EMBRYOLOGICAL STUDIES IN COMPOSITAE

IV. Heliantheae

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INTRODUCTION

The various aspects of the embryology of the tribe Heliantheae, one of the largest tribes of the family Compositae, are rather inadequately investigated. For example, the previous accounts do not contain definite information about the first division of the primary endosperm nucleus as to whether it is accompanied by wall formation or not. The observations of Merrel (1900), Dahlgren (1920) and Carano (1921) were based on well-developed endosperm and are contradictory. Bhargava (1935) worked out the male and female gametophytes in Tridax procumbens and observed irregularities in the microsporogenesis and Normal type of embryo-sac. Venkateswaralu (1941) recorded integumentary vascular traces in Zinnia elegans, Cosmos bipinnata and Tridax procumbens. Maheshwari and Srinivasan (1944) reported Fritillaria type of embryo-sac development in Rudbeckia bicolor. Semigamy was observed in Rudbeckia speciosa and R. laciniata (Battaglia, 1946 and 1947). Both monosporic and bisporic types of embryo-sacs occur in Tridax trilobata (Hjelmqvist, 1951). Maheshwari and Roy (1952) reported Normal type of embryo-sac development and polyembryony in Tridax procumbens. Vernin (1952) studied endosperm and embryo development in Madia sativa, but could not decide the type of the endosperm development. Hjelmqvist and Holmberg (1961) studied the development of embryo-sac in Sanvitalia procumbens. The archesporium is multicellular. The development of the embryo-sac in some ovules is of the Polygonum type while in others it is of the bisporic type, the upper dyad in some and the lower in others functioning to develop into an 8-nucleate embryo-sac.

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MATERIALS AND METHODS

The materials were collected from plants grown in the Botanical Gardens of the Andhra University, Waltair, and fixed in Formalin-acetic-alcohol or Acetic-alcohol. The usual methods of infiltration and embedding were followed. Sections were cut at a thickness of 8–14 μ and stained with Delafield's Haematoxylin.

ORGANOGENY

Except in Xanthium strumarium the heads are heterogamous and bear the peripheral ray florets and central disc florets. In Xanthium strumarium the heads are homogamous and bear one kind of flowers either the male or the female flowers. The male heads bear a large number of flowers and the female heads contain only two flowers enclosed in a prickly gamophyllous involucre (Fig. 3, A), only the styles protecting out through openings in the two horns of the involucre.

The sequence of the floral whorls in the bisexual flowers is petals, stamens and sepals followed by gynoecium. In the female flowers also the same sequence is observed except that no stamens are developed.

MICROSPOROGENESIS AND MALE GAMETOPHYTE

The structure and development of the anther and pollen is closely similar in all the species investigated and resembles that described in Helieineae (Venkateswarlu and Maheswari Devi, 1955 b). The primary archesporium in each anther lobe consists of a row of 7–10 cells in longitudinal section (Fig. 1, A) and a single cell in transverse section. In the structure of the anther the epidermis is followed by two wall layers and a tapetum which surrounds the sporogenous tissue (Fig. 1, E–G). The tapetum is of the periplasmodial type (Fig. 1, H). In Cosmos sulphureus and Helianthus debilis nuclear fusions of the tapetal cells occur resulting in a large nucleus with many nucleoli. The hypodermal layer develops into the fibrous endothecium (Fig. 1, M). In previous papers published by Venkateswarlu and Maheswari Devi (1955 a and 1955 b) and Maheswari Devi (1957) it was reported that no fibrous endothecium was differentiated in the anthers of Tagetes patula, Gaillardia picta, Flaveria australasica, Launaea pinnatifida and Gerbera jamesonii. On critical re-examination of fresh preparations by Prof. Venkateswarlu and myself, it has been found that in all these cases also fibrous endothecium becomes differentiated in the mature anthers.

The primary sporogenous tissue undergoes a few mitotic divisions in all planes resulting in a moderately extensive mass of pollen mother cells
(Fig. 1, B–F). In *Bidens pilosa* the primary sporogenous cells divide transversely and only a single row of pollen mother cells is formed (Fig. 1, G) as in *Launaea pinnatifida* (Venkateswarlu and Maheswari Devi, 1955 a). Pollen mother cells divide in a simultaneous fashion (Fig. 1, I). Both bilateral and
tetrahedral types of pollen tetrads are formed. Cytokinesis is by furrowing (Fig. 1, I). The pollen grains are three-celled and triporate (Fig. 1, J and K) at the time of shedding.

In Bidens pilosa, Zinnia pauciflora, Cosmos sulphureus, Xanthium strumarium and Helianthus debilis a few cases of pollen tetrads are met in which one or two or three pollen grains are found to be degenerating (Fig. 1, L).

**Ovary and Ovule**

The ovary is bicarpellary, syncarpous, unilocular and inferior with a basal ovule which is anatropous, unitegmic and tenuinucellate (Fig. 3, B).
The inner layer of the integument becomes differentiated as the integumentary tapetum. Three types of integumentary tapetum are recognised. In the first type, as in *Cosmos sulphureus*, *Xanthium strumarium*, *Zinnia pauciflora* and *Coreopsis tinctoria* the integumentary tapetum consists of
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a single layer of uninucleate cells (Fig. 3, L). In the second type, to which Bidens pilosa belongs the integumentary tapetum remains uniseriate, but the cells later on become multinucleate followed by nuclear fusions (Fig. 3, P). In the third type, the integumentary tapetum is multiseriate with multinucleate cells, as in Helianthus annuus and H. debilis (Fig. 3, D). The multiseriate condition in H. annuus is restricted mostly to the middle region of the embryo-sac.

Integumentary vascular traces are present in Helianthus annuus and H. debilis, Zinnia pauciflora, Cosmos sulphureus and Xanthium strumarium (Fig. 2, A–H). The vascular bundle in Xanthium strumarium at the funicle branches into three bundles which in their turn divide and form a number of bundles (Fig. 2, A–G). These vascular traces ramify all over the integument and supply nourishment to the ovule.

MEGASPOROGENESIS AND FEMALE GAMETOPHYTE

The hypodermal archesporium in the ovule is one-celled. It enlarges and functions directly as the megaspore mother cell (Fig. 3, B). A linear tetrad of megaspores is formed consequent upon the two meiotic divisions in the megaspore mother cell (Fig. 3, C). The chalazal megaspore of the tetrad develops into the eight-nucleate embryo-sac according to the Polygonum type (Fig. 3, C and D). The synergids are hooked (Fig. 3, D). The antipodals show much variation (Fig. 3, D–J). In Bidens pilosa, Coreopsis tinctoria and Cosmos sulphureus antipodal haustoria are formed. Soon after fertilisation the antipodal cells begin to grow in size, become haustorial, crush and absorb the cells of the integument but for a thin membrane (Fig. 3, K–M).

Degeneration of entire embryo-sacs were observed in few cases of Bidens pilosa.

In a few cases of Bidens pilosa, multicellular archesporium and multiple embryo-sacs were encountered (Fig. 3, N–P). Figure 3, O shows four embryo-sacs, two of which are in the two-nucleate condition and the other two in the four-nucleate condition. In still other cases two four-nucleate embryo-sacs are seen (Fig. 3, P).

FERTILISATION

Fertilisation is porogamous. The pollen tube in Cosmos sulphureus, Coreopsis tinctoria, Xanthium strumarium and Eclipta erecta, discharges its contents into one of the synergids (Fig. 4, A) as in Heliantheae (Venkateswarlu and Maheswari Devi, 1955 b). In Bidens pilosa, however, the pollen
tube touches the tip of the one of the synergids and empties its contents into
the synergid through a terminal pore (Fig. 4, G). The pollen tube in *Zinnia pauciflora*, after its entry into the embryo-sac, passes between the egg and one
of the synergids and discharges its contents directly into the vicinity of the
egg and secondary nucleus. The pollen tube in *Helianthus annuus* is sickle-
shaped (Fig. 4, B) as in *Taxacum kok-saghys*.

Details of the fusion of the two male gametes with the egg nucleus and
secondary nucleus are similar to that described in Heliantheae (Venkateswarlu
and Maheswari Devi, 1955 b). Triple fusion is completed much earlier
than syngamy. In some cases like *Helianthus annuus* and *H. debilis* syngamy
is completed only after the first or second division of the primary endosperm
nucleus is completed (Fig. 4, C and D). In *Cosmos sulphureus* syngamy and
triple fusion are completed more or less simultaneously (Fig. 3, Q).
In one case of *Bidens pilosa*, in addition to the normal two sperms one extra sperm is noted in the embryo-sac near the two polar nuclei (Fig. 4, G). In this case, the two polar nuclei, unlike in the normal cases, remain unfused even after the discharge of the sperms into the embryo-sac.
The endosperm is Nuclear in all the species studied except in *Eclipta erecta* where it is Cellular. The primary endosperm nucleus divides earlier than the fertilised egg. In the orientation of the spindle of the primary endosperm nucleus *Helianthus annuus* and *H. debilis* resemble *Tagetes patula* (Venkateswarlu and Maheswari Devi, 1955b) and *Gerbera jamesonii* (Maheswari Devi, 1955). In all species studied the endosperm eventually enters the cellular phase (Fig. 4, E) and absorbed by the embryo in the mature seed.

**Fig. 6**
The endosperm in *Eclipta erecta* is of the Cellular type. The first division of the primary endosperm nucleus is followed by a transverse wall and two cells are formed. Further divisions in these four cells take place and a massive tissue is formed filling the whole of the embryo-sac.

In *Bidens pilosa* in one case, however, "the primary endosperm nucleus" (secondary nucleus ?) remains undivided even after a few-celled embryo is formed in the embryo-sac (Fig. 4, F).

**Embryo**

The development of the embryo, in all the species investigated, is essentially similar to that described in *Launaea pinnatifida* and Helenieae (Venkateswarlu and Maheswari Devi, 1955 a and 1955 b). Hence a detailed description is not given in this account.

Details of the development of the embryo are shown in the following schematic representation:

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Fertilised egg --> ca
       ^  ^
       m  n
       cb  ci
       n'  o
       p

Cotyledons and stem tip
Entire hypocotyledonary region and plerome initials of root
Root tip, root cap and dermatogen of root
Suspensor
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Thus in all the plants studied, the first division of the fertilised egg is transverse and both the terminal cell *ca* and the basal cell *cb* contribute to the development of the embryo (Figs. 5, A–V and Fig. 6, A–P). Thus the embryo development conforms to the Asterad type. The cell *m* gives rise to the entire hypocotyledonary region and plerome initials of the root and this feature is characteristic of the senecio variation of the Asterad type.

The cell *p* undergoes two or three transverse divisions resulting in an uniseriate suspensor in *Coreopsis tinctoria* and *Bidens pilosa* (Fig. 5, F–K), while in the remaining forms the cell *p* either directly forms the suspensor cell (Fig. 6, O and P) or undergoes one transverse division resulting in two suspensor cells.
In the structure of the seed the members investigated in the present study resemble *Launaea pinnatifida*, Helieae (Venkateswarlu and Maheswari Devi, 1955a and 1955b) and *Gerbera jamesonii* (Maheswari Devi, 1957).

**DISCUSSION**

Integumentary vascular traces are known to occur in a number of Compositae. The presence of integumentary vascular traces was once looked upon as primitive feature, but its presence in an undoubtedly advanced family like Compositae is evidenced that this feature may not always be indicative of primitiveness, but may be a device for efficient supply and transport of water and nourishment to the developing ovule and embryo.

In three percent of the cases in *Tagetes patula* there are found two ovules per ovary which condition is unusual in Compositae. In the allied families included in Asterales, namely, Valerianaceae, Dipsacaceae and Calyceraceae also, as in Compositae, the ovary is uniovulate. In the other allied orders Rubiales and Campanales the ovary is multiovulate and the occasional occurrence of the two ovulate condition in *Tagetes patula* seems to be a derived condition from that in Rubiales and Campanales.

Though the occurrence of multicellular archesporium is a primitive feature, it is retained in some members in the otherwise advanced family Compositae. Multiple archesporium is known to occur in a few cases of *Bidens pilosa* (present study), *Lonas inodora*, *Erigeron*, *Chrysanthemum*, *Anthemis*, *Cladanthus*, etc. (Harling, 1950, 1951a and 1951b). In all these cases, it appears that multiple embryo-sacs develop due to the further functioning of two or more archesporial cells of an ovule. In *Haploppapus* (Harling, 1951), *Tagetes patula* (Venkateswarlu and Maheswari Devi, 1955b) and *Gerbera jamesonii* (Maheswari Devi, 1957), multiple embryo-sacs develop from the further functioning of more than one megaspore of a tetrad as in these cases there is no multiple archesporium. Bhargava (1935) reported synergids without hooks in *Eclipta erecta*. A careful re-examination of synergids, in the same species, revealed hooks.

Both Nuclear and Cellular types of endosperm development have been reported in the family. Dahlgren (1920) reported Cellular type of endosperm development in *Tagetes signatus*, *Bidens tripartitus* and *Xanthium spinosum*. But my observations on *Tagetes patula*, *Bidens bilosa* and *Xanthium strumarium* show nuclear type of endosperm formation and the statement made by Dahlgren seems erroneous.
Senecio variation of Asterad type of embryo development is invariably found in all Compositae so far investigated.

Embryological features in this family do not aid either in distinguishing one tribe from the other or in tracing the evolutionary tendencies within the family. For instance, both primitive and advanced features like the occurrence of an extensive sporogenous tissue in the anther, presence or absence of an integumentary vascular trace, uni- or multicellular archesporium in the ovule, various types of embryo-sac development, antipodal cells with and without haustorial structures and both Nuclear and Cellular types of endosperm development are known to occur in different members of the same tribe.

Regarding the systematic position of the family Compositae different views were put forth by various authors. Engler (1926) included Compositae in the order Campanulate along with Companulaceae, Goodeniaceae, Brunoniaceae, Stylidiaceae and Calyceraceae. Bentham and Hooker (1862–83) included the family in the order Asterales along with Valerianae, Dipsaceae and Calycereae, while, Hutchinson (1926) incorporated the Adoxaceae also in the Asterales. According to Rendle (1938) the order Campanulales contains the families Campanulaceae, Goodeniaceae and Compositae. He placed the families Valerianaceae and Dipsacaceae in the Rubiales along with three other families.

In all the above-mentioned systems of classification, the family Compositae is treated as highly specialised. The families included in the order Asterales resemble one another in their exomorphic features to a greater extent than families included in the above-mentioned orders. The family Adoxaceae differs in its morphological features from the rest of the families of Asterales (Hutchinson, 1926). Adoxaceae is characterised by the head inflorescence with 4–6 merous flowers, 4–6 stamens, which split at the base to form double the number and contain single-celled anthers, semi-inferior ovary with 3–5 locules, pendulous ovules and the fruit which is a drupe. In the embryological features the family differs from the rest of the families included in Asterales by the Adoxa type of embryo-sac development and resembles Compositae in the Asterad type of embryo development.

In the embryological features the family Compositae shows close resemblances to the families Dipsacaceae and Valerianaceae. In the two families the anther tapetum is of the amoeboid type. In the presence of integumentary tapetum Compositae resembles Dipsacaceae. The endosperm is cellular in Dipsacaceae and Valerianaceae and also in some members of Compositae. Valeriana olitoria, Centranthus ruber and C. angustifolium show close resemblances to Senecio vulgaris in their embryo development. To some extent
the irregular embryo of *Scabiosa succisa* resembles the embryo of *Valeriana olitoria*. Thus embryological and taxonomical evidence is in support of retaining the family in Asterales (Hutchinson, 1926) along with Dipsacaceae, Valerianaceae and Calyceraceae as proposed by Vernin (1952).

Notwithstanding the inclusion of the families Valerianaceae, Dipsacaceae, Calyceraceae and Compositae in the order Asterales, the systems of classification of Bentham and Hooker (1862–83) and Hutchinson (1926) differ in the following respect. Bentham and Hooker (1862–83) place the order at the bottom of the Gamopetalae next to the Rubiales, while in Hutchinson’s system Asterales is considered to be the most advanced among Gamopetalae.

In the embryological features also the family Compositae shows specialisation in the reduction of male archesporium to a single row of cells, presence of amoeboid anther tapetum, spinescent exine of the pollen grains, reduction of nucellus to a single layer of epidermal cells, absence of parietal cell, presence of integumentary vascular traces in some members, formation of antipodal haustoria in some members and a great variation of antipodal cells and nuclei in each of them and in the absence of endosperm in the seed. Thus, embryological features favour Hutchinson’s treatment of the Asterales as the most advanced of the gamopetalae.

The families Companulaceae, Goodeniaceae and Stylidiaceae which include the Campanulatae of Engler (1926) and Campanulales of Rendle (1936) differ from the Compositae in their morphological features.

In the embryological features also the above families differ from Compositae in the presence of more than one row of archesporial cells in the same anther lobe, glandular anther tapetum, smooth exine of the pollen grains, constant occurrence of three antipodals which degenerate before fertilisation, in the cellular type of endosperm development with both chalazal and micropylar haustoria, presence of starch as reserve food in the endosperm (in most members of Lobeliaceae and Goodeniaceae), Solanad type of embryo development.

Thus, both morphological and embryological features are not in favour of inclusion of the family Compositae either in the Campanulatae of Engler (1926) or in the Campanulales of Rendle (1938).

The family Compositae is divided into a number of separate families by systematists like Bessey (1915) and Gundersen (1950). According to Bessey (1915) the Asterales comprises Heliantheae, Ambrosiaceae, Heleniaceae, Arctotidaceae, Calandulaceae, Inulaceae, Asteraceae Vernoniaceae, Eupa-
toriaceae, Anthemidaceae, Senecionidaceae, Carduaceae, Mutisiaceae and Lactucaceae. He raised each tribe to a family rank, while Gundersen (1950) raised the tribe Cichorieae to a separate family status based on the characters like the presence of latex, flowers always ligulate and mostly yellow. He incorporated this family Cichoriaceae in the Asterales along with Calyceraceae and Compositae. In this connection it may be well to quote Johansen (1950) who says “Some embryologists have segregated tribes within the family; others have split into a number of separate families. If the latter procedure were accepted it is believed that the embryology of the entire group could be established on a more satisfactory basis”. Since the above opinion was expressed by Johansen (1950), the embryological knowledge gained in the various tribes of the family Compositae (Heliantheae, Helenieae, Astereae, Anthemidae, Senecioneae, Calanduleae, Cynereae, Mutisieae and Cichorieae) lends no support for the views of Bessey and Gundersen (1915 and 1950) to split the Compositae into small separate families by raising one or more tribes to the status and rank of separate families.

**Summary**

The present paper deals with the embryology of the following members of Heliantheae: *Halianthus annuus, H. debilis, Bidens pilosa, Coreopsis tinctoria, Xanthium strumarium, Eclipta erecta, Cosmos sulphureus* and *Zinnia pauciflora*.

The sequence of development of floral whorls is corolla, androecium, calyx and gynoecium.

The anther shows an epidermis, two wall layers, amoeboid anther tapetum of parietal origin and sporogenous tissue. The pollen mother cells are arranged in a single row in *Bidens pilosa*. In the other species the sporogenous tissue is extensive. The pollen mother cells divide in a simultaneous manner and cytokinesis is by furrowing. The pollen grains are shed in the three-celled stage. The exine is echinate and shows three germ pores.

The ovary is bicarpellary syncarpous and unilocular with a single unitegmic, tenuinucellate and anatropous ovule. An integumentary vascular trace occurs in the ovules of *Cosmos sulphureus, Zinnia pauciflora, Halianthus annuus* and *H. debilis*. Branched vascular traces are present in *Xanthium strumarium*.

The female archesporium is one-celled in all the species investigated except in *Bidens pilosa* where in a few cases it is multicellular. A linear tetrad of megaspores is formed and the chalazal megaspore develops into an eight-nucleate embryo-sac according to the Polygonum type. The number of
antipodal cells varies from two to three and the number of nuclei in each of them varies from one to six. In *Helianthus debilis*, frequently the nuclei fuse to form a single nucleus containing many nucleoli. In *Xanthium strumarium* three uninucleate antipodal cells occur. In *Bidens pilosa*, *Coreopsis tinctoria* and *Cosmos sulphureus* antipodal haustoria are formed.

In *Bidens pilosa* multiple embryo-sacs develop from the further functioning of more than one archesporial cells of an ovule.

Fertilisation is porogamous. Syngamy and triple fusion take place more or less simultaneously in *Cosmos sulphureus*. In other species triple fusion is completed much earlier than syngamy. Pollen tube persists until a few-celled embryo is formed in the embryo-sac. Endosperm is of the Nuclear type in all the species except in *Eclipta erecta* where it is of the Cellular type. The nuclear endosperm becomes cellular at an early stage and is completely consumed in the mature seed.

Embryo development conforms to the Asterad type and keys out to the Senecio variation.

One case of an embryo-sac with young embryo and undivided "primary endosperm nucleus" (secondary nucleus?) and one case of an embryo-sac with three sperms are met with.

Embryological features are not of service either in distinguishing the tribes from one another or in tracing the evolutionary tendencies within the family.

On embryological grounds retention of the family Compositae as one of the families of Asterales (Hutchinson, 1926) seems to be justifiable. Embryological evidence does not support the elevation of various tribes to the rank of independent families as done by Bessey (1915) and Gundersen (1950).

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**REFERENCES**


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EXPLANATION OF FIGURES


A. L.s. anther lobe showing primary archesporium, ×465. B. T.s. anther lobe showing primary sporogenous cells and primary parietal layer below the epidermis, ×465. C. L.s. part of anther lobe showing two wall layers, tapetum and sporogenous tissue, ×500. D. T.s. anther lobe showing pollen mother cells, ×465. E. L.s. part of anther lobe showing degenerating wall layers, tapetum and pollen mother cells in meiotic prophase, ×465. F. T.s. anther lobe with epidermis, wall layers, tapetum and pollen mother cells, ×465. G. T.s. anther lobe showing pollen mother cell surrounded by tapetum and two wall layers, ×625. H. L.s. part of anther lobe showing tapetal periplasm and one nucleate pollen grains, ×465. I. Pollen tetrad showing cytokinesis by furrowing, ×1,455. J and K. Three-nucleate pollen grains, ×1,455. L. Pollen tetrad with one of the microspores degenerating, ×1,455. M. T.s. anther lobe showing fibrous endotheleum, ×465.


A. L.s. upper part of embryo-sac showing triple fusion. The second sperm is not yet discharged, ×465. B. L.s. embryo-sac showing integumentary tapetum, syngamy and free endosperm nuclei, ×465. C. L.s. upper part of embryo-sac showing syngamy and two endosperm nuclei. Pollen tube persisting ×465. D. L.s. upper part of embryo-sac showing nuclear endosperm and zygote nucleus in telophase. Pollen tube persisting, ×465. E. Embryo-sac showing well-developed embryo and cellular endosperm, ×62. F. L.s. upper part of embryo-sac showing a well-developed embryo and a large “primary endosperm nucleus” (Secondary nucleus ?), ×465. G. L.s. upper part of embryo-sac showing the egg and two polar nuclei. Three sperm nuclei close to the polar nuclei, ×465.
