EMBRYOLOGICAL STUDIES IN THE COMPOSITÆ

I. *Launaea pinnatifida* Cass.

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INTRODUCTION

COMPOSITAE, the largest family of the flowering plants, comprising about 900 genera with over 1,300 species (Willis, 1948) enjoys a worldwide distribution. The majority are herbaceous and prefer open spaces while a smaller number are forest forms. A few are cultivated ornamental plants.

The family is of great interest to embryologists. As many as five different types of embryo-sac development, namely—Normal (Polygonum), Scilla (Allium), Peperomia, Drusa, and Fritillaria—occur within the family (Schnarf, 1931), besides some unclassified types in genera like *Balsamita vulgaris* (Fagerlind, 1939) and *Chrysanthemum cinerariaefolium* (Martinoli, 1939). The structure of the embryo-sac also presents some variations in the number of the antipodals, in the number of nuclei in them, and in the formation of antipodal and synergid haustoria in various members of the family. Polyembryony, apogamy and parthenocarpy are also known in some species. Apart from these interesting variations there is a great uniformity in the embryological features within the family.

In spite of extensive work in the family, some tribes have not received much attention and some aspects of embryology are rather poorly known. For instance, until recently a complete account of the detailed development of the embryo is only available in a few species like *Senecio vulgaris* (Souëges, 1920) and *Lactuca sativa* (Jones, 1927). Writing on this aspect Johansen (1950) says, "Despite a wealth of investigations on species belonging to the Asteraceae, the embryonomy of the family is in none too satisfactory a condition. The family, for one thing, is too large and unwieldy. Some taxonomists have segregated tribes within the family; others have split it 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. There is only one completely detailed investigation (that on *Senecio vulgaris*)."
based on modern embryological conceptions; certain of the older accounts, notably those of CARANO, indicate that there are significant minor departures which would warrant the segregation of several variations, from the accepted Senecio variation if the splitting into several families were followed. The whole problem requires more critical consideration than can be given to it in the present connection; moreover, certain of the groups (tribes or separate families) include no carefully investigated species". Since the publication of Johansen’s book, an account of the embryo development in twenty-eight species distributed in twenty genera and representing seven tribes (Astereae, Heliantheae, Anthemideae, Senecioneae, Calenduleae, Cynarieae, Chorieae) is given by Vermin (1952).

Even so, the development of embryo in the tribes Helenieae and Heliantheae remains unknown. There remain several genera belonging to these and other tribes of Compositae growing in India in respect of which little or no embryological information is available. In the present studies it is hoped to work out the embryology of as many of them as possible.

The present paper deals with Launaea pinnatifida Cass., belonging to the tribe Cichorieae. Embryologically this tribe is better known than the rest in the family. Such interesting phenomena as apogamy (Hieracium and Taraxacum), polyspermy (e.g., Taraxacum and Crepis) and poly-embryony (Crepis) are known in this tribe (Maheshwari, 1950). Launaea pinnatifida grows wild on the sandy beach of Visakhapatnam and Waltair, and bears delightful yellow capitulae on which all flowers are ligulate.

**Material and Methods**

The material of Launaea pinnatifida was collected from plants growing at Visakhapatnam and fixed in Nawaschin’s fluid and F.A.A. and sectioned following customary methods. Delafield’s Hæmatoxylin was used for staining the sections. Some preparations on the basis of which the senior author (J. Venkateswarlu, 1939) published a note on the embryo-sac development in this plant have also been used.

**Observations**

**Microsporogenesis and Male Gametophyte**

In the very early stages of development each anther consists of a homogeneous mass of meristematic cells. The primary archesporium consists of a single hypodermal row of prominent cells which differentiates in each of the four lobes when the anther begins to show a four-lobed contour.
Soon the archesporial cells undergo a periclinal division (Fig. 1) giving rise to a primary parietal layer of cells to the outside and a layer of sporogenous cells to the inside. Once again the primary parietal layer divides periclinally to form two layers (Figs. 2 and 3). The inner of these layers directly becomes the anther tapetum while the outer divides periclinally and gives rise to two wall layers below the epidermis. Even in mature anthers no fibrous endothecium is differentiated in this plant. This has been verified by teasing the wall of the mature anther and examining the wall layers after clearing with chloral hydrate. Similar absence of endothecium was reported previously in *Oryza* (Juliano and Aldama, 1937), *Ditepalanthus* (Fagerlind, 1938) and *Balanophora* (Fagerlind, 1945).

**Figs. 1-9.** Structure and development of the anther and pollen: Fig. 1. L.S. anther lobe showing a row of archesporial cells, × 707; Figs. 2 & 3. L.S. & t.S. anther lobes respectively showing single layer of P.M.C., and two wall layers beneath the epidermis, Fig. 2. × 527; Fig. 3. × 707; Fig. 4. L.S. anther lobe showing a single row of P.M.C., in II meiotic division. The radial walls of some tapetal cells have dissolved and there is only a single wall layer of cells under the epidermis, × 527; Fig. 5. T.S. of anther lobe showing a little later stage, × 527; Fig. 6. L.S. of anther lobe showing periplasmodium around the pollen grains. The nuclei of the periplasmodium are not in quite healthy condition, × 527. Fig. 7. Cytokinesis by furrowing in tetraneucleate pollen mother cell, × 707; Fig. 8. Section of pollen grain showing first division of the nucleus, × 707; Fig. 9. Section of a three-nucleate pollen grain showing three germ pores in the exine, a large vegetative nucleus and two sperms, × 707,
The tapetum is a single layer of prominent cells which are binucleate (Figs. 4 and 5). The cells are at first uninucleate. Their nuclei undergo a mitotic division at about the time when pollen mother cell nuclei are in their prophase and the tapetal cells become binucleate. At about the time when uninucleate pollen grains are formed the inner and radial walls of the tapetal cells dissolve and the cytoplasm flows out into the anther lobe forming a periplasmodium (Fig. 6). The nuclei of the periplasmodium do not remain healthy for a long time but degenerate soon. Tapetal periplasmodium is found in Blumea laciniata (Banerji, 1942), Eclipta erecta (Bhargava, 1935) and many other Compositae (Schnarf, 1931). The periplasmodium diminishes as the microspores develop further and disappears finally in the mature anther.

The cells of the inner layer arising from the first periclinal division of the archesporial cells divide transversely and only a single row of pollen mother cells is formed. The nuclei of these show one or two nucleoli. The division of the pollen mother cell is of the simultaneous type and meiosis does not show any unusual features. Cytokinesis is by furrowing (Fig. 7). Both bilateral and tetrahedral types of pollen tetrads are met with. The young 1-nucleate pollen grains are filled with cytoplasm, but soon a large central vacuole is developed and the centrally placed nucleus moves to a peripheral position. It divides there to produce a large vegetative nucleus and a small generative nucleus. The spindle has two similar poles (Fig. 8). This division is followed by the formation of a curved wall which demarcates a small lenticular generative cell, but the wall disappears soon and the generative nucleus migrates inwards and divides to give rise to two spindle-shaped male cells. The pollen grains are shed at this stage (Fig. 9). The mature pollen grains are spherical. The exine is echinate and has three germ pores (Fig. 9).

Megasporeogenesis and Female Gametophyte

The ovule is anatropous, unitegmic and tenuinucellate. In young ovules with primary archesporial cell the integument is three to six celled thick in the basal region but in advanced stages of the ovule it is more massive. It does not contain any vascular trace such as known in some Compositae (Schnarf, 1931; J. Venkateswarlu, 1941).

The primary archesporium consists of a single conspicuous hypodermal cell (Fig. 10). This elongates and directly becomes the megaspore mother cell without cutting off a parietal cell (Fig. 11). A linear tetrad of megaspores is formed consequent upon the two meiotic divisions in it. The chalazal megaspore of the tetrad develops further and the three upper megaspores
of the tetrad degenerate (Fig. 12). The development of the embryo-sac is according to the Polygonum type. By the time the two-nucleate embryo-sac is formed the degenerating megaspores vanish completely (Fig. 13). The 8-nucleate embryo-sac grows rapidly and presses upon the nucellar epidermis which is completely destroyed excepting at the basal region where the crushed nucellar cells can still be seen at the mature embryo-sac stage (Figs. 14 and 15). The cells of the innermost layer of the integument become differentiated as a glandular layer of cells with rich cytoplasm and large nuclei forming the integumentary tapetum such as found in other
investigated Compositae and Sympetalae in general. The cells of the integumentary tapetum are 1-nucleate. The embryo-sac is spindle-shaped and tapers towards either end. The cells of the egg apparatus are rather elongated. The egg cell shows the characteristic prominent micropylar vacuole and basally placed nucleus. The synergids are without hooks and show nuclei above the basal vacuoles. The antipodals are three in number and are uninucleate (Figs. 14 and 15). They persist for a long time (Fig. 16).

**Fertilisation, Endosperm and Embryo**

Fertilisation is porogamous. Only one pollen tube enters the ovule and it persists for a long time. Fig. 15 shows a case of an ovule with a persistent pollen tube and in this ovule a many-celled embryo is already developed. The pollen tube shows a small apical pore which is formed to facilitate the discharge of its contents into the embryo-sac. Endosperm is of the cellular type (Figs. 16 and 17). The primary endosperm nucleus divides earlier than the fertilised egg. In very old ovules the endosperm is completely consumed by the growing embryo.

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**Figs. 18-27.** Various stages in the development of the embryo: ca & cb=apical and basal cells of the two-celled proembryo; q=Quadrants derived from ca; m=Upper daughter cell arising out of the first division of cb; n=Upper daughter cell derived from ca; n'=Lower daughter cell derived from ca; o & p=Upper and lower daughter cells derived from n' of which p forms a row of suspensor cells; Fig. 18, 20-25, × 527; Fig. 19. × 291; Fig. 26. × 172; Fig. 27. L.S. of cypsela, × 24; pc=pericarp; sc=Crushed remains of the seedcoat. e=embryo.
The first division in the fertilised egg is transverse (Fig. 18). Consequently a proembryo of two superposed cells, the terminal ca and the basal cb, is formed. The former divides by a vertical wall and the latter by a transverse wall to form a T-shaped tetrad. The derivatives of cb may be designated as m and ci. The former divides by a vertical wall and the latter by a transverse wall (Fig. 19). Thus ci later gives rise to a superior daughter cell, n, and an inferior one, n' (Fig. 19). The latter further divides transversely forming two superposed cells o and p (Figs. 20 and 21).

The terminal cell ca first undergoes two vertical divisions in which the walls are formed at right angles to each other producing quadrants in the tier q (Fig. 20). The four cells of the tier q divide by obliquely oriented walls (Figs. 20 and 21) and form octants. The cell m undergoes two vertical divisions at right angles to each other (Fig. 21). The cell n also divides similarly. In the tiers q and m periclinal divisions take place demarcating the dermatogen (Fig. 22). Later on further divisions take place in these tiers and periblem and plerome become differentiated (Figs. 24 to 26). The derivatives of q give rise to the cotyledons and stem tip and those of m to hypocotyledonary region and plerome initials of the root. The cells n and o undergo two vertical divisions at right angles to each other (Figs. 23 to 25). Their derivatives contribute to the formation of the root tip, root cap and dermatogen of the root. The cell p undergoes a few transverse divisions and forms a uniseriate suspensor of six cells. The lowest cell of the suspensor is larger and slightly vesicular (Fig. 26).

In Launaea pinnatifida 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 proper. Thus the embryo development conforms to the Asterad type. The cell m (superior daughter cell of cb) 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 (Johansen, 1950).

Fruit and Seed

In a fully developed seed the endosperm is completely absorbed. Even the seed-coat is almost completely destroyed except for the outermost layer of cells or two which remain in a crushed state between the embryo and the pericarp (Fig. 27).

Summary

The development of the anther and pollen, megasporogenesis, female gametophyte, fertilisation, endosperm and development of the embryo of Launaea pinnatifida have been studied.
Embryological Studies in the Compositae—1

The primary archesporium in the anther consists of a single row of hypodermal cells. The structure of the anther shows epidermis, two wall layers, amœboid tapetum and a single row of spore mother cells. No fibrous endothecium is differentiated. The division of the pollen mother cell is simultaneous. Cytokinesis is by furrowing. The mature pollen grains are three-nucleate. The exine is echinate and has three germ pores.

The ovule is unitegmic, tenuinucellate and anatropous. An integumentary tapetum is differentiated. The primary archesporium is one celled. It directly becomes the megaspore mother cell without cutting off a parietal cell. A linear tetrad of megaspores is formed. The chalazal megaspore of the tetrad is functional. Embryo-sac development is according to the Polygonum type. Three persistent one-nucleate antipodals are formed.

Fertilisation is porogamous. The pollen tube is persistent.

Endosperm is cellular.

Embryo development takes place according to the Asterad type and keys out to the Senecio variation. Details of development are shown in the following schematic representation:

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Fertilized egg
  \_ ca--------q ................. ........ Cotyledons and stem tip
  \n  \_ cb
  \n  \_\_ m ...................... Entire hypocotyledonary
                 region and plerome
               initials of root

  \_ cl
  \n  \_\_ n ....................... Root tip, root cap and
dermatogen of root

  \_ p ................. Suspensor
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The seed is exalbuminous. Even the seed-coat is completely crushed by the embryo except one or two outer layers.

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