Further Studies on Aeginetia indica.

By

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With Plate XI and XII.

In my former paper (1903) some accounts were given of the morphology, anatomy, and biology of *Aeginetia indica.* So far as my observations went, this parasite showed no special character in the manner of its development, which can be distinguished from that of *Orobanche* as thoroughly investigated by Koch (1883). When I undertook during the past year a further study of this parasite, particularly as regarded the germination of the seeds and the development of the seedlings, I could show that at an early stage of development *Aeginetia* displayed many peculiarities, some of which are perhaps unique. As the results obtained appear not only interesting in themselves, but also contribute something to the knowledge of phanerogamic parasites, I think it advisable to give them briefly in the present paper.

Very little has yet been published on the early stage of development of the *Orobanchaceae.* In *Lathraea* Heinricher (1894, 1895) made some experiments on the germination of the seeds and the development of the seedlings. According to him, the seeds show no feature during germination and further development that is worthy of special mention. The vegetative organs are very much reduced in form, but the embryo does not differ essentially in structure from that of most autophytic plants, being provided apparently with a pair of cotyledons and a radicle. In germination the radicle first grows into a filamentous root which soon branches into numerous rootlets. The rootlets then produce haustoria where they come in contact with the host-root (Heinricher, 1894, p. 128). Further he ascertained that the seeds require in germination the presence of proper host-root which he believed to exert a chemical stimulus.

Koch (1883) extended our knowledge on *Orobanche,* and succeeded in raising seedlings from the seeds laid on or near a proper host-root. In this plant the embryo is so much reduced in form as to appear like a younger stage of a dicotyledonous embryo (Koch, 1878, p. 259), being merely an oval cell-mass, and the changes that take place during germination show certain peculiarities. At first the radicular half of the embryo develops into a filamentous root (Koch, 1883, p. 189), while the plumular half remains throughout in the endosperm, acting as an absorbing organ. Differing from *Lathraea*-seedling the parasitism of this seedling is effected by the root-tip, provided it abuts on a host-root lying before its course. In his culture-experiments Koch (1883) assumed that in germination the seeds required a chemical stimulus from the host-root. Such being all that we know, at present, about the early stage of development of the *Orobanchaceae,* it appears to me to be not the less interesting to extend our study on *Aeginetia* which exhibits a close resemblance to the last mentioned species of *Orobanchaceae,* on account of the structure of the seeds as well as the vegetative organs, and to ascertain how far what was found on the latter plant is applicable to the former.

While the present study was carried out with this end in view, I have never undervalued the problem about the condition which the seeds of such holoparasite require in germination. Although it has been ascertained by the above mentioned authors that the stimulus of the host-root is invariably neccessary to germination in plants of this family, the nature of the stimulus has not yet been studied with accuracy. Concerning this point I can not yet express any definite view, but as it seems to me that the results of a few incidental experiments are suggestive for a further study on this subject, I will note them briefly in the present paper.

Methods.

The seed of *Aeginetia* being very fine and pulverous, a special treatment is required in observing its germination. In order to observe easily the successive stages of germination, and of the development of the seedlings, I transplanted, a month or two previously, some vigorous host-plants in pots of 15—20 cm in diameter. These being kept sufficiently moist, the plants began to produce after a while young rootlets mainly traversing between the wall of the pots and the soil inside. When a thick mesh-work was thus formed by the rootlets I lifted up carefully the plants from the pots, laid the seeds of *Aeginetia* upon the meshes, and then put the plants again in the pots as before. By taking the plants from time to time out of the pots without disturbing the arrangement of their root-system on which the seeds were laid, I was able to follow in detail the changes that took place during the germination and subsequently.

The seeds used in the experiment were collected in the preceding year and kept dry. Under favourable conditions they germinated within two weeks in the early summer. However I could observe no germination to take place in seeds preserved in a dry state for two years. It has not yet been ascertained how long the germinating power can be kept intact in seeds kept moist. This is a practically important matter in connection with the protection of the cultivated plants (Kusano, 1903), in case they should be invaded by this parasite.

Embryo.

The embryo is microscopically small and enclosed in the endosperm packed with starch. In order to take it in toto out of the endosperm the seed was treated a day or more with a concentrated solution of chloralhydrate. If such a seed be gently pressed under the cover glass, the endosperm would escape easily from the testa, and the embryo from the endosperm. The mature embryo thus taken out consists simply of a few isodiametric parenchymatous cells of nearly equal size. It is somewhat oval in form with its narrow end directed towards the microphylar end of the seed. No morphological differentiation into plumule, radicle or cotyledons being invisible, it represents, as it were, the younger stage of an embryo of a phanerogamic plant. Optical section shows that at most two but often a single row of cells in the direction of the long axis of the embryo is enclosed by the epidermal cells (Figs. 1, 2). Very simple as it may be in structure, still it is not difficult to point out both the radicular and plumular ends in the embryo. These become evident in a germinating seed; the narrow end, which often consists of smaller cells, corresponds to the radicle, while the other end represents the plumule. As a whole the embryo of *Aeginetia* has quite the same structure as that of *Orobanche* (Koch, 1878; Smith, 1901, p. 118).

Seedling.

It is a noteworthy fact that in spite of a great similarity in structure of the seed in *Aeginetia* the mode of germination is very divergent. In *Orobanche* germination is brought about by the multiplication of cells in the embryo, so that a filamentous seedling of 1—2 mm in length is the result. Both the radicular and plumular ends are seen to consist in longitudinal section of four rows of cells enclosed by the epidermis (Koch, 1878, Figs. 17—19). The connection of the seedling with the host is effected by the tip of the radicle. The tip on coming in contact with any host sends out its epidermal cells in the form of papillae (Koch, 1883, p. 189), and the subjacent initial cells then commence to proliferate and produce the tissue of the primary haustorium. In *Aeginetia* the changes are quite different. In the first place we can scarcely recognize multiplication of cells or longitudinal growth in the seedling before it finds out the proper host, and in the second place the development of the radicular end is very characteristic. The first change that can be observed as the sign of germination consists only in that two or three large, hyaline globular cells appear outside the testa at the micropylar end of the seed (Figs. 3, 4). These are highly turgescent with abundant cell-sap. The nuclei are large and conspicuous, and the cytoplasm radiate from them. At an advanced stage the globular cells increase in number generally up to 15 approximately (Fig. 12). As can be seen in Figs. 1, 2 and 6, these are not a new tissue, but only the epidermal cells of the radicle, but swollen up to nearly 4 times the original diameter. Simultaneously with this changes all the other cells swell up more or less making the embryo much larger in size; and judging from the number of cells seen in an optical section of the embryo before and after germination (compare Figs. 2 and 6), it is very improbable that a multiplication of cells may be partly concerned in the increase of the size. An accumilation of starch more especially in the tissue under the globular cells is perhaps connected not with the cell-division in this place, but with the further development of the globular cells.

Now follows the outgrowth of the globular cells one by one. Their external wall protrudes so as to make them first conical and then papillalike in form (Figs. 7, 9, 10). The outgrowths proceed further until they become slender hairs growing at times up to 1 mm in length. The diameter of the hairs is much smaller than that of the globular cells, measuring 38 μ on the average while the latter measure generally 115 μ in diameter. Although they belong morphologically to the category of trichomes, yet they are not identical in structure and even in function with the typical roothairs (Schwarz, 1883); they are often septate or even branched (Figs. 8, 9, 14), resembling rather the rhizoids of some cryptogamic plants (Haberlandt, 1904, p. 200). If undisturbed, they are all straight and radiate from the radicular end in all directions as shown in Fig. 8, but if one of them during its further prolongation should come in contact by its tip with a young host-root, it seems to attach itself firmly to the latter and then to coil or contract through its whole length, whereby the seedling is drawn closer to the host (Fig. 10). This is evidently an advantageous contrivance for the parasite to facilitate its organic connection with the host, that is to say, the formation of the primary haustorium. In Fig. 9 is shown one of the hairs just adhering to a host-root, and about to bend itself, while in Figs. 10 and 12 are shown hairs in a much contracted condition with the radicular end brought much nearer to the host.

By what means the tip of the hair fixes itself to the host has not yet been made out exactly. It is not impossible that a cementing substance is secreted by the hair, but there has actually come under my observation such a case as shown in Figs. 9 and 10, where the fixation was effected by a slight penetration of the tip of a hair between the epidermal cells. My observations, however, are not extended enough to justify the conclusion that this is a general case with *Aeginetia*.

So far as I know, such an organ has not hitherto been described in phanerogamic parasites. Analogous but not homologous cases may perhaps be found in the root-hairs that develop previous to the formation of haustoria on the typical root of some hemi- and holo-parasites, such as *Melampyrum* (Leclerc du Sablon, 1887), *Lathraea* (Heinricher, 1895, p. 381), *Santalum* (Barber, 1906). In all these cases the root-hairs appear to serve simply for the fixation of the root of the parasite to the host. The cushion-cells in *Cuscuta* (Peirce, 1893) may be considered to perform the similar function. In *Aeginetia* it is quite obvious, as already stated, that the hairs serve first of all as a „tentacle“, and after contact with the host, as a „prehensile organ“, besides drawing the seedling closer to the host. In function, therefore, they possess all the characters of a typical tendril (i. e., *Cucurbitaceae*), and hence I venture to propose for them the name of „hair-tendrils“.

In the root-system a similar function has already been known to appertain to the so-called root-tendrils (see Pfeffer, 1904, p. 416). They are not, however, identical morphologically with the hair-tendrils; for in typical root-tendrils the entire root plays a part of a tendril, while in hair-tendrils an appendage of the radicle comes into play. In origin, again, the hair-tendrils may be homologous to the papilla-like cells at the tip of the radicle in the seedling of *Orobanche* (Koch, 1883, p. 189). However, in structure and function the latter organ seems to be different from the former showing a rather close resemblance to the cushion-cells of *Cuscuta*.

The kind of stimuli required in causing the curvature of the tendrils remains still unknown. But on the basis of my culture-experiments it seems highly probable that, unlike the true root-hairs (see Pfeffer, 1904, p. 459), mere contact with sand- or soil-particles remains quite ineffectual, but that some chemical stimulus must be concerned, to which the tip of the tendrils coming in contact with the host-root must respond. That normal tendrils may respond to chemical stimuli has already been ascertained by Correns (1896, p. 16).

In almost all cases the globular cells do not appear to develop all into the hair-tendrils: some of them remain unchanged, while some are arrested from further development after reaching the conical or papillae stage. As for the most probable ground of such variable development of the globular cells, my observations of a number of seedlings have led me to the conclusion that the number of tendrils that are formed in a seedling must depend more or less upon the chances of meeting with an appropriate host. In fact I have found that when a seedling came on contact with a host by a premature development of some tendrils the remaining ones were more or less arcested from further development and the globular cells from forming further tendrils (Figs. 9, 10, 12); while when a seedling remained away from the host long enough many tendrils were observed to develop at once and in full length, or many globular cells to give rise to tendrils (Fig. 7). This fact makes it most probable that the seedling develops as many tendrils as possible in several directions until it finds out a host thus securing as many chances to meet with a desired host-root, but that as soon as one of the tendrils comes in contact with it the seedling does not need the development of further tendrils.

Usually only the apex of the tendril is responsive to the stimulus, but that the other portions may also react may be seen in Fig. 11, where a tendril is shown twining around a root-hair of a proper host-root (*Zingiber*).

The tendril on coming in contact with the host seems to be retarded in growth as in the typical tendril (Fitting, 1903, p. 604), and it seems to wither and die away if kept indefinitely away from a proper host.

In view of all these facts there can be any doubt that the hair in *Aeginetia*-seedling is quite different both morphologically and physiologically from the true root-hair, and that it most closely resembles the typical tendril in its function.

While the changes described above are taking place at the radicular end, we can not find any notable change at the plumular end except for a slight increase in size. The general form of the embryo at this stage is then as reproduced in Fig. 12. It is perhaps the last stage to which an embryo can develop without coming in contact with the host-root. Much starch-granules still remain in the embryo and endosperm, and serve as the reserve material for the further development of the seedling.

Tubercle and Primary Haustorium.

When a seedling as above described comes in contact with a host-root by means of a hair-tendril further development follows immediately. By a rapid multiplication of cells the seedling grows so as to become visible to the naked eye. The newly produced tissue gives rise. besides a primary haustorium, to a tubercle from which the shoot and root-system of the plant are afterwards formed. What is remarkable is that the multiplication of cells does not take place unless the seedling becomes attached by one of the tendrils to the host. Since the seedling is otherwise entirely incapable of further development in spite of the presence of the reserve material left in the endosperm, it follows that the further development of the seedling is associated with the stimulus of the host.

The multiplication of cells occurs under the tendril-cells. The parenchymatous tissue thus derived pushes and finally breaks the latter, and comes to lie in direct contact with the tissue of the host-plant. Until an organic connection becomes established between the seedling and the host-tissue the multiplication of cells must be due to the reserve material in the seed. The maximal size to which the cell-mass can thus attain is less than 1 mm in diameter, approximately the same as that to which the seedling of *Orobanche* can reach with the help of its endosperm alone (Koch, 1883, p. 189).

The cell-mass thus formed becomes a tubercle generally of a spherical or oval form (Figs. 13, 14). It forms a large part of the seedling, making the plumular end, globular cells and tendrils highly inconspicuous. The formation of the tubercle has already been observed in *Orobanche,* in which however only one fifth of the whole length of the seedling is transfered into it.

The frontal portion of the tubercle penetrates into the young cortex of the host-root and becomes differentiated into a primary haustorium which is completed by the formation of tracheids in direct connection with the conducting system of the host-root. On the completion of the haustorium the tubercle derives nourishment from the host, and there ensues a vigorous development. The further development of the tubercle — formation of the shoot and root-system — is quite the same as in *Orobanche* (Koch 1883).

Germination-Experiments.

As has been quoted above, there is no doubt that in the germination of the Orobanchaceae, as ascertained in *Orobanche* and *Lathraea,* a chemical stimulus comes into play. Still it has not been conclusively shown that whether the stimulus in question is due to the character of the roots as such, or is entirely peculiar to the root of the proper host. Although Koch has expressed the opinion that „die Samen der Orobanchen keimen nur im Anschluß an die Wurzel einer geeigneten Nährpflanze“ (Koch, 1883, p. 188), it seems to me that a sufficient number of plants has not been tested with this point in view. Heinricher (1894) succeeded in raising the seedling of *Lathraea* on the roots of a very few kinds of trees. From his experiments we cannot conclude that the roots of all trees can stimulate the seed to germination. A further study is also needed to decide whether the seed germinates on the roots of herbaceous plants. But when we consider that these parasites thrive only on certain plants¹) one might consider himself justified in assuming that the germination takes place only on these plants. Likewise, as only monocotyledonous plants are at present known as the hosts of *Aeginetia* in the field²), one might be led to the same assumption. This has, however, been proved to be quite incorrect by the germination-experiments now to be described. As these experiments were originally planned to verify what we had assumed, they were not so extended as were afterwards found desirable.

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¹) Among more than 300 species enumerated by von Beck (1890) as the hosts of *Orobanche* no monocotyledonous plant is mentioned as the proper host.

²) So far the following plants have been ascertained to serve as the host: *Canna indica* L. (Dandoku). *Carex lanceolata* Boott. (Hikagesuge). *C. Morrowi Boott.* (Kansuge). *C. transversa* Boott. (Ko-onisuge). *Imperata arundinacea* Cyr. var. *Koenigii* (Benth.) Hack. (Chugusa). *Miscanthus sinensis* (Anders.) (Susuki). *M. sacchariflorus* Hack (Ogi). *Oryza sativa* L. (Upland form) (Okabo). *Panicum miliaceum* L. (Kibi). *P. flumentaceus* L. (Hie). *Saccharum officinarum* L. (Satokibi). *Setaria italica* Kth. var. *germanica* Trin. (Awa). *Zea Mays* L. (Tomorokoshi). *Zingiber Mioga* Rosc. (Myoga).

1. Germination of the Seeds on Pot-Plants.

Aeginetia-seeds were laid on the roots of several pot-plants. The experiments were made in July and the germination took place within two weeks. The plants used comprised several species of Phanerogams and Cryptogams, two pots being prepared for each.

a. Pteridophytes: *Selaginella involvens* Spring. (Iwahiba) and *Aspidium rhomboideum* Wall. (Kanawarabi) have rather weakly developed roots. After two weeks some of the seeds laid on them were seen to have produced a few globular cells outside the testa but no further development took place even after four weeks or more.

b. Gymnosperms: *Cryptomeria japonica* Don. (Sugi) and *Thujopsis dolabrata* S. et Z. (Asunaro) were used. Although the roots are not very vigorously developed, yet a few of the seeds produced globular cells. Further development remained uncertain.

c. Monocotyledons: Keeping in mind that *Aeginetia* grows in the field exclusively on plants of this group I have used for my purpose several species from various families, comprising also the well-known hosts for control[1]).

Juncaceae.

Luzula campestris Dc. var. *capitata* Miq. (Suzumenohie).

Cyperaceae.

Carex japonica Thunb. var. *chlorostachys* (Don.) Kük. (Shirasuge).
C. Morrowi Boott. (Kansuge)*.

Gramineae.

Arundinaria Simoni Riv. (Medake).
Calamagrostis arundinacea Both. (Chigusa).
Miscanthus sinensis (Anders.) (Susuki)*.
Oryza sativa L. (Upland form) (Okabo)*.
Panicum miliaceum L. (Kibi)*.
Setaria excurrens Miq. (Inuawa).
Zea Mays L. (Tomorokoshi)*.

Araceae.

Acorus gramineus Ait. (Sekisho).

Commelinaceae.

Pollia japonica Hornst. (Yabumyoga). Thick, soft and vigorous roots with densely developed root-hairs.
Rhoeo discolor Hce. (Murasakiomoto).

Liliaceae.

Allium fistulosum L. (Negi). Vigorous development of roots.
Hemerocallis fulva L. (Yabukwanzo).
Ophiopogon japonicus Ker. (Janohige). Roots dense but not vigorous.

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[1]) The natural hosts are marked with an asterisk.

Iridaceae.
Iris tectorum Max. (Ichihatsu).
Dioscoreaceae.
Dioscorea sativa L. (Marubadokoro). The development of roots far less vigorous than other plants.
Zingiberaceae.
Zingiber Mioga Rosc. (Myoga)*. Roots very vigorous.
Cannaceae.
Canna indica L. (Dandoku).

With the exception of *Ophiopogon* all the plants above mentioned gave the required stimulus, and the seed attained after two weeks to a stage similar to that shown in Fig. 4. The percentage of germination seemed to be larger on plants which produced vigorous roots. In *Zingiber* and *Pollia* young roots were constantly and luxuriantly produced during the experiment, so that almost all the seeds laid on them came to germination. As for *Ophiopogon* the roots were not very active during the experiment, and the necessary stimulus, if present, seemed to have been too feeble.

c. Dycotyledons: Only a few plants were taken here. This was due to the circumstance that more plants had not been prepared as pot-plants for my purpose.

Plumbaginaceae.
Armeria maritima Willd.
Araliaceae.
Fatsia japonica Dcne. et Planc. (Yatsude). The roots were very few and not vigorous.
Geraniaceae.
Pelargonium zonale Willd. (Montenjikuaoi).
Rosaceae.
Pirus Malus L. var. *tomentosa* Koch. (Ringo). Roots evry few, not vigorous.
Prunus Mume S. et Z. (Mume). Roots very few, not vigorous.
Solanaceae.
Solanum tuberosum L. (Bareishod). Roots very scanty.
Leguminosae.
Pisum sativum L. (Endo).
Compositae.
Chrysanthemum sinense Sab. (Kiku).
Solidago occidentalis Torr. et Gray. (Oawadachiso).
Taraxacum officinale Wigg. var. *glaucescens* (Koch). (Tanpopo). The development of roots not vigorous).

Of these plants *Fatsia* and *Taraxacum* did not bring the seed to germination. This might perhaps be due to a comparatively weak development of the roots as above noticed. On the other hand, the seeds laid on all the other plants mostly germinated just as they did on Monocotyledons. It must, however, be remarked that the germination did not all proceed so far in their development so to produce the hair-tendrils: stopping at the stage shown in Fig. 4, they ultimately came to death, mainly owing to mould fungi or other microorganisms.

The foregoing experiments show, contrary to our natural expectation, that the stimulus necessary for the germination of *Aeginetia*-seed is not peculiar to particular species of plants, but is given by all vigorously developing roots, whether of Phanerogams or Vascular Cryptogams. If it be admitted that a chemical stimulus is concerned here, it is most probable that the stimulant is an excretion of the roots. The following experiments afford some evidence for this view.

2. Germination of Seeds wrapped in Paper on Pot-Plants.

This experiment was undertaken to ascertain whether the direct contact of the seed with the host-root is neccessary for germination or not. The seeds were wrapped in one or several sheets of well washed filter-paper and laid among the root meshes of the pot-plants. For control seeds prepared in the same manner were kept at the same time in a moist chamber, and again unwrapped seeds were laid directly on the roots of the same pots. The seeds wrapped in 3—5 sheet sof paper did not germinate about the time that the unwrapped seeds germinated vigorously. However those wrapped in one sheet and laid on *Zingiber* and *Pollia* germinated partly. In the mean time the control seeds in the moist chamber remained entirely unchanged.

From this experiment we see that direct contact of the seeds with the host root is by no means an indispensable condition in bringing them to germination, and that the germination is associated with a certain substance or substances excreted by the host-root and diffused into the surrounding medium. That the percentage of germination is smaller in the case of the wrapped seeds than in those laid directly on the root, and that it becomes less with the increase of the sheets of paper are strong evidences that the amount of the diffusible substance depends upon the nature of medium through which it must pass to reach the seeds.

3. Germination of Seeds without Host-Root.

The seeds were kept in water (tap-water or destilled water) or in a moist chamber. They were also sown in soil without any visible plant. In either case I was not able to observe any sign of germination. If such seeds were afterwards brought on the root of any plant, the germination took place easily. Hence it follows that the seed of *Aeginetia* always requires a stimulus from the roots for germination.

4. Germination of Seeds in Chemicals.

This is only a preliminary experiment to find out a stimulating substance among chemicals, and only a few substances were tested. Under a bell jar one end of a piece of filter-paper moistened previously with destilled water, on which the seeds were placed, was immersed in a given solution of the substance to be tested in a small vessel. By capillary action the given solution diffuses up the paper so that the seeds are acted on by the substance in various degrees of concentration at different parts of the paper. For control tap-water and destilled water were tested in the same manner. The results were entirely negative, and no germinating seeds were observed after two weeks or more. The seeds were attacked by mould fungi and destroyed. The chemicals tested and their concentration in the vessels were the following:

Hydrochloric acid	1/100 and 1/500 mol.
Phosphoric acid	1/100 and 1/500 mol.
Tartaric acid	1/100 and 1/500 mol.
Citric acid	1/100 mol.
Formic acid	1/100 and 1/500 mol.
Malic acid	1/10 and 1/500 mol.
Monopotassium phosphate	1/100 mol.
Sodium hydroxide	1/100 and 1/1000 mol.

It would be of great interest and importance to extend the above experiments and to determine, if possible, a chemical or chemicals that would stimulate the *Aeginetia*-seed to germination. If such a substance be found out, it is highly probable that it is one of the excretions of the roots. Much difficulty must certainly lie in the way of such a study. It is generally known that roots excrete acidic substances (Czapek, 1905, p. 873), and recently Schreiner and Reed (1907) have found out that a very slight amount of substances is excreted by roots, which act deleterious to their growth [1]). The amount is so exceedingly small that it can not be detected by chemical analysis, but its presence is revealed by the chemotropism of roots. The method proposed by the last named authors is very ingenious, and it leads us to think that our germination-experiments, if extended further, might perhaps be applicable to the investigation of root-excretions.

Development of Tubercle and Selection of Host.

Although it is clear from the foregoing accounts that all roots can stimulate *Aeginetia*-seed to germination, still the facts obtained both from field-observations and culture-experiments clearly show that *Aeginetia* cannot grow on all plants. This is proved by my experiments. By careful examination at intervals of the pot-plants on which the seeds were laid, we could ascertain that the germinating seeds did not develop equally well on Cryptogams, Gymnosperms and Dicotyledons. Again, among Monocotyledons different plants acted very differently. The plants of this group that induced the seedlings to form tubercles were *Luzula*, both species of *Carex, Calamagrostis, Miscanthus, Setaria, Oryza, Panicum,*

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[1]) For the literature on root-excretions see Schreiner and Reed's paper.

Pollia, Zingiber and *Canna,* most of them being already known as natural hosts[1]). Again the development of the tubercles was not only very unequal on these plants, but even in the same species it was different on different individuals. After two weeks all the seedlings reached the stage shown in Fig. 4, but the size of the tubercles during the next two weeks was very variable, some attaining to the size of poppy grains and others to that of the corn. The growth of the tubercles were especially vigorous on *Zingiber* and *Pollia.* It was also observed that the development of the parasite was less rapid on pot-plants than on those in the field: in September it was all in flower in the field while the shoots scarcely appeared above ground in the pots. It follows that the growth of the parasite is most intimately connected with that of the host, and in particular with the activity of its roots.

I have already remarked that the host-root induces no germination when too feebly developed. The same cause must not be assigned for the nondevelopment of tubercles on some of the plants used in the experiment. For instance, *Allium, Iris, Acorus, Hemerocallis,* and others produced numerous vigorous rootlets and appeared always to be much more rapid in growth than some natural hosts such as *Carex* and *Miscanthus.* It is certain, therefore, that there are fit and unfit plants as the host of *Aeginetia.*

As for the intimate relation between the seedlings and the proper hosts, or plants unfit as the host, I have no evidence to bring forward. It may be that the roots of some plants are unfit for inducing the formation of the primary haustorium, the hair-tendrils, or perhaps the tubercles. Which of these assumptions holds true must be settled by further investigations. At present I can go no farther than to state that the stimulus which causes the seeds to germinate and the stimulus which causes the seedlings to develop further are of a quite different nature.

General Remarks and Summary.

On looking over what have been described above, we see that *Aeginetia* presents many remarkable characters which must be due to its parasitic life. In the first place, the formation of the hair-tendrils is a most specialised contrivance for finding out the host. It may be that in *Lathraea* and *Orobanche* the seedlings can not easily reach the host, unless the seeds are placed close to the host-root so that their radicles lie against the latter. Otherwise, the tip of the radicles may diverge from the host-root more and more as they grow further and further so as to make the development of the seedlings impossible, just as the same organ of *Viscum* would do if it should be insensitive to light, or the same organ of autophytic plants if insensitive to light and gravity.

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[1]) See foot-note in the preceding page.

In *Aeginetia* the formation of the hair-tendrils is alone sufficient to avoid such a danger.

In the second place, *Aeginetia* shows some transitional states between autophytic and the most advanced parasitic life. In most hemiparasites, or more strictly speaking, green parasites such as Santalaceae (Kusano, 1906, Barber 1906, 1907), Rhinanthaceae (Heinricher, 1901, 1902) and Loranthaceae, the germination is neither associated with the presence of the host, nor have they any marked tendency to select their host. But some holoparasites or at last Orobanchaceae, hitherto studied, have acquired the habit of not developing and even of not germinating without the presence of the roots of their proper host. While thus the intimate relation of the parasite and host-root is in this case restricted to certain limited species of plants, *Aeginetia* shows itself to be many-sided in this respect: In *Orobanche* and *Lathraea* the selection of the host takes place already at the period of germination, it takes place in *Aeginetia* at a later period. Thus certain variations observed to occur in the Orobanchaceae in their behaviour towards the host-roots a study of other species of the same family is very desirable.

The chief results of the experiments described in the foregoing pages may be summarised as follows:

1. The germination of *Aeginetia*-seed does not take place in water, moist chamber or soil. It requires always the stimulus of the root of other plants.
2. The seed kept dry for two years loses its germinating power.
3. The plants which stimulate the seed to germination may be Vascular Cryptogams, Gymnosperms, or Angiosperms.
4. The stimulant is an unknown substance that is perhaps excreted by active roots of all higher plants.
5. The development of the seedlings takes place only on certain species of Monocotyledons. Its conditions are entirely different from those that are necessary for the germination of the seeds, the former being fulfilled only by certain plants while the latter are found in the roots of all higher plants.
6. The first change that takes place during the germination is the swelling of the epidermal cells at the radicular end of the embryo and their transformation into the hair-tendrils.
7. The seedlings are much reduced in form, and before they are connected with the host no multiplication of cells take place.
8. The seedlings develop, when attached to the host, spherical tubercles. They are formed by the meristematic tissue under the hair-tendrils.
9. For the multiplication of cells in the seedlings certain stimulus from the host-roots to which the hair-tendrils are sensitive seems to be required.
10. The tubercles become differentiated first into the primary haustorium at the frontal portion, and then into the shoot and root-system at the other portions.

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Explanation of Figures.

All figures except Figs. 13—16 are drawn with the aid of the camera lucida from the fresh materials and magnified 130 times.

Fig. 1. An adult embryo in a ripe seed.

Fig. 2. The same shown in optical section. Fragments of testa are attached to the radicular end,

Fig. 3. A seed at the beginning of germination, with some swollen epidermal cells at the radicular end appearing outside the testa.

Fig. 4. A seed at somewhat later stage.

Fig. 5. An embryo in the germinated seed as shown in Fig. 3.

Fig. 6. The same in the seed shown in Flg. 4 (optical section) Starch-granules accumulate at the median portion.

Fig. 7. Radicular end of a seedling showing one of the globular cells protruded into a papilla.

Fig. 8. The same with full grown tendrils.

Fig. 9. The same showing one of the tendrils attached to a host (*Zingiber).* Its apex is penetrating between two epidermal cells of the host.

Fig. 10. The same with a much shrinked tendril.

Fig. 11. The same with a tendril twined round a root-hair of a host *(Zingiber).*

Fig. 12. Two seedlings at advanced stage. In the right is shown an entire embryo taken out df the endosperm.

Figs. 13—15. Tubercles at several stages of development. ca. 40.

Fig. 16. A shoot and roots derived from a tubercle. Nat. size.

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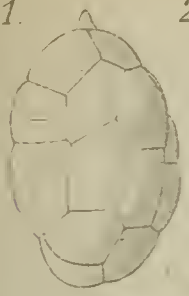

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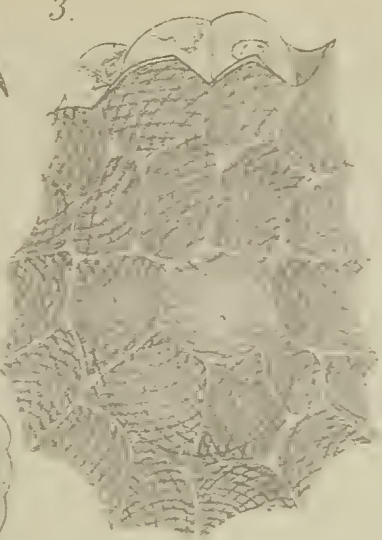

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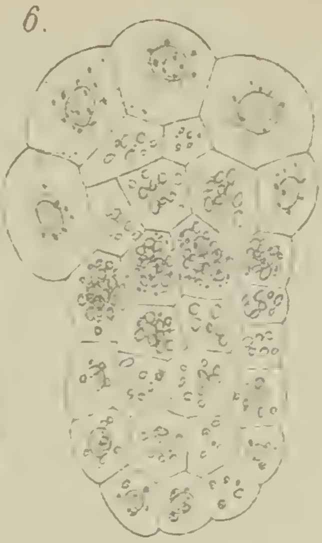

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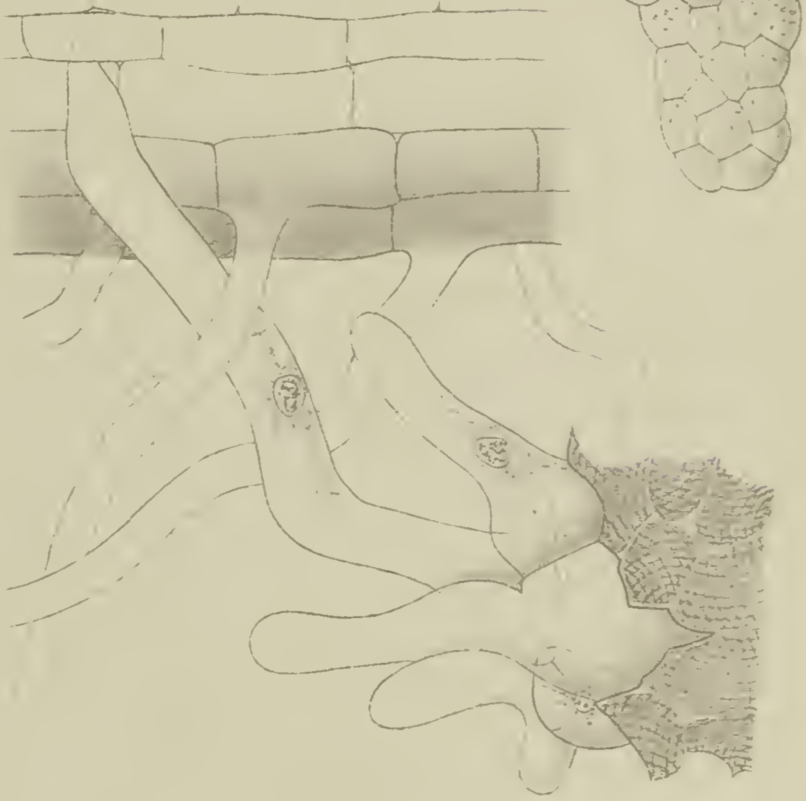

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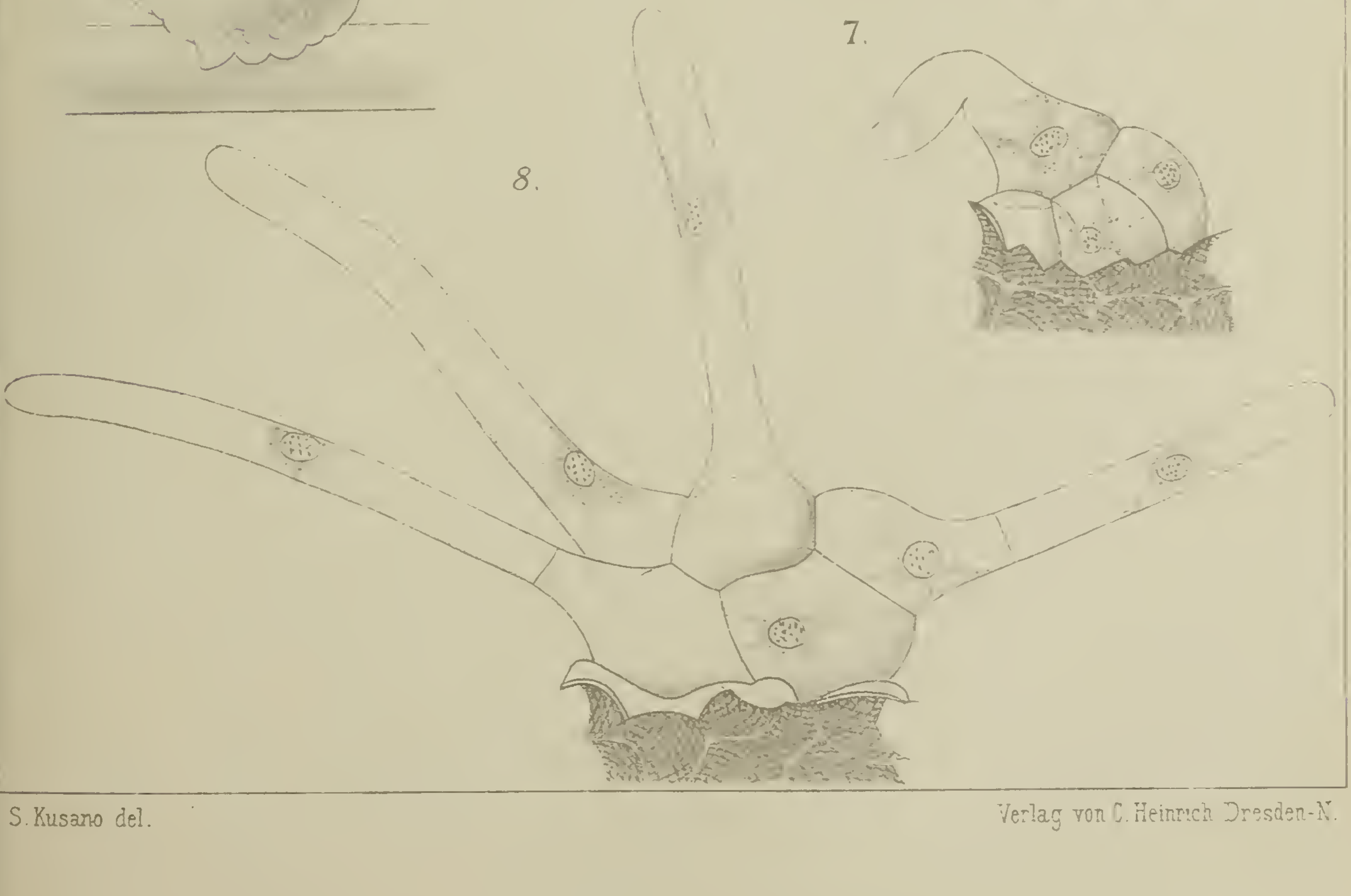

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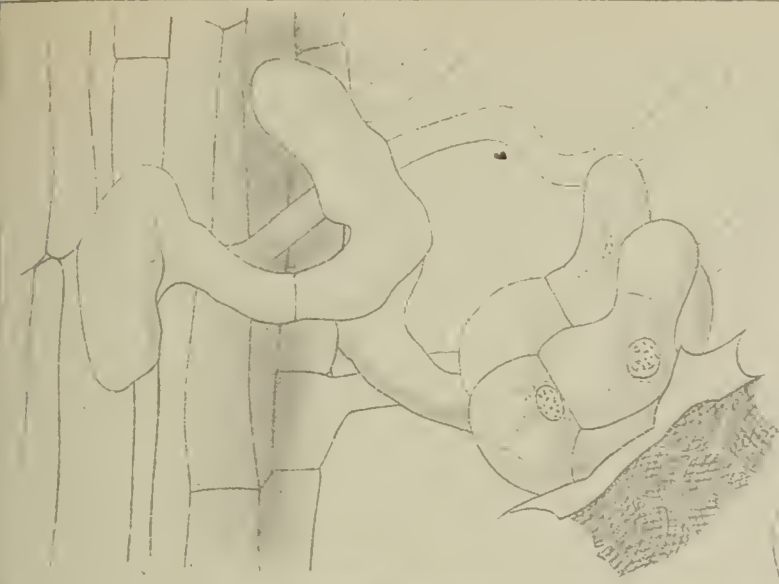

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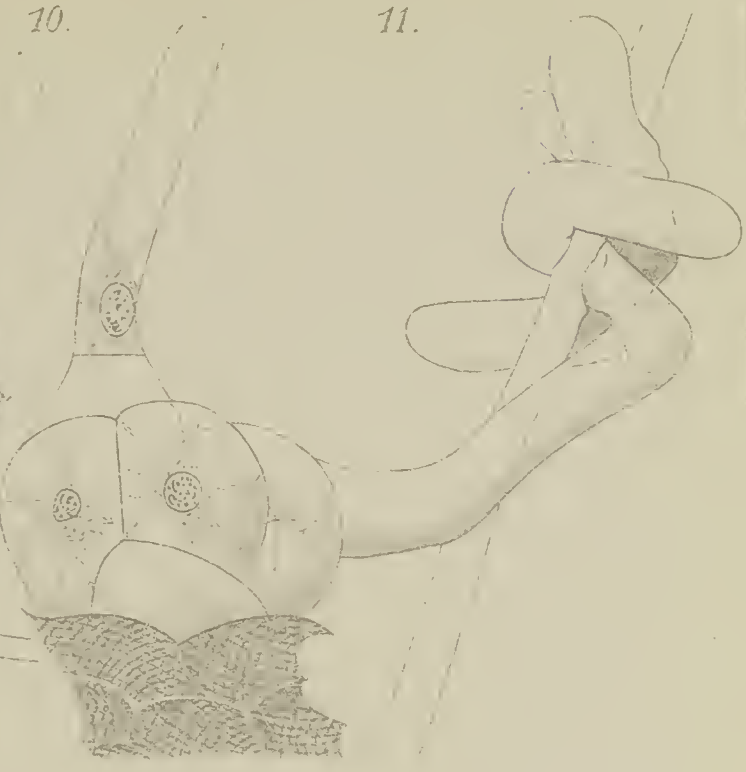

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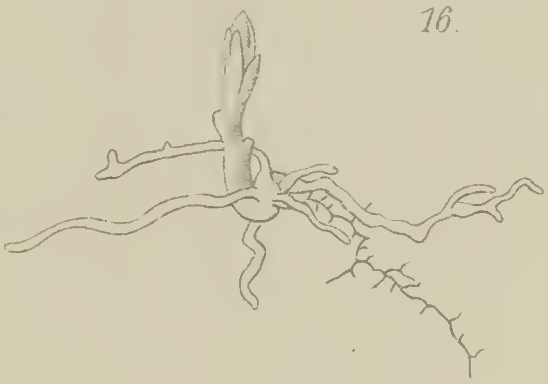

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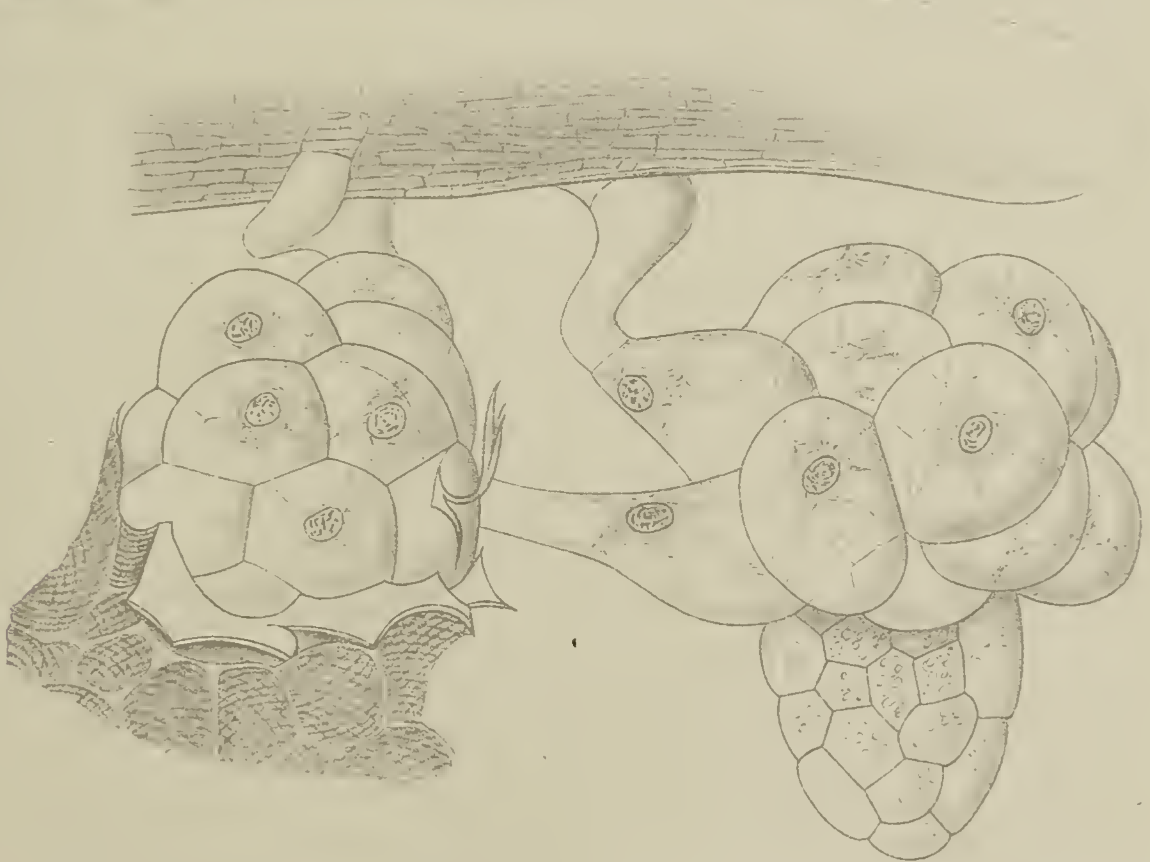

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