EMBRYOLOGICAL STUDIES IN ERIOCaulON QUINQUANGULARE LINN.

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ABSTRACT

An account of sporogeneses, development of gametophytes, endosperm and embryo in Eriocaulon quinquangulare Linn. is presented.

The unisexual flowers are borne on a terminal globose head. The development of floral parts is acropetal.

The hypodermal archesporium in an anther is one to two-celled. The wall of the mature anther is four-layered; the innermost of these layers functions as the glandular tapetum. The microspore tetrads are of isobilateral and decussate type. A well-developed stomium is present. The pollen grains are generally shed at two-celled stage.

The tenuinucellar ovules are bitegminal and pendulous. The primary archesporium is hypodermal and functions directly as the megasporocyte. The megaspore tetrads are of linear, obliquely linear and T-shaped type. The chalazal megaspore is functional and develops into a Polygonum type of embryo-sac. The antipodals form the most conspicuous part of the embryo-sac and are linear in arrangement.

Endosperm is free nuclear and becomes cellular later. Embryo development is of Asterad type.

INTRODUCTION

The family Eriocaulaceae is referred as the Compositae of monocotyledons because of the constancy of occurrence of the typical inflorescence in the form of globose head with involucre of bracts of different colours. It has been of great taxonomical interest for a long time and a large number of species of Eriocaulon have been described by Fyson (1921). Anatomical details have also been worked out by Solomon (1931). A study of the available literature reveals that very little work has been done on the embryology of the genus Eriocaulon. Only three species have been worked out by Smith (1910), Patel (1964) and Begum (1965).
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The family includes six genera according to Engler (1897). The genus *Eriocaulon* is placed under the tribe Diplantherae with about 193 species (Ruhland, 1903) of which about 50 species are found in South India (Fyson, 1921).

*Eriocaulon* is an extensive genus being found in swampy tracts of land with herbaceous habit. The stem is highly condensed and bears a tuft of radical leaves which in the present species are pinkish in colour.

**Material and Methods**

The material was collected from the marshy areas in the vicinity of Bangalore, during the months of September and November and fixed in Formalin-Acetic-Alcohol. Customary methods of dehydration, infiltration and embedding were carried out. The sections were cut at 4–15 microns thickness. Considerable difficulty was experienced in cutting the material due to the presence of silica. The material was treated with a mixture of 2–4% Hydroflouric acid and 70% alcohol for one week to facilitate cutting. The sections were stained in Heidenhein’s Iron Alum Haematoxylin and Delafield’s haematoxylin with Eosin and Erythrosin as counter stains.

**Observations**

*Flower.*—The unisexual, trimerous flowers are borne on a terminal globose head wherein staminate and pistillate flowers are intermingled.

*Staminate flower.*—The staminate flower consists of six perianth lobes arranged in two whorls of three each. The perianth lobes of the inner whorl are fused to form a tube. There are six stamens surrounding a rudimentary pistil.

*Pistillate flower.*—The pistillate flower has six perianth lobes in two whorls. But unlike the staminate flowers, the perianth lobes of the inner whorl are free and are gland dotted. The ovary is superior, tricarpellary and trilocular with a solitary, pendulous ovule in each locule. The style ends in three radiating stigmatic branches. Staminodes in the form of small projections are seen at the base of the ovary.

The development of floral parts in both pistillate and staminate flowers is in an acropetal succession.

*Microsporogenesis and the development of male gametophyte.*—A young anther is composed of a homogeneous mass of cells. The hypodermal
FIGS. 1–21. Sporogeneses and the development of gametophytes in Eriocaulon quinquangulare Linn. Figs. 1–11. Microsporogenesis and the development of male gametophyte. Fig. 1. T.s. anther showing the archesporium, × 1,455. Fig. 2. T.s. anther lobe showing the sporogenous cells and the parietal cells under division, × 1,455. Fig. 3. T.s. anther lobe showing wall layers, tapetum and the sporogenous cells, × 1,455. Fig. 4. L.s. anther lobe showing binucleate tapetal cells and mature sporogenous cells, × 1,455. Fig. 5. Decussate microspore tetrad, × 1,455. Fig. 6. Isobilateral microspore tetrad, × 1,455. Fig. 7. Uninucleate pollen grain, × 1,455. Fig. 8. Pollen grain showing the first nuclear division, × 1,455. Fig. 9. 2-celled pollen grain, × 1,455. Fig. 10. T.s. anther showing the stomium, × 387. Fig. 11. Portion marked × in Fig. 10 enlarged showing the endothecium and the stomium, × 1,455. Figs. 12–21. Megasporogenesis and the development of female gametophyte. Fig. 12. Portion of the ovule showing the archesporium, × 1,455. Fig. 13. Megasporocyte, × 1,455. Fig. 14. Dyads under meiosis II, × 1,455. Fig. 15. Linear tetrad of megaspores, × 1,455. Fig. 16. Functional megaspore, × 1,455. Fig. 17. Two-nucleate embryo sac, × 1,455. Fig. 18. Four-nucleate embryo sac, × 1,455. Fig. 19. Eight-nucleate embryo sac, × 1,455. Fig. 20. Mature embryo sac, × 1,164. Fig. 21. Mature embryo sac showing the fused antipodal cells, × 1,455. (FAC = Fused antipodal cell.)
archesporium is one to two-celled and becomes differentiated even before
the four lobes of the anther become recognizable (Fig. 1). Periclinal
divisions of the archesporium result in the outer primary parietal layer
and an inner primary sporogenous layer (Fig. 2). The primary parietal
layer by further anticlinal and periclinal divisions (Fig. 2) adds to the wall
of the anther which consists of an outer epidermis, endothecium, a single
middle layer and tapetum (Fig. 3). The tapetal cells are uninucleate to
start with but become binucleate at about the time the microsporocytes
are ready for meiosis (Fig. 4).

The primary sporogenous cells directly function as microsporocytes
and by successive meiotic divisions from tetrads. The tetrads are mostly
of the isobilateral type (Fig. 6). However, decussate tetrads are also seen
(Fig. 5). Cytokinesis takes place by cell plate method. The tapetal cells
separate from one another and develop dense contents.

A young microspore is spherical with a conspicuous nucleus in the
centre of the dense cytoplasm (Fig. 7). The nucleus is pushed towards
the periphery due to the formation of a vacuole, where it divides (Fig. 8)
resulting in a large vegetative cell and a small lenticular generative cell.
The latter detaches itself from the wall and comes to lie near the nucleus
of the vegetative cell (Fig. 9). The pollen grains are triporate with thick
exine having very fine projections. They are generally shed at the two-celled
stage. A rare instance was observed where the generative nucleus had
already divided to form the two male cells.

In a mature anther, the middle layer and the tapetum get disorganized
completely and only the epidermis and fibrillar endothecium persist. The
endothecium lacks fibrillar thickenings at the region of dehiscence where
the epidermal cells are enlarged constituting a stomium. The rest of the
epidermal cells assume an irregular shape with dark contents (Fig. 11).
The two pollen sacs become confluent due to the disorganization of the
tissue between them (Fig. 10).

*Megasporogenesis and the development of the female gametophyte.*—
The ovular primordia arise as small protuberances from the placenta
and assume a bent position with the micropyle directed towards the base
of the ovary. The ovules are bitegminal and tenuinucellar. Usually a
single hypodermal archesporial initial becomes distinguishable in the scanty
nucellus before the integumentary primordia appear (Fig. 12). Soon the
nucellus becomes invested by two integuments of which the outer stops
short of the inner, which forms the micropyle. Although, both the integuments remain two-layered for most of their length, during the post fertilization phase, the micropylar part of the inner integument becomes slightly dilated due to the enlargement of the cells. The cells of the inner layer of the inner integument enlarge considerably and become filled with dense cytoplasm and function as endothelium (Fig. 20). The endothelial cells show conspicuous nuclei.

The archesporial initial enlarges and directly functions as a megaspore cyte (Fig. 13). Meiotic divisions result in linear, obliquely linear and T-shaped tetrads of megaspores (Figs. 14, 15). The chalazal megaspore functions further and the other three invariably degenerate (Fig. 16). The functional megaspore enlarges and pushes aside the neighbouring nucellar cells which get crushed and degenerate. Its nucleus divides mitotically resulting in a two-nucleate embryo sac (Fig. 17). At the four-nucleate stage of the embryo sac, a central vacuole develops between the nuclei (Fig. 18). The gametophyte comes in direct contact with the endothelium.

In the prefertilization organization of the embryo sac, the polarization in groups of four is very clear (Fig. 19). The development of the gametophyte conforms to the Polygonum type (Maheshwari, 1950).

In a mature embryo sac the egg apparatus comprises a pair of large, hooked synergids which are filled with dense cytoplasm and a rounded egg. The behaviour of the antipodals is rather peculiar in this species. They not only form the most conspicuous part of the embryo sac showing linear arrangement (Fig. 20) but also fuse to form one large cell in the later stages (Fig. 21). They, however, disappear early without leaving any trace. Sometimes the embryo sac gets highly compressed and the antipodals in such embryo sacs occupy 2/3rds of the sac (Fig. 21). The two polar nuclei fuse before fertilization and the secondary nucleus lies very close to the antipodals.

Fertilization is porogamous. Traces of the pollen tube are seen upto the two-celled stage of the embryo. The degenerating synergids are seen as black masses covering the zygote (Fig. 25).

Endosperm.—The primary endosperm nucleus migrates to the chalazal end of the embryo sac and divides earlier than the zygote. The divisions are rapid and the endosperm nuclei are seen to be distributed along the periphery at the micropylar end. They tend to aggregate at the chalazal end (Fig. 23). Endosperm is therefore free nuclear (Fig. 22) but becomes
cellular at later stages due to centripetal wall formation (Fig. 24). The endosperm cells are full of starch grains.

Figs. 22-38. Development of endosperm and embryo in Eriocaulon quinquangulare Linn. Figs. 22-24. Development of Endosperm. Fig. 22. four-nucleate endosperm, × 645. Fig. 23. Multinucleate endosperm showing the aggregation of nuclei at the chalazal region, × 645. Fig. 24. L.s. fruit showing the cellular endosperm and mature embryo, × 387. Figs. 25-37. Development of embryo. Fig. 25. Zygote, × 1,455. Fig. 26. Zygote nucleus under division, × 1,455. Fig. 27. Two-celled embryo, × 1,455. Fig. 28. Three-celled embryo, × 2,182.5. Fig. 29. Divisions in ca and cb, × 2,182.5. Fig. 30. 3-celled embryo showing cb under division, × 2,182.5. Fig. 31. Proembryonal tetrad, × 2,182.5. Fig. 32. Formation of quadrant, × 2,182.5. Figs. 33-36. Stages in the development of embryo, × 2,182.5. Fig. 37. Mature embryo, × 1,455. Fig. 38. Portion of the fruit showing pericarp, seedcoat and endosperm, × 1,455.

(Agg. End. N. = aggregated endosperm nuclei; SC = Seedcoat; End. = Endosperm; II = Inner integument; OI = outer integument).
Embryo.—The first division of the zygote is transverse (Figs. 25, 26) and occurs only after a considerable amount of endosperm is formed. It results in two cells, *viz.*, *ca* and *cb* (Fig. 27). The terminal cell *ca* divides vertically much earlier than the basal cell *cb* to form two juxtaposed cells (Fig. 28). The basal cell *cb* also divides vertically forming an isobilateral pro-embryonal tetrad (Figs. 29, 30, 31). Thus no suspensor is formed. The next division is at right angles to the previous one (Figs. 32, 33), so that the embryo passes through a regular octant stage. Periclinal walls are laid down in the cells derived from *ca* which cut off the dermatogen (Figs. 34, 35, 36).

Divisions are not simultaneous in the two halves of the embryo (Fig. 36). They are irregular and more rapid in the basal region resulting in an embryo with flaring edges (Fig. 37). The sequence of cell division follows the Penea variation of the Asterad type (Johansen, 1950).

*Pericarp and the seedcoat.*—The fruit is a capsule with oblong seeds. The pericarp is composed of two layers. The cells of the inner layer are large with conspicuous fibrillar thickenings, while the outer layer shows thin-walled, radially stretched cells (Fig. 38).

Both the integuments contribute to the formation of the seedcoat. In the early stages of development of the seed, the cells of the outer integument stretch considerably along their long axes and in later stages become highly compressed. The inner layer of the outer integument and the outer layer of the inner integument are lignified along their outer tangential walls. The cells of the inner layer of the inner integument elongate and contain dense contents (Fig. 38).

**DISCUSSION**

The archesporial initials in the anther of *Eriocaulon quinquangulare* differentiate as a single row unlike *E. cinerum* (Patel, 1964) where the archesporium is reported to be in two rows. The occurrence of four-layered wall of the anther is also shared by *E. septangulare* (Smith, 1910). The tapetal cells become binucleate at later stages of development in *E. quinquangulare* whereas they remain uninucleate throughout in *E. cinerum* (Patel, 1964). A well-developed stomium found in *E. quinquangulare* has, however, not been reported in *E. cinerum* (Patel, 1964). The pollen grains are usually shed at the two-celled stage in the present species unlike *E. septangulare* (Smith, 1910) and *E. cinerum* (Patel, 1964) where they are shed at the three-celled stage. However, one instance was observed where the pollen grain was three-celled.
In the ovule, the archesporial initial directly functions as the megasporocyte as in the other species of *Eriocaulon* worked out so far. The central vacuole in the embryo sac appears at the four-nucleate stage as in *E. septangulare* (Smith, 1910). Contrary to this, Patel (1964) has reported the occurrence of the vacuole at the two-nucleate stage of the embryo sac. The polarization of the nuclei in groups of four at the time of organization of the embryo sac is very clear unlike *E. cinerum* (Patel, 1964) where it is not clear. The antipodals are very conspicuous and form the most remarkable feature of the embryo sac in the present species as they fuse to form one cell in later stages, while *E. septangulare* and *E. cinerum* (Smith, 1910; Patel, 1964) show very inconspicuous antipodals.

The mature embryo is undifferentiated as in other species and conforms to the Penea variation of the Asterad type. This feature is shared by all the three species of *Eriocaulon* worked out so far, *viz.*, *E. septangulare* (Smith, 1910), *E. cinerum* (Patel, 1964) and the present species *E. quinquangulare*. Polyembryony is, however, absent here while it was observed by Smith (1910) in *E. septangulare*.

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