D. Sarada* & T. Pullaiah*: Embryology of Anaphalis subdecurrens Gamble (Compositae)

The genus *Anaphalis* belonging to the tribe Inuleae of the family Compositae comprises of 13 species. Although considerable literature is available on the embryology of the tribe Inuleae (see Pullaiah 1984), information on the genus *Anaphalis* is inadequate. Of the 13 species of this genus only *Anaphalis busna* has been studied embryologically and that too concerned with the development of male and female gametophytes only (Pullaiah 1979). Information is completely lacking on fertilization, endosperm and embryo development of the *Anaphalis*. Hence the present study has been undertaken.

**Material and methods** The material was collected by T. Pullaiah from the forests of Doddabetta in Nilgiris and fixed in formalin-acetic-alcohol (F. A. A.). Usual methods of dehydration, infiltration and embedding were followed. Serial longitudinal and transverse sections were cut at a thickness of 2-6 μ and stained in Delafield's haematoxylin. Voucher specimens No. TP 1285 were deposited in the Herbarium of Sri Krishnadevaraya University, Anantapur and in the Herbarium of Botanical Survey of India, Southern Circle, Coimbatore (MH).

**Observations**

Microsporangium, microsporogenesis and male gametophyte. The anther is four-lobed (Fig. 1A). The primary archesporium in each lobe is confined to a single hypodermal row of four to six cells (Fig. 1B). Each archesporial cell cuts off a parietal cell towards the outside and the primary sporogenous cell towards the inside. The cells of the primary parietal layer divide anticlinally and periclinally to form two layers; one adjacent to the epidermis divides once again periclinaly. In this way the primary parietal layer forms 3 layers according to the Dicotyledons type (Fig. 1C-E). The layer in the hypodermal position develops into the fibrous endothecium (Fig. 1H). The cells of the

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Fig. 1. Anaphalis subdecurrens. A. Tetrasporangiate anther. B. Longitudinal section of anther lobe showing archesporial cells. C. Longitudinal section of anther lobe showing parietal and sporogenous layers. D. Transverse section of anther lobe showing 2 parietal layers and sporogenous cells. E. Transverse section of anther lobe showing wall layers and pollen mother cell. F. Longitudinal section of the part of anther lobe showing wall layers and pollen mother cells in meiosis. G. Longitudinal section of the part of anther lobe showing periplasmodium and one-nucleate pollen grains. H. Fibrous endothecium. I-L. Meiotic divisions in the pollen mother cells. M. Tetrahedral pollen tetrad. N. Decussate pollen tetrad. O. Isobilateral pollen tetrad. P. One-nucleate pollen grain. Q. Three-celled pollen grain. R. Sterile pollen grain.
middle layer get crushed at the time of meiotic divisions in the pollen mother cells. The inner most layer is the tapetum and it is of the periplasmodial type (Fig. 1G). The cells of the anther tapetum become multinucleate. The tapetal cells are still intact at one-celled pollen grain stage. When the pollen grains have already developed thick exine, the walls of the tapetal cells break down and the cytoplasm flows into the anther locule forming periplasmodium. It is absorbed by the developing pollen grains and no trace of it is left at maturity.

The primary sporogenous cells undergo only transverse divisions resulting in a single row of pollen mother cells (Fig. 1F). The pollen mother cells undergo two meiotic divisions and the cytokinesis is simultaneous. Tetrahedral pollen tetrads are more common, however decussate and isobilateral tetrads also occur (Fig. 1M-O). Quadripartition of the microspores occurs by furrowing. The pollen grains after their release from the tetrad enlarge and develop a thick exine and thin intine (Fig. 1P, Q). Pollen grains are 3-celled at the shedding stage with thick spinous exine and with three germ pores (Fig. 1Q). Rarely sterile pollen grains have been observed (Fig. 1R).

Ovary and ovule. The ovary is inferior, bicarpellary syncarpous and unilocular with a single basal ovule. The ovule is anatropous, unitegmic (Fig. 2A, B) and tenuinucellate. At about the time of megaspore tetrad formation an integumentary tapetal layer is differentiated (Fig. 2D). This layer remains uniseriate with uninucleate cells throughout further growth (Fig. 2F).

Megasporogenesis and female gametophyte. The archesporium is hypodermal and single celled. It functions directly as the megaspore mother cell (Fig. 2C). When the integument completely encloses the nucellus, the megaspore mother cell enlarges considerably and undergoes meiosis resulting in a linear tetrad of megaspores (Fig. 2D). Of the four, the micropylar three megaspores degenerate and the chalazal megaspore becomes functional. The nucleus of the chalazal megaspore undergoes three mitotic divisions and results in eight nuclei (Fig. 2E). These nuclei organize into 3-celled egg apparatus, three antipodal cells, while the remaining two polar nuclei fuse in the centre to form a secondary nucleus (Fig. 2F). The embryo sac development thus follows the monosporic Polygonum type. The synergids are pear-shaped. Antipodals are three in number which are arranged in ‘T’-shaped manner.

Fertilisation, endosperm and embryo. Entry of the pollen tube is porogamous. Syngamy and triple fusion occur more or less simultaneously. Endosperm devel-
Development is of the Nuclear type. The primary endosperm nucleus undergoes a few free nuclear divisions and the nuclei are more in number at the micropylar region when compared to the chalazal region (Fig. 3A, B). Wall formation commences from the micropylar region and proceeds towards the chalazal end (Fig. 3C). The endosperm is completely absorbed by the growing embryo but for one or two layers.

Fig. 2. *Anaphalis subdecurrens*. A. B. Ovule. C. Megaspore mother cell. D. Megaspore tetrad. E. 4-nucleate embryo sac. F. Mature embryo sac.
Fig. 3. *Anaphalis subdecurrens*. A–C. Stages in the development of endosperm.
The zygote divides transversely resulting in two cells, the basal cell cb and the terminal cell ca (Fig. 4A, B). The cell cb undergoes a transverse division resulting in two cells, m and ci (Fig. 4C). The cell ca undergoes two vertical divisions at right angles to one another resulting in the formation of quadrants q (Fig. 4C, D). Further divisions in the quadrants q occur obliquely resulting in octants (Fig. 4F-I). The derivatives of q contribute to the stem tip and cotyledons. The cell m divides twice vertically, the wall being oriented at right angles to one another (Fig. 4D, E). The derivatives of this tier contribute to the formation of hypocotyledonary region and a part of root (Fig. 4F-I). Meanwhile the cell ci divides transversely and two superposed cells n and n' are formed (Fig. 4D). Further divisions in cell n contribute to the upper part of root (Fig. 4F-I). The cell n' undergoes another transverse division and produces two cells o and p (Fig. 4E). The derivatives of the cells n and o contribute to the completion of the root and those of p to the suspensor (Fig. 4F-I). Thus the development of the embryo follows the Senecio variation of Asterad type according to Johansen (1950) and Grand period I, Megarchetype II, series A, subseries A in the first embryonic group according to Souèges system (Crété 1963).

Discussion Anthers in Anaphalis subdecurrens (present study) are tetrasporangiate. In the tribe Inuleae the anthers are tetrasporangiate, but bisporangiate anthers have been reported in Blumea membranacea (Pullaiah 1979). Anther wall development in all the members of Compositae so far studied is of the Dicotyledonous type (Pullaiah 1984). Anther tapetum in Anaphalis subdecurrens (present study) is of the Periplasmodial type. But glandular anther tapetum has been reported in Chrysothamnus (Snow 1945, Anderson 1970), Vernonra (Tiagi & Taimni 1963), Hypochoeris (Kaul 1972), Tragopogon (Singh & Kaul 1974) and Sonchus (Kaul et al. 1975). But these reports, as Pullaiah (1984) pointed out, are erroneous. Pollen grains in Anaphalis subdecurrens (present observation) are shed at 3-celled stage. All those reports that the pollen is shed at 2-celled stage in Compositae (Sundara Rajan 1968, Walter & Kuta 1971, Kaul et al. 1975) are found to be erroneous.

Ovule in the family Compositae is unitegmic, crassinucellate and anatropous and Anaphalis subdecurrens is in conformity with this.

In the tribe Inuleae both Nuclear and Cellular types of endosperm development have been reported (Pullaiah 1979, 1984) and in Anaphalis subdecurrens
endosperm is of the Nuclear type. The development of the embryo in *Anaphalis subdecurrens* is in conformity with all other Compositae in showing *Senecio* variation of Asterad type.

Fig. 4. *Anaphalis subdecurrens*. A–I. Stages in the development of embryo.
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Anaphalis (ヤマハハコ属) については発生学の研究が少なく、A. busna があるのみである。しかもこれは雌雄の配偶体に関するもので、受精や胚乳と胚の発生には触れていない。それ故ここに A. subdeccurens について詳しく研究した。


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