

Pistillody of the stamens in *Nicotiana*

BY

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With Plate VII.

Although in the teratological literature a good many cases have been registered of stamens either having been replaced by pistils or showing various stages of the process, it attracts attention on closer inspection, that many descriptions of the intermediate stages are not accurate enough as to admit of the forming of a clear notion of the metamorphosis. Through the kindness of Dr. Burck, who in the autumn of 1906 sent me a few monstrous flowers of *Nicotiana affinis*, I have been enabled to study all the degrees of pistillody of the stamens in the said plant. I will try both by description and illustration to give an impression of my observations.

The structure of the *normal* flowers of *Tobacco* needs no explanation: merely for the sake of contrast with the abnormal flowers it should be mentioned that in the case under consideration their length amounted to 75 c.M., that the stigma extends just beyond the anthers and that one of the stamens is a little shorter than the four others ¹⁾.

In fig. I an anther is represented twice magnified, to which should be added that the outer loculamenta or pollen-cavities are not inconsiderably larger than those

1) In many Solanaceae the stamens have unequal lengths (Eichler, Blüten-diagr. I. p. 204).

pointing to the centre of the flower, from which circumstance it is clear that the slits of dehiscence are not perfectly lateral but turn a little inwards.

The *abnormal* flowers are all a little shorter, not exceeding 60 c.M., moreover the sepals of the same flower differ more in length as well in width. Besides the corolla may show various degrees of dialysis and the insertion of the stamens irregularities.

The pistil always proved undisturbed, both in structure and in relative length.

The greatest disturbance is, however, shown by the anthers: so e.g. in fig. II the anther bears a curved appendage at top with a stigma-like end. When we trace the origin of this appendage it proves to be in connection with both thecae. Fig. III represents a stamen, from which one of the thecae has been taken away enabling us in this way to see the side of dehiscence as well as the opposed one. The top bears a threadlike appendage without stigma. Although this theca opened at the time of its examination, only a small quantity of pollen was produced; in the split, however, a hard, brown, grainy little body (o) was seen at the base, and even at the edges on the opposite surface. This brown corpuscle stands out more clearly in fig. IV where it coincides with indubitable distinctness with the style and stigma-like appendage already described. The thecae have the aspect of dehiscence while the brown corpuscles coalesce.

As the brown corpuscles in the other figures are also marked with o, their further indication will be superfluous. It is worth mentioning that the stronger this corpuscle is, the less is the quantity of pollen in the same anther. In figures V and VI two other derangements incidental to the said phenomenon are represented. In fig. V it is a strong twisting, evidently in consequence of a difference in rate of growth between the filament and an additional

product of the torus, coalesced with the former. In fig. VI the thing is somewhat complicated as the outgrowth springing from the filament under the anther splits into a style and a peduncled anther-like corpuscle.

Finally I found in the first set of monstrous Tobacco-flowers in a flowerbud of scarcely 2 c.M. in length besides two normal stamens three others, of which the anthers at their base showed a quite small spot, the very beginning of the anomaly repeatedly pointed out (fig. VII).

MICROSCOPIC EXAMINATION.

Although the appendages with the small knob show all the outer characteristics of style and stigma, I wanted to put their true nature beyond doubt. For this reason I enclosed after the necessary preparation a few specimens in paraffine and by means of a microtome cut a series of longitudinal sections. The same thing was done with the style proper. The comparison of the two sets of preparations showed that not a single difference could be discerned between the styles proper and the style-like appendages of the anther. So we may safely conclude that in our *Nicotiana* more or less developed styles have grown out from the anthers.

A similar investigation was executed into the nature of the brown excrescences. The supposition readily presented itself that they might be made up of ovules, a supposition supported by two circumstances, firstly the style-like appendage indubitably springs from the valves belonging to different thecae or in other words from the adjoining (either outer or inner) loculaments. From this the notion arose of two carpels having been created, divided from one another by the plane through the anther-splits. Where there are carpels, there must or at least *can* also be ovules, albeit at the same time with pollen in this particular case.

The first work was, accordingly, to cut the anther, drawn in fig. VII, in a great number of transverse slices and to examine if the brown corpuscles consisted of ovules. This first operation was a failure, the paraffine not having penetrated in a sufficient degree and consequently the preparation lacking distinctness. In order to be quite sure a second time, the anther, represented in fig. III, remained immersed in absolute alcohol for three days, then in turpentine, next for several days in a fluid mixture of turpentine and paraffine and finally during twenty hours in paraffine of 60° C. After this the anther was enclosed and cut into a long series of thin slices without any difficulty. Three of these slices are represented in fig. VIII, a, b and c. In the first the filament is to be seen without any connection with the anther-cells, in b a slight connection is visible, whereas in c the connective holds the two thecae together.

The lines *a*, *b* and *c* in fig. III indicate the relative places of the slices.

The principal feature of this and the other sections, either higher or lower, is that they show a kind of placenta growing forth out of the tissue ¹⁾ towards which — before the dehiscence — the valves of the anthers curve. These placentas have the greatest development at the base of the anther and gradually decrease in the direction of the top where they are reduced to the normal dimensions of the said tissue. As soon as the placentas, to which the connective sends out a special set of small cells, have assumed certain proportion, they commence producing ovules, which according to our figures instead of being anatropous, seem to be not quite normal.

1) Turpin called this tissue at the time „trophopollen” holding that it was the producer of pollen (H. von Mohl, Verm. Schr. bot. Inh. p. 31).

The cavities of each separate theca — the loculaments — are inverse to the placentas, i. e. the larger the latter, the smaller, the former are. In the lowest sections they are but little circles at large distances and containing only a few pollengrains.

Quite at the base of the anther they have altogether disappeared and with them the pollen. Such is the case with the stamens represented in figures III—VII. But in figures IX—XII the transformation goes on much farther.

A transition between the two sets is to be seen in fig. IV. The ovules of the two splits touch one another, caused, as is evident, by the anterior loculaments growing smaller compared with the outer ones, i. e. the loculaments pointing away from the centre of the flower. In fig. IX this shrinking becomes still more obvious, besides this ovules appear on the filament, a phenomenon which I often came across.

When the anterior loculaments disappear altogether — a not unfrequent occurrence — only one carpel-like part (*bu*) remains, which part corresponds with the outer anther-valves with which the two placentas are firmly connected. The figure moreover shows that the style (with the stigma) is continuous from the top of the carpel in its very middle. For clearness' sake we might once more point out that *bu* is a transformation of the outer anther-valves, belonging of course to different thecae, whereas the origin of *bi* is to be found in the inner valves.

The latter (*bi*) do not always disappear: in fig. X and XI it is, indeed, much narrower but present without a doubt. It may even happen that it ends into a style with stigma and also that it is split up into both its components, which lengthen into ribbon-like lobes. But ovules are as a rule absent, because the placentas remain in connection with *bu*. The more remarkable are therefore the exceptions, of which one is represented in fig. XII.

In this case both *bu* and *bi* are covered with ovules, numerous in *bu*, only a few with *bi*. The striking feature of the case is that *bu* and *bi* have grown together thus forming a kind of closed ovary with two parietal placentas. Only *bu* has a strongly developed style with stigma. In this cases the transformation of a stamen into a pistil has attained its height, the more striking as the filament has almost disappeared and the pistiloid stamen stands on the same level as its more perfect prototype. For differences between model and imitation distinctly persist. But which are the carpels now? Judging from the placentation it must be admitted that *bu* and *bi* do *not* correspond to the carpels, but are to be considered as consisting of two different halves as e. g. the valves of the capsule of the pansy.

According to this conception it would be the thecae having been transformed into carpels and the anther consequently comparable to two leaves! In the life-time of Agardh and Endlicher this conclusion would certainly have found a ready acceptance, for as von Mohl calls to mind in his „Vermischte Schriften”, already cited, it was those famous botanists, who looked upon the filament as an axial formation producing two opposed leaves.

Hugo von Mohl¹⁾ who together with all the other botanists of his time had manifested himself as an adherent of Goethe's doctrine of metamorphosis, opposed Agardh's and Endlicher's opinion, remarkably enough appealing to the very subject now under discussion, viz. pistillody of stamens. He argued that if a pistil can pass into a stamen and a stamen into a pistil and the latter must needs be considered as a leaf, a stamen must necessarily itself be of foliaceous origin.

The plants used by von Mohl for his argument are

1) l. c. p. 32.

especially *Sempervivum tectorum*¹⁾ and *Papaver orientale*. The examination of *Sempervivum* deserves special attention by its accuracy and completeness, illustrated moreover by excellent figures. The degrees of transformation from stamen to pistil are the following: broadening of the connective, by which process the thecae become more separated; shrinking and final disappearing of the pollen-cavities; appearance of ovules in the clefts between them; increased growth of the back of the connective resulting in a bending over towards the pistil, disappearance of the front anthervalves and at last an open carpel with two parietal placentas. These placentas may grow into one and in this way complete a perfect pistil²⁾.

In *Papaver* almost the same changes were observed, that is to say, that also in the widening clefts there appeared ovules and the pollen-cavities receding before the increasing placentas. But whilst in *Sempervivum* the ovules are born in the gradually deepening clefts, in *Papaver* the cellular tissue comes forth out of the cleft and brings the ovules to the surface.

Our *Tobacco* may in all respects be compared with *Sempervivum* and *Papaver*, for also in *Tobacco* the placentas arise simultaneously with the disappearance of the four pollen-cavities on both sides of the connective.

For all that there remains one noticeable difference, for whereas in the cases described by von Mohl the final outcome is only one carpel, our figures show that, although the inner

1) Du Petit Thouars seems to have been the first to observe the pistillody of the stamens of *Sempervivum tectorum*, viz. in 1807. Comp. A. P. de Candolle, Organ. Végét. T. I, p. 546.

2) Also Masters gives on p. 351 of his Veg. Teratology (German transl.) drawings of the pistillody of the stamens of *S. tectorum*. Although his figures are inferior to von Mohl's, yet they express the same way of transformation: production of ovules in the lateral clefts, falling off of the loculaments and broadening of the connective.

valve (bi) tends to disappear, it can, indeed, be the bearer of ovules and even unite with the outer (bu) to a closed whole. In this cases we may decidedly speak of a compound pistil.

It cannot, of course, occur to a botanist of the present day to infer from this fact that each stamen should be comparable to two leaves, at best one could admit of a splitting up of the connective in tangential direction.

It we have succeeded in proving that in *Nicotiana* as well as in *Sempervivum* and *Papaver* the ovules have arisen at both sides of the connective, the question remains whether in botanical literature also other kinds of pistillody of stamens have been registered.

We leave, of course, the leap-variations unmentioned, because the process of transformation defies observation.

In the *Mémoires de l'Académie de Toulouse*, 5 Série, T. III (1859) p. 105 D. Clos describes a tulip in which one of the stamens was pistilloid, but in such a way that the ovules arise between the cells of the anther, on the connective. As figures are wanting it is better for a right understanding to quote the exact words of the author:

„En effet, au dessus du filet on distingue la base des deux loges de l'anthère que surmontait une rangée d'ovules imparfaits: ceux-ci naissaient à la jonction du filet et de la loge anthérale avortée. Deux stigmates se trouvaient au sommet de ce corps....

Cette observation démontre que les ovules n'occupent pas la place du pollen, mais naissent à la jonction des loges de l'anthère avec le connectif.”

The similarity to *Nicotiana* is in my opinion complete, even where two stigmas occur. Both back and front of the anther appear to have developed into a sort of carpel, a fact also repeatedly found in *Nicotiana*.

As an appendage to the interesting paper on the green Rose (a monstrous variety of *Rosa diversifolia*) A. Gris

in the „Annales des sc. nat., IV^e Série (Botanique) T. IX (1858) p. 76 deals with some cases of pistillody of stamens in *Macleya* (*Bocconia*) *cordata*, which, I think, ought to be classed with the cases described and cited above. Gris says e. g.: „une étamine n'offrait qu'une seule loge normale à l'anthère, l'autre étant très réduite, irrégulière, sinueuse, et aboutissant par une de ses extrémités à la base d'un ovule monstrueux représenté par un corps central irrégulier (nucelle) qu'entouraient deux enveloppes courtes et évasées”.

About another case he says: „l'anthère d'une autre étamine monstrueuse n'avait qu'une seule loge fertile, tandis qu'un renflement verdâtre occupant la place de l'autre loge portait deux ovules bien développés”.

In perusing the literature on this subject within my reach I have not met with more cases offering sufficient similarity to those already mentioned. Often the descriptions are too incomplete and defectively illustrated as to yield a due insight into the transformation. Nevertheless it seems to me acceptable that the manner of alteration as shown in Tobacco and so on may be looked upon as the most usual, also in those cases which at present, owing to insufficient examination, seem to justify some different opinion.

How far the method of Klebs ¹⁾ of artificially creating monstrosities may be useful in this direction should be tested by other plants than *Sempervivum* for the very reason that the transitions of stamens to pistils made known by von Mohl, Masters and other students, are of frequent occurrence and belong so to say almost to the normal character of that plant.

1) G. Klebs. Ueber künstliche Metamorphosen (Abh. der naturf. Gesellschaft zu Halle 1906 Bd. 25, S. 133—294) ref. by O. Damm in Naturw. Rundschau, 27 Juni 1907.

Also the American botanist, Mel. T. Cook, known by his studies on galls, points out the necessity of obtaining data about the physiological conditions under which teratological deviations arise and of undertaking experiments in order to attain that end. ¹⁾

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POSTSCRIPT.

The ovules of the Solaneae being anatropous as also appears from my preparations, my attention was drawn by the fact that in the pistillodic anthers some ovules were abnormal and seemed to be orthotropous and without any integument. Quite aware of the difficulty of making a decisive statement regarding microscopic preparations when direction and place of section are not accurately known, I have repeatedly undertaken the same task but always come back to the same impression that, although many ovules are anatropous, there are plenty of them too of which the development is incomplete. In the above quotations the same thing has been mentioned as having been found by other authors.

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1) Teratología de la Piña (Tomado del Primer Informe Anual de la Estación Central Agronómica de Cuba, publicado el 1° de Junio de 1906.

