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CONTENTS.

Botany. — *"On the biological significance of the secretion of nectar in the flower."* By Dr. W. BURCK.

(Communicated in the meeting of November 28, 1908.)

In an article in the Recueil des travaux botaniques Néerlandais vol. IV. [1]) I have explained in detail, that DARWIN in 1859 put forward the hypothesis, that a cross with another individual is indispensable for the species and that, at the time, he considered the structure of flowers to be generally such as to ensure, or at least to favour, cross-fertilisation, but that in later years he, however, left this stand-point. I showed from his later writings, that the observations and experiments of many years had brought him more and more to the conclusion, that a much greater significance should be attached to self-fertilisation, than he had at first imagined; I also showed that, at the close of his studies, he was not very far from giving a negative answer to the question whether floral structure favours cross-fertilisation. Since then, observations have been made on a number of tropical plants, the flowers of which are always closed, so that in such plants the possibility of cross-fertilisation is

1) An abstract of this may be found in Biolog. Centralblatt. Bd. XXVIII. N⁰. 6. 1908.

excluded and I further pointed out, that from these results there can be no question of a natural law in the sense imagined by DARWIN. Furthermore, the view that cross-fertilisation might be advantageous to the species, has been rendered untenable by our present knowledge of the structure of the nucleus, and its function in the life of the plant, and also by our modern ideas concerning the nature of fertilisation.

Suppose we now give up this view, and fall back on the fundamental hypothesis, which was put forward by GÄRTNER in 1849, that only by self-fertilisation, vigour and fertility of the species are preserved, since a cross may lead to hybrid-formation, which diminishes the fertility of the plant. It then follows, that floral biology, which has started in its considerations from the opposite view, has lost its basis and must be built up anew. We have been led astray by our ideas regarding the significance of the properties of the perianth — its shape and dimensions, its colour and odour — and regarding the various mechanisms of the flower — dioecism, monoecism, heterogamy, dichogamy, hercogamy and self-sterility — all of which we thought we could explain as useful adaptations for visiting insects in order to ensure cross-fertilisation; it must be possible to explain them in another way. I have already shown in my previous paper that diclinism and hercogamy can be explained by *mutation* and that protandry and protogyny must be considered as characters of organisation, and not of adaptation.

With regard to the phenomenon of self-sterility I limited myself to pointing out, that this should be considered primarily as the result of hybridisation, rather than as a special adaptation.

In order that we may now obtain a better conception of the qualities of the floral envelopes, we must again adopt the view of the older biologists, who regarded these envelopes as organs for the protection of the sexual apparatus.

We must therefore consider to what extent the sexual organs require the protection of the perianth, not only when they originate and develop, but also during the flowering period. Hitherto we have been accustomed to look for a connexion between the various properties of the perianth and its significance in the attraction of insects. Now we shall have to test these same properties, especially of shape, dimension, position and the distribution of fragrant vapours, by the question, how they may be considered to be of importance to an organ, which is intended to protect the sexual organs from unfavourable external influences. More than has hitherto been the custom in floral biology, we shall have to pay attention to the anatomical structure and the physical and chemical properties of the floral envelopes, to the way in which the floral leaves are arranged in the bud, with reference to each other, (the aestivation) to mutual coalescence, to the presence of scales, hairs and glands, to the secretion of water, honey, mucilage, etc. Also, if we give prominence to the protection of the generative organs as the basis of our considerations, we shall have to investigate whether the *secretion of nectar* is not connected with this protective function.

This connexion may be inferred all the more readily on account of the unmistakable correspondence of the secretion of nectar during the flowering period to that of water or of a mucilaginous fluid in the so-called water-calyces, the latter secretion being considered a means of protection of the sexual organs.

With regard to this secretion of water I beg to recall, that 20 years ago TREUB first drew attention to the remarkable phenomenon that the floral buds of *Spathodea campanulata* BEAUV., a tropical *Bignoniacea*, are filled with a watery liquid, secreted by a large number of glands, which cover the inner surface of the calyx, so that the petals, stamens and ovaries develop under the protection of this fluid. The liquid contains traces of the hydrochlorides, carbonates, nitrates and sulphates of potassium, sodium and calcium, has an alkaline reaction and contains traces of ammonia; sugar was not found in it.

A similar secretion of water in the closed flower-bud was afterwards also observed in other plants. We may mention the papers of LAGERHEIM, GREGOR KRAUS, HALLIER, KOORDERS, SHIBATA and SVEDELIUS, to whose investigations I do not propose to refer here in further detail, as I intend to publish my own observations on this subject before long. From these it will be evident, that the phenomenon is not limited to the tropics, but can also be studied here.

I only wish to emphasize, however, that all naturalists, who have occupied themselves with the subject, have accepted the opinion of TREUB, that the secretion of water is a means of protecting the sexual organs against the unfavourable consequences of too strong transpiration, and that my personal observations, especially in this country, have shown me the connexion between the secretion of water and of nectar, and have gradually confirmed me in the conviction, that by the nectar-secretion the sexual organs are protected.

I wish briefly to explain the train of thought, from which I started my investigation.

The observations on plants with water-calyx and especially the detailed investigations of KOORDERS have taught us, that already long before the corolla and the sexual organs are laid down, the very

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young calyx (the development of which in all these plants is hurried on, before that of the other parts of the flower) is protected against the dangers of exposure to the atmosphere; sometimes the calyx is protected by glands, which may or may not be active, sometimes by a thick covering of hairs, which retains air, sometimes by both these means. It is intelligible, that this young organ, the vascular bundles of which are as yet unperfectly developed and therefore unable to compensate adequately for the loss of water through transpiration, should require a special, temporary protection, in so far as it is not surrounded by bracts.

Now we see at a later stage, in which the calyx has already acquired certain dimensions and in which its anatomical structure is nearing completion, that the same glands appear on the *inner surface*, and by their activity more or less fill the cavity of the calyx with water; this secretion of water supplements the protective function of the calyx towards the other parts of the flower, which are now beginning their development.

Later, in older buds, when the stamens and ovaries have already made considerable progress, the same glands appear on the outer- and on the inner surface of the *corolla*. The former, the *outer* glands, are especially active in protecting the petals against excessive transpiration in the short period, between the bursting open of the calyx and the development of the petals to their full size — temporarily therefore [1]. The significance of the hairs on the *inner surface* would then be, that in the same period they keep the sexual organs in a moist space.

When we see therefore, that the flower is carefully protected against transpiration from the first stages of its development to the moment of opening, the question naturally arises, whether at the opening and during the flowering-period, the sexual organs are under such especially favourable conditions, that they require no protection?

This is certainly not the case; during the flowering period the ovary is not placed in favourable conditions.

When opening, the flower enters upon a period, in which the stamens and the ovaries — exceptions apart — have reached their highest stage of development, do not require food for further growth and are in a state of rest; the ovaries are awaiting fertilisation in order to be called to new life by that stimulus; the stamens in a state of maturity, await the evaporation of the superfluous water from the anthers.

[1]) This opinion will later be supported by examples; I propose to show, that at this stage, when the corolla is still completely closed, water or nectar is found in many flowers.

At the opening of the flower the perianth, and especially the corolla, are in very different condition, the latter generally not having reached anything like its full size, when the sepals move apart. In a very short time, the corolla grows out to its normal dimensions, to be afterwards during the whole flowering period the seat of various physiological processes, consisting partly, in the transformation to its own use of material laid down in its tissues in the bud, and partly in the continuous production of fragrant vapours, which the flower gives off in that period, very often also in the production of nectar etc. If we further remember, that the considerable quantity of water which the corolla gives off to the atmosphere by transpiration, is continually replenished by fresh supplies, while the stamens on the other hand receive less water from the thalamus than they give off, it becomes clear, that the nutrition-stream moves principally in the corolla.

The consideration suggests the following questions: What means are at the disposal of the ovary for escaping the harmful consequences of too strong transpiration? Is the secretion of nectar perhaps to be regarded as one of these means?

I venture to think that I have obtained an affirmative answer to the last question and hope that I may succeed in obtaining acceptance of my opinion.

I wish to preface a description of the flower and of nectar-secretion in *Fritillaria imperialis*.

Fritillaria imperialis bears large, bell-shaped flowers turned with the opening downwards, and consisting of a perianth of two trimerous whorls, a superior ovary with a long style and tripartite stigma, and 6 long stamens, with filaments entirely enclosed in the bell, but with anthers protruding outside. Generally the style is somewhat longer, so that the stigmas are under the anthers and outside the flower. The cylindrical ovary escapes observation, as it is wholly surrounded by the fleshy filaments of the stamens, which form a close-fitting tube around it.

Not until fertilisation has taken place and the perianth has withered, do the flowers become erect; the fruits afterwards are also erect.

Each perianth-leaf bears close to its base a large saucer-shaped, shiny, white nectary, which is surrounded by an elevated border, and secretes heavy drops of fluid during the flowering-period.

The whole of the perianth is very rich in glucose, not only at the time of flowering, but already much earlier. A section through the middle of an adult perianth leaf, about half-way between base and top, shows, that the mesophyll, which is here 13—14 cells thick, consists of thin-walled cells, which leave large intercellular spaces between them. The vascular bundles are strongly developed and take up almost the whole thickness of the leaf. In no part of the transverse section can starch be detected, but the whole of the mesophyll is very rich in glucose; starch occurs only in the nectary. In a section through the nectary, 4 different parts can be made out even at low magnification. First there is the honey-secreting tissue proper, consisting of 3—4 layers of small close-fitting cells, densely filled with protoplasm and containing large nuclei. Under this there is a tissue, 8 or more cell-layers thick, composed of larger cells with very distinct intercellular spaces; these cells are crowded with numerous small starch-grains. Outwards or downwards there follows the region of the vascular bundles, where the mesophyll still contains starch. Finally the latter tissue gradually passes into that containing chromatophores, which again consists of considerably smaller cells and is closed off on the outside by an epidermis, consisting of pinacoid cells, the outer wall of which, in this region, is much thicker than in any other part of the perianth.

The starch which collects under the secretory layer, is already found in sections of very young nectaries, for instance in buds about 2.5 cm. long.

That it is from this material that nectar is afterwards formed, becomes evident on the examination of nectaries, which have already been forming honey-drops for some days; a distinct diminution of starch may then be observed, and at the end of the flowering no starch whatsoever is found.

A section through a stamen shows, that the latter is traversed by a comparatively thin vascular bundle, and that for the rest the tissue consists of large cells, which give a very strong reaction with FEHLING's test-solution for glucose. Externally the tissue is enclosed by a small-celled epidermis with a comparatively thick outer wall, which presents a granular cuticle. It may be, that by being enclosed by stamens, which are rich in glucose, the ovary is not so completely protected against the harmful consequences of exposure to the atmosphere as an inferior ovary is by the thalamus, but nevertheless the two kinds of protection are comparable; in any case the ovary thus receives considerable protection during development.

It may be of interest to note, that the stamens continue to enclose the ovary, when the anthers have fallen off. The filaments remain fresh and in their original position, as long as flowering continues.

The secretion of nectar begins soon after the perianth-leaves separate, and the tips of the anthers protrude out of the flower.

The secretion is very abundant. Generally large drops hang down from the nectaries in plants in the open. If a cut flowering specimen be placed in a glass of water, under a high bell-jar — in a fairly moist space therefore, where evaporation is limited — drops may be seen to fall down from time to time. When plants which have been grown in pots, are placed in a dark room some time before the opening of the flowers, it is found that the secretion of nectar is quite independent of light and continues day and night. If the nectar be removed by means of a pipette, the drops are renewed as well and as quickly as in the light. The nectar can be removed for several days; each time new drops appear again. From this we may deduce, that the evaporation of nectar in plants in the open air is fairly considerable, and that the nectaries continue to act as long as the flowering-period lasts.

Fritillaria imperialis is one of those plants, in which the dehiscence of the anthers depends on loss of water by transpiration. Although in many orders, such as the *Papilionaceae, Antirrhineae, Rhinanthaceae, Malvaceae* the dehiscence of the anthers is independent of the hygroscopic condition of the atmosphere, and the pollen is equally well liberated in a moist flower as in dry air, this is not the case in *Fritillaria*. As has been said above, the tissue of the filament indeed contains a considerable quantity of glucose, but nevertheless the osmotic action, which the sugar exerts in abstracting water from the anthers, is evidently not enough to make them dehisce. If a young flower be enclosed in a moist glass box, or a cut plant be placed under a high bell-jar in surroundings, which are only moderately damp, the anthers remain closed during the whole of the flowering period, whereas in the open air they often dehisce on the first day in bright, dry, spring weather, after having lost 90°/₀ of water. It follows from this experiment, that the anthers can dehisce, because they protrude from under the flower. If this were not the case, if the filaments were a few centimetres shorter, the moist air, inside the flower, would prevent the dehiscence of the anthers. That during the flowering-period there is a strong current of water through the vascular bundles of the perianth-leaves, which continually supplies the latter with water to compensate for the loss by transpiration, needs as little proof as the fact, that this watercurrent has been turned away from the stamens. If this were not so, there could be no question of the dehiscence of the anthers.

I now come to the conclusion, that the *Fritillaria*-flower is to be regarded as a cup in which the air is continually kept moist during the flowerlng period by the evaporation of 6 large drops of fluid, secreted in its upper parts by as many nectaries, the transpiration-loss of which is made good by fresh supplies of fluid, day and night, as long as flowering continues.

Inside this moist cup there are the ovary and the stamens, which remain in a state of rest during the flowering period, and receive only a small supply of water from the thalamus. For to the extent that they are enclosed in the cup (the ovary for its full length, and the stamens with the exception of the anthers) they are protected against dessication by damp surroundings, whereas the anthers, hanging out of the cup, are exposed to evaporation.

According to the analysis of BONNIER the nectar is very rich in water and contains at most 5—7 % of sugar. If there were no sugar at all in the fluid, one would not hesitate to call the nectaries of *Fritillaria* perianth-hydathodes, and to consider them quite similar to the calyx-hydathodes of *Spathodea campanulata* and similar plants.

In *Fritillaria* the nectar does not come into direct contact with the ovary, but is found outside the sexual organs. This method of nectar-secretion, which I purpose to call, for the sake of brevity, a peripheral one, is not the most general. A number of plants may indeed be cited, which agree with *Fritillaria* in this respect, such as *Trollius, Abutilon, Lilium* and *Helleborus*, but in most plants the nectar is secreted in such a way, that the ovary is directly moistened by it, as in *Labiatae, Boraginaceae, Solanaceae* and other orders. In contradistinction to the peripheral, I wish to call this a central secretion of nectar. Very often the nectar is secreted in more than one part of the flower; in such cases there is a combination of the peripheral with the central method.

In numerous plants the moistening of the ovary is greatly increased by a thick covering of soft hairs or by a thick felt, which covering is saturated with nectar in various ways. Sometimes the nectar is secreted by the ovary-wall, and ascends between the hairs, as is for instance, the case in most species of *Verbascum* and in *Helianthemum vulgare,* which are wrongly called nectarless plants. In other cases the covering itself consists of hairs which secrete glucose; this occurs for instance in the species of *Paeonia,* another genus which is wrongly considered to be devoid of nectar. Often, however, the nectar which saturates the ovary-covering, is brought up from the thalamus, as for instance in *Pulsatilla* and other *Ranunculaceae,* which will be considered below. Especially when such covered ovaries are close together (e.g. in *Pulsatilla* each flower has about 100 ovaries) it may be readily imagined, that by evaporation of the nectar the ovaries are always in a moist atmosphere. By this I mean, that one may assume, not only that the nectar is continually replenished by fresh secretion (this can indeed be observed in many plants) but also that on increased concentration, the nectar never dries up, be it, that it absorbs aqueous vapour from the air, or abstracts water from the ovary itself. This moistening of the ovary reminds us vividly of certain well-known mechanisms for protecting an organ against excessive transpiration, such as a covering of wax, or of mucilage-secreting glands. In this connexion I may point out that among plants without nectar, there are indeed some, in which the ovary is protected by wax, as in *Papaver*, *Eschscholtzia*, and *Glaucium* or by mucilage, as in species of *Lysimachia*, *Ononis spinosa*, and *Verbascum Blattaria*. It thus becomes intelligible, that these plants can do without nectar. In *Verbascum Blattaria* the ovary, which is fairly deeply hidden, is covered from top to bottom with compound glands, which correspond in structure with lupulin- and *Ribes* glands, continually pouring out a layer of mucilage over the ovary.

This is the more remarkable and important, since, as was mentioned above, the ovary of all other *Verbascum*-species is covered with a felt, rich in glucose. We find therefore in different species of the same genus two different means of protection, to which the same biological significance must be attached.

I now wish to explain further, by some notes on *Ranunculaceae* and *Malvaceae*, what was said above with reference to the secretion of nectar in different parts of the flower.

Let us consider first of all the flower of *Trollius europaeus* L.

In *Trollius* the 11 or 13 large, hemispherical sepals with overlapping edges, form an approximately ball-shaped envelope round the sexual organs. The petals, generally 10 in number, are yellow and spatulate, and secrete honey on the middle of their inner surfaces. The stamens numbering about 160 and placed in numerous whorls, surround about 30 ovaries. Except for a small opening, facing upwards, the flowers are closed; only the stigmas come wholly or partially into view.

At the beginning of the flowering period the anthers are at about the same height as the stigmas, and the ovaries are surrounded and protected by the column of stamens.

Later this is not the case to the same extent, although a few whorls of the inner stamens, the anthers of which do not come to complete development, retain their places.

As in *Fritillaria*, the ovaries of *Trollius* are in a moist space, and are furthermore protected laterally by the stamens. Whereas, however, the humidity of the flower in *Fritillaria* does not interfere with the dehiscence of the anthers, because these are outside the flower, this is not so in *Trollius*, where the dehiscence of the anthers is equally dependent on the evaporation of superfluous water into the air, for in *Trollius* the stamens are enclosed within the calyx.

This is the explanation of the remarkable phenomenon, that the stamens, beginning with those of the outer whorl and then gradually from the periphery to the centre, become elongated soon after the opening of the flower and bend inwards, until their anthers are near the opening; the anthers of the inner staminal whorl then come to lie immediately above the stigmas. If one places a young flower in a closed glass box, the phenomenon may be followed step by step, and one observes at the same time, that as long as the flower remains in the glass box, the anthers remain closed. In an open box on the other hand, the anthers are seen to dehisce as soon as they have come under the opening of the flower, and their pollen is seen to be scattered on the stigmas. Observation in the field likewise proves, that the anthers remain closed in damp weather.

Honey is not secreted in any place other than the petals. In the main the arrangement of the flower is quite like that of *Fritillaria*. The closed condition of the corolla can hardly be explained otherwise than as a device to prevent the rapid evaporation of the nectar into the air and is connected with the erect position of the flower [1]).

As a second example of the methods of nectar-secretion in *Ranunculaceae*, I now choose the flowers of *Clematis* and of *Anemone*, which do not possess petals, but where the calyx takes the place of the corolla, and where no nectar is observed on the periphery of the flower. This is the reason, why they are referred to as nectarless plants in the literature on the biology of the flower. That this is by no means correct, is at once evident when we wash the ovaries, which are thickly covered with silky hairs, for a moment with a drop of distilled water on a slide, and then warm the water with a drop of FEHLING's solution; we then obtain a strong glucose-reaction, proving that the hairy covering of the ovary is saturated with nectar. Further investigation shows, that this nectar is derived from the interstaminal portion of the thalamus.

The droplets of nectar, which are secreted here, are sucked up between the stamens and the ovaries and are retained, especially by the hairy covering of the latter.

I must now recall that many years ago, BONNIER already drew

[1]) I believe that this is also the explanation of the closed flowers of *Calceolaria*, *Fumariaceae*, *Antirrhineae*, *Rhinanthaceae* etc.

attention to the interstaminal secretion of nectar in *Anemone nemorosa*. He stated that the thalamus contains much sugar, and that its interstaminal portion is covered with numerous thin walled papillae, from which, under favourable conditions, minute drops of nectar are seen to exude. My own investigations have shown me that what BONNIER [1]) observed, may be called a pretty general phenomenon in the order of *Ranunculaceae* i.e. in many genera, nectar is secreted from this portion of the .thalamus.

The flowers of *Anemone* and of *Clematis* may therefore be contrasted with those of *Trollius*, as regards secretion of nectar. Here the nectar comes into direct contact with the ovaries and it is evident, that the numerous drops of honey, which are found everywhere between the stamens, and which are constantly renewed, contribute not a little to the maintenance of a certain degree of humidity in the neighbourhood of the ovaries.

It is remarkable, that in many other *Ranunculaceae* the nectar is secreted in the flower in two places, so that a peripheral and a central secretion may be distinguished. It should be noted, that in some genera the two methods of secretion are of about equal importance to the plant, but that in other genera the peripheral one is much the least important.

The flower of *Aconitum* may serve as an example of a plant in which both secretions are of importance for the protection of the sexual organs.

At the beginning of the flowering-period the 3—5 quite glabrous ovaries have not yet reached their full development. They can scarcely be discerned, as they are enclosed by the numerous stamens. These stamens are distinguished by broad filaments, which are very rich in glucose, and which, being closely pressed against the ovaries, protect the latter against external influences. The sexual organs are kept moist by a secretion of nectar from the interstaminal portion of the thalamus. [2]) The sepals and petals are also rich in glucose.

The two superior petals are metamorphosed to nectaries with long stalks and during the time of flowering these secrete a copious supply of honey. The two superior, dark blue sepals have coalesced to form a helmet-shaped hood, which, as long as the flower is still in bud, encloses it for the most part and further, during the

[1]) BONNIER, G,. Les nectaires. Annales des sciences naturelles. Botanique. Tome VIII. 1879. p. 141.

[2]) Not unfrequently the nectar-drops can be detected on the stamens with a simple lens; the presence of nectar between the stamens may moreover be easily demonstrated chemically, by depriving a young flower of its calyx and corolla, and washing it with water.

flowering-period, acts as a protective roof to the two nectaries and the sexual organs below them, while the latter are surrounded by the remaining sepals and petals. The secretion of nectar has once more rendered the flower a moist chamber, in which the sexual organs are protected against the dangers of dessication. At first the stamens, with anthers bent downwards and closed, lie turned away from the entrance of the moist chamber. Later they become erect; afterwards they become elongated, and so bring the anthers to the entrance of the flower, where they can give up their excess of moisture to the air, at least when the latter is not too damp. As they dehisce, the stamens again bend downwards with empty anthers. The broadened parts of the filaments do not, however, bend in this way, but retain their original position and protect the ovaries throughout the whole of the flowering period. It is not until this stage that the stigmas, which are now fully developed, come to the entrance of the flower.

Although the corollar-nectaries of *Aconitum* are not much less important than the thalamus, as regards secretion of nectar, this is not so in all genera of *Ranunculaceae*, as has already been pointed out. In *Ranunculus, Batrachium*, and *Ficaria* the corollar-secretion is of much less significance and that of the thalamus certainly much more important. In *Pulsatilla* the corollar-secretion is still further reduced and in the genera *Paeonia, Caltha, Anemone*, and *Clematis* the corollar-nectaries no longer occur; here the honey-secretion of the thalamus has become of primary importance.

In *Caltha palustris* secretion of nectar can be observed in the flower in three places: first at the periphery of the thalamus, where in the allied *Helleboreae* the stalked corollar-nectaries are placed; secondly at the interstaminal part of the thalamus; thirdly on the wall of each ovary. The ovaries of *Caltha* are glabrous, but on both sides of each ovary there is a spot, covered by hundreds of delicate papillae with very thin walls. Each of the latter secretes a minute droplet of nectar, and the large drop, which is formed by the fusion of the droplets, can easily be detected with a lens between any two adjacent ovaries. The parietal papillae here replace the hairs of other genera.

The extent of the reduction in the peripheral nectar-secretion of other genera is best observed in *Ranunculus* and in *Pulsatilla*.

The flower of *Ranunculus acer* for instance, agrees with that of *Trollius* both as regards the position of the stamens relative to the ovaries and the elongation and inward-movement of the stamens. The nectar-secretion at the base of the petals cannot contribute to the protection of the sexual organs by keeping the flower moist, except possibly on the first day of flowering, when the corolla is still cup-shaped. In no case can this secretion be of importance during subsequent stages, when the corolla is spread out. If there were here no nectar-secretion at the interstaminal portion of the thalamus, the ovaries would be in danger of rapid destruction owing to dessication.

In *Ranunculus auricomus* the peripheral secretion is still much less important. Here often one or two and sometimes all petals are wanting, and with them the nectaries; frequently, moreover, the nectaries are rudimentary.

In the genus *Pulsatilla* the peripheral nectar-secretion is likewise insignificant (its seat is in the metamorphosed anthers of the outer whorl). In *Pulsatilla vulgaris, P. pratensis* and *P. vernalis* it has been observed, that the nectaries frequently do not secrete any nectar; here nectar-containing and nectarless plants are found; *P. alpina* is quite free from nectar, according to SCHULZ. The nectar-secretion from the thalamus is therefore, also in this genus, of primary importance; during the flowering period the numerous ovaries are each, as it were, covered by a mantle saturated with glucose.

In the natural order of *Malvaceae* the true significance of nectar-secretion is not less clear than among *Ranunculaceae.*

I shall not be able to consider this subject in detail in the present communication, but may recall, that BEHRENS showed in 1879, that in *Abutilon, Althaea,* and *Malva* the bottom of the calyx bears a nectary, consisting of a large number of closely crowded multicellular "Sekretions-Papillen", which together form a large secreting surface. Each "Papille" consists of a large number of cells, placed in a row, e. g. in *Abutilon insigne* 12—14. What BEHRENS thus describes probably applies, as far as my own investigation extends, to all *Malvaceae.* I found these nectaries also in the genera *Hibiscus, Kitaibelia, Malope, Anoda* and *Sidalcea.*

Whether in general, however, secretion is a constant phenomenon in these calyx-nectaries, is doubted by various authors. Of many species it is not known whether they ever contain nectar, and of other species the accounts are contradictory; in the case of some, it might be assumed, that the individuals of the same species differ among themselves. Thus, for instance, KIRCHNER could not find any nectaries in *Abutilon Avicennae,* whereas in this country the same plant is so rich in nectar, that the latter can be seen with the naked eye. As regards *Hibiscus,* those species, which are best known in Europe, namely *H. syriacus, H. Trionum,* and *H. esculentus* are regarded as nectarless. The large flowers of *Abutilon* are however very rich in nectar, so much so, that the nectar is removed by honey-birds.

Being peripheral, the secretion of the calyx-nectaries may be compared with that of the corollar-nectaries of *Ranunculaceae.* My investigations have now shown me, that in the order of *Malvaceae* a central secretion of nectar may also be observed, which in most genera gives the impression of being the more important — perhaps in all genera except *Abutilon.*

As is well known, the stamens in *Malvaceae* are united to form a tube. This staminal cylinder, which extends upwards round the ovary, is, at its base, joined to the corolla in such a way that their common tissue encloses the ovary and hides it from view. If the ovary be now liberated from its little "house", its wall, in almost all *Malvaceae,* is found to be thickly covered with nectar-secreting trichomes of the same structure as those, which constitute the calyx-nectary (Sekretionspapillen of BEHRENS) and these trichomes continually pour a layer of glucose on the ovary. In *Hibiscus esculentus* and in *H. Trionum* these ovarial trichomes are even larger than those of the calyx-nectary, and consist of 28 cells. The ovaries are therefore not only enclosed in the staminal tube, but are always confined in a space, kept moist by nectar-secretion.

I hope afterwards to return to a detailed study of this order, which is so extremely interesting as regards nectar-production.

Before closing this communication, I still wish to call attention to two important matters. In the first place to the secretion, which takes place in many flowers, while they are still in bud. We are accustomed to assume, that secretion only begins at or after the opening of the flower, but I have found many exceptions to this rule. The phenomenon may be observed in *Ranunculaceae* especially. The ovaries of *Clematis Viticella,* covered with silken hairs, the ovaries of *Paeonia, Pulsatilla* and of *Aconitum* are bathed in nectar, long before the opening of the bud, and it may probably be assumed with safety, that the secretion of nectar, which already takes place in the bud, serves here to protect the sexual organs, and is therefore comparable to the secretion of water in flowers with a water-calyx. In the flowers of *Aconitum* I found that indeed the central, but not the peripheral, secretion may be observed before the opening; this suggested to me that the latter secretion serves more especially to keep the flower moist during the flowering period. Further investigation will be required to show, whether this difference can also be traced in other plants with a double secretion of nectar.

Before there is any question of the flower's opening, a copious secretion of nectar may also be observed in other plants, such as *Melandrium album* (*Lychnis vespertina*), *Hyoscyamus niger*, *Galanthus nivalis*, many *Papilionaceae* and *Epilobium angustifolium*.

In the second place I think it may be useful to refer briefly to the so-called nectarless plants, because it might be argued that these do not support the truth or general validity of the hypothesis, put forward above.

I have already had an opportunity of pointing out, that some plants, which do not contain nectar, have their ovarian-wall covered with *wax*, and others with *glands secreting mucilage*; to these secretions the same biological significance is attached as that, which I think should be attributed to nectar-secretion. Furthermore, I have already mentioned a number of plants, which are recorded as nectarless, but which, nevertheless, must certainly be reckoned among those containing nectar, namely species of *Anemone*, *Clematis*, *Pulsatilla*, and *Paeonia* in the order of *Ranunculaceae*, also *Helianthemum vulgare* and the various species of *Verbascum* and *Hibiscus*. I will only add, that it can be easily shown by chemical means, that the so-called nectarless *Rosaceae*: *Rosa*, *Poterium*, *Agrimonia*, *Aruncus* and *Spiraea* have been wrongly included in this class. Here indeed the nectar is often difficult to observe, but it is none the less present, as in other *Rosaceae*. If the flowers are extracted with water, so that the nectar, which has been thickened by evaporation, passes into solution, the presence of glucose may readily be demonstrated in all these plants. Finally it may be pointed out in this connexion, that very many plants do not require a special protection by nectar, either because the ovary continues its growth without interruption, (on account of early fertilisation, which often already takes place in the bud) or because it is not exposed to the air during the flowering period.

The latter case occurs especially in the genera *Plantago* and *Luzula*, in *Nymphaea alba* and *Erythraea Centaureum*, in *Iuncus*, in most Grasses and in other anemophilous plants.

Mathematics. — "*On a theorem of* PAINLEVÉ'S." By Prof. W. KAPTEYN.

1. PAINLEVÉ, in his well-known memoirs on differential equations of the first order, investigated the question when the integrals possess a definite number of values or branches if the independent variable turns round the critical parametric (not the fixed) points.

For differential equations of the first degree

$$\frac{dy}{dx}=\frac{P(x,y)}{Q(x,y)} \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (1)$$