# NOTES ON CYPHIA VOLUBILIS, WILLD.

BY

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When I was working out the *Campanulaceae* for Engler and Prantl's "Natürliche Pflanzenfamilien," (1) I was struck with the absence of any detailed information on the plants which form the sub-order of "*Cyphioideae.*" I was unable to find anything about them beyond their mere descriptions. As I had at that time only dried material at my disposal, I was not in a good position for extending our knowledge of these plants. This was the more to be regretted since they are generally considered to form a connecting link between the *Campanuloideae* on the one hand and the *Lobelioideae* on the other hand, because their flowers, being as a rule, zygomorphic, have the general appearance of those of the latter and have free anthers, which is the rule in the former. The following notes may therefore serve as the first step to fill up this gap in botanical literature.

My observations have mostly been made on specimens, which had been kept in spirit for a short time. I may mention that I have only observed the variety with sub-entire leaves and hairy anthers. (2)

The vegetative organs of the plants, which I examined, were very simple. The stem never branches in its lower portion. It rises from the ground not much thicker than ordinary twine. As soon as it reaches a support it begins to twist round it. On its lower portion it bears about half a dozen very tiny toothlike leaves, and above these about as many more foliage leaves. (Fig. i). It is terminated by a simple racemose inflorescence (without terminal flower like the racemose inflorescences of the Lobelioideæ), which is also twining. In rare cases one or two lateral inflorescences are formed just below the terminal inflorescence, which have the same simple structure as the latter. The taproot, which has about the same thickness as the stem, is at its lower extremity (usually 2—3″ below ground) thickened into a more or less globular tuber of $\frac{1}{2}$—$\frac{3}{4}$″ diameter. This tuber has, therefore, morphologically speaking the same value as the tubers known in other members of the *Campanulaceae.* (3) Both the tuber and the upper portion of the taproot bear a number of rootlets.

The anatomical structure of the stem is very much the same as in

(1). IV. Theil, 5. Abtheilung, pp. 40—70.

(2). Compare Harvey and Sonder, Flora Capensis iii, p. 604.

(3). It is a root and not a stem as in the potato.

the majority of the *Campanuloideae* and *Lobelioideae.* Medullary rays and haid bast are absent. The laticiferous tubes, which are articulated as in all *Campanulaceae*, accompany the soft bast usually in 3 or 4 groups. In many cases (though not in all) laticiferous tubes are also found in the centre of the pith. This will appear somewhat remarkable, however, among *Campanuloideae* there are also a number of species in which different specimens possess a somewhat different anatomical structure (1). It may be mentioned that the structure of the stem does not exhibit any peculiarity produced by its twining habit.

I found the main root always to be tetrarch. Its structure was quite normal. Secondary thickening does not take place. The tuber is composed almost entirely of parenchymatous tissue in which the vascular bundles pursue a rather irregular course. It is completely surrounded by a typical cork-layer composed of about 6—10 layers of cells. Separated from it by a few layers of parenchymatous cells there is a group of laticiferous tubes, which form a complete circle in transverse section. A small number of such tubes is irregularly distributed in the interior of the tuber. At the time when my investigations were carried out, *i.e.*, when the plant was in flower, the tubers contained a fair amount of Inuline as reserve material. Starch was absent. The discovery of Inuline in a member of the *Cyphioideae* is of some interest, as the same substance has been proved to occur in the *Campanuloideae*, *Lobelioideae*, *Goodeniacae* and *Candolleaceae*, besides the well-known occurrence of Inuline in *Compositae.*

The inflorescence is composed of about half a dozen flowers, which have a tendency of placing themselves in a straight line. The inflorescence thus becomes frequently unilateral and is more conspicuous than it would be if the flowers were turned in all directions. Each flower is preceded by two very minute bracteoles, which are always sterile as in the majority of *Lobelioideae.* The bracts of the flowers resemble the foliage leaves, but decrease in size from below upwards.

The flowers are two lipped, the upper lip being composed of three parts, the lower lip of two. In *Lobelioideae* (with the exception of the genus *Monopsis* and a few other cases, which I have pointed out in my paper quoted above) we find just the reverse (2). Here the lower lip is composed of three parts and the upper lip of two. The odd petal in the *Lobelioideae* is therefore anterior, whereas in *Cyphia volubilis* it is placed in a posterior position. In *Campanuloideae* (3)

(1). Natürliche Pflanzenfamilien iv., 5. p. 41.

(2). "Natürliche Pflanzenfamilien," iv., 5 p. 67, 69, 70.

(3). With very rare exceptions. Eichler ("Blütendiagramme i., p 294) mentions that in *Specularia* the parts of the flower are sometimes found in the same position as in *Cyphia volubilis.*

we find the parts of the flowers in the same position as in the *open* flowers of the *Lobelioideae.* I have underlined the word *open* because the flowers of *Lobelioideae* are always formed in the same position as in *Cyphia volubilis* (with posterior odd petal), but just before and during anthesis a twisting of the pedicel takes place, which reverses the position of the parts of the flowers. They are turned through an angle of 180° (as in many Orchids) (Figs. ii and iii). Baillon (1) has stated that resupination (as the process through which this reversal is effected is called) also takes place in the *Cyphioideae.* An examination of the specimens contained in the Oxford Herbarium, however, showed me that he was mistaken (2) and I am glad that the examination of fresh specimens of at least one species of *Cyphia* has confirmed my opinion that his statement was not correct, but of course, in order to upset it completely, a larger number of species would have to be observed in a living state. It is true that a slight displacement of the flowers usually takes place consequent upon the tendency of the inflorescence of becoming unilateral, but no such decided reversal as in most species of *Lobelioideae* takes place.

When a flower is about to open the anthers though not connected with one another are placed so close together as to form a tube the bottom of which is closed by the thickened upper portion of the style which is densely covered with hairs (Fig. iv and v). As soon as the flower opens the pollen is shed by the anthers, and deposited on the style. So far everything is the same as in the majority of the *Lobelioideae* and to a certain extent as in *Campanuloideae* (3). In *Lobelioideae* the style has, as a rule, not completed its growth by this time. (Fig. vi.—ix.). It goes on elongating, pushing the pollen gradually out of the tube formed by the anthers. Insects visiting the flowers come into contract with the pollen, which is prevented from falling by a number of hairs placed around the entrance of the tube (Fig. vi.). By and bye the style itself has reached sufficient length to protrude out of the tube. As soon as this stage is reached it developes its two stigmatic lobes (Figs. viii., ix.), which then and not till then are ready to receive pollen for the fertilisation of the flower. As will easily be seen, the flower was therefore at first in a male state (Fig. vi.) and passes into the female state after the stigmatic lobes are developed (Fig. viii). It is distinctly

(1). "Histoire des Plantes," viii. p. 337.

(2). "Natürliche Pflanzenfamilien," iv, 5, p. 61.

(3). I may here mention that in the South African species of Campanuloideae (belonging to the genera *Wahlenbergia* and *Lightfootia*), which I hitherto had an opportunity of observing, pollination is effected in exactly the same way as in the genus *Campanula.*

proterandrous and cross-fertilisation must therefore as a rule take place for the production of seeds.

In *Cyphia volubilis*, however, the style has reached its final length when the flower opens, and as no change is perceptible after the pollen has been deposited on the top of the style even if it is examined with a lens, I was for some time under the impression that we have here a very marked case of self-fertilisation, which was the more strange as all species of *Campanulaceae* which have hitherto been examined show very elaborate arrangements for cross-fertilisation, although self-fertilisation is in many cases not excluded. The microscopic examination of the style, however, revealed some arrangements, which to say the least must sometimes ensure cross-fertilisation and these arrangements are quite unique as far as my knowledge goes. Any longitudinal section through the upper portion of the style (Fig. x.) will show that it contains a cavity in its thickened part, and if such a section be made exactly in its median plane, it will reveal the existence of a narrow channel at its posterior portion (Fig. x *c*.), through which the cavity communicates with the open air. I will call this cavity the "stigmatic cavity."

I said before that the anthers are placed closely together, and the pollen is kept in the tube, which is formed by them. The slightest touch on the anthers or filaments will, however, open the tube. Insects visiting the flowers can therefore not fail to dust themselves with pollen if they touch these parts, and as the pollen is frequently entirely removed from the flowers, I do not think that we can imagine any other agency which can effect this. At a comparatively early stage there appear at the mouth of the stigmatic cavity drops of a slimy substance (Fig. v *e*), and the cavity itself is also filled with the same substance, which appears to be produced by the breaking down of the walls of the cells lining the cavity, and of the hairs placed round the entrance, in very much the same way as the slimy substances in many fruits are formed. However, the exact nature and the precise mode of the formation of this slime remain to be determined. In this slime we see in older flowers a number of pollen grains germinating (Fig. x), and the pollentubes pass from the cavity into the "conducting tissue" of the style. I have never seen a pollentube passing from the top of the style into it although I have diligently searched for such cases, and although it sometimes happens that a few pollengrains which have been left there, begin to push out their tubes. It will now be apparent why I have called the cavity "the stigmatic cavity." It acts like a stigma by receiving the pollen for fertilisation by giving it an opportunity of germinating and allowing the pollentubes to pass into the style. The question now arises what is the biological meaning of this structure? I believe that all these arrangements are there to ensure crossfertilisation. It will be seen from Fig. iv. and v., that the pollengrains deposited on the top of the style can hardly reach the entrance of the stigmatic cavity. There remains further the fact that the pollen is frequently removed, which can only be done by insects (although I must admit that with the exception of a little butterfly I have not seen any insect visiting the flowers), and insects, laden with pollen from other flowers, will probably leave some of it on the slime round the entrance of the stigmatic cavity. However, this has to be confirmed by actual observation before it can be accepted as representing the full truth; besides as the male and female conditions of the flowers are not so sharply separated as in most *Lobelias*, it is quite possible that self-fertilisation may also sometimes be effected either with or without the aid of insects.

One curious fact remains to be mentioned. Pollengrains are not only found at the mouth of the "stigmatic cavity," but also inside it. I have found them there so frequently that it is almost impossible to imagine that they got there accidentally when my sections were prepared. I may suggest that the slime dries up a little occasionally, and that the pollengrains are thus drawn in by the slime reducing its volume. Fresh slime being formed other pollengrains are caught, and the same game may be repeated. To quote a somewhat analogous case I may mention that in many *Coniferae* the pollengrains are also caught by a drop of fluid at the mouth of the micropyle and drawn down on to the top of the nucellus when the fluid dries up.

The structure of the style besides giving a hint as to how pollination is effected in *Cyphia volubilis*, is also very interesting from another point of view. Harvey, in his "Genera of South African plants" ([1]), and Sonder in "Flora Capensis" ([2]), say that the "stigma" of *Cyphia* has an "obsolete ciliate indusium" and this character probably induced them to place the tribe of "*Cyphieae*" next to the "*Goodenovieæ*" their 4th tribe of *Campanulaceae*. The latter tribe is only represented in South Africa by a species of the genus *Scaevola*, a widely spread sea-shore plant. Most species of the "*Goodenovieæ*" are Australian. *Bentham* and *Hooker* separated the *Goodeniaceæ* from the *Campanulaceæ* as an order, following in this respect almost all previous botanical authors, who had had occasion to treat of them. Baillon ([3]) united them again without, however, recognizing that the "*Cyphieæ*" possessed any structure corresponding to the "indusium" of the "*Goodenieæ*." In his description of the style of *Cyphia* he simply says "stylo apice stigmatoso obliquo vel 2-lobo." Now as long as no plant was known among the

([1]). 2nd ed. p. 215. ([2]). iii. p. 597. ([3]). "Histoire des plantes," viii p. 369.

*Campanulaceæ* (as defined by Bentham and Hooker), which possessed any structure corresponding undoubtedly to the "indusium" which forms such a marked character in *Goodeniaceæ*, I did not think it right to include the latter among *Campanulaceæ*. I was well aware that some writers (1) had maintained that certain *Lobelioideæ* possessed an "indusium." However, a minute investigation of a great many species of the latter convinced me that there was only an external resemblance between the tufts of hairs on the styles of many *Lobelioideæ* and the "indusium" of the *Goodeniaceæ* and consequently (although erroneously) I considered at the time the remarks of Harvey and Sonder as regards the "indusium" of the *Cyphioideae* to be also founded only upon vague analogies, and thought myself quite justified in keeping the *Goodeniaceae* as a separate order, especially as in taking this course I had the approval of Baron Ferdinand von Mueller, the greatest living authority on these plants. However, I have altered my opinion now. I shall show presently that *Cyphia volubilis* at all events (and probably also the other species of *Cyphia*) possesses a structure homologous with the "indusium" of *Goodeniaceae* and that, therefore, the latter have to be included among *Campanulaceae*. As an objection to the advisability of this step one might only bring forward the fact that the *Goodeniaceae* do not possess any laticiferous tubes. But this objection loses considerably in force when we consider that in *Compositae* also (an order very nearly allied to the *Campanulaceae*) there are many forms possessing laticiferous tubes, while others are entirely without them.

To make the foregoing remarks a little more intelligible I will refer briefly to the structure and development of the "indusium" in *Selliera radicans*, (a species of *Goodeniaceae* occurring in Australia, New Zealand and South America, which I was enabled to study in fresh specimens). The style having reached a certain stage in this species developes round the apex an oval protuberance (several cell-layers in thickness), which grows considerably until it forms a cup, which opens at the top by a narrow slit. A number of hairs are placed round the entrance of the cup. This cup is called the "indusium." Now if we imagine the entrance to it to be a roundish hole instead of a slit, and its position shifted to one side, we have very much the same what we find in *Cyphia volubilis*, the tissues surrounding the "stigmatic cavity" in the latter may therefore even from analogy be considered as corresponding to the tissues of the "indusium" in *Selliera* and other *Goodeniaceae*, and this view is considerably strengthened by the fact, which I was able to ascertain, that their

(1). F. i. Urban in "Jahrbuch des K. botan. Gartens zu Berlin," Vol. i, p. 260.

development proceeds on the same lines as in *Selliera.* Apart from the unimportant differences as regards position and shape of the entrance to the "indusium," we have to take also into account another difference, which I will briefly discuss.

In *Selliera* and probably in many other (if not in all) *Goodeniaceae* the pollen is deposited in the "indusium" after having been discharged by the anthers. But shortly afterwards two stigmatic lobes begin to be developed, pushing the pollen out of the cup, whence it is carried away by insects in very much the same way as in *Lobelia.* The stigma does not become receptive until it has grown through the entrance of the cup ; in fact, the latter has the same biological function as the tube formed by the anthers in *Lobelia.* Now in *Cyphia volubilis* no stigmatic lobes are developed, and it is the inside of the "indusium," which performs the function of a stigma. But even this difference can, I believe, not shake the conclusion that what I have now called the "indusium" in Cyphia volubilis is homologous to what we are accustomed to call the "indusium" in *Goodeniaceae.* But to satisfy even the most scrupulous morphologist one might perhaps say that the structure enclosing the "stigmatic cavity" is homologous with the combined stigma and indusium of *Goodeniaceae.*

It would be interesting to know for certain whether the other species of *Cyphia* also possess a similar "indusium," although one may conclude from Harvey and Sonder's description that this is the case, and if found in all of them this character might be used as a test whether the American genera *Nemacladus, Parishella* and *Cyphocarpus* are so nearly allied to *Cyphia,* as is frequently supposed, because the structure of the flower is somewhat similar in all of them. I have, however, already expressed my doubts whether these 4 genera really form a natural group(1).

## Summary.

1. The anatomical structure of the stem of *Cyphia volubilis* is broadly speaking the same as in *Lobelioideae* and *Campanuloideae.* The tuber contains Inuline as reserve-material.

2. The flowers are not resupinated.

3. The style contains a cavity in its upper portion, which communicates laterally with the open air by a narrow channel. The tissues surrounding it are homologous with the combined stigma and "indusium". of *Goodeniaceae.*

4. It is advisable to include the *Goodeniaceae* among *Campanulaceae.*

(1). "Natürliche Pflanzenfamilien," iv., 5 p. 61.

5. Fertilisation is only effected through the open entrance of the "stigmatic cavity." Pollengrains are caught at the mouth of this entrance by a slimy substance formed by the cells lining the "stigmatic cavity," and by the hairs surrounding its mouth.

6. Cross-fertilisation probably often takes place through the agency of insects.

## Description of Plate.

Fig. i.—*Cyphia volubilis*, Willd. Whole plant $\frac{1}{3}$ natural size, $l$ = line separating root and stem, $t$ = tuber.

Fig. ii.—Diagram of flower of *C. volubilis* and of *Lobelia coronopifolia*, L., before resupination has taken place in the latter $a$ = axis ; $b$ = bract ; $\alpha, \beta$ = prophylls ; $s$ = sepal ; $p$ = petal ; $a$ = stamen ; $o$ = ovary.

Fig. iii.—Diagram of flower of *Lobelia coronopifolia*, L., after resupination.

Fig. iv.—Upper portion of the stamens of *C. volubilis*, slightly magnified. They surround the style completely.

Fig. v.—Upper portion of the style of *C. volubilis*, slightly magnified, $e$ = entrance to the stigmatic cavity closed up by a drop of a slimy substance.

Fig. vi.—Stamens of *Lobelia coronopifolia*, L., slightly magnified, from the flower in male condition. The growing style has pushed a number of pollengrains out of the tube formed by the anthers. They are collected at the top.

Fig. vii.—Style of the same flower.

Fig. viii.—Stamens of *L. coronopifolia*, L., slightly magnified, from a flower in female condition. The style has grown through the staminal tube and has unfolded its two stigmatic lobes.

Fig. ix.—Style of the same flower.

Fig. x.—Median section through the upper portion of the style of *Cyphia volubilis*, $c$ = canal leading into the stigmatic cavity, which is filled with a slimy substance. A quantity of this substance is collected round the entrance. Four pollengrains (p). which have sent out their pollentubes are represented.

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