The pollination of European Orchids Part 3: *Limodorum* and *Epipactis*

Jean Claessens & Jacques Kleynen

In the second part of this series we treated the primitive orchid genera *Cypripedium* and *Cephalanthera*. In this article we introduce two further representatives of the primitive orchids. We will discuss the development of a specific organ intended for attaching the pollinia to a pollinator.

Limodorum

The representatives of the genus *Limodorum* are tall, slender plants, resembling an *Asparagus* when not in bloom. The flowers open wide or stay closed, depending on the climatic conditions or the pollination mode; allogamous or autogamous. Open flowers are attractive − the lateral sepals are spread and the bipartite lip is horizontal, providing a good landing place for visiting insects (Fig. 1). The long, downward curved spur contains copious nectar. The long column is bent over the lip and on its ventral side is a large, triangular-rounded stigma, glistening with stigmatic fluid. On the flattened top of the column lie the pollinia, covered by the hinged anther cap. In the genus *Cephalanthera* we saw that the pollinia are transported by means of the stigmatic fluid, gluing the pollinia to the back of the pollinator. In the genus *Limodorum* pollinia are attached to the pollinator by means of a specific structure.

The stigma of most European orchid genera consists of three parts, a condition best viewed in young flowers, when the stigma is not yet covered with stigmatic fluid. In *Limodorum* (Fig. 2), part of the stigma is converted into the rostellum, a tissue that can form a viscid structure, termed the viscidium, for attaching the pollinia to the pollinator. The viscidium is a rounded, whitish convex structure at the upper rim of the stigma. It consists of viscid fluid covered by a thin membrane. When an insect visitor of L. *abortivum* (Violet Limodore**)** lands on the lip the protruding, hinged part bends downwards, forcing the visitor to crawl further forward in order to reach the nectar in the spur (Fig. 3). Thus, the pressure on the lip is reduced and it swings up into its original position. The chance is high that the visitor pushes against the viscidium. The covering membrane ruptures and the pollinia are glued to the insect's

Fig.1 : *Limodorum abortivum,* La Bouverie, France, 4th May 2009
Fig.2: Column of *Limodorum abortivum*
[A=anther, P=pollinia, V=viscidium, S=stigma]
Fig.3: *Limodorum abortivum* with an *Anthophora* bee that has landed on the lip, searching for nectar. La Bouverie, France, 4th May 2009
Fig.4: The flower of *Limodorum abortivum* is well adapted to its pollinator, *Anthophora biciliata*, which has pollinia attached to its back. The pollinia are in the exact position for touching the stigma. La Bouverie, France, 7th May 2008


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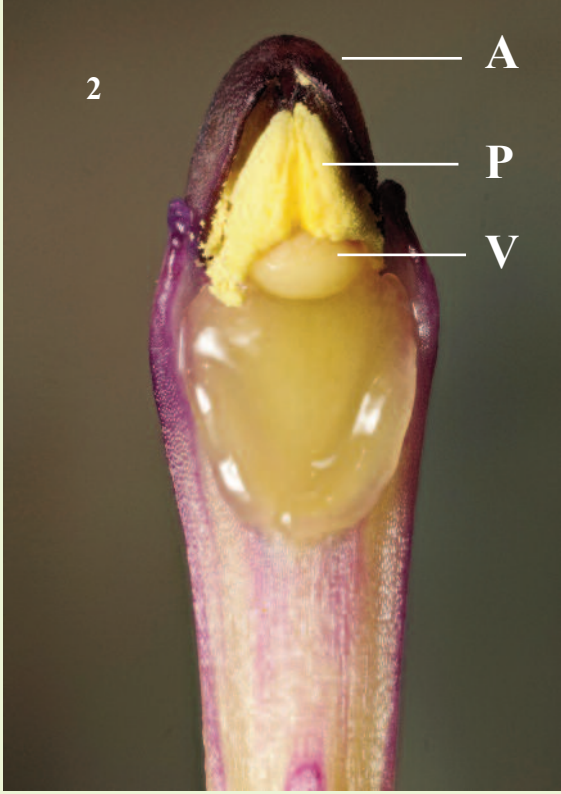
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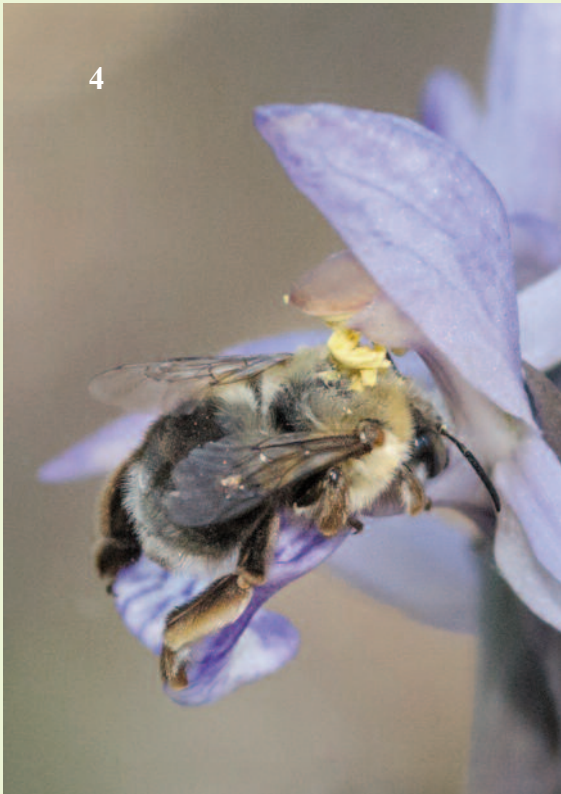
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back (Fig. 4). Due to the retreating movement of the insect, the hinged anther lifts, freeing the pollinia, and they can be transported to another flower. Main pollinators are male *Anthophora* bees, which include the plants of *L. abortivum* in their patrol routes. While flying around checking if there are any females available, they land now and then on the orchid and search for nectar. Many of the males we have observed already had pollinia glued to their back. The visiting frequencies seem to be specific for a locality, as in other nearby populations we saw no pollinators patrolling or visiting the flowers. Other reported pollinators are *Bombus terrestris* (Fig. 5), *Anthidium septemdentatum* (Fig. 6) and *Lasioglossum* sp. (Claessens & Kleynen 2011). During either cold, rainy or very hot periods the flowers hardly open or can stay completely closed. In that case, the flowers of *Limodorum abortivum* can auto-pollinate. The pollinia are rather friable and can lose coherence, so that the pollen grains, united in packages of four, can pass the viscidium and contact the stigmatic surface.

In its sister species *Limodorum trabutianum* (Fig. 7) autogamy is the rule. The stigma is situated right under the anther and is perpendicular to the axis of the column. When the anther is mature and dehisces the pollinia fall directly onto the underlying stigma. There is a viscidium, but this is covered by a tongue-shaped outgrowth of the column, blocking the passage to the viscidium.

Epipactis

The genus *Epipactis* comprises allogamous, autogamous as well as transitional species. The structure of the stigma and the viscidium plays an important role in the pollination mode. We will take *Epipactis helleborine* (Broad-leaved Helleborine) as an example to illustrate the construction of an *Epipactis* flower (Fig. 8). The flower perianth is bell-shaped and has a bipartite lip with a more or

Fig.5 : A bumblebee (*Bombus terrestris*) searching for nectar. The articulated lip bends down under its weight. La Bouverie (F), 6th May 2009
Fig.6: *Anthidium septemdentatum* landing on the lip of *Limodorum abortivum.* La Bouverie, France, 4th May 2006
Fig.7 (above): Flower of *Limodorum trabutianum* with a sepaloid lip and a ventral outgrowth covering up the stigma.

less triangular part that serves as a landing place for insects (the epichile), and a basal, cup shaped part where nectar is secreted (the hypochile). The column is horizontal; the large, concave, quadrangular stigma is placed on the underside. The top of the column is concave, forming a pollen bed in which the pollinia are deposited when the anther is ripe. On the protruding part of the column sits a rounded structure, the viscidium (Fig. 9). As in *Limodorum*, it consists of sticky fluid, covered by a thin membrane. When the flower opens, the viscidium is already connected to the pollinia. The viscidium has a double function. It glues pollinia to the pollinator and prevents pollinia from sliding out of the anther and contacting the stigmatic surface.

Wasps almost exclusively visit and pollinate *E. helleborine* (Figs. 10 & 11). Wasps often visit rotting fruit and after crawling over the fruit they can transport yeast bacteria from the fruit to the *Epipactis* plants. The nectar is infected with the yeast and starts fermenting, producing small quantities of alcohol. This attracts the bees and makes them more sluggish, extending the time they spend on the *Epipactis* plants (see a video at http://www.youtube.com/watch?v=GIbB2_MUFs8). Due to this phenomenon the fruit set of *E. helleborine* is quite high. Other species that depend on insect visitors for their pollination include *E. atrorubens* (Dark-red Helleborine) and *E. purpurata* (Violet Helleborine).

In *E. palustris* (Marsh Helleborine, Back Cover Photograph), we can observe both allogamous and autogamous pollination. The conspicuous flowers produce large amounts of nectar in the hypochile and are pollinated by a wide range of insects (see Wilcox 2010). In order to enable autogamy the pollinia must be able to contact the stigma. The pollinia stick out beyond the point of attachment to the viscidium and cohere well in young flowers (Fig. 12). However, if a flower gets older and is not yet pollinated, the pollinia lose cohesion and pollen packages can reach the stigma below the tips of the pollinia.

Fig.8 (above): *Epipactis helleborine*, Geulle, The Netherlands, 26th July 2011
Fig.9: *E. helleborine* close-up [A=anther, V=globular viscidium, S=stigma]
Fig.10: Wasp presses pollinia, attached to its head, firmly against the stigmatic surface while drinking nectar, Geulle, The Netherlands, 5th August 2013
Fig.11: Wasp drinking nectar from the hypochile, Geulle, The Netherlands, 5th August 2013


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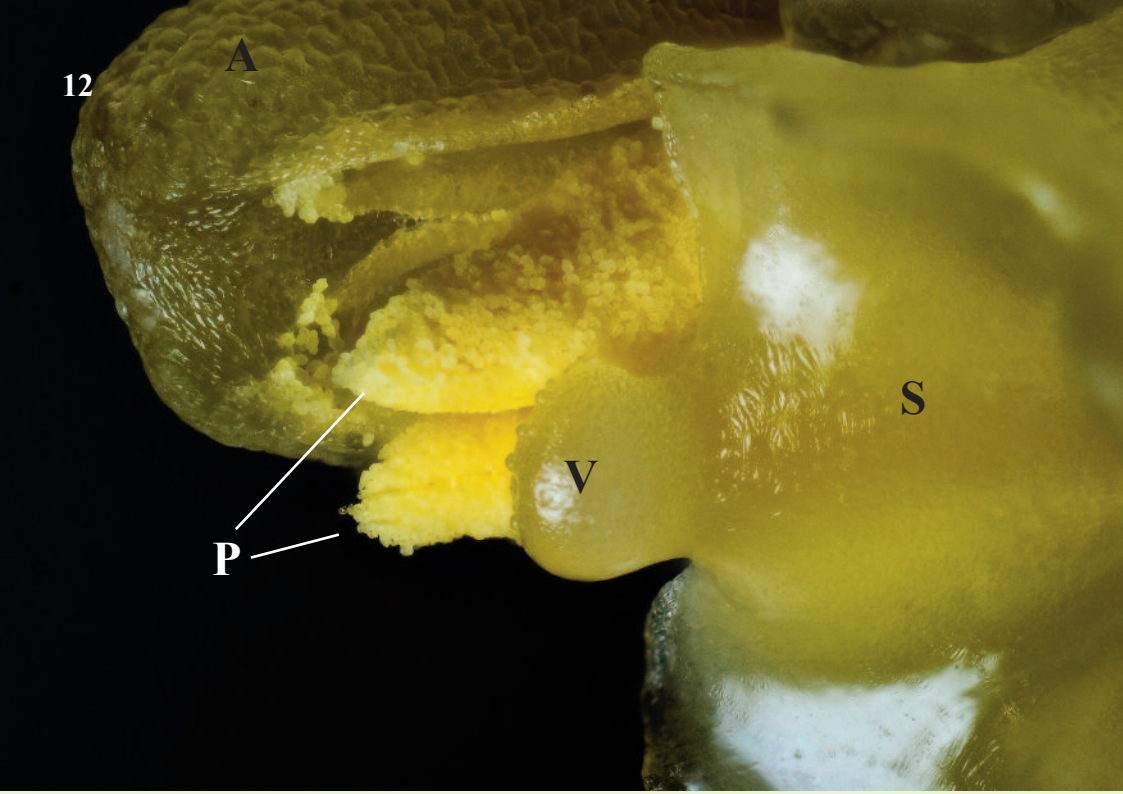
The cohesion of the pollinia, the functionality of the viscidium and the form of the stigma determine the pollination mode of the various species. In recent orchid literature, there is a torrent of new "species", many of which are autogamous taxa. They all show pollinia that easily fall apart, a viscidium that is either ineffective, has shrunk or has completely disappeared and a stigma that is reduced. Instead of forming a broad platform for the pollinia, there is only a small, triangular pollen bed left so that the pollinia can easily contact the stigma (Fig. 13). Examples of autogamous species are *E. leptochila* (Narrow-lipped Helleborine) or *E. microphylla* (Small-leaved Helleborine). Autogamy enables those species to occupy forests with few or hardly any insect visitors.

In *Epipactis muelleri* (Mueller's Epipactis), the pollen bed has almost completely disappeared. When the anther dehisces the pollinia fall directly onto the underlying stigma (Fig. 14). Because of the lack of a viscidium, transport of the pollinia is impossible. Hybrids can occur if the pollinia of an allogamous species are deposited on the stigma of *E. muelleri*.

References

Claessens, J. & Kleynen, J. (1991): Het geslacht Epipactis in de Benelux: bloembiologische beschrijvingen en soorttypische kenmerken. *Eurorchis* 3: 5-38.
Claessens, J & Kleynen, J. (2011): *The flower of the European orchid – Form and Function*. Self Published, Geulle.
Godfery, M. J. (1933) *Monograph & Iconograph of Native British Orchidaceae*. Cambridge.
Kugler, H. (1977) Zur Bestäubung mediterraner Frühjahrsblüher. *Flora* 166: 43-64.
Nieschalk, A & Nieschalk, C. (1970) Die Gattung Epipactis (Zinn) Sw. em. L. C. Rich. in Nordhessen. *Abh. Ver. Naturk. Kassel* 63: 1-40.
Richards, A. J. (1982) The influence of minor structural changes in the flower on breeding systems and speciation in Epipactis Zinn (Orchidaceae). in Armstrong, J.A., J.M. Powell & A.J. Richards: *Pollination and Evolution*. Sydney 47-53.
Wilcox, Y. (2010) *Epipactis palustris* et ses pollinisateurs en Vendée. *Bulletin Soc. Franc. d'Orchidophilie Poitou-Charentes et Vendée* 8-26

Fig.12 : Part of the *Epipactis palustris* column, seen from below. The pollinia exceed the upper rim of the stigma and have a rather loose structure. [A=anther, P=pollinia, V=globose viscidium, S=stigma]
Fig.13: *Epipactis leptochila* column showing the reduced stigma allowing the pollinia to contact the stigmatic surface. The pollinia are powdery, easily falling apart and the viscidium is ineffective. [A=anther, V=viscidium, S=stigma]
Fig.14: Longitudinal section of an *Epipactis muelleri* bud showing the column. The pollinia have fallen out of the anther directly onto the underlying stigmatic surface.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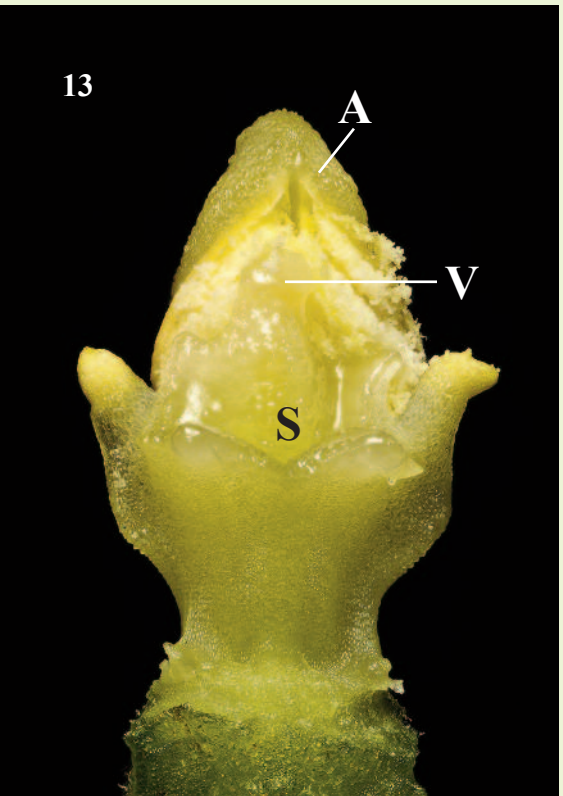
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