

On the relative position of the divisions of stigma and parietal placentae in the compound ovarium of plants / by Robert Brown.

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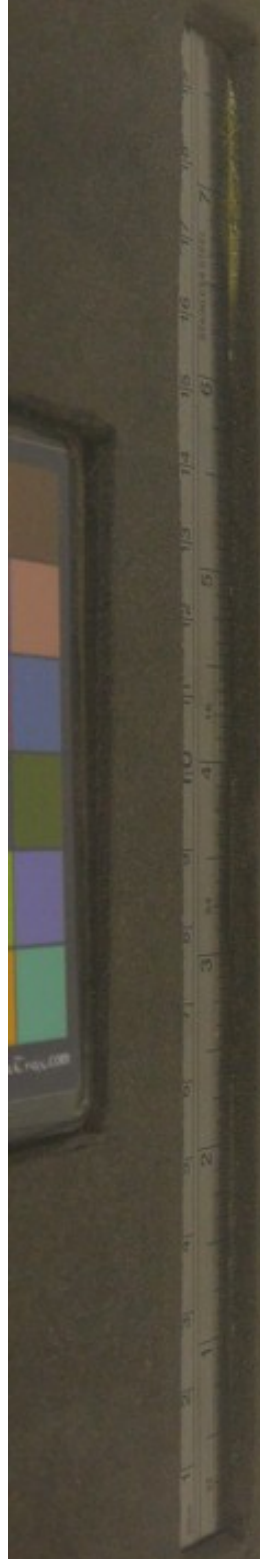
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Position of the Sigma and Parietal

having a width of about an inch at the back of the cross bar might prevent the post-holding papers from being held with a lid at the top, and sliding boxes supporting. Work. Fine well does with dried; gas-welding prepared might perhaps do so not at present used either material. A servant to take out, dry, and replace the slides without having plain.

The uncorrected remark and I have finished provided with a coarse lining, which I take care to in very winter, to supply much of that moisture to the diffuse into the air from the contained plus further provided with a covering of canvas to be a suitable when it is wanted to keep the box cool by its surface.

Woolen, New York, November 1862.

XI.—On the relative position of the Division Parietal Placenta in the Compound Ovarium
 ROBERT BROWN, F.R. & L.S.*

To estimate correctly the importance of the relative positions of the Sigma and the parietal placenta in the compound ovum, namely, whether when they are placed opposite to or alternate with each other, it is necessary to take into consideration the theory which appears the most probable of the origin of a simple ovum, and that of the stigma, besides well as the various kinds and degrees of confusion the real nature of both organs, but especially the other observed.

It is at present, I believe, universally agreed that the polygamous legumen is that state of the ovum which best exemplifies the hypothetical view of this organ generally adopted; namely, that it is a modification of a leaf folded inwards and united at the base, which in most cases are the only parts of the ovum; or, at least, where this power of folding is not absolutely confined to the margins, it generally includes them.

The exceptions to the structure as here stated are of two kinds—

* The article, which is referred to at p. 255 of No. 66, in Mr. Brown's volume of *Cryptogamia*, given in the second part of his "Pteris Javanica Benth." published in 1860. This article was distributed in December, 1859.

having a cavity of about an inch at the back of the shelves (two cross bars might prevent the plant-holding papers from being pushed too far back) with a lid at the top, and sliding in one or more frames supporting Welsh Plane well dosed with the chloride and dried; gun-wadding prepared might perhaps do as well, but I have not at present tried either material. A servant might occasionally take out, dry, and replace the slides without having access to the plants.

One unconnected remark and I have finished: my vasculum is provided with a canvass lining, which I take care to have well-wetted in warm weather, to supply much of that moisture that would otherwise diffuse into the air from the contained plants alone. It is further provided with a covering of canvass to be used only in hot sunshine when it is wetted to keep the box cool by evaporation from its surface.

Woodloes, near Warwick, November 1842.

XI.—*On the relative position of the Divisions of Stigma and Parietal Placentæ in the Compound Ovarium of Plants.* By ROBERT BROWN, F.R. & L.S.*

To estimate correctly the importance of the relation between the divisions of the Stigma and the parietal placentæ of the compound ovarium, namely, whether when agreeing in number they are placed opposite to or alternate with each other, it is necessary to take into consideration the theoretical view which appears the most probable of the origin or formation of a simple ovarium, and that of the stigma belonging to it, as well as the various kinds and degrees of confluence by which the real nature of both organs, but especially the latter, is so often obscured.

It is at present, I believe, universally agreed to consider a polyspermous legumen as that state of the simple ovarium, which best exemplifies the hypothetical view of the formation of this organ generally adopted; namely, that it consists of the modification of a leaf folded inwards and united by its margins, which in most cases are the only parts of the organ producing ovula; or, at least, where this power of production is not absolutely confined to the margins, it generally commences with or includes them.

The exceptions to the structure as here stated are of two kinds:—

First. Where the whole internal surface of the carpel is

* This article, which is referred to at p. 255 of No. 65, is extracted from Mr. Brown's account of *Cyrtandrea*, given in the second part of Dr. Horsfield's '*Plantæ Javanicæ Rariores*,' published in 1840. Separate copies of this article were distributed in December, 1839.

equally ovuliferous, which is the case in a few families of very small extent, as *Butomeæ*, *Nymphæaceæ* and *Lardizabaleæ*.

Secondly. Where the production of ovula is limited to the external angle of the cell or axis of the leaf supposed to form the carpel.

A case of this kind is found in a portion of one of those families in which the whole surface is generally ovuliferous, namely, in *Hydropeltideæ*, which I have always regarded as merely a section of *Nymphæaceæ**; and from the nature of these differences in placentation, which are more apparent than real, an argument might even be adduced in favour of that opinion.

A placenta apparently limited to the outer angle of the cell also occurs in the greater number of species of *Mesembryanthemum*. As this structure, however, is certainly not without exception in that very natural genus, several species, among which are *Mesembryanthemum crystallinum*, *cordifolium*, *papulosum* and *nodiflorum*, having the placenta confined to the internal angle of the cell or margins of the carpel; and as in some of those species in which the outer angle is placentiferous, the production of ovula is not confined to it, but extends to the lower half of the inner angle;—this apparent deviation from ordinary structure may perhaps be explained by assuming cohesion of the inflected portion of the carpel with the wall of the cell;—an hypothesis, in some degree supported by the fact, that in several species the termination of the assumed inflected portion is free and not ovuliferous.

But whatever opinion may be adopted as to the relation of this seemingly anomalous to the ordinary structure, it cannot, as M. Fenzl proposes†, be employed as the essential character of a distinct natural family limited to the Linnæan genus *Mesembryanthemum*.

The placenta then of a simple ovarium in its usual state, according to this view, is necessarily double; though by the complete suppression of ovula in one of its two component parts, and their diminished production in the other, the ovarium is not unfrequently reduced to a single ovulum. That such is the origin of the single ovulum is at least manifest in a monstrosity of *Tropæolum majus*, in which the stamina are converted into pistilla; but the complete action being impeded by the presence of the regular trilocular pistillum, and the two marginal cords of each open ovarium remaining di-

* Gen. Rem. in Flinders's Voy. vol. ii. Append. p. 598.

† Annal. des Wien. Mus. vol. i. p. 349.

stinct, the origin of the ovulum from one only of these cords is satisfactorily shown.

An ovarium with two or a greater number of cells, whose placentæ project into the cavities more or less from their inner angles, is an organ, the composition of which is sufficiently obvious.

But a compound ovarium may be differently constructed; and, first, instead of each simple organ forming a complete cell by the union of its own margins or adjoining portions of its surface, the corresponding margins or adjoining portions of surface of the proximate component parts may unite together so as to form a parietal placenta, often apparently simple, but in reality double in all cases. This view of the composition of a unilocular ovarium having two or more parietal placentæ is also very generally received. But exceptions, supposed to prevail in whole families, in which the disc and not the margins are placentiferous, have lately been assumed by Professor Lindley, *Orchideæ* and *Orobancheæ* being the examples of this structure to which he more particularly refers.

The accurate determination of this question appears to me of great importance to the theoretical botanist, but the subject will be most advantageously discussed after treating of the origin and modifications of stigmata.

An ovarium less manifestly compound is that in which the centre of the cavity is occupied by a placenta entirely unconnected with its sides; the supposed inflected portions of each component organ, according to the view here adopted, being removed, or reabsorbed so completely in a very early stage of its development as to leave no trace of their existence either on the walls of the cavity or on the surface of the central placenta, which may either be polyspermous, or produce only a smaller and definite number of ovula having a relation to its supposed component parts, or, lastly, in some cases be reduced to a single ovulum.

These are the principal modifications of the compound ovarium when forming a simple series; but it is necessary to observe that both surfaces of the inflected and included portions of the carpels are not unfrequently equally productive of ovula, a structure which is manifest in many *Cyrtandraceæ*, especially *Cyrtandra*, although in several other genera of the same family the production is confined to the inner or upper surface of the margin. In other cases the polyspermous ovuliferous portion or placenta is connected with the inner angle of the cell by a single point only, which may proceed either from the apex or base of the cavity. This modification of

structure, though in some families hardly of generic importance, seems to me to assist in explaining the apparently anomalous structures of *Hydnora*, *Rafflesia*, and *Brugmansia*.

On the subject of the origin and type of Stigma, my first observation is, that the style where present can only be regarded as a mere attenuation, in many cases very gradual, of the whole body of the ovarium. Hence the idea naturally suggests itself, that the inner margins of the carpel, which in the lower part are generally ovuliferous, in the upper part perform the different, though in some degree analogous, function of stigma. As the function, however, of this organ implies its being external, and as in different families, genera, and even species, it has to adapt itself to various arrangements of parts destined to act upon it, corresponding modifications of form and position become necessary; hence it is frequently confined to the apex, and very often, especially in the compound ovarium with united styles, appears to be absolutely terminal.

In such cases, as it must always include and be closely approximated to the vascular cord of the axis, it has by some botanists been considered as actually derived from it, which it is, however, only in the same manner as the marginal placentæ are derived from the axis of the carpel. But according to the notion now advanced, each simple pistillum or carpel has necessarily two stigmata, which are to be regarded, not as terminal, but lateral.

That the stigma is always lateral may be inferred from its being obviously so in many cases; and in one genus at least, *Tasmannia*, it extends nearly the whole length of the ovarium, so as to be commensurate with and placed exactly opposite to the internal polyspermous placenta.

That the stigma is always double appears probable from those cases in which it is either completely developed, as in the greater part of *Gramineæ* where the ovarium is simple; in the compound ovarium in *Urena*; and from those in which the development, though less complete, is still sufficiently obvious, as in many *Euphorbiaceæ* and in several *Irideæ*. This degree of development, however, is comparatively rare, confluence between the two stigmata of each carpel being the more usual structure; and in the compound pistillum a greater degree of confluence often takes place in the stigmata than in the placentæ;—a fact, which in all such cases is obviously connected with adaptation of surface to the more complete performance of function.

Another difference frequently occurs between the mode of confluence of placentæ and stigmata, namely, that in the com-

pound but unilocular ovary, while the placentæ of the adjoining carpels are united, the stigmata of each carpel are generally confluent. But this rule admits of exceptions, as in *Parnassia*, in many *Cruciferae*, and in *Papaveraceae*: in all these cases the stigmata as well as placentæ of the adjoining carpels are confluent, a structure satisfactorily proved in *Cruciferae* by several cases of monstrosity, in which the stamina are transformed into pistilla; and in *Papaveraceae* by a series of modifications of structure as well as by a like transformation of stamina.

A similar confluence of stigmata in the compound multilocular pericarpium is of much rarer occurrence; it is found, however, in the majority of *Irideae*, in which the three stigmata alternate with the cells, and consequently with the placentæ of the trilocular ovary. That this is the correct view of the composition of the stigmata in *Irideae* is at least probable from their occasional deep division, and more particularly still from the bifid petal-like styles or stigmata which are opposite to the cells of the ovary in other genera of the same family, as in *Iris* and *Moræa*. In both these arrangements the adaptation to the performance of function is equally manifest.

If the correctness of these observations be admitted, it follows that characters dependent on the various modifications of stigmata are of less value, both in a systematic point of view as determining the limits of families, and theoretically in ascertaining the true composition of organs, than those derived from the analogous differences in the ovaria or placentæ.

In those cases in which the nature of the composition of the ovary is doubtful, it may, in the first place, be remarked, that wherever in the compound unilocular pistillum the placentæ are double or two-lobed, it is more probable that such placentæ are derived from two adjoining carpels, and are consequently marginal or submarginal, than that they occupy the disc of one and the same carpel: this being entirely the appearance in many cases where the marginal origin of placentæ is admitted; while in the greater part of those in which the disc is known to be ovuliferous, the ovula are never collected in two distinct masses, being generally scattered equally over the surface.

But the double placentæ are manifest in *Orchideae*, the principal family in which Mr. Lindley considers the ovula as occupying the disc and not the margins. In this family also the alternation of stigmata with placentæ is that relation which is most usual in compound unilocular ovaria, where the apparent number of stigmata and placentæ is equal; and that

in *Orchideæ* each apparent stigma is formed by the confluence of the two stigmata of one and the same carpel, is proved by tracing to their origins their vascular cords, which are found to coalesce with those of the three outer foliola of the perianthium.

This view of the composition of the ovarium in *Orchideæ* is confirmed by finding that it agrees with the ordinary arrangement in monocotyledonous plants; namely, the opposition of the double parietal placentæ to the three inner divisions of perianthium*, while in *Apostasia* the three placentæ of the trilocular ovarium are opposite to the three outer divisions; and it is further strengthened on considering what takes place in *Scitamineæ*, where the same agreement is found both in the placentæ of the trilocular ovarium, which in this family is the ordinary structure, and in the unilocular, which is the exception.

I am aware that the agreement of *Orchideæ* with the usual relation of parts in Monocotyledones is not admitted by M. Achille Richard, nor by Mr. Lindley, who has adopted his hypothesis respecting the structure of the flower in this family. According to M. Richard, the outer series of perianthium is generally wanting, being found only in one genus, *Epistephium*: the three outer divisions actually existing in the whole order, according to this view, become petals, and the three inner divisions sterile petaloid stamina.

I have some years ago† stated several objections to this hypothesis; at present I shall advert to one of those only, considering it as conclusive; namely, the position of the two lateral stamina, which are generally rudimentary, but in some cases perfectly developed, in this family. In several species of *Cypripedium*, which is one of these cases of perfect development, I had then ascertained, by means of numerous transverse sections made at various heights in the column and at its base, that their vascular cords united with those of the two lateral inner divisions of the flower, while that of the third, generally the only perfect stamen, is manifestly opposite to the anterior division of the outer series. The position of stamina, therefore, so far from being regular, as the hypothesis in question considers it, is absolutely without example, two of the inner series being opposite to two of the supposed outer series of stamina.

A very different view respecting the formation of the ovarium in *Orchideæ* is that first advanced by Mr. Bauer and

* Denham, Trav. in Afr. Append. p. 243.

† Linn. Soc. Trans. vol. xvi. p. 698.

adopted by Mr. Lindley, namely, that it consists of six carpels, of which three, placed opposite to the outer series of perianthium or sepals, are sterile; the remaining three, opposite to the inner series, or petals, being fertile, and bearing their placentæ on their axes or discs.

The chief argument in support of this view is no doubt derived from the very remarkable dehiscence of the capsule into six valves. But I have elsewhere pointed out cases where an analogous dehiscence occurs, in which, however, a similar composition has never been supposed to exist: and if the presence of six vascular cords in sections of the ovarium be likewise adduced in favour of the opinion, I may add that I have in the same place remarked that these vascular bundles belong not to the ovarium only, but also to the perianthium and stamina, and are equally observable in other families with adherent ovarium, as *Irideæ*, in which a similar composition has never been inferred.

With regard to the second family, in which Mr. Lindley believes the disc of the carpel to be ovuliferous, namely, *Orobancheæ*, I find no other argument advanced in support of this view than that derived from the bursting of the capsule into two lateral valves: but an opinion founded on dehiscence only may be said to be a mere begging of the question; division through the axis of carpels, especially in the families related to *Orobancheæ*, being nearly as common as separation of their margins. In this family also, as in *Orchideæ*, the placentæ are double, an argument in favour of their submarginal origin: and although, whether the carpels be regarded as lateral, or anterior and posterior, the placentæ are not strictly marginal, yet there are other families where a similar position of placentæ is found, but in which the structure assumed in this hypothesis has never been suspected. As to the supposed affinity of *Orobancheæ* with *Gentianeæ*, which might be adduced in support of this view, as far as it is founded on the assumed agreement of the two orders in the lateral position of their carpels, the argument, even if correct, would hardly be conclusive; for in *Gentianeæ* there is at least one genus having quadrifid and another with quinquefid flowers, in which the carpels are not lateral, but anterior and posterior, as I believe them to be in *Orobancheæ*; nor has it ever been supposed that in *Gentianeæ* the disc or axis is ovuliferous.

In the account now given of the modifications of ovarium and stigma, I have, in conformity with the ordinary language of botanists, employed the term *confluence*, by which, however, is not to be understood the union or cohesion of parts originally distinct, for in the great majority of cases the sepa-

ration or complete development of these parts from the original cellular and pulpy state has never taken place. But with this explanation the word may still be retained, unless connate should be considered less exceptionable.

I have also assumed that ovula belong to the transformed leaf or carpel, and are not derived from processes of the axis united with it, as several eminent botanists have lately supposed. That the placentæ and ovula really belong to the carpel alone is at least manifest in all cases where stamina are changed into pistilla. To such monstrosities I have long since referred in my earliest observations on the type of the female organ in phænogamous plants*, and since more particularly in my paper on *Rafflesia*†: the most remarkable instances alluded to in illustration of this point being *Sempervivum tectorum*, *Salix oleifolia* and *Cochlearia armoracia*, in all of which every gradation between the perfect state of the anthera and its transformation into a complete pistillum, is occasionally found.

XII.—On the Structure of the Capsule of *Papaveraceæ*; and on the Nature of the Stigma of *Cruciferæ*. By J. W. HOWELL, Esq., M.R.C.S.

To the Editors of the *Annals of Natural History*.

GENTLEMEN,

IN reference to your notes appended to my paper "On the Structure of the Stigma of the *Papaveraceæ*," &c. in your last Number, wherein it would appear that I had been anticipated by M. Kunth, '*Flora Berolinensis*,' published 1838, in the description of the apparently anomalous relation of the parietal placentæ to the stigmatic rays—permit me to observe, that my observations on this interesting subject were made in 1832.

In respect to your statement that "those of Mr. Howell's observations which relate to the opposition of stigmata to placentæ in *Papaveraceæ*, and to the composition and cohesion of stigmata, had already been published by Dr. Brown in his account of *Cyrtandraceæ* in Horsfield's '*Plantæ Javanicæ*,'" which work I have not yet seen, but have learned that it was published in 1840—justice to myself compels me to inform you, that the paper I sent you was published *verbatim* in the '*Bath and Cheltenham Gazette*' in October 1840, and was sent for republication in the '*Annals*,' from a conviction that the subject was new, and worthy of a more extended circulation than a local paper could ensure.

* In Linn. Soc. Trans., vol. xii. p. 89.

† Ibid. vol. xiii. p. 212, note.



