Pl. Syst. Evol. 137, 203–214 (1981)

Plant Systematics and Evolution [©] by Springer-Verlag 1981

From the Andhra University, Waltair, India

Studies in the Embryology of Heliantheae (Compositae)¹

By

T. Pullaiah, Waltair, India

(Received November 26, 1978, in revised form March 28, 1980)

Key Words: Compositae, Heliantheae.—Embryology.

Abstract: The embryology of Lagascea mollis, Zinnia angustifolia and Galinsoga parviflora has been studied. The anther archesporium is hypodermal and consists of a single row of 6-8 cells, there are two layers below the epidermis of the anther and a periplasmodial tapetum. Ripe pollen grains are tricolpate and 3-celled. The ovary contains a single ovule, but in a few cases of Galinsoga parviflora two ovules have been found. The female archesporium is unicellular, but sometimes more than one archesporial cell occurs in Lagascea mollis and Zinnia angustifolia. The embryo sac development is of the Polygonum type, the synergids are hooked, antipodal cells show great variation. The endosperm development is cellular in Galinsoga parviflora and peripheral layer persists in the mature seed. The embryo development conforms to the Senecio variation of the Asterad type. The pericarp structure and embryological features support the disputed systematic position of Lagascea within Heliantheae.

The tribe *Heliantheae* of the family *Compositae* is of special interest to embryologists because of the occurrence of a number of variations. As many as three different types of embryo sac development—i.e. Polygonum, Allium, and Fritillaria type—occur in this tribe (MAHESH-WARI & SRINIVASAN 1944, ROSEN 1944, HJELMQUIST 1951, HJELMQUIST & HOLMBERG 1961, CESCA 1961, MAHESWARI DEVI 1963, PULLAIAH 1978). Antipodal variations, apomixis, polyspermy, semigamy and polyembryony etc. also are known from some species (GELIN 1934, ESAU 1946, BATTAGLIA 1945, 1946, 1963, MAHESWARI DEVI & PULLAIAH 1976, PULLAIAH 1978).

¹ Part of a Ph.D. thesis, accepted at Andhra University.

¹⁴ Pl. Syst. Evol., Vol. 137, No. 3

In spite of this extensive work, a number of genera and species in the tribe have remained uninvestigated. Doll's (1927) observations on the embryology of Lagascea mollis are limited and include a reference to cellular endosperm development. Embryological investigations on the genera Zinnia and Galinsoga are confined to single species, i.e. Zinnia pauciflora (MAHESWARI DEVI 1963) and Galinsoga ciliata (HARRIS 1935, POPHAM 1938). DAHLGREN (1920) has investigated the development of endosperm in a number of Compositae and reports cellular endosperm in Galinsoga perviflora, while HARRIS (1935) and POPHAM (1938) have observed nuclear endosperm in G. ciliata. Very little is known about the structure and development of the anther, male gametophyte, fertilization and embryo development in Lagascea, Galinsoga, and also in Zinnia. As DAVIS (1964) pointed out, a considerable amount of purely descriptive work still remains to be carried out before any generalization can be made. Hence, the present investigation was undertaken to study the embryology of three species, Lagascea mollis CAV., Zinnia angustifolia HBK. and Galinsoga parviflora CAV.

Materials and Methods

The material of *Lagascea mollis* was collected from plants growing in the Andhra University campus and that of *Zinnia angustifolia* from the plants cultivated in the gardens of Andhra University. Capitula of *Galinsoga parviflora* were collected from the Anantagiri hills in Visakhapatnam district. Voucher specimens were deposited in the Herbarium of the Botany department, Andhra University, Waltair. Heads at different stages were fixed in Formalin-Acetic-Alcohol (F. A. A.). The involucral bracts were removed before fixation. Dehydration infiltration, embedding and sectioning were done by the customary methods (JOHANSEN 1940). The sections were stained in Delafield's haematoxylin.

Observations

Microsporangium, Microsporogenesis and Male Gametophyte. The anthers contain four microsporangia. The primary archesporium consists of a single hypodermal row of 6-8 prominent cells in each of the four lobes of the anther (Fig. 2A). The development of anther wall follows the dicotyledonous type (Figs. 1A-C, 2B-D). The epidermis is much stretched and persists at maturity. The sub-epidermal layer develops into the fibrous endothecicum (Figs. 1D, 2H, 3C). The middle layer is ephemeral. The cells of the tapetum show great variation in their nuclear behaviour. The nucleus of the tapetal cells undergoes nuclear divisions and fusions resulting in multinucleate and polyploid cells. The tapetum is of the periplasmodial type (Figs. 2G, 3B).

The primary sporogenous cells undergo few mitotic divisions in all planes resulting in a moderately extensive mass of pollen mother cells

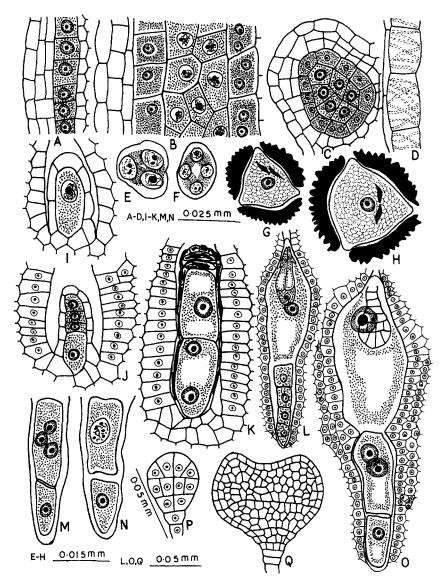


Fig. 1. Lagascea mollis. A L.s. part of anther lobe showing epidermis, wall layers and sporogenous layer; B, C L.s. and T.s. of anther lobes showing epidermis, wall layers and pollen mother cells; D fibrous endothecium; E, F tetrahedral and isobilateral pollen tetrads respectively; G, H mature pollen grains of different sizes; I megaspore mother cell in meiotic prophase; J megaspore tetrad showing chalazal functional megaspore; K two- and one-nucleate embryo sacs are developed from the chalazal and third megaspores respectively; L mature embryo sac; M, N antipodal cells; O embryo sac showing a few-celled embryo and an undivided primary endosperm nucleus; P, Q young and heart shaped embryos

(Figs. 1B, C, 2D) except in Galinsoga parviflora where the pollen mother cells are 2-seriate (Fig. 3A). Pollen mother cell meioses are simultaneous and produce either tetrahedral (Figs. 1E, 2I, 3D) or isobilateral tetrads (Figs. 1F, 2J, 3E). Cytokinesis is by furrowing. The pollen grains are tricolpate and 3-celled at the shedding stage (Figs. 1G, H,2K, 3G). In Galinsoga parviflora sometimes one, two or even three microspores of a tetrad degenerate (Fig. 3E, F).

Ovary and Ovule. The ovary as characteristic of *Compositae* is bicarpellary, syncarpous, unilocular and inferior with a single basal ovule. But in Galinsoga parviflora, the ovary occasionally contains two ovules which have a common funicle and are arranged face to face. Each of these ovules contain a mature embryo (Fig. 3H). The ovule is anatropous, unitegmic and tenuinucellate. At about the time of the megaspore tetrad formation the innermost layer of the integument becomes differentiated as the integumentary tapetum. Three types of integumentary tapetum are recorded: 1) in Galinsoga parviflora, the integumentary tapetum consists of a single layer of uninucleate cells and this remains unaltered throughout. i.e., until it is completely absorbed by the growing embryo (Fig. 3M). 2) In Zinnia angustifolia the integumentary tapetum becomes biseriate, but the cells remain uninucleate (Fig. 2P). 3) An additional type is seen in Lagascea mollis: The integumentary tapetum becomes multiseriate near the middle of the embryo sac and the cells remain uninucleate (Fig. 10). In all the species investigated integumentary vascular traces are recorded.

Megasporogenesis and Female Gametophyte. The female archesporium is hypodermal and single-celled. But in Lagascea mollis and Zinnia angustifolia a multicellular archesporium is occasionally formed (Fig. 2L). The archesporial cell directly develops into the megasporial cell (Fig. 3I) and the meiotic divisions produce a linear tetrad of megaspores (Figs. 1J, 2M, 3J). The chalazal megaspore (Fig. 1J) produces an 8-nucleate, spindle-shaped embryo sac of the Polygonum type (Figs. 2N, O, 3K-M). In Lagascea mollis occasionally more than one megaspore of the tetrad develop embryo sacs (Fig. 1K). After formation of the secondary nucleus, the embryo sac widens considerably near the region of the egg apparatus so that the extreme apex appears as a beak-like protuberance. The synergids are hooked and degenerate soon after fertilization. There are either two or three antipodal cells (Figs. 10, 20, P, R, 3M, N). If two occur, one of them is binucleate; if three, all are uninucleate. In Galinsoga parviflora the original condition of the antipodals remains unchanged (Fig. 3M, N). In Zinnia angustifolia the number of antipodals remains constant, but due to nuclear divisions multinucleate cells are formed (Fig. 2Q). Occasio-

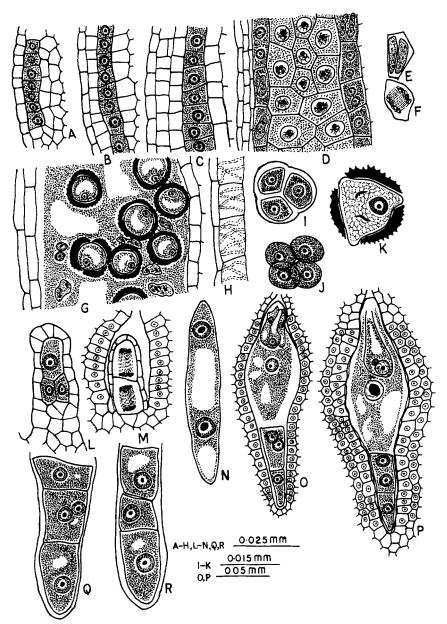


Fig. 2. Zinnia linearis. A L. s. part of anther lobe showing archesporium; $B \rightarrow D$ L. s. of anther lobes showing development wall layers; E, F anther tapetal cells showing nuclear divisions; G L. s. part of anther lobe showing periplasmodium and one-nucleate pollen grains; H fibrous endothecium; I, J tetrahedral and isobilateral pollen tetrads respectively; K mature pollen grain; L three-celled female archesporium; M megaspore dyad, the two cells are in telophase; N, Otwo-nucleate and mature embryo sacs respectively; P embryo sac showing syngamy, triple fusion nucleus; Q, R antipodal cells

nally, in Lagascea mollis the number of cells increases up to 5-6 and these become multinucleate and polyploid (Fig. 1L-O). Antipodal cells persist up to the time of formation of a heart-shaped embryo in the embryo sac.

Fertilization, Endosperm and Embryo. Fertilization is porogamous. Triple fusion is completed before syngamy (Fig. 2P). The synergids degenerate before fertilization.

The development of the endosperm has been studied in *Galinsoga* parviflora. The first division of the primary endosperm nucleus is followed by a transverse wall and two cells are formed. Further divisions in these two cells take place in all directions and a massive tissue is formed filling the embryo sac with cellular tissue (Fig. 3N, O).

At the stage of a globular embryo in Lagascea mollis and Galinsoga parviflora the endosperm cells divide and form a narrow layer of small peripheral cells which resemble the integumentary tapetal cells in their appearance and in their glandular nature. But the integumentary tapetal cells are elongated radially, while the peripheral endosperm cells are elongated longitudinally (Figs. 3O, 4F). Excepting its peripheral layer, the entire endosperm, is consumed by the growing embryo (Fig. 4G). In a single instance of Lagascea mollis an embryo sac with few-celled embryo and undivided primary endosperm nucleus is recorded (Fig. 1O).

Development of embryo, seed coat and pericarp has been studied only in Lagascea mollis and Galinsoga parviflora. A transverse division of the zygote results in two cells, the basal cb and the terminal ca (Fig. 4A). The latter divides vertically and forms two juxtaposed cells while the former undergoes a transverse division producing two superposed cells m and ci. Thus a four-celled "T" shaped proembryo is formed (Fig. 4B). The two juxtaposed cells of the tier ca divide once more vertically and produce quadrants which divide obliquely and give to octants (Fig. 1P). The cell m also undergoes two vertical divisions at right angles to one another and produces quadrants. The cell ci divides transversely to n and n'. The latter, after one more transverse division produce o and p(Figs. 1P, 4C).

The tier q gives rise to the cotyledons and stem tip, the tier m contributes to the formation of hypocotyledonary region and plerome initials of the root, and n and o to the formation of root tip, root cap and dermatogen of the root (Figs. 1P, Q, 4C, D). The cell p undergoes two or three transverse divisions and produces an uniseriate suspensor of 4-8 cells (Fig. 4D). Thus the embryogeny conforms to the Senecio variation of the Asterad type (JOHANSEN 1950).

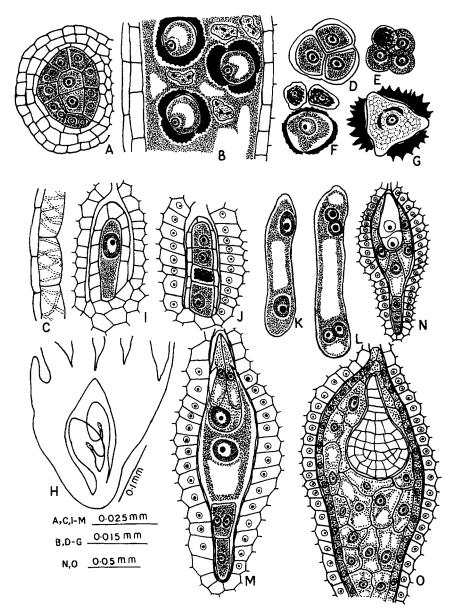


Fig. 3. Galinsoga parviflora. A T.s. anther lobe showing epidermis, wall layers and pollen mother cells; B L.s. of part of anther lobe showing periplasmodium and one-nucleate pollen grains; C fibrous endothecium; D tetrahedral pollen tetrad; E isobilateral pollen tetrad showing one degenerating microspore; Ftetrahedral tetrad showing two degenerating microspores; G mature pollen grain; H L.s. ovary showing two ovules; I megaspore mother cell; J megaspore tetrad; K, L two- and four-nucleate embryo sacs respectively; M mature embryo sac; N embryo sac showing two-celled embryo and cellular endosperm; O embryo sac showing globular embryo and cellular endosperm

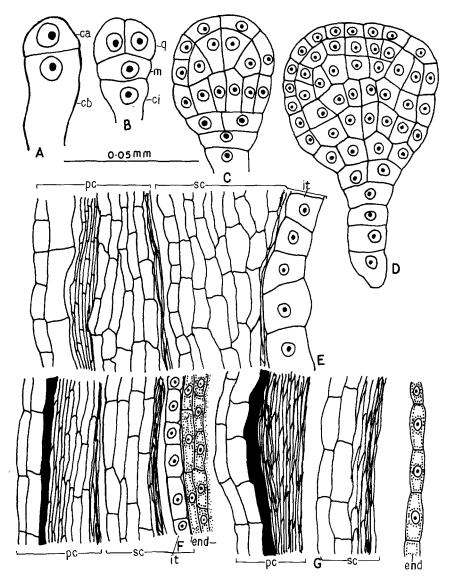


Fig. 4. Galinsoga parviflora. A - D Various stages in the development of the embryo; E L. s. of a portion of seed coat and pericarp at organised embryo sac stage; F, G L. s. of a portion of seed coat and pericarp at heart-shaped and dicotyledonous embryo stages respectively (end endosperm, it integumentary tapetum, pc pericarp, sc seed coat)

Seed Coat and Pericarp. The integument at the organised embryo sac stage is 8-10 layered including the integumentary tapetum (Fig. 4*E*). After fertilization a few layers of cells of the integument next to the endothelium become enlarged, loose their contents and become obliterated (Fig. 4*F*). In a mature seed, except for a few layers of cells and the epidermis, the layers of the integument are crushed and absorbed by the growing embryo. Thus the seed coat is made up of the epidermis and a few layers of the integument (Fig. 4*G*).

The ovary wall, which consists of parenchymatous cells at the megaspore mother cell stage, becomes differentiated into three zones by the time a mature embryo sac is formed in the ovule (Fig. 4E). The outer zone includes epidermis and hypodermis, the latter with larger cells. The middle zone consists of a few layers of elongated fibrous cells, the inner zone of a few layers of parenchymatous cells. After fertilization schizogenous cavities develop between the hypodermis and the inner layers of cells. A brown resinous substance exudates into this space, finally becomes hard and forms a dark cementing layer. Meanwhile the inner parenchymatous zone dissolves. In the mature achene the epidermis, hypodermis and a few fibrous layers form the pericarp.

Discussion

The structure and development of the anther and male gametophyte in Lagascea mollis, Zinnia angustifolia and Galinsoga parviflora are typical of that reported for the Heliantheae (BANERJI & PAL 1963, DESHPANDE 1960, 1962, 1964, GHOSH 1962, MAHESWARI DEVI 1963, MAHESWARI DEVI & PULLAIAH 1976, PULLAIAH 1978). The archesporium consists of a single row of hypodermal cells. Only for Blainvillea rhomboidea the occurrence of two rows of archesporial cells reported SUNDARA RAJAN (1972).

In Galinsoga parviflora two ovules per ovary were occasionally observed. Although occurrence of two ovules per ovary is reported in a number of Compositae belonging to different tribes (VENKATESWARLU & MAHESWARI DEVI 1955, MESTRE 1957, KAPIL & SETHI 1962a, ENGELL 1970, MAHESWARI DEVI & PULLAIAH 1977, PULLAIAH 1979b), this is the first case for the tribe *Heliantheae*.

The female archesporium is normally single-celled in the tribe. However, in a few species, for example, *Bidens pilosa* (MAHESWARI DEVI 1963), *Scalesia divisa*, *S. gummifera*, *S. helleri* (ELIASSON 1974), *Melampodium divaricatum* (MAHESWARI DEVI & PULLAIAH 1976), multicellular archesporia also occur.

In the majority of the *Heliantheae* the development of the embryo sac follows the Polygonum type. But in *Tridax trilobata* (HJELMQUIST 1951) and Sanvitalia procumbens (HJELMQUIST & HOLMBERG 1961) both Polygonum and Allium types of embryo sac development have been recorded. In Tridax glabellus (see DAVIS 1966) embryo sacs are either monosporic or tetrasporic. In the genus Rudbeckia — R. hirta (PALM 1934), R. amplexicaulis, R. laciniata (FAGERLIND 1939, ROSEN 1944), R. bicolor (FAGERLIND 1939, ROSEN 1944, MAHESHWARI & SRINIVASAN 1944), and R. missouriensis (CESCA 1961) — the development of embryo sac follows the Fritillaria type.

Both nuclear and cellular endosperm occur in the tribe *Heliantheae*. DOLL (1927) for *Lagascea mollis* and DAHLGREN (1920) for *Galinsoga parviflora* report cellular endosperm, as is confirmed in the present investigation. In contrast, HARRIS (1935) and POPHAM (1938) have observed nuclear endosperm development in *G. ciliata*. Such intrageneric variation of endosperm development was earlier recorded for *Blumea* (PULLAIAH 1978), also a member of the *Compositae*. In some cases the primary endosperm nucleus remains undivided, when the embryo reaches a few celled stage e.g. in *Tridax procumbens* (MAHESH-WARI & ROY 1952), *T. trilobata* (KAPIL & SETHI 1962b), *Bidens pilosa* (MAHESWARI DEVI 1963), *Sigesbeckia orientalis* (MISBA 1965), and *Lagascea mollis* (present study).

Two different views were expressed regarding the systematic position of Lagascea. CASSINI (1815), LESSING (1832), DECANDOLLE (1836), SCHULTZ-BIPOTINUS (1861) and MERXMÜLLER (1954) included the genus Lagascea in the tribe Vernonieae. BENTHAM (1873), HOFFMANN (1894) and others place Lagascea in the tribe Heliantheae. Recently STUESSY (1976) on the basis of morphologgical and chromosomal studies, supports the assignment of the genus Lagascea to Heliantheae. Embryological characters and especially pericarp structure are also in favour of its retention in the tribe Heliantheae. In Heliantheae generally three different zones are distinguished in the pericarp (MISRA 1972b, present data). Between the middle and outer zones characteristic schizogenous cavities develop which fill with a brown resinous and hardening substance. Such schizogenous cavities are absent in Vernonieae (MISRA 1972a, PULLAIAH 1979). In addition, Heliantheae have a well developed integumentary tapetum which is poorly developed in Vernonieae.

References

- BANERJI, I., PAL, S., 1959: A contribution to the life history of Synedrella nodiflora. — J. Linn. Soc. Lond. Bot. 55, 810—817.
- BATTAGLIA, E., 1945: Fenomeni citologici nuovi nella embriogenesi (Semigamia) e nella microsporogenesi (doppio nucleo di restituzione) di Rudbeckia laciniata. — N. G. Bot. Ital. 52, 34—38.

- BATTAGLIA, E., 1946: Ricerche cariologiche ed embriologiche sul genere Rudbeckia. 1-5. Il gametofito femminile e maschile di R. bicolor, R. hirta, R. hirta var. meine freude, R. amplexicaule e R. purpurea (Echinacea purpurea).
 N. G. Bot. Ital. 53, 1-26.
- 1963: Apomixis. In MAHESHWARI. P., (Ed.): Recent advances in the Embryology of Angiosperms, p. 221—264. — Delhi.
- BENTHAM, G., 1873: Notes on the classification, history and geographical distribution of Compositae. J. Linn. Soc. (Bot.) 13, 335-577.
- CASSINI, H., 1815: Précis d'un second mémoire sur les Synanthérées, contenant l'analyse des étamines. — J. Bot. (Paris), ser 2, 4, 231—254.
- CESCA, G., 1961: Ricerche embriologiche su Rudbeckia missouriensis. Caryologia 14, 129—139.
- DAHLGREN, K. V. O., 1920: Zur Embryologie der Kompositen mit besonderer Berücksichtigung der Endospermbildung. — Z. Bot. 12, 481—516.
- DAVIS, G. L., 1964: Embryological studies in the Compositae. 4. Sporogenesis, gametogenesis and embryogeny in Brachycome ciliaris. — Aust. J. Bot. 12, 142—151.
- DECANDOLLE, A. P., 1836: Compositae, part I. In Prodromus Systematis Naturalis Regni Vegetabilis 5. — Paris.
- DESHPANDE, P. K., 1960: Studies in the family Compositae. Male and female gametophytes of Parthenium hysterophorus. J. Biol. Sci. 3, 26—29.
- 1962: Studies in the life history of *Glossocardia bosvallia*. Bull. Bot. Soc., Coll. Sci. Nagpur, 3, 84—91.
- 1964: A contribution to the embryology of *Bidens biternata*. J. Indian Bot. Soc. 43, 149—157.
- Doll, W., 1927: Beiträge zur Kenntnis der Dipsacaceen und Dipsacaceenähnlichen Pflanzen. — Bot. Arch. Königsberg 17, 107—146.
- ELLASSON, U., 1974: Studies in Galapagos plants XIV. The genus Scalesia. Opera Botanica 36, 1—117.
- ENGELL, K., 1970: Embryological investigations in Arnica alpina from Greenland. — Bot. Tidsk. 65, 225—244.
- ESAU, K., 1946: Morphology and reproduction in guayule and certain other species of *Parthenium.* Hilgardia 17, 61—101.
- GELIN, O. E. V., 1934: Embryologische und cytologische Studien in Heliantheae-Coreopsidinae. — Acta Hort. Berg. 11, 99—126.
- Gноян, R. B., 1962: A contribution to the life history of Wedelia calendulacea. J. Indian Bot. Soc. 41, 197—206.
- HARRIS, C. J., 1935: The development of the flower and seed in *Galinsoga ciliata*.
 Univ. Pittsburgh Bull. 32, 131—137.
- HJELMQUIST, H., 1951: The embryo sac development of *Tridax trilobata*. Bot. Notiser 1951, 180—187.
- HOLMBERG, U., 1961: The development of the embryo sac in Sanvitalia procumbens. - Bot. Notiser 1961, 353-360.
- HOFFMANN, O., 1894: In ENGLER, A., PRANTL, K., (Eds.): Die natürlichen Pflanzenfamilien IV/5: 87-391.
- JOHANSEN, D. A., 1940: Plant Microtechnique. New York: McGraw Hill.
- 1950: Plant embryology. Waltham, Mass.
- KAPIL, R. N., SETHI, S. B., 1962a: Gametogenesis and seed development in Ainsliaea aptera. — Phytomorphology 12, 222—234.
- 1962b: Development of seed in Tridax trilobata. Phytomorphology 12, 235—239.

LESSING, C. F., 1832: Synopsis Generum Compositarum. — Berlin.

- MAHESHWARI, P., Roy, S. K., 1952: The embryo sac and embryo of Tridax procumbens. — Phytomorphology 2, 245—252.
- SRINIVASAN, A. R., 1944: Contribution to the embryology of *Rudbeckia* bicolor. New Phytol. 44, 135-142.
- MAHESWARI DEVI, H., 1963: Embryological studies in Compositae. 4. Heliantheae. — Proc. Indian Acad. Sci. Ser. B. 58, 274—290.
- PULLAIAH, T., 1976: Embryological investigations in the Melampodinae I. Melampodium divaricatum. — Phytomorphology 26, 77—86.
- 1977: Embryological abnormalities in *Carthamus tinctorius*. Acta Bot. Ind. 5, 8—15.
- MESTRE, J. C., 1957: (The presence of two ovules in the ovary of some Cynareae. Observations on Centaurea collina and Carduus defloratus). — Bull. Soc. Bot. France 104, 37—40.
- MERXMULLER, H., 1954: Beiträge zur Taxonomie der Compositen. Ber. Deutsch. Bot. Ges. 67, 23—24.
- MISRA, S., 1965: Floral morphology of the family Compositae. 3. Embryology of Sigesbeckia orientalis. — Aust. J. Bot. 13, 1—10.
- 1972a: Floral morphology of the family Compositae. 4. Tribe Vernonieae Vernonia anthelmintica. — Bot. Mag. Tokyo 85, 187—199.
- 1972b: Floral morphology of the family *Compositae*. 5. The seed coat and pericarp in *Verbesina encelioides*. J. Indian Bot. Soc. 51, 332-341.
- POPHAM, R. A., 1938: A contribution to the life history of *Galinsoga ciliata*. Bot. Gaz. **99**, 543—555.
- PULLAIAH, T., 1978: Embryology of *Tithonia*. Phytomorphology 28, 437-444.
- 1979a: Embryology of Adenostemma, Elephantopus and Vernonia (Compositae). — Bot. Notiser 132, 51—56.
- 1979b: Studies in the embryology of *Compositae*. IV. The Tribe *Inuleae*. Amer. J. Bot. **66**, 1119—1127.
- Rosen, W., 1944: The embryo sac of *Rudbeckia*. Acta Hort. Goteb. 15, 267—273.
- SCHULTZ-BIPOTINUS, C. H., 1861: Cassiniaceae uniflorae, oder Verzeichnis der Cassiniacean mit l-blüthigen Köpfchen. — Jahresber. Pollichia 18—19, 161—190.
- STUESSY, T. F., 1976: A systematic review of the subtribe Lagasceinae (Compositae, Heliantheae). — Amer. J. Bot. 63, 1289—1294.
- SUNDARA RAJAN, S., 1972: Embryological studies in Compositae 3. A contribution to the embryology of Blainvillea rhomboidea. — Proc. Indian Acad. Sci. Ser. B. 75, 167—176.
- VENKATESWARLU, J., MAHESWARI DEVI, H., 1955: Embryological studies in Compositae. 2. Helenieae. — Proc. Nat. Inst. Sci. India Ser. B. 21, 149—161.

Address of the author: Dr. T. PULLAIAH, Department of Bio-Sciences, S.V.U. Autonomous P.G. Centre, Anantapur 515003, A.P. India.