II. *On the Ovulum of Santalum album.* By WILLIAM GRIFFITH, Esq.,
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THE following observations were made at the Botanic Garden, Calcutta, in the early part of July, 1835.

The ovarium as well as the fruit of this genus corresponds with the structure laid down by Mr. Brown as one of the principal distinguishing marks of *Santalaceæ*, of which order I presume this genus is the type.

I allude to the central free placenta, bearing towards its apex a definite number of pendulous ovula. Yet Roxburgh has mistaken the structure entirely, and has evidently described the placenta together with the ovula, which he did not see, for the *ovulum*. This author, in his *Flora Indica*, vol. i. p. 443, describes the ovulum as "Germ. semi-superum, one-celled, containing one conical seed attached to the bottom of the cell." This mistake is perpetuated in the Botanical Magazine, new series, t. 3235, in which Roxburgh's description is quoted, and said to be faithful. The error of Jussieu with regard to the *ovulum* of *Santalaceæ*, first pointed out by Mr. Brown in his *Prodromus Floræ Novæ Hollandiæ*, and subsequently in the Appendix to Captain Tuckey's Expedition to Congo, p. 453, might have partly originated from an examination of *Santalum*, in which the ovula from their situation and direction may very easily be overlooked.

The placenta in this species is conical, rather obtuse in the young flowers, but prolonged considerably in those that are matured. Its apex corresponds at this period to the termination of the canal, occupying the centre of the style, but not opening between the stigmata in the fully developed flowers. The ovula are attached near the base, and not towards the apex, as in the other genera of this family. Mr. Brown's statement in Captain Flinders's

Voyage, in the Appendix to vol. ii. p. 569, that the ovula are attached to the apex of a central receptacle, must therefore be received with slight limitation.

The ovula in this genus have, I believe, in general a marked correspondence in number with the stigmata, the number of both being most commonly three. In the very young buds, as, for instance, those of a line in length, the future ovula are indicated by papilliform bodies of a homogeneous pulpy structure. They are, as it were, appressed to the surface of the placenta; they soon, however, become elongated, and appear truncate at the apex, which is minutely papillose. The next change takes place apparently with great rapidity, and consists in the protrusion of a tubular membrane from the centre of the apex of the ovulum, in which no opening could be detected previously. This tubular membrane passes down at first in the direction of the axis of the ovulum, but becomes immediately recurved, and passes up on one side of the ovulum, and in close apposition to the placenta.

I have not hitherto seen this membrane in the earlier stages of its formation. At the period to which I have alluded above, the tube may be traced to the point of attachment of, or base of the ovulum, where it ends, or rather begins, in a cul de sac. Immediately at its exit it is somewhat enlarged, but the diameter soon narrows, and continues so until it dilates again at the apex, which frequently shows a tendency to division. Throughout the ascending part of its course it is in close apposition with the placenta. Generally each tube reaches to the apex of this body; and at this point, and occasionally throughout other portions, mutual and tolerably firm adhesion takes place. Each tube is a simple, membranous, closed sac, containing a great number of molecules, which are exceedingly active, especially about the time of expansion of the flower. These molecules vary much in size, the variety depending apparently upon degrees of combination, the very small ones being alone simple. The motion consists of a rapid oscillation, and is frequently accompanied with considerable change of place; the molecules frequently approaching each other and then receding, the line or course which they describe being very irregular. The motion is much more vivid in those parts of the tubes in which the least aggregation of the molecules has taken place. These always appear to be least abundant in that part of the tube contained

within the body of the ovulum. At the period of their greatest activity they are more mobile when contained in the tubes than when they are made to escape into the fluid medium surrounding them. No change, excepting in size, occurs in the ovula up to the period of the application of the male influence to the stigmata. The tubes remain in apposition to the placenta, and continue to be simple, membranous, elongated, closed sacs. There is, perhaps, a tendency in many of the molecules to become aggregated in the dilated apices of the tubes.

Shortly after the period above alluded to exceedingly fine filaments are visible in the canal existing in the centre of the style, down which they pass to the apex of the placenta and become firmly applied to the extreme points of the tubes, more than one being generally found in apposition with each tube. From a solitary entrance I imagine them to terminate in dilated cul de sacs, or rather, to use the French term, in a *pâté d'oie*; I must remark, however, that in most cases they have appeared blended with the substance of the tubes, although in no case do they appear to *perforate* the membrane. At this time the molecules will be almost invariably found to have lost their motion and to have become densely aggregated into a grumous, opaque, central body, reaching from the apex of the tube to the apex of the ovulum. This is, however, frequently interrupted, but I believe that this is to be attributed to pressure during the operation of separating the ovula from the placenta. The tubes now adhere to the placenta, especially throughout the upper two thirds of their length; and on separating them, portions of the cellular tissue of the placenta to which they were applied become detached, and are visible adhering to the membrane of the tubes. Owing to this adhesion the tube itself appears to be occasionally cellular. A vesicle, generally of a globular form, and frequently appearing to contain mobile granules or molecules, is now visible in, and occupying the chief part of the apex of the tube. I have not been able to trace any continuity between this vesicle and the filaments stated to descend through the style to the tubes. The lower margin of this vesicle is in apposition with the upper portion of the grumous, opaque, central mass, which I have described above as resulting from an aggregation of the molecules. The part of the tube adjoining the apex of the nucleus is now visibly enlarged. In addition to the molecules which it contains a small central cell is apparent,

which cell is an extension of the inner wall of the corresponding part of the tube, and cuts off the base of this from communication with the ascending portion. Although the fruit of *Santalum* is monospermous, yet the above changes are not, as this would lead one to imagine, confined to one ovulum. The application of the filaments, as might indeed be expected from the situation of the points of the tubes, takes place frequently on all the ovula.

The abortion of these ovula is certainly, therefore, not ascribable to the non-agency of the male influence; neither is it to be attributed to pressure, or indeed to any appreciable cause.

The remaining changes, which in fact constitute the history of the ovulum, are limited, in accordance with the structure of the ripe fruit, to one ovulum. They take place within the dilated part of the tube, in which the single cell, as stated above, is first developed; and they consist in a further development of cells, and in a corresponding increase of size of this portion of the tube itself. It appears at this period opaque, owing to its being crowded with molecules, which are aggregated into distinct groups, perhaps corresponding with some cellular division of the interior of this part of the tube. At a still later period this portion is distinctly cellular, and most of the molecules have disappeared; at the same time, the constricted or narrow portion of the tube presents indications of a cellular subdivision. As the development proceeds the cells become more distinct, and end by occupying the whole of the tube. They are developed from below upwards. When these cells are completely developed, the membrane of the tube is not apparently visible; but we have a lax cellular body, corresponding to it in shape, which still remains attached to the ovulum. I should here mention that the tube, from the site of the development of the small cell to its origin at the attachment of the ovulum, never undergoes any change, except, perhaps, a diminution in the number of its molecules. This cellular body continues enlarging, especially at its base, and subsequently becomes a globose body with an apiculus, the point of which continues applied to the apex of the placenta: the original attachment continues perfect. When the young fruit is further advanced, the placenta will be found pushed to one side, and nearly inclosed in a depression of the cellular body. The original attachment of the base of the ovulum and of the tube still continues perfect, and this latter may be found towards the centre of the

depression. As the development proceeds, the cellular body, which has undergone scarcely any change in shape, enlarges and becomes firmer; at its apex a cavity will be seen, which is partially occupied by an oblong, minute, cellular, grumous body, the rudiment of the future embryo. This is attached by its superior margin to the corresponding part of the apex of the cavity, which is formed by excavation: as it continues to enlarge it extends downwards, and its attachment becomes considerably narrower and very slight, and at a rather later period it appears completely detached. As the cellular body continues to enlarge, it becomes whiter and of a firmer texture, and the embryo becomes oblong and cellular, the tissue towards its apex is more grumous and dense, and immediately above this part there is a degree of constriction visible. As the fruit advances towards maturity, the endocarp, which has already assumed the appearance of albumen, diminishes, and the mesocarp begins to be indurated. The cellular body is now nearly globular, white, and of a dense texture; its component cells being loaded with granules of fecula. The apex of the embryo now becomes lobed, indicating the commencement of a cotyledonary division; its attachment is exceedingly fine, and it is itself evascular. The subsequent changes in the fruit consist in a still further diminution of the endocarp, which is subsequently reduced to a spongy lax coating, adhering both to the now osseous mesocarp and to the albumen. The sarcocarp terminates by becoming baccate. In the seed they consist of an enlargement of the albumen (originally the cellular body); its apiculus finally almost totally disappearing. The division of the cotyledons increases, and has reached to a considerable extent before the tissue of the radicle becomes, as it were, condensed. The cotyledons are, during the first part of their development, somewhat conduplicate; they terminate by becoming elongated and plane on their internal appressed faces. The perfect radicle is ovate, tapering to a fine point.

From this statement it will at once appear that the mode of development of the ovula of *Santalum* is different from that which usually obtains. The cellular oblong bodies which are attached to the placenta are evidently the ovula, and have the appearance and cellular structure of the nuclei of ordinary ovula. The membranous tube from its anatomy answers, I think, to the sac of the *anmos*, which in ordinary structures lines the cavity formed in the

nucleus at some period previous to fecundation, and which, at least in its earlier stages of development, is the only coat that is membranous. If this view be correct, the anomalies will be reduced to the formation of the albumen, or rather, tissue of the amnios and embryo externally to the nucleus, and to the application of the male influence to the apex of the sac of the amnios instead of to that of the nucleus.

This seems to me to be the best explanation of this anomalous development, although there is no appreciable reason why such an extraordinary modification should be adopted. The mode of development has some analogy to that of *Loranthus* and *Viscum*, with which it agrees in especial in the albumen being destitute of a proper integument. I may, perhaps, be borne out in giving it as my opinion that *Santalum* forms the connecting link between the simplest form of ovulum, as exemplified by *Loranthus* and *Viscum*, and the ordinary and more complicated form of these organs. Another mode of explanation is obvious, by adopting which the male influence would be supposed to operate on the usual spot, viz. the apex of the nucleus; but as the anatomy of these parts does not confirm the supposition, and as the number of anomalies are not reducible to such an extent by this as by the explanation adopted above, I prefer the opinion that the ovula are reduced to nuclei, and that the "seed" of botanists is developed externally to this, and consists of, or is reduced to a naked albumen and an ordinary embryo.

I shall not enlarge on the changes that take place after the supposed action of the male influence until at a subsequent period I have demonstrated the continuity of the filaments with the grains of pollen adhering to the stigmata. The fitness of the present subject for attempting to ascertain rigorously what the first changes incident on this action actually are, is at once very obvious, and close examination will probably put us in possession of very important results.

EXPLANATION OF THE PLATES.

I beg to remark, that with regard to the measurements, they are all taken from the base of the proper pedicle of the bud, or ovarium, or fruit to the

apex of the perianth, or the apex of the remains of the style. No dependence is, however, to be placed on mere measurement, since the development of the ovulum does not always correspond to that of the fruit.

TAB. I.

Fig. 1. Represents the obtuse placenta from a flower-bud $\frac{1}{2}$ a line long, towards the base of which 2 ovula are visible; these are at this period papilliform, and have no indications of distinction of coats or openings through these.

Fig. 2. Ditto of a flower-bud, $\frac{2}{3}$ rds of a line long. The placenta is now elongated towards its apex. The ovula have assumed their mature form. There is still no trace of distinct coats, or of openings in them.

Fig. 3. Ovulum detached, with a portion of the placenta, from a bud of about the same size ($\frac{2}{3}$ rds of a line long). It is a cellular mass, somewhat truncate, the cells being most lax at the apex. It resembles in form and structure the nucleus of the ovulum of other plants.

Fig. 4. Represents the placenta of a flower-bud about a line long.

The placenta is still more elongated. Towards its base two ovula are visible, the corresponding two being necessarily concealed. *a.* Represents the part of the tube at its exit, and when its course is downwards, nearly in the direction of the axis of the ovulum.

b, b, b, b. The upper portions of these prolongations, which terminate in cul de sacs, and contain, as it appears, at least with a small magnifying power, grumous matter. These tubes are separated artificially from the placenta; they have not as yet completed their growth.

Fig. 5. Placenta and ovula of a flower some time after expansion, and when the segments of the perianth have become of a dark blood-colour. Two ovula are seen *in situ*. The tubular prolongations from the bases of the ovula upwards to their apices are somewhat detached, owing to the object having been immersed in water. Several exceedingly fine filaments are visible attached to the apex of the placenta, and to the corresponding parts of the tubular membranes. The molecules have become aggregated, and appear to form (in the right hand ovule at least) a grumous opaque line of communica-

tion between the apex and the exerted part of the tubular membrane.

Fig. 6. Ovulum about the same period, highly magnified, and cut through longitudinally. The included part of the tubular membrane and its origin in a cul de sac are traceable. The exerted part is slightly swollen. The molecules were beginning to become aggregated in this part and in the apex. They were all highly mobile, especially those in the narrow portion of the membrane.

TAB. II.

Fig. 7. Ovulum from the placenta of an ovarium just after the fall of the perianth. In this the filaments are seen attached to the extreme apices, and are apparently intimately confounded with the structure of the membranes. Within the dilated apex a very distinct vesicle or sac is visible, attached apparently by its superior margin, and containing a few mobile molecules. The appearance of molecules in this vesicle may, and probably does result from the presence of some between the vesicle and upper surface of the tube. Extending downwards from its inferior margin, there is a grumous irregular process, which reaches to the dilated exerted portion. It is broken in several places, probably from pressure. Near its apex and adjoining the vesicle globular bodies are seen adhering, of the nature of which I am entirely ignorant. Within the dilated exerted portion, and which is nearly transparent (with the exception of one part), the outlines of an internal sac are visible, which appears to taper superiorly towards the point where it is in contact with the grumous process. This process I have stated before to arise from an aggregation, or rather agglutination, of the originally distinct and active molecules. Within this fine cellular outline, and in juxtaposition with the apex of the ovulum, there is a cellular grumous body of a nearly globular form. The included portion of the tubular membrane is traceable.

Fig. 8. The fecundated ovulum from a placenta of an ovarium two lines long. The apex of the ovulum remains *in situ*; part of the included portion

of the tube is visible from the ruptured apex, of which molecules are escaping. To the dilated apex of the tube two filaments and some remains of cellular tissue are seen to adhere; cells are likewise seen adhering to the margins of the upper half of the tube. The vesicle is visible within the dilated apex, and appears to be continuous with the grumous process. At its base 4 globules are seen. The upper half of the grumous process is very distinct; below this, however, it is broken up. The commencement of the development of the basilar inner cell is distinct, but its intrusion has not yet taken place.

Fig. 9. Represents the dilated exerted part of the membranous tube of an ovulum, from an ovarium $2\frac{1}{4}$ lines in length. This is torn partially, so as to expose what appears to be a large cell with very fine walls. Within this the innermost small cellule is visible, and appears filled with grumous matter. The faint line visible at its base, and which appears continuous with the second fine cell, marks its line of origin. The constricted, or rather, narrow exerted portion, is occupied also by molecules in a state of aggregation. The apex of the nucleus remains.

I may here remark that I am by no means certain of the existence of the fine large cell above mentioned. The innermost small cellule exists, I may almost say, invariably.

Fig. 10. Represents an ovulum from an ovarium $2\frac{1}{4}$ lines in length. The apex of the ovulum alone remains. The base of the membranous tube is much enlarged, and has evidently become cellular. At the same time there is much less granular matter (molecules) observable in its tissue. This cellular part appears to be prolonged upwards in the form of 2 or 3 cells. *a, a, a*. Between this part and the apex there is much grumous matter, composed almost entirely of small granules, and which presents traces of subdivision, the tendency to subdivision being most distinct at the apex. Adhering to the margins of the tube towards its apex, remains of the cellular tissue of the placenta are visible. The vesicle is very distinctly seen within the apex, the extreme part of which appears sphacelated. To it a filament is seen adhering.

Fig. 11. Represents the fecundated ovulum of an ovarium 3 lines long. A portion of the nucleus remains, beyond which can be seen the termination of the inclosed part, or rather, the origin of the tube. The attachment of this is visible by an expanded portion at *a*, and no change is seen to have taken place from this part to the origin of the tube. Two grumous irregular masses are visible between the apex of the ovulum and the attachment of the unchanged portion of the tube. The still more enlarged exerted portion, and rather more than the lower half of the tube, have become cellular, the cells containing a good deal of grumous matter. The upper part of the tube likewise appears cellular; but this, I think, results from the adhesion of the cells of the surface of the placenta. On one side of the apex of the tube a protuberance is seen; the only instance that has hitherto occurred.

To its apex a filament is seen adhering, and this part is of a yellowish brown colour. The vesicle is not visible. Three small cellular-looking bodies are seen within the apex. I should remark, that the edges of the upper finely-cellular portion of the tube appeared to be double.

TAB. III.

Fig. 12. Placenta of an ovarium upwards of 3 lines in length. It is at this time of a decided brown tint, the green having disappeared. A fecundated ovulum is visible *in situ*, of which almost the entire original membranous tube has become cellular. On the opposite side of the placenta the apex of an unchanged tube is seen to project upwards.

Fig. 13. Placenta and fecundated ovulum of a fruit $2\frac{1}{3}$ lines long *in situ*. The placenta is pushed towards one side of the cell of the fruit, and is a good deal compressed. It is attached chiefly by branched fibrous tissue, which contains molecules.

Fig. 14. Longitudinal section of an ovarium $3\frac{3}{4}$ lines long. No induration has taken place in the pericarpial walls. The endocarp is white, fleshy, of considerable thickness, and closely resembles albumen. A brownish line is seen passing through the remaining base of

the style to the apex of the cell. The placenta is pushed completely to one side, and from the enlargement downwards of the cellular body, their bases do not correspond, as in fig. 13. A cavity is apparent at the apex of the cellular body.

Fig. 15. Represents its longitudinal section.

Fig. 16. Embryo in a very young state from the same; it is somewhat dilated, and more dense at its inferior free extremity.

Fig. 17. Ovulum and placenta of a fruit $3\frac{1}{2}$ lines long, showing the situation of the placenta.

Fig. 18. Barren (or rather abortive) ovulum from the placenta of the same; very few globules or molecules are visible, and they are either stationary or sluggish.

With this exception it agrees with the abortive ovula examined in earlier stages.

Fig. 19. Represents a long section of the cellular body at a period later than that of fig. 15. The embryo is seen *in situ*.

Fig. 20. The same embryo detached. The apex of the cellular body remains, and to this the embryo is seen to be attached. There is an evident commencement of the cotyledonary division visible at its lower extremity.

Fig. 21. Embryo from an ovarium 4 lines long. The fruit is now nearly at its full development; the mesocarp is indurated, and the endocarp is reduced to a spongy coating, which adheres to the indurated, nearly osseous mesocarp, and likewise to the "albumen." This body now occupies the entire cavity of the fruit, and has assumed its mature form; it is white and fleshy, and abounds with fecula. The embryo is about 2 lines long, it is included in the "albumen," but is not exactly axile. The apex or radicle is ovate and attenuate, and points to the upper portion of the "albumen," and towards the apex of the placenta, which is still visible, lodged in a depression on its surface. The cotyledons are plano-convex, mutually applied by their plane faces. The plumula is inconspicuous.

I trust that the accompanying sketches will be found sufficient.

The structure of the fruit is sufficiently well understood, and hence figures of this are unnecessary. My principal object has been to show the changes that take place in the ovulum throughout its earlier stages, and especially to point out the extraordinary situation of the embryo.

The explanations of the figures are carried down to the nearly mature state of the fruit ; the only considerable subsequent change being the conversion of the tissue between the now osseous mesocarp and the cuticle into a baccate pulp.

Fig. 11.

Fig. 10.

Fig. 8.

Fig. 9.

Fig. 7.

Fig. 12.

Fig. 13.

Fig. 14.

Fig. 18.

Fig. 15.

Fig. 20.

Fig. 16.

Fig. 17.

Fig. 21.

Fig. 19.