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Botany. — *"On the influence of the nectaries and other sugar-containing tissues in the flower on the opening of the anthers."* By Dr. W. BURCK. (Communicated by Prof. F. A. F. C. WENT.)

(Communicated in the meeting of September 29, 1906).

The consideration that the opening of the anthers is preceded by a very considerable loss of water [1]) and that with very many plants, e.g. *Compositae, Papilionaceae, Lobeliaceae, Antirrhineae, Rhinanthaceae, Fumariaceae* and further with all plants, chasmogamous as well as cleistogamous, which fertilise in the bud, this opening takes place within a closed flower and consequently cannot be caused by transpiration to the air, gave rise to the question whether perhaps the nectaries or other sugar-containing tissues in the flower, which do not secrete nectar outwardly, have influence on the withdrawal of water from the anthers.

My surmise that also among the plants whose anthers only burst after the opening of the flower, some would be found in which this process is independent of the hygroscopic condition of the air, was found to be correct. If the flowers are placed under a glass bell-jar, the air in which is saturated with water-vapour, the anthers of many plants burst at about the same time as those of flowers which are put outside the moist space in the open air.

This led me to arranging some experiments, yielding the following results:

1. If in a flower of *Diervilla* (*Weigelia*) *rosea* or *floribunda*, which is in progress of unfolding itself, one of the stamens is squeezed by means of a pair of pincers, so that the drainage of water from the stamen downwards is disturbed, the four anthers whose stamens have remained intact, spring open, but the fifth remains closed. With this plant it is not necessary to place the flower in a moist space; the same result is generally obtained if the flower remains attached to the plant.

If a flower is placed in the moist space together with the loose

[1]) This loss of water amounts e.g. with *Fritillaria imperialis* to 90 $^0/_0$ of the weight of the anthers, with *Ornithogalum umbellatum* to 86 $^0/_0$, with *Diervilla floribunda* to 87 $^0/_0$, with *Aesculus Hippocastanum* to 88 $^0/_0$, with *Pyrus japonica* to 80 $^0/_0$, with different cultivated tulips 59—68 $^0/_0$, etc. With plants whose anthers burst in the flower, the loss is smaller; the anthers and the pollen remain moist then. With *Oenothera Lamarckiana* the loss amounts to 41 $^0/_0$, with *Canna hybrida grandiflora* to 56 $^0/_0$, with *Lathyrus latifolius* to 24 $^0/_0$.

anthers of another flower, those which are attached to the flower spring open; the loose ones don't. If only the corolla with the stamens attached to it is placed in the moist space, the anthers open as well as those of the complete flower. Consequently the nectary which is found in the middle of the flower at the side of the ovary, exerts no direct influence on the bursting of the anthers. If further a stamen is prepared in its full length and placed in the moist space together with some loose anthers, the anthers of the stamen burst, whereas the loose anthers remain closed.

From these experiments we infer that the anthers open under the influence of the stamen whether or not connected with the corolla. Now an investigation with FEHLING's solution shows that as well the stamen as the whole corolla and even the corollar slips, show the well-known reaction, indicating glucose.

Of *Digitalis purpurea* two of the anthers of a flower in the moist chamber, were separated from the corolla by an incision. The uncut anthers burst open, but the other two remained closed. A stamen prepared free over its full length causes the anther to burst in the moist chamber; loose anthers, on the other hand, remain closed.

An investigation with FEHLING's solution showed that here also the corolla contains glucose everywhere, but in especially large quantities where the stamens have coalesced with the corolla. Also the stamens are particularly rich in sugar over their entire length.

Of *Oenothera Lamarckiana*, the anthers of which burst already in the bud, a flower-bud was deprived of sepals and petals. One of the stamens was taken away from the flower in full length; of another stamen only the anther was removed. These three objects were placed together in the moist chamber. The anthers of the stamens which had remained connected with the tube of the calyx and those of the loose stamen sprang open; the loose anther, however, remained closed. An examination with FEHLING's solution gave the same result as was found above with *Digitalis*.

Similar experiments were made with the flowers of *Antirrhinum majus* L., *Lamium album* L., *Glechoma hederacea* L., *Salvia argentea* L., *Nicotiana affinis* Hort. and *sylvestris* Comes., and *Symphytum officinale* L., which all gave the same results, while with the flowers of *Ajuga reptans* L., *Stachys sylvatica* L., *Scrophularia nodosa* L., *Cynoglossum officinale* L., *Anchusa officinalis* L., *Echium vulgare* L., *Calceolaria pinnata*, *Hibiscus esculentus*, *Anoda lavateroides*, *Malva vulgaris* Tr., *Torenia asiatica*, *Corydalis lutea* Dc., *Colchicum autumnale* L., *Lysimachia vulgaris* L., *Atropa Belladona* L. and *Rhinanthus major* Ehrh. the experiments were restricted to showing that with all of them the anthers spring open in a space, saturated with water-vapour. With all these plants the corolla and stamens react very strongly with FEHLING's solution.

These experiments indicate that the water is withdrawn from the anthers by an osmotic action, having its origin in the glucose-containing tissue.

I remark here that the presence of glucose — in so far as we may infer it from the precipitate of cuprous oxide after treatment with FEHLING's solution — in other parts of the flower than the nectaries proper and especially in the corolla, is a *very common* phenomenon (to which I hope to return later) and that it is not restricted to those flowers in which stamens and corolla have coalesced. There is rather question here of a quantitative difference than of a special property, peculiar to these flowers.

2. With *Stellaria media* the epipetalous stamens are mostly abortive, while of the episepalous ones only three have remained, as a rule. These three stamens bear at the base on the outside, a gland, secreting nectar.

If a flower is placed in the moist chamber and one of the stamens is injured with the pincers, the anthers of the uninjured stamens will afterwards burst, but the other remains closed. And when loose anthers from the flower are placed in the moist chamber, together with an intact flower, the loose anthers remain closed, while the anthers of the flower open. As well the petals as the stamens precipitate cuprous oxide from FEHLING's solution; also the tissue at the base of the sepals reacts with it. But the bursting of the anthers stands in no relation to this; if the petals are removed, this has no influence on the result of the just mentioned experiment.

The experiment indicates that the water is withdrawn from the anthers by the osmotic action, proceeding from the nectary.

In this connection it deserves notice that the nectaries of the epipetalous whorl and also those of the missing stamens of the episepalous whorl are abortive together with the stamens. The same is observed with *Cerastium semidecandrum* L., *C. erectum* L. and *Holosteum umbellatum* L.; here also the nectaries of the missing stamens have disappeared as a rule.

With the *Papilionaceae,* of which I investigated *Lupinus luteus L., Lupinus grandifolius L., Lathyrus odoratus L., Lathyrus latifolius L.* and *Vicia Faba L.,* the anthers are known to open already in the closed flower. The petals precipitate cuprous oxide from FEHLING's solution, but exert no influence on the opening of the anthers. Flower buds of *Lathyrus latifolius* and *Lathyrus odoratus* were deprived of their petals and placed in the moist chamber together with loose anthers. The loose anthers remained closed, but the others burst open.

In the same way as the flowers of *Stellaria media* and the mentioned *Papilionaceae,* behave with respect to the opening of the anthers in a space, saturated with water-vapour :

Stellaria Holostea L., St. graminea L., Cerastium Biebersteinii C. arvense L., Cochlearia danica L., Sisymbrium Alliaria Scop., Crambe hispanica L., Bunias orientalis L., Capsella Bursa pastoris Mnch., Hesperis violacea L., H. matronalis L., Thlaspi arvense L., Alyssum maritimum Lam., and further *Lychnis diurna Sibth., Silene inflata* Sm. *Galium Mollugo L., Asperula ciliata Rochl., Campanula media L., C. latifolia L.*

With all these plants the bursting of the anthers must, in my opinion, be ascribed to the influence of the nectaries.

With *Hesperis* two large nectaries are found at the inner side of the base of the two short stamens and between these and the four long stamens. If a flower of *Hesperis violacea* or *H. matronalis L.*, after being deprived of its petals and sepals, is placed in the moist chamber, nearly always the four long stamens only burst; the other two remain closed.

It has been repeatedly observed that the secretion of nectar begins as soon as the stamens open.

In connection with what was stated above, one would be inclined to infer from this that flow of water from the anther causes the secretion of nectar. If, however, with *Stellaria media,* the anthers are removed before they have discharged water to the nectaries, one finds all the same the nectaries amply provided with honey, when the flower opens. The same may be observed in the male flowers of *Aesculus Hippocastanum.* In the still nearly closed flowerbud the nectary is dry yet. When the flower continues to open small drops of liquid are seen to appear on the surface of the nectary, still before the anthers extend halfway from the bud. These droplets increase in size as the anthers approach the moment in which they open. By weighing it may be proved that the anthers have already lost part of their original weight when the first droplets of nectar appear on the surface of the nectary. From this circumstance also one would be inclined to infer that the water of the anthers comes out again as nectar. When, however, from very young buds, whose nectary is not moist yet, the anthers are removed, yet at a later stage of development of the bud, secretion of nectar is found in them as in buds that have kept their anthers.

With *Fritillaria imperialis* I found the same; but here the secretion of nectar was not so abundant as in buds, the anthers of which had not been removed. In my opinion these observations indicate that the sugar, stored up in the nectaries or other sugar-containing tissues of the flower, at the moment when it begins to exert its osmotic action, attracts water not only from the anthers but also from other parts of its surroundings.

3. With the following plants the anthers remain closed in a space, saturated with water-vapour. In so far as they possess nectaries, these latter appeared to exert no influence on the bursting of the anthers.

Ranunculus acris L., *R. bulbosus L.*, *Aquilegia vulgaris L.*, *Clematis Vitalba L.*, *Chelidonium majus L.*, *Brassica oleracea L.*, *Geranium molle L.*, *G. Robertianum L.*, *G. macrorhizum L.*, *Geum urbanum L.*, *Rubus caesius L.*, *Philadelphus coronarius L.*, *Heracleum Sphondylium L.*, *H. lanatum Michx*, *Aegopodium Podagraria Spr.*, *Carum Carvi L.*, *Pimpinella magna L.*, *Valeriana officinalis L.*, *Ligustrum vulgare L. Majanthemum bifolium Dc.*, and *Iris Pseudacorus L.*

It is remarkable that *Brassica oleracea L.* forms an exception to what is otherwise generally observed with the Cruciferae; the position of the stamens with respect to the nectaries which secrete honey abundantly, would make us expect that in a moist chamber they would behave like the others. The same remark holds for the species of *Geranium*.

The secretion of nectar in the flower attracted the attention of various investigators many years before SPRENGEL published his view of the matter. Also after SPRENGEL, in the first half of the preceding century, it has many times been the object of investigation. All these investigators agreed in being convinced that, apart from the significance of the honey-secretion for the fertilisation of the flowers by the intervention of insects, to which SPRENGEL had drawn attention, the sugar-containing tissues and the secreted liquid were still in another respect useful to the plant.

After DARWIN had in 1859 brought to the front again SPRENGEL'S observations on the biological significance of the various properties of the flower — which observations were falling more and more into oblivion — and had accepted their consequences by bringing them into relation on one hand with his conceptions about the necessity of cross-fertilisation for the maintenance of the vital energy of the species, on the other hand with the theory of natural selection, the investigation of still another significance of the nectaries for the plant was for a long period entirely abandoned.

Not until 1878 this subject was again broached by BONNIER [1]) who, in his extensive paper on the nectaries, in which as well the anatomical as the physiological side of the problem were submitted to a very extensive investigation, proved that sugar-containing tissues in the flower and especially in the immediate vicinity of the ovary are not only found with plants which regularly secrete nectar during the flowering, but also with such plants as under normal conditions never secrete such a liquid. With these plants, which in the literature on flower biology are called "pollen flowers", since the insects find no nectar in them, he found as well sugar-containing tissues as in the so-called "insect flowers". Even with anemophilous plants he found "nectaires sans nectar", e. g. with *Avena sativa, Triticum sativum* and *Hordeum murinum*. A number of plants which under ordinary conditions of life contain no nectar, he could induce to nectar-secretion by placing them under conditions, favourable for this purpose.

At the end of his paper he reminds us that an accumulation of reserve materials, wherever a temporary stagnation in the development exists, may be considered a very general and well characterised phenomenon. When a plant stops its further development at the end of its growing period, it has stored up reserve material in its subterranean, parts and when the seed has finished its development, it has accumulated nourishing substances in the endosperm or in the cotyledons of the embryo. These reserve materials, turned into assimilable compounds, then serve for the first nutrition of the newly formed parts.

He then arrives at the conclusion that in the vicinity of the ovary saccharose is stored up, and that this reserve substance after fertilisation and in the same proportion as the fruit develops, passes partly or entirely into the tissue of the fruit and into the seed, after having first been changed, under the influence of a soluble ferment, into assimilable compounds.

Investigation showed me also that the accumulation of saccharose as a reserve substance in the flower is a very common phenomenon [2]).

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[1]) GASTON BONNIER. Les nectaires. Étude critique, anatomique et physiologique. Annales des sciences naturelles. Tome VIII. 1878.

[2]) On this point see also: PAUL KNUTH, Über den Nachweis von Nektarien auf chemischem Wege. Bot. Centralbl. LXXVI. Band, 1898, p. 76 and ROB. STÄGER, chemischer Nachweis von Nektarien bei Pollenblumen und Anemophilen. Beihefte zum Bot. Centralbl. Band XII. 1901, p. 34.

But besides the function, discovered by BONNIER and the significance of the secreted nectar for the fertilisation, it has become clear to me that as well the glucose, formed from saccharose, as the outwardly secreted nectar, are also in other respects of great importance to the plant. The observations, here communicated, point already to one very important function, i. e. *to enable the stamens to bring their pollen to the surface at the right time, independent of the hygroscopic condition of the air.*

I hope before long to be able to point out still another function.

The secretion of nectar now appears in another light. The view that it must be considered as an excretion of "a waste product of chemical changes in the sap" [1]), which in the course of time has become more marked through natural selection, as a useful adaptation for promoting cross-fertilisation, since this liquid was eagerly taken away by insects, has to give way to the conception that, preceding any adaptation, it has in its further development kept pace with the sexual organs.

Anatomy. — "*On the relation of the genital ducts to the genital gland in marsupials.*" By A. J. P. v. D. BROEK. (Communicated by Prof. L. BOLK).

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In the following communication the changes will be shortly described which the cranial extremities of the genital ducts in marsupials undergo during the development and their relations in regard to the genital gland. In more than one respect the ontogenetic development differs in these animals from what can be observed in other mammals.

It is especially a series of young marsupials of Dasyurus viverrinus in successive stadia of development from which the observations are derived. The preparations of other investigated forms (Didelphys, Sminthopsis crassicaudata, Phascologale pincillata, Trichosurus vulpecula, Macropus ruficollis) correspond however completely with the conditions we meet in Dasyurus.

In our description we start from a stadium schematically represented in figure 1 that still prevails for both sexes, (Dasyurus, Didelphys, Macropus). The genital gland (Figure 1 *k*) is situated at the medial

1) CH. DARWIN. Origin of species. Sixth Edition. 1872. Chap. IV, p. 73 and The effects of Cross and Selffertilisation. Edition 1876. Chap. X, p. 402.