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Embryology of *Scleria foliosa* (Cyperaceae)

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Abstract: The embryology of *Scleria foliosa* A. RICH. is described and several features have been recorded for the first time in the family. The endosperm having both micropylar and chalazal haustoria and embryo with characteristic cotyledon bearing papillate outgrowths are unique features noted in this taxon. The epicotylary and cotyledonary sectors are adjacently placed and occupy a terminal position on the embryonic axis. Taxonomic implications of the embryological findings with particular reference to the problem of circumscription of *Scleria* are discussed.

Scleria is a pantropical genus belonging to the tribe *Sclerieae* of the family *Cyperaceae*. There is no unanimity of opinion among the cyperologists in respect of its circumscription. Based on gross morphology, some authors transposed *Becquerelia* (BOCKELER 1874, CLARKE 1908) and *Diplacrum* (BENTHAM 1878, KERN 1961) to *Scleria*, while others (GOEBEL 1888, CORE 1936, BLAKE 1954, KOYAMA 1967, HAINES & LYE 1983) accorded a generic status for each of them (cf. KERN 1961, KOYAMA 1967).

A perusal of literature pertaining to the embryology of *Scleria* reveals that the available information is too inadequate and fragmentary. Therefore, a thorough study is needed before one could attempt to circumscribe this genus from embryological standpoint in order to reinforce the macromorphological evidence already on hand. The previous embryological work on this taxon has been reviewed by DAVIS (1966) and NIJALINGAPPA & NAGARAJ (1980). More recently a few reports have appeared (MAKDE 1981a, 1981b, 1982, NIJALINGAPPA & AREKAL 1983, MAKDE & BHUSKUTE 1984) but again of fragmentary nature. The present

Figs. 1-9. *Scleria foliosa*: Fig. 1. Transverse section (t.s.) of an young anther lobe. - Fig. 2. t.s. of microsporangium showing the formation of tapetum. - Fig. 3. t.s. of microsporangium showing a 4-layered wall and microspore mother cells. - Figs. 4-6. Stages in the formation of microspores. - Fig. 7. 2-celled pollen grain. - Fig. 8. Portion of anther showing thickenings in the endothecium and 2-celled pollen grain with generative cell in division. - Fig. 9. 3-celled pollen grain. - *ac* = archesporial cells, *e* = epidermis, *en* = endothecium, *gc* = generative cell, *mc* = male cells, *ml* = middle layer, *mmc* = microspore mother cell, *ppc* = primary parietal cell, *psc* = primary sporogenous cell, *ram* = remnants of abortive microspores, *spl*₁ & *spl*₂ = outer and inner secondary parietal layers respectively, *t* = tapetum, *vc* = vegetative cell

investigation dealing with microsporogenesis, megasporogenesis, development of male and female gametophytes, endosperm and embryo in *S. foliosa* A. RICH. was undertaken with the prime objective of providing a clear picture of the embryology of *Scleria* and to ascertain how far this would be useful while taking taxonomic decisions.

Material and Methods

The material for the present study was collected from paddy fields near Bannerghatta (Bangalore District) and fixed in formalin-acetic-alcohol, dehydrated in alcohol-xylol series and embedded in paraffin wax. Sections were cut at 6–12 μ m and stained with HEIDENHAIN's haematoxylin and orange G. For the study of endosperm haustoria, wholemounts of endosperm were also examined to supplement the details obtained from sectioned preparations.

Results

Microsporangium and Male Gametophyte. The anther is tetrasporangiate. One or two densely cytoplasmic hypodermal archesporial cells are differentiated at each of the four corners of a young anther, as seen in transection (Fig. 1). Each archesporial cell divides periclinaly and forms a primary parietal cell and a primary sporogenous cell (Fig. 1). Periclinal division in the former results in the formation of two secondary parietal layers (Fig. 2). Of these the outer divides anticlinally forming an endothecium whose cells enlarge and develop characteristic thickenings (Fig. 8). The inner secondary parietal layer divides both anticlinally and periclinaly producing two layers of which the outer becomes a middle layer and an inner together with cells of the connective adjacent to the sporogenous tissue develops into a glandular tapetum (Figs. 2 and 3). The cells of the latter remain uninucleate throughout. Thus the anther wall becomes four-layered and follows the Monocotyledonous type of development (DAVIS 1966). At maturity, all wall layers except epidermis and endothecium degenerate (Fig. 8).

Concomitant with these changes in the anther wall, the primary sporogenous cells divide and form microspore mother cells (Figs. 1–3). Each microspore mother cell undergoes meiosis producing four microspore nuclei which become separated into microspores by simultaneous cytokinesis (Figs. 4–6). The microspore tetrad has three smaller abortive microspores and a larger functional microspore (Fig. 6). The former degenerate in situ while the latter divides producing a generative cell and a vegetative cell (Fig. 7). To begin with, the generative cell is lenticular and situated just above the abortive microspores but later moves into the vegetative cell where it divides and forms two male cells (Figs. 7–9).

Figs. 10–17. *Scleria foliosa*: All longisections. — Fig. 10. Young ovule with the sporogenous cell (stippled). — Fig. 11. Nucellus showing megaspore mother cell. — Fig. 12. Linear tetrad of megaspores. — Fig. 13. Functional megaspore and 3 degenerating megaspores. — Figs. 14–16. 2-, 4-, and 8-nucleate female gametophytes respectively. — Fig. 17. Mature female gametophyte. — *dm* = degenerating megaspores, *fm* = functional megaspore

Megasporogenesis and Female Gametophyte. The ovule is anatropous, bitegmic and crassinucellate. At the megaspore mother cell-stage, a group of funicular cells become papillose and grow in the direction of the micropyle and form an obturator which covers the outer opening of the micropyle as a sort of canopy (Fig. 19). The obturator is noticeable up to a young globular-stage of the embryo and later degenerates. After fertilization, a group of cells at the chalazal region become thick-walled and form a hypostase (Fig. 24).

A single hypodermal archesporial cell is differentiated in the ovular primordium. It divides transversely forming a primary parietal cell and a sporogenous cell (Fig. 10). The former by further divisions produces 5- to 6-layered parietal tissue. The sporogenous cell enlarges and functions as the megaspore mother cell (Fig. 11). The latter divides meiotically and forms a linear tetrad of megaspores of which the chalazal one functions while the other three degenerate (Figs. 12 and 13). The functioning megaspore undergoes three successive mitoses forming two-, four- and then eight-nucleate embryo sac of the *Polygonum* type (Figs. 14–16). The polar nuclei fuse and form the secondary nucleus (Fig. 17). The antipodal cells persist up to the two-celled stage of the proembryo and then degenerate (Figs. 18–20).

Fertilization. Fertilization is porogamous. One of the synergids degenerates during fertilization and the other follows suit soon after (Figs. 18 and 19). Syngamy and triple fusion are synchronous and result in the formation of zygote and primary endosperm nucleus respectively.

Endosperm. Endosperm is of the Nuclear type. During the first division of primary endosperm nucleus, a tubular extension of the embryo sac appears near the zygote and grows towards the micropyle (Fig. 18). It comes into contact with the obturator and functions as a micropylar haustorium (Fig. 19). Soon, the latter becomes separated from the obturator as the micropyle gets occluded by the growing integuments (Fig. 20). The haustorium remains enucleate throughout and maintains cytoplasmic continuity with the rest of the endosperm until a wall is laid at the point of its attachment with the latter (Figs. 19 and 20).

Simultaneously with these changes in the micropylar region, the endosperm nuclei undergo several free-nuclear divisions which maintain a perfect synchrony till their number reaches 128. Then, the wall formation begins around the embryo and later extends towards the chalazal region but confines only to a third of the endosperm which constitutes the endosperm proper. The remaining free-nuclear portion functions as a

Figs. 18–25. *Scleria foliosa*. — Fig. 18. 2-nucleate endosperm showing the initiation of micropylar haustorium. — Fig. 19. 4-nucleate endosperm with micropylar haustorium in contact with an obturator. — Fig. 20. Multinucleate endosperm showing wall formation. — Figs. 21–22. Endosperm with micropylar and chalazal haustoria. — Fig. 23. Chalazal end of endosperm marked in Fig. 22 is enlarged to show cellular details. — Fig. 24. Longitudinal section of a mature seed with a cavity in the center of the endosperm. — Fig. 25. A portion marked x in Fig. 24 is enlarged to show the details. — *ant* = antipodal cells, *ce* = cellular region of the endosperm, *ch* = chalazal haustorium, *emb* = embryo, *h* = hypostase, *mh* = micropylar haustorium, *obt* = obturator, *pt* = pollen tube, *sc* = seed coat, *sy* = synergoid, *z* = zona.

chalazal haustorium (Figs. 18–23). Both micropylar and chalazal haustoria are recognizable up to the late globular stage of proembryo and later degenerate.

As the development proceeds, the cells of the central region of the endosperm which fail to keep pace with those at the periphery disintegrate and form a large cavity surrounded by endosperm tissue (Fig. 24). At maturity, the cells of the latter show abundant reserve food materials in the form of darkly stained bodies of various sizes (Fig. 25).

Embryo. The zygote divides by a transverse wall forming a terminal (ca) and a basal (cb) cell (Fig. 26). The latter divides transversely while the terminal cell undergoes a vertical division resulting in a proembryonal tetrad (Fig. 27). Each of the derivatives of the terminal cell divides at right angles to the previous division forming a quadrant (Fig. 28). The cells of the quadrant undergo periclinal divisions and give rise to an octant having four axial cells overarched by four protodermal cells (Fig. 29). In later stages of development, the cells of the octant exhibit an unequal rate of growth—one-half being slower than the other—leading to the differentiation of epicotylary and cotyledonary sectors. The latter shows a rapid growth and overtops the quiescent epicotylary sector. As a result, the terminal region of the embryo becomes occupied by the cotyledon pushing the epicotyl to a lateral position (Figs. 30–32 and 36–38).

Meanwhile, the middle cell (m) of the proembryonal tetrad (Fig. 27) undergoes two vertical divisions one at right angles to the other forming four circumaxial cells which by further divisions contribute to the formation of hypocotyl and radicle (Figs. 28–30). The proximal cell (ci) of the tetrad divides and forms a row of eight to ten cells which constitute the suspensor which later degenerates (Fig. 33).

As the development proceeds, the cells bordering the epicotyl form an annular rim around the latter and contribute to the formation of coleoptile which enwraps the plumule (Figs. 32 and 33). The opening of coleoptile becomes gradually shifted from lateral to a sublateral position as the radicle is displaced in the direction away from the epicotyl from its original basal position to a sublateral position. The cotyledon, however, remains terminal assuming a characteristic shape with a circular disc bearing a central cone (Fig. 34). This distinctive apical part of the embryo has numerous papillate outgrowths and constitute a major zone of absorption of cotyledon (Fig. 34). The peripheral cells of this zone are filled with fine granular contents and appear lightly stained than those of the interior which have denser contents (Fig. 35). The disposition of embryonal regions in the mature embryo corresponds to the *Schoenus* type (VAN DER VEKEN 1965).

Figs. 26–38. *Scleria foliosa*: Successive stages in the formation of embryo (Figs. 26–35: longisections; Figs. 36–38: transections).— Fig. 26. 2-celled embryo.— Fig. 27. Proembryonal tetrad.— Figs. 28–29. Quadrant and octant-stages respectively.— Figs. 30–32. Globular embryos.— Fig. 33. Differentiated young embryo.— Fig. 34. Mature embryo.— Fig. 35. One of the cotyledonary papillae shown in Fig. 34 is magnified to show the cellular details.— Figs. 36–38. Transections of embryos to show epicotylary (single hatched) and cotyledonary sectors.— *ca* and *cb* = terminal and basal cells of the 2-celled embryo respectively; *ci* = proximal cell of the proembryonal tetrad; *cot* = cotyledon, *cs* = cotyledonary sheath (coleoptile), *em* = epicotylary meristem, *fl* = first leaf, *l*₂ = second plumular leaf, *m* = middle cell of the proembryonal tetrad, *pz* = papillate zone, *q* = quadrant, *r* = radicle, *s* = suspensor

Discussion

The development and structure of male and female gametophytes in *Scleria foliosa* are similar to the pattern already established for the family *Cyperaceae*.

The endosperm in all the members of *Cyperaceae* including the present one is of the Nuclear type. Whereas the wall formation in the endosperm is complete in most of the species of the family, it is incomplete in species of *Scleria* (NIJALINGAPPA & DEVAKI 1979, MAKDE & BHUSKUTE 1984) and *Rhynchospora* (NIJALINGAPPA & TEJAVATHI 1983). The latter two taxa stand apart from the rest of the *Cyperaceae* in having endosperm with haustoria. The combination of nuclear ontogeny and the presence of both micropylar and chalazal haustoria as seen in *S. foliosa* has not been reported in any other angiosperm examined so far.

The embryo in *Cyperaceae* exhibits a high degree of uniformity in respect of early stages of its ontogeny. However, opinions differ with regard to the origin of epicotyl and its topographic relations with the cotyledon. While some authors believe that the cotyledon and epicotyl are derived from the superposed tiers, *l* and *l'* respectively (SHAH 1965, SHAH & NEELAKANDAN 1971, JUGUET 1970, UNTAWALE & MAKDE 1984), others derived them from the two adjacently placed vertical halves of the terminal tier of the embryo (NIJALINGAPPA 1977, NIJALINGAPPA & DEVAKI 1978, TEJAVATHI 1980). The present study is in agreement with that of the latter authors and conforms to the concept of terminal origin of epicotyl and cotyledon as reported in other monocotyledons (HACCIUS 1952, SWAMY 1963, HACCIUS & LAKSHMANAN 1966, PHILIP & HACCIUS 1976, RAMASWAMY & AREKAL 1981, 1982a, 1982b, RAMASWAMY & al. 1980).

The characteristics of mature embryo in *S. foliosa* correspond to the *Schoenus* type (VAN DER VEKEN 1965) as reported in *S. levis* (SHAH & NEELAKANDAN 1971 as *S. hebecarpa*). On the contrary, the embryo of *S. alata* has been assigned to the *Scirpus* type by SCHNEIDER (1932) when the *Schoenus* type of VAN DER VEKEN (1965) was not yet known. Furthermore, the papillose cotyledon observed in *S. pergracilis*, *S. lithosperma* and *S. foliosa* (NIJALINGAPPA & AREKAL 1983, present work), a feature unknown elsewhere in the family but appears to be quite consistent among the species where present, serves as one of the embryological characteristics of diagnostic value.

The circumscription of the genus *Scleria* is highly debatable. Whereas some authors expanded its limit by adding other genera, *Becquerelia* (BOCKELER 1874, CLARKE 1908) and *Diplacrum* (BENTHAM 1878, KERN 1961) to it, others (GOEBEL 1888, CORE 1936, BLAKE 1954, KOYAMA 1967, HAINES & LYE 1983) recognized each one of them as distinct. For want of embryological data *Becquerelia* has been omitted from further con-

sideration and the present discussion is, therefore, confined to *Scleria* and *Diplacrum* for which embryological information is available (see NIJALINGAPPA & NAGARAJ 1980).

Morphologically, *Scleria* and *Diplacrum* can be distinguished from each other in the structure of inflorescence, number of stamens, number of glumes enveloping the nut and distribution of bulliform cells in the leaf epidermis (KOYAMA 1967). Embryologically too, they have some differences in respect of endosperm and embryo. In *Scleria*, the endosperm has both micropylar and chalazal haustoria which are absent in *Diplacrum*. The latter is characterized by a highly precocious wall formation—at the eight-nucleate stage—in the endosperm which is not the case in *Scleria* where cellularization occurs only after 128 nuclei are formed. Furthermore, in *Scleria* the mature embryo is of the *Schoenus* type while in *Diplacrum* it conforms to the *Scirpus* type. Another notable difference pertaining to embryo is that in *Scleria* the cotyledon is highly differentiated and papillose but in *Diplacrum* it is simple having a smooth surface. These embryological differences are quite distinctive enough to strengthen those obtained from morphological and anatomical studies and substantiate the views of earlier cyperologists who maintained *Scleria* and *Diplacrum* as independent genera.

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References

- BENTHAM, G., 1878: *Cyperaceae*. In: Flora Australiensis. 7, 427.
 BLAKE, S. T., 1954: The *Cyperaceae* collected in New Guinea by S. J. BRASS IV. — J. Arnold Arb. 35, 203–238.
 BOCKELER, O., 1874: Die Cyperaceen des Königlichen Herbariums zu Berlin. — Linnaea 38, 410–544.
 CLARKE, C. B., 1908: New genera and species of *Cyperaceae*. — Kew Bull. Add. Ser. 8, 1–196.
 CORE, E. L., 1936: The American species of *Scleria*. — Brittonia 2, 1–105.
 DAVIS, G. L., 1966: Systematic embryology of the Angiosperms. — New York: John Wiley.
 GOEBEL, K., 1888: Morphologische und biologische Studien III. Über den Bau der Ährchen und Blüten einiger Javanischer Cyperaceen. — Ann. Jard. Bot. Buitenz. 7, 120–140.
 HACCUS, B., 1952: Die Embryoentwicklung bei *Ottelia alismoides* und das Problem des terminalen Monokotylen-Keimblattes. — Planta 40, 443–460.
 — LAKSHMANAN, K. K., 1966: Vergleichende Untersuchung der Entwicklung von Kotyledo und Sproßscheitel bei *Pistia stratiotes* und *Lemna gibba*, ein Beitrag zum Problem der sogenannten terminalen Blattorgane. — Beitr. Biol. Pflanzen 42, 425–443.

- HAINES, R. W., LYE, K. A., 1983: The sedges and rushes of East Africa. — Nairobi: East African Natural History Society.
- JUGUET, M., 1970: Développement de l'embryon chez quelques Cypéracées africaines. — *Adansonia* **10**, 271–288.
- KERN, J. H., 1961: Florae Malesianae Precursores XXX. The genus *Scleria* in Malaysia. — *Blumea* **11**, 140–218.
- KOYAMA, T., 1967: The systematic significance of leaf structure in the tribe *Sclerieae* (Cyperaceae). — *Mem. New York Bot. Garden* **16**, 46–70.
- MAKDE, K. H., 1981a: Endothecium in *Cyperaceae*. — *Curr. Sci.* **50**, 98–99.
- 1981b: Hypostase in *Cyperaceae*. — *Curr. Sci.* **50**, 421–422.
- 1982: Obturator in the *Cyperaceae*. — *Curr. Sci.* **51**, 525–527.
- BHUSKUTE, S. M., 1984: Trends of specialization in endosperm of the *Cyperaceae*. — *Curr. Sci.* **53**, 504–506.
- NIJALINGAPPA, B. H. M., 1977: Post-pollination studies in some *Cyperaceae*. — *Proc. Indian Acad. Sci.* **85 B**, 391–398.
- AREKAL, G. D., 1983: On the papillate cotyledonary surface of *Scleria foliosa* HOCHST. ex A. RICH. (*Cyperaceae*). — *Curr. Sci.* **52**, 816–817.
- DEVAKI, N., 1978: Embryological studies in *Diplacrum caricinum* R. BR. — *Beitr. Biol. Pflanzen* **54**, 215–225.
- — 1979: Endosperm of *Scleria foliosa* HOCHSTETTER ex A. RICHARD. — *Curr. Sci.* **48**, 451–452.
- NAGARAJ, M., 1980: Glimpses of embryological studies in *Cyperaceae*. — In: NAGARAJ, M., MALIK, C. P., (Eds.): *Current Trends in Botanical Research*, pp. 51–58. — New Delhi: Kalyani Publishers.
- TEJAVATHI, D. H., 1983: Occurrence of haustorium in *Rhynchospora corymbosa* (L.) BRITTON (*Cyperaceae*). — *Curr. Sci.* **52**, 262–263.
- PHILIP, V. J., HACCIUS, B., 1976: Embryogenesis in *Bambusa arundinacea* WILLD. and structure of the mature embryo. — *Beitr. Biol. Pflanzen* **52**, 83–100.
- RAMASWAMY, S. N., AREKAL, G. D., 1981: Embryology of *Eriocaulon setaceum* (*Eriocaulaceae*). — *Pl. Syst. Evol.* **138**, 175–188.
- — 1982a: Embryology of *Eriocaulon xeranthemum* MART. (*Eriocaulaceae*). — *Acta Bot. Neerl.* **31**, 41–54.
- — 1982b: On the embryogeny of three taxa of *Paepalanthoideae* (*Eriocaulaceae*). — *Ann. Bot.* **49**, 99–102.
- SWAMY, B. G. L., AREKAL, G. D., 1980: From zygote to seedling in *Eriocaulon robusto-brownianum* RUHL. (*Eriocaulaceae*). — *Beitr. Biol. Pflanzen* **55**, 179–188.
- SCHNEIDER, M., 1932: Untersuchungen über die Embryobildung und Entwicklung der Cyperaceen usw. — *Beih. Bot. Centralbl.*, I. Abt. **49**, 649–674.
- SHAH, C. K., 1965: Embryogeny in some *Cyperaceae*. — *Phytomorphology* **15**, 1–9.
- NEELAKANDAN, N., 1971: Embryogeny in some *Cyperaceae* II. — *Beitr. Biol. Pflanzen* **47**, 215–227.
- SWAMY, B. G. L., 1963: The origin of cotyledon and epicotyl in *Ottelia alismoides*. — *Beitr. Biol. Pflanzen* **39**, 1–16.
- TEJAVATHI, D. H., 1980: Cyto-embryological studies in some members of *Cyperaceae*. — Ph.D. Thesis, Bangalore University.

UNTAWALE, A. G., MAKDE, K. H., 1984: A contribution to the embryology of *Scirpus roylei* NEES. — J. Indian Bot. Soc. **63**, 298–305.

VAN DER VEKEN, P., 1965: Contribution à l'embryographie systématique des *Cyperaceae-Cyeroideae*. — Bull. Jard. Bot. État. Brux. **35**, 285–354.

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