

Jean Claessens and Jacques Kleynen

Column structure and pollination of *Corallorrhiza trifida* Châtelain (Orchidaceae)

Keywords

Corallorrhiza trifida, *Orchidaceae*, stipes, hamulus, autogamy.

Zusammenfassung

Claessens, J. & J. Kleynen (1998): Column structure and pollination of *Corallorrhiza trifida* Châtelain (Orchidaceae).-Jour.Eur.Orch. 30(3): 629-637. *Corallorrhiza trifida* besitzt eine typische Säulchenstruktur, wodurch die Autogamie ermöglicht wird. Das Rostellum bildet eine hackenförmige Verlängerung, der Stipes (vom Hamulus- Typ). Die vier Pollinien werden mittels vier dünnen, elastischen Pollenstielchen mit dem Stipes verbunden.

An der Basis vom Stipes befindet sich das Viscidium, das aber nur sehr kurze Zeit, noch vor der Anthese, funktioniert. Die Selbstbestäubung, die bei *C. trifida* die Regel ist, wird ermöglicht, indem die Antherenkappe austrocknet und sich gleichzeitig erhebt. Die Pollinien fallen dann, fest verbunden mit den elastischen Pollenstielchen, auf die Narbenfläche, wo sie kleben bleiben.

Summary

Claessens, J. & J. Kleynen (1998): Column structure and pollination of *Corallorrhiza trifida* Chatelain (Orchidaceae).-Jour.Eur.Orch. 30(3): 629-637. *Corallorrhiza trifida* has a particular column structure, which facilitates autogamy. The rostellum forms a hook-like prolongation, the stipe (of the hamulus-type). The four pollinies are connected to the rostellum by means of four thin, elastic caudicles.

There is a viscidium at the base of the stipe, which functions only a very short time, before anthesis. Autogamy, which is general practice with *C. trifida*, is realised by the simultaneous dessication and lifting of the anther cap. This

enables the pollinies, firmly joined to the caudicles, to fall on the stigmatic surface, where they keep sticking.

Resumé

Claessens, J. & J. Kleynen (1998): Column structure and pollination of *Corallorrhiza trifida* Châtelain (Orchidaceae).-Jour. Eur. Orch. 30(3): 629-637. La structure du gynostème de *Corallorrhiza trifida* est bien typique pour l'espèce, et permet l'autogamie. Le rostellum modèle un prolongement en forme d'un crochet, la stipe (du type hamulus). Au moyen de quatre caudicules minces, élastiques, les masses polliniques sont reliées à la stipe. A la base du stipe se trouve le viscidium, qui ne fonctionne qu'une très courte période, bien avant l'anthese.

L'autofécondation, qui est la règle chez *C. trifida*, est réalisée par la dessiccation et puis la monte du capuchon de l'anthere. Les masses polliniques tombent, bien unies aux caudicules élastiques, vers la surface stigmatique, où ils restent collés.

* **

Previous studies

The genus *Corallorrhiza* has its main area of distribution in northern and central America, where we can find ten species. Only one species, *Corallorrhiza trifida*, can be found in Europe. It is widely spread from the arctic to the submeridional zone and can rarely be found in the meridional zone BUTTLER (1986).

The little, yellowish-green plant has no leaves, just some sheath-like scales. Its name refers to the coralloid rhizome. *C. trifida* was before often described as being saprophyte. e.g. in HEUKELS (1911) and VERMEULEN (1958), but is in reality a mycoparasite, because the plants don't get their nutrition directly from the organic material, but "their interaction with fungi is facilitated by the coralloid rhizome" FREUDENSTEIN (1994). The rootless rhizome is a typical feature of this species.

Concerning the possible pollinators of *C. trifida*, there can be found several indications in literature. SILÈN (1906) observed the visit of several Syrphids and other small insects. He suggested that, because the pollinies do not possess a

viscidium (an assumption that is false, as we will point out later), they can neither be attached to a visitor's head nor to a pencil tip.

KIRCHNER (1922) observed, how the anther cap drops off very easily, thus allowing the pollinies to fall, passing both sides of the very small rostellum, right onto the nearby stigma. Descriptions of later authors, e.g. SUMMERHA YES (1951), DAVIES et al (1983) and LANG (1989) are based upon the observations of KIRCHNER and do not bring any new knowledge as far as the process of autogamy is concerned.

They too report about visiting insects: SUMMERHAYES (1951): hoverflies and other small insects (*Hymenopteres*); LANG (1989) too observed hoverflies and dungflies (*Scatophaga*). But very important is the fact, that none of the authors could actually observe, whether the visitors were actual pollinators.

The very high rate of fruit set is a clear indication for autogamy. According to SUMMERHAYES (1951), 85-100 % of the flowers set fruit. CATLING (1983) held the plants of *C. trifida* in insect-proof cages, and found an autogamy-rate of 50 %. The observations of FREUDENSTEIN (1992) also affirm the high degree of autogamy. He found, that 50 % of the open flowers had self-pollinated. Only 6,8 % of the open flowers had their pollinia removed.

Although there are various descriptions of potential pollinators and of the degree of autogamy, one looks in vain in European literature if one tries to find a clear description of the way in which pollination or autogamy takes place. The studies of FREUDENSTEIN (1992, 1994a, 1994b) have filled up this lack, but it was not until after we completed our own observations, that we heard of his studies.

Morphology and function

Let's first describe the morphology and function of the column of *C. trifida*. The column is about 2.0-3.3 mm long, slightly curved forward, having a ventral shallow, gutter-shaped central channel. The stigma is oblong-elliptic-cordate, lying in a cavity, perpendicular to the column axis. The anther cap is fugacious, whitish-yellow when fresh, later on turning brown FREUDENSTEIN (1992).

The different European authors do not agree about rostellum, pollinies and their connection. CAMUS (1929): *C. trifida* has a bilocular anther without appendage or rostellum.

SCHLECHTER, in describing the subtribe of the *Corallorrhizinae*: "Die Pollinien sind immer wachstartig und von fester Konsistenz und kleben bei

manchen Gattungen mit ihren Spitzen zusammen, oder aber es ist eine deutliche Kaudikularbildung zu sehen, die manchmal als eine viereckige Platte beschrieben wurde. Jedenfalls handelt es sich offenbar dabei weder um einen Stipes noch um ein Viscidium" SCHLECHTER (1970, pA08). A little further, when describing *C. trifida*, he says: "Die vier Pollinien hängen zusammen, und manchmal wird ein kleines, etwa viereckiges Kaudikulum gebildet" SCHLECHTER (1970, p. 412). Perhaps he meant the four caudicles, when speaking about a four-edged "Kaudikulum". ZIEGENSPECK (1936) doesn't mention caudicles or viscidium. He points out that, judging by the construction of the flower, it should be well pollinated by insects. However, autogamy seems to be the rule. After ZIEGENSPECK the pollinies fall apart when growing older and then fall onto the stigmatic surface. This process is facilitated by the fact that, when the pollinies des integrate, the column bends forward.

VERMEULEN (1958) mentions a little, roundish rostellum and says nothing about the connection with the four pollinia.

In more recent literature the authors agree about the composing elements of the column, but do not give information about the functioning of those elements. LUER (1975): "The column is compressed and the anther is terminal, with four yellow, waxy, subspherical pollinia, all of which are connected by a single, microscopic, elastic band to a detachable viscidium". The only element lacking in his description is the presence of a stipes. REINHARD et al (1991): " ... die vier Pollinien hängen zusammen, das Viscidium ist ablosbar; der Stipes ist klein und schmal. Details des Säulenbaus sind wenig erforscht".

DRESSLER (1993) classifies *Corallorrhiza* in the tribe *Calypsoeae*, a tribe characterized by four superposed pollinia, stipe and viscidium. DELFORGE (1994) states that the pollinies are connected with the pollinia by means of an elastic caudicle.

Observations

In studying *C. trifida*, we experienced, that it is very important to study the flowers in the very early stages of development, that is to say long before anthesis. For several years we studied the development of the column of *C. trifida*.

It proved, that the development of the rostellum is of crucial importance, since this organ determines the way in which pollination can take place. In *C. trifida* the rostellum develops a prolongation, the stipes (photo 1). The difference between caudicles and stipe is the place where they are formed. The caudicles are made in the anther and consist of elastoviscin (the elastic material which keeps united the pollengrains) and pollengrains. Their function is to unite

pollinium and viscidium. In e.g. the genus *Orchis* we can see two caudicles, connected with one common viscidium. The caudicles are an extension of the pollinies and may often be yellowish.

The rostellum in its turn can also form a connection with the caudicles, which is called stipes. So the stipes is an extension of the rostellum, and consists of cellular tissue of the rostellum. In our case, the different colour of stipe (whitish) and caudicles (yellowish) is an indication for the different place of initiation of both structures, although one cannot always be able to state that two structures are different in origin, just on the basis of colour and consistency (DRESSLER pers. comm.). Their different origin can best be seen in anatomical sections, where it is clear that the stipes is cellular, while the caudicles are essentially just a secretion (FREUDENSTEIN, pers. comm.)

RASMUSSEN (1985, 1986) distinguishes two types of stipes. The tegula is a connecting strap, consisting of an only several layers, derived from the dorsal epidermis of the rostellum. A hamulus is the entire distal portion of the rostellum, prolonged into a stalk (FREUDENSTEIN 1994). Because of its delicacy and its position the tegula is much more difficult to observe than a hamulus. FREUDENSTEIN (1994a, 1994b) shows beautiful microscopic cuts that demonstrate stipes of the tegula-type (*Calypso bulbosa*), and of the hamulus-type (*Corallorrhiza*). Here one can clearly see the hook-like shaped stipes.

As soon as the anther cap opens, about one week before anthesis, one can observe the position of the four pollinia, superposed, with the members of a pair stacked, one on top of the other (photo 2 + 3). They are lense-shaped and flattened on the side where they are pressed together. The pollinia are separated by a very thin, horizontal layer (the septum), which later in development desiccates, shrinks and then is hardly visible any more. The pollinia form four very thin, elastic caudicles which, as soon as the anther opens, contact the hook-like stipes.

Unlike SILEN (1906), we were able to remove the pollinaria of *C. trifida* with a needle, although this was only possible for a short time, directly after pollinia and viscidium, with the help of the stipes, were connected with each other (photo 4). In FREUDENSTEIN (1994a, p. 5, ill. a) one can clearly see, that the viscidium is placed at the basis of the stipes. So pollination is basically possible, but as far as we could observe, the viscidium only functions with a newly opened anther, when the flower is still closed. It seems that when growing older, the viscidium loses its adhesive power.

In *C. trifida* auto-pollination usually takes place before or directly after anthesis. As soon as the anther cap has opened and the pollinaria are connected with the stipes, the anther cap lifts upward, dries out and very soon falls off. The pollinia

then lie quite loose in the clinandrium and the least vibration is sufficient to make them fall down to the stigmatic surface (photo 5). In this process the elastic caudicles play an important role: because of their elasticity they easily allow the pollinia to fall down. They have exactly the right size to make the pollinia land on the stigma. So on one hand they give the pollinia a great freedom of movement, but on the other hand they guarantee, that the pollinia will sooner or later fall onto the stigmatic surface. In BAUMANN & KÜNKELE (1982, p.51) the illustration shows very well, how the pollinia have fallen down and are already partly sticking onto the stigma.

FREUDENSTEIN (1994b) reports that "C. trifida rotates its stipe with attached pollinia to contact the stigma very soon after anthesis". During our observations we didn't observe this phenomenon. In the plants we observed, the stipes kept its place, and the contact between pollinia and stigma was achieved only by means of the elastic caudicles.

Soon after making contact with the stigma, the pollinia are soaked with stigmatic fluid. This can very well be observed by the colour of the pollinia: they become more whitish and more or less melt together with the stigmatic surface.

We often observed that at the same time the stipes more or less disappeared, as if being dissolved from the stigmatic fluid. What's left is just a little, roundish structure, just as VERMEULEN (1958) described it. He probably saw *C. trifida* only in late stages of its development.

Acknowledgements

We sincerely wish to thank Dr. Robert L. Dressler, Dr. John V. Freudenstein, Dr. Finn N. Rasmussen, Hans R Reinhard and Jürgen Reinhardt for their great help, references to literature as well as for their constructive remarks. We also thank Dr. Eckhard Willing and Henk ten Brinke for their help in providing literature.

Bibliography

BAUMANN, H & S. KÜNKELE (1982): Die wildwachsenden Orchideen Europas. Stuttgart.

BUTTLER, K.P. (1986): Orchideen.- München.

CAMUS, E.G & A. (1921-1929): Iconographie des Orchidees d'Europe et du bassin méditerranéen.- Paris.

CATLING, P.M. (1983): Autogamy in eastern Canadian Orchidaceae: a review of current knowledge and some new observations.- *Naturaliste Canadien* 110: 37-53.

DAVIES, P & J and A.HUXLEY (1983): Wild orchids of Britain and Europe.- London.

DELFORGE, P. (1984): Guide des Orchidées d'Europe, d'Afrique du Nord et du Proche Orient.- Lausanne.

DRESSLER, R.L. (1993): Phylogeny and classification of the orchid family.- Cambridge.

DRESSLER, R.L. (1961): The structure of the orchid flower.- *Missouri Botanical Garden Bulletin* 49: 60-69.

FREUDENSTEIN, J.V. (1992): Systematics of *Corallorrhiza* and the *Corallorrhizinae* (Orchidaceae).- PhD. dissertation, Cornell University. Ithaca, NY.

FREUDENSTEIN, J.V. (1994a): Gynostemium structure and relationships of the *Corallorrhizinae* (Orchidaceae: Epidendroideae).- *Plant Systematics and Evolution* 193: 1-19.

FREUDENSTEIN, J.V. (1994b): Character transformation and relationships in *Corallorrhiza* (Orchidaceae: Epidendroideae). 11. Morphological variation and phylogenetic analysis.- *American Journal of Botany* 81(11): 1458-1467.

HEUKELS, H. (1911): De flora van Nederland. Deel 1, *Orchidaceae*.- Leiden/Groningen.

KIRCHNER, O. (1922): Zur Selbstbestäubung der Orchidaceen.- *Ber. Deutsch. Bot. Ges.* 40: 317-321.

LANG, D. (1989): A guide to the wild Orchids of Great Britain and Ireland.- Oxford, New York.

LUER, C.A. (1975): The native orchids of the United States and Canada, excluding Florida.- New York.

RASMUSSEN, F.N. (1985): Orchids.- In: DAHLGREN, R.M.T. et al: The families of the Monocotyledons - Structure, evolution and taxonomy.- Berlin, Heidelberg, New York, Tokio.

RASMUSSEN, F.N. (1986): On the various contrivances by which pollinia are attached to viscidia.- *Lindleyana* 1: 21-32.

REINHARD, H.R et al. (1991): Die Orchideen der Schweiz und angrenzender Gebiete.- Egg.

SCHLECHTER, R (1970): Die Orchideen, 3.Auflage.- Berlin und Hamburg.

SILEN, F. (1906): Blombiologiska iagttagelser i södra Finland. *Medd. Soc. pro Fauna e Flora Fennica*, Bd. XXXII, 120-134.

SUMMERHAYES, V.S. (1951): Wild Orchids of Britain.- London.

VERMEULEN,P. (1958): Flora Neerlandica 1/5, *Orchidaceae*. Koninklijke nederlandse Botanische Vereniging.

ZIEGENSPECK,H. (1936): *Orchidaceae*. In: KIRCHNER,O.VON et al: *Lebensgeschichte del Blütenpflanzen Mitteleuropas*, Band 1.- Stuttgart.

Authors' addresses

Jean Claessens
Moorveldsberg 33
NL - 6243 AW Geulle

Jacques Kleynen
Pr. Constantijnlaan 6
NL - 6241 GH Bunde

Figures (phot. pag. 637, photos by Jean Claessens and Jacques Kleynen)

1	2
3	5
4	

photo 1: *C. trifida*: column in very early state of development, before anthesis (flower opened manually).

photo 2: *C. trifida*: front view of a column with newly opened anther. Stipes and caudicles well visible.

photo 3: *C. trifida*: column side view showing stipes, caudicles and pollinia.

photo 4: *C. trifida*: column with newly opened anther (before anthesis, flower opened manually). Pollinaria removed with the help of a needle.

photo 5: *C. trifida*: Older stage of the column. Anther cap lifted, pollinia already partially sticking onto the stigmatic surface.

