The pollination of European orchids
Part 1: Introduction and the genera *Orchis* and *Dactylorhiza*

Jean Claessens and Jacques Kleynen

Introduction

Wild orchids inspire many people and incite them to undertake long journeys to find and photograph those beauties of nature. Far less people travel to find and study the pollinators, which is quite understandable as it inevitably takes much time and the chance of finding nothing at all is quite large. Unfortunately there are no GPS data available for sites where you are certain to find a specific pollinating insect. Yet the study of pollination is a very interesting and fulfilling subject, a new dimension that can help to understand why a certain orchid has a certain appearance and habitat

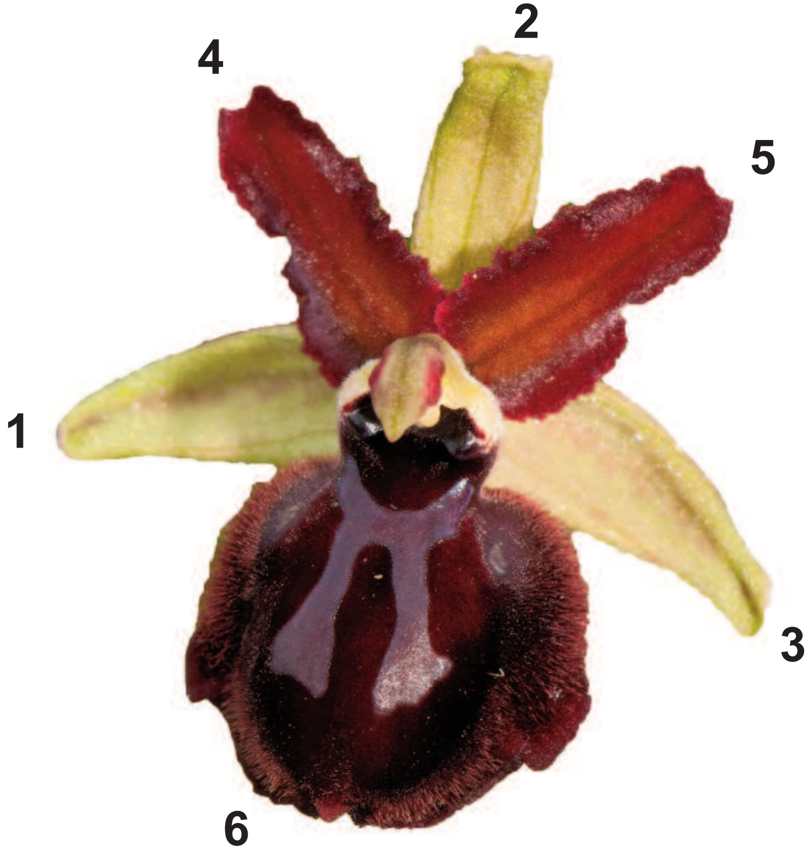

Fig. 1: Flower of *Ophrys garganica*. Numbers 1, 2 and 3 are the sepals, numbers 4 and 5 are the petals and number 6 is the lip.
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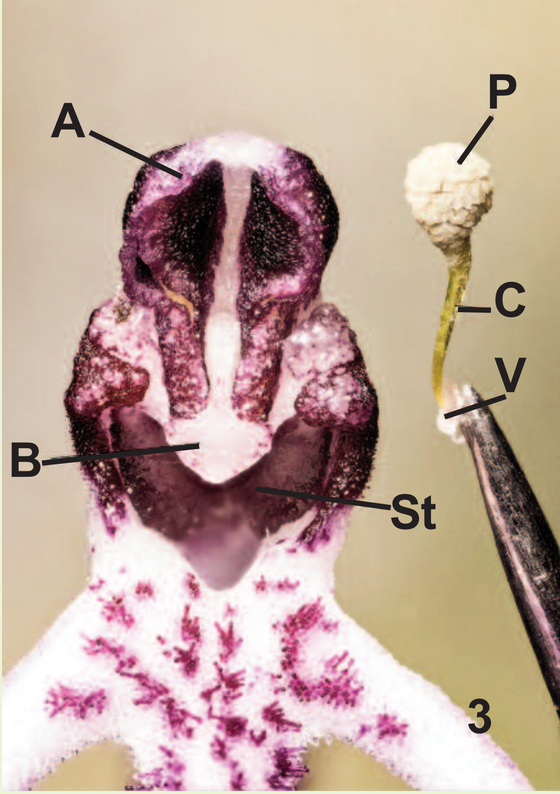
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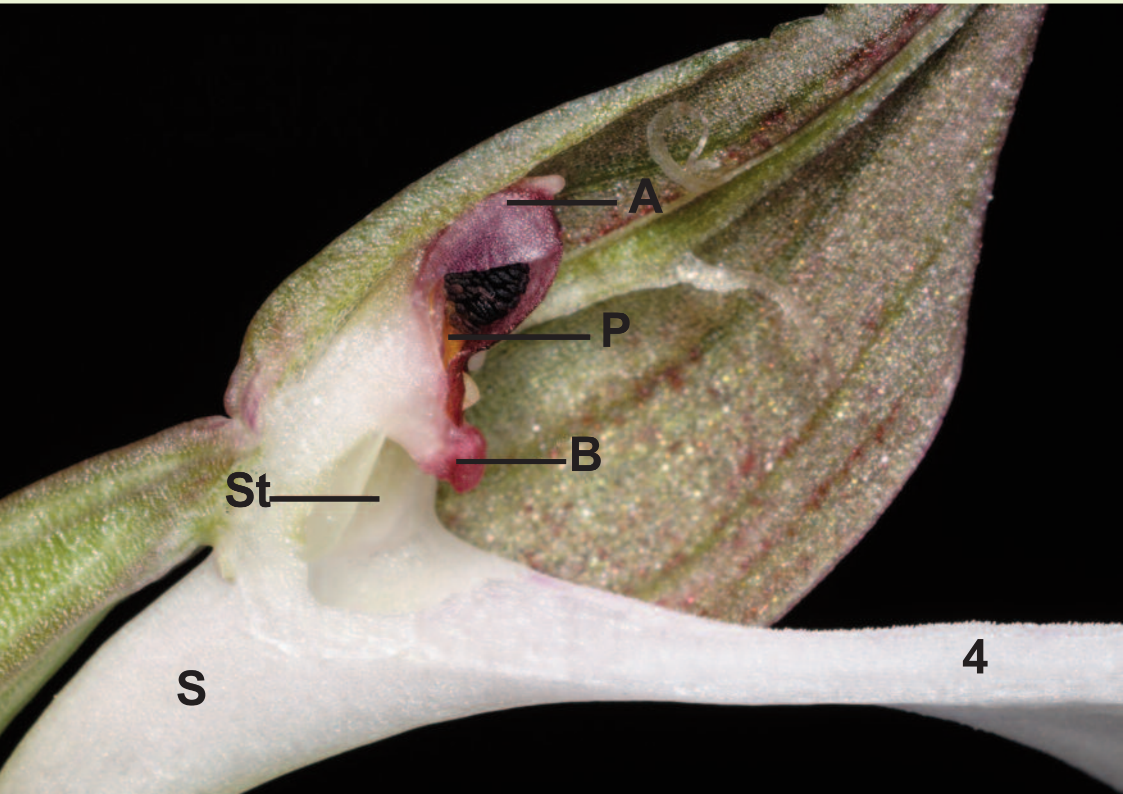
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demands. In this series of articles we will try to clarify those relationships. Each article will treat a certain genus and the adaptations of the orchid flower to meet the requirements of the pollinator.

Terminology

In this first article we will explain and illustrate the terms used. The flower morphology shows a general pattern, but we will see that there are many modifications of this ground pattern. Always, an orchid flower has two whorls of flower parts. The outer whorl has three sepals (Figure 1, labelled 1, 2 & 3), which generally are about equal in form and colour. The sepals on the left and right are called lateral sepals, while the one in the middle is the median sepal. Also, the inner whorl consists of three flower parts: two identical, generally short petals (Figure 1, labelled 4 and 5) and a third petal that has changed into the most conspicuous part of the orchid flower, the lip (Figure 1, labelled 6). In most orchid genera the lip points downwards. When an orchid flower is in bud the lip points upwards, but due to the twisting of the flower pedicel or the bending over of the flower, the lip becomes the lower part. In this position it can function as a suitable landing place for visiting insects.

Inside the flower is the column (Figures 3 and 4), a special organ that arose from the fusion of stamen and stigma. In general in the European orchids there is only one stamen left from the three stamens of the primitive orchids. The stamen is bipartite and is stored in an equally bipartite anther. The pollen grains can be single (monad), in packages of four (tetrad) or in much larger packages (massulae). They are held together by a very sticky fluid, the elastoviscin, and form a pollen package, called the pollinium. A pollinium can have a round or filiform, yellow elongation, the caudicle. The caudicle in turn is connected to a viscid disc, the viscidium. The combination of pollinium, caudicle and viscidium is called a pollinarium (Figure 2). The viscidium is not necessarily disc-like; we will see that it can have different shapes. Its function however is the same: fixing the pollinium or pollinarium to a visiting insect. In some orchids the viscidium (or if there are two, the viscidia) is protected by a pouch-like membrane, the bursicle.

Fig. 2: Pollinarium of *Ophrys scolopax*, sticking to a sepal.
Fig. 3: Column and pollinarium of *Orchis purpurea*. A=anther, B=bursicle containing the viscidia, St=stigma, P=pollinium, C=caudicle, V=viscidium (viscid disc).
Fig. 4: Longitudinal section of a flower of *Himantoglossum comperianum*. A=anther, P=pollinarium partly visible inside the anther, B= protruding bursicle, St=stigma, S=spur, O=ovary.

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The lower part of the column is the stigma, which generally is situated below the anther and the viscidium. It often lies in a stigmatic cavity and is covered with glistening stigmatic fluid which is capable of retaining pollen fragments. The lip may have a short or long, tube-like extension, the spur, which may contain nectar. The spur entrance generally is under the stigma. The column is connected to the ovary, which contains a large number of ovules.

Orchis* and *Dactylorhiza

The principle of pollination is often illustrated by referring to Charles Darwin's ground breaking book "*The Various Contrivances by which Orchids are Fertilized by Insects*", published in 1877. Darwin used drawings of *Orchis mascula* to illustrate the pollination process.

In *Orchis* and *Dactylorhiza* the flower and column structure are quite similar (figure 5 and 6). Both genera have flowers that are readily accessible for insects. Sepals and petals form a loose helmet and the lip is bent downwards, providing a good landing place for insects. The insect is lured to visit the flowers by means of scent, the stimulus for approaching the flowers. The lip is the organ used to attract insects from nearby, and often it has a distinct pattern of dots and lines, the so-called honey guides. They lead towards the spur entrance in the centre of the flower. The spur can be bent downwards or upwards and contains no nectar. *Orchis* and *Dactylorhiza* are called deceit flowers because they offer their visitors no nectar reward. The lip surface is covered with fine papillae, giving the insect visitors a good hold.

When approaching the spur entrance, the insect visitor meets the column. In *Orchis* and *Dactylorhiza* the anther is upright and extends in a bursicle containing two viscid discs. Underneath lies a stigmatic cavity created by the opening of the spur. The large, more or less rectangular to triangular stigma is situated at the "ceiling" of the spur, right above the spur entrance. In order to reach the supposed nectar the insect has to bend forward. In doing so, there is a great chance that it will touch the protective bursicle. This is pushed backwards, thus freeing the viscidia which are glued to

Fig. 5: Flower of *Orchis spitzelii*. S=sepal, P=petal, C=column, St=stigma
Fig. 6: Column of *Orchis mascula*, sideview. The bursicle is pushed backwards, freeing the two viscidia. The pollinarium sticks to a needle and has bent forward. It can now reach the stigmatic surface behind the bursicle.
Fig. 7: The bumblebee (*Bombus terrestris*) in vain tries to remove the extremely flexible pollinia of *D. praetermissa*.
Fig. 8: A bumblebee (*Bombus pascuorum*) pollinates *Orchis mascula*. It has 8 pollinaria attached to its head. Valkenburg (The Netherlands), 3rd May 2012

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the insect's head when it touches them. The glue covering the viscidia instantly hardens and then it is no longer possible for an insect to remove the pollinarium. This obviously bothers the insects, for we observed many times how they tried to get rid of the pollinaria by grooming intensely. But the caudicles are very flexible and can be stretched up to ten times their length without breaking (Figure 7). The pollen fragments are held together by the elastoviscin threads. Generally, it is impossible for the insects to remove the pollinaria. After grooming they go on to visit the next flower of the same plant or they move towards another orchid plant.

When the pollinaria are withdrawn, they stand upright on the insect's head, just like their position within the anther. But in order to reach the stigma, they have to bend forward by about 90 degrees. This is accomplished by the dehydration of the base of the caudicle, which makes the caudicle base contract, causing the bending movement. Darwin placed a forward bent caudicle in water and observed how it went back to its original position (Darwin 1877, page 191). This is a quite interesting experiment which you can carry out yourself easily. Just put a pin into the flower, collect one pollinarium and observe how it bends forward within 20 to 50 seconds (Claessens & Kleynen 2011). Then place it into some water and see the opposite movement. This little experiment gives you better understanding of the bending mechanism of the caudicle.

Fig. 9: A honeybee (*Apis mellifera*) pollinating *Dactylorhiza sphagnicola*
Brunssum (The Netherlands), 8th June 2010
Photos by Jean Claessens and Jacques Kleynen

When visiting another flower the pollinium is in the right position to touch the stigma. The stigmatic fluid has an even larger viscid force than the viscidium or the elastoviscin strands, for when the pollinium is pushed against the stigma it retains fragments of the entire pollinium. The rest of the pollinium stays on the insect's head ready for pollination of other orchid flowers.

References

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Yet Another Article on Bee Orchid Variants

Stan Jordan

Over the past year there has been a spate of articles on the Bee orchid (*Ophrys apifera*). Now here is another one, but this one is about the ability of *Ophrys apifera* to vary from one year to the next. It is now well known that a normal Bee orchid can change over the winter period and appear the following year as a variant. This is fairly frequent on the limestone outcrops of the Cotswolds, particularly between a normal Bee orchid and an *Ophrys apifera* var. *belgarum* or even a *trollii* variant. The variant that has eluded me for years is the "brown bee" or *atrofucsca/fulvofusca* type. A couple of years ago an *atrofusca* variant appeared in Weymouth. My wife and I went down to see Lorne and Sheila Edwards, who showed us the plants. While we were looking at the plants my eye wandered over the vegetation in the area around the plants, especially the small bushes. The reason for this is some plants do have an effect on the symbiotic fungus that feeds the orchid. There was no plant that immediately stood out regarding this aspect.

Many years ago I wrote an article on a pseudanthial Common Spotted-orchid, (*Dactylorhiza fuchsii*) that appeared close to where I live (Jordan, 2008). In that article I mentioned the arrival at that site of four flowering Bee orchids and many non flowering plants. The following information refers to *Ophrys apifera* at that site. As this site is the closest to where I live, I visit it quite frequently during the orchid flowering season. The Bee Orchids vary in number and the most that have flowered was fourteen, but most years there are eight or nine. One particular plant has always stood out from the rest, because of its very dark colouring, so every year when I go there I always photograph this particular plant. I have even put metal markers in the ground to mark where it was. I have now progressed to making a map/plan of the