The Pollination of European Orchids: Part 2: _Cypripedium_ and _Cephalanthera_
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**Introduction**
In the first part of this series we discussed and illustrated the construction of an average European orchid flower. Much of this applies to many European orchids. In this part we will show two orchid genera that deviate from the general pattern.

*Cypripedium calceolus*, the Lady’s slipper orchid
This orchid certainly is the orchid lover’s favourite with its brownish perianth and the beautifully contrasting yellow slipper. The Lady’s Slipper is a primitive orchid, the only European species that has two anthers. The pollen is not mealy, but instead the loose pollen grains are packed into a viscid fluid. The stigma is quite large, dry and covered with minute pointing papillae (Figure 1). The yellow slipper serves as a means of attraction from afar. The flower emits a scent, but colour is the key attraction mechanism. The crimson spots on the white staminode and on the veins in the bottom of the lip (Figure 2) are false nectar guides (Nilsson 1981). _C. calceolus_ is above all visited and pollinated by *Andrena* bees. Visitors generally land on the lip which has margins covered with an oily substance. They either fall into the pouch losing their balance or they fly into the flower searching for nectar. Once inside the bees find out there is no nectar and show a disturbed behaviour, making efforts to escape. They try to climb the inside of the pouch, but this is covered with a film of oil as well, preventing them from getting out. They also try to escape by climbing the slippery staminode, but always fall back into the flower. There are only two exits from the flower, two small orifices left and right of the column (Figure 3). Near the lip base are various translucent spots on both sides of the slipper. They help to guide the bees towards the exits.

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**Fig. 1:** _Cypripedium calceolus_, column showing the large, shield-like stigma. Behind it is the staminode; under the stigma are the two anthers with the pollen smear.

**Fig. 2:** _Cypripedium calceolus_, lip. The visiting insect leaves through one of the two openings behind the staminode.

**Fig. 3:** Longitudinal section of the slipper showing the translucent sections and the arching stigma and staminode. Near the base of the stigma is one of the two anthers.

**Fig. 4:** A female of *Andrena carantonica* leaving the slipper with stigmatic smear on its back.

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After discovering the way out, there is hard labour ahead for the insect. In order to get out it first has to pass the stigma. If the insect has already visited another flower, it will carry some pollen smear on its back which now is scraped off by the pointed papillae of the stigma. Then it encounters one of the anthers, which partly block the exit. The insect must have enough power to push back the flower tissue to fight its way past the sticky anther. It inevitably touches the surface of the anther and some pollen smear will stick on its back (Figure 4). We often saw the bees grabbing the hairs on the bases of the petals in order to pull themselves out. When the insect is halfway things go very quickly. It climbs out and rests for some moments or disappears at once. We never saw them visiting another nearby flower directly after climbing out of the flower. The whole pollination process is quite stressful for the insects and revisits leading to pollination are quite low. The Lady’s Slipper-orchid mainly propagates vegetatively.

The genus *Cephalanthera*
Three species of *Cephalanthera* grow in Great Britain – the Sword-leaved Helleborine (*C. longifolia*), the Red Helleborine (*C. rubra*) and the White Helleborine (*C. damasonium*). The first two species are allogamous, that is they rely on insects for pollination, whereas the third species is autogamous, self-pollinating. We will discuss the pollination mode of the Sword-leaved Helleborine, which also applies to the Red Helleborine.

The perianth segments of the Sword-leaved Helleborine do not open wide. Generally the lateral sepals spread a bit more. All *Cephalanthera* species have a long column with a large stigma and a hinged anther with two bipartite pollinia (Figure 5). The lip consists of two parts: the front part or epichile and the rear part or hypochile. The connection between epichile and hypochile is hinged. On its tip the epichile is ornamented with yellow-orange longitudinal ridges. They imitate pollen and are meant to tempt insects to visit the flower. Also, the rear part of the hypochile is equally coloured yellow-orange. The column is long and slender and more or less horizontal. The pollinia are banana-shaped, have no caudicles or viscidia and lie free in the anther (Figure 8, left column). The stigma is placed near the anther, on the underside of the column and is large and rounded.

**Fig. 5:** *Cephalanthera longifolia*, longitudinal section. The orange parts are imitations of pollen. A=anther, L=lip, St=stigma, O=ovary

**Fig. 6:** A female *Lasioglossum laeve* that has just left the flower. The banana-shaped pollinia stick to its back.

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An insect visitor, attracted by the pseudo-pollen of the lip, will have to bend forward in order to reach the rear part of the hypochile, searching for nectar. When it finds out there is no nectar, it retreats and lifts its body. In doing so it touches the stigmatic surface. It scrapes off some of the stigmatic fluid. When it continues its bow-shaped retreat it touches the pollinia which remain in the anther. Due to the stigmatic fluid on the back of the insect the pollinia are pulled out of the anther and stick to the insect’s back (Figure 6). The two little banana-shaped pollinia cannot be removed by the insect. When it visits another flower, the forward sticking pollinia are pushed against the stigma and pollination is completed. Regular pollinators are small *Halictus* or *Lasioglossum* bees. Pollination of the Red Helleborine takes place in the same way as described. Pollinators are various small bees like *Chelostoma, Dufourea, Heriades* or *Osmia*.

The White Helleborine has flowers that hardly open. The epichile and hypochile are similarly coloured and ornamented as in the previous species (Figure 9). The column closely resembles that of the Sword-leaved Helleborine, but there is one small but decisive difference. The upper rim of the stigma of the Sword-leaved Helleborine is covered with a thin layer of tissue, preventing the contact between pollinia and stigmatic fluid. The White Helleborine lacks this tissue and as a result the pollinia can directly contact the stigmatic fluid as soon as the anther opens (Figure 8, right column). This takes place before the flower opens, making this species totally autogamous. Even if an insect enters the flower, it will not be able to collect any pollen, because this is already soaked with stigmatic fluid and can no longer be transported (Figures 9 and 10). If there are hybrids with one of the other species, then the pollen most likely was imported from the allogamous species. For this species autogamy is an advantage, because it means that it can grow in unfavourable conditions (dark woods and heavy shade) where few pollinators are available.

**Fig. 7:** *Cephalanthera longifolia*
**Fig. 8:** Columns of *C. longifolia* (left) and *C. damasonium* (right). In *C. longifolia* the contact between pollinia and stigma is prevented by a thin membrane covering the upper stigmatic rim. The pollinia of *C. damasonium* are already soaked with stigmatic fluid.
**Fig. 9:** *Cephalanthera damasonium*, flower opened manually to show the pollinia sticking onto the stigma.
**Fig. 10:** *C. damasonium*, column. The pollinia have fallen out of the anther and stick to the stigma.

Photos by Jean Claessens & Jacques Kleynen
The Oxwich Epipactis
Mike Clark

In July 2012, I surveyed the Oxwich Burrows NNR for Epipactis as I had heard that historically E. phyllanthes had grown in the slacks. I discovered large numbers of Epipactis helleborine var. neerlandica in certain areas, and in a remote spot I found 13 plants in open-ground keying down to E. phyllanthes var. cambrensis, described by Charles Thomas (Thomas 1941, 1950). I returned to the site this August and found 5 more plants in open-ground on a 40m north-east facing slope growing in Early Hair-grass with Round-leaved Wintergreen, Yellow Rattle, Restharrow and a small amount of Dewberry. Figures 1 and 2 are of one of the plants, which was 25.5 cm tall, with a 7cm inflorescence made up of eleven flowers. The plants have a definite ‘jizz’ and tend to be more yellowish than the woodland phyllanthes plants, with undulate margins to the leaves which are long, well-keeled and convexing. The flowers are also greenish yellow with pale greenish white hypochile and the epichile can reflex quite early into flowering, looking like a small white boxing glove. The height of the plants seems to depend on the surrounding sward and age of the plant but most are under 21cm. My own personal observation of this plant is that it is a woodland plant that has adapted itself to surviving in open ground and has altered its appearance accordingly. I appreciate this view is not accepted by every one and that it is a good taxon and not just an ecotype.

References

Fig. 1: Spike close-up of E. phyllanthes var. cambrensis
Fig. 2: Whole plant of E. phyllanthes var. cambrensis
Fig. 3: Habitat of E. phyllanthes var. cambrensis
Photos by Mike Clark