PREVIOUS WORK
One of the earliest embryological studies pertains to the work of Hofmeister (1849) who studied the development and structure of the female gametophyte in *Helianthus annuus*. Schnarf (1931) summarized the scattered and rather meagre embryological data then known for the family. In 1966 Davis brought together the more salient embryological features of the family in her book "Systematic Embryology of Angiosperms". Since then, the notable contribution is that of Pullaiah (1984) who published a monograph "Embryology of Compositae". In the present chapter an attempt has been made to review, in a concise way, the embryological and histochemical works with a stress on recently published papers.

Asteraceae are characterised by the occurrence of tetrasporangiate anthers (Davis, 1966), but bisporangiate anthers have also been recorded (Deshpande, 1960b; Davis, 1962; Sundara Rajan, 1974; Pullaiah, 1976, 1979b, 1982a,b, 1983). Kaul (1973) depicted the co-occurrence of bi- and trisporangiate anthers in *Youngia japonica*.

Male archesporial cells are commonly arranged in a single row (Schnarf, 1931; Davis, 1966; Pullaiah, 1984). A single instance of the occurrence of archesporial cells in three rows has been illustrated in *Minuria integerrima* (Davis, 1964a).
Occurrence of the dicotyledonous type of anther wall development is the rule in the family (Davis, 1966; Pullaiah, 1984). Davis (1961a) described the occurrence of calcium oxalate crystals in the developing endothecium of Podolepis jaceoides. In the year 1962, Dormer made a detailed study on the fibrous layer in the anthers of Compositae. Endothecial thickenings are reported to be absent in Emilia sonchifolia and Erigeron bonariensis (Sehgal, 1966; Sundara Rajan, 1968a). There are sporadic reports on the occurrence of glandular tapetum in the family (Snow, 1945; Kapil & Sethi, 1962a; Tiagi & Taimni, 1963; Anderson, 1970; Walter & Kuta, 1971; Kaul, 1972, 1973; Kaul et al., 1975; Prakasa Rao et al., 1979; Sood & Thakur, 1984). Behaviour of the anther tapetal cells varies in different members of the family (Schnarf, 1931; Davis, 1966). Polyploid tapetal nuclei of various shapes are observed in Podolepis jaceoides (Davis, 1961a) and Helichrysum bracteatum (Sarada & Pullaiah, 1986). Pollen sterility due to anomalous behaviour of certain tapetal cells is also on record (Davis, 1968). Bambacioni (1941) is of the opinion that anther tapetum contributes to the formation of exine. Gelin (1934) described the phenomenon of cytomixis in Coreopsis tripteris.

Anthesis generally occurs at 3-celled stage (Davis, 1966). In 1973, Pandey & Singh studied the shape of the
male gametophytes in Compositae. Degeneration of 1 to 3 microspores of a tetrad is also known in the Compositae (Bhargava, 1935; Maheswari Devi, 1963; Misra, 1965; Smith, 1969; Maheswari Devi & Pullaiah, 1976b). Based upon their ultrastructural investigations on surface patterns of exine, Skvarla & Turner (1966) and Skvarla et al. (1978) recorded Helianthoid, Senecioid, Arctotoid and Anthemoid types of patterns in the asteraceous taxa.

Normally one ovule per ovary is the feature of Asteraceae, but Maheswari Devi & Pullaiah (1977a) recorded as many as six ovules in *Carthamus tinctorius*. Tip of the integument is swollen and protrudes towards funicular side in *Carthamus tinctorius*, (Maheswari Devi & Pullaiah, 1976c) and *Vicoa auriculata* (Pullaiah, 1979b). Differentiation of funicular and integumentary obturator has so far been described in six asteraceous taxa (Dahlgren, 1920, 1924; Kapil & Sethi, 1962a; Maheswari Devi & Pullaiah, 1977a; Pullaiah, 1976; Pandey & Chopra, 1979). In most of the cases endothelium is differentiated at the time of megaspore tetrad formation and remains uniseriate with uninucleate cells throughout the length of the embryo sac (Pullaiah, 1984). Structures simulating embryos originate from the endothelium in *Melampodium divaricatum* (Maheswari Devi & Pullaiah, 1976b).
Ultrastructural studies of Newcomb (1973) reveal the occurrence of small numbers of free ribosomes, mitochondria, rough endoplasmic reticulum and vacuoles in the megaspore mother cell. The chalazal megaspore functions and embryo sac is of the Polygonum type (Davis, 1966). Allium type of embryo sac has been reported by Hjelmqvist (1951). Harling (1951) reported all the three types viz., mono-, bi- and tetrasporic embryo sacs in Erigeron. In Minuria denticulata (Davis, 1963) embryo sac is of Drusa type. Abnormal embryo sacs occur in Calotis cuneifolia and C. lappulacea (Davis, 1961c, 1968) and Helichrysum rupestre var. messerii (Veillari, 1987a). Antipodals show interesting variations (Davis, 1961b; Sundara Rajan, 1974). An interesting instance pertaining to the occurrence of two eggs, two synergids and five sperms has been recorded in the embryo sac of Tithonia rotundifolia (Pullaiah, 1978b).

Maheswari Devi & Padma (1985a) described the co-existence of synergid, antipodal and embryo sac haustoria in one and the same ovule of Echinops echinatus.

The polars do not fuse in Brachycome ciliaris and Minuria integerrima (Davis, 1964a,b). Fertilization of more than one cell of the egg apparatus has been observed in Carthamus tinctorius (Maheswari Devi & Pullaiah, 1976c).
The family exhibits both cellular and nuclear types of endosperm development. Considerable variation with regard to the orientation of the first wall in the primary endosperm nucleus in the cellular development has been described in Composites (Davis, 1966). Occurrence of functional endospermous haustoria is seen in *Taraxacum officinale* (Sood & Sud, 1992) and *Galinsoga parviflora* (Sood and Tandon, 1992).

The embryogeny corresponds to the Asterad type of Johanson (1950). The suspensor is filamentous, consisting of 3 to 8 cells. The mature embryo is straight, dicotyledonous and completely fills the seed (Davis, 1966; Pullaiah, 1984).

Davis (1967, 1972) reviewed apomixis in Compositae. Apomixis in non-reduced embryo sacs (recurrent) has been observed in a number of Compositae while apomixis in reduced embryo sacs (non-recurrent) has been reported in only one member, *Brachycome iberidifolia* (Sharma & Murthy, 1977).

False polyembryony occurs in *Minuria integerrima* (Davis, 1964a,b). The additional embryo in the seed has been reported to develop from synergids in *Calotis lappulacea* (Davis, 1968), *Carthamus tinctorius* (Maheswari

Earliest contributions on the structure and development of the seed-coat are those of Lavaille (1912) and Briquet (1916) who studied some of the taxa belonging to Cichorieae, Cynareae, Mutiseae and Anthemideae. Netolitzky as early as in 1926 showed the taxonomic importance of seed. Singh (1964) reviewed the Indian work on the asteraceous seeds. Corner (1976) brought together the then existing literature on the subject in his book, "Seeds of Dicotyledons". The seed-coat shows great variation in its organisation. Mostly, it is formed from epidermis and a layer or two of the hypodermal cells of the massive integument (Deshpande, 1970). The epidermal cells possess annular bands on their radial walls in *Flaveria repanda*, *Vernonia anthelmintica*, *Verbesina encelioides* (Misra, 1964, 1972a,b), fibrous thickenings in *Blumea malabarica* (Pullaiah, 1979b) and palisade-like macrosclereids in *Onopordum nervosum* (Perez-Garcia & Duran, 1987). Seed-coat is reported to be absent by Tiagi & Taimni (1960, 1963) and Pullaiah (1979b) whereas it is reduced to a non-cellular pellicle in *Vicoa indica* (Pandey et al., 1983). In Heliantheae, the seed-coat is 1-5 layered (Madeshwari Devi & Padma, 1985b), but Pandey (1977) and Pandey et al. (1986) recorded as many as eight
layers in *Tagetes patula* and fifty one in *Cosmos bipinnatus*. Formation of periendothelial zone in the seed-coat has been observed in some members of the family (Kapil & Sethi, 1962a,b; Sundara Rajan, 1974; Maheswari Devi & Padma, 1985b; Pullaiah, 1982a, 1983; Pandey et al., 1986). The inner tangential wall of the epidermal cells of the seed-coat bulges out to form peg-like projections in *Xanthium strumarium* (Chopra, 1968) *Tagetes patula*, *T. erecta*, and *Tithonia rotundifolia* (Pandey, 1977). Maheswari Devi & Ranjalkar (1979) observed druses in the integument of *Blainvillia acmella*.

The pattern of pericarp development and differentiation in the members of the family show features like, schizogenous splitting of the ovary wall into variable number of zones, exudation of tanniniferous substance in the schizogenous space, reapproximation of zones and formation of mechanical zones (Misra, 1972a,b; Pandey, 1976; Pullaiah, 1979b, 1981a; Rajashekar, 1980; Pandey & Singh, 1983a,b; Singh & Pandey, 1984; Maheswari Devi & Padma, 1985b). Hypodermis of the pericarp is multiplicative in *Eclipta alba* and *Synedrella nodiflora* and non-multiplicative in *Cosmos sulphureus* and *Tridax procumbens* (Maheswari Devi & Padma, 1985b). A net-work like configuration of the cell contents has been recorded in the outer layers of pericarp
(Rajashekar, 1981). Mechanical zone is present below ribs in Youngia japonica, Crepis biennis, C. blattarioides and as a continuous layer beneath the epidermis in other investigated taxa (Pandey, 1977; Pandey et al., 1986). Maheswari Devi & Ranjalkar (1979) reported formation of periderm with lenticel like structures in Wodelia urticaefolia. According to Kondo (1919), a range of variations in the fruit colour of Lactuca is due to the presence of a brownish pigment in the epidermal cells of coloured fruits and its absence in light-coloured ones.

The pioneering work on developmental histochemical changes in plants was that of Jensen (1962). Southworth (1971) showed abundant sugars in the tapetum of Gerbera. Based upon their histochemical studies, Panchaksharappa & Rudramuniyappa (1974, 1975) suggested transitory storage nature of the tapetum. Nanda & Gupta (1981) studied the distributional pattern of total carbohydrates of insoluble polysaccharides in wall layers, specially the tapetum periplasmodium in relation to developing pollen grains in microsporangia of Helianthus annuus. Starch grains are reported to occur in the connective of an anther at the sporogenous stage in Carthamus tinctorius (Bhandari & Sharma, 1983). Studies of Rudramuniyappa (1985, 1991) negate the occurrence of storage polysaccharides in the sporogenous tissue, meiocytes and in microspore tetrads.
Young microspores showed reduced contents of RNA and proteins which increased later at the maturity of microspores. Besides the high concentration of PAS +ve and AA granules, the tapetum also showed high concentration of RNA and proteins.

Blankovaskaya & Mironchak (1969) recorded clusters of starch grains in the cells of integument between outer and inner epidermis. According to Plisko (1971), in *Calendula officinalis* the central cell possesses both starch and lipids while the egg shows high concentration of starch grains and the synergids are rich in lipids. Endothelial cells exhibit PAS +ve response in *Bellis perennis* (Engell & Peterson, 1977). In 1980 Bhandari et al. dealt with the qualitative histochemical analysis of insoluble polysaccharides, starch, RNA and total proteins during the development of female gametophyte in *Argemone mexicana* and concluded that the antipodals are most metabolically active among the constituents of the embryo sac. Mature embryo is rich in protein bodies of different shapes and sizes in *Lactuca sativa* (Paulson & Srivastava, 1968).