The Pollination of European Orchids Part 5: *Himantoglossum* and *Anacamptis*, Two Examples of Deceptive Pollination Jean Claessens & Jacques Kleynen

Introduction

Many orchids produce nectar in order to attract insects. However, in the European orchids there are a considerable number of orchids which produce no nectar. Why would an orchid shift from reward to no reward, as this pollination mode clearly attracts less insects? We will discuss this on the basis of two non-rewarding orchid genera, *Himantoglossum* and *Anacamptis*.

Many orchids provide some kind of reward for their visitors like nectar, pollen or oil. European orchids only present nectar to their visitors. A number of orchids do not present any reward at all; they are called rewardless or deceptive orchids. The best known forms of deception are: food deception, shelter imitation (in the genus *Serapias*) and sexual deception, well known from the genus *Ophrys*. In this article we will only discuss food deception, where a plant attracts pollinators despite the fact that it does not present a food reward.

Himantoglossum

Because the Lizard Orchid (*H. hircinum*) is the only species of the genus growing in Great Britain, we will use this species to illustrate the pollination biology. The plants are 30-80 cm high, carrying 15-80 flowers (photo on back cover). The leaves appear in September, and by the time the flowers are in full bloom the rosette has withered. The orchid's name refers to the flowers with the long, twisted lip, reminiscent of a lizard. A feature you remember, once you have seen this orchid, is its pungent, goat-like smell. In most European countries it is therefore called "goat orchid". The sepals and petals form a hood and the upright, large column is readily accessible to visiting insects. The long, brownish, strap-shaped lip has a white basal part with purplish tufts of hairs, acting as honey guides (Fig. 1). They are also said to be osmophores, emitting an attractive scent. The lip forms a short, downward curved spur which contains no nectar. The anther contains two pollinia which are connected to a common viscidium by two long, curved caudicles. The viscidium is stored in a bursicle, a protective membrane. The large stigma is oblong to oval and concave.

Fig. 1: *H. hircinum*; lip with tufts of purple hairs (Selogney, France 12-5-2007). Fig. 2: *H. hircinum*, longitudinal section showing the protruding bursicle (red arrow).

Fig. 3: Honeybee (*Apis mellifera*) pollinating *H. hircinum* (Gilsdorf, Germany, 1-6-2012).

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Insects encounter two obstacles when visiting the flower. The viscidium protrudes and, when searching for nectar in the spur, an insect will most certainly bump its head against it (Fig. 2). The vertical, narrow spur entrance is reduced by two rows of long, white hairs, narrowing the entrance considerably. This causes the pollinators to bend well forward. In doing this they touch the protective bursicle, which is pushed backwards and then touch the viscidium, which is generally attached to the forehead. If they already have pollinaria attached (Fig. 3), the pollinium is pushed against the stigma, and the massulae (the packages of pollen composing the pollinium) stick into the stigmatic fluid.

In the literature a variety of pollinators is mentioned like hoverflies, various bees, wasps, ants, beetles, butterflies and moths. However, our observations supplemented with other data clearly show that bees, above all the genus *Andrena*, are the legitimate pollinators of *H. hircinum* (Figs. 4 and 5). All other European *Himantoglossum* species like *H. robertianum* or *H. adriaticum* are also exclusively pollinated by various Hymenoptera.

Anacamptis

Two main flower types are recognised in species of the genus *Anacamptis*, each adapted to specific pollinators. We will discuss the Pyramidal Orchid (*A. pyramidalis*) and the Green-winged Orchid (*A. morio*) as representatives of those types.

Fig. 4: *Andrena* cf. *carantonica* pollinating *H. hircinum* (Gilsdorf, Germany, 3-6-2009).

Fig. 5: *Andrena* sp. grooming; the worn pollinaria indicate that it has visited several other flowers and deposited fragments of pollen (St. Paul-en-Forêt France, 2-5-2008.)

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Fig. 6: A. pyramidalis (Treffort, France, 15-6-2015).

Fig. 7: A. pyramidalis (Barbières, France, 14-5-2007).

Fig. 8: *A. pyramidalis*, close-up of the lip with guide plates and narrow spur entrance.

Fig. 9: *A. pyramidalis*, pollinaria; the viscidium is curled around the tip of a needle.

Fig. 10: Small tortoiseshell (*Aglais urticae*) with pollinaria attached to its proboscis (Eys, Netherlands, 2-6-2014).

Fig. 11: Meadow fritillary (*Melitaea parthenoides*) with pollinaria of *A. pyramidalis* (Barbières, France, 29-5-2008).

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Fig. 12: Zygaena filipendulae, a regular pollinator of A. pyramidalis (Seyssinet-Pariset, France, 16-6-2015) Photo by Jean Claessens & Jacques Kleynen

A. pyramidalis is 10-25 cm high and has a pyramidal-shaped inflorescence with closely packed, pink to purple flowers (Figs. 6 and 7). Dorsal sepal and petals form a loose hood; the lateral sepals are spreading. The three-lobed lip has two prominent upright guide-plates at its base, leading to the long, slender spur (Fig. 8). The anther is erect and contains two pollinia attached by yellow caudicles to a common, saddle-shaped viscidium, covered by a bursicle of the same form. The stigma is not placed under the column but instead is composed of two stigmatic lobes, placed on each side of the column.

A. pyramidalis is pollinated by a wide variety of butterflies. Various *Zygaena* species are regular pollinators. Flower morphology is well adapted to butterflies: the guide-plates lead the proboscis towards the narrow spur entrance. The long spur (containing no nectar) and the narrow entrance incite the pollinator to stick its head deep into the flower, where it touches and

pushes the bursicle backwards. The saddle-shaped viscidium is a beautiful adaptation to the butterfly tongue: when touched it curls around the proboscis, firmly securing the pollinaria which bend sidewards due to the curling movement of the viscidium (Fig. 9). At the same time, they bend forward, bringing the pollinia to the exact position for touching the two stigmatic lobes left and right of the column base. This process takes about 30 seconds, and when the butterfly visits another flower, it will certainly push the pollinia onto the two stigmatic lobes. Butterflies often use the inflorescence as a landing platform from which they start probing the flowers for nectar (Figs. 10, 11 & 12). It does not matter that they insert the proboscis upside down; the spur entrance is so narrow that the pollinia reach the stigma in whatever position the butterfly has adopted.

Fig. 13: A. morio (Padalu, France, 8-4-2013).
Fig. 15: Solitary bee pollinating A. morio (Fayence, France 1-5-2008).
Fig. 14: Honeybee (Apis mellifera) inspecting the flowers of A. morio subsp. picta (Bois du Rouquan, France, 5-5-2008).
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With some exceptions all other species of the genus *Anacamptis* are deceit-flowers, that is they do not have any nectar. The pollination of *A. morio* is similar to the process as described in Part 1 for *Orchis*. The broad, slightly three-lobed, violet-purple lip has a lighter, more whitish centre with violet-purple spots creating the the honey-guides (Fig. 13). The spur is long and upward-curving. Darwin (1877) supposed that the insects pierced the inner spur wall to suck the fluid stored between the membranes of inner and outer spur wall, however this assumption was proved to be false. Pollinators are newly emerged, naïve bees who still have to learn which flowers are good food sources (Fig. 14 and 15). They soon learn that the orchids provide no food whatsoever and then avoid the orchids. The early flowering period of *A. morio* is advantageous, because there are few nectar producing plants and the bees have not yet established a fixed food plant preference.

Deceptive orchids are recognisable by the irregular seed set: a bee visits some flowers and then finds out it is deceived and leaves. Often fruit set of the lower half is higher than the upper half, illustrating the learning process of the inexperienced bees. Deception is a widespread strategy among orchids. Production of nectar costs much energy, which in deceit species can be invested in the formation of the fruit. Another advantage is the improvement of the "fitness "of the plants. Orchids with nectar are visited for a longer time and insects tend to creep longer from one flower to another on the same flower spike, causing a much higher degree of geitonogamy. In deceptive orchids the insects visit few flowers and fly much faster to the next plant, thereby promoting cross-pollination, bringing about a higher gene exchange. This is important for maintaining a healthy population.

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