

# STUDIES IN THE CAPPARIDACEÆ

## VII. The Floral Morphology of *Crataeva religiosa* Forst.

BY PROF. T. S. RAGHAVAN, M.A., PH.D. (LOND.), F.L.S.

(Head of the Department of Botany, Annamalai University)

AND

K. R. VENKATASUBBAN, M.Sc.

(Annamalai University)

Received February 14, 1941

### CONTENTS

	PAGE
I. Introduction .. .. .	235
II. The ovary .. .. .	236
III. The origin and development of the integument .. .. .	238
IV. Macrosporogenesis and macrogametophyte .. .. .	239
V. The microsporangium .. .. .	241
VI. Chromosome number .. .. .	242
VII. Summary .. .. .	242

#### I. Introduction

THIS is a continuation of the series of papers on the morphology and cytology of some important Indian members of the Capparidaceæ (Raghavan, 1937, 1938 *a*, 1938 *b*, 1939 and 1941). The only paper that has appeared on this family since the publication of the above-named papers is that of Billings (1937). It deals with a very unusual type of embryo development of *Isomeris arborea*.

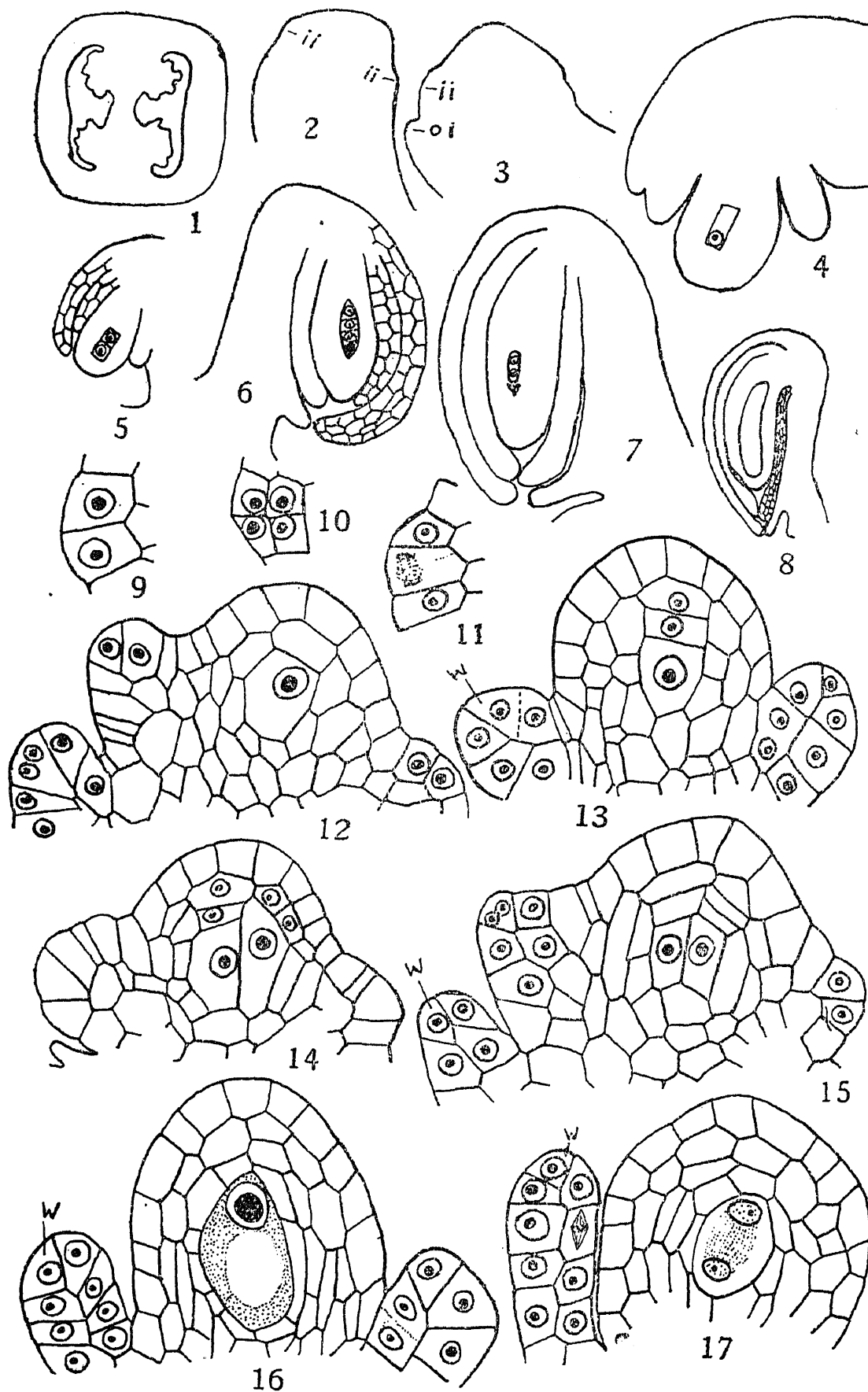
*Cratæva* is a Linnean genus named after Cratevas, an obscure writer on medicinal plants at the beginning of the first century B.C. There are ten species most of which are of medicinal value. The bark of *C. gynandra* (garlic pear) blisters like cantharides (Bailey, 1933). The bitter aromatic leaves and bark of *Cratæva religiosa* are used as a stomachic by natives (Oliver, 1868). The specific name presumably owes its origin to the plant being held sacred and as such are grown in temple compounds. *Cratæva religiosa* is commonly found in almost all the districts, although it is said to be a native of the Malabar coast.

It is a spreading unarmed deciduous tree of moderate size, flowering during the hot season when the plant is bare of foliage.

The present paper is a report of observations on the development of the microsporangium, and the macrogametophyte with incidental reference to the origin and development of the integuments.

## II. The ovary

Typically the ovary is composed of two carpels by whose marginal fusion two parietal placentas result on which the ovules arise in about four rows (Fig. 1). In *Cratæva*, while normally the gynæcium is bicarpellary, there occur not infrequently ovaries which at first appear to be tricarpellary. Plate I, Figs. 1 and 2 which are photo-micrographs of young ovaries, show at A of Fig. 1, the incomplete marginal fusion of the adjacent carpels. In Fig. 2 a small crescent-shaped loculus has developed (A'), and this undoubtedly has resulted from the production of what may be termed a secondary tissue arising out of an incomplete fusion of the carpellary margins. For this reason, while the two lateral loculi bounded by the adjacent carpels are equal in size, the loculus A' is very much smaller, being merely the outgrowth tissue A of Fig. 1. The gynæcium therefore though tri-carpellary in appearance, is to be looked upon as only bi-carpellary, the placenta B only being the normal production of the fusion of the adjacent carpellary margins, while B' and B'' represent individual unfused carpellary margins. Further support is lent to this interpretation of the nature of these "abnormal gynæcia by the occurrence of two separate vascular bundles at A of Fig. 1, indicating the unfused marginal strands of the carpels. Such gynæcia were also recorded in *Gynandropsis pentaphylla* (Raghavan, 1939) where, in addition, apparently tetracarpellary conditions were seen. In such cases diagonally placed carpels are equal in size and one set is much bigger than the other. The smaller loculi represent the secondary tissue arising out of a lack of fusion of the carpellary margins. While in tri-carpellary condition fusion has taken place on one side resulting in a normal placenta, in the 'tetracarpellary' gynæcium no fusion has taken place on either side, so that the four placentas represent the unfused margins of the two adjacent carpels. A diagrammatic representation of this interpretation, has been given in the previous paper (Raghavan, 1939). These observations in another genus of the same family only go to confirm the classical bi-carpellary concept of the Capparidaceous gynæcium, based on a monomorphic interpretation. Further detailed ontogenetic and anatomical investigation, a report of which forms the subject-matter of a separate communication, also supports this concept.



TEXT-FIGS. 1-17

Fig. 1. T.S. of very young gymcium at a lower level showing the replum-like septum. Note  
 vules originating in four rows on either side of each placenta.  $\times$  ca 75. Figs. 2 and 3. The

initiation of the integumental primordia; *ii.*, = inner integument; *oi.*, outer integument.  $\times 750$ . Figs. 4-7. Development of the integuments, at megaspore-mother cell, dyad, tetrad and bi-nucleate embryo-sac stages. Fig. 4  $\times 750$ ; the rest  $\times 350$ . Fig. 8. Just after fertilization, the ovule begins the campylotropous curvature and also the inner integument becomes three-layered.  $\times 150$ . Figs. 9-11. Integumental primordia and their behaviour; explanation in the text.  $\times 1700$ . Fig. 12. Megaspore-mother cell having cut off the primary parietal cell. Note also the development of the integuments.  $\times 1700$ . Fig. 13. Do. two wall layers cut off periclinally.  $\times 1700$ ; *W.*, wedge-shaped apical cell of the integument. Fig. 14. Two juxtaposed megaspore-mother cells one of which has cut off two tangential wall cells, the other two anticlinal wall cells.  $\times 1700$ . Fig. 15. Do. both the mother cells have cut off parietal cells by successive  $\times 1700$ . Fig. 16. Megaspore-mother cell in synesis.  $\times 1700$ . Fig. 17. Dyad formation. Periclinal divisions. Telophase of the heterotypic division.  $\times 1700$ .

### III. *The origin and development of the integument*

The primordium of the inner integument makes its appearance slightly earlier than the outer (Text-Fig. 2 *ii*) which soon arises as a protuberance on the convex side of the ovule (Text-Fig. 3 *oi*). Though the outer integument (*oi*) is slightly later in its origin, it soon overtakes the inner (Text-Figs. 4 and 5), and by the time the linear tetrad is organized it completely envelopes it (Text-Fig. 6). The halves of the inner integument come together some time later when the embryo-sac is in its bi-nucleate condition (Text-Fig. 7), and the massive micropyle thus formed is more or less straight and not zigzag as in *Cleome Chelidonii* (Raghavan, 1937).

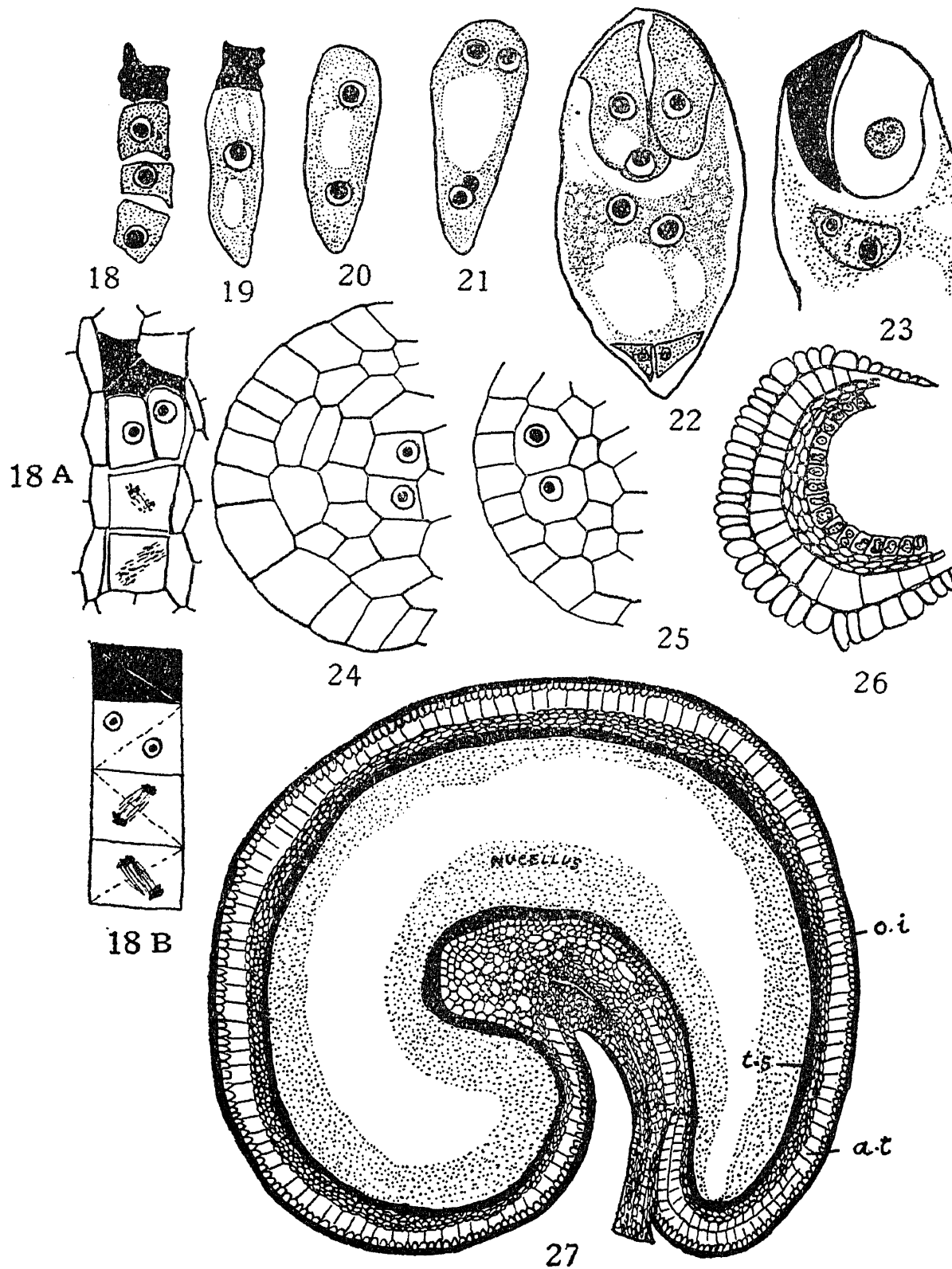
The integument initial is a superficial cell which by its larger size and richer protoplasmic contents can readily be recognised from the epidermal cells above which it protrudes slightly. This soon divides by a radial wall resulting in two juxtaposed cells bigger than the rest (Text-Fig. 9). By a tangential wall four cells are formed (Text-Fig. 10). One of the upper cells by an oblique wall cuts off a wedge-shaped cell. Sometimes the oblique wall-formation preceded the division of the juxtaposed cell (Text-Fig. 11). By a further series of tangential divisions a two-layered integument results (Text-Figs. 12-17), but the wedge-shaped apical cell always persists (*w*), till a comparatively late stage when essentially by its activity a massive micropylar region is built up. The outer integument remains two-layered throughout, while the inner integument till fertilization remains also two-layered and then becomes three-layered (Text-Fig. 8). In a mature seed (Text-Fig. 27) the two integuments forming the testa could yet be recognised. The outer integument (*oi*) is still two-layered of which the outer layer has become sclerotic. The inner integument is about six-layered of which the cells of the outermost layer are radially elongated and constitute the aqueous tissue (Text-Fig. 27, *a*, *t*) as in *Cleome Chelidonii*. The innermost layer lining initially the nucellus, and then the embryo is sclerotic and forms the tracheary sheath (*t*, *s*). These two layers of the inner integument doubtless play an

important part in the economy of the seed. The former is helpful in the storage of water in the initial stages of the development of the seed, while the latter, possessing as they do the structure of tracheids, function first as accessory water supply system for the embryo on account of the layers' close association with the vascular structure of the funicle, later acting as a sponge, absorbing moisture through the micropyle and constituting a kind of water jacket surrounding the embryo.

#### *IV. Macrosporogenesis and macrogametophyte*

The differentiation of the archesporium is slightly later than that of the integuments (Text-Fig. 12). The primary archesporium consists of a single hypodermal row very often of two cells (Text-Figs. 14, 15). The primary parietal cell is cut off by the usual tangential division (Text-Fig. 12). Most usually this parietal cell cuts off by successive periclinal divisions a number of wall cells (Text-Figs. 13, 15), though occasionally anticlinal division follows the primary parietal cell division (Text-Fig. 14). About four layers of wall cells are organized before the megaspore-mother cell enters upon its division (Text-Fig. 16). Text-Fig. 17 shows the megaspore-mother cell in telophase of the heterotypic division. Linear tetrad is organized in the usual manner (Text-Fig. 18). T-shaped tetrads are also of frequent occurrence.

One very interesting case was found in which there were eight megaspores being formed instead of the usual four (Text-Fig. 18 A and Pl. XII, Fig. 6). And the interesting thing about them is that the planes of division of successive cells were at right angles to one another, so that the four walls of these eight cells formed a zigzag line. In other words, the two daughter cells resulting from the division of the mother cell were diagonally placed instead of vertically as is usually the case. This is diagrammatically represented in Text-Fig. 18 B. In Text-Fig. 18 A the uppermost two cells have degenerated. The next two cells have been fully organized while the remaining two are in telophase of division. No later stage than this was found and it is likely that these represent two superimposed linear or rather diagonal tetrads, having been organized by two megaspore-mother cells which were originally placed one above the other. Support is lent to this interpretation by the upper tetrads being in a more advanced stage of division than the lower. If this is accepted the embryo-sac formation must be considered as of the normal type belonging to the usual monosporic eight-nucleate kind (Maheshwari, 1937). If on the other hand all the eight cells are regarded as having originated from a single mother cell, then there will be one division more than in the normal type in reaching the eight-celled embryo-sac stage.



TEXT-FIGS. 18-27

Fig. 18. Linear tetrad with the micropylar megaspore degenerating.  $\times 1700$ . Fig. 18A. The abnormal megaspore formation. Explanation in the text.  $\times 1700$ . Fig. 18B. Diagrammatic representation of the same to show that the planes of division of successive cells are at angles to one another. Note also that the top four cells are in a more advanced condition than the lower two. Fig. 19. Uni-nucleate embryo-sac.  $\times 1700$ . Fig. 20. Bi-nucleate embryo-sac.  $\times 1700$ . Fig. 21. Tetra-nucleate embryo-sac.  $\times 1700$ . Fig. 22. Mature embryo-sac;

as photographs, Figs. 5 A and 5 B, Plate XII.  $\times 1700$ . Fig. 23. Fertilization. The dark streak is the relic of the pollen tube. Of the two nucleoli in the egg cellulose belongs to the male cell.  $\times 1700$ . Figs. 24 and 25. The archesporium of the anther consisting of two hypodermal cells which are seen to have cut off three layers of wall cells, while they themselves have not commenced to divide.  $\times 1700$ . Fig. 26. Fully formed anther sac. Note the hypodermal endothecium composed of radially elongated cells, three layers of small thin-walled cells and the tapetum lining the anther sac. The nuclei of the tapetal cells are in various stages of division.  $\times 350$ . Fig. 27. A mature ovule. Note the fusion of the funicle with the micropylar side of the ovule; *oi.*, outer integument; *at* = aqueous tissue; *t.s.*, tracheary sheath.  $\times 75$ .

The further development of the embryo-sac conforms to the usual type laid down for dicotyledons (Text-Figs. 19–22). The chalazal megaspore functions (Text-Fig. 19) and the mature embryo-sac is of the normal type. The egg-apparatus consists of two prominent synergids in each of which the nucleus is located above a well-defined vacuole (Text-Fig. 22 and Pl. XII, Figs. 5 A and 5 B). They possess the “Hakenförmige Leistenbildung” (Dahlgren, 1928), a feature which was found in the other two Cappariidaceous genera investigated, *Cleome* and *Gynandropsis* (Raghavan, 1937, 1938 *a*). It would appear to be a characteristic feature of the Cappariidaceæ (Pl. XII, Fig. 7). The egg is normal with a prominent nucleus surmounted by a large vacuole (Text-Fig. 22). The polar nuclei are large and fuse comparatively late and the fusion nucleus takes up a position just below the egg. Text-Fig. 23 represents ostensibly a stage in fertilization, the dark patch representing the remains of the pollen tube, and one of the two nucleoli in the egg belongs to the male cell.

#### V. The microsporangium

The archesporium consists of groups of two hypodermal cells below each of the four corners of the anther (Text-Fig. 25). These cut off primary parietal cells (Text-Fig. 24) and these like those of the megasporangium are more active at first than the microsporangogenous cells, so that about four layers of wall cells are organised while the sporogenous cells are yet in an undivided condition. In a mature anther about six layers of wall cells are organized (Text-Fig. 26) of which the innermost layer lining the anther sac functions as the tapetum. The epidermal cells become radially elongated, so do the cells of the hypodermal endothecium. The tapetal cells also become somewhat radially elongated while the intermediate three layers of cells being thin-walled, become crushed.

The tapetal cells are uni-nucleate initially, but very soon they become bi-nucleate even before the microspore-mother cells have entered upon their meiotic stages. Plate XII, Fig. 4 shows the tapetal cells in various stages of mitotic division. Soon they become tetra-nucleate but the nuclei seldom

remain separate (Pl. XII, Fig. 3). This confirms the careful results of Bonnet (1912). In the same tapetal layer one meets with almost all the conditions, bi-nucleate separate, tetra-nucleate separate and all stages of fusion of the four nuclei. After this the fusion nucleus gradually degenerates; so do the cells and presumably the contents are discharged into the anther sac to be utilized by the dividing microspore-mother cells. No definite periplasmodium was recognised. By the time homotypic divisions are completed the tapetal layer is completely disorganized.

#### VI. Chromosome number

The haploid chromosome number is thirteen. Plate XII, Fig. 8 shows a first metaphase plate. An account of the meiotic details has already appeared (Raghavan and Venkatasubban, 1939).

#### VII. Summary

The haploid chromosome number of *Crataeva religiosa* Forst., is thirteen. Further ontogenetic evidence based upon the occurrence of 'tricarpeillary' gynæcea and their interpretation, is adduced in support of the classical concept of the carpel and the bicarpeillary nature of the Capparidaceous ovary.

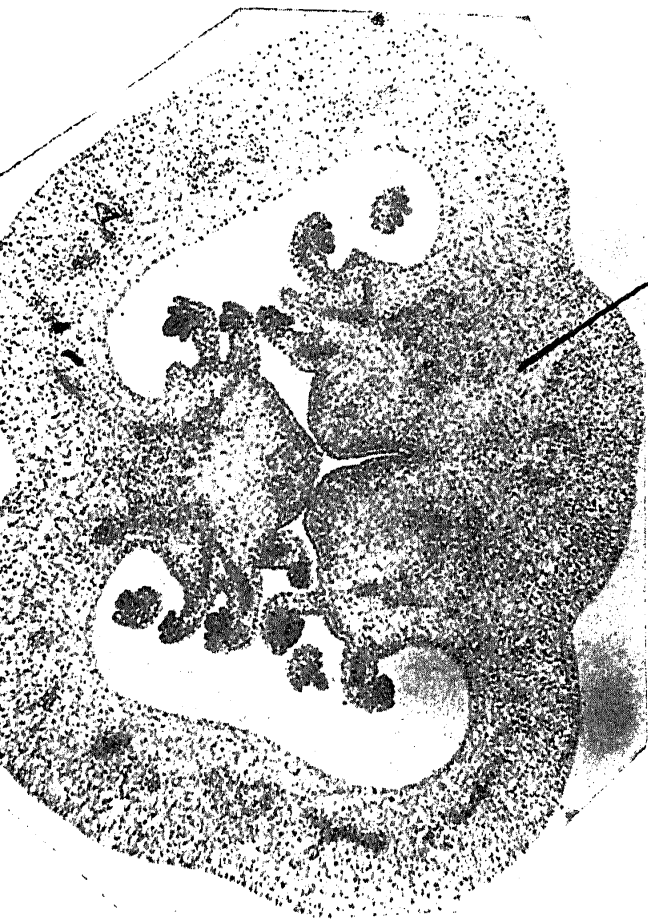
The development of the macrogametophyte is described with a detailed description of the origin and development of the integuments right up to the mature stage of the seed.

The development of the microsporangium with details of the behaviour of the tapetal cells is described.

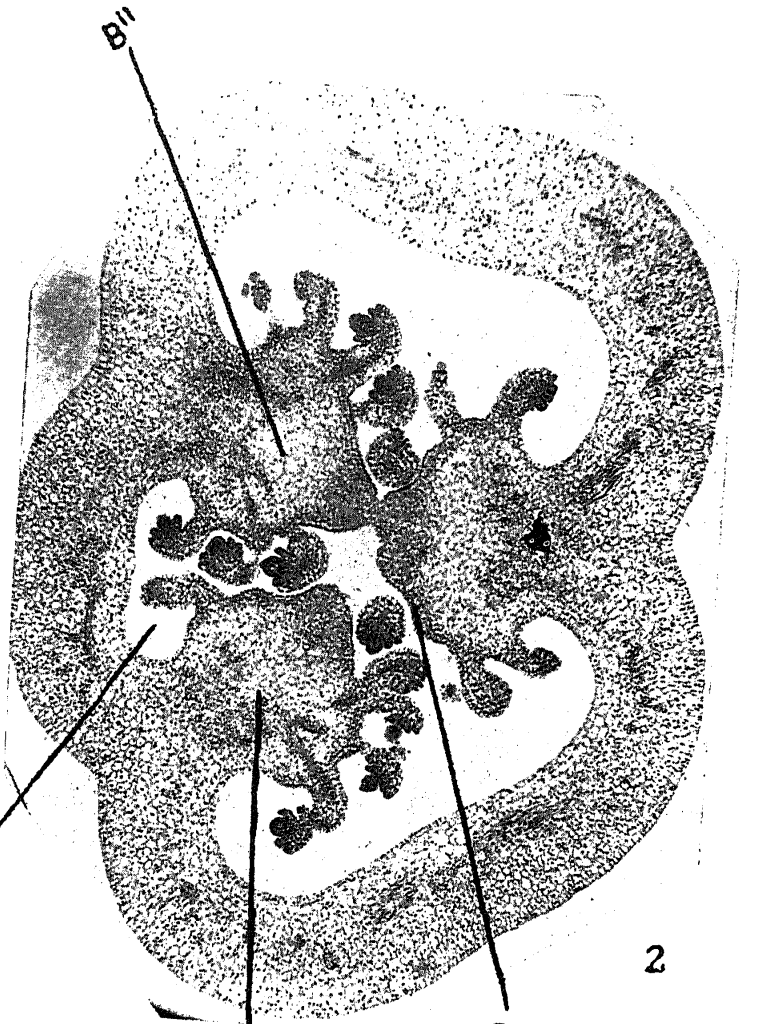
#### REFERENCES

- Bailey, L. H. .. *The Standard Cyclopaedia of Horticulture* (Macmillan), 1933, 1, 889.
- Billings, F. H. .. "Some new features in the reproduction and cytology of Angiosperms as illustrated by *Isomeris arborea*," *New. Phyt.*, 1937, 36, 301.
- Bonnet, J. .. "Recherches sur l'évolution des cellules nourrie'res du pollen chez les Angiosperms," *Arch. f. Zellforsch.*, 1912, 7, 604.
- Dahlgren, K. V. O. .. "Hakenförmige Leistenbildungen bei der Synergiden," *Ber. Deutsch. Bot. Ges.*, 1928, 49, 434.
- Maheshwari, P. .. "A critical review of the types of embryo-sac in Angiosperms," *New. Phyt.*, 1937, 36, 359.
- Oliver, D. .. *Flora of Tropical Africa*, 1858, 80.
- Raghavan, T. S. .. "Studies in the Capparidaceæ; I. The life-history of *Cleome Chelidonii* Linn.," *fil. Journ. Linn. Soc. Lond.*, 1937, 51, 43.





1



2



3



4



5 B



- Raghavan, T. S. .. "Studies in the Capparidaceæ II. Floral morphology and cytology of *Gynandropsis pentaphylla* DC.," *Ann. Bot. Lond.*, New ser., 1938a, 2, 75.
- \_\_\_\_\_ .. "Studies in the Capparidaceæ III. Prochromosomes of *Polanisia tracyperma* Torr et Gray and *Gynandropsis pentaphylla*," *Cytologia*, 1938b, 8, 563.
- \_\_\_\_\_ .. "Studies in the Capparidaceæ IV. Floral anatomy and some structural features of the Capparidaceous flower," *Journ. Linn. Soc. Lond.*, 1939, 52, 239.
- \_\_\_\_\_ and Venkatasubban, K. R. "Studies in the Capparidaceæ V. The cytology of *Crataeva religiosa* Forst.," *Cytologia*, 1939, 10, 23.
- \_\_\_\_\_ .. "Studies in the Capparidaceæ VI. Floral Structure in *Crataeva religiosa* Forst., with special reference to the Morphology of the Carpel," *Proc. Ind. Acad. Sci. Ser. (B)*, 13, 109.

EXPLANATION OF PLATE XII

- FIG. 1. T. S. of young ovary basal portion. The tissue at A shows the incomplete fusion of the adjacent carpellary margins. Note also the two vascular strands of that region while on the opposite side they have fused to form a single bundle. × 85.
- FIG. 2. T. S. of a slightly older ovary and at a slightly higher level. Loculus A' is the outgrowth tissue A of figure 1. B is a normal placenta while B' and B'' represent the unfused carpellary ends. × 85.
- FIG. 3. Tapetal cells showing the nuclei in various stages of division and fusion, bi-nucleate, tetra-nucleate conditions being the most common. Note that the p.m.c. in its first metaphase. × 600.
- FIG. 4. Tapetal cells in various stages of mitosis. × 600.
- FIG. 5 A and 5 B. Fully developed embryo-sacs. The antipodals have degenerated; their remains could be seen only in 5 B; the polar nuclei have not yet fused. Note the prominent vacuole below the nucleus in the synergid. × 550.
- FIG. 6. The abnormal case of megaspore formation. Explanation in the text. × 600.
- FIG. 7. The synergids alone enlarged to show the Hakenförmige Leistenbildung. × 800.
- FIG. 8. First metaphase plate greatly enlarged. Thirteen bivalents could be clearly counted × 5200.