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The Cobalt Sodium Hexanitrite Reaction for
Potassium in Plant Cells

by

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Organographie der Pflanzen insbesondere der Archegoniaten und Samenpflanzen. Von Dr. K. Goebel, Prof. an der Universität München. Zweite, umgearbeitete Auflage. Drei Teile.

- I. Teil: **Allgemeine Organographie.** z. Zt. vergriffen
- II. Teil: **Spezielle Organographie. Archegoniaten.** Zwei Hefte.
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- III. Teil: **Spezielle Organographie der Samenpflanzen.** Drei Hefte. Mit 431 Abbild. im Text. IX, S. 1209—1789 1923 Rmk 17.—, geb. 19.—
1. Heft: **Vegetationsorgane.** Mit 220 Abbild. im Text. 284 S. gr. 8° (S. 1209—1492 des ganzen Werkes) 1922 Rmk 9.—
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3. Heft: **Die Sporangien der Angiospermen.** Mit 71 Abbild. im Text. 95 S. gr. 8° (S. 1693—1789 [Schluß] des ganzen Werkes) 1923 Rmk 3.—
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Naturwissenschaftliche Wochenschrift, 1916, Nr. 24: Von Goebels Buch gilt im eigentlichen Sinne, daß es in keiner botanischen Bibliothek fehlen sollte, wie es ja tatsächlich kaum in einer fehlt. Es gibt trotz des bewußten Verzichtes auf jede Zusammentragung, der alles und jedes zu sammeln das höchste Ziel ist, wegen des Reichtums der eigenen Beobachtungen und Erfahrungen die wichtigste Quelle, die uns in der pflanzlichen Morphologie fließt. Man findet nicht viele Bücher von dem Umfange des Goebelschen, die so eng mit dem Autor verwachsen sind, ein so starkes persönliches Gepräge tragen. Mit der Sicherheit eines Herrschers, der seinen Titel aus einer umfassenden, ins einzelne wie ins allgemeine dringenden Forschertätigkeit herleitet, wird das Gesamtgebiet der Pflanzengestalten geschildert, die Organographie, wie Goebel diesen Zweig der Pflanzenkunde nennt.

H. Mische.

Die Entfaltungsbewegung der Pflanzen und deren teleologische Deutung.

Ergänzungsband zur „Organographie der Pflanzen“. Von Dr. K. Goebel, Prof. an der Universität München. Zweite, neubearbeitete Auflage. Mit 278 Abb. im Text. X, 565 S. gr. 8° 1924 Rmk 20.—, geb. 22.—

Inhalt: 1. Einleitung. 2. Die Verschiedenheit in der Blütengestaltung der Papilionazeen und ihre biologische Bedeutung. 3. Art der Entfaltung, Gelenke und Schwellkörper. 4. Entfaltungsbewegungen der Sprosse (Sproßnutationen). 5. Entfaltungsbewegungen der Blätter. 6. Entfaltungsdrehungen (Morphologie des Unsymmetrischen). 7. Resupination der Blüten. 8. Die Reihenfolge der Entfaltung. 9. Entfaltungs- und Reizbewegungen in Blüten. 10. Die Sensitiven. 11. Die Schlafbewegungen. — Namen- und Sachregister.

Zeitschrift für Botanik, 1921, Heft 5: Verf. führt uns in diesem Buche ein gewaltiges Material vor. Überall hat er, überaus fein beobachtend, neue Tatsachen gefunden und stellt nun auf Grund einer fast verblüffenden Kenntniss namentlich der älteren Literatur dar, was er von gewissen ökologischen Fragen hält. . . Oltmanns.

Die Naturwissenschaften, 1920, Heft 32: . . . Noch mehr als die Fülle seines Inhalts zeichnet das Buch die Vielseitigkeit der Gesichtspunkte aus, welche der Verfasser seinem Thema abgewinnt: vergleichende Morphologie, Entwicklungsgeschichte, Reizphysiologie und Anatomie spielen in dem Buche ihre gleich wichtige Rolle; hierzu kommen das Interesse des Verfassers an der Geschichte seiner Wissenschaft, das er mit großem Geschick zu Worte kommen läßt, und vor allem die Ausführlichkeit, mit der er auf die schon im Titel des Buchs genannten „teleologischen Deutungen“ seiner Phänomene eingeht. Die Erklärungen, welche frühere Autoren den Entfaltungsbewegungen gegeben haben, werden eingehend und kritisch erwogen, neue Deutungen vorgeschlagen, die Unzulässigkeit irgendwelcher Zweckmäßigkeitsdeutung für viele Fälle konstatiert. Besonders wertvoll und beherzigenswert sind die allgemeinen Betrachtungen über teleologische Deutungen, mit welchen Verfasser sein Buch einleitet.

E. Küster, Bonn.

The Cobalt Sodium Hexanitrite Reaction for Potassium in Plant Cells¹).

By Francis E. Lloyd,
Macdonald Professor of Botany, McGill University.

With Plate V.

In 1905 Professor A. B. Macallum announced his adaptation of cobalt sodium hexanitrite for microchemical purposes, and in a considerable paper gave details of his observations on various plant and animal cells. The contention made by this author, and which here concerns us, was that the reagent in question permits the observer to determine the localization of potassium in the living cell. The method has been fully described and discussed by Professor Macallum in his various publications on the subject, and he has in addition published more recently (1922) a critique of the method, wherein, however, the earlier claims appear to have received some modification. It is unnecessary for the purposes of this paper to say more than that the conditions laid down by Professor Macallum for the proper use of the reagent have been scrupulously adhered to. Prolonged washing, however, has been found necessary for the purpose of eliminating so far as possible all traces of the reagent, the double cobalt salt. The writer has had the advantage of having for his use a supply of the reagent prepared by Professor Macallum with whom, also, he has taken counsel so that no oversight on his part might lead to error. He is indebted to Professor Macallum for courtesies extended.

Since Professor Macallum made his announcement in 1905 there has been only one critical study of the method from the botanical point of view, viz., by Th. Weevers in 1911. O. Tunmann also appears to have tested the reagent with much the same results as those obtained by Weevers. At all events Tunmann's contribution (1913) to the matter is slight and demands no more than a mere reference. He rightly regarded the reagent in question as the most sensitive available for the determination of the presence of potassium.

1) Presented originally before Sect. V. Royal Society of Canada, May 1923, and subsequently elaborated.

Weevers used cobalt sodium nitrate in the place of the nitrite. Whether this substitution would result in failure to duplicate the earlier observations of Professor Macallum I do not undertake to say. It does not seem likely, however, when my own observations are compared with those of Weevers', that such was the case. Accepting therefore Weevers' observations at their full value, he found evidence of the presence of potassium in almost everything he looked at; the only exceptions were Cyanophyceae, chloroplasts, aleurone bodies, and the nucleus. In this connection attention is drawn particularly to certain features of Weever's observations.

He found that root hairs exhibited an accumulation of the potassium triple salts inside their tips. He explains this localization on the ground that the reagent penetrating at this point would naturally lead to an accumulation of the precipitate. He properly argues that this vitiates any conclusion that might be drawn as to localization in the living cell, for when the root hairs were plasmolyzed the potassium was found to be equally distributed about the cell.

With regard to less specialized cells such as those of the epidermis of *Allium*, Weevers has generally found evidences of potassium in the cytoplasm. He thinks, however, that this was due to the migration of the very mobile potassium ions to meet the entering reagent. Indeed in the case of *Spirogyra* Weevers observed the formation of a precipitate in the outer zone of the vacuole just where the plasma threads lay hold on the chromatophore. It seemed to Weevers unlikely that the formation of the precipitate in the region of the chromatophore has the significance suggested by Macallum. Indeed Weevers never found any evidence of potassium in the chloroplasts or in the nucleus; that is to say, because no precipitate was ever found to have been produced within these bodies, Weevers infers potassium to have been absent from them. He cites in this connection particularly the case of *Noctiluca* in which the nucleus lies close to the cell wall, and consequently in a favourable position for the reagent to affect the potassium before its escape from the nucleus were it there. Here, however, no evidence was found.

With reference to the localization of potassium in the guard cells of stomata, Weevers was unable to see eye to eye with Macallum since he found irregularities and variations of behaviour which at all events prevented him from drawing any definite conclusion beyond general disagreement. He appears to see some unknown factor at work in the case of guard cells.

It was indeed the apparently peculiar distribution of potassium in the guard cells of stomata which furnished the stimulus to my own studies of stomata, epidermis and leaf chlorenchyma.

We presently turn to the results obtained by myself. In the first place I present categorically a summary of my observations.

1. **Cyanophyceae.** — The results obtained on these forms were very various save in one or two details. In the same preparation, in organisms apparently of the same age, one could find hundreds of individuals showing no sign of precipitate while a varying percentage showed darkened granules in the peripheral zone, generally lying near the cell wall. Adequate illumination showed that these darkened granules were often not solid suspensoids but seem to be rather due to a coating of black precipitate at the interface between the spherical granules and the adjacent cytoplasm. I found such granules in *Cylindrospermum*, *Oscillatoria*, *Tolypothrix* and in some others. The deposition of precipitate upon granular bodies finds its analogue in the similar deposition on chloroplasts, and on foreign bodies as will be seen later. Weevers, it may be recalled, failed to obtain the reaction in the Cyanophyceae.

For the rest I found an almost constant appearance of the precipitate in the pore or pit extending between the heterocyst and the spore in *Cylindrospermum*. The shape of the black mass was nearly constant, appearing as two truncated cones of different slope, top to top; occasionally also a black broad patch or band could be seen either in the inner cell wall or in the interface between this and the outer cell wall. Under plasmolysis these two walls separated easily in the spores of *Cylindrospermum*. These dark patches or bands I have seen both in the heterocyst and in the spore. Evidence of the same thing was found in the cell wall of *Oscillatoria*. Both the dark plugs and dark bands in the cell wall are duplicated in the cell walls of trichomes of the higher plants. Particularly instructive in this respect is the fact that, in *Cylindrospermum*, between a half-developed spore and the heterocyst I observed a conical black plug, and within the wall of the heterocyst some distance from the pore a well defined band of ppt.¹).

1) Weevers records seeing some granules on the outside of the wall. I wish to emphasize that I have observed the ppt. in the wall in these small forms, (the observation of which is attended with some difficulty) as well as in thick walls in other plants where mistake is hardly possible.

This could be explained by assuming that the wall of the heterocyst is less permeable than that of the spore. Fully matured spores do not have the black plug.

The thick mucilaginous walls of forms such as *Gloeocapsa*, and similar colonial forms appear dark even after 24 hours washing previous to applying ammonium sulphide. This appears due to the adsorption of the reagent by the walls.

2. Diatoms. — Several species and genera were examined. Under some conditions the interstices of the shell of *Bacillaria* and others were found loaded with precipitate; sometimes also the edge of the valves carried precipitate. In practically no instances could the precipitate be found within the protoplast. On the other hand I found a large diatom in the food vacuole of a *Vorticella*, and in this, as also within the cytoplasm of the *Vorticella*, very minute black granules could be seen. The nucleus of the *Vorticella* was also covered with granules of precipitate. In *Navicula* there were observed two elongate arrow-shaped groups of minute granules fitting apparently between the chloroplasts; and around the wall near one end a partial band, perhaps in a fissure. The occurrence of ppt. within the protoplast in this form was found fairly constantly, but in others not a trace could be found, save, as above said, attached to the shells.

3. Chlorophyceae. -- In *Chaetophora* I found generally that a black precipitate of unequal thickness was formed on the pyrenoid bodies. In addition occasional large masses of precipitate occurred irregularly in position.

Young colonies of *Hydrodictyon* were exposed to the reagent. The articles of the colony, which of course are syncytial, showed very uneven results, and it was discovered that when this is the case the cuticle had frequently become cracked. The course of diffusion of the reagent was, naturally, through the opening so formed. As a result of this I frequently found, in the vicinity of the break, a dense mass of precipitate, either irregular or in the form of a transverse band, this band being more or less extensive according to the time of exposure to the reagent. Thus different colonies of the same age were exposed to the reagent for 5, 10, 20, 40 and 80 seconds, after which they were thoroughly washed and the ammonium sulphide applied, with the result that every stage of penetration of the reagent could be followed. Aside from this there is nothing particular to mention beyond that the general result is comparable to those found for other Algae, viz., that

granules of precipitate are formed in the vacuole and collect on the cytoplasmic membrane. I have seen evidence that the precipitate may also become entrained in the protoplasm. This, however, appears to be secondary.

In *Spirogyra* the precipitate was frequently found along the margins of the chloroplast (fig. 6.) as recorded by Macallum, but also on the cytoplasm in the interspaces. Although I have observed cells in which the precipitate occurred with the regularity represented by Macallum, the same preparation, and others, showed no such occurrence; and it is difficult to understand, why, for instance, the precipitate occurs on one margin of the chloroplast and not on the other. A possible explanation of the frequent occurrence of the ppt. along the margins of the chloroplast is suggested by the presence of the vacuole lying along the sulcus of the latter, especially since the ppt. generally, if not always, lies within the limb of the chloroplast, apparently within the angle formed by the wall layer of cytoplasm and that covering the chloroplast. The potassium affording this ppt. is probably, in life, in solution in the sap of the sulcus vacuole. My colleague, Professor G. W. Scarth has also observed that under certain circumstances the precipitate collects in two large masses, one at each end of the cell. This was evidently due to the formation of two vacuoles (artefacts) which, contracting, mass the precipitate formed in the original vacuole, and appears to follow when the *Spirogyra* has been subjected to the action of trivalent ions. The precise conditions, however, matter less than the fact that different conditions in the organism induce strikingly different results on applying the reagent. I have also observed the massing of the precipitate at the ends of cells in various other algae, (*Cladophora*, *Ulothrix*, *Zygnema*) sometimes with regularity¹).

Diffusion along the transverse walls appears to be one of the conditions determining the result in these forms. The course of vacuolization undoubtedly is of much importance. Much importance has been attached to the consideration that in the position of maximum curvature of surface there is also a concentration of potassium (Macallum, 1905, 1912). Examples of cases in which this condition is supposed to occur are the point of emergence of the growing rhizoid cell in germinating spores of *Equisetum*, (see beyond) and in the analogous

1) I have recently observed that the outer cell-wall of *Zygnema* betrays physico-chemical gradients due to age, differences which may be demonstrated by staining (fig. 13). Such differences may permit local penetration of the reagent and thus account for the pptn. at the ends of cells.

surfaces of outgrowing conjugation tubes in the Zygnemaceae. Dense masses of precipitate are said by Macallum to occur at such points; (see his figures, 1912, plate 1, figs. 2—4, 7, e.g.). If potassium has, indeed, any peculiar and necessary function in such position; or if for any reason it needs must accumulate there; if, that is, such regions are of low surface tension, then it should always be detectable by means of a method which deserves recommendation for that purpose, when properly used. An abundance of conjugating material of *Spirogyra* afforded an opportunity of making a careful test of the point. The material was subjected to the reagent for 15 min. and washed on a small filter with ice water for various periods (15 min. to 1½ hrs.) until, at least, the filtrate showed no trace of reaction with the reagent. I repeated the test a dozen or more times, always with the same result, namely, an entire lack of regularity in the position of the precipitate. In very few instances indeed one may find a mass of precipitate in the critical position; but the number of cases in which the opposite is the case is so great as to render any conviction that potassium occurs in such position with definiteness and regularity impossible (figs. 5—7). I present for consideration photographs in which the appearances are well portrayed. Further comment on these is unnecessary.

***Equisetum arvense*.** — The ungerminated spore, and various stages of development of the young prothallus were studied. The material, which had been grown on sand, was collected on a small filter and after washing thereon was subjected to the reagent for 10 to 20 min. After thoroughly washing away the reagent with ice-water, ice being kept in the filter the while, the ammonium sulphide and glycerin mixture was applied on the filter. The material was then mounted for examination.

In the ungerminated spore there were frequently observed dense lenticular masses of ppt. lying against the wall. Sometimes round cakes of the same were seen lying in the wall itself. Within the cytoplasm, a minute, evenly distributed ppt. or few masses, irregular as to size and form, could be seen. Perhaps the most general statement which I can make is that in the spores the ppt. most usually lies as rounded plaques against the inner wall surface.

In the two-celled stage of germination, no constant evidence of the massing of ppt. at the growing point could be observed. Such masses occurred, as a matter of fact, anywhere in the rhizoid cell, though not infrequently a group of several granules of ppt. could be seen lying near but not at the apex of the rhizoid (figs. 8, 11). On

the other hand, the agglomeration of ppt. on the upper side of the first transverse wall was not uncommon, and this was repeated on other transverse walls as the prothallus became larger (figs. 8, 10, 12). These aggregations took the form of rounded cakes, frequently lying as well on the peripheral (fig. 9) as on the transverse walls. These cakes were also usually thinner in the middle and so appeared as rings (fig. 9), and were clearly to be regarded as diffusion figures. The result was the production of most bizarre appearances (e. g. fig. 10), which can only be referred to the local penetration of the reagent through restricted points in the cuticle, there or nearby to be met by the diffusing potassium ions, and thus laying down the resultant curious precipitation forms. It was fairly uniformly evident that such pptn. membranes are very likely to occur on the upper side of the transverse walls as shown in fig. 12. The explanation seems to lie in the probable more rapid entrance of the reagent at the rhizoid end of the prothallus, where there is little cutinization.

In no case was any ppt. observed in the nucleus, which was usually quite distinct and easily observed after the action of the reagent, and had then a pink coloration, as described by Macallum.

Higher-Plants. — Particular attention has been paid to stomata, epidermis and chlorenchyma. I have verified Weevers' observation that when sap is gathered, invariably a precipitate occurred on applying the reagent.

Stomata. — I have examined an extensive series of stomata including *Allium*, *Norantea*, *Clusia*, *Ficus*, *Tradescantia*, *Phaseolus*, *Pelargonium*, etc. For the sake of brevity I forbear from describing in detail each of these, and present my observations in summary form. Some stomata show a precipitate on the outer wall of the guard cells¹⁾ quite regularly. This condition, which is the one observed and laid stress upon by Macallum in *Tulipa*, may frequently be seen in some plants almost uniformly — *Allium* is such an one. On the other hand in the same piece of epidermis the precipitate may be found massed at the end walls, or it may be scattered in the form of fine granules apparently throughout the whole cytoplasmic mass. More careful observation will generally discover however that the precipitate occurred on or near the lower wall, to all of which must be added

1) By the "outer wall" I mean the lateral curved walls as the stomata are viewed from above or below, that is, looking through the pore. By "end wall" I mean the wall between the ends of the guard cells. By the "lower" wall I mean the wall next the chlorenchyma.

that exceptions are bound to be found to any general statement. Nevertheless one gets a definite impression that there is on the whole a fairly uniform behaviour in any particular species, that is to say, when one finds the precipitate in a particular place in one stoma one may rather expect the same condition in other stomata. The fact that no precipitate at all occurs in many instances appears to be due to the accidental circumstances that a bubble of air in the sub-stomatal space prevents the reagent from reaching the stomata. In particular I would point out that in the accessory cells in grasses (*Zea*) the precipitate is frequently found on or near the wall between the accessory cell and the next laterally placed epidermal cell. The precipitate is frequently scattered in small granules or massed in large ones in various positions in these cells, but speaking broadly the picture afforded by the accessory cells is much the same as that by guard cells of other plants. I frequently found one or a very few granules of precipitate in the bulbous end of the guard cell.

In interpreting the above results one must always take into account the presence of cuticle which, as is well known, not only clothes the outer walls of the epidermis but also those of the stomatal pore and the inner faces of the guard cells, and even of the accessory cells, at least in some cases. My observations compel me to the conclusion that no interpretation of the behaviour of the cobalt reagent can be accepted without due regard to the distribution of cuticle. It is quite obvious that the entrance of the reagent into guard cells will generally be through the outer walls, although one can easily conceive behaviours resulting in the more rapid wetting of other parts of the guard cell. In accordance with this general belief I have observed that the most uniform results are generally to be obtained when the chlorenchyma has been entirely removed in making preparations of the epidermis.

Roots. — Whole seedling root systems were carefully exhumed, washed in tap water, rinsed in distilled water, exposed to the reagent and washed for three hours in ice-cold distilled water. *Trifolium*, *Chenopodium*, *Chaetochloa* and several others were used.

An abundant ppt. was always found. Granules and irregular clumps occurred in the root-cap cells, including the detached moribund cells. Cells of epidermis and cortex frequently show massing of granules on transverse walls, and it is evident in all these that the black ppt. tends to form a coating on plastids or other bodies, including starch grains and nuclei, these latter less frequently. Two details should be especially mentioned, (1) Curious precipitation membranes are formed

in the cell walls. I have observed these in the cortex and within the central cylinder, and are undoubtedly the same as those seen in epidermis walls. (2) I have observed in *Chaetochloa* also Liesegang rings formed in the central cylinder each precipitation band filling the entire space within the endodermis (fig. 4), but not bridging the tracheid lumen, from which I infer that the lumina of other cells were free. This condition corresponds perfectly with that found in trichomes. In other cases I found large clumps of ppt. within the lumen of trachea, in which also the annulae, resp. spiral thickenings often appear black.

The root-hairs on the other hand have generally been found free of ppt. though cases of its occurrence have been found as by Weevers. In one instance a band of granules was observed on the wall near the apex of the hair.

The internal tissues of the nodules on *Trifolium* roots were entirely free of ppt. though in the light of Miss Dowding's work (1924) it is probable that if sections were used a positive result would follow.

While the presence of potassium in the root is thus indicated, here also cutinized membranes must be taken into account. But even when cells are at once open to the attack of the reagent on all sides, as are the exfoliated cells of the root-cap, the results are not definitely indicative of particular localization within the cell. In many plant cells in which tannin is present, the course of the reagent is interfered with. I noticed in such leaf tissues that instead of a black ppt. a dark brown colloidal vitreous mass occurred. If a solution of tannin and KNO_3 and of the cobalt reagent be brought together on a glass slip, a dense ppt. is formed, which more or less clings in a mass. If then ammonium sulphide be added, a vitreous mass is formed. Microscopically however, the characteristic granules of potassium double salt will be seen deeply blackened. If however the cobalt reagent is allowed to stand in contact with strong tannin plus KNO_3 , a membrane of vitreous appearance is formed which contracts spontaneously. After washing, I still found the precipitate embedded in a colloidal mass, so that, if we may follow the analogy, we should find the typical ppt. in tannin bearing cells embedded in a similar colloidal mass. I have however failed to find the ppt. in *Clusia* and other forms in which tannin occurs. The question demands further study. I take account only of forms in which the above complication does not occur.

Trichomes. — Trichomes of *Pelargonium*, *Begonia*, *Gloxinia*, *Saint Paulia* and *Sicyos* furnished the material. Epidermis was stripped

off, or transverse sections were cut and after treatment were subjected to four hours washing in ice-cold distilled water, in a refrigerator.

In many cells the ppt. occurs as granules entrained in the cytoplasm, with no definite position, but a wide variety of behaviour aside from this was observed. Small irregular creeping precipitation membranes in the wall beneath the cuticle were common, e. g. in *Gloxinia*. Liesegang bands were beautifully developed, often throughout the whole length of the trichome, and the rates of diffusion of the reagent through the whole length of the trichome could be determined. E. g., in one case each band was formed in a trifle less than seven seconds. The bands themselves lay either within the cellulose wall or in the cytoplasm or both. When in the wall, the bands were usually frustums of cones in form with the apex of the cone directed toward the apex of the trichome (figs, 1, 2). This evidently indicates gradients of diffusion. When the reagent met a transverse septum, the next band was further away than it would have been otherwise. These bands were formed as clearly in dead and empty cells as in living ones, and even in the multicellular trichomes of *Begonia*. Collapsed cells indeed showed every variety of behaviour seen in Liesegang rings developed on gelatine plates or in rods. Since we have here primarily nothing to do with the physics or chemistry of the Liesegang phenomenon, further mention of details would be fulsome. I can only recommend plant trichomes as convenient capillary tubes in which this behaviour may be studied with great ease and satisfaction.

Disregarding the banded precipitate as clearly not contributing evidence of localization of potassium for the moment, and regarding only trichomes in which no such banding was seen, and only cells which were in sound condition, including the glandular trichomes of course, one may say without fear of contradiction only that the cobalt-potassium reaction does occur in the cells, but the position in which the ppt. occurs teaches us nothing further. Particularly to be noted is that, in addition to the above mentioned banding, the ppt. formed in the cell may also be laid down in periodic fashion (fig. 3). I observed this in the trichomes of *Pelargonium*. As to the nature of the precipitate in the Liesegang rings. There can be no doubt that these rings are caused by the periodic reaction between the cobalt reagent and the entering sulphite, because of the failure to wash out the former. This is, of course, due to the cuticle encasing of the trichome. When the trichome is broken, the reagent enters here, as well as at the base, and two sets of Liesegang bands, approaching each other, are formed

Epidermis. — The approach of the reagent with respect to the epidermis is always from the chlorenchyma side and the ppt. usually lies on or near the inner wall. According to the amount of chlorenchyma present, the penetration of the reagent is more or less impeded. Air in the intercellular spaces likewise hinders its penetration. A rapid treatment with absolute alcohol, previous to applying the cobalt reagent, insures a more even result, without however altering the net issue. This method is open to some, if perhaps little, objection, since the alcohol certainly affects the protoplasmic membrane.

Leaves with very large epidermal cells (as *Platysynaphia*) permit cutting away the outer epidermal walls, opening all the cells. When such a preparation is made and treated, the ppt. is found clinging to the cut edges of the syncinal walls. Elsewhere, the ppt. clings to the cytoplasmic utricle, and this condition prevails generally, when the cells are not damaged. The granules may be small and fairly evenly distributed or larger and fewer may occur, as in the accessory cells of *Scindapsus*, which belongs to the *Commelina* type of Porsch (1905). The epidermis of this plant is peculiarly instructive, for the accessory cells show a heavy potassium content, but certainly with no suggestion of definite localization in the living cells, though betraying segregation of granules during the reaction, in that these find their way into odd corners formed by cell walls. Curiously enough, the guard-cells are apparently devoid of potassium if we may judge solely from the objective appearances.

Not infrequently the outer epidermal walls contain black circular or lobulated precipitation membranes, similar to those seen in roots and in the walls of trichomes. The walls of the ends of the guard-cells of *Zea*, even after prolonged washing, appear dark, distinctly darker than the walls elsewhere.

Chlorenchyma etc. Nothing of note is discoverable in the cells of the chlorenchyma by which they may be brought into contrast with other cells in regard of the potassium reaction.

In no case have I seen unequivocal evidence that potassium is to be found in the chloroplasts, but the accumulation of ppt. on their surface is common enough. This is seen readily in the large "water" cells which occur just beneath the lower epidermis in *Scindapsus*, which are poor in chlorophyll, but the plastids of which stand out as spores of black ppt. In *Zea* however the chloroplasts are quite clear. The chlorenchyma of *Platysynaphia* I found particularly rich in ppt., the granules being indiscriminately scattered about among the chloro-

plasts, apparently, but in reality, I think, sticking to the inner cytoplasm. The appearances in a word are practically identical with those seen by Macallum, but his observations do not cover the whole matter, as e. g., the occurrence of a single granule of ppt. in a chlorenchym cell, or a huge clumping of ppt. in one place, as may be seen frequently where two cell walls meet where obviously they are not concerned in the serious business of conjugation. In *Allium* the chlorenchyma gave an abundant reaction, but afforded poor evidence for any inference beyond merely that the potassium was there.

Nucleus. — With Weevers and Macallum I have not found a ppt. in the nucleus but often the nucleus is covered by a fine granular ppt. Why may it not be argued that this was formed by the reagent meeting the potassium as it diffused out of the nucleus? And if not, where in fact was the potassium? It seems hardly possible to escape the idea that, because of the great mobility of K-ions, the penetration of the reagent at the walls would be accompanied by migration of potassium toward the walls, hence depriving the nucleus of that substance. This consideration led Weevers to experiment with *Noctiluca*, the nucleus of which, on account of its position, would favor detection within it of the potassium if present, but without positive results. For the present, therefore, the facts as maintained by the authors cited must be granted until contrary evidence is gained.

Indeed so confusing are the facts gleaned in the course of the work that I sought for some explanation of the results in the technique. I therefore did the following experiments to determine the character of the interaction between the reagents themselves and between the cobalt reagent and potassium.

Ammonium sulphide was allowed to diffuse into gelatin with cobalt hexanitrite in it. Liesegang "rings" — preferably here one should say bands or zones — were formed. The details of the structure obtained duplicated those obtained in the trichomes (figures 1, 2). The cobalt reagent was also allowed to diffuse into gelatin with potassium nitrate in it. I here obtained small yellow droplets which showed some angularity especially, of course, the larger. It may be supposed that at the temperature prevailing these were concentrated solutions partly crystallized. At all events, they were apparently similar to the ppt. formed in cells (which sometimes also appear crystalline) but, what is more important, no periodicity comparable to the Liesegang effect was seen. If fragments of cotton fiber are present in the gelatine, the ppt. accumulates on the surface of the fiber.

I then made a preparation of gelatin and potassium salt, placed a small drop on a glass slip, covered it with a thin cover and after setting, I applied the cobalt reagent to the edge of the cover. After the reaction above noted was completed for a zone of two or three mm. I placed the preparation in running water (t. 10° C.) for several hours to wash out the excess of cobalt reagent. I then applied ammonium sulphide to the edge of the cover. I now got both banding and blackening of the ppt. In one such preparation after standing overnight I found beautiful yellow crystals, single, in pairs, and in various forms of cluster, even in the form of a druse, (in the sense of the plant histologist).

The obvious and inescapable conclusion is that the Liesegang rings I obtained in trichomes were due to the persistence of the cobalt reagent, which reacts with ammonium sulphide to form a black salt. The remedy obviously was to attempt to wash out the cobalt reagent thoroughly, but this was more easily proposed than achieved. However, I found that, after prolonged washing the trichomes of *Pelargonium* (lemon scented var.) showed no more the dark bands in the walls, but, on the other hand, did show that the precipitation of potassium had, apparently produced the Liesegang effect, since the granules were sometimes definitely laid down in clusters of dendritic appearance in periodic fashion (fig. 3). I say that the potassium was thus precipitated, since the washing (in ice water for over four hours) had apparently cleared the cobalt reagent out of the walls. In other trichomes the ppt. was evenly scattered, and this would be adduced as evidence of the occurrence of the potassium. Either therefore potassium was absent from the trichomes in which the ppt. fell out in the Liesegang fashion, and we have to thank the presence of the cobalt reagent for the result, or the potassium was thrown out periodically.

The Liesegang bands in the central cylinder of roots may also be due to the persistence of the cobalt reagent in spite of the washing of a root 1 mm in diameter for two hours, and checking the washing by testing the final wash water, as in all cases demanding the more critical technique. Further work may throw a clearer light on this and on the occurrence of the curious precipitation membranes frequently seen in roots and elsewhere.

It is further also possible that the dark plugs and bands seen in the Cyanophyceae were of the same nature, but when it is stated that these minute objects were washed for three hours in distilled water, frequently changed and kept ice cold, either much must be said for the persistence of the cobalt reagent, or little for the method, unless

it should turn out that potassium in very truth does occur in the manner indicated in the body of this account.

It would appear therefor that the application of the method under consideration to the study of the distribution of potassium in plants is attended with peculiar difficulties not hitherto properly evaluated by previous observers. Until we know more about the matter, theoretical considerations are superfluous. The following conclusions may however be drawn, subject to correction always, but reasonable in the light of the observed facts.

Plant organs, tissues, and even cells, have peculiarities of structure which permit or hinder diffusion currents. The cellulose wall may adsorb the reagent in question¹⁾ or it may be held by capillarity in minute interstices (such as the pore in the Cyanophyceae, or in the pits or fissures of the diatoms), whence removal is peculiarly difficult. Accidental circumstances such as fissures in the cuticle, allow an uneven entrance of the reagent leading to results explicable only when this fact is known.

Coupled with the foregoing is the difficulty of freeing the tissues of the cobalt reagent. It was found that, even after prolonged washing (4 hours) evidence of the cobalt reagent could be found in the occurrence of Liesegang bands in trichomes and roots. Even when these were not observed in trichomes whence after long washing the cobalt had been dispelled, we may infer, the precipitate supposed to indicate potassium was frequently also found in bands. That the ppt. was indeed of a potassium-cobalt origin may be questioned, but an admission to the contrary does not remove the quandary, one which is not lessened by the fact that periodic precipitations have been observed in such minute objects as the blue-green algae.

Tannin appears to interfere with the behaviour of the cobalt reagent. In some tissues where tannin occur, no evidence of ppt. could be found.

When, by prolonged washing, it is reasonably certain that the cobalt reagent has been completely eliminated, the distribution of the ppt. of the double salt of potassium and cobalt in the cell does not permit the drawing of any inferences as to the distribution of potassium in the living cell, beyond the one conclusion, made by Weevers, and to which from my own observations I can subscribe, that the ppt. occurs in the vacuole, and becomes secondarily attached to the cytoplasm or to plastids, nucleus etc. Potassium may occur in the cytoplasm as

1) This view was also advanced by Czapek, *Biochemie der Pflanzen*, 2, p. 533, 1920.

obviously it must during the migration of potassium ions through the cytoplasm, but even if it were caught here, it would collect to form granules, droplets or crystals of visually appreciable size, if they are to be observed. Having collected, they would not be as in life, analogously to the precipitation of potassium in gelatin.

In particular also, regarding the distribution of potassium in the guard cells of stomata, it has been suggested that (Macallum, 1912) the potassium salts collect according to the principle of surface concentration on the outer convex surface of the guard cell. If this is the case it is unfortunate, if the principle is to be applied, since, as a matter of fact, the greatest convexity of surface is to be found, not on the outer convex wall, but on the thin wall adjacent to the stomatal pore, namely, on the diametrically opposite side of the cell. Since the stoma is an osmotic mechanism, well enough understood so far as its cruder workings are concerned, to call on surface concentration seems superfluous.

Furthermore, growing points are regions of less cuticularization, and hence points of more ready entrance of reagents. The inferences in this regard need no further amplification.

Summary.

The purpose of the foregoing account is to present an evaluation of the cobalt-sodium-hexanitrite method of determining the localization of potassium in the living cell. It has been found that for this purpose, the reagent in question is inadequate as at present used. The position of the ppt. appears to depend upon various conditions, important, if not chief, among which is the local entrance of the reagent through portions of the wall which for one reason or other permit a more rapid diffusion than elsewhere.

The absorption of the reagent by cellulose and mucilaginous walls is evidently another disturbing factor, as is also the great difficulty of washing out the reagent from cul-de-sac positions such as occur in trichomes.

That the reagent may however be used for the purpose of determining the localization of potassium in various tissues is another and quite different question. Recently Miss E. S. Dowding, working in Professor F. J. Lewis' laboratory, has found the reagent of great value for this purpose, as she showed at the recent (Toronto) meeting of the British Association for the Advancement of Science. Her paper is still unpublished so that only cursory reference may at present be made to it.

It may properly be added that, in certain details no evidence has been found to controvert the conclusions earlier reached by Macallum and by Weevers.

Evidence of potassium in the Cyanophyceae in the peripheral region, as observed by Macallum, was obtained, in contradistinction to Weevers.

The nucleus was never found to contain the ppt. (Macallum, Weevers).

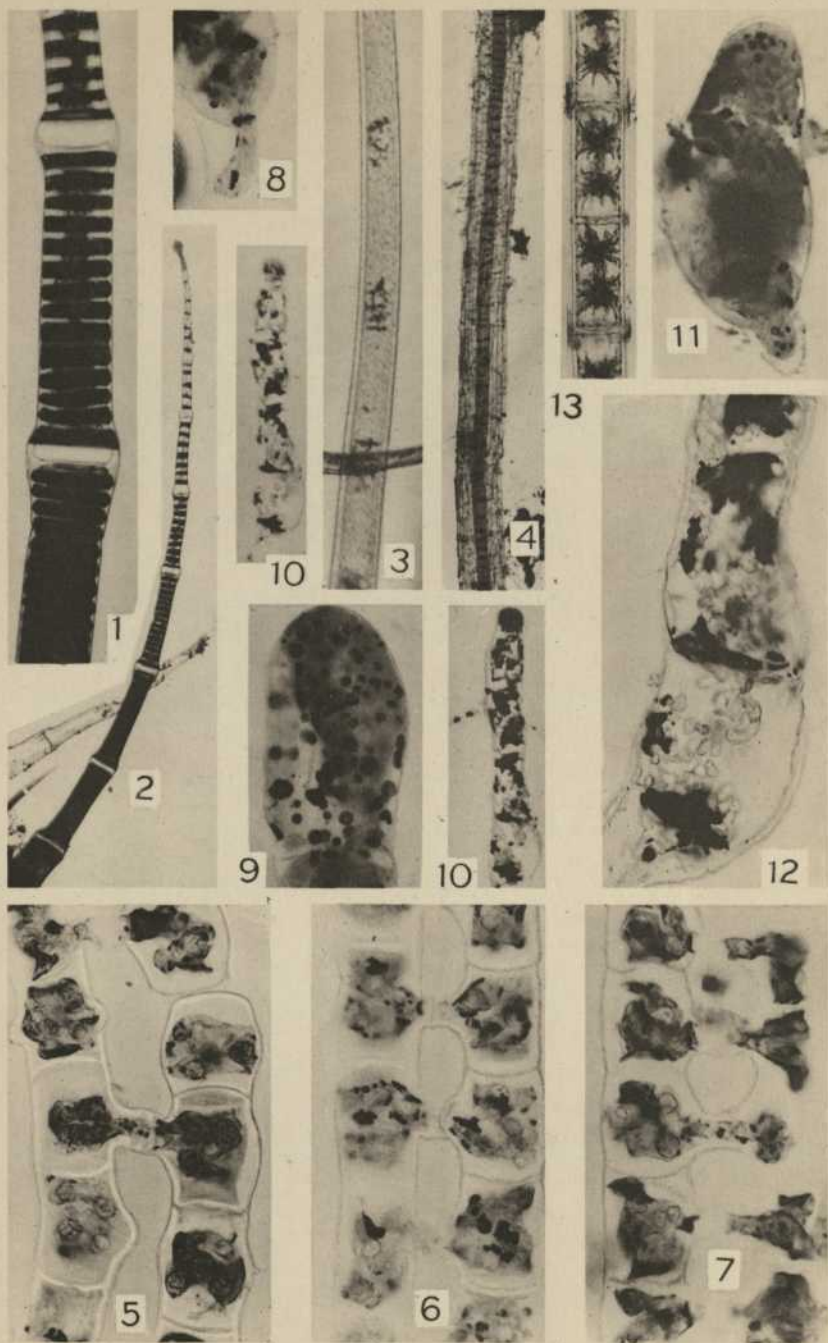
With Weevers, I have to believe that there is no evidence of definite localization of potassium in the cytoplasm. The evidence rather shows that the salt is contained chiefly in the vacuoles. Chloroplasts were also found to lack ppt., so that, in common with the nucleus, we must at present suppose them free of potassium.

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Explanation of figures (plate V).

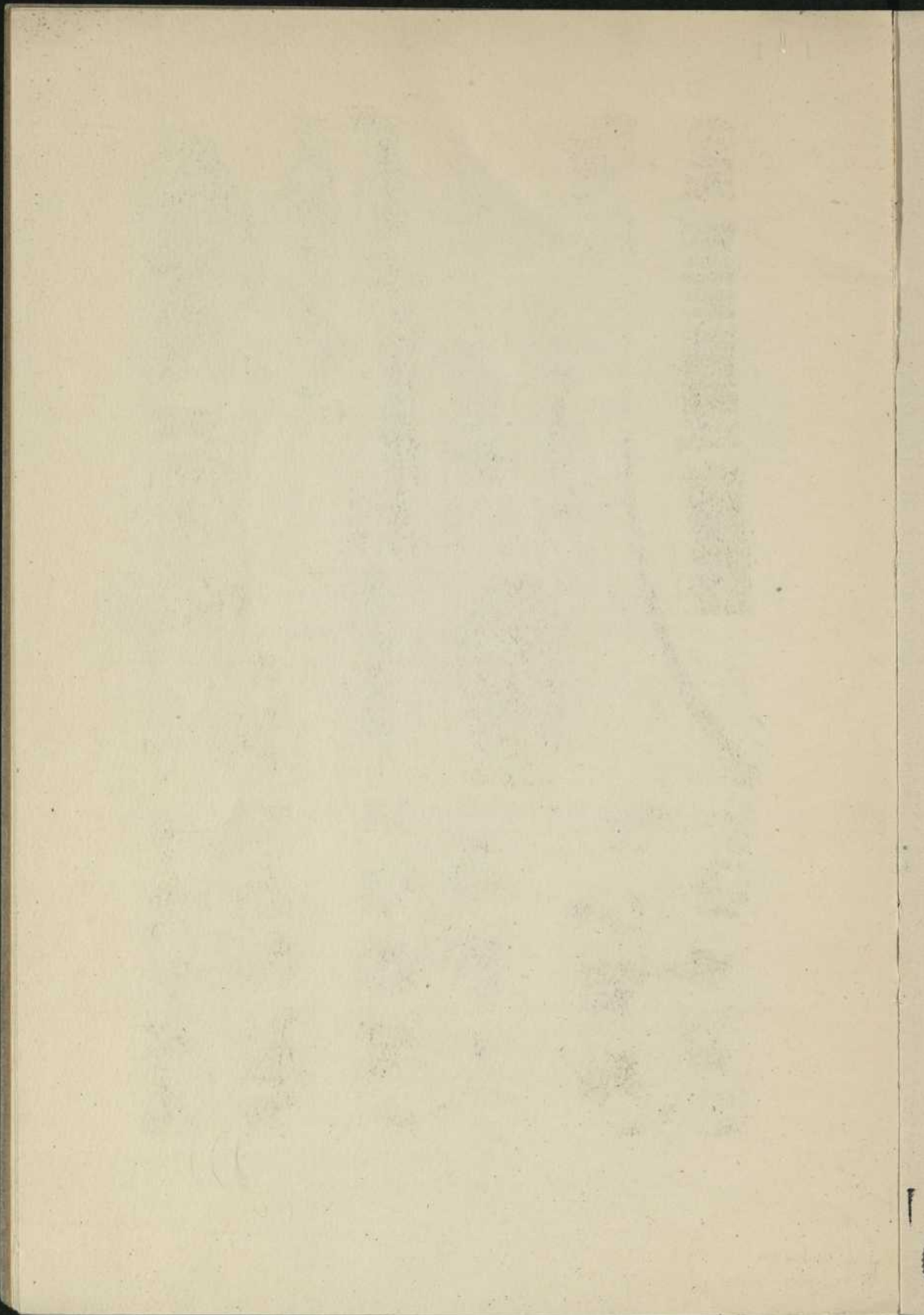
- Fig. 1. *Saintpaulia* sp. Trichome with Liesegang bands formed by the reaction of ammonium sulphide with cobalt-sodium-hexanitrite in the walls.
- Fig. 2. A similar trichome, at lower magnification. The entrance of the reagent at the base is so rapid that visible periodic pptn. does not occur.
- Fig. 3. *Pelargonium* sp. Rhythmic precipitation of potassium (?) within the cytoplasm.
- Fig. 4. *Chaetochloa* sp. Rootlet with rhythmic pptn. in the stele. The reagent moved forward from both ends of the rootlet.



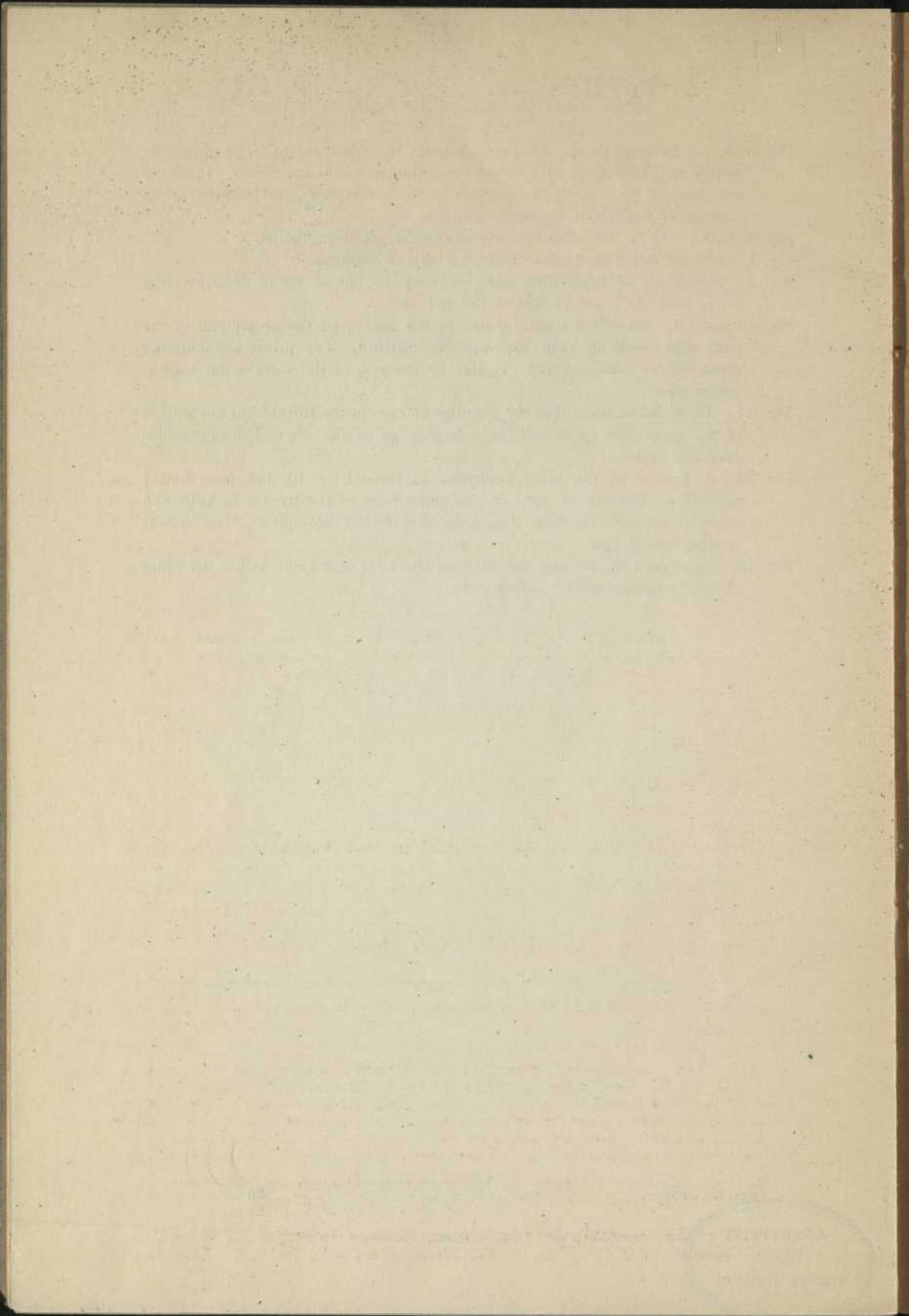
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- Fig. 5, 6, 7. *Spirogyra* sp. Conjugation-tubes in various stages. The potassium double salt, blackened with ammonium sulphide stands out clearly. Instances are seen of pptn. along the margins of the chloroplasts, and elsewhere; no massing of the salt at the apex of tubes.
- Fig. 8, 9, 10, 10', 11, 12. *Equisetum arvense*: young prothallia.
- Fig. 8. Rhizoid cell with masses of ppt. in various positions.
- Fig. 9. Apical cell of four-celled stage, showing the ppt. as round disks or rings on or near the inner surface of the cell-wall.
- Fig. 10 and 10'. Six-celled stage. Owing to the density of the protoplasm in the more apical cells an even exposure was difficult. Two prints are therefore given of the same negative. In fig. 10' the ppt. in the more apical cells is better seen.
- Fig. 11. Three-celled stage showing granules of ppt. in the rhizoid but not massed at the apex. The apical cell has a large mass on one side and some granules near the apex.
- Fig. 12. A portion of the same prothallus as that of fig. 10, but more highly magnified. Massing of ppt. on the upper faces of the transverse walls and cakes of the same clothing or partially clothing the chloroplasts. The nucleus is seen free of ppt.
- Fig. 13. *Zygnema* sp. showing the different character of the cell-wall in the zones of the transverse walls. Iodine-eosin.
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Botanische Abhandlungen

Herausgegeben von Professor **Dr. K. Goebel**, München.

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Die Untersuchungen gehen von der Frage aus, ob sich in der Anordnung der „Blattnerven“ und der Spaltöffnungen Gesetzmäßigkeiten erkennen lassen; sie sind gleichzeitig eine wesentliche Ergänzung zu den Ausführungen des Verfassers über den gleichen Gegenstand in seiner „Organographie“.

Heft 2: Die sterile Kultur der höheren Pflanzen. Von **G. Klein** und **J. Kisser**. Mit 20 Abbild. im Text. (Aus dem Pflanzenphysiologischen Institut der Wiener Universität.) 58 S. gr 8° 1924 Rmk 2.40

Eine Reihe von biochemischen Fragen hat ihre Durcharbeitung noch nicht finden können, da hierfür eine leichte und absolut sichere Kulturmethode höherer Pflanzen Voraussetzung ist. Wohl gibt es eine Anzahl von Methoden, aber diese sind entweder zu unsicher, zu kompliziert, andere sogar unbrauchbar. Die vorliegenden Untersuchungen geben zunächst eine kritische Darstellung aller bekannten Methoden. Im Anschluß hieran wird eine neue Methode mitgeteilt, die die Verfasser auf Grund vieler Versuche ausgearbeitet haben und die auf das Interesse aller Biologen, vor allem aber der Botaniker rechnen kann.

Heft 3: Blütenmorphologische Untersuchungen an den Euphorbiaceen unter besonderer Berücksichtigung der Phylogenie der Angiospermenblüte. Von **Dr. P. Michaelis**, Jena. Mit 41 Tafeln. 150 S. gr. 8° 1924 Rmk 16.—

Zur Einführung in die vorliegenden Fragen gibt der Verfasser zunächst eine Darstellung der wichtigsten z. Z. bestehenden Ansichten über die morphologische Natur der Blüte und ihre Bildung im phylogenetischen Sinne (Pseudanthienlehre Wettsteins, Euanthienlehre Halliers und Arber-Parkins', sowie die von Karsten und Celakovsky vertretenen Anschauungen). Alsdann behandelt er seine eigenen Untersuchungen innerhalb der Familie der Euphorbiaceen und erörtert an ihrem Beispiele die Frage nach dem Bildungsgange ihrer Blüten. Anhangsweise werden einige Versuche experimenteller Richtung angeführt. Zum Schluß bespricht der Verfasser noch die Frage nach der Phylogenie der Angiospermen im allgemeinen. Außer einem Literaturverzeichnis sind der von der Universität München preisgekrönten Schrift noch 41 Tafeln im Schwarzdruck mit nahezu 500 Zeichnungen und ausführlichen Erklärungen beigegeben.

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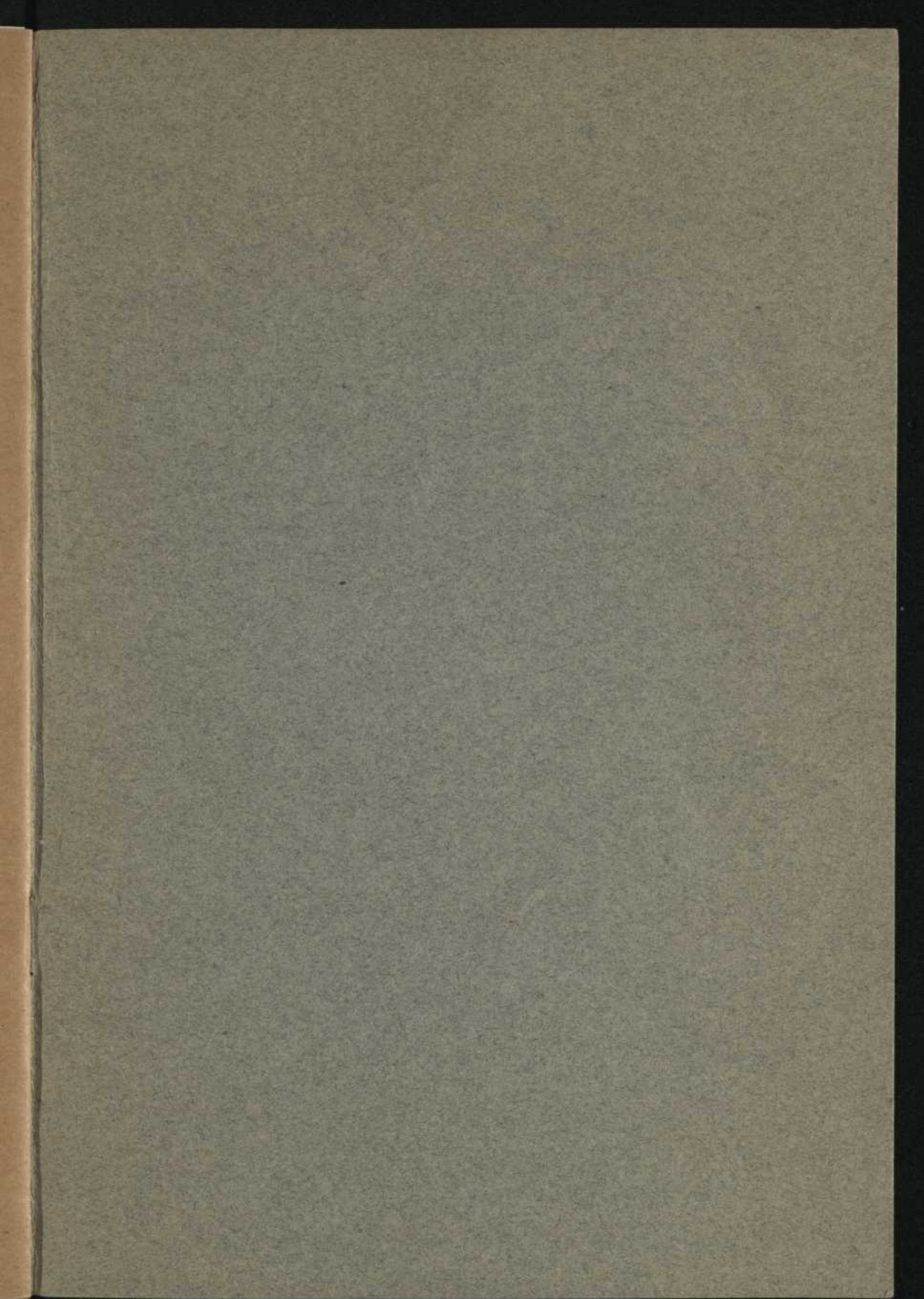
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