A CONTRIBUTION TO THE LIFE-HISTORY OF
OROXYLUM INDICUM VENT

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INTRODUCTION

Oroxylum indicum VENT, a plant belonging to the family Bignoniaceae, is grown as an ornamental plant in many gardens. It is a tree with large, beautiful bilabiate flowers and long sword-shaped fruits.

The earlier literature on the embryology of the Bignoniaceae has been reviewed by Schnarf (1931). Since then the following important contributions have been made. Mauritzon (1935) has described the formation of the embryo-sac and endosperm in six genera and has recognised two main types of endosperm development. Soueges (1940) for the first time, studied in detail the development of the embryo in Catalapa kæmpferi. Swamy (1941) has given an account of the embryology of Bignonia megapotamica and later Govindu (1950) described in detail the embryology of Jacaranda mimosæfolia, Parmentiera cerifera, Tecoma stans and Kigelia pinnata.

The literature on the cytology of the family is comparatively meagre. The earlier cytological investigations as reported by Wang (1940), Raghavan and Venkatasubban (1940), Venkatasubban (1945) and Darlington and Janaki Ammal (1945) refer mainly to the chromosome numbers of the various genera of the family.

The present work gives an account of the cytology and embryology of Oroxylum indicum. The development of the wing on the seed has also been studied.

MATERIAL AND METHODS

The material used in the present investigation was obtained from a plant growing in the University College campus.

For cytological studies, temporary and permanent preparations of anthers and root-tips were made. Meiotic division was frequent between 9 A.M. and 11 A.M. For permanent preparations, anthers were treated in equal proportions of 0.002 M Oxyquinoline and Nawaschin's fluids (Sharma and Ghosh, 1951) at 18°C. for two hours and then kept at room temperature.
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for overnight. Temporary smears of anthers in acetocarmine were not satisfactory.

Temporary mounts of root-tips were treated in a mixture of saturated solution of paradichlorobenzene and water in the proportion of 1:4 with a drop of formalin for 45 minutes at room temperature; heated in a mixture of 2% aceto-orcein and N.HCl (9:1) and squashed in 1% aceto-orcin. Very clear metaphase plates were obtained by this method. For permanent mounts, fixation of root-tips in a mixture of equal amounts of 1% platinic chloride and 10% formalin gave satisfactory results.

For embryological studies, ovaries in different stages of development were fixed in Nawaschin's fluids. Dehydration, clearing and embedding were done in the usual way. Sections were cut 8–16 μ thick depending on the stage required for study.

Newton's crystal-violet-iodine and Heidenhain's iron-alum hæmatoxylin were used for staining.

Pollen grains were stained and mounted in methyl-green-glycerine jelly for study.

For studying the nature of the cells composing the wing of the seeds, these were macerated in 5% chromic acid and also in saturated solution of caustic potash.

Observations

The Somatic Chromosomes

The diploid number of chromosomes as determined from root-tip cells was found to be 28 (Fig. 1). On the basis of relative length, the chromosomes could be arranged under three categories:

(i) One pair of long chromosomes 3·67 μ in length.

(ii) Eight pairs of medium-sized chromosomes varying in length from 2·45 μ to 1·53 μ.

(iii) Five pairs of short chromosomes varying in length from 1·42 μ to 1·12 μ.

An idiogramatic representation of the chromosomes reveals the following types: (Fig. 2)

Type A.—One pair of long chromosomes with submedian primary constriction and secondary constriction on the shorter arm.

Type B.—One pair of medium-sized chromosomes with satellites. Primary constrictions are median.
Type C.—One pair of medium-sized chromosomes with satellites and sub-median primary constriction. Satellites are situated on the shorter arm.

Type D.—One pair of medium-sized chromosomes with submedian primary constriction and secondary constriction on the shorter arm.

Type E.—One pair of medium-sized chromosomes with sub-median primary constriction.

Type F.—One pair of medium-sized chromosomes with satellites and sub-median primary constriction. Secondary constriction is on the longer arm.

Type G.—One pair of medium-sized chromosomes with sub-median primary constriction.

Type H.—One pair of medium-sized chromosomes with median primary constriction.

Type I.—One pair of medium-sized chromosomes with sub-median primary constriction.

Types J and M.—Two pairs of short chromosomes with median primary constrictions.

Types K, L, and N.—Three pairs of short chromosomes with sub-median constrictions.

MEIOSIS AND THE POLLEN GRAINS

In the hypodermal layer a row of single-layered hypodermal archesporial cells becomes distinguishable during the lobation of the anther (Fig. 3). The archesporium is recognisable by the larger size, denser cytoplasm and more prominent nuclei of its cells. It divides periclinally to produce an outer layer of parietal cells and an inner of sporogenous cells (Fig. 4). By further divisions of the parietal cells, at least nine layers of cells are produced in the mature anther of which the innermost forms a secretory tapetum (Figs. 5 and 6). The outer layer forms the conspicuous hypodermal endothecium which later becomes multilayered below and show the characteristic endothecial bands. The epidermal cells show prominent radial elongation and conspicuous cutinization on the outer surfaces.

Before the differentiation of the microspore-mother-cells, the sporogenous tissue divides only once producing two layers (Figs. 4, 5 and 6). This division of the sporogenous layer takes place before the maturity of the tape- tum (Figs. 4 and 5). The tapetal cells which are uninucleate at the initial stages, become binucleate (Figs. 6 and 7). Some of these cells later become
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Text-Figs. 1–12. Fig. 1. Somatic metaphase, ×2,450. Fig. 2. Idiogram of the somatic chromosomes, ×4,900. Figs. 3–6. Differentiation of parietal and sporogenous tissue in the anther initial, ×500. Fig. 3. Hypodermal archesporium in the anther, ×500. Figs. 4–5. Division of the parietal and the sporogenous tissues, ×500. Fig. 6. Differentiation of the tapetal cells, ×500. Fig. 7. Binucleate tapetal cells, ×1,050. Fig. 8. Tri- and Quadrinucleate tapetal cell, ×1,050. Fig. 9. Diakinesis in a P.M.C., ×1,050. Fig. 10. Meiotic metaphase I, ×2,450. Fig. 11. Meiotic metaphase II, ×2,450. Fig. 12. A pollen grain, ×750.

Quadrinucleate (Fig. 8). The tapetal cells begin to degenerate after the formation of the pollen grains.

Meiosis does not show any unusual feature. At diakinesis fourteen bivalents are seen, of which three are attached to the nucleolus (Fig. 9).
The bivalents are somewhat irregular in form but show size differences and lie mostly towards the periphery of the nucleus. The nucleolus shows progressive reduction in size and disappears along with the disappearance of the nuclear membrane. During metaphase I, the chromosomes are regularly arranged on the equatorial plate of the bipolar spindle and become much condensed. A polar view of an equatorial plate shows fourteen bivalents (Fig. 10). The anaphasic separation of the chromosomes appears to be regular. On the completion of the first division, the two daughter nuclei are organised with distinct nuclear membranes and the chromosomes pass through an interkinetic stage. Second division is of the simultaneous type, fourteen chromosomes appear like dots in polar view at metaphase II (Fig. 11). On the completion of the second division, four daughter nuclei are formed arranged in a tetrahedral manner. Cytokinesis takes place by the process of furrowing.

The mature pollen grains are tricolpate, spheroidal-prolate, length of the longest axis varies from 70 μ-80 μ; reticulate, sexine is entire, annular and thicker than the nexine (Fig. 12). The pollen grains are binucleate, the vegetative nucleus being much bigger in size than the generative nucleus.

**Development of the Ovule**

As is characteristic of the Bignoniaceae, the ovary is distinctly superior, subsessile, bicarpellar and bilocular with a single style and a bilobed flattened stigma. A thick, annular disc occurs at the base of the ovary.

The ovules are unitegmic, tenuinucellate and mostly anatropous. A few hemianatropous ovules have also been noted. The ovules are borne on the two slightly projecting placentas. The placentas are parietal in the beginning (Fig. 13) but very soon become axile due to the later development of a sterile, central bridge connecting the two fertile, massive projections (Fig. 14).

The ovule at first arises as an uniform mass of a papillate protrusion of the placenta and curves inwards before the differentiation of the archesporium and the integument. The direction of curvature of the ovules is opposite to each other on the two sides of the sterile partition wall (Fig. 14).

A hypodermal archesporial cell differentiates before the integument is developed (Fig. 15). The integument arises from the base of the nucellus (Fig. 16) when the ovule has rotated about ninety degrees. The integument at its inception is composed of only two layers of cells and extends to about half the length of the nucellus. The cells composing the integument divide rapidly and the tip is soon seen to be composed of four layers of cells which
undergo further divisions in later stages. Most of the ovules turn through an angle of 180 degrees and become completely anatropous before the integuments are fully developed.

The nucellus in the initial stages of development of the ovule is composed of a few layers of cells. With the increase in size of the ovule, a multi-layered, massive and elongated nucellus results. It is interesting to note in this connection that generally from the four-nucleate stage of the female gametophyte onwards, disintegration of the nucellar epidermis starts. It proceeds from the micropylar end and extends towards the chalazal region, because of the maximum dilation of the gametophyte at the former end. At the mature embryo-sac stage, almost all of the nucellar cells become destroyed. The innermost cells of the integument which come in contact with the embryo-sac, elongate radially and form the endothecium. This has also been noted in other plants of the family by previous workers. It is further significant to note that at the chalazal end below the embryo-sac, a hypostase is formed. The vascular strand is unbranched and terminates at the chalazal region, a little above the hypostase.

**MEGASPOROGENESIS**

The single archesporial cell which differentiates in the hypodermal layer (Fig. 15) can be easily made out on account of its bigger size and prominent nucleus. It directly functions as the megaspore mother cell (Fig. 16). The position of the nucleus inside the megaspore mother cell is not fixed, as it has been found to lie towards the top or bottom or sometimes in the centre. It is interesting to note that Banerji (1940) noted a similar condition in *Costus speciosus*. On the completion of the usual reduction divisions, a linear tetrad of megaspores is formed (Fig. 17). The upper three megaspores degenerate and only the lower chalazal one becomes functional. The increase in size of the functional megaspore is accompanied with increased vacuolation. After the first meiotic division, the two daughter nuclei move apart to opposite poles and become embedded in a mass of copious cytoplasm (Fig. 18).

The next division gives rise to the four-nucleate stage, when two nuclei are arranged at each pole in a dense cytoplasmic mass. During this period, a large central vacuole occupies the central region of the sac. It may be mentioned that the nuclei lying towards the micropylar region are comparatively larger than those occupying the chalazal end. The embryo-sac at this stage becomes dilated at the micropylar end, and gradually tapers towards the chalaza. It becomes more or less club-like in appearance (Fig. 19). Division of the four nuclei gives rise to the eight-nucleate embryo-sac of the
Figs. 13-26
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Text-Figs. 13–20. Fig. 13. Development of placenta, ×39. Fig. 14. Development and curvature of ovules, ×39. Fig. 15. Nucellus showing archesporial cell, ×475. Fig. 16. Megaspore mother cell, ×475. Fig. 17. Linear tetrad, ×475. Fig. 18. Two-nucleate embryo-sac with degenerating megaspores, ×475. Fig. 19. Four-nucleate embryo-sac, ×475. Fig. 20. Mature embryo-sac, ×475.

Figs. 21–26. Fig. 21. Primary endosperm nucleus in division, ×475. Figs. 22–26. Stages in the development of the endosperm. Figs. 22–24, ×475. Figs. 25–26, ×300. Fig. 26. Chalazal haustorium of the endosperm; note zygote in resting condition.

Polygonum-type (Maheshwari, 1948). The mature embryo-sac is somewhat cylindrical in shape with maximum dilation near about the middle (Fig. 20). The two synergids are slightly hook-shaped in appearance with pointed apices and big basal vacuoles. Synergids of similar form have been recorded by Mauritzon (1935) in Catalapa, by Swamy (1941) in Bignonia megapotamica and by Govindu (1950) in four other genera. The egg-nucleus is much bigger in size than the synergid-nuclei. It is situated below the synergids. The polar nuclei fuse together to form the secondary nucleus of the embryo-sac. The antipodals are three in number and ephemeral in nature. The early degeneration of the antipodals has also been observed by Mauritzon (1935) and by Swamy (1941) but not by Govindu (1950) in Jacaranda mimosefolia, Parmentiera cerifera and in Tecoma stans.

Fertilization

Fertilization is porogamous. Plasmogamic condition of the egg and the male generative nucleus is delayed in comparison to that between the second male gamete and the fusion nucleus. The fusion of the egg and the sperm-nucleus does not appear to take place earlier than the 12-celled stage of the endosperm. The fertilized egg remains undivided for a long time. It divides after the division of the primary endosperm nucleus has taken place.

Development of the Endosperm

Before division, the primary endosperm nucleus migrates towards the chalazal region. It divides much earlier than the egg. Transverse wall-formation demarcates a small, basal, primary chalazal chamber and an upper large micropylar one (Fig. 21). The next division is synchronous and vertical in both the chambers, forming two tiers of two cells in each (Fig. 22). Subsequently, vertical walls are laid down in the two primary tiers at right angles to the previous plane of division. As a result, eight cells are formed with four cells in each tier (Fig. 23). The cells of the chalazal tier do not appear to divide further. They elongate enormously to form the highly conspicuous chalazal haustoria. The four cells of the micropylar tier usually divide transversely to form eight cells; thus the developing endosperm becomes composed of three tiers consisting of four cells each.
(Fig. 24). By repeated divisions of the cells of the middle tier, an extensive endosperm tissue is formed (Fig. 25). The uppermost micropylar cells, formed towards the beginning of endosperm-development, gradually lose their protoplasmic contents and have no haustorial function (Fig. 25). The nucellar tissues in contact with the chalazal haustorium gradually disorganise. The cells below this degenerated zone in the chalazal part, arrange themselves in regular rows which are rich in protoplasmic contents and take deep stain (Fig. 26). Such radiating arrangement of cells at the chalazal region has been reported in *Bignonia megapotamica* by Swamy (1941).

The mature endosperm tissue, prior to division of the fertilised egg is composed of a large number of cells. These cells may be grouped as follows into four zones, based on the size, compactness and protoplasmic contents (Fig. 26).

1. Four-celled haustorium at the chalazal region.
2. Just above these, a compact mass of small, more or less rectangular, parenchymatous and prominently nucleated cells. These serve as proper endosperm in which the fertilised egg lie embedded before division.
3. A mass of loosely arranged cells of larger size and lesser protoplasmic contents which stain feebly.
4. Lastly, at the micropylar end, the remnants of broken walls of the disintegrated cells.

**EMBRYOGENESIS**

The fertilised egg lies embedded in the mature endosperm tissue. The zygote nucleus enlarges in size and migrates towards the lower part of the cell before division (Fig. 27). The first division of the zygote is transverse giving rise to a basal cell $Cb$ and a terminal cell $Ca$ (Fig. 28). The former divides transversely and the latter longitudinally, resulting in a 1-shaped pro-embryo composed of four cells (Fig. 29). Occasional occurrence of a linear row of four cells is also noticed (Fig. 30).

After the pro-embryo stage, the two upper cells divide transversely. These engender four quadrants disposed in a vertical plane (Fig. 31). The quadrants thus formed, next segment vertically to produce four upper octants and four lower ones (Fig. 32). The upper octants produce the cotyledonary portion of the embryo, undergoing first periclinal and then anticlinal divisions to separate the dermatogen (Fig. 33). Later, two layers of cells are differentiated beneath the epidermis. The lower octants produce the hypocotyledonary portion (Fig. 32).
The hypophysis originates from the cell \( d \), a daughter cell of \( m \) (Figs. 33–35). The tissues produced by it are deeply embedded in the body of the embryo. To begin with, the hypophysis cell \( h \), although similar in shape to the other cells of the suspensor, soon becomes somewhat rounded at the lower end. It divides transversely to form two daughter cells, each of which undergoes two divisions by walls at right angles to one another (Figs. 34–35). Of the resulting eight cells, the lowest four form the initials of the root cortex and the upper four produce the root cap and the root epidermis.

The suspensor is long and filamentous. At maturity it consists of about fifteen cells, the lowest few of which divide lengthwise. Each cell thus produced has a prominent nucleus and is longer than broad (Fig. 35).

In the mature seed, the cotyledons are large, massive, more or less obcordate in shape (Fig. 36) and completely fill up the seed.

**Development of the Wing**

The seeds of *Oroxylum indicum* are characterised by the presence of a thin, membranous structure called the "Wing". It forms an outer fringe, composed of a single layer of mostly thin-walled cells. Its maximum extension is on the two lateral sides of the seed. The delicate, almost transparent, fringe is supported on brownish, rib-like radiating strands composed of thick-walled cells (Zones III and I in Fig. 36), which encircle the cotyledons completely. In between these two zones, the area of the wing is occupied mainly with thick-walled cells and partly with thin-walled ones (Zone II in Fig. 36). That the thickening appears to be due to deposition of cellulose has been ascertained by microchemical tests.

The early stages in the development of the wing is indicated by the elongation and increase in the size of the two tip-cells at the chalazal end of the ovule before fertilization (Fig. 37). The process becomes accentuated after syngamy (Fig. 38). During the initial stages of the development of the endosperm, the chalazal tip-cells and the lateral epidermal cells of the integument divide both longitudinally and transversely and become more active. This is accompanied by an elongation of these cells. As a result broad, multicellular outgrowths are formed surrounding the ovules during the earlier stages of endosperm development. The cells produced from the chalazal tip elongate rapidly as slender columns, closely adpressed with each other. After attaining considerable length, these become curved and interwined (Fig. 39). The development of the wing thus proceeds mainly on two aspects: (1) from the chalazal tip and (2) from the outermost integumentary cells on the lateral sides of the ovules (Fig. 40). These two zones composed of thin-walled cells ultimately coalesce forming the major part
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Text-Figs. 27-35. Stages in the development of the embryo. Figs. 27-33, ×550. Figs. 34-35, ×300.

Text-Figs. 36-45. Fig. 36. Mature winged seed, ×½. Figs. 37-39. Chalazal tip-cells of the ovule elongating. Figs. 37-38, ×300. Fig. 39, ×77. Fig. 40. Lateral integumentary cells of the ovule dividing, ×77. Fig. 41. Intermingling of integumentary strands from the chalazal end and the lateral sides, ×300. Fig. 42. Micropylar strands, ×75. Fig. 43. Funicular strand, ×75. Fig. 44. Pitted thickening in the inner cells of the wing, ×475. Fig. 45. Distribution of thick-walled tissue, remnant of endosperm and mature embryo, ×23. Tk., Thick-walled; Tn., Thin-walled; End., Endosperm.

of the fringe of the mature wing (Fig. 41). The integumentary cells of the micropylar end are less active during this period. These begin to increase in number first laterally and then terminally towards the later stages of endosperm development (Fig. 42). Multicellular, strand-like outgrowths are also produced from the funicular base (Fig. 43). These micropylar and funicular outgrowths overlap the filamentous strands already produced as described earlier. All these cells appear to be thin-walled and constitute the fringe of the wing.

Thickenings of various types, mostly with pits, appear in the long, fibre-like inner (Fig. 44) integumentary cells during the later stages of the development of the embryo. Thickenings start from the chalazal and the micropylar ends simultaneously. The deposition of additional cellulose then proceeds upwards and downwards from the chalazal and the micropylar ends respectively. Finally the multi-layered thickened cells completely encircle the mature embryo (Fig. 45). This thick-walled tissue lies innermost to the thin-walled cells previously formed and radiates in the midst of the latter. As a result, in the mature seed, the central part of the wing surrounding the cotyledons (Zone I in the Fig. 36) is only composed of thick-walled cells. Occasional radiations emanate from this zone rendering a ribbed appearance to the fully-formed wing.

Conclusion

The somatic chromosome number of Oroxylum indicum as determined in the course of the present investigation is not in conformity with observation of Venkatasubban (1945). He mentions 2n = 30, but does not give gametic confirmation. No information regarding the morphology of the somatic chromosomes of Oroxylum indicum is available in his report. So far as the present writer is aware, apart from Venkatasubban, no other investigator has recorded the chromosome-morphology of Oroxylum indicum. According to him the genera approaching Oroxylum in chromosome numbers are Spathodea with 2n = 26 and Millingtonia with 2n = 30.
Venkatasubban (1945) observed multinucleate condition and intrusive nature of the tapetal cells in *Dolichondrone rheedii* which agree in the observations made in the present material.

Erdtman (1952) gives a full account of the morphology of the pollen grains of Bignoniaceae. It is interesting to note that the broad characteristics of the pollen grains of *Oroxylum indicum* agree in general with those observed by others in the family Bignoniaceae.

Based on the floral evolution among the Sympetalae (Wernham, 1913), the origin of the Bignoniaceae has been traced from the apocynal plexus and it is placed among the Tubiflorae. The dendroid habit and woody follicles in some members of the Bignoniaceae are put forth as reminescent of similar conditions which predominate in the Apocynaceae. When the embryological findings of both the families are considered, the differences are so wide apart that the two families seem to be far removed.

On the contrary, Bignoniaceae resemble more clearly the families like Verbenaceae and Boraginaceae which are all included under Engler’s Tubiflorae and under the Personales by Bentham and Hooker (1862-67) and also by Hutchinson (1926).

Each of these families has cellular endosperm, whereas the endosperm of the Apocynaceae is nuclear and becomes cellular only at later stages. As observed in the course of this investigation and also recorded by all other previous workers, in the family Bignoniaceae, one of the most noteworthy features in the embryology is the development of the endosperm tissue.

In *Oroxylum indicum*, the early development of the endosperm upto the 4-celled stage follows the *Catalapa* type of Mauritzon (1935). But it differs in the more active, important and aggressive role of the chalazal haustorium. The haustorial activity of the chalazal cells of *Tecoma stans* and *Jacaranda mimosifolia* (Govindu, 1950) resembles that of *Oroxylum indicum*. But *Tecoma stans* (Govindu, 1950) differs from the other two genera in having only two cells at the micropylar end instead of four. *Oroxylum indicum* differs from *Bignonia megapotamica* (Swamy, 1941) and *Parmentiera cerifera* (Govindu, 1950) because the latter two genera have only two cells composing the chalazal haustorium.

In *Oroxylum indicum* the inconspicuousness of haustorial activity of the topmost micropylar cells is a characteristic feature. The pronounced haustorial activity of the micropylar cells of *Catalapa bignoniioides* (Mauritzon, 1935) may be stated to have become reversed in *Jacaranda mimosifolia* (Govindu, 1950) and in *Oroxylum indicum*. It is further
interesting to note that the last trace of insignificant haustorial activity of the four cells at the micropylar region of *Jacaranda mimosaefolia* (Govindu, 1950) has been lost altogether in *Oroxylum indicum*.

The observations on the development of embryo of *Oroxylum indicum* confirm those of Souege (1940) and probably of Swamy (1941). The variations in the total number of suspensor cells as well as in the vertical division of the lower ones of *Oroxylum indicum* are not recorded by the previous workers.

The development and the structure of the wing on the seeds of *Oroxylum indicum* follow in general outline those of *Jacaranda mimosaefolia* and *Tecoma stans* (Govindu, 1950) which, however, have not been studied in detail. Moreover, the thickenings on the inner cells of the wing of *Oroxylum indicum* appear to be due to heavy deposition of cellulose and not of lignin as noted in *Tecoma stans* by Govindu (1950).

**SUMMARY**

The paper gives an account of the cytological and embryological investigations on *Oroxylum indicum*.

1. The diploid number of chromosomes is 28. A detailed morphological study of the somatic chromosomes shows the presence of one pair of long chromosomes, eight pairs of medium-sized chromosomes and five pairs of short chromosomes. There are five pairs of chromosomes with secondary constrictions of which three medium-sized pairs are with satellites.

2. Meiosis is normal and 14 bivalent chromosomes have been recorded. Pollen-formation is of the simultaneous type. The pollen tetrads are mostly tetrahedral in arrangement; sometimes decussate tetrads have been noted. The pollen grains are binucleate, spheroidal-prolate, tricolpate with sexine thicker than the nexine.

3. The anther-wall at maturity is made up of the cutinised epidermis, generally three-layered endothecium with fibrous bands and a minimum of four middle layers.

4. The tapetum is of the secretory type. The tapetal cells are 2 to 4 nucleate.

5. The ovules are unitegmic, tenuinucellate and mostly anatropous. Hemitropous ovules have also been observed.

6. The single archesporial cell is hypodermal in origin and functions directly as the megaspore mother cell which undergoes the reduction divisions and produces a monosporic embryo-sac of the "Polygonum type".
(7) Fertilization is porogamous. Stages of fertilization have been observed.

(8) The endosperm is cellular from the beginning and corresponds to the *Catalapa* type of Mauritzon (1935) with minor variations. The four-celled chalazal haustorium is functional.

(9) The development of the embryo is primarily of the *Capsella* type with secondary variations commonly observed in members of Solanaceae.

(10) The outer integumentary cells of the ovule take part in the development of the wings on the seeds. At first the chalazal tip-cells elongate, divide both longitudinally and transversely and form columnar strands. These intermingle with tissues formed later by the cells on the lateral sides, of the micropylar end and also on the funicular part of the fertilised ovule.

At a later stage cellulose thickenings, mostly with pits, are laid down on the inner cells of the wings.

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