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curve of the binary system formed by *D* and *L*, so to speak "thermi analyses of their solutions, which might have been compared with polarimetric ones. It is to be regretted that these investigators have not applied this check as now it cannot, provisionally, be decided whether their isotherms exhibit the true form or not. From my results with the strychnine tartrates, I think I may decide upon the latter view. The truth may, however, be revealed by a determination of the complete isotherms or, perhaps with sufficient accuracy, by melting point determinations of the residues left on evaporation.

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Botany. — "Contribution to the knowledge of water-secretion in plants.
By Dr. W. BURCK.

(Communicated in the meeting of October 30, 1909.)

II. Secretion of water in the flower.

After TREUB¹⁾ showed in 1890 that the flower-buds of *Spathod campanulata* Beauv. are filled with a watery fluid, a similar secretion of water in closed flower-buds has also been observed in a few other tropical plants.

LAGERHEIM²⁾ observed the same phenomenon in a South-American Solanacea, *Jochroma macrocalyx* Benth. GREGOR KRAUS³⁾ soon afterwards described the water-calyces of *Parmentiera cerifera* Seem., and HALLIER⁴⁾ those of *Leea amabilis*. Later a detailed paper was published by KOORDERS⁵⁾ on the flower-buds of the Bignoniaceae: *Parmentiera cerifera* Seem., *Crescentia Cujete* Linn., *Kigelia pinnata* DC., *Heterophragma adenophyllum*, Seem., *Stereospermum hypostictum* Miq.; of the Solanaceae: *Juanulloa parasitica* Ruiz et Pav., *Nicandra physaloides* Gärtn.; of the Verbenaceae: *Clerodendron Minahassae* T. et B. and of a Scrophulariacea *Illysanth* spec. Afterwards there followed important contributions by SHIBATA

¹⁾ TREUB, M. Annales du Jardin botanique de Buitenzorg. Vol. VIII. 1890

²⁾ LAGERHEIM. Zur Biologie der *Jochroma macrocalyx* Benth. Berichte der deutsch. bot. Gesellsch. Bd. 9, Jahrg. 1891.

³⁾ KRAUS, G. Wasserhaltige Kelche bei *Parmentiera cerifera* Seem. Flora B 81, p. 435—437.

⁴⁾ HALLIER, H. Ueber *Leea amabilis* und ihre Wasserkelche. Annales du Jardin botanique de Buitenzorg. Vol. XIV. 1897.

⁵⁾ KOORDERS, S. H. Ueber die Blütenknospen—Hydathoden einiger tropischer Pflanzen. Annales du Jardin botanique de Buitenzorg. Vol. XIV 1897.

⁶⁾ SHIBATA, K. Zur Kenntnis der Kelch- und Knospenhydathoden. Bot. Centralblatt 1900. Bd. LXXXIII.

on the secretion of water in *Tecoma grandiflora* Loisel and *Katalpa Kaempferi* S. et Z. and on the Verbenaceae: *Clerodendron trichotomum* Thunb. and *Cl. squamatum* Vahl and by NILS SVEDLIUS¹⁾ on the water-calyces of tropical Convolvulaceae especially in *Stictocardia tiliæfolia* (Choisy) Hallier and *Operculina Turpethum* (L.) Peter.

Amongst other results these investigations have shown:

1. that glands which secrete the water, often at first produce mucilage, as was also found to be the case with the epidermal glands of the leaves, and that only in a single case i. e. in *Tecoma grandiflora*, the calyx-water reduced FEHLING'S solution.

2. that the secretion of water on the inner surface of the calyx can begin at widely different stages of development of the flower; in many of the plants mentioned it begins very early, when the corolla and the sexual organs are first laid down, and ends towards the flowering period, but in *Sochroma macrocalyx*, *Clerodendron Minahassae* and *Jurulloa parasitica* the secretion of water continues during the time of flowering even up to the formation of the fruit. SVEDLIUS afterwards showed that in the above-mentioned Convolvulaceae the real secretion of water only begins after fertilisation, when the calyx-leaves continue to grow with the fruit.

3. that trichomes, of the same structure as those which secrete water on the inner surface of the calyx, may also be found elsewhere in the flower, especially on the outer surface of the calyx and the inner- and outer surfaces of the corolla.

This last point is especially important in interpreting the phenomenon.

KOORDERS mentions in this connexion, that such trichomes occur in large numbers on the outside of the calyx in *Nicandra physaloides*, *Kigelia pinnata*, *Stereospermum hypostictum* and *Clerodendron Minahassae*. They are laid down at a very early age, earlier than those of the inside, but often they already begin to die off, when those of the inner surface have scarcely begun to secrete water.

SHIBATA made the same observation with regard to the flowers of *Tecoma grandiflora* and SVEDLIUS observed also in *Stictocardia tiliæfolia* that, at a very early stage, the outside of the calyx is already covered with many small peltate glands.

Concerning the glands on the corolla, TRÉUB mentions that in *Spathodea campanulata*, the cushion-shaped trichomes of the inner surface of the calyx are afterwards reduplicated on the inside of the corolla, when the flower-buds have already undergone considerable development; KOORDERS found similar corollar glands in most of the

¹⁾ NILS SVEDLIUS. Ueber das postflorale Wachstum der Kelchblätter einiger Convolvulaceen. Flora, Bd. 96. Jahrg. 1906.

plants examined by him. In *Stereospermum hypostictum* Miq. he found them on the inside of the corolla; in other plants, viz. *Clerodendron Minuhassae* T. et B., *Heterophragma adenophyllum* Seem., *Nicandra physaloides* Gärtn. and *Juanulloa parasitica* Ruiz et Pav. only on the outside and in *Parmentiera cerifera* Seem., *Crescentia Cujete* Linn. and *Kigelia pinnata* DC. both on the inside and on the outside.

In other respects but little is known concerning these epidermal trichomes. Whether the glands which cover the outside of the calyx secrete water, has not been further investigated. As regards the corollar glands, KOORDERS has indeed put forward the suggestion that they may participate in the production of the calyx-water and that in the older flowerbuds the function of secreting water may pass from the glands of the calyx to those of the corolla, but no definite conclusion was reached on this point; in any case the function of glands on the outside of the corolla had to remain hypothetical.

Experience shows that, as was already shown above, there is not only a close agreement in external shape and anatomical structure between epidermal waterglands and mucilage- and resin glands, but also between trichomes¹⁾ which secrete water and those secreting nectar; hence the mere presence of glands on the corolla does not enable us to infer the nature of these glands.

It is nevertheless quite possible that, in some of the plants examined by KOORDERS, the glands on the outside of the corolla secrete water during the bud-stage.

I am the more ready to assume this, because I am acquainted with a plant, in which, as will immediately be seen, the whole of the calyx water is derived from the corollar glands; for the rest this subject requires further investigation, because conditions may differ from plant to plant. As far as my experience extends to corollar glands in plants with and without water-calyces, these glands are not always water-glands and in those cases, where they really are,

¹⁾ For the sake of brevity I only refer to what has been observed by HABERLANDT concerning the similarity of structure and shape of water- and nectar-secreting trichomes in connection with the stipular nectaries of *Vicia sepium* and the trichome-hydathodes on the upper surface of the leaflets; further I refer to the observations of KOORDERS concerning the so-called extranuptial nectaries on the calyx of *Kigelia*, *Crescentia*, *Parmentiera* and *Stereospermum* compared with the water-glands of these plants and to the observations of SCHWENDT on the extrafloral nectaries of *Muehlenbeckia sagittifolia* and various species of *Polygonum*, *Gossypium brasiliense* and other species of *Gossypium*, *Tecoma radicans* and *Ligustrum Regelianum*. (in Beihefte zum bot. Centralblatt Bd. XXII Heft 3. 1907.)

the secretion may also take place later, when the flower has emerged from the bud-stage.

This, for instance, is the case in *Nicandra physaloides*, to which further reference will be made.

In *Malva silvestris* and in *Sidalcea candida*, where numerous glands occur on the margin and on the lower surface of the petals, I have only observed the production of mucilage. In *Hibiscus esculentus* there is secreted, in addition to mucilage, glucose from the apical cell of the corollar glands; as we shall see, this case of glucose secretion does not stand by itself.

I now wish to show, by means of a few examples, that the trichomes on the outside of the calyx are most probably always real glands, and that therefore in plants with water-calyces water, or mucilage, or both, may not only be secreted on the inside of the calyx, but also in other parts of the flower. Now investigation has shown that we must not consider this a peculiarity distinguishing plants with water-calyces from other plants; we must remember that generally, in many plants, the same glands occur in the so-called floral region as on the vegetative parts and that secretory trichomes are sometimes found on the axis of the inflorescence, on the bracts or on the peduncle, on the outer or inner surface of the calyx or corolla and not uncommonly on the sexual organs themselves.

I already pointed out above that on the young flowerbuds of *Fuchsia* exactly the same thin-walled, more or less club-shaped trichomes occur as may be found on the surface of the youngest leaves, and that secretion of watery mucilage also takes place on the surface of the flowers, when a cut plant is placed in a space saturated with aqueous vapour. What has here been said of *Fuchsia*, applies also to other plants; sometimes the secretion of water, and sometimes that of mucilage predominates, although the water-secretion generally occurs in glands which originally produced mucilage.

For the following examples I have selected by preference those which refer to plants with so-called water-calyces; as will be seen, they are not limited to the tropics. I first however, give an example of a plant, in which nectar-secretion, mucilage-secretion and water-secretion can all three be observed, and in which (as I have not often found to be the case) mucilage and water are secreted by different glands.

Finally some observations on the secretion of water by stamens will be added.

Abutilon Darwinii Hook f.

The Malvaceae do not belong to the plants, which have water-calices, although in many respects they resemble them.

Instead of water, honey is here secreted on the inner surface of the calyx. This secretion is especially copious in the species of *Abutilon*. If an adult flowerbud be enclosed overnight in a glass-box, a fairly large quantity of nectar will be found on the broad flat bottom of the calyx, when the flower has opened next morning. In the hanging flower the nectar runs down along the inner surface of the calyx. Without having previously satisfied ourselves, that we are here dealing with glucose, we might suppose that *Abutilon* belonged to the plants with water-calices.

In 1879 BEHRENS¹⁾ gave a detailed description of this nectary at the bottom of the calyx in *Malvaceae*.

It consists of a tender-walled tissue of small, irregular cells, of which those which constitute the epidermis have grown out to a multicellular thread-like trichome to which BEHRENS gave the inappropriate name of "Sekretions-Papille". As the apical cells of these papillae secrete, they together constitute an extensive secretion area. Now BEHRENS observed that the outflow of nectar is preceded by production of mucilage in the apical cell, taking place with formation of collagen. It is remarkable that trichomes of exactly the same shape as BEHRENS' "Sekretions-Papillen", which compose the nectary, are found in different places, both in the flower and outside.

NESTLER, who in his paper on the water-secretion of the leaves of *Malvaceae*²⁾, mentioned the various trichomes which may be found in these plants, distinguishes them as "lang-gestielte, mehrzellige Drüsenhaare", but only found them in *Abutilon* in comparatively small numbers, probably because he did not examine the very youngest parts for the presence of these glands.

On the outside of the young calyx, which in addition bears a thick covering of long, pointed, stellate hairs (Buschelhaare, Sternhaare) they are found in relatively small numbers, but the outside of the corolla, the very young peduncle and petiole, the young stipules and the very youngest leaves are thickly covered by them.

Besides these long pointed hairs and "Sekretions-Papillen" the young calyx has an abundant covering of much smaller glands of elliptical shape, which consist of one or two stalk-cells and 4 secre-

¹⁾ BEHRENS, W. J. Die Nectarien der Blüten. Regensburg. 1879.

²⁾ NESTLER, A. Die Ausscheidung von Wassertropfen an den Blättern der Malvaceen und anderer Pflanzen. Sitzungsber. der Kais. Akad. der Wissenschaften Band CVI, Heft 1, S. 387.

tory gland-cells. These are the "kurze, mehrzellige blasig-kopfig gestaltete Haare" of NESTLER's paper.

If now, in order to convince ourselves of the secretory activity of these various glands we place a cut branch, bearing young flowers as well as young leaves, under a glass bell-jar kept moist, we can observe in a few hours that practically every "Sekretions Papille" of the peduncles, petioles, stipules and youngest leaves bears at its apical cell a large drop of mucilage, clear as a crystal, while the leaves are further covered with a watery layer of mucilage. The older full-grown leaves are almost dry on their upper surfaces, while their lower surfaces are covered with large drops, as already described by NESTLER.

From the young flowers under the bell-jar heavy drops soon hang down, and are replaced when they are removed by filter-paper.

The liquid does not contain glucose, nor is it mucilaginous. It is water, which is secreted by the smaller glands of elliptical shape, which behave from the beginning like true water-glands. Even there, where these glands occur on the very youngest leaves and flower-buds, they never form subcuticular mucilage or resinous products. The outer wall of the cells is always very thin; the cuticle is never seen to be raised by a substance formed inside the wall.

Three kinds of glands can therefore be distinguished in *Abutilon Darwinii*:

1. multicellular, thread-like trichomes, the "Sekretions-Papillen" of BEHRENS, which form the nectary at the bottom of the calyx, and which at the beginning of flowering, secrete glucose with mucilage from the apical cell.

2. glands of exactly the same structure, which secrete mucilage and also a little water; these are placed on the outside of the calyx and of the corolla, on the peduncle and petiole, on the stipules and on the youngest leaves.

3. glands on the outside of the calyx and on the under surface of the leaves, which only secrete water.

In other *Malvaceae* the same kinds of glands are generally found, but with a different local distribution.

In *Mulva silvestris* the waterglands predominate; the leaves of the epicalyx, the outside of the calyx proper and the peduncles are thickly covered with them.

In the moist space under the bell-jar the young flowerbuds next morning have their epicalyx and calyx covered with water. The secreted water gradually increases to such an extent, that it literally drips down from the flowers.

Calystegia sepium R.Br. (*Convolvulus sepium* L.)

NILS SVEDELIUS made important observations on the secretion of water on the inner surface of the sepals of tropical *Convolvulaceae*, particularly *Stictocardia tiliaefolia* (CHOISY) HALLENB. and *Operculina Turpethum* (L.) PETER. Similarly the inner surface of the sepals of our indigenous *Calystegia sepium* is always moist and sticky, both in the bud and during the flowering stage. It may readily be observed that the slimy liquid is secreted by cushion-shaped or peltate glands, which are distributed over the inside of the calyx in relatively large numbers. These glands are here only partially arranged in groups of 1—5; most of them are distributed more or less uniformly over the inner surface. They do not occur on the outer surface of the sepal, but they are found in fairly large numbers on the outside of the bracts, and to a less extent on the inside of the bracts, on the petioles and on the leaves.

Under ordinary conditions there is rarely found so much liquid in the flower-buds, that it can be pressed out in drops between the fingers; nevertheless I have been able to observe this a few times. I do not know whether mucilage or water is also secreted after fertilisation, during the period of the ripening of the fruit, as in *Stictocardia tiliaefolia* and *Operculina Turpethum*. *Calystegia sepium* gives the impression of an impure, hybrid plant, its power of sexual reproduction is evidently much weakened and fruit formation by self-fertilisation rarely takes place.

If a branch of *Calystegia sepium* is placed with the cut surface under water in a moist bell-jar the glands on the surface of the bracts, on the petiole and on the leaves soon begin to secrete water and after a few hours the upper and lower surfaces of the leaves are covered with numerous droplets of water, which soon increase in size. By the coalescing of these drops both sides of the young leaves are soon covered with a layer of water and in the terminal bud in which the leaves cover one another wholly or in part, they are as it were in a water-bath, together with the enclosed axillary flower-buds, which themselves also secrete water on the inside and outside of the leaves.

The glands which secrete the water, secrete mucilage in the bud, when they are still very young; in this respect, therefore, they agree with the glands of the inner surface of the calyx. They are the "Trichomzotten" of HANSTEIN, which afterwards become water-glands.

Datura Metel L., *D. Stramonium* L.

The water-calycies of some other Solanaceae have been described by LAGERHEIM and by KOORDERS viz. *Jochroma macrocalyx* Benth., *Nicandra physaloides* Gärtn, and *Juanulloa parasitica* Ruiz et Pav.; the very large flower-buds of *Solanandra grandiflora* are also always filled with a considerable depth of water. Similarly it may be said of the genus *Datura* that the corolla, stamens and ovary are developed in a water-containing calyx. Although the secretion of water in the species of this genus is not so abundant as in *Solanandra grandiflora* or even in *Nicandra physaloides*, still a not inconsiderable quantity of water may always be found in the buds, and also later, during the flowering-period. But, whereas in other Solanaceae the water is secreted on the inner surface of the calyx, we find in *Datura* the peculiar modification, that the glands cover the outside of the corolla, whereas the inner surface of the calyx, while having many stomata, bears neither glands nor other trichomes. Nor is the glandular outer surface of the corolla free from stomata. In external shape and in internal structure these glands agree fairly well with those which are found in other Solanaceae; the secreting part in the glands of *Datura* also consists of three layers, but generally the middle cell is divided vertically in two, so that the glands are spherical rather than elliptical. In *Datura Metel* these waterglands are hidden between numerous long pointed hairs consisting of three or four cells.

In other plants with water-calycies, the calyx shows a much more advanced growth and earlier development than the other parts of the flower, so that when the calyx already forms a fairly considerable space filled with water, the other floral organs only just begin to appear on the thalamus. In *Datura*, however, this is not the case.

In very young buds of 3 mm. the corolla has already a length of $1\frac{1}{2}$ mm. and at this stage the water-glands are first formed.

When the corolla has reached a length of 5 mm. it is covered from top to bottom, and especially on the teeth of the limb, with glands of various sizes in various stages of development.

The outside of the calyx of *Datura* bears glands of approximately the same structure as those on the outside of the corolla and the same applies to the peduncle.

Further the leaves are covered on both sides, from their earliest youth, with glands which only differ from the glands of the corolla in a subsidiary character i. e. the shape of the secreting part. In somewhat older leaves, which are already more or less unfolded, they are especially numerous and closely packed on both surfaces

of the basal half of the leaf. For the rest the outside of the calyx, as also the leaf and the peduncle are covered with long hairs, which, from a broad base, run out into a point, - are generally composed of 4 cells and have a highly refractive content; these hairs are especially numerous on the upper surface and are more or less limited on the under surface to the course of the veins.

Now if a cut young plant is placed for a few hours in a moist space, numerous droplets are secreted on the leaf especially on the basal portion; by the running together of these drops the leaves are soon covered with a layer of water. Such waterdrops appear at the same time on the outside of the young flowerbuds. The secretion of water is only absent from the very youngest leaves of the bud, but instead a mucilage-secretion takes place from the walls of the glands.

The waterglands of *Datura* are therefore originally mucilage-glands (Trichomzotten) which afterwards secrete water.

The long, erect, conical trichomes do not take part in the secretion of water. Not infrequently, however, a clear drop of mucilage is found on some of these hairs, on the apical cell or on one of the other cells.

Nicandra physaloides Gärtn.

As was already shown by KOORDERS the water-secretion of *Nicandra physaloides* agrees with that of *Spathodea campanulata* and of other plants in as much as the water-secreting trichomes are here also found on the inner surface of the calyx, and the secretion already begins when the other floral organs have scarcely been laid down. The plants grown here do not secrete any less than at Buitenzorg; the young buds are generally completely filled with water.

KOORDERS has already mentioned, that club-like trichomes, similar to those secreting the water on the inner surface of the calyx, are also found in almost as great numbers on the outside of the calyx and of the corolla.

I now add, that the young leaves also, from the earliest bud-stages onwards, are covered on either side with these trichomes, and that, as in *Datura*, they are afterwards found especially in large numbers on the basal half of the leaf.

In *Nicandra* also they are laid down very early; the very young leaflets of the bud, of no greater length than 1 mm., are already thickly covered with them. Likewise they are found to be originally mucilage-glands.

Nicandra further agrees with *Datura* in this respect, that the leaves — but here only on their upper surface — bear large conical

hairs of 3-4-cells, with highly refractive content; the distribution of these hairs is not determined by the veins. They no longer occur on the adult leaves.

In a moist space *Nicandra physaloides* behaves exactly like *Datura*.

After a few hours the young flowers and leaves — except the very youngest leaves of the bud — are covered with a layer of water, while the conical hairs show themselves to be mucilage-glands. The mucilage-secretion is slight, however; small droplets only occur, on a few hairs. This is not only observed in a moist space, but also on young plants, cut off and placed in a glass of water, but not covered by a bell-jar. Finally we may also observe in the moist space that the glands on the lower surface of the corolla secrete water during the flowering period, as was mentioned above.

Dahlia spec. et var. div.

As long as the capitula of *Dahlia* are still in the bud, the youngest florets are covered by the inner bracts of the involucre. Generally we may easily observe at this stage, that the hanging capitula are moist below, and that drops of liquid, between the involucre bracts and the florets, are discernible through the translucent bracts and may be moved to and fro by the slight pressure of a lead-pencil. Not infrequently a drop of liquid may also be seen hanging down from the capitulum, especially when the sky is overcast.

The droplets consist of water.

This secretion of water, although not inconsiderable, is much greater after fertilisation. The capitulum, which had opened out during the flowering period, once more closes up, while the involucre bracts grow considerably. The capitulum after flowering assumes the shape of a hanging top.

At the apex of the top a drop of water can nearly always be observed during the whole period of the ripening of the fruits; after removal this drop is renewed, in proof that water is continually excreted somewhere in the capitulum.

Further investigation shows that all ovaries and all corollae in the capitulum are covered on the outside with long trichomes, consisting of a row of about 15 cells with dense content, and reminding one of the nectar-secreting glands of Malvaceae. These trichomes are the glands which secrete the water.

In *Dahlia* every floret is placed in the axil of a bract. This bract completely enclosing the flowerbud, does not bear glands or other trichomes and does not take part in the secretion of water.

The ray-florets, which are folded longitudinally in the bud in peculiar manner, bear most water-glands on their veins, but for the rest the latter are distributed over the whole outer surface. The water-glands appear in much smaller numbers on the disc-florets and are limited on the corolla-tube to the junction of the narrow and wide portions. It cannot be determined at which stage of the bud the water-secretion begins. In very young capitula the drops escape on observation, or may not yet be present. They cannot be observed until the outer whorl of the involucre curves outwards. During flowering the secretion of water cannot, of course, be observed on account of evaporation. It is not until after fertilisation, when the capitulum again contracts, and the involucre bracts grow out and again approach one another, that the secretion once more becomes evident.

Coreopsis tinctoria Nutt., *Coreopsis lanceolata* L. *Cosmos hybridus* Hort. ¹⁾

In the genus *Coreopsis* and in *Cosmos hybridus* Hort., as in *Dahlia* the young capitula are enclosed and covered by the inner whorl of involucre bracts which are here generally light-brown. If the capitulum be opened at this stage, the florets in *Coreopsis* and in *Cosmos hybridus* are found to be in a bath of fluid as in *Dahlia*.

In *Dahlia* the involucre bracts are superposed in two rows without coalescing, but in *Coreopsis* and this species of *Cosmos* arranged in a single row, they close up more tightly with the edges. This closing makes the extrusion of a drop here much rarer than in *Dahlia*.

After fertilisation the capitulum does not close again in these plants and a secretion of fluid during the ripening of the fruit does not occur.

Further investigation shows that here also the corolla is covered with the same long trichomes composed of 15 cells, as in *Dahlia* but in these plants the young ovaries are free from trichomes. It is very remarkable, however, that in *Coreopsis* and in *Cosmos hybridus* these trichomes do not secrete water, but a fluid which when heated with FEULING'S solution, gives a very marked reaction for glucose. In this respect therefore the secretion agrees with that found by SHIBATA in the calyx of *Tecoma grandiflora*.

¹⁾ I doubt somewhat whether this plant has been correctly included in the genus *Cosmos*. It appears to me rather to be a *Coreopsis*.

I shall be able to show afterwards, that it is by no means a rare case that glands, which might superficially be regarded as water-glands, secrete nectar. The agreement between water- and sugar-secreting glands is by no means limited to their external shape and anatomical structure (see foot-note, p. 402) but extends further.

It may be remembered that HABERLANDT¹⁾ expressed the view that there might be a phylogenetic relationship between nectar-glands and water-glands. HABERLANDT supposes that water-glands are very much older and that in many cases nectaries may safely be assumed to have been formed from them. He starts from the supposition that the difference between water- and nectar-secreting trichomes does not so much lie in the difference in composition of the product (for the cell-content of water-secreting trichomes also occasionally gives a reaction for glucose) as in the dependence on the hydrostatic pressure of the water-conduct system in the case of the secretion from water-glands, which dependence would not exist in the case of nectaries.

The gradual evolution of nectaries from hydathodes was regarded as giving to the plant the advantage that the secretion became independent of the root-pressure. We have already seen in the first part of this communication that the basis of this theory is incorrect and that it is difficult to defend any longer the hypothesis of a phylogenetic connexion between water-glands and nectaries.

In returning from this digression to observations I must point out that the left and right side of the tongue-shaped ray-florets are folded over in the bud towards their middle and that they are covered with secretory trichomes especially on the veins.

In the tubular disc-florets they are found especially on the limb (*Coreopsis tinctoria*) or only on the lowest portion of the corollar tube (*Coreopsis luciniata* and *Cosmos hybridus*).

Finally I wish to observe that in *Dahlia* and in *Cosmos* the corolla of the tongue-shaped ray-florets is not only covered with these long, glucose-secreting glands, but in addition with short stalked club-like glandular hairs. I did not find these in the two species of *Coreopsis*. They are not coloured by dilute stains, whereas the other glands take up stains. In shape they agree with those, which according to SOLEREDER are common among Compositae. The character of the walls suggests the secretion of mucilage; probably they only function later during the flowering-period.

From analogy with what may be learnt from *Calystegia*, *Datura* and *Nicandra* it might be expected that the trichomes which secrete

¹⁾ HABERLANDT, l. c. p. 58.

water or glucose on the outside of the florets in the capitula of those Compositae, might also be found in other places.

This expectation has been realized. In *Cosmos hybridus* and also in *Dahlia*¹⁾ the leaves are already covered in very early youth by two kinds of trichomes, firstly with such as correspond structurally to the water- and glucose-secreting glands of the florets and secondly with longer (*Dahlia*) or shorter hairs (*Cosmos*), which from a broad base are continued to a conical point, and have a thick wall with a striped cuticle. The former consist of a row of 15—20 thin-walled cells, succeeding one another somewhat like a chain of pearls, which in the middle of the trichome are as long as broad but which gradually become longer towards the apex. These cells, especially those of the upper half of the trichome, are filled with dense granular protoplasm. They are readily stained by aniline-dyes (methylene blue, rosaniline violet). In *Dahlia* they are chiefly found above the median and lateral veins, pressed against the surface on both sides of the leaf. In *Cosmos hybridus*, where the leaf-segments are very narrow, they are also found in largest numbers on the upper surface of the leaves above the vein, but here and there also on the lower surface. The other hairs have a different shape in *Cosmos* and in *Dahlia*, but it is not always constant in different parts of the same plant.

In *Cosmos* those occurring on the lower surface and on the margin of the leaf are composed of 6 cells; they arise from a broad and occasionally multicellular base, are conically pointed and curved like a sickle; the content is more or less highly refractive and the cuticle, especially that of the apical cell, is striped.

In *Dahlia* sickle-shaped trichomes occur on the margin of the leaf-segments, but those on the upper and lower surface of the leaf are much longer, are not curved and are not restricted in their distribution to the veins; the cuticle of all cells is striped. These hairs are much more numerous on the lower surface of the leaf than on the upper.

It is easy to verify that in the very youngest leaves the glandular hairs secrete mucilage (resin or balsam). In a somewhat more advanced state of development the glands above the median and lateral veins are partly, as it were, surrounded by mucilage; the cells of the upper half of the trichome have not infrequently perished during the mucilage secretion.

With cut plants placed in a glass of water under a bell-jar we observe exactly the same phenomenon as in *Calystegia* and the Solanaceae.

¹⁾ In *Coreopsis* I did not investigate this point.

The folded leaf-segments of both species are soon covered on their inner and outer surfaces with a layer of mucilagenous water, but the secretion is not so abundant as in the other plants. In this case I did not succeed in producing the formation of drops.

Hence the glandular hairs, which in the capitula of *Dahlia* secrete water and those of *Cosmos* glucose, secrete a watery mucilage when they occur on the leaves. In this mucilage I could not find glucose, either in *Dahlia* or in *Cosmos*.

Melandrium album Garcke, (*Lychnis vespertina* Sibth.).

The female form of *Melandrium album* may also be reckoned among plants with watercalyces, but here there is the peculiarity that the secreted water takes the place which elsewhere is occupied by the nectar.

If a completely closed, immature flowerbud of the female plant be opened, the claws of the petals, and the walls of the ovary and calyx are found to be covered with numerous drops.

On superficial inspection the flower might be considered very rich in nectar, but if these droplets are sucked up by a strip of filter paper in order to test the paper with FEHLING'S solution for nectar on the slide, not a trace of glucose is found.

In the male flower the various enclosed parts are also covered with numerous drops of liquid, long before the bud is ready to open, but here the droplets consist of nectar, which is secreted from the fleshy ring at the base of the stamens.

In other respects the nectary of the female flower appears fully developed; it resembles that of *Melandrium rubrum*, both in shape and in size, but it does not produce nectar, and the tissue is free from glucose.

A comparison of the two sexual forms of *Melandrium album* further shows that the female calyx, which is a little larger than the male and is somewhat constricted towards the top, is thickly covered on its inner surface with two kinds of hairs i. e. with elongated hairs of 3—4 cells, which terminate in a rounded gland-cell and with very similar hairs, which do not bear a gland-cell and terminate in a pointed apical cell.

These two kinds of hairs are not found on the inner surface of the calyx-tube; the margin and the inside of the limb alone are covered with glandular hairs.

Similar hairs, but generally having a somewhat longer stalk, cover also the outside of the calyx in both sexual forms.

After fertilisation, when the corolla has fallen off, the young fruit

is enclosed by the calyx which keeps pace with its growth and one can then observe that during the ripening of the fruit the space between the calyx-wall and the ovary is filled with a layer of very sticky mucilage, derived from the glandular hairs, which during this stage are fully active.

As regards the water, which is found in the female bud and in the open flower, I feel justified in assuming that this is secreted by the other, pointed hairs of the inner surface of the calyx; I feel the more ready to assume this, because in *Melandrium rubrum* there are only found on the inside of the calyx the mucilage-secreting hairs and not the pointed ones. Now in the female flowers of the latter species the inside of the calyx is also covered at all stages of development with a large number of glandular hairs, which evidently already secrete mucilage in the young buds; the fruits are also surrounded by a layer of mucilage, but no water is secreted in the flowers during the flowering period, presumably owing to the above mentioned absence of the pointed hairs¹⁾.

I now wish to show by means of two examples, that the secretion of water in the flower is not dependent on the outer or inner surface of the calyx, nor on the outside of the corolla (*Datura*), but that it can also occur on the stamens.²⁾

1) It is possible that water is also secreted in the female flower of *Silene Otites* Sm. With regard to this plant SCHULTZ mentions, that in Germany the nectar-secretion of the female flower is almost always absent, and that of the male flower very often, but that in the Tyrol the male (and the hermaphrodite) flowers, like the female ones, secrete honey at the outside of the ring which unites the bases of the stamens.

According to SCHULTZ insects can easily reach the honey of the male flower on account of its small depth and fairly wide mouth, but in the female flower this is probably always quite impossible, because the calyx and the petals are closely applied to the ovary.

I shook 50 male and as many female flowers of this plant with distilled water and tested the water for glucose. I found that the male flowers are abundantly provided with nectar, but that the water from the female flowers had not taken up a trace of glucose.

I did not succeed in observing drops of fluid in the female flower and cannot say whether water is secreted here as in *Melandrium album*. It seems to me most probable that we are here dealing with a flower which is wholly devoid of nectar and of water; this is the more likely because the trichomes on the inside of the calyx, which might possibly secrete water, do not occur in *Silene Otites*.

2) With regard to the occurrence of "Trichomzotten" on the surface of the ovary e.g. in species of *Lysimachia*, in *Ononis spinosa* and in *Verbascum Blattaria* I must refer for the sake of brevity to my previous communication. Proceedings of the meeting of Nov. 28, 1908.

Secretion of water by the stamens.

Verbascum. If an almost fully grown bud of *Verbascum* be carefully opened, a clear drop of fluid will certainly be found in it.

KERNER¹⁾, who observed this phenomenon in *Verbascum phoeniceum* and *V. Blattaria*, considered it a very peculiar method of nectar-secretion, in which extremely minute droplets of honey were supposed to exude from the stomata.

If the fluid is sucked up with filterpaper and tested with FEHLING'S solution it is found to contain no trace of glucose.

I have observed this secretion in the closed flowerbud of all species of *Verbascum* which I have been able to examine namely: *V. phlo-moides* L., *V. Thapsus* L., *V. thapsiforme* Schr., *V. Phoeniceum* L., *V. Blattaria* K. and a hybrid of *V. Phoeniceum*.

The water may be most readily observed in buds which are about to unfold; in young buds it escapes observation or it is not yet present.

The source of this water cannot be indicated with absolute certainty. KERNER'S view, that it is secreted by the stomata of the corolla, is erroneous, because stomata do not occur in the corollar epidermis of *Verbascum*. Neither are glands or other trichomes on the corolla.

I think, however, that I am justified in assuming that the water is secreted by the long hairs which cover the stamens. These hairs are generally coloured and have a peculiar structure; they consist of a single club-shaped cell with a long stalk and a finely marked cuticle. DELPINO regarded these hairs as "Handhaben zum Anklammern der blütenbesuchenden Insekten", whereas KNÜTH considered, that they serve in addition to enhance the "Augenfälligkeit" of the *Verbascum* inflorescence, at least in those cases where the colour of the hairs differs from that of the corolla.

I consider them to be water-glands.

With FEHLING'S solution they only give a very faint reaction for glucose and often the presence of glucose cannot be demonstrated at all. Occasionally a vertical, or more rarely horizontal slit is found in the club-shaped end; this is not a constant character, however.

I do not mean by this, that KERNER is wrong in saying that honey may be found in the flower of *Verbascum*. This genus is indeed considered to be nectarless, but with the exception of *V. Blattaria* an abundant secretion of honey is found on the wall of the ovary, which is covered with a dense felt of branched hairs with very thick walls. The honey which is excreted by the ovary-wall, is

¹⁾ KERNER VON MARILAUN. Pflanzenleben. Zweiter Band. Neuer Abdruck. S. 159.

sucked up by this covering and retained through capillarity, so that during the flowering the ovary of *Verbascum* may be said to be covered by a mantle saturated with glucose.

Tradescantia virginica L.

Exactly the same phenomenon of the constant occurrence of a clear drop of fluid in the flower-bud may be observed in *Tradescantia virginica*. Here the phenomenon is even more striking, because there can be no question of the secretion of honey in the *Tradescantia*-flower. Nectaries are not found in the whole order of *Commelinacea*.

On sucking up the fluid with a strip of filter-paper and warming the paper on the slide with a drop of FRÄGLING's solution, we find in this case also, that the fluid does not contain a trace of glucose.

Just as I pointed out the probability that the drop of water in *Verbascum* is secreted by the hairs with which the stamens are covered, so I have reason to believe in the case of *Tradescantia*, that the staminal hairs, so well-known in physiology, secrete fluid in their capacity of water-glands.

Before concluding this communication I consider it necessary to explain briefly why the expression "Hydathode" has only been used exceptionally. It may be remembered that HABERLANDT brings together under this expression all "Apparate" and places, where secretion of water in the liquid state takes place in the plant, no matter in which way the water is set free, whether by active or by passive cells.

HABERLANDT supposed that the whole water-secretion of the plant, both at the apex and the teeth of the leaf and superficially by external or internal glands, is especially intended to prevent an injection of the intercellular spaces, whenever the water which the roots take up from the soil has caused an increase of hydrostatic pressure in the vascular bundles; HABERLANDT evidently meant to indicate by the expression "hydathodes or water-ways" the ways by which the excess of water is again got rid of.

It has been pointed out above that this conception is incorrect and that the activity of the internal and external glands is not directly related to the bleeding-pressure. The expression could therefore only be retained for places of least resistance, which allow the water which the roots have pumped up, to pass out when transpiration is impeded; for all other places we should, for the sake of clearness, speak of glands.

For the places of least resistance MOLL¹⁾ has, however, already

¹⁾ MOLL, J. W., Untersuchungen über Tropfenausscheidung und Injection bei Blättern Verslagen en Mededeelingen der Koninkl. Akad. v. Wetensch. te Amsterdam Dl. XV, 1880.

introduced into the literature the expression *Emissarium* or *outlet of water*, which more clearly indicates the notion than the word "*Hydathode* or *water way*".

It is thus evident from the second part of this communication on the secretion of water in the plant, that a secretion of liquid not only takes place in the leaves, but often also in the floral region and on various parts of the flower.

These observations place in a different light the well-known phenomenon of water-secretion in the flower-bud of plants with so-called water-calyces

Formerly we considered, that the secretion of water in the flower-bud was to be regarded as a useful arrangement, arisen in the struggle for life by natural selection, in order to protect the enclosed parts of the flower against desiccation.

We now see that it is related to the phenomenon of the secretion of liquid on the surface of the plant and that the presence of water in the calyx is to be explained thus, that the water secreted by the glands of calyx and corolla is less exposed to evaporation in the closed calyx and so can collect there.

In other words, the secretion of water in the flower-bud did not arise because it is useful to the plant, but it may nevertheless be of advantage to the plant in these cases where the enclosed parts of the flower or the young fruits are exposed to the danger of desiccation.

Chemistry. — "*Contribution to the knowledge of catalytic phenomena*". By Prof. J. BOESEKEN. (Communicated by Prof. A. F. HOLLEMAN).

(Communicated in the meeting of October 30, 1909).

I.

Through the researches of Perrier (Thesis 1896 and Comt. rend. **116**, p. 1300) and of myself (Rec. 1900, p. 19) it has been shown that in the reaction of FRIEDEL and CRAFTS it is not the aromatic hydrocarbon but the chloride or the anhydride which is attacked first by the aluminium chloride, as in many cases additive products could be isolated. These are then converted by the benzene derivative. Afterwards I have pointed out (Proc. 1907, p. 613), that the formation of these intermediate products cannot, as such, serve to explain the