STUDIES IN THE CÆSALPINIACEÆ

I. A Contribution to the Embryology of the Genus Cassia

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OUR present knowledge of the embryology and cytology of the three families Mimosaceæ, Cæsalpiniaceæ and Papilionaceæ belonging to the order Leguminosæ (if we follow the classification of Hutchinson, 1926), chiefly on account of their different distribution, is very unequal. The Papilionaceæ being cosmopolitan and abundant both in Europe and N. America have received much attention, while the more tropical Mimosaceæ and Cæsalpiniaceæ have been only meagrely investigated. This fact has prompted the author to take up the study of the Cæsalpiniaceæ. The present paper deals with the structure and development of the ovule and embryo-sac of *Cassia* species. The author has started with this genus not only because it is the largest in the family and is represented by many species in this country, but also because the few observations that have been made by the earlier workers are in several cases contradictory.

PREVIOUS WORK

The earliest reference to the embryology of the Cæsalpiniaceæ is found in the work of Braun (1860), who observed polyembryony in a species of *Cassia*. Later Guignard (1881) in his extensive studies on the embryology of the Leguminosæ also made some observations on the genera *Cæsalpinia, Cassia, Cercis, Gleditschia* and *Ceratonia*. He observed in *Cercis siliquastrum* both the chalazal megaspores often becoming 2-nucleate and each having the capacity of developing into a mature embryo-sac. Some further observations on the embryo-sac of *Cassia* were made by Hubert (1896).

Saxton (1907) worked out the structure and development of the ovule and embryo-sac of *Cassia tomentosa*. He observed a deeply situated primary archesporial cell which functions as the megaspore-mother cell without cutting off any primary wall cell. The megaspore-mother cell undergoes the two meiotic divisions in the normal manner and forms a linear tetrad of megaspores. The second megaspore from the chalazal end develops into the embryo-sac according to the *Normal* type. The mature embryo-sac at the chalazal end forms a tubular-extension which becomes filled with a row of antipodal cells, as happens in some Compositæ.

Ghose and Alagh (1933) studied *Cassia purpurea*. They found hypodermal primary archesporial cell in the ovules and the formation

of a primary wall cell. The second megaspore from the chalazal end, as in *Cassia tomentosa*, was found to develop into the embryo-sac.

Datta (1935) investigated *Cassia tora*. He found in the ovules sub-hypodermal primary archesporial cells, absence of the primary wall cells, and organisation of a linear tetrad of megaspores, out of which the chalazal one developed into the 8-nucleate embryo-sac. The antipodals, even though they were found to persist till fertilisation, remain only as free nuclei and are not organised into cells.

The latest work on the embryo-sac of the Cæsalpiniaceæ is a paper by Paul (1937) dealing with *Tamarindus indica*. He reports the differentiation of the primary archesporium from the sub-hypodermal layer, formation of the primary wall cell and a normal tetrad of megaspores from the megaspore-mother cell. The chalazal megaspore is the functional one and develops into the embryo-sac according to the *Normal*-type.

Material and Methods

During the course of the present investigation material of the following species of Cassia has been investigated.

1. *C. occidentalis* Linn.
2. *C. abtusifolia* **Linn.**
3. *C. glauca* Lamk.
4. *C. glauca* Lamk. var. *suffruticosa* Koenig.
5. *C. marginata* Roxb.
6. *C. siamea* Lamk.

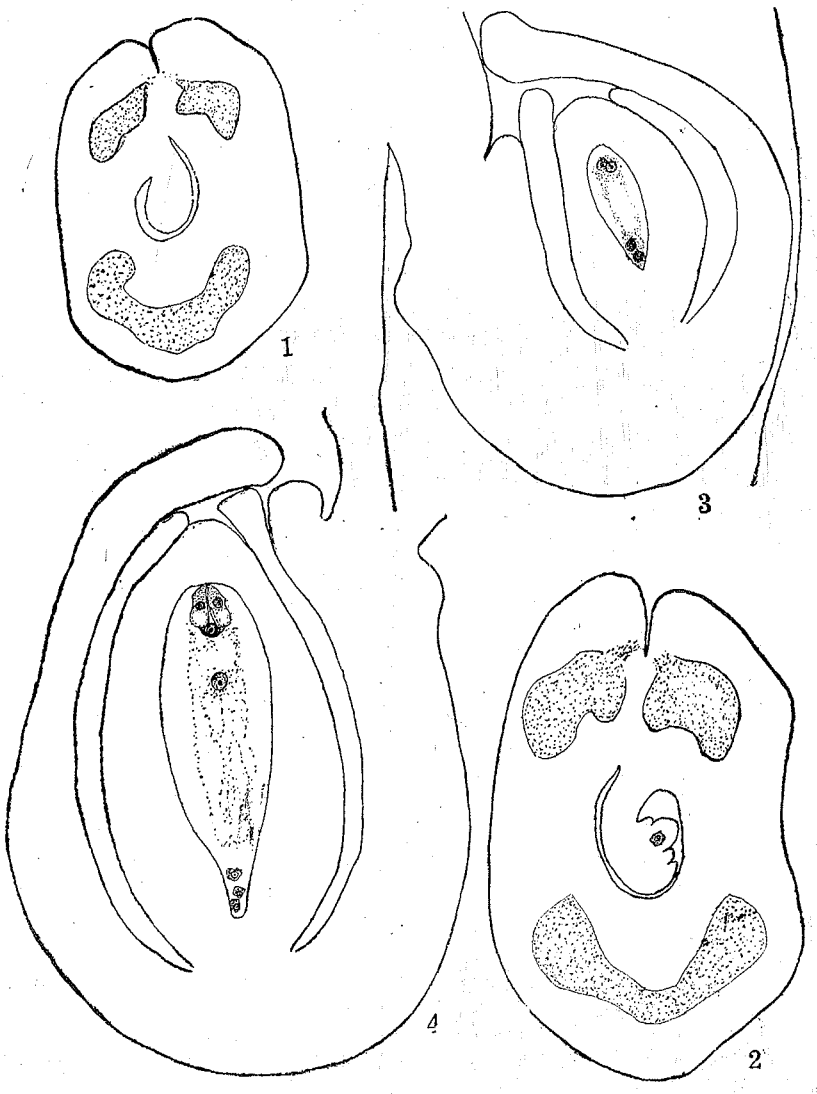
The first two species grow abundantly at Benares, particularly during the rainy season in waste places, and their material was collected from plants growing wild in the Benares Hindu University area. The material of *Cassia glauca* was obtained from a plant cultivated in the Benares Hindu University Botanical Garden, and that of *C. glauca* var. *suffruticosa* from a plant growing in the Sri Sita Ram Krishishala, Benares. The material of *C. marginata* was collected by Dr. A. C. Joshi from a tree growing in one of the gardens at Allahabad and that of *C. siamea* from trees planted on road-sides in the Benares Hindu University campus.

In all cases the material was fixed in Nawaschin's fixative between 12 noon and 3 p.m. during the months of September, October and November, 1940. An exhaust syringe was employed to cause the rapid immersion of the material in the fixative ; 12–18 hours after fixing, the material was rinsed in water four or five times and then transferred to 70% alcohol. The further dehydration and embedding in paraffin was carried out according to the customary methods. Sections were cut 8–16μ thick. Delafield's Hæmatoxylin and Newton's Iodine Gentian Violet were employed as stains.

Structure and Development of the Ovule

The ovules in all species of *Cassia* are borne in two rows along the ventral suture of the monocarpellary unilocular gynœcium, the ovules

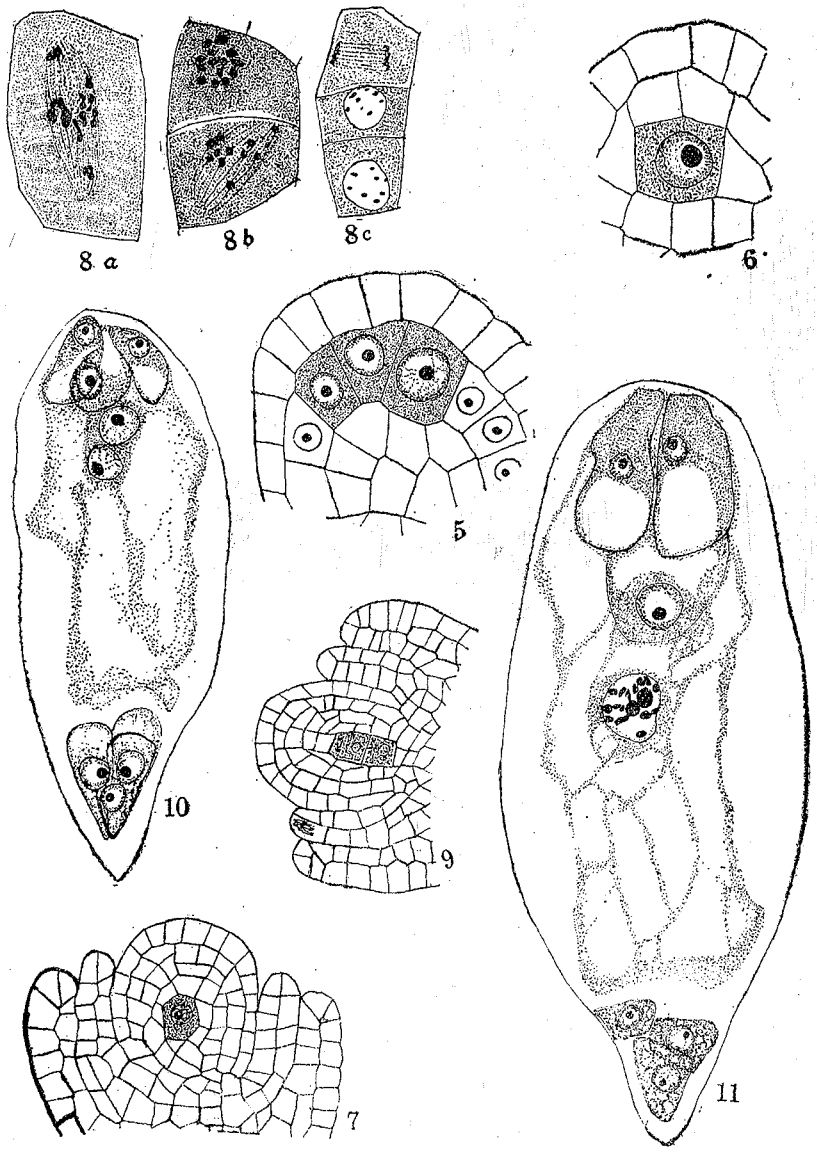
of the two rows alternating with one another. The number of ovules in a carpel varies slightly with each species, but it may be stated that on the average there are 30–50 ovules in a carpel.



Figs. 1–4. *Cassia occidentalis*.—Figs. 1 and 2. Transverse sections of young ovaries showing early stages in the development of the ovule. The vascular bundles of the carpel are stippled. Fig. 3. An ovule at the 4-nucleate embryo-sac stage. Fig. 4. An ovule at the mature embryo-sac stage. Figs. 1 and 2, × 800; Figs. 3 and 4, × 150.

The ovules first arise as small papillæ from the margins of the carpel, which has at this stage the form of a linear structure folded upwards along the midrib, a fact which agrees with the classical interpretation of carpel morphology. The two margins of the carpel are still free from each other and the carpel is open on the posterior side (Fig. 1). The development of the ovule primordia results chiefly from the activity and rapid division of groups of hypodermal cells, and after their differentiation these primordia are seen protruding into the ovary cavity (the space enclosed by the wall of the carpel). The ovule primordia at first are quite straight, but soon during further growth the cells develop more actively on one side than on the other. Consequently the young ovules bend towards the apex of the ovary, and gradually assume an anatropous form (Fig. 3). Reeves (1930) in *Medicago* observed that the curvature of the ovules is conditioned by mechanical pressure. He found as long as there is space for free development, the ovule remains orthotropous, but as soon as the ovule during its growth comes in contact with the dorsal wall of the carpel opposing it, its straight growth comes to end and it curves generally towards the base. Maheshwari (1931) in *Albizzia Lebbek* describes the young nucellus as growing at first straight and at right angles to the placenta (ventral suture), but when it approaches the dorsal wall of the carpel it begins to curve upwards. Singh and Shivapuri (1935) describe the same condition in *Neptunia oleracea*, a member of the Mimosaceæ. In a few cases, in which the carpel was found to remain open throughout its development, the ovules were found to remain permanently orthotropous. Great significance has been attached to this fact by Joshi (1935) in the evolution of the anatropous form of the ovule. In *Cassia* species studied during the course of the present investigation, however, no such relation has been found. The primordia of the ovules begin to bend towards the apex of the ovary even when these are quite away from the dorsal wall of the ovary.

The mature ovules in all *Cassia* species, even after the development of embryo, are anatropous with a slight tendency towards amphitropy (Figs. 3 and 4). They possess two integuments. The inner integument in the flowering plants generally differentiates from the ovule primordium almost simultaneously with the differentiation of the primary archesporium, but in all *Cassia* species investigated by the writer it did not appear till the primary archesporial cell had cut off the primary wall cell and had reached the megaspore-mother cell stage. The development of the integuments thus in the genus is considerably delayed. The primordium of the inner integument arises just below the level of the megaspore-mother cell (Fig. 2). Soon after its differentiation, the primordium of the outer integument appears just below that of the inner integument. In spite of the late start, the outer integument soon outgrows the inner by its faster development, so that by the time of tetrad formation the outer integument has attained a slightly greater length than the inner (Figs. 25 and 31). While the outer integument by this time has reached the level of the nucellus apex, the inner integument is seen to end somewhat below the level of the nucellus. The disparity between the growth of the two integuments is maintained



Figs. 5–11. *Cassia occidentalis*.—Various stages in the development of the embryo-sac.—Fig. 5. Apex of the nucellus showing a group of primary archesporial cells. Fig. 6. Formation of the primary wall cell and its division by an anticlinal wall. Fig. 7. An ovule showing the megaspore-mother cell. Fig. 8 *a–c*. Three stages in the development of a tetrad of megaspores; (*a*) I meiotic division in the megaspore-mother cell; (*b*) the II meiotic division; (*c*) a stage showing the formation of a T-shaped tetrad of megaspores. Fig. 9. The ovule from which the T-shaped tetrad shown in Fig. 8 *c* has been sketched. Fig. 10. A young 8-nucleate 7-celled embryo-sac. Fig. 11. A mature embryo-sac after the fusion of the polar nuclei. Figs. 7 and 9, × 800; the rest, × 1700.

even in the later stages, so that in the mature ovule (an ovule at the time of fertilisation) the micropyle is mostly formed by the outer integument. The inner integument contributes only to a very small length of the micropyle (Fig. 4). There are two further peculiarities of the micropyle. Firstly, the passage formed by the outer integument is not quite opposite to that formed by the inner. It is rather to one side, so that the micropyle is not straight but somewhat zig-zag. Secondly, at the micropyle the outer integument is never in direct contact with the inner integument. In this region there is always a small space between the two integuments. Both the integuments in all species are two layers of cells thick except near the micropyle, where both the integuments are 4–5 cells thick.

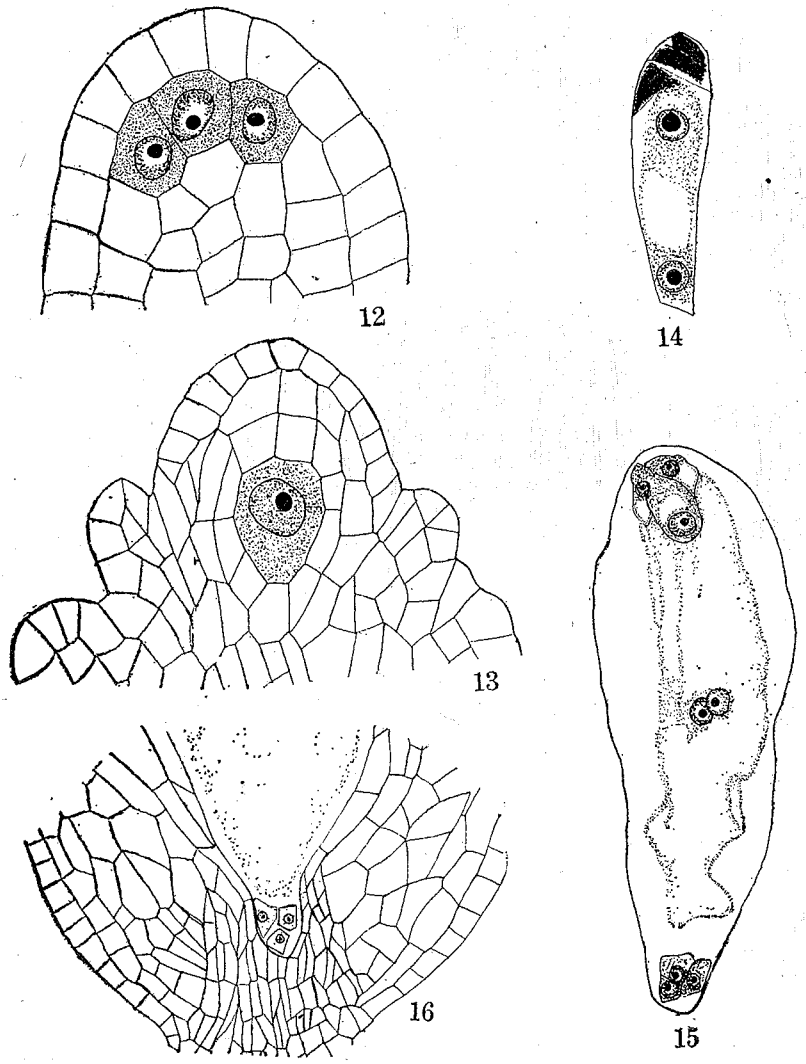
The nucellus in species of *Cassia* is massive from the very beginning. At the tetrad stage there are approximately 4–5 layers of nucellus cells above the tetrad, 3–5 layers on the sides, and 4–5 layers beneath the tetrad (Figs. 9 and 31). By the time the embryo-sac reaches the 4-nucleate stage the number of cells in the nucellus above the embryo-sac has increased to 8–10 layers due to divisions in the parietal cells. Before fertilisation many of these parietal cells are gradually crushed by the growing embryo-sac, but the number of cell layers above the micropylar end of the embryo-sac remains the same due to periclinal divisions in the epidermal cells of the nucellus. As the parietal cells are crushed at this end, the epidermal cells divide to restore the number of layers destroyed. This growth gives rise to considerable pressure inside the ovule, so that the epidermal cap shortly before fertilisation begins to project as a small beak into the micropyle of the ovule (Fig. 4). This pushes outwards the inner integument and leads to considerable decrease in the size of the air-space found between the two integuments close to the micropyle of the ovule. The formation just before fertilisation of an epidermal cap at the micropylar end of the nucellus with a small beak projecting into the micropyle seems to be a characteristic feature of all the Cassias examined by the author. I have seen it also in a number of other Cæsalpiniaceæ and perhaps this feature is characteristic of the whole family. There are approximately 6–7 layers of cells below the chalazal end of the embryo-sac, and 7–8 on the sides of the embryo-sac at the time of fertilisation. To a large extent these cell layers are soon crushed by the post-fertilisation growth of the embryo-sac.

Another characteristic feature of the ovule of Cassias is that the epidermis of the funicle and the adjacent part of the outer integument on the outer side (*i.e.*, the side on which the ovule does not bend) remains meristematic for a long time. At the tetrad stage these cells are quite distinct from the other cells of the ovule, possessing as they do dense cytoplasm and no conspicuous vacuoles. Further close to the hilum these cells grow out into a short hump-like outgrowth, which persists throughout the life of the ovule.

Development of the Embbyo-Sac

As the ovule begins to curve, but before the appearance of the integument primordia, the primary archesporium differentiates from

the other cells of the nucellus. In the flowering plants in general the curving of the ovule, the appearance of the integument initials and development of the primary archesporium are almost synchronous.



Figs. 12–16. [*Cassia obtusifolia*.—Fig. 12. Nucellus showing a group of archesporial cells. Fig. 13. An ovule at the megaspore-mother cell stage. Fig. 14. A 2-nucleate embryo-sac, with three degenerating micropylar megaspores. Fig. 15. An 8-nucleate, 7-celled embryo-sac. Fig. 16. Antipodal region of an embryo-sac showing the tubular extension of its chalazal end. Fig. 15, × 1400; the rest, × 1700.

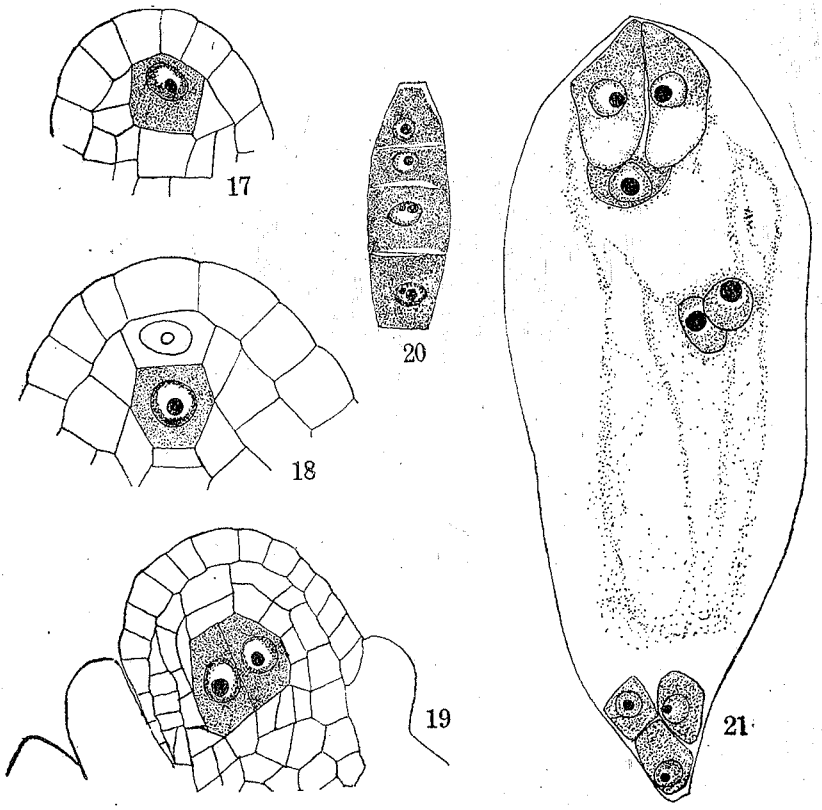
In all Cassias, however, as has been stated before, the integuments begin to develop rather late, only after the differentiation of the megaspore-mother cell in the ovules. The primary archesporium in all species

was found to be of hypodermal origin. In *Cassia glauca* and *C. glauca* var. *suffruticosa* a single primary archesporial cell is quite prominent from an early stage and can be easily distinguished from the surrounding cells (Figs. 17 and 22). In other species all the cells of the hypodermal layer are equally prominent and look just alike. They all show dense cytoplasm and possess almost equally large nuclei (Figs. 5, 12 and 26). One of these cells, however, generally the most centrally situated one, divides by a periclinal wall into an outer parietal cell and an inner megaspore-mother cell. This cell may be said to act as the primary archesporial cell (Figs. 6, 13, 18, 23, 29 and 30).

Describing the primary archesporium of the ovule, Coulter and Chamberlain (1903) state: "The archesporium is recognized by the increasing size and different reaction to stains of one or more hypodermal cells. Doubtless all of the hypodermal cells are potentially archesporial, and there is reason for believing that the deeper cells of the nucellus, most of which are probably derivatives from the original hypodermal layer, may be also. In the vast majority of the cases, however, only cells of the hypodermal layer show those changes that are characteristic of archesporial cells. It is not always easy to determine just how many hypodermal cells are to be included in the archesporium, for there is often complete gradation from cells with the size and staining reaction of undoubted archesporial cells to those showing neither increase in size nor the characteristic staining reaction. This is to be expected in case all the hypodermal cells are potentially archesporial, and there is no definite point in its history when such a cell ceases to be merely hypodermal and becomes clearly archesporial." While examining the ovules of the different species of *Cassia* for the primary archesporial stages, I have felt exactly like Coulter and Chamberlain. In the beginning in most species all the hypodermal cells at the apex of the nucellus are just similar. Then one of them cuts off a parietal cell and may be said to function as stated above as the primary archesporial cell.

Saxton (1907) noted in *Cassia tomentosa* that the primary archesporial cell is deep-seated, *i.e.*, sub-hypodermal and functions directly as the megaspore-mother cell without cutting off any parietal cell. Datta (1935) has described the same feature in *Cassia tora*. From the uniform hypodermal origin of the primary archesporium that I have noticed in the species examined by me, I am led to believe that the observations of both these authors are probably incorrect. This error has been made by them very likely from an examination of too old material, in which the parietal tissue had already begun to develop. I have not been able to see the paper by Saxton, but from examining the figures of Datta I find the Fig. 3 of his, which is almost at the same stage as Fig. 2 (and the latter is supposed to represent the primary archesporium). In the material examined by me the ovule has always developed up to the megaspore-mother cell stage by the time the integument primordia differentiate. Further, *Cassia obtusifolia* examined by me is very closely related to *C. tora*. In *Cassia obtusifolia*, I have clearly seen the hypodermal origin of the primary archesporium and the formation of a primary perietal

cell. It is not possible to believe that two such closely related species can show such a great difference in their embryological characters. What Datta regards as the primary archesporial cell is really the megaspore-mother cell after the cutting off of the primary wall cell. The observations of Ghose and Alagh (1930) on *Cassia purpurea* agree with mine. They also noted hypodermal archesporium and the formation of the primary wall cell. This character, therefore, may be taken as characteristic of the genus. Paul (1937) has reported sub-hypodermal origin of the primary archesporium in *Tamarindus indica*. I consider his observations also doubtful.



Figs. 17–21. *Cassia glauca*.—Fig. 17. The primary archesporial cell. Fig. 18. The differentiation of the primary wall cell. Fig. 19. An ovule showing two megaspore-mother cells. Fig. 20. A linear tetrad of megaspores. Fig. 21. A mature embryo-sac. Fig. 19, × 800; the rest, × 1700.

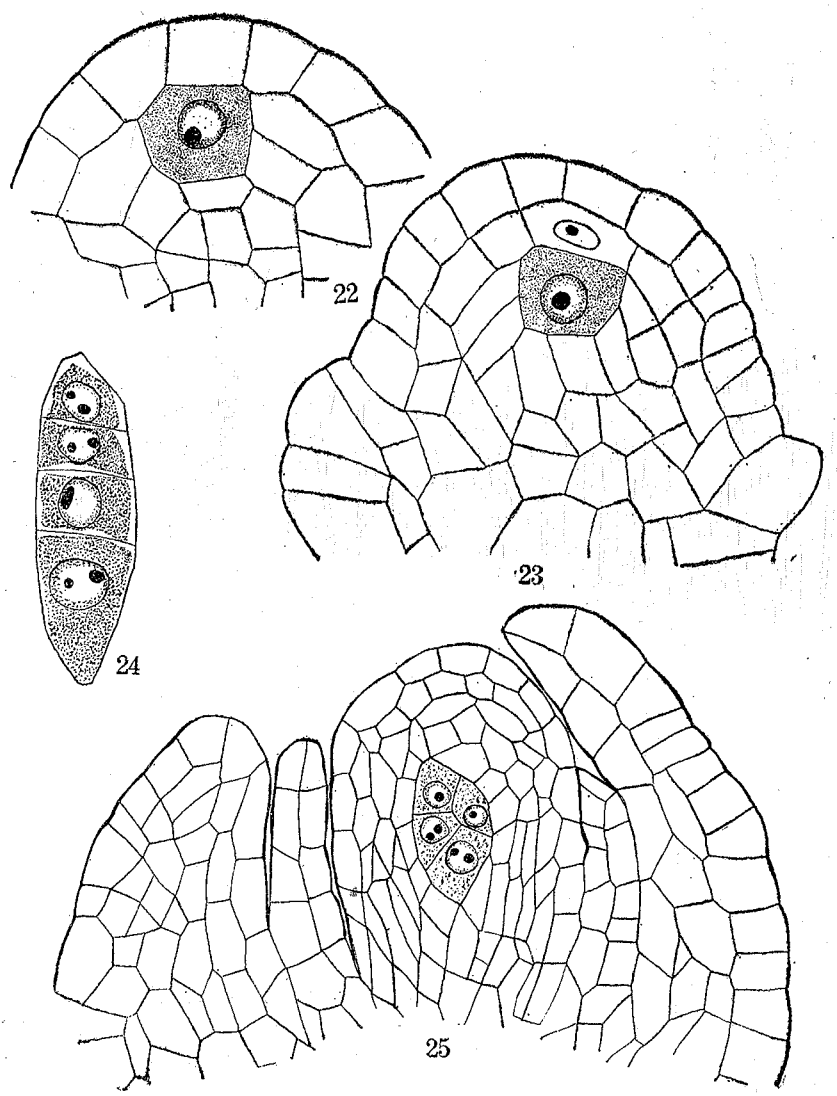
One functional archesporial cell and one megaspore-mother cell is the general character of the ovules of the different Cassias, but the occasional occurrence of two megaspore-mother cells has been observed in *Cassia glauca* (Fig. 19), *C. glauca* var. *suffruticosa* and *C. siamea*. Perhaps such exceptional cases are likely to occur in other species also

if a larger amount of material is examined. However, whenever two megaspore-mother cells were observed in an ovule, only one was seen to develop up to the tetrad stage. I did not come across any case of two tetrads or multiple embryo-sacs in an ovule. Occurrence of more than one megaspore-mother cells in an ovule has been previously noted by Datta (1935) in *Cassia tora*, and there are many similar instances reported among other Leguminosæ, *e.g.*, *Albizzia Lebbek* of the Mimosaceæ (Maheshwari, 1931), *Medicago sativa* (Reeves, 1930), *Melilotus alba* (Cooper, 1933), etc., belonging to the Papilionaceæ.

The primary parietal cell divides in all planes and by the time the two meiotic divisions in the megaspore-mother cell are completed, it gives rise to 4–5 layers of parietal cells (Figs. 9 and 31). Later the number of these layers increases to 8–10. Such extensive development of the parietal tissue seems to be characteristic of the Cæsalpiniaceæ and Mimosaceæ. In the Papilionaceæ, on the other hand, the parietal tissue is poorly developed. This agrees with the primitive character of the first two families and the more advanced position of the last family in the order.

The megaspore-mother cell after its differentiation undergoes a considerable period of rest and growth without any nuclear changes. It increases considerably both in length and breadth. The ovule also increases considerably during the megaspore-mother cell stage, so that the megaspore mother-cell becomes deep-seated. The meiotic divisions in all investigated species proceed in the normal manner. In *Cassia occidentalis* 14*n* chromosomes were counted during these divisions (Fig. 8 *a*). After the first meiotic division the mother cell is divided into two dyads by a transverse wall, which does not lie exactly in the middle (Figs. 8 *a*, *b* and *c*). The dyads are thus of unequal size, the chalazal one being larger. The second meiotic division in the two dyad cells generally does not proceed simultaneously. It starts earlier and proceeds more actively in the chalazal dyad than in the micropylar, so that in some cases even when the division has been completed in the chalazal dyad, the micropylar dyad is in the telophase stage (Fig. 8 *c*). Due to the difference in the size of the dyads, the megaspores formed from them also show slight size differences. The two chalazal megaspores are slightly larger than the two micropylar ones. The four megaspores are generally arranged in a linear order (Figs. 20, 24 and 31), but a T-shaped arrangement of the megaspores (Figs. 8 *c* and 9) was also seen in several instances in almost all species. In addition to this variation, in one ovule of *Cassia glauca* var. *suffruticosa* one megaspore-mother cell was observed to have given rise to an isobilateral tetrad of megaspores (Fig. 25). In this ovule there were two megaspores. One of these had formed this exceptional type of tetrad. The other was still in the megaspore-mother cell stage. It is not illustrated in the figure. Exceptional occurrence of isobilateral tetrads of megaspores in the flowering plants has been previously observed by Ducamp (1902) in *Fatsia japonica*, Greco (1930) in *Myrtus communis*, and Capoor (1937) in *Urginea indica*.

In all the species studied during the course of the present investigation the chalazal megaspore is found to develop into the embryo-sac (Figs. 14 and 31). The other megaspores degenerate, but the traces of the degenerating cells may be seen up to the 2-nucleate stage of the



Figs. 22–25. *Cassia glauca* var. *suffruticosa*.—Fig. 22. The primary archesporial cell. Fig. 23. Formation of the primary wall cell. Fig. 24. A linear tetrad of megaspores. Fig. 25. An ovule showing an isobilateral tetrad of megaspores. Fig. 25, × 900 ; the rest, × 1700.

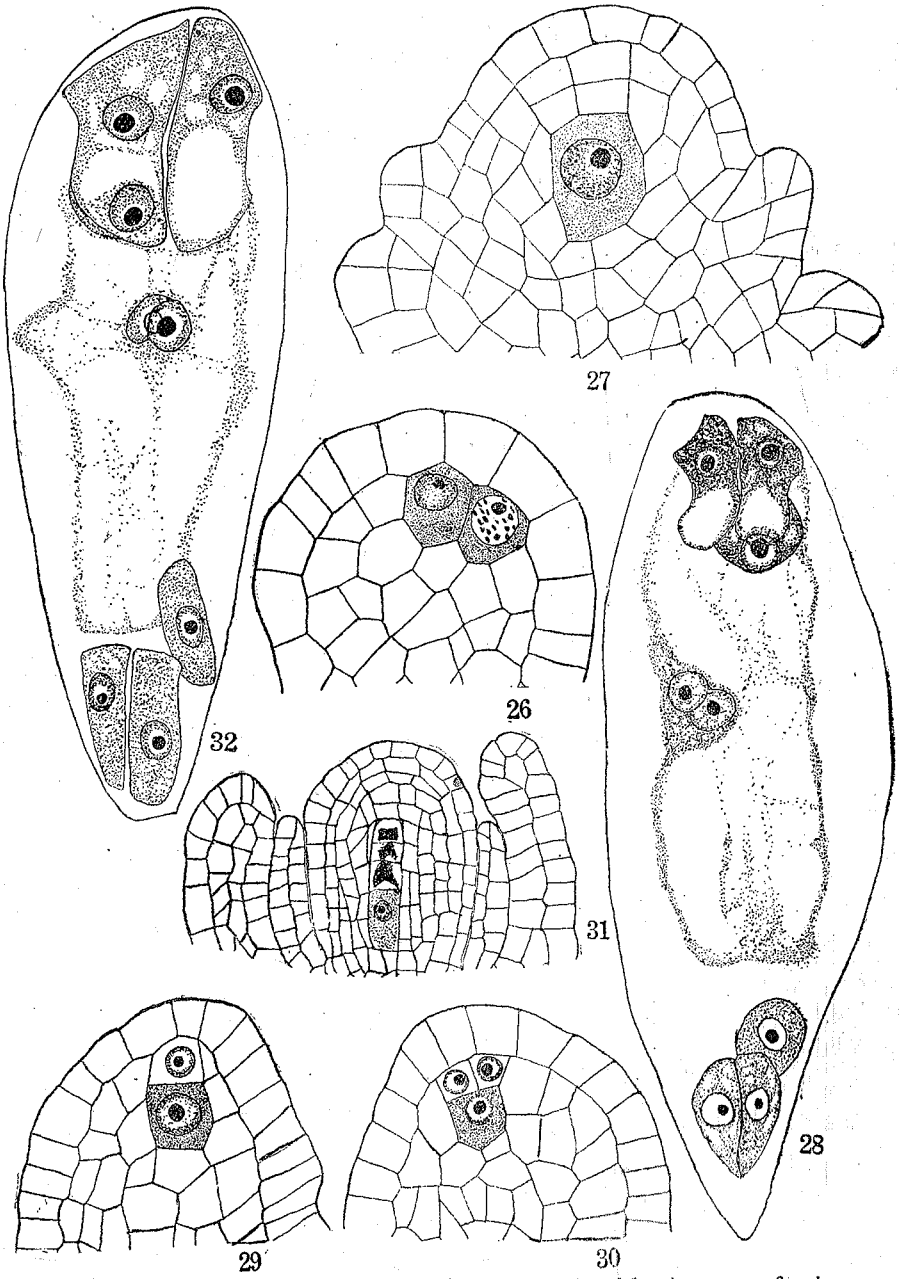
embryo-sac. Datta (1935) observed the same feature in *Cassia tora*, but Saxton (1907) and Ghose and Alagh (1933) found in *C. tomentosa* and *C. purpurea* respectively the second megaspore from the chalazal end developing into the embryo-sac. Such variation in the selection of the megaspores is common in the whole order Leguminosæ and was observed as early as 1881 by Guignard. From a study of about 40 species he concluded that in the Leguminosæ of the four megaspores of the tetrad either the innermost or the one next to it is the functional one.

The functional megaspore develops into the embryo-sac according to the *Normal*-type. It increases in size. Along with this vacuoles develop both above and below the central nucleus. The latter divides. The daughter nuclei move to the two poles of the embryo-sac and a central vacuole becomes prominent. The two nuclei at the poles undergo two more mitotic divisions, so that an 8-nucleate embryo-sac is formed with four nuclei at either end. Three nuclei at the micropylar end organise into the egg-apparatus, three at the chalazal end into antipodals and the two polar nuclei are left in the central cell (Figs. 10, 15, 21, 28 and 32).

Both the egg and the two synergidæ are nearly pyriform. The egg is slightly larger than the synergidæ. It shows a large vacuole towards the micropylar end, while the nucleus and the cytoplasm are pressed towards the chalazal end. The synergidæ show a large vacuole in the chalazal half, while the micropylar half is densely filled with cytoplasm. The nucleus is found embedded in the cytoplasm just above the vacuole. In all species the synergidæ show prominent hooks and a distinct "filiform apparatus" at the time of fertilisation (Figs. 11, 21, 28 and 32).

The antipodals form definite cells (Figs. 10, 11, 21, 28 and 32). Datta (1935) reports that in *Cassia tora* the antipodals are not organised into cells but remain as free nuclei. As I have observed antipodal cells in all the species investigated by me, his observations appear to me quite erroneous. Even in one of his own figures he has represented one of the antipodals as a cell with a cell-wall around it. In all the Leguminosæ investigated so far the organisation of antipodal cells has been noted. The antipodals in all Cassias are quite prominent and persist till the time of fertilisation. They often develop large vacuoles. In *Cassia glauca* var. *suffruticosa* they are sometimes even more prominent than the egg-apparatus. In *Cassia tomentosa*, Saxton (1907) mentions the presence of more than three antipodals, but I have not come across any such case in my material.

The two polar nuclei meet near the egg-apparatus or the middle of the embryo-sac. Here they remain together for a long time, but fuse only just before fertilisation. In *Cassia occidentalis*, the two polar nuclei just before fusion have been observed to enter the prophase stage and show the chromosomes quite distinctly (Fig. 11).



Figs. 26–32.—Figs. 26–28. *Cassia marginata*.—Fig. 26. A group of primary archesporial cells. Fig. 27. Apical region of an ovule with a megaspore-mother cell. Fig. 28. Mature embryo-sac. × 1700. Figs. 29–32. *Cassia siamea*.—Fig. 29. An ovule showing the differentiation of a primary wall cell and the megaspore-mother cell. Fig. 30. The same as Fig. 29 but showing the anticlinal division of the primary wall cell. Fig. 31. An ovule showing a linear tetrad of megaspores. Fig. 32. A mature embryo-sac. Fig. 31, × 900; the rest, × 1700.

SUMMARY

The development of the ovules and embryo-sac has been studied in *Cassia occidentalis* Linn., *C. obtusifolia* Linn., *C. glauca* Lamk., *C. glauca* Lamk. var. *suffruticosa* Koenig., *C. marginata* Roxb. and *C. siamea* Lamk. The ovules in all species are anatropous, with a slight tendency towards amphitropy, and bitegmic. The integument initials appear only after the primary archesporial cell has cut off the primary wall cell. The micropyle is somewhat zigzag and is formed largely by the outer integument. Further, in the region of the micropyle the outer integument for a short distance is separated from the inner by a small air-space. The nucellus is quite massive. The formation just before fertilisation of an epidermal cap at the micropylar end of the nucellus with a small beak projecting into the micropyle is characteristic. The epidermis of the funicle and the adjacent part of the outer integument on the outer side remains meristematic for a long time and close to the hilum grows out into a short hump-like structure, which persists throughout the life of the ovule.

The primary archesporium in all species is hypodermal and a primary wall cell is always formed. The earlier records about the occurrence of sub-hypodermal archesporium in some species of *Cassia* appear to be all doubtful. The megaspore-mother cell gives rise to a linear or T-shaped tetrad of megaspores, of which the chalazal develops into an 8-nucleate embryo-sac according to the normal type. In one instance in *C. glauca* var. *suffruticosa* an isobilateral tetrad of megaspores has been observed. The synergidæ are prominently hooked and show the filiform apparatus. The egg is pyriform and slightly larger than the synergidæ. The antipodals are definite cells and persist till the time of fertilisation. The two polar nuclei meet near the egg-apparatus. They fuse only just before fertilisation.

In conclusion I wish to express my sincere thanks to Dr. A. C. Joshi for his kind advice and help throughout the progress of the work.

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