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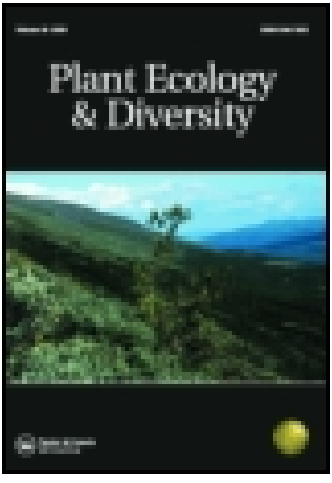

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VIII. On the Ovule of Euphrasia officinalis

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VIII. *On the Ovule of* Euphrasia officinalis. By G. Dickie, M.D., Lecturer on Botany in the University and King's College of Aberdeen.

Read 13th January 1848.

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In a communication submitted to the Society two years ago, an attempt was made to prove that in certain plants, tubes observed in connexion with ovules are not really in every case derived from the pollen, as stated by some physiologists, but prolongations from some part or other of the ovules. This statement had reference only to a few plants, and the same restriction is still adhered to: it would be rash to generalise in the matter. It was argued in favour of this opinion, that the number and position of the ovules would present obstacles to the pollen-tubes entering their foramina. An argument, it may be said, of greater value was employed, viz. that the development of such a tube might be traced at an early stage projecting from the exostome in the form of a papilla, ending in a blind extremity, afterwards increasing in length and coming in contact with the placenta. The observations of the late Mr. Griffith on *Santalum* were quoted in favour of the idea in question, that acute observer having proved the true nature of the tube sent up to meet the pollen-tube, it being a prolongation of that part which is usually denominated embryo-sac. It was not in my power to speak so emphatically regarding the nature of the tubes in those plants in which they were seen; in *Narthecium, Bartsia* and *Euphrasia* I expressed however my belief that they might be prolongations of the apex of the nucleus. It was considered sufficient at that time to show that prolongations like pollen-tubes might be sent up from the ovule. I have repeatedly examined ovules of *Euphrasia* and have found them uniformly present. I had originally set out with the view of tracing pollen-tubes into the ovule, and if possible observing them in contact with the embryo-sac, and even in the act of causing introflexion of that part. When I say, if possible, the expression has reference to myself; observers of great experience and of high authority in points relating to vegetable physiology had made such statements, and implicit confidence was placed in them. Tubes were observed, but for the reasons alluded to I felt convinced that they had origin from the ovule itself.

Additional observations have led me to change the opinion formerly expressed respecting the part of the ovule from which these organs in *Euphrasia* are derived, and the present communication has reference to that point, and to a peculiarity in the structure of the ovule of that plant, which, so far as I am aware, has not been hitherto described.

The substance of the nucleus is very thin about the period of fecundation, the embryo-sac which lines it becoming highly developed. This sac is attenuated at the posterior extremity; its body tapers gradually upwards into a neck, which is bent at an obtuse angle, and near the apex it is bulbous; at this apex or anterior extremity there is the appearance of a fissure or cleft bounded by two or three rounded lobes. In the interior of the neck and bulb of the sac there is distinctly seen a tube which is narrow below, but somewhat dilated at the part corresponding to the bulb of the sac. This tube I have observed in several instances prolonged upwards, passing out at the terminal fissure and ending in a papilla closed at the extremity. I have traced it some way into the interior of the body of the sac, but the presence of the cellular contents has prevented me from being able clearly to see its relation to the very minute embryo, whose outline might be seen shining through. In one preparation in my possession there is an appearance which seems to indicate a connexion between the embryo and the tube, but I cannot decidedly assert that they are continuous. Lying parallel to the embryo-sac, and on the side next the short podosperm, there is another organ similar in structure; it may be compared to a Florence flask in shape; the necks of the two are quite continuous.

The nature of this remarkable appendage was not easily comprehended at first. I am inclined to believe that the arrangement of the parts in *Euphrasia* is somewhat similar to that in some species of *Veronica*, and which has been described and illustrated by M. Planchon, to the accuracy of whose descriptions and delineations I can bear testimony from my own observations. In the earlier stages of the ovule in *Veronica* the upper end of the sac is bulbous, below this it tapers into a neck, then becomes again somewhat dilated at the part in which the embryo afterwards appears, and which may be called the body of the sac; towards the posterior end it gradually becomes narrower and ends in a sharp point. At more advanced stages the neck of the sac presents several varicose appendages. The large appendage already described as lying parallel to the embryo-sac in *Euphrasia*, and continuous with its neck, is merely a process of that part. In *Euphrasia*, however, the embryo-sac does not appear externally, as in the advanced stages of that of *Veronica*.

The tube already described as traversing the bulb and neck of

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the sac, and passing some way into the interior of the body of the same organ, is certainly not the least remarkable part of the arrangement. The principal argument against its origin from the pollen has been already alluded to, viz. its closed papilliform end projecting from the fissure in the extremity of the bulb. It is certainly very difficult to pronounce a decision respecting the nature of the extremity of a transparent membranous tube less than a three-thousandth of an inch in diameter. I have come to the conclusion mentioned, after repeated careful examination under various powers of a microscope (by Brunner of Paris) varying from 250 to upwards of 600 diameters. Figure 1 represents a preparation in my possession, in which two tubes are lying beside each other; one of them is evidently broken across, the other is closed at the end; the latter may be traced to the exostome of an ovule, part of which only is represented. The ruptured tube belonged to another ovule which is not represented in the figure. But for the fact just mentioned, I should feel constrained at once to admit, that appearances are much in favour of Schleiden's opinion, excepting that part which has reference to the introflexion of the embryo-sac.

It will now be evident, therefore, that in *Euphrasia*, the ovule tubes are not prolongations of the apex of the nucleus, but proceed from the interior of the embryo-sac. As already mentioned, I am not at present prepared to state positively the relation between the tube and the embryo.

The majority of observers seem to agree respecting the presence of pollen-tubes in the tissue of the stigma and style; and they have been traced into the interior of the ovarium. That part of the subject which has reference to the presence of such tubes connected with the ovule, and their nature, has given rise to much difference of opinion.

Mirbel long ago pointed out the existence of tubular prolongations proceeding from some part of the ovule. Those observed by Mr. Brown in the *Orchideæ* were supposed to have their existence determined by the action of the pollen, but not to be directly derived from it. Schleiden spoke emphatically respecting the pollen-tubes reaching the embryo-sac, and the same was admitted by Meyen, though they differed respecting the subsequent relations of the two. Griffith demonstrated the presence of both pollen- and ovule-tubes. Hartig admitted the existence of three kinds in connexion with the ovules in different plants: first, true pollen-tubes, as in the *Coniferæ*; second, prolongations of the conducting tissue of the style, as in some *Cruciferæ*; lastly, tubes proceeding from some part of the ovule itself, as in certain *Cupuliferæ*. Gasparrini alludes to their presence in connexion with the ovule, but supposes them to be derived from the con-

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ducting tissue of the style; Hartig and he are therefore agreed in this, in regard to some plants at least. In *Orchideæ*, Amici, Mohl and Müller have all recently traced the pollen-tube through the foramina of the coats to the embryo-sac. Hoffmeister has made similar observations in the *Œnothereæ**. Tulasne says he has traced the pollen-tube into the interior of the embryo-sac. The opinions respecting them are therefore three: first, they are true pollen-tubes, an opinion supported by Schleiden, Meyen, Amici, Mohl, Müller, Gelesnow, Tulasne and others; second, they are derived from the conducting tissue of the ovarium, a view supported by Gasparrini, and also by Hartig, in reference at least to certain plants; third, they are derived from some part of the ovule itself, issuing from it, not directed towards it; this opinion derives support from the observations of Griffith and Hartig, and in the first part of this communication I have expressed the same in reference to *Euphrasia*.

Admitting that the pollen-tube reaches the embryo-sac†, the opinions respecting their subsequent relation to each other are the following. The view first promulgated by Schleiden was, that the pollen-tube pushed the summit of the embryo-sac before it and became invested by it. Hoffmeister admits that the tube in some instances where the embryo-sac is very delicate does push it inwards a little distance, but he also speaks of the tube becoming distorted by the resistance of the embryo-sac. Gelesnow, and subsequently Tulasne, state that the tube actually penetrates the embryo-sac and lies within it, and Schleiden has recently admitted the possibility of this in certain cases. Amici, Mohl, Müller and others state that it is merely applied to the sac at or near the apex; Meyen went a step farther, and supposed that their respective membranes were absorbed at the point of contact, thus permitting the direct mixture of the contents of both.

The action of the pollen in regard to the origin and subsequent development of the embryo may next be alluded to. It may however be observed, that the universality of a law having reference to the necessity for the action of the pollen is not now tenable, after the statement of Mr. Smith respecting the female plant of *Cœlebogyne*, and the still more recent observations of Gasparrini on the cultivated Fig. These statements will also diminish the tendency to call in question the observations on the Hemp long since recorded. Still, the action of the pollen, whatever be its nature, cannot generally be set aside.

It will be necessary to allude briefly to the stages through

* An account of the observations of Amici, Mohl, Müller and Hoffmeister, by Mr. Henfrey, is published in the 'Annals of Nat. Hist.' for Jan. 1848.

† Amici applies the term 'embryonal vesicle' to the earliest stage of this organ.

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which the embryo passes. The first or earliest condition is that of a simple cell, the germinal vesicle of Amici and others; it may be compared to the reproductive cells of some of the Algæ, and might be denominated with propriety the *sporoid* stage. The appendage termed 'suspensor' is worthy of notice; it is usually very highly developed in the sporoid embryo, and more so in some plants than in others; in some of the *Cruciferæ*, for example, it attains considerable dimensions. I have seen an embryo of *Draba verna* $\frac{1}{440}$ of an inch long, with a suspensor three times that length. Mr. Griffith describes the embryo in *Gnetum* as being attached to an enormously long, tortuous, but irregularly twisted cellular suspensor, its length varying from $3\frac{1}{2}$ to 5 inches; the whole length of the seed being about 1 inch.

Different opinions are entertained respecting the true nature of this appendage. According to Schleiden's view it is part of the pollen-tube; in the *Orchideæ* it would seem from Amici's observations to be part of the embryo-sac; he states that the part of the sac which was in contact with the pollen-tube becomes elongated upwards, dividing likewise into cells, which are transparent and situated one above another, so as to form a large confervoid filament; thus traversing in the opposite direction the course followed by the pollen-tube, becoming enlarged and passing through the orifices of the tegmen and testa, and being prolonged even as far as the placenta. According to Mohl the suspensor is essentially connected with the embryo, both being produced by the growth and division of the germinal vesicle, the lowest cell, the embryo, growing faster than the others. In *Tropæolum*, however, the development of the suspensor seems to precede that of the embryo; such at least is the result of Mr. Wilson's observations upon that plant*. It has been already stated that the embryo in its first stage may be compared to the spore of an Alga; future observations may afford greater reason than at present for saying, that the sporoid embryo of some phænogamous plants germinates *in situ*, emitting a confervoid filament, and requiring no transference to a new nidus, but finding in the interior of the embryo-sac all the conditions necessary to its existence and future development as a spore up to a certain period. In such Algæ as *Vaucheria, Derbesia*, &c., the spores usually escape from the cell in which they are produced; being furnished with cilia they are enabled to disperse themselves abroad, after a time they become fixed, and produce a plant like the parent. We may suppose that such change of circumstances is necessary to their proper development; the very fact of number alone would in certain cases be an obstacle to their

* London Journal of Botany, vol. ii. p. 623.

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growth in their original situation. In some instances however they do germinate *in situ*; these form the exception and not the rule. The sporoid embryo is usually solitary (*Citrus, Coniferæ*, &c. present exceptions); it does not require to change its place, but begins to germinate *in situ*, producing a confervoid filament, the embryo suspensor, which is usually directed towards the apex of the nucleus. But it may be objected to this idea, that spores do not germinate from any special fixed point; this however is not proved, for who has yet demonstrated that they have not a fixed point for the origin of the thread they produce? Sometimes however the suspensor is not directed towards the micropyle, but away from it; Gasparrini has observed this in *Citrus*, and Griffith observed that in *Osyris* the part corresponding to the suspensor has a direction quite opposed to the point reached by the pollen-tube. In the ovule of *Euphrasia*, the peculiarities of which have been already described, it is probable that the tubular filamentous appendage which protrudes from the apex of the embryo-sac is a prolongation of the terminal joint of the suspensor; at all events it cannot be derived from the pollen for reasons already given; at the same time it is not denied that the pollen-tube may reach and come in contact with the apex of the sac, though I have hitherto failed in detecting its presence. In a former communication an opinion was expressed that the jointed appendage of the embryo in the *Orchideæ* is no part of the pollen-tube, as supposed by Schleiden, but a process from the embryo itself; it was also added, that a tubular prolongation of its terminal joint might account for the presence of those tubes so abundant upon the placenta, and which had been by most observers considered to be derived from the pollen. From the observations of Mohl and others it would appear that the statement alluded to was only partially correct, their observations having confirmed the first part, but shown the second to be erroneous. For reasons already mentioned it would be premature to state that the production of the confervoid filament or suspensor, in other words, the germination of the sporoid embryo, forms the second stage of its development.

This stage appears to be quite independent of the action of the pollen. Mirbel and Spach in 1839* demonstrated that the first appearance of the embryo, the germinal vesicle, called by them primary utricle, precedes the application of the pollen. This early formation of the germinal vesicle, the first outline of the embryo, was proved by them in a large number of *Gramineæ*. Its independence of the pollen need scarcely be spoken of in *Cœlebogyne* and *Citrus* already alluded to. The ob-

* Report by M. Giraud in 'Annals of Nat. Hist.' vol. v.

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servations of Mohl on the *Orchideæ* lead to the same conclusion; those of Müller on the same family have a similar import. Mr. Henfrey in his report already quoted observes, "The whole question appears to be narrowed to the determination of the point, whether the germinal vesicle does actually exist before impregnation, since if that can be proved, all appearances yet observed may be reconciled by allowing for very slight errors in interpreting and delineating them."

The most careful and trustworthy observers speak with caution respecting the real nature of the action produced by the pollen-tube upon the ovule in impregnation. We have seen that at least one stage of embryo-life is independent of the contact of the pollen-tube with the embryo-sac; this I have ventured to denominate the sporoid stage. In some few cases, viz. *Cœlebogyne* and others, all the stages are equally so; generally however the future progress of the embryo is determined by the action of the pollen, whatever the nature of that action may be. The production of true radicle, cotyledons and plumule will constitute the last stage of embryo-development, and it is in reference to it that the best instruments cease to afford us any precise information. We can trace the progress of the organs in question, but we cannot state precisely in what way the action of the pollen influences their development. We do not derive any very clear information from such statements as those of Oken*, when he tells us that "the pollen electrifies, animates or inspirits the ovarium—that the male imparts nothing in impregnation but the solar ray or fluid nervous mass in its semen, which awakes, animates and inspirits the quiescent female—that the pollen is a most highly differenced electrical product; the seed-granule a wholly indifferent and tranquil mucous mass. The pollen falls upon the stigma of the pistil, and irradiation has taken place; the material fruit-capsule gains thereby so much polarity, that saps enough ascend, in order to develope the germless seed-vesicles."

The theory of Schleiden had the advantage over all others that it directly accounted for the presence of the embryo. Some observations of Mr. Griffith seemed to lead to a conclusion nearly similar, the difference being that the embryo is not developed directly from the end of the pollen-tube, but from cells produced by that part. It is presumed that no one has hitherto traced a tube through its whole length, connected with the pollen-grain at one end and with the embryo at the other.

* Oken's Philosophy of Nature, Ray Society, 1847.

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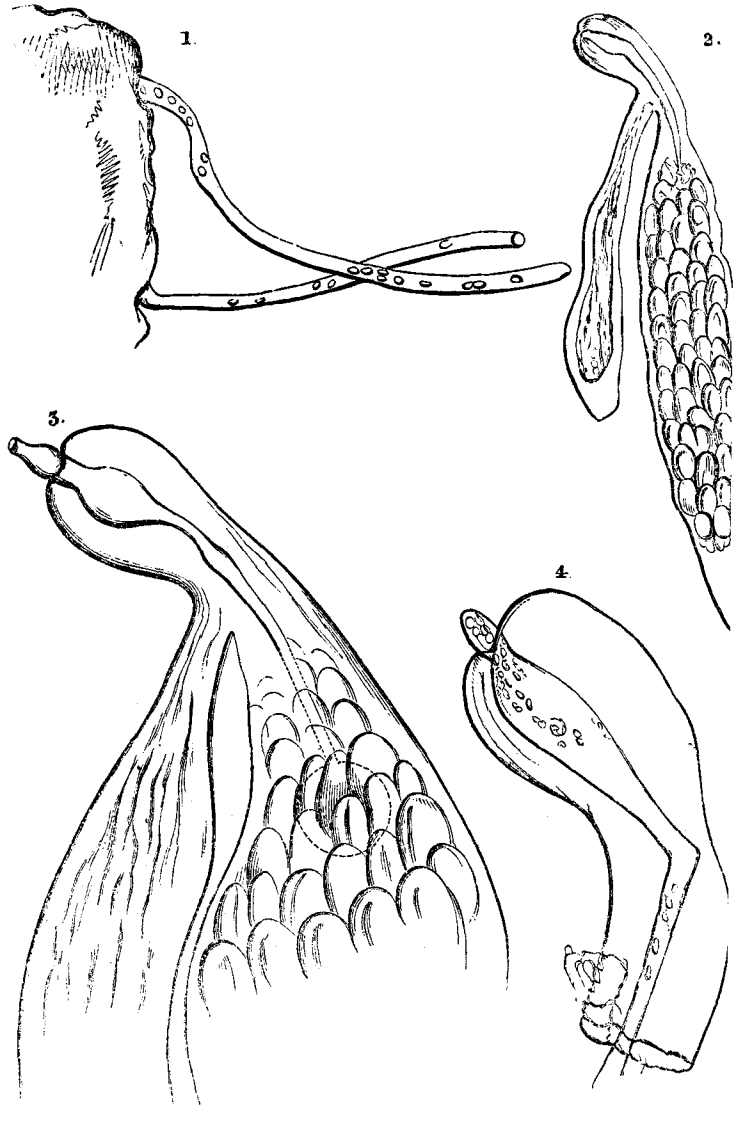

Fig. 1. Part of an ovule with a tube issuing from the foramen and terminating in a closed extremity.
Fig. 2. Embryo-sac and appendage.
Fig. 3. Part of another more highly magnified, showing the tube which traverses the sac.
Fig. 4. Neck and bulb of the sac with tube more highly magnified.

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