STUDIES IN EMBRYOLOGY OF CYPERUS TEGETUM ROXB.

BY M. D. PADHYE AND S. K. MOHARIR

(Department of Botany, College of Science, Nagpur)

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INTRODUCTION

One of the most interesting points in the embryology of the Cyperaceae is the development of the pollen grains. In contrast to all other angiosperms, only one microspore in a tetrad comes to maturity while the other three degenerate. The nuclei of the degenerating microspores besides, are enclosed within the wall of the functioning pollen grain, but it is doubtful whether or not the nucleus of the functioning microspore is separated from the remaining nuclei by a wall. Further, it is debatable whether the degenerating nuclei themselves are separated from each other by distinct septa. According to Piech (1928) the nucleus of the functioning microspore in Scirpus paluster is not separated from the remaining three nuclei by a cell-wall. Neither any cell-wall exists delimiting the three non-functioning nuclei. Tanaka's (1939 b) observations on Fimbristylis cericea agree with those of Piech (1928). In his later work Tanaka (1939 a and 1940), however, has demonstrated the formation of such separating walls in species of Carex and Scirpus. According to Dnyansagar and Tiwari (1956) delimiting walls exist between the functioning and non-functioning nuclei of the pollen grain and the septa are also present between three non-functioning nuclei. The present investigation, therefore, has been undertaken with a view to learn the correct state of affairs in respect of these points in Cyperus tegetum. While studying these features the authors could gather detailed information on the development of the female gametophyte and consequently these observations are also included in the present communication.

MATERIAL AND METHODS

Cyperus tegetum Roxb. is a robust sedge growing abundantly in water-logged or marshy areas along the banks of the rivers and tanks throughout India. Flowers and fruits are available for about eight to nine months in a year from July to February.
The material was fixed in Formalin-acetic-alcohol at about 11 A.M. It was dehydrated and embedded in paraffin as per routine methods. Sections were cut at the thickness of 8–12 μ. Heidenhain’s iron-alum-Hæmatoxylin was used as stain. The slides were destained in a saturated solution of picric acid and counterstained with fast green, especially to study the cell-walls between the nuclei enclosed in a common envelope of the pollen grain.

**MICROSPOROGENESIS**

The anther is bithecous. The hypodermal archesporium in the anther appears at four places and consists of 2 to 5 rows of cells extending over the whole length of anther (Fig. 1). The archesporium divides periclinaly forming primary parietal and primary sporogenous layers. The primary parietal layer forms three layers, viz., the tapetal layer, the early degenerating middle layer and the layer of fibrous endothecium (Figs. 2–4). Numerous globular markings appear on the inner tangential walls of the endothecial cells during later stages as in many other angiosperms (Fig. 6). The cells of the anther epidermis do not present uniform dimensions and at anthesis they are completely filled with yellow deposits.

Anther tapetum is of the secretory type and the cells finally become binucleate. Prior to degeneration the small yellow-staining globules (In slides stained with Hæmatoxylin) appear in large number on the inner tangential walls of the tapetal cells much before they appear on the fibrous endothecium. Such granules are now recorded in several angiosperms. For detailed information on this point reference may be made to the works of Ubisch (1927), Kosmath (1927), Kajale (1940), Puri (1941) and Singh (1950).

The primary sporogenous cells increase in size and divide once to multiply their number. The most unusual feature of the pollen mother cells is their shape as seen in transverse section. They appear triangular in outline with their apices meeting in the centre (Figs. 4 and 5). In longitudinal section, however, they look oblong and are arranged in two rows. During meiosis numerous irregularly distributed black staining bodies appear in pollen mother cells (Figs. 7, 9 and 10). In some cases these bodies disappear from the cytoplasm at a stage shown by Fig. 8; but they reappear during second meiosis. In others they continue to exist throughout the two meiotic divisions. The exact nature of these bodies is not known. Whatever be their nature or behaviour during earlier stages, no such bodies are seen in the young pollen grains.

According to Piech (1928) the pollen mother cells are elongated and the first meiotic spindle is parallel to its long axis. In *Cyperus tegetum*, on the
other hand, axes of the spindles during both the meiotic divisions are not oriented in any definite direction as in species of *Scirpus* (Piech, 1928). The four nuclei formed after the meiotic divisions lie free for some time in the cytoplasm and show no difference in their size at this stage (Fig. 11). The three nuclei now migrate to the tapering or proximal end of the pollen mother cell (Figs. 12 and 13). These are the non-functioning nuclei of the microspores. The functioning nucleus increases in size. All the non-functioning nuclei are of equal size and do not show any increase in their dimension. The septa are soon organized in between them and the four nuclei become separated from each other unlike in *Fimbristylis cericea* (Tanaka, 1939). Sometimes an additional septum may also be organized in between the functioning and three non-functioning nuclei (Fig. 12).

Thus as in other angiosperms, no regular tetrads are organized in the Cyperaceae. These tetrads are termed as cryptotetrads by Erdtman (1952); though Selling (1947) prefers to call them pseudomonads as the pollen grains in the Cyperaceae in general according to this author, are not homologous to those of other angiosperms.

The three non-functioning nuclei degenerate in course of time and their traces may be seen even beyond the two-celled stage of the pollen grains (Fig. 14). The uni-nucleate pollen grain gradually becomes vacuolate. Its nucleus divides to form a generative cell. The nucleus of the latter is slightly smaller than that of the other cell. In cross-section the generative cell looks circular as in *Scirpus lacustris* (Piech, 1928) (Fig. 15). It further divides and forms two male cells. The mature pollen grains in *Cyperus tegetum* are thus three-celled at anthesis (Fig. 16).

**Megasporangium**

The family is characterized by a single unilocular pistil having a solitary basal ovule (Lawrence, 1951). The latter is bitegmic as in other species of *Carex, Cyperus, Heliocharis* and *Scirpus* (Schnarf, 1931). Only the inner integument forms the micropyle and the outer one up to the mature embryo-sac stage takes no part in its organization. The integuments during the early stages of development appear in acropetal succession from below the level of archesporium (Fig. 18).

**Megasporogenesis and Embryo-sac**

The hypodermal archesporium is one-celled (Fig. 17). It cuts off a parietal cell which generally divides periclinally before the megaspore mother cell forms the megaspores (Figs. 18 and 19). Sometimes, however, the
parietal cell divides anticlinally forming two cells which become elongated parallel to the long axis of the ovule as shown in Fig. 20. Later on, however, these cells divide in both directions to form a parietal tissue of few cells in thickness.

The megaspore mother cell forms dyad (Fig. 20). Both the cells are of equal size and divide transversely once again to form a linear row of four megaspores (Fig. 21). The functioning (chalazal) megaspore increases more in length than in breadth (Fig. 21). The nucleus after three mitotic divisions forms an eight-nucleate embryo-sac of the Polygonum-type (Maheshwari, 1950) as reported by Hicks (1929) in Cyperus natalensis and by Dnyansagar (1956) in species of Fimbristylis. According to Schnarf (1931) species of Carex also have the Polygonum-type of embryo-sac.

The egg is flask-shaped and much vacuolated (Fig. 26). The two synergids have usual structure and are hooked (Fig. 25).

The antipodals are three small cells and are housed in a small chalazal pouch on either side of which as seen in longitudinal section the part of the embryo-sac becomes dialated (Figs. 25 and 27).

The polar nuclei meet somewhere in the centre of the embryo-sac. After fusion the secondary nucleus shows considerable increase in size (Figs. 24 and 25).

HYPOSTASE

An unusual feature, hitherto unrecorded in the Cyperaceae, is the differentiation of the group of meristematic cells at the chalazal end of the embryo-sac surrounding the pouch and its chalazal part (Fig. 27). These cells are rich in cytoplasm and stand out more prominently than the remaining cells of the nucellus. This is homologous to the hypostase.

SUMMARY

The paper deals with the development and structure of anther, pollen grain, ovule and male and female gametophyte of Cyperus tegetum.

The male archesporium consists of two to five rows of cells. It cuts off a parietal layer which divides further and forms three layers of the anther wall excluding the epidermis. The cells of the latter contain yellow deposits in them. The tapetal cells are uni-nucleate but later on become bi-nucleate and degenerate. The tapetum is of the secretory type. Globular markings on the inner tangential walls of the tapetum and fibrillar endothecium are noted.
Pollen mother cells in transverse section are triangular in shape with their apices meeting in the centre of the anther loculus. The divisions in them are simultaneous. Numerous black-staining bodies appear in the cytoplasm of the pollen mother cells during meiosis.

The three nuclei of the microspores are delimited by cell-walls and may or may not be separated by an additional wall from the functioning microspore nucleus. The three nuclei are cut off on the proximal side. Pollen grains are three-celled at anthesis.

Ovules are crassinucellate, bitegmic and anatropous. The micropyle is formed by the inner integument. The hypodermal archesporium is a single cell. Parietal cell is cut off. The megaspore mother cell forms a row of four megaspores. The chalazal megaspore develops into an embryo-sac of the Polygonum-type. The egg is flask-shaped with narrow neck. The synergids have a normal structure and are hooked. The antipodals are three cells present at the chalazal end in a pouch-like structure. The hypostase consisting of parenchymatous cells is developed below the chalazal end of the embryo-sac.

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EXPLANATION OF TEXT-FIGURES

Figs. 1–27. Cyperus tegetum. Figs. 1–4. T.S. of anther lobes showing various stages in the development of anther wall. Note the radial arrangement of sporogenous cells in Fig. 4. Fig. 5. T.S. anther lobe showing two-layered anther wall, degenerating tapetal cells and pollen mother cells in meiosis II. Note that meiotic spindles are not orientated in any definite plane. Fig. 6. Part of anther wall showing fibrous endothecium with punctate markings. Figs. 7–10. Pollen mother cell showing meiotic divisions. Note the presence of darkly stained bodies in the cytoplasm of the pollen mother cells and the perinuclear zone surrounding the spindle. Fig. 11. Pollen mother cell showing four free microspore nuclei. Figs. 12 and 13. Pollen grain showing three microspores delimited by cell-wall. Note also the additional septum between the functioning and non-functioning nuclei in Fig. 12. Fig. 14. Two-celled pollen grain showing two out of the three degenerating non-functioning microspores. Fig. 15. The same as above showing generative cell in cross-section. Note that the nucleus is preparing for division. Fig. 16. Pollen grain showing tube nucleus and the dividing generative nucleus. Fig. 17. L.S. apex of nucellus showing single archesporium. Fig. 18. The same as above showing megaspore mother cell and anticlinal division in the parietal cell. Fig. 19. Same as above at an advanced stage. Fig. 20. L.S. apex of nucellus showing meiosis II in dyad cells. Note the enlargement of the parietal cells. Fig. 21. Uninucleate embryo-sac with three degenerating megaspores on the micropylar side. Figs. 22 and 23. Two- and four-nucleate embryo-sacs. Fig. 24. Micropylar part of embryo-sac showing two young synergids and two polar nuclei. Fig. 25. Embryo-sac showing two synergids, secondary nucleus and three antipodals in chalazal pouch. Fig. 26. Same as above showing egg. Fig. 27. Chalazal part of the embryo-sac showing three antipodals and hypostase. Fig. 5, × 350; Figs. 1–4, 6 and 17–27, × 600; Figs. 7–16, × 935.