Also, there is a second instalment from Svante Malmgren and John Haggard with more original material on orchid hybridisation and lastly a detailed account of *Dactylorhiza* species found in Saaremaa from local expert Tarmo Pikner. This builds on Simon Tarrant's recent article in *JHOS* on his visit to Estonia. It is interesting to read a detailed account of the variation found in this part of the Baltic region and the perspective of a local botanist on *Dactylorhiza* taxonomy. Bear in mind that some of the orchid species' names may seem different from our own as this is a view from a different part of the orchid world. The remaining field trip reports from 2012 are held over for January as Malcolm Brownsword is talking about them at the forthcoming Kidlington meeting.

Chairman's Note

Greetings. I hope you've all managed to get out and enjoy our native orchids this summer. The cypripediums and dactylorhizas I grow in the garden have had a long season of growth in the cool, wet weather, so I hope they're building up their strength for a good show next year. The exception was the *Dactylorhiza fuchsii* and some of the *Dactylorhiza* hybrids that met an unpleasant end with what I think was Black Death. I shall need to ask our experts some questions about this at the Kidlington meeting, when a Growing Forum is on the programme. The booking form for the November meeting was circulated with the July Journal. If you've lost it and haven't booked yet, you can download both a programme and a booking form from the HOS website.

I greatly enjoyed the Seed Sowing Workshop held in August. This is the third year we've run this and it gets better all the time as we listen to and implement feedback from those who come. I was amazed that members came from as far away as Ayrshire, Abergavenny and Hampshire. All felt they had a worthwhile day, while one participant was coming for the second time. We could look at a venue further south next year if that would help enough members, but further north would be more difficult as John Haggart, our excellent tutor, lives on the south coast. Do let me know if this is important to you.

My thoughts now turn to next year and particularly our AGM in the spring. In 2013 and again in 2014 there will be vacancies on the committee as long serving members move on. I am concerned that we do not currently have a Vice Chairman as no one has yet come forward to take on this role; I hope that this lack of volunteers is not a reflection of lack of interest on the part of our members. I have enjoyed being on the HOS committee more so than with any other society, as my fellow committee members have always been an enthusiastic group who work well together. Even committee meetings have been interesting rather than merely functional. If you might like to join the committee, please email me (celia.wright@tiscali.co.uk) or phone (01743 884576) and I'll be glad to discuss it. My best wishes to you all.



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The Most Exciting Day of 2005

Rosemary Webb

Now that we are in the second decade of the 21st century, I have been thinking about the many excursions I have taken to look for orchids during the last half century. When I was a child, if something special happened, I would often feel in my excitement, that it was 'the best day of my life'. As one gets older, this enthusiasm gets overwhelmed and life becomes more complex. However, there are a few occasions when one is in the wild and natural world where this feeling can still be experienced. This happened to me on Sunday 5th June, making it the most exciting day of 2005. I was looking forward to this particular Sunday as the Hampshire and Isle of Wight Wildlife Trust had organised a walk to look for orchids in a privately owned wood. I had visited it once before and remember seeing magnificent spikes of Greater Butterfly Orchid (*Platanthera chlorantha*) along the edges of the rides. I thought that I would take my camera as I remembered the orchids being easily accessible.

In one's memory, June was always warm and sunny and good things happened on fine, warm days. It was quite disappointing to find that the day dawned overcast and the forecast was for the weather to deteriorate as the day progressed. I was not going to let this put me off. I stowed the camera gear in the car and set off. The sky was heavy, there did not seem to be any chinks for the sun to shine through but it was still and at least it was dry for the present.

The wood is on a low hillside and we set off up a gravel ride with thick vegetation on either side. There were a number of Common Spotted Orchids (*Dactylorhiza fuchsii*), some just coming into flower but mostly still in bud. The ground rose to our right and this part of the wood had been largely felled and cleared. A lot of vegetation was growing up amongst planted saplings cocooned in their protective, plastic tubes. The cleared ground was rich in plants. Primroses (*Primula vulgaris*) and Wood Anemones (*Anemone nemorosa*) were over but many other plants were coming into flower. There were some magnificent spikes of Greater Butterfly Orchid all in perfect condition and in some places these formed groups of several flowering spikes. The light, which had been let in by the felling of the old trees, had certainly been good for them. There were some Common Spotted Orchids on tall, stately stems, in more advanced flower here in the open than those by the track. Some Twayblades (*Neottia ovata*) were competing with them for height.

Figs. 1 & 3: Common Spotted Orchid, *Dactylorhiza fuchsii*

Fig. 2: Greater Butterfly Orchid, *Platanthera chlorantha*

Fig. 4: Twayblade, *Neottia ovata*

Photos by Rosemary Webb





As we descended down the hillside towards the track at the bottom we were told to look out for the curious brown Bird's-nest Orchid (*Neottia nidus-avis*) in the wood on the other side of the ride. No-one found any. It had been a cool, dry, cloudy spring and the ground underfoot is very dry indeed, not the best conditions for this particular orchid. I have not seen any really fine specimens so far; it seems to be a poor year for them. We walked on, returning across the fields to the cars and lunch at a local inn. It had been a very pleasant morning with some lovely orchids.

By the time we had finished lunch, the weather was getting cooler, a breeze was beginning to blow and the clouds were getting thicker and thicker. It was starting to

rain, not heavy rain but fine, penetrating rain and the cloud-base had descended considerably. It seemed a pity to go home, so four of us decided to visit another nearby wood, which is well-known locally for its orchids. This is also privately owned, but a bridleway runs along the edge and a footpath runs close by. The wood faces north-east on a chalky slope. We took a footpath which immediately enters a small patch of woodland before continuing through more open areas with grassy edges, wild roses, brambles and other shrubs such as Spindle, Dogwood and Hawthorn.

The path follows the ridge of the hill and quite quickly we reached the wood. The shrubby area gives way to some big, old beech trees and the tracks veer off into the wood. The first find for the afternoon was in the grass on the edge of the path. There was a lovely, tall, stately spike of Bee Orchid (*Ophrys apifera*) with the lowest flower perfectly out and many more buds to come. It was a Bee Orchid on another Hampshire hillside (Portsdown) that started my enduring love for orchids: I was twelve at the time and I remember that excitement, the feeling that this was 'the best day of my life'! I was entranced by this little flower which looked so much like an insect and was such a beautiful colour. It was incredible, so interesting and so

Fig. 5 (above): Greater Butterfly Orchid, *Platanthera chlorantha*

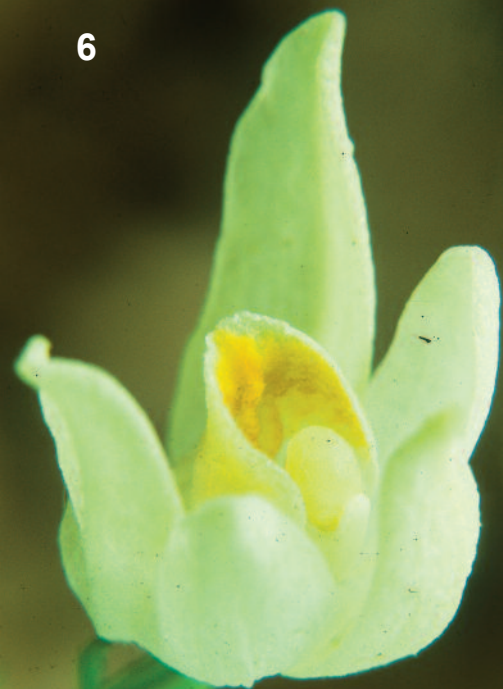
Figs. 6 & 7: White Helleborine, *Cephalanthera damasonium*

Fig. 8: Fly Orchid, *Ophrys insectifera*

Fig. 9: Bee Orchid, *Ophrys apifera*

Photos by Rosemary Webb

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extraordinary. Today, although I have seen so many Bee Orchids, I still felt that frisson of excitement and the memories came flooding back into my consciousness.

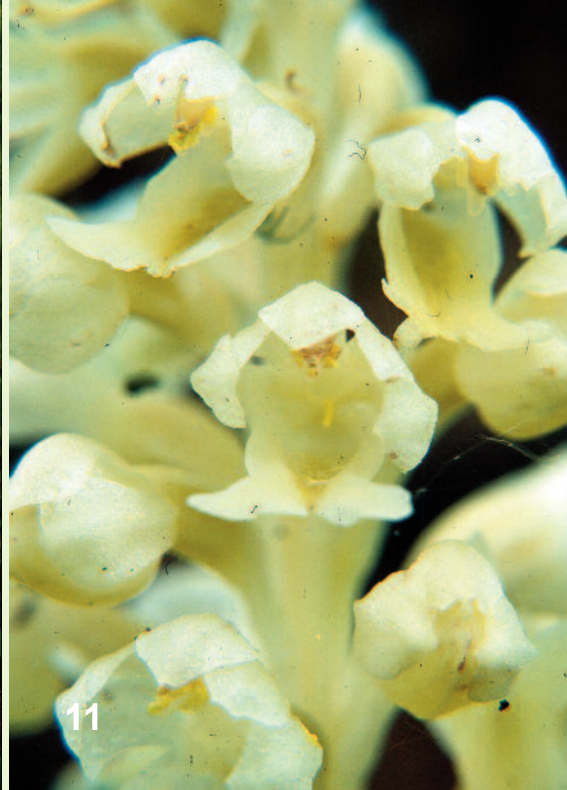
Having admired the Bee Orchid we turned our attention to the wood. There are some tall beech trees here, their pale, silvery-green trunks looking very light in contrast to this dull weather. The damp has made the leaf-mould beneath them an almost burnt orange. Beneath the trees, large spikes of Bird's-nest Orchid were in good light, growing out of the leaf-litter. A quick count revealed that at least twenty three large spikes were flowering in this small area, making excellent photographic possibilities had not been so wet. I was interested to note that the strong, sweet, almost sickly perfume was very evident even here on the edge of the wood, where the rain was actually falling on the flowers.

We walked on, down the hillside, through the wood. This is really a rather neglected area. We made our way through, heading north west and came to a large fallen tree whose branches had nonetheless sprouted into leaf, that lovely soft green of the newly emerged beech. Coming round the end of this fallen tree, I could see a large area of beech litter, some big, mature beech trees and more Bird's-nest Orchids, their honey-brown colour really matching the leaf litter. There were also some flowering spikes of White Helleborine (*Cephalanthera damasonium*) growing near some beech trees.

This is classic habitat for both these species. But the real excitement of the day could be seen – standing erect and isolated in the middle of the open beech wood floor. There, shining out like a beacon was something that I have always wanted to see – a white spike (albino) of Bird's-nest Orchid (*Neottia nidus-avis* var. *pallida*). I held my breath, I blinked, I rubbed my eyes – could I really be seeing what I thought I was seeing? The emotion was overwhelming. I wanted to shout, I wanted to jump, I was so excited. I have looked for this for over 30 years, ever since I saw a picture in a German orchid book. I never really thought that I would ever see one here as it was not mentioned in British orchid books until Derek Turner Ettliger published “*Notes on British and Irish Orchids*” in 1997. Here it is referred to but not in Hampshire.

I was stopped in my tracks, I was in awe. I felt overwhelmed by presence, the need for quiet and respect. There was an aura of silence around it. I get a great feeling of excitement and energy whenever I think of that moment, that afternoon. I can see it when I close my eyes, that striking white spike in the gloom of a dull day and the contrast of this pure spike with the brown of the leaf litter. It stood there, like a ghost – Hampshire's own ‘Ghost Orchid’. The whole spike was a uniform creamy-white

Figs. 10 & 12: Bird's -nest Orchid, *Neottia nidus-avis*
Figs. 11 & 13: Albino Bird's -nest Orchid, *Neottia nidus-avis* var. *pallida*
Photos by Rosemary Webb





Bird's-nest Orchid,
Neottia nidus-avis
Photos by Rosemary Webb

colour, stem and flowers the same. Looking the flower 'in the eye' one can see that the nectar-producing, bowl-shaped depression at the base of the lip is a little darker, pale yellow, unlike the deeper brown of the normal plant. The pollinia are also very pale, unlike the normal, deep golden yellow of the brown florets. This was truly one of those 'best day of my life' moments – this was magical. I think one appreciates something that has been difficult to find, so much more. I wish I could keep that moment forever. In a way, I can. Photographs show the stark contrast of the plant and its setting. The moment is caught, it can never be repeated and that initial excitement can never be re-created either. I often revisit this wood. Last year there were more ordinary Bird's-nest Orchids here than there are this year but '*pallida*' was not there. Will it be here next year? Who knows? It could be here next year, it may re-appear in the future or it may be fleeting – like a ghost!

After this excitement, everything else was an anti-climax. Suddenly the impressive quantity of normal Bird's-nest Orchids seemed mundane. The large White Helleborines were almost ignored. We walked on, to the far side of the wood. Bird's-nest Orchids were everywhere. In a patch of Ivy, Sanicle and seedling shrubbery were six, tall spikes of Fly Orchid (*Ophrys insectifera*). In woodland settings these are often difficult to see, their subdued colour, purple-brown and light green, camouflages them so well in the low light.

This has been a wonderful day. The weather has been irrelevant. I have seen many of my favourite orchids and the *Ophrys apifera* has reminded me how my passion for these plants began. Every time I have seen Bird's-nest Orchids I have thought of the elusive var. *pallida* and wished that I could find one. Today, I have found a magnificent specimen, a good size and in perfect condition – glowing like a beacon on the dark woodland floor. I think the dullness of the day was actually an advantage, as it enhanced the contrast. I have searched for this orchid every year since but to date it has not re-appeared. I can definitely say that for me, the best day of 2005 was finding *Neottia nidus-avis* var. *pallida*.

Much Ado About Almost Nothing? Part 2

Svante Malmgren & John Haggar

Continuing with our discussion of artificially propagated orchid hybrids and their relevance to naturally occurring species and hybrids, we now turn our focus to the genus *Ophrys*. With very few exceptions, it seems that any two species can be crossed successfully, producing viable F1 hybrid plants. In the wild, different *Ophrys* species are isolated pre-zygotically to a great extent by virtue of their pollinator specificity, but natural hybrids are nonetheless fairly commonly found. One of us (SM) has experimentally produced at least ten different F1 *Ophrys* hybrids, including crosses between Swedish *Op. insectifera* and four species from Greece. The F1 hybrids described are crosses between truly different *Ophrys* species well separated by DNA analysis, as described by Devey *et al.* (2008), and not between splitters' species separated by minor morphological differences as, for example, according to Delforge (2006).

Most *Ophrys* hybrids exhibit the frequently seen hybrid vigour (some cultivated plants are still living after more than 15 years), but with very few exceptions they do not produce viable seed upon self-pollination. In two cases (*Op. argolica* × *cornuta* and *Op. cretica* × *fuciflora*), viable seed did form but the percentage germination was very low. The first-mentioned F2 hybrids proved to be weak and slow growers on soil and all five plants died after flowering only once. In 2010, the self-pollination was repeated, but only ten plants were successfully grown to tubers from one entire seed capsule. These were potted in soil in May 2011. In the second case a dozen plants grew healthily on sterile medium *in vitro* and were potted up in 2002. Since then they have progressively died off and although one plant still lives a decade later, not one has ever flowered. Interestingly though, and in contrast with all other F1 *Ophrys* hybrids tested, the pollen of these crosses is fertile. It can be used to fertilise other species and hybrids, and in some cases strong F2 hybrids are obtained.



Ophrys cretica × *fuciflora* F1 (right) & F2 (left) generations
Photo by Svante Malmgren

Selfing of *Op. lutea* × *tenthredinifera* produced a small amount of apparently viable seed which germinated on sterile medium, but all the plants quickly became malformed and none survived to be weaned from flask. As some seeds did germinate they would probably have passed the TTC test, but this just confirms the unreliability of this test for our purposes as discussed in Part 1 (Haggar & Malmgren, 2012).



Hybrid vigour
Ophrys apifera × *scolopax*
Photo by Svante Malmgren

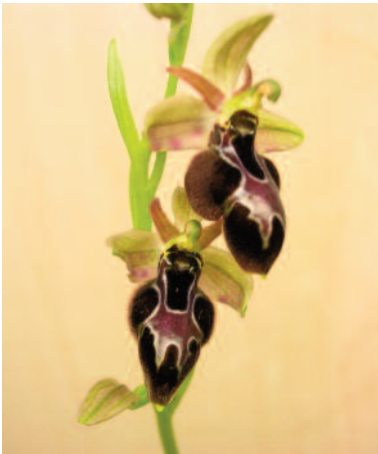
The very vigorous hybrid between *Op. apifera* and *Op. scolopax* produces large seed capsules when selfed, though there is no viable seed. These similar parent species are easily distinguishable morphologically and the failure to produce an F2 generation experimentally strongly suggests that they are well separated by post-zygotic isolation. Back-crossing has so far not been done.

Although the pollen of virtually all F1 *Ophrys* hybrids is incapable of enabling fertilisation, “new” *Ophrys* hybrids can be made by using the hybrids as mother plants and fertilising them with the pollen of true species. In this way new species can be added to a hybrid in a stepwise fashion, generation by generation. Three different lines have been created in this manner and hybrids incorporating up to seven different *Ophrys*

species have been grown to flowering size. It is important to note, though, that not one of the hybrid forms successively produced has proved fertile when self-pollinated (i.e. the pollen remains defective). Such entities in a wild setting would represent a genetic dead end and no such population could be self-sustaining.

One possible method whereby introgression might occur in *Ophrys* is by fertilising the F1 hybrid with pollen from one of the parents of the hybrid. This experiment has been done with seven different species pairs, using the original mother species as the pollen donor. In all cases an entire seed capsule was sown in order to record even rare germination events. *Ophrys* (*cretica* × *fuciflora*) × *cretica* has just been sown and currently (November 2011) a large number of protocorms have germinated on medium. In the case of *Op.* (*argolica* × *cornuta*) × *argolica*, however, only one seed germinated from the entire capsule. *Ophrys* (*lutea* × *speculum*) × *lutea* produced seed with an appreciable germination percentage but *Op.* (*lutea* × *fuciflora*) × *lutea* only gave rise to a couple of protocorms. The other three back-crossings resulted in no viable seed at all, or even in empty seed capsules.

In 2012 we will see whether the F2 plants are viable on medium and soil. In spring 2014 we might have flowering *Ophrys* plants whose DNA is mainly from one species but with some DNA “introgressed” from other species, but will these plants grow normally and be healthy? More to the point, will they yield fertile pollen and ovules and so be able to pair successfully with plants of the major contributor



Multiple hybrid
Ophrys insectifera × *tentredinifera* × *speculum* × *cretica* ×
holoserica × *spruneri*
Photo by Svante Malmgren



Multiple hybrid
Ophrys insectifera × *tentredinifera* × *speculum* × *cretica* ×
holoserica × *argolica* × *cornuta*
Photo by Svante Malmgren

species? In all other tested “multiple” *Ophrys* hybrids, no two plants are similar and all are infertile when fertilised with their own pollen.

Introgression in *Ophrys* species in nature has been demonstrated in DNA analysis by Stökl *et al.* (2007). However, they describe only introgression in what Devey *et al.* would call different types within the *fusca* complex; for example, *Op. lupercalis* × *Op. iricolor* and *Op. bilunata* × *Op. fabrella*. Some might regard these as subspecies or varieties of one species, so we are not surprised by those findings (Devey *et al.*, 2008). To illustrate this point, SM has produced fully fertile hybrids when crossing two morphologically different *Op. fuciflora* variants and two morphologically different *Op. fusca* forms. In conclusion, although *Ophrys* appears to readily produce primary (F1) hybrids, healthy second generation (F2) hybrids are a real rarity and may never produce fertile pollen. In our opinion it is unlikely that new *Ophrys* species arise from pre-existing hybrids and introgression between well-defined species is a very rare phenomenon.

What is the situation in the genera *Orchis* and *Anacamptis*? Although found much less commonly in the wild than are *Dactylorhiza* and *Ophrys* crosses, many naturally occurring hybrids are documented and several more have been artificially propagated in the laboratory as horticultural specimens. *Orchis* and *Anacamptis* species have many more pollinators in common than do *Ophrys* (Cozzolino and Scopece, 2008) and reproductive isolation is more dependent on post-zygotic isolation (i.e. genetic mis-fitting). *Orchis* × *hybrida* (*Orchis purpurea* × *militaris*) is a well known hybrid where lady and



Orchis × *hybrida*
(*Orchis purpurea* × *militaris*)
Photo by John Haggar



Anacamptis × *kallithea*
(*Anacamptis sancta* × *fragrans*)
Photo by John Haggar

military orchids grow together. The cross has been propagated by SM and it is evident that the hybrid grows significantly more vigorously than either parent. The plants are yet to flower, but this is a consequence of the cool Swedish climate rather than genetics. We hope it will not be long before flowers are available for pollination tests.

In at least one orchid flora it has been suggested that *Anacamptis coriophora* could be the final result of hybridisation and introgression between *A. sancta* and *A. fragrans* (Mossberg & Nilsson, 1980). Strong, healthy hybrids between *A. sancta* and *A. fragrans* (*A. ×kallithea*) may be seen at several wild sites and one particularly fine colony containing both parents (the *A. fragrans* is rare) was formerly to be seen at Mykali beach on the Greek island of Samos. *Anacamptis ×kallithea* has been reproduced by SM but when these plants were self-pollinated no seed at all was produced. In addition, no seed resulted when the hybrid was back-crossed with pollen from the *A. sancta* mother plant. Similar results were obtained from the hybrids *A. sancta* × *papilionacea* (SM) and from *A. morio* × *laxiflora* (JH), both crosses proving to be sterile when selfed. In these cases no back crosses were done.

A very strongly growing primary hybrid is *Anacamptis ×gennarii* (*Anacamptis morio* × *papilionacea*), large specimens of which can reach almost 40cm in height, much bigger than either parent. Supposed hybrid swarms have been described as having emerged from this hybrid in the wild in Cyprus (Bateman, 2006). We have both reproduced this hybrid and, on more than one occasion, have self-pollinated it without successfully producing any viable seed. In addition, SM has back-



Anacamptis morio (left),
& its hybrid with *A. laxiflora*
Anacamptis × *alata* (centre &
right)

Photo by John Hagger

crossed it with both parents without success. In the case of *A. ×gennarii* × *morio*, seed was produced in large quantity but not a single seed contained an embryo of normal size and, of course, no germination occurred. The two parent species actually have different numbers of chromosomes so these results are hardly surprising. Our interpretation of the so-called hybrid swarms would be that they are likely to consist entirely of “dead end” F1 hybrids and do not contain fertile F2 hybrids.

Apart from anecdotal reports, we have been unable to find much information in the literature relating to back-crossing of F1 hybrids

in *Anacamptis* and *Orchis*. Cozzolino *et al.* referred to a population of *O. mascula* and *O. provincialis* in which back-crossing had supposedly occurred but there was no mention of the methods used to ascertain their claim (Cozzolino and Scopece, 2008). The distributions and habitats of *A. morio* and *A. longicornu* overlap on Sicily, where they are said to form fertile hybrids and to introgress one another (Cozzolino and Scopece, 2008). This is another case, however, like *Dactylorhiza incarnata* and *D. aristata*, where two related species, normally pre-zygotically isolated are inter-fertile.

Now back to the question of the Hartslock *Orchis* hybrids. In late summer 2010, SM received seed from an area in Eastern Europe where *O. purpurea*, *O. simia* and *O. ×angusticuris* grow together. A seed capsule from the hybrid (of unknown pollen parentage) was examined microscopically and found to contain seed, 30 to 40% of which had embryos of normal appearance and size. A large amount of the seed was sown, and more than a year later there was still no sign of germination. Using appropriate methods and media, *O. simia* normally would germinate within 4 weeks and *O. purpurea* not later than 5 months after sowing. Most primary orchid hybrids grow from seed that behaves in the same manner as the mother plant when it comes to germination characteristics. Currently two protocorms appear to have formed from the many thousands of seed sown, but their longer term viability remains to be seen.

So, despite a few exceptions (some predictable in very closely related taxa and some unpredictable in others), most hybridisation in European terrestrial orchids stops after the primary (F1) hybrids. It would appear that infertility past the F1 generation and the consequent rarity of introgression between moderately closely related species is the very mechanism whereby genetic incompatibility produces post-

zygotic isolation in European orchids. The fact that even quite distantly related species from different genera can form primary hybrids though, tells us that genetic distance is not the sole cause and that other factors are involved. Experiments can help us to clarify the exceptions to this generalisation. With any particular species pair, the chances of introgression occurring must be very unlikely if we cannot demonstrate even rare examples of back-crossed F2 hybrid fertility. In addition, of course, continued seed, somatic and particularly pollen viability proceeding into later generations are essential prerequisites.

In the case of *O. ×angusticuris* in Oxfordshire, we would anticipate that the most likely outcome is that the hybrid will prove to be a dead-end taxon that will not influence the genetic integrity of the *O. simia* at the site in the long term. We, the authors, would be pleased to sow seed from the Hartslock hybrids, preferably from plants in which controlled pollination had been done, if interested parties wish to follow this course to investigate the true likelihood. Obviously though, for as long as the “foreign” *O. purpurea* remains at the site, the hybrid will persist and this could potentially influence the *O. simia* population numerically by diverting the pollinators from their “proper” targets. Some may say that pollinator availability is unlikely to be a limiting factor, but it is certainly thought that the Hartslock Monkey Orchid population began to expand in the mid 1990’s at least in part as a result of systematic hand pollination at the site from 1977 onwards (Harrap & Harrap, 2005).

It remains an unlikely possibility that a partially fertile back-crossed (with *O. simia*) F2 generation plant might appear that could back-cross again to produce a later generation with a genome similar enough to the native plants for normal recombination to occur. If this should happen then a fully fertile monkey orchid with a small amount of introgressed DNA from the *O. purpurea* might arise. After all, genetic studies do tell us that it has happened in the past (Bateman *et al.*, 2008) and SM has demonstrated that the seed of *O. ×angusticuris* is not totally infertile. The novel genes could then be passed gradually to the remaining population, but it would take many generations and decades for this to occur and in appearance the plants would remain essentially normal monkey orchids.



Orchis simia first year in soil
Photo by Svante Malmgren

We will discuss the implications of this observation in more detail later but it is worth remembering that *O. simia* and *O. purpurea* co-exist in many Continental sites without any obviously significant phenotypic changes. This suggests that genetic drift due to mutual introgression is not a real problem for the survival of either species. In some populations, F1 hybrids may dominate locally (in the French Vercors, for example),

but the true species are still common there and remain clearly identifiable as such. In the authors' opinions, the emergence of a fertile back-crossed F2 hybrid in anthropomorphic *Orchis* species is a rare event that is unlikely to have any significant effect on local populations other than on those equally rare occasions when the hybrid's genetic make-up confers significant adaptive advantage to its progeny.

In the third and final part of this paper, we will discuss the general implications of the introduction of alien genetic material into native orchid populations.

References

- Bateman, R.M. (2006) The Origin of (Pseudo) species by Means of Natural Selection: a Cypriot Conundrum. *JHOS* 3 (41): 80-82.
- Bateman, R.M., Smith, R.J. and Fay, M. (2008) Morphometric and population genetic analysis elucidate the origin, evolutionary significance and conservation implications of *Orchis* × *angusticuris* (*O. purpurea* × *O. simia*), a hybrid orchid new to Britain. *Botanical Journal of the Linnean Society* 157: 687-711.
- Cozzolino, S. and Scopeze, G. (2008) Specificity in pollination and consequences for postmating reproductive isolation in deceptive Mediterranean orchids. *Philosophical Transactions of the Royal Society B* 363: 3037-3046.
- Delforge P. (2006) *Orchids of Europe, North Africa and the Middle East* (3rd edn), A & C Black, London.
- Devey, D.S., Bateman, R.M., Fay, M and Hawkins, J.A. (2008) Friends or relatives? Phylogenetics and Species delimitation in the controversial European orchid genus *Ophrys*. *Annals of Botany* 101: 385-402.
- Haggard, J. & Malmgren, S. (2012) Much ado about almost nothing? Part one. *JHOS* 9 (65): 85-90.
- Harrap, A. & Harrap, S. (2005) *Orchids of Britain & Ireland*, A. & C. Black, London
- Mossberg, B and Nilsson, S (1980) *Syd- och Mellaneuropas orkidéer*, Wahlströmmoch och Widstrand, Stockholm.
- Scopeze, G., Musaccio, A., Widmer, A. and Cozzolino, S. (2007) Patterns of reproductive isolation in Mediterranean deceptive orchids. *Evolution* 61(11): 2623-2642.
- Stöckl J. (2007) Pollinator driven radiation in sexually deceptive orchids of the genus *Ophrys*. Dissertation, Ulm.

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Taxonomic Diversity of *Dactylorhiza* on Saaremaa

Tarmo Pikner

When reading “Orchid Hunting on Saaremaa” by Simon Tarrant (Tarrant, 2011), an interesting sentence caught my attention – “The Estonians recognise a number of marshland *Dactylorhiza* species, but I lack the confidence to be more precise!” I decided to try to contribute this knowledge in the current article. In addition, this complements the series of articles by John Haggard (Haggard, 2003a; 2003b; 2004a; 2004b; 2005a; 2005b), on northern European *Dactylorhiza* distribution. Readers will get an insight into different positions on the taxonomy of this complicated genus, especially on the extremely polymorphic *Dactylorhiza incarnata* complex.

Saaremaa, the largest Estonian island, belongs to the Baltic or north-central European floristic region, whereas most of the mainland belongs to the Sarmatic one. The maritime influence gives rise to a milder climate on Saaremaa and littoral areas, which is visibly reflected in the distribution of wild orchids. Most of the sites are concentrated on islands and the western coastal mainland of Estonia, where orchids find a mild climate and suitable habitats on the calcareous ground. Wetlands, marshy landscapes, meadows and grasslands provide habitats for many orchids.

Since 1818, when the flora of Saaremaa aroused the interest of researchers, 37 species of orchids have been found flowering on the island. The mainland offers only one additional species (*Dactylorhiza ruthei*) to the total number of Estonian orchids. Unfortunately, four species are extinct on Saaremaa. Still, the island with its 33 flowering orchid species has a remarkable and important status in the northern European orchid world.

Genus *Dactylorhiza*

Dactylorhiza is taxonomically the most problematic and controversial complex of wild orchids. This is complicated by the great morphological variability within species and a high frequency of hybridisation between species. The borderlines between the numerous species remain unclear. Nowadays, molecular analyses aid identification and distinguish those with the stabilised characteristics of a species and those produced by unstable hybrid swarms. It is worth mentioning that *Dactylorhiza* species are very sensitive to environmental changes, and human land management may result in reduction and isolation of marsh orchid populations. In turn, this may even influence the morphological features of the species.

The most widespread taxonomy of the genus *Dactylorhiza* divides the family into three groups. The *D. incarnata* group (e.g. diploid *D. incarnata* and *D. coccinea*) and the *D. maculata* group (including diploid *D. fuchsii* and autotetraploid *D. maculata*) are connected by a number of allopolyploid taxa, forming the third group of

allopolyploids. These allopolyploid taxa originate from repeated hybridisation processes involving the diploid ancestors *D. fuchsii* and *D. incarnata*. The group of hybrid allopolyploids is in turn divided into three smaller groupings: the *D. majalis* grouping, the *D. praetermissa* grouping and the *D. traunsteineri* grouping. Besides the three major groups, there is a sister section – the diploid *D. sambucina* group, whose morphology and ecology is distinct.

The most intriguing question is why allopolyploids that have the same pair of parental species (*D. fuchsii* and *D. incarnata*) can exhibit different morphology, ecology and distribution. The differentiation of the taxa has strong ecological and biogeographical components and they can operate as distinct evolutionary units (Pillon et al. 2007). At issue is whether the allopolyploids are one single species, different species, subspecies, varieties or just swarms of hybrids. Different schools treat the issue differently; very generally, “morphologists” prefer the concept of a species while “molecularists” prefer division into subspecies. Here the hierarchical ranking of “species”, “varieties” and “forms” is used for *Dactylorhiza* taxa (Pikner 2011).

With respect to Saaremaa it is fortunate that valuable wetlands and marshes still remain after the long period of collective farming during the Soviet times. Today, nature conservation and orchid protection measures sustain the necessary biotopes for the populations of *Dactylorhiza*. Only the meadow species *D. sambucina* and *D. (Coeloglossum) viridis* are unfortunately extinct due to grasslands having become overgrown with brushwood and trees, mainly pine. Today, the diversity of *Dactylorhiza* includes 8 species and 13 varieties.

***Dactylorhiza incarnata* group**

The dominant representative of the group, *Dactylorhiza incarnata*, is an abundant species, and not only on Saaremaa. However, not all widespread orchids are as varied as this one. The polymorphism of this taxon includes the size of the whole plant and inflorescence, the size, colour and form of flowers (lip & spur), bracts, leaves, and stem, as well as the number of flowers and leaves. It is interesting to note that one characteristic of *Dactylorhiza incarnata* is remarkably stable – the horse-shoe pattern, a dark red double loop on the lip. The latter is never stable in allopolyploid species in which one parent is *D. incarnata* – the horse-shoe pattern is transformed into different appearances of stripe and line patterns in allopolyploids.

The nominate taxon with pale pink flowers is a conspicuous minority in the whole of Estonia, especially on Saaremaa. The nominate taxon accounts for less than 1% of the whole population of *Dactylorhiza incarnata* on the island. Nearly all of the remaining population belongs to the nominate taxon with dark purple flowers. For example, at the Undva site there are only 1–8 pale pink specimens among the population of 2000 - 3000 specimens with dark purple flowers, as seen during the

author's ten years of field surveys. In Western Europe, the dominant nominate taxon has pale pink flowers, whereas in Estonia it is considered to be a rare variation of *D. incarnata*. Several authors report that the nominate taxon with dark purple flowers dominates also in Scandinavian regions, including Öland and Gotland (e.g. Haggard 2007). In this respect, the author can easily understand Linnaeus's description of the type specimen from the year 1755, which we today know as *D. incarnata*, where he stated that the species occurs "rarely" in meadows (in eastern Sweden, probably on Öland). The pink flowered specimen of *D. incarnata* is really rare there, as it is on Saaremaa.

In comparison to the nominate species with dark purple flowers, wet seaside meadows in flooded landscapes are the habitat of a shorter taxon with a height of 16-23 cm. This has fewer, smaller and flatter leaves and even darker violet flowers. These are smaller but the lip has an elongated median lobe and notably reflexed lateral lobes. This taxon is *D. incarnata* var. *borealis* (Neumann) Hylander, described from Sweden by Neumann. In a certain respects, *D. incarnata* var. *borealis* could be comparable to the taxon *D. incarnata* var. *pulchella* described from Hampshire, England by Druce, and to *D. incarnata* var. *serotina* described from Germany by Haussknecht. *D. incarnata* var. *borealis* colonizes the western coastal meadows and flooded areas of the island of Saaremaa (sites Kuusnõmme, Eeriksaare). As the taxon *D. incarnata* var. *borealis* originates from Sweden, it is found in Scandinavian coastal regions, including Öland and Gotland, where it is better known as *D. incarnata* var. *serotina* type (Mossberg & Lungqvist 1994; Hedren & Nordström 2009). The above mentioned variations could most probably be treated as genetic differentiations correlated with their biogeographic origin.

Scattered in swampy rich marshes (e.g. site Küdema), a very robust taxon appears. It is mainly tall, with a height of 60-80 cm (sometimes rather dwarfed to 40-50 cm), a very thick stem with a diameter of 1.5-2 cm and large lush leaves with a width of 3-4.5 cm. The inflorescence is massive, with big flowers having a wider flat lip and side lobes that are not reflexed. This taxon is *D. incarnata* var. *latissima* (Zapal.). It has also been described on Öland and Gotland (Mossberg & Lungqvist 1994; Hedren & Nordström 2009). The variety is also known under the names *D. incarnata* var. *sublatifolia* (Rchb.) Soo and *D. incarnata* var. *macrophylla* (Schur) Soo.

A taxon with long, straight and erect leaves, spotted on both sides, is *D. incarnata* var. *hyphaematodes* (Neumann) Läjtnant. In comparison with *D. cruenta*, the taxon

Fig. 1 *Dactylorhiza incarnata* nominate taxon with purple flowers

Figs. 2: *Dactylorhiza incarnata* var. *latissima*

Fig. 3: *Dactylorhiza incarnata* var. *borealis*

Fig. 4: *Dactylorhiza incarnata* f. *ovata*

Photos by Tarmo Pikner



is taller, with bigger straight leaves and fewer, paler spots. It grows in similar habitats to *D. incarnata*, sometimes together with the latter but forming a separate colony (site Kõruse). Elsewhere, the two taxa form mixed populations (site Tagamõisa). In rich marshlands, specimens can be very succulent and robust (site Küdema). On the islet of Manija, county of Pärnu, a small population of a very robust variant has appeared, which here is called *D. incarnata* var. *hyphaematodes* f. *latissima*. A similar taxon to *D. incarnata* var. *hyphaematodes* with leaves spotted only on the upper side is *D. incarnata* var. *haematodes* (Rchb.) Soo, also known under the name of *D. incarnata* var. *reichenbachii* Gathoye & Tyteca. The variety prefers dryer biotopes, where it appears rarely as a single specimen.

Another taxon, named *D. incarnata* f. *ovata*, is described here for the first time. This form prefers wooded plains with a dryer biotope and it grows in separated colonies, not accompanied by the nominate taxon of *D. incarnata* [site Kuusnõmme]. It has a remarkable oval, flat lip that is not lobed and the double loop pattern is transformed into a single loop. It has a more slender, rounded stem, a height of 20-26 cm, narrower and comparatively longer leaves, and a shorter, lax inflorescence with fewer (15–20) flowers.

Dactylorhiza ochroleuca

Dactylorhiza ochroleuca, the species with yellow flowers without lip markings, is often considered to be a variety of *D. incarnata*. In fact, these two taxa are clearly distinguishable from each other by their ecological needs, habitats, floral morphology and phenology. *D. ochroleuca* prefers very calcareous, rich fens and the delimitation of these two taxa is well defined by Delforge (2006). One reason for taxonomic misinterpretation is the increasing loss of the habitats similar to the original *locus classicus* of *D. ochroleuca*. This has led to the extinction of populations with nominate specimens. For example, habitat drainage in Britain has reduced representatives of the taxon and this complicates the identification of yellow flowered specimens (Foley 2000).

Dactylorhiza ochroleuca is represented on Saaremaa by some independent populations of 100-600 specimens. Sometimes these are close to a site of *D. incarnata*, where they form separate colonies (sites Kuusnõmme, Viidumäe), and occasionally mixed populations with *D. incarnata* (sites Kurevere, Jaagarahu). Usually however,

Fig. 5: *Dactylorhiza incarnata* var. *hyphaematodes*

Fig. 6: *Dactylorhiza cruenta*

Fig. 7 *Dactylorhiza incarnata* f. *alba*

Fig. 8: *Dactylorhiza incarnata* f. *ochrantha*

Photos by Tarmo Pikner



it has its own distinct sites due to its habitat preference. A fascinating habitat for the taxon is situated on a seaside marshy reed-bank (site Küdema). Here a massive population of 300-600 specimens forms a separate colony with a bigger colony of 1000-2000 specimens of *D. incarnata* only a few dozen metres away, where the biotope is not so swampy but rather flooded. *D. ochroleuca* on Saaremaa is a robust plant, with a height of 35-60 cm and short, very erect leaves, placed against the stem. The middle leaves are slightly warped sideways but remain erect. The inflorescence is more lax and flowers are a little bigger than those of *D. incarnata*, with a clearly 3-lobed lip and longer median lobe. Bracts are smaller and not so dominant. It is said that *D. ochroleuca* produces no or few hybrids (Delforge & Kreutz 2005). The author has made a survey of different populations of *D. ochroleuca* in relation to *D. incarnata* for over a decade. Very generally, the results are the following:

- (1) In sites with an independent population of *D. ochroleuca*, where a population of *D. incarnata* was more than 10 metres away, no hybrids were detected, nor were there any yellow marks on the lip of *D. incarnata* specimens (sites Küdema, Kuusnõmme).
- (2) In sites where *D. incarnata* specimens were closer than 5 metres to specimens of *D. ochroleuca*, the hybridisation percentage between these taxa was 20% on a 10 × 10 m plot (sites Karala, Viidumäe).
- (3) In a site with a mixed population, where the distance between the specimens of the two taxa was 1-3 metres, the hybridisation percentage was 60% on a 10 × 10 m plot (site Kurevere).

In the latter case, samples were taken from hybrids and molecular analysis showed that they were genetically similar to *D. ochroleuca* but different from *D. incarnata* at the same site. This was reflected in the plants' appearance, which was closer to *D. ochroleuca* (Hedren & Nordström 2009; Hedren pers. comm.). The hybrids in the centre of this "melting pot" were really robust, with a height of 40-50 cm. They have a thick stem (1-1.5 cm), an inflorescence with up to 100 flowers in an orange-red colour and a lip that is not folded, with somewhat wavy borders. From this, a conclusion can be formulated that the bumblebees pollinating these two taxa do not focus on different flower colours at short distances, but do so at longer distances. This could complement previous understanding of pollination leading to *D.*

Fig. 9: *Dactylorhiza ochroleuca*
 Fig. 10: *Dactylorhiza incarnata* × *ochroleuca*
 Fig. 11: *Dactylorhiza baltica*
 Fig. 12: *Dactylorhiza baltica* var. *kuzkenembe*
 Photos by Tarmo Pikner

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ochroleuca hybridisation and the pollinators and the food plants on which they are dependent (Pedersen 1998; Delforge & Kreutz 2005; Hedren & Nordström 2009). It is emphasized that no yellow-orange marks appear on the lip of *D. incarnata* specimens from colonies without the proximity of *D. ochroleuca* specimens – for example, among the thousands of specimens of *D. incarnata* on site Undva.

The distinction between *D. ochroleuca* and *Dactylorhiza incarnata* f. *ochrantha* is a frequently debated issue – is the latter a yellow-whitish hypochromic form of *D. incarnata* or does it correspond to a faded taxon of *D. ochroleuca*? On the basis of morphological and ecological features, it belongs to the taxon *D. incarnata*, sharing the same habitats and possessing similar features. The colour of the lip is paler yellow, closer to whitish and somewhat translucent. The lip is flatter, slightly 3-lobed and not folded and the plant is smaller than *D. ochroleuca* with more yellowish-green bracts and stem. It is said that yellow-flowered plants arise because they lack the ability to synthesise anthocyanins, the pigments that confer red and purple colour to the flowers (Bateman & Denholm 1985). Resulting from this, some authors consider *D. ochroleuca* to be a component of the *D. incarnata* complex (Haggard 2005b). On Saaremaa, *D. incarnata* f. *ochrantha* appears rarely as single specimens in a dryer biotope than normal *D. incarnata*. Concerning the taxonomic controversy surrounding *D. incarnata* f. *ochrantha*, molecular analyses place it closer to the taxon *D. ochroleuca* than to *D. incarnata* (Hedren pers. comm.). I suggest that it should be treated under the taxon *D. ochroleuca*.

Sometimes the pure white-flowered form of *D. incarnata* is considered to be the same variation as *D. incarnata* f. *ochrantha*, but here it is designated *Dactylorhiza incarnata* f. *alba*. This variant appears extremely rarely on Saaremaa, mainly in more shaded habitats. It is clearly distinguished from the variant *D. incarnata* f. *ochrantha* due to an absolute lack of yellow and also red colours. In other morphological features, the plant is analogous with *D. incarnata*, including deep green bracts and stem.

Dactylorhiza cruenta

The species with leaves heavily spotted on both sides, rather as if dark lilac colour has been poured over them to give the appearance of dried blood, is *Dactylorhiza cruenta*. Here another debate starts – is the taxon *D. incarnata* var. *hyphaematodes* or just a variety of *D. incarnata*? In fact, *Dactylorhiza cruenta* is distinguished from *D. incarnata* var. *hyphaematodes*. It differs from the latter by a smaller stem and shorter, remarkably curved leaves of lilac colour – especially in early stages when the leaves are totally dark lilac. The inflorescence is shorter with substantially fewer flowers. The taxon is restricted to very calcareous, rich fens, growing almost in water. This is again one reason for misinterpretation, caused by loss of the habitats similar to the original *locus classicus*. Usually the taxon is not accompanied by *D.*

incarnata and does not form mixed populations, which makes determination easier. The author's judgement is that the determination of *D. cruenta*, which has mainly dark purple flowers, is easier in western and central Europe because the majority of *D. incarnata* have pale pink flowers. In Scandinavian regions *D. incarnata* tends to have dark purple flowers which are similar to the flowers of *D. cruenta*. However, on Saaremaa these two taxa are easy to distinguish as they form comparatively independent populations. Sometimes, *D. cruenta* is accompanied by specimens of *D. ochroleuca* (sites Kuusnõmme and Eeriksaare). On Gotland and Öland, *D. cruenta* is morphologically distinguishable from *D. incarnata s.l.* (Hedren & Nordström 2009).

***Dactylorhiza maculata* group**

Dactylorhiza fuchsii

On Saaremaa, the large-flowered species *Dactylorhiza fuchsii* is widespread in different habitats that include calcareous to neutral wetlands, alkaline fens, meadows and woodlands. It is a species, together with *Orchis militaris* and *Epipactis atrorubens*, that in recent decades has occupied wet roadsides and ditches. Sometimes it is difficult to distinguish diploid *D. fuchsii* from its relative, the autotetraploid *D. maculata*, because intermediate forms occur. In terms of floral morphology, the best distinguishing feature of *Dactylorhiza fuchsii* is the deeply 3-lobed lip with a prominent median lobe, as wide as but longer than the side lobes. Another distinguishing feature is the broad obovoid lowest leaf. Moreover, their habitat preferences are different and usually they are not found together. As to the hypochromy of Dactylorchids, then *D. fuchsii* most frequently produces specimens with pure white flowers. On a roadside at site Odalätsi, a population of 700 specimens appeared with 10% of the form *D. fuchsii* f. *alba*. Scattered in flooded salty coasts, a very small variety, *D. fuchsii* var. *psychrophila*, appears. The plant is very short, with a thin stem and a height of 10-15 cm. It has two narrow leaves and 5-7 flowers, which are smaller than in the normal taxon. This variety is also reported in northern Scandinavia.

Dactylorhiza maculata

Acidiphilous *Dactylorhiza maculata* is easily distinguished from calciphilous *D. fuchsii* by its habitat preference. In terms of floral morphology, *D. maculata* has a less lobed and more rounded lip with a small median lobe that does not protrude between the side lobes. The lowest leaf is narrower, longer and has a lanceolate shape. The taxon occupies spring fens (sites Odalätsi and Viidumäe) with small populations. In a rather wooded fen on site Viieristi, a pure white form *D. maculata* f. *alba* has appeared among thousands of normal specimens. A much more slender variant with fewer flowers, the taxon *D. maculata* var. *ericetorum*, is present on sites Kuusnõmme and Viidumäe.

Group of allopolyploids

Dactylorhiza baltica

Dactylorhiza baltica originates from the Baltic region and is fairly widespread on Saaremaa's western coastal wetlands, fens, and reed-banks, where there is a neutral or slightly calcareous substrate. The taxon prefers oxygen-rich water to marsh waters. Among the very polymorphic allopolyploids, *D. baltica* is the most stable species in both its vegetative and floral features. Within *Dactylorhiza*, only *D. ochroleuca* could compete with *D. baltica* in the stability of its morphological features. The peculiarity of the taxon is its regularly and spirally positioned flowers in a cylindrical inflorescence. The flowers are pink-violet with a broad oval lip and wide, rounded lateral lobes. Heavy leaf spots are evenly orientated crosswise. The most exciting populations are littoral, in reed-banks with over a thousand relatively robust specimens (sites Kuusnõmme and Küdema). *D. baltica* is an exceptional species which is expanding its distribution area and increasing its populations (Pikner 2011). Nevertheless, it is interesting to note the clear northern-western segregation line in the distribution of this taxon. This runs from the northern coast of the Estonian mainland to the western coast of Hiiumaa and then to the western coast of Saaremaa and the eastern coast of the Baltic Sea down to Lithuania. On the right of this line, massive populations of *D. baltica* appear, whereas on the left there are none at all, except for doubtful single reports from Sweden and Finland. It should be noted that the taxon is still quite rare in Hiiumaa. Another interesting thing to note is that this same segregation line functions for *Dactylorhiza sambucina*, but in reverse. *D. baltica* may be called an Estonian endemic orchid because J. Klinge described the type specimen, collected from Livonia in 1898.

Some authors have drawn parallels between *D. baltica* and *D. majalis*. Indeed, both of them have spotted leaves but even this feature has differences. It should be noted that the segregation line in the distribution of these two taxa runs from the east-southern coast of the Baltic Sea, through northern Poland towards Russia. *D. baltica* grows above the segregation line and below the line there is *D. majalis*. What happens when the borders of the two distribution areas meet can be seen in several populations of intermediate forms and hybrid swarms of allopolyploid taxa in northern Poland (Pikner 2011). Also, the northern border of the distribution area of *D. majalis* includes the Baltic Sea islands. The taxon is missing on northern islands and starts to appear on Bornholm and Rügen. The central-western European species *D. majalis* is becoming replaced with *D. baltica* in north-eastern Europe.

A new variety of the taxon has recently been discovered by the author: *Dactylorhiza*

Fig. 13: *Dactylorhiza osiliensis* Pikner

Fig. 14: *Dactylorhiza russowii*

Fig. 15: *Dactylorhiza maculata* f. *alba*

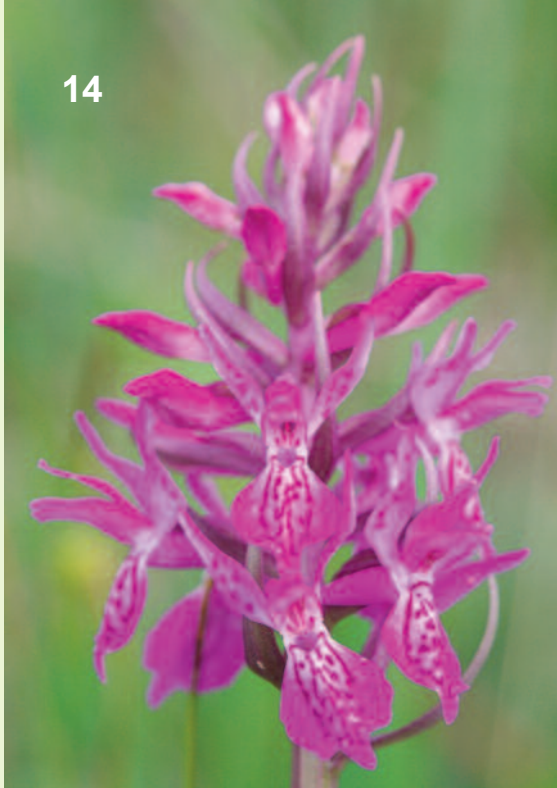
Fig. 16: *Dactylorhiza ruthei*

Photos by Tarmo Pikner

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baltica var. *kuzkenembe* Pikner (Pikner 2011). The newly discovered variety has unspotted leaves, a shorter, thinner and more conical inflorescence and darker flowers with downwards orientated lateral lobes and a median lobe that is not rounded. Also, the lateral sepals are longer and narrower, with backwards turned concave sides. *D. baltica* var. *kuzkenembe* prefers a more shaded habitat (sites Kuusnõmme and Kaarmise).

Dactylorhiza russowii

In contrast to the previously mentioned species, *Dactylorhiza russowii* is the most unstable and polymorphic *Dactylorhiza* species, having many populations on Saaremaa. If *D. incarnata* has at least one stable feature – a double loop on the lip, then *D. russowii* has nothing which could be said to be stable. This has led to a situation where the same or very similar taxa have been given different names at different times. A very similar taxon, *D. traunsteineri*, was described from the Austrian Tyrol by Sauter ex Rchb in 1830. Then, *D. curvifolia* was described from Finland by Nylander in 1844. Then comes *D. lapponica*, described from Swedish Lapland by Laestadius ex Rchb in 1850. Then, *D. russowii* described from Palmse, Estonia by Klinge ex Russow in 1893. While he was working at Tartu University, the Baltic-German botanist J. Klinge defined 73 different varieties and forms of the taxon, mainly on the basis of surveys in Estonia, including site Viidumäe on Saaremaa (Klinge 1899). *D. russowii* as a very polymorphic taxon that may occupy diverse habitats like wooded bogs (site Viidu), spring fens (sites Viidumäe and Küdema) and neutral wetlands, sometimes close to habitats of *D. maculata* but not forming mixed populations with the latter (site Viieristi). One feature of *D. russowii*, less described in the literature, should be noted – dark lilac-brown dots on the upper side of narrow curving leaves are concentrated towards the edges of the leaves, while the very edge of the bluish-green leaves is only just dark lilac.

In order to reduce the confusing nomenclature for the taxon, the author here suggests that the taxa under all the above-mentioned names be treated as *Dactylorhiza traunsteineri*. Otherwise, the situation is created where several regions have their own “traunsteineri” under different names. Although distinguishable features can be found, they are probably caused by the influence of local biogeographical factors.

***Dactylorhiza osiliensis* Pikner**

The endemic species *Dactylorhiza osiliensis* Pikner was discovered by the author on Saaremaa in 2003. Some large populations of the new species were found in the swampy, wooded marshes of the western littoral of the island (site Kuusnõmme). The robust, large-flowered taxon of deep purple-violet colour is surprisingly homogeneous and is obviously distinct from other allopolyploids (Pikner & Delforge 2005). Sometimes the taxon is associated with the western European allopolyploid species *D. praetermissa* but this is wrong. *D. osiliensis* has been determined clear-



Dactylorhiza osiliensis Pikner
Photo by Tarmo Pikner

ly and proved by molecular analyses (Hedren pers. comm.). Still, a question may arise as to how it is possible to find a new species nowadays. On the one hand, during the Soviet time, the littoral area was comparatively closed for visits to potential habitats and hence some sites were not well investigated. On the other hand, several authors say that various allotetraploids are still being synthesized locally (e.g. Pillon et al. 2007) and some comparatively young taxa may appear. It should be noted that the report of the taxon with the name *Dactylorhiza praetermissa* described on Saaremaa's neighbouring island Hiiumaa in 1989 (Schmeidt 1996, Tuulik 1998) was mistaken. Studies have shown that it was a small population of an unstable hybrid swarm, and the primary association is almost extinct today (Delforge & Kreutz 2005; Pikner unpublished observations).

***Dactylorhiza sambucina* group**

Unfortunately, the species *Dactylorhiza sambucina* is extinct on Saaremaa. The last specimen was collected for a herbarium in 1901. One reason for its loss is the decrease in coastal meadows where the taxon used to grow. From the conservation point of view, it should be mentioned that even botanists have contributed to the extinction of this taxon. Several herbarium examples of *D. sambucina* collected from Saaremaa have been found in St. Petersburg and Riga. In 1989, an attempt to re-introduce the population was initiated and some plants were brought from Aland Island and planted in potential habitats. The result has not been very successful with only leaves of 2-3 cm of some plants appearing year by year (Pikner observations).

***D. (Coeloglossum) viridis* group**

Recently, the species *Coeloglossum viride* was added to the *Dactylorhiza* genus as *D. (Coeloglossum) viridis*. On Saaremaa, the taxon is extinct but I am sure that one day this grass-green species will be found in the green grass.

The bonus: *Dactylorhiza ruthei*

It was stated above that *Dactylorhiza ruthei* does not grow on Saaremaa, but it can be found not far from the island, and it is appropriate to introduce the species here. The only authentic population of the taxon has been determined on the littoral of

western Estonia. *D. ruthei* was first described from Swinemünde, Germany, by M. Schulze ex Ruthe in 1897. The taxon disappeared for many decades. In 1952, a similar taxon was collected near Virtsu in the mainland of Estonia and it was determined as *D. ruthei* by V. Kuusk in 1974. In 1997, a taxon with the same name appeared in Peenemünde (Usedom, Germany), about 45 km from the original *locus classicus* in Swinemünde, which is built over today. Observations have shown that the Peenemünde taxon differs both from the type specimen of *D. ruthei* and from the Estonian *D. ruthei* (Pikner & Kuusk 2008). The current position is that the only population of the taxon grows in Estonia, not far from Saaremaa. *D. ruthei* with its large pale violet-purple flowers is a really outstanding taxon. Exceptionally, the lip seems to lack markings, yet a closer observation reveals very small dots. It has very long bracts and pale green linear leaves that extend to the centre of the inflorescence.

Conclusion

Several surveys and molecular analyses of the origin of *Dactylorhiza* taxa have been carried out in order to clarify their relationships. It is evident that some taxa in northern Europe have different features from what are principally the same taxa in central or southern Europe or in the British Isles. There is a hypothesis on the migration of the parental species of numerous allopolyploids to northern Europe after the last glaciations and on when they arrived and whether they immigrated from the south or north-east. These factors have probably influenced the continuous evolution of orchids. Also, it has to be taken into consideration that there is a high level of genetic variation among the allopolyploid taxa, caused by habitat preferences and fragmented locations (e.g. Nordström & Hedren 2009).

One explanation for allopolyploids with the same parents yielding different results could be that allotetraploids could have profoundly affected both the form, flower colour and habitat preferences of one of the parental species, especially considering the polymorphic nature of *Dactylorhiza incarnata* (Haggard 2007). There is still room for different interpretations of the taxonomy of *Dactylorhiza*, starting with the authenticity of the type specimen of *D. incarnata* and ending with defining newly appearing allopolyploid species. Hopefully, this article will show that one “smelting furnace” of wild orchids has been working on the western littoral of Saaremaa.

References

- Bateman, R.M. & Denholm, I. (1985) A reappraisal of the British and Irish dactylorchids. 2. The diploid marsh-orchids. *Watsonia* 15: 321-355.
- Delforge, P. & Kreutz, C.A.J. (2005) Remarks on Estonian orchids. *Les Naturaslistes Belges*, 86 (Orchid. 18): 21-56.
- Delforge, P. (2006) *Orchids of Europe, North Africa and the Middle East*. A&C Black, London: 172-243.
- Foley, M.J.Y. (2000) *Dactylorhiza incarnata* (L.) Soo subsp. *Ochroleuca* (Wüstneii

- ex Boll) P.F. Hunt and Summerh. (Orchidaceae): A comparison of British and European plants. *Watsonia* 23: 299-303.
- Haggar, J. (2003a) The Early Marsh-orchid (*Dactylorhiza incarnata*) in Northern Europe. I. *HOS Newsletter* 27: 4-9.
- Haggar, J. (2003b) The Early Marsh-orchid (*Dactylorhiza incarnata*) in Northern Europe. II. *HOS Newsletter* 29: 17-22.
- Haggar, J. (2004a) The Early Marsh-orchid (*Dactylorhiza incarnata*) in Northern Europe. III. *JHOS* 1(31): 18-23.
- Haggar, J. (2004b) The Early Marsh-orchid (*Dactylorhiza incarnata*) in Northern Europe. IV. *JHOS* 1(32): 45-51.
- Haggar, J. (2005a) The Early Marsh-orchid (*Dactylorhiza incarnata*) in Northern Europe. V. *JHOS* 2(36): 51-59.
- Haggar, J. (2005b) The Early Marsh-orchid (*Dactylorhiza incarnata*) in Northern Europe. VI. *JHOS* 2(38): 116-124.
- Haggar, J. (2007) The Early Marsh-orchid (*Dactylorhiza incarnata*) in Northern Europe. VII. *JHOS* 2(44): 52-57.
- Klinge, J. (1899) Die homo- und polyphyletischen Formenkreise der Dactylorchis. *Acta Horti Petropolitani*, vol. XVII, Fasc. II, N. 6.
- Kuusk, V. (1984) Orchidaceae. *Eesti NSV floora, IX. Tallinn*: 376-396.
- Mossberg, B. & Lundqvist, A. (1994) Öländska ängsnycklar. *Swensk Botanisk Tidskrift* 88 (2): 84-96.
- Nordström, S. & Hedren, M. (2009) Evolution, phylogeography and taxonomy of allopolyploid *Dactylorhiza* (Orchidaceae) and its implications for conservation. *Nordic Journal of Botany* 27: 548-556.
- Pedersen, H. (1998) Allozyme variation and genetic integrity of *Dactylorhiza incarnata* (Orchidaceae). *Nordic Journal of Botany* 18 (1): 15-21.
- Pikner, T. & Delforge, P. (2005) The Dactylorchid of the island of Saaremaa (Estonia), Pikner sp. Nova. *Les Naturalistes Belges* 86 (Orchid. 18): 65-80.
- Pikner, T. & Kuusk, V. (2008) *Dactylorhiza ruthei* (M. Schulze ex Ruthe) Soó versus *Dactylorhiza vironii* Kreutz. *Ber. Arbeitskr. Heim. Orch.* 25(2): 119-150.
- Pikner, T. (2011) Northern European polyploid species of *Dactylorhiza baltica* (Klinge) Orlova ex Averjanov, a new variety of *Dactylorhiza baltica* var. *kuzkenembe* nova and their comparison with the other polyploid species of *Dactylorhiza* (Orchidaceae). *Ber. Arbeitskr. Heim. Orch.* 28(2): 233-262.
- Pillon, Y., Fay, M. F., Hedren, M., Bateman, R. M., Deveyl, D.S., Shipunov, A. B., van der Bank, M., Chase, M. W. (2007) Evolution and temporal diversification of western European polyploid species complexes in *Dactylorhiza* (Orchidaceae) *Taxon*, 56: 1185-1208.
- Schmeidt, O. (1996) *Eestimaa orhideed*. Varrak, Tallinn.
- Tarrant, S. (2011) Orchid Hunting on Saaremaa. *JHOS* 8:101-106.
- Tuulik, T. (1998) *Hiiumaa orhideed*. BKHK, Kärdla.

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