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VII.—*On Relative Position ; including a new Arrangement of Phanerogamous Plants.* By B. CLARKE, F.L.S. &c.

[With a Plate.]

PART I.

On the Position of the Raphe.

THE position of the raphe in anatropal ovules is a character which has hitherto attracted but partial attention, yet is, as will be seen, one of much constancy, being rarely variable in the same natural order, and the exceptions also, in most if not in all instances, being readily explained.

For the purpose of giving to this physiological character a more definite form, I will endeavour in the first place to show what is the most usual position of the raphe, where each margin of the carpel bears a single row of ovules, as in *Paonia*, and afterwards notice the variations of its position, more especially where the ovule is single.

The most usual position of the raphe where the ovules form two rows—one row to each margin of the carpel—is the same throughout the families of phanerogamous plants, viz. the raphes of the two opposite rows lie in apposition with each other in the mesial line of the carpel, or, in other words, are turned towards each other, and the ovule bends downwards so as to be in contact with the parietes. And hence it may be a question whether this is not the normal position, as it is common to Endogens and Exogens, of which Amaryllideæ, Liliaceæ, Ranunculaceæ, and Passifloraceæ contain well-marked examples.

But when anatropal ovules are very numerous in consequence of each placenta bearing more than a single row, this regularity

of position is not always observable, further than that the raphe usually retains its lateral position as in Cucurbitaceæ; and campylotropal ovules also not unfrequently have an equivalent character in the direction of their curvature.

It is chiefly therefore when the ovule is reduced to one, that characters of much importance can be derived from the relative position of the raphe to the placenta; and for the purposes of arrangement, the positions of the anatropal ovule may be described under the following variations, each of them including also some instances in which the ovules are two, or three, or more numerous.

1. Ovule pendulous with the raphe turned away from the placenta.

2. Ovule pendulous with the raphe lateral, so that it appears as if it were turned sideways in the cell.

3. Ovule pendulous with the raphe next the placenta.

4. Ovule horizontal with the raphe on the upper surface.

5. Ovule horizontal with the raphe lateral.

6. Ovule horizontal with the raphe on the under surface.

7. Ovule erect with the raphe next the placenta.

8. Ovule erect with the raphe on one side, that is, neither in apposition with the placenta, nor yet turned directly away from it.

9. Ovule erect with the raphe turned away from the placenta.

1. *Ovule pendulous with the raphe turned away from the placenta.* This character was first observed by Mr. Brown in *Euo-nymus*, and subsequently by Dr. Schleiden in Ranunculaceæ (Annals of Natural History, vol. v. p. 164), who, referring to Mr. Brown's researches, remarks: "As far as I am aware, no one has profited by his inquiries in order to solve similar anomalies which obscure the clear principles of affinity," and adds some further observations, describing it as "*ovulum spurie pendulum anatropum raphe aversa.*"

The researches of Dr. Schleiden have already shown that in the Typhaceæ the raphe is averse, and as the Ranunculaceæ so nearly approach Endogens, it might be supposed that it would be of frequent if not constant occurrence in this class; and I am able to add that in *Chamædorea elegans*, although the ovule is not completely pendulous, the raphe is next the dorsum of the cell; that in *Potamogeton* the ovule shows a decided tendency to it in the direction of its curvature; and that the numerous ovules of Araceæ also show a tendency to it by the raphe being frequently on the upper surface. There are, however, apparent exceptions afterwards particularly alluded to.

In Exogens it occurs more frequently as Endogens are approached, which the following enumeration will show:—1. *Ne-*

lumbium. 2. Hydropeltideæ (ovules two, one above the other). 3. Ranunculaceæ. 4. Monimiaceæ. 5. Lauraceæ. 6. Anacardiaceæ. 7. *Coriaria* (Pl. II. figs. 1 & 2). 8. Malpighiaceæ (in those genera in which the funiculus is next the dorsum of the cell). 9. Celastraceæ. 10. Ternströmiaceæ (ovules two, collateral). 11. Ebenaceæ (ovules two, collateral). 12. Icacinæ. 13. Loranthaceæ (Pl. II. fig. 3, and see also Part III.). 14. Plumbaginæ. 15. Illecebraceæ. 16. Chenopodiaceæ. 17. Amaranthaceæ. 18. *Geissoloma* (ovules two, collateral). 19. Cyrtolaceæ. 20. *Helwingia*. 21. *Aucuba*. 22. Cinchonaceæ (Pl. II. fig. 4). 23. Tetragoniaceæ. 24. Calyceraceæ. 25. *Dipsacus*. 26. Onagrarieæ (ovules three or four).

The campylotropal ovule in which the radicle of the embryo subsequently formed is turned towards the placenta, as in *Amaranthaceæ*, is a character which deserves especial attention, if it is equivalent to that of the raphe averse in the pendulous anatropal ovule, and that it is so, *Statice* and *Plumbago* seem to prove. That *Plumbago* is a genuine instance of the raphe averse there appears no reason to doubt, because it is constantly so,—the raphe being always on the side of the ovule which is directly away from the funiculus, the latter coiling round the edge of the foramen to join it. And if its occurrence in the ovule of *Plumbago* is admitted, then there can scarcely remain a doubt of the correctness of the inference in question, because in *Gomphrena* and *Philoxerus*, where the ovule is equally suspended as in *Plumbago*, the foramen and subsequently the radicle are always next the funiculus. It may be added also, that in *Scleranthus annuus* the ovule as regularly curves away from the funiculus, as in *Gomphrena* it curves towards it (see also Part III. and the accompanying figures); and this question is almost set at rest, when it is considered that no distinction which is absolute exists between anatropal and campylotropal ovules, as in *Trianthema* the ovules are simply campylotropal, but in the nearly allied genera *Galenia* and *Tetragonia* a short raphe is present, although the ovule is curved as in the former case*.

2. *Ovule pendulous with the raphe lateral*. This has been

* Since the above was written, I have ascertained that in *Atriplex* the same inversion of the ovule takes place as in *Euonymus* and *Ranunculaceæ* when it is single and pendulous; thus in *A. angustifolia* the seed is erect and the cotyledons next the placenta, being on that side of the ovary to which the short funiculus is adherent; in *A. laciniata* the seed is attached above the middle of the wall, so that being vertical, the cotyledons are on the upper surface, and the radicle underneath curving up so that its extremity reaches to the hilum; and in *Halimus pedunculatus* (olim *A. pedunculata*) the inversion is complete, the seed being pendulous and the cotyledons turned away from the funiculus.

already noticed as occurring in *Cornus* and *Marlea*, and the following enumeration will show that it is one of the more frequent variations of the position of the raphe.

1. *Pontederia lanceolata*. 2. Aquifoliaceæ (*Ilex*). 3. Styra-
ceæ (*Halesia*—ovules two). 4. Oleaceæ (ovules two). 5. *Mal-*
pighia and other genera of Malpighiaceæ in which the funiculus
(representing the raphe) is constantly lateral (Pl. II. fig. 5).
6. *Nitraria* as figured by Prof. Lindley. 7. Santalaceæ. 8. Myo-
poraceæ (ovule single or two). 9. Illecebraceæ. 10. Cheno-
podaceæ. 11. Epacrideæ (*Acrotriche*). 12. Caprifoliaceæ.
13. *Globularia*. 14. Dipsaceæ. 15. Valerianaceæ. 16. Hip-
purideæ (*Goniocarpus*). 17. Hamamelideæ. 18. Bruniaceæ.
19. *Schizandra*.

In *Corrigiola* the cotyledons are lateral, that is, neither next the funiculus nor yet directly removed from it, and therefore if the ovule were completely inverted the raphe would be lateral. In *Paronychia*, however, the cotyledons are turned away from the funiculus and the radicle in relation with it; but as the raphe averse, and the raphe lateral, occur in the same family, as in *Aucuba* and *Cornus*, and equivalent characters also in Malpighiaceæ, this offers an explanation of the variable relation of the cotyledons to the funiculus in Illecebraceæ, and also tends to show that the raphe averse the placenta and the cotyledons averse it (*i. e.* next the dorsum of the cell) are characters of equivalent value.

3. *Ovule pendulous with the raphe next the placenta*. This, as is well known, is the ordinary position of the raphe in pendulous anatropal ovules; but although it is the more common, it is of rare occurrence in the Heterocarpous families, as will be seen from the Tables.

4. *Ovule horizontal with the raphe on the upper surface*. Of this position I have hitherto observed only three instances. 1. A species of *Macleya* in which the ovules are six, three on each placenta, having the raphe constantly on the upper surface. 2. Araceæ. Where they are numerous, many of the ovules have this character, but in others the raphe is lateral. 3. *Fumaria officinalis*. The ovule, although not anatropal, has the equivalent character of the foramen, being always directly below its attachment to the wall of the ovary. To these perhaps should be added *Paris quadrifolia* as the ovules are scarcely ascending, the raphe being frequently on the upper surface but sometimes lateral, thus agreeing with Araceæ; and also the ovules on the upper portion of the placenta in *Swietiana*, where in the early stages they are horizontal.

5. *Ovule horizontal with the raphe lateral*. Of this no instance has been observed where the ovule is single, except in Chenopo-

diaceæ, the ovules of which have an equivalent character in those genera in which the seed subsequently produced is horizontal; and even when they are two it is very rare, having been only observed in *Talauma* among Magnoliaceæ and *Trianthema*, the latter of which is afterwards more particularly noticed.

6. *Ovule horizontal with the raphe on the under surface.* Of this no instance has been observed where the ovule is single, nor yet where they are two, unless it is that in *Geranium Robertianum* they are in their early stages nearly horizontal; and Asclepiadeæ and Apocynaceæ are the only ascertained instances where the ovules are numerous.

7. *Ovule erect with the raphe next the placenta.* This, as is well known, is the ordinary position of the raphe in erect anatropal ovules, and occurs I believe not unfrequently where they are numerous, as in *Cuphea* and *Reaumuria*.

8. *Ovule erect with the raphe lateral.* This character, which was first observed by Mr. Bennett in Rhamnaceæ, and by that gentleman attributed to torsion of the funiculus, obtains to a considerable extent among Exogenous families, but is very rare in the Endogenous, *Calamus viminalis* being the only instance hitherto observed.

1. Elæagnaceæ. 2. Rhamnaceæ. 3. Staphyleaceæ (ovules in two rows). 4. Stilbaceæ. 5. Portulacæ (ovules campylotropal). 6. *Justicia* (ovules two, one above the other). 7. Labiatae and Verbenaceæ?*. 8. Jasminaceæ (ovules two). 9. *Trianthema decandra* (ovules campylotropal). 10. Goodeniaceæ (ovules two or more, numerous).

9. *Ovule erect with the raphe turned away from the placenta.* Since my first Dissertation on the Position of the Raphe was read at the Linnæan Society, several additions have been made to the instances of the raphe having this position then particularly adverted to, and it is not improbable that others remain as yet unobserved. 1. *Limnocharis Humboldtii* (ovules numerous). 2. *Pennisetum fruticulosa* (ovules two, Pl. II. fig. 8). 3. *Geissoloma* (ovules four, Pl. II. figs. 6 & 7). 4. *Berberis vulgaris* (ovules two). 5. *Geranium* (ovules two). 6. *Nolana*. 7. *Calytrix virgata* (ovules two). 8. Compositæ (Pl. II. fig. 9). 9. *Chrysobalanus* (ovules two).

In Compositæ the raphe in several genera examined proved to be always on the anterior side of the ovule, and consequently in relation with the anterior angle of the ovary, and hence it is averse from the placenta, supposing the anterior to be the fertile

* In such species of Labiatae as I have examined, the raphe is not in relation with the inner angle of the achenium, but inclines more or less away from it as it ascends.

carpel (see Part III. *Compositæ*). It may be interesting, however, here to add, that in *Aster* and *Centaurea* the ovule arises from the base towards the posterior side of the ovary always more or less distinctly.

In such *Cichoraceæ* as I have examined, the raphe is for the most part or always lateral (that is, towards one side of the ovary), in no instance posterior ; but as the carpels in this section of *Compositæ* are right and left the axis, the position of the raphe might be expected to be different. In *Calytria virgata* the raphe is not so completely averse as in the other instances, being intermediate between lateral and averse ; but in *Berberis vulgaris* I have since ascertained it is always next the dorsum of the carpel.

Causes of the Variations.

The cause of the first of these variations has already been demonstrated by Dr. Schleiden (*loc. cit.*), and each of the others being also especially deserving of attention as influencing the value of the characters derived from the position of the raphe, I would suggest the following as the most frequent, if not unexceptionable.

1. That a single ovule pendulous with the raphe averse, being, as first observed by Mr. Brown, an erect ovule pressed or growing downwards, may result from the cavity of the ovary elongating in that direction, while its upper part remains stationary. As tending to show that it may be produced by pressure, I have met in *Sassafras officinale* with an instance in which the ovule had apparently forced its way through the upper part of the ovary as it was growing from its external surface,—the ovary having again closed and the cavity still remaining, but empty. It may be further suggested, however, that it is only when an erect ovule has the raphe next the placenta, that it has the raphe averse when it thus becomes pendulous.

2. That a single pendulous ovule with the raphe lateral is an ovule originally extending horizontally from the placenta with the raphe lateral (as in *Ranunculaceæ*, where the ovules are numerous, and in *Cucurbitaceæ*), and subsequently becoming pressed downwards in consequence of the ovary elongating in that direction more than upwards. By the raphe lateral in horizontal ovules, it is to be understood that it is not on the upper surface towards the stigma, nor beneath it towards the base of the ovary.

3. That a single pendulous ovule with the raphe next the placenta may possibly be an ovule originally extending in a horizontal direction from the placenta, having the raphe on the under surface, and should perhaps be regarded as the only truly

pendulous ovule, including however those pendulous campylo-tropal and amphitropal ovules with the foramen and (in the seed) the radicle of the embryo turned away from the placenta, while the cotyledons are in relation with it.

4, 5 & 6. That these three positions may perhaps be equally regarded as normal, although the 4th and 6th are comparatively so rare. It may here be observed that an ovule horizontal with the raphe on its upper surface is doubtless equivalent with an ovule pendulous with the raphe averse, and the same observation may apply to those having the raphe on their under surface, as compared with those which are pendulous with the raphe next the placenta.

7. That an erect ovule with the raphe next the placenta is usually an ovule raised into that position without any torsion taking place in the funiculus, but that torsion may, in this instance, sometimes have taken place, its normal position in such a case being lateral. It here becomes an interesting question as to whether or to what extent twisting of the funiculus may take place; two positions there are at least in which in all probability it does take place,—in some of those instances where the ovule is longer than its raphe, and the funiculus so short that the ovule appears as it were sessile; thus in *Geum urbanum*, the ovule in growing erect must have the raphe next the placenta, as its apex or foramen projects much below its point of attachment to the ovary, and the ovule of *Cliffortia ilicifolia* must for the same reason in being pendulous have its raphe next the placenta; and as far as my own observations have gone, I believe a very slight degree of pressure will occasion twisting of the funiculus, so that the form of the ovary or winged seeds might give rise to an alteration of position. But whether it ever takes place spontaneously, as in the filament of *Lopezia*, remains a question, as the funiculus has very rarely any appearance of being twisted; *Dodonaea* and other Sapindaceæ, and part of Rhamnaceæ, as referred to by Mr. Bennett, being the only instances particularly noticed where it seems likely that the position of the ovule is to be attributed to that cause.

8. That a single ovule erect with the raphe lateral is a horizontal ovule spontaneously becoming erect or pressed upwards by the ovary remaining contracted below while its upper part expands; this is distinctly shown to take place in Tetragoniaceæ (in an equivalent character), where *Trianthema micrantha* has two seeds horizontal, one above the other, the cotyledons being lateral, and *T. decandra* two erect seeds, one completely above the other, the cotyledons also in each of them being lateral.

9. Ovule erect with the raphe turned away from the placenta. This position is to be accounted for on the same principles as the

foregoing, *i. e.* either from the peculiar form of the ovary or by the spontaneous growth of the ovule; and in the case of *Limncharis* it appears rather to arise from the latter, as the ovary makes no pressure on the greater part of the ovules. The position of the raphe in the seed of *Geranium Robertianum* is however rather produced by pressure, as it is forced to become ascending in consequence of being attached near the base of the cavity, and in *Nolana* the external side of the ovule (on which the raphe is situated) curves forward, giving it somewhat the appearance of having been forced upwards in its growth.

Value as a Differential Character.

Should further observation show the position of the raphe when differing from its ordinary relation to the placenta to be a character without exception in the families in which it occurs, it will form an important distinction between many of them which otherwise nearly approach each other; thus Lauraceæ and Daphnaceæ have usually been considered as almost conterminous, and the Urtical Orders have by most botanists been compared with Chenopodiaceæ and its allies. It may also tend to a more definite distribution of the Orders in Alliances, as for instance of those related to Rutaceæ, Sapindaceæ, Rhamnaceæ, and Clusiaceæ, as showing *Erythroxylon* to differ from Malpighiaceæ, *Spondias* from Aurantiaceæ, &c.

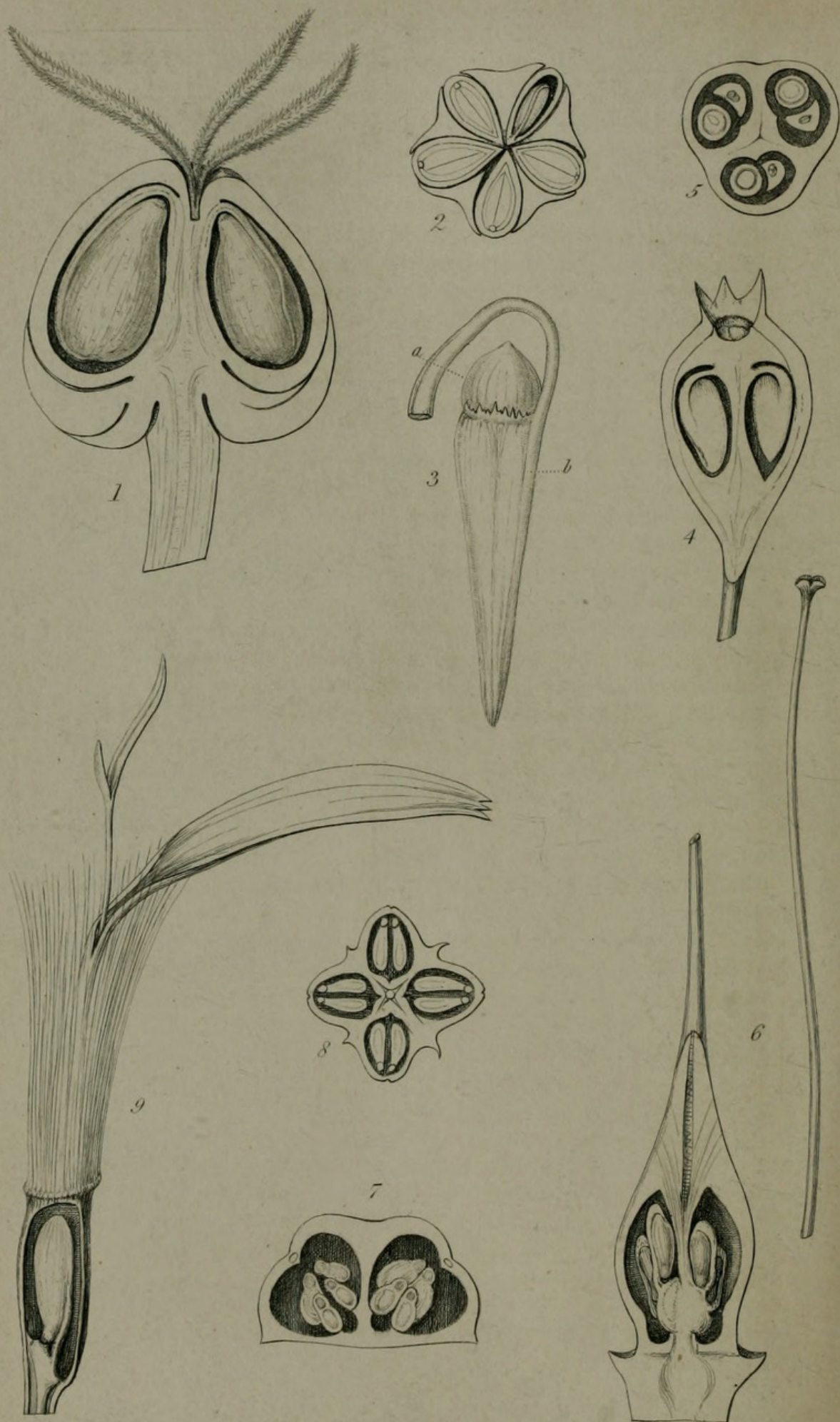
Berberis differs from Ranunculaceæ in having the raphe away from the placenta, and *Hedera* from *Cornus* in its being next the placenta as in Umbelliferæ.

It may also show a distinction between *Nolana* and Convolvulaceæ, and its near approach to Boragineæ, as the short raphe in the latter family is next the placenta.

The raphe next the placenta also separates some minor families from others in or with which they have been included, as Selagineæ from Myoporaceæ, Scleranthaceæ (the position of the cotyledons being equivalent) from Illecebraceæ; and differences in this character between many others usually regarded as in near affinity will be seen by the Tables.

As to whether a single pendulous ovule having the raphe next the placenta ever occurs among Endogens is not fully ascertained, as in *Tamus* the ovule is longer than the raphe, which also in a very early stage has more or less the appearance of being lateral; and in *Dioscorea* and *Rajania*, where the raphe is also next the placenta, the seeds are winged. These may be compared with *Menispermum* where the raphe is very short, so that the ovule in having its foramen superior must have it next the placenta, or if the raphe is wanting, have an equivalent character; so that it







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