Floral Morphology and Embryology of ***Melianthus major*** LINNAEUS

By

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With 70 Figures

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Contents

1. Introduction

BENTHAM & HOOKER 1862 regarded *Melianthaceae* as a part of *Sapindaceae.* The genera comprising the *Melianthaceae* were treated as a distinct family by GÜRKE 1896, who regarded them as having affinities with *Sapindaceae.* HALLIER 1912 treated *Melianthaceae* as a taxon very distinct from but quite closely related to *Sapindaceae.* In recent years also *Melianthaceae* has been regarded as a family distinct from *Sapindaceae* (COPELAND 1957, LAWRENCE 1958, HUTCHINSON 1959 and PORTER 1959). Practically there is no previous work on the embryology and floral anatomy of *Melianthaceae.* MAURITZON 1936 has studied the megasporogenesis of the *Melianthus.*

2. Materials and methods

Melianthus major was collected from Ootacamund in the year 1959 and fixed in formalin-acetic-alcohol. Dehydration and embedding was followed according to the xylol ethyl alcohol paraffin method. Sections were cut at 6—15 μ. For embryological purpose staining was done with combinations of safranin and fast green; safranin and light green and Heidenhains iron-alum haematoxylin counterstained with safranin. While for the floral anatomical purpose the combination erythrosine and crystal violate gave better results.

3. Observations

3.1. External morphology

The marcoon coloured bracteate, bisexual and zygomorphic flowers are borne on densely clustered racemes. There are five laterally compressed unequal and imbricate sepals united at the base. The anterior sepal is sub-saccate. Petals are four and clawed. A crescent-shaped nectar secreting disc with teeth-like projections is present which lines the inner side of the anterior sepal. There are four stamens, two being attached only at the base to the two posterior sepals and the other two being attached at the base to the two posterior petals. The tetracarpellary ovary is tetralocular at the base having two alternate rows of ovules in each locule. The single, filiform style is deeply cleft into four at the apex.

3.2. Floral anatomy

Pedicel has a ring of vascular tissue (Fig. 1 and 2)*). The central vascular tissue in the receptacular region gives out the first set of eight traces to the sepals and petals (Figs. 3 and 4). For the sake of convenience these traces are designated as 'a', 'b', 'c' to 'h' as in Figs. 4, 5 and 6. The trace 'a' later on divides into two (Figs. 6 and 7) forming the laterals of the two posterior sepals. The trace 'b' enters one of the posterior sepals to form the midrib.

Trace 'c' gives off two branches which form the laterals of the two adjacent sepals i. e. one posterior and the other lateral. After giving off these two branches, the trace 'c' enters one of the posterior petals (Figs. 12, 13, 14 and 16).

Trace 'd' divides into two, the branch which is on the outer side, traverses radially towards the lateral sepal side just below the level of the sepal it divides into two, one of the branches enters the lateral sepal forming its

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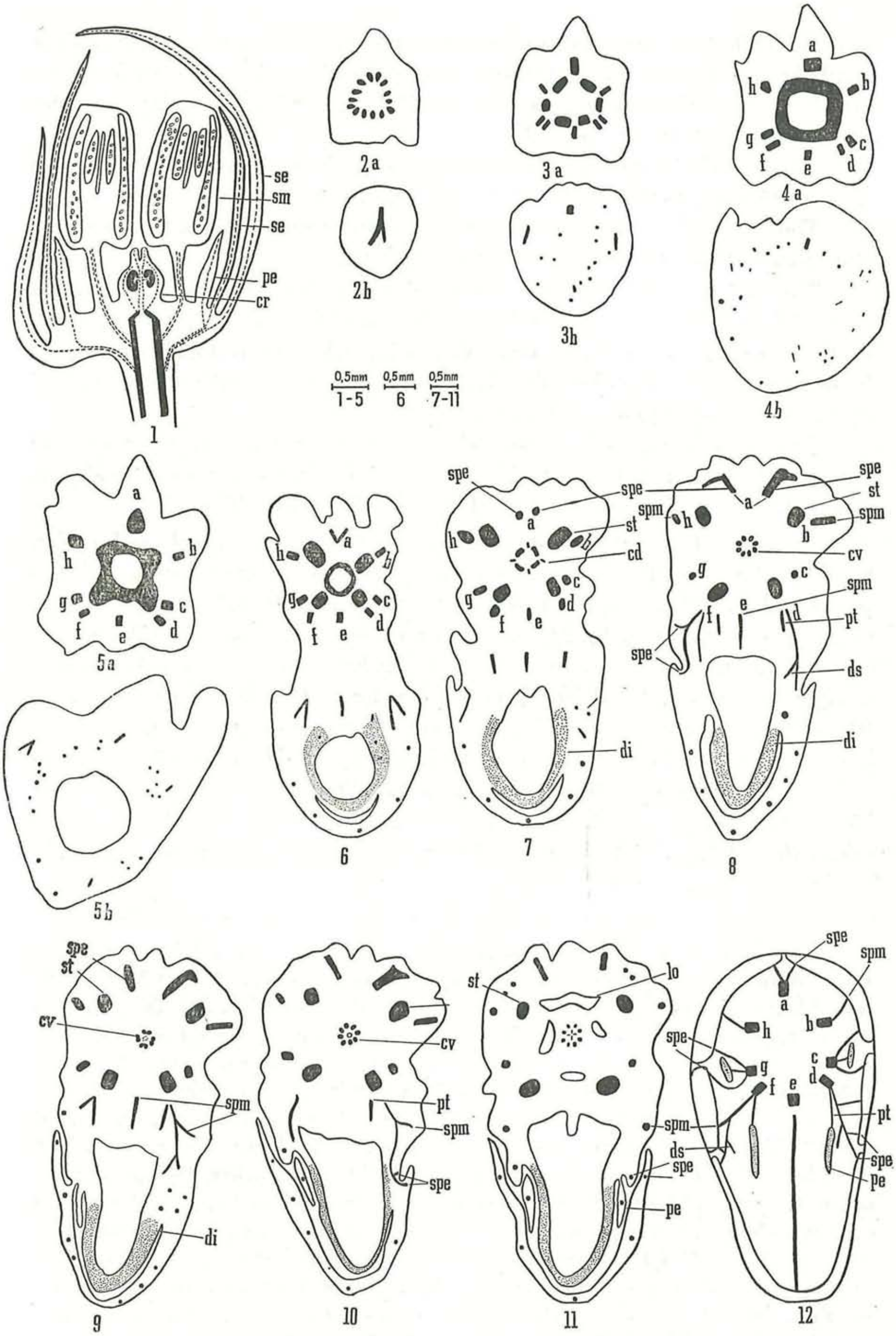
*) Abbreviations in figures 1—70: anp = antipodal, cd = carpel dorsal, cr = carpel, cv = carpel ventrals, di = disc, ds = disc supply, eg = egg, end = endosperm, ent = endothecium, ep = epidermis, ii = inner integument, lo = locule, nc = nucellar cap, nu = nucellus, oi = outer integument, pe = petal, pn = polar nuclei, pt = petal trace, pt' = pollen tube, se = sepal, sm = stamen, spe = sepal lateral, spm = sepal dorsal, st = staminal trace, sn = secondary nucleus, syd = synergids, tp = tapetum, vb = vascular bundle, zy = zygote.



Figs. 1—12 *Melianthus major*. — Fig. 1, L. S. of the flower. — Figs. 2—11, Serial transections of the flower from pedicel upto the middle of the ovary region. — Fig. 12, Diagrammatic sketch showing supply of calyx and corolla.

midrib, while the other one traverses downwards. On its way, it gives off a small branch to the disc. Later on it divides radially into two to form the two laterals of the two sepals i. e. one lateral sepal and another anterior sepal (Figs. 8, 9, 10, 11 and 12).

The branch of the trace 'd' traverses down for a short distance to enter the anterior petal (Figs. 8, 9, 10, 11 and 12).

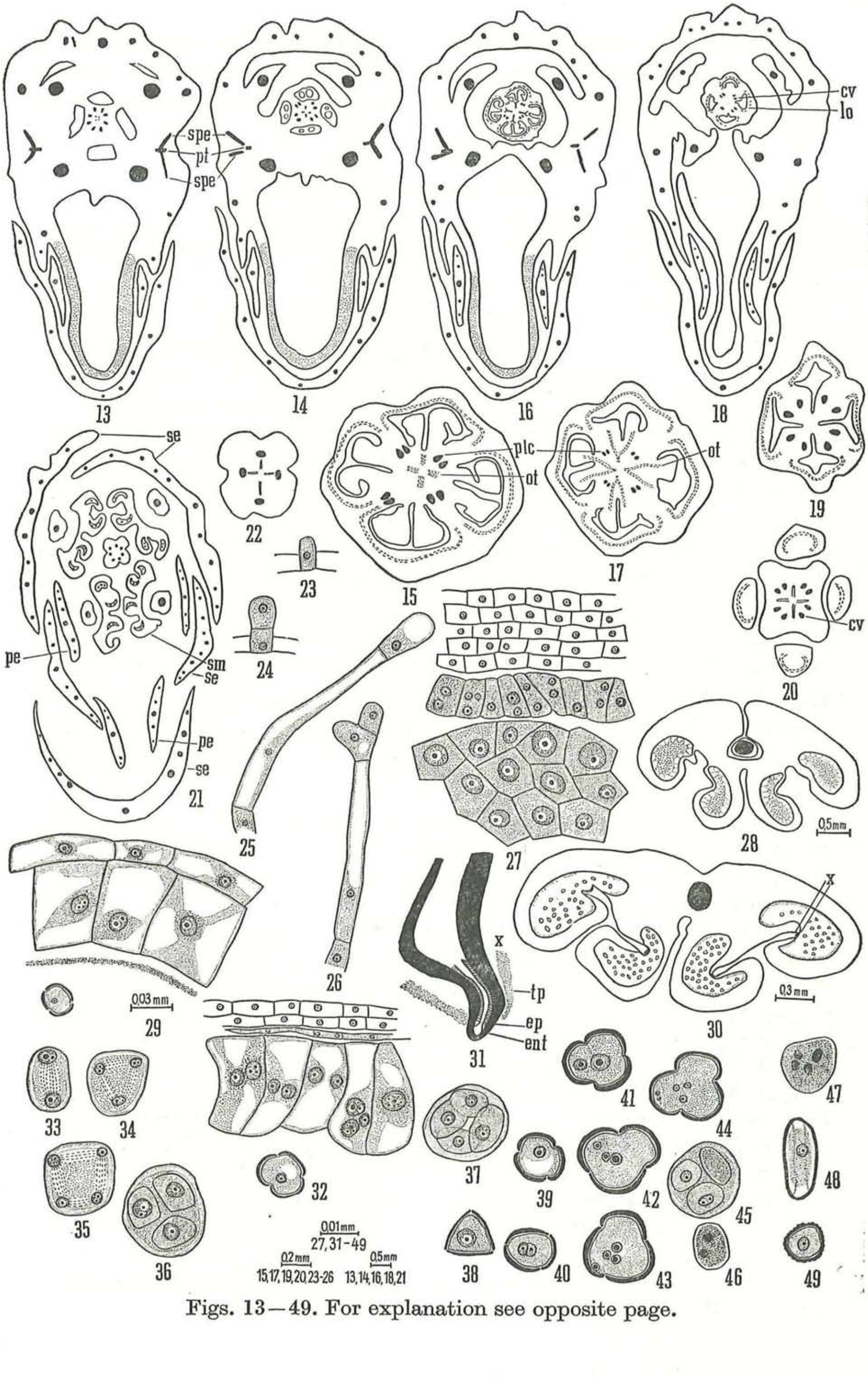
The trace 'e' forms the midrib of the anterior sepal, but before entering the sepal it gives off small branches to the disc.

The pattern taken by trace 'f' is similar to that of trace 'd' and those of traces 'g' and 'h' are similar to those of traces 'c' and 'b' respectively. Thus, each sepal may have later on eight to ten lateral veins and each petal may have three to five bundles. The diagrammatic representation of the sepal and petal supply is given in Fig. 12.

At a slightly higher level after giving out the combined sepal and petal traces, the central stele gives out four traces to the four stamens (Figs. 5, 6 and 7). Next it gives off four dorsal traces to the carpel (Fig. 7).

The central vascular tissue soon after resolves into eight bundles (Fig. 8). These bundles in order to become inversely oriented come close in pairs towards their xylem ends and then turn up thus resulting in eight inversely oriented bundles (Fig. 9). During this process each of the bundles leaves some of vascular tissue in the centre, which later on forms a sort of a ring in the centre (Figs. 9 and 10). This ring breaks up into four distinct strands which later on supply the ovules. At this level the lower portion of the locules is seen (Figs. 11 and 13), and the inversely oriented bundles move in pairs into the septal radii (Figs. 14 and 15). Each of the vascular strands left in the centre now bifurcates and supplies the ovules of one carpel (Figs. 16 and 17), the dorsals bundles in the higher regions were not clearly made out.

Figs. 13—49, *Melianthus major* (contd.). — Figs. 13—22, Serial transsections of the flower from the middle of the ovary region onwards. (In Figs. 15, 17, 19, 20 and 22, the sepals; petals and stamens are avoided). — Figs. 23—26, Development of glandular hairs. — Fig. 27, T. S. of anther lobe showing the wall layers and the sporogenous layer. — Fig. 28, T. S. of an anther showing an almost horse-shoe-shaped anther lobe. — Fig. 29, Vacuolated epidermis, endothecium and degenerating tapetum is shown at uninucleate pollen grain stage. — Fig. 30, T. S. of the mature anther which is about to dehisce. — Fig. 31, It is an enlargement of a portion marked as 'x' in Fig. 30, showing the cutinization of the endothecial layer at the region of the dehiscence. — Fig. 32, The cells of tapetum elongated, showing their multinucleate and multinucleolate condition. — Figs. 33—35, Meiotic divisions in the microspore mother cell. — Figs. 36—37, Tetrahedral and isobilateral tetrads. — Figs. 38—39, Uninucleate pollen grains. — Figs. 40—41, Bicelled pollen grains. — Fig. 42, Pollen grain with three nuclei. — Figs. 43—44, Polyspermy. — Figs. 45—47, Degenerating dyads and tetrads. — Fig. 48, Whole mount of pollen grain. — Fig. 49, Same cut in T. S.



Figs. 13–49. For explanation see opposite page.

The ventrals continue throughout the style into the stigma (Figs. 18, 19, 20 and 21), where they fuse into pairs and constitute its supply (Fig. 22). The anther lobes make their appearance only when the stylar region of the ovary starts (Fig. 21).

3.3. Embryology

Glandular hairs with simple as well as branched terminal cells are present on the inner side of the ovary wall (Figs. 23—25). The upper club-shaped, head cell of the glandular hair divide vertically giving rise to another cell which gives it an appearance of a branch (Fig. 26). The floral organs develop in the sequence sepals, petals, disc, stamens and gynoecium.

3.3.1. Microsporangium and male gametophyte

The young anther is four-lobed, the sporogenous layer lies five layers below the epidermis (Fit. 27). Each pollen sac is somewhat horse-shoe-shaped when seen in the transverse section, and the walls of the two sacs of each side do not become confluent at the maturity but each anther lobe dehisces independently (Fig. 28). The cells of the epidermis are narrow and thin walled with prominent nuclei. The sub-epidermal layer functions as the endothecium, while the innermost wall layer functions as the tapetum and the intervening three layers form the middle layers. The cells of the endothecium are vacuolated and later become more broad as well as more radially elongated than those of epidermis (Fig. 29). At this stage the pollen grains are uninucleate in the anther. The endothecium cells do not develop the usual fibrous thicknings which are formed in most of the plants at the

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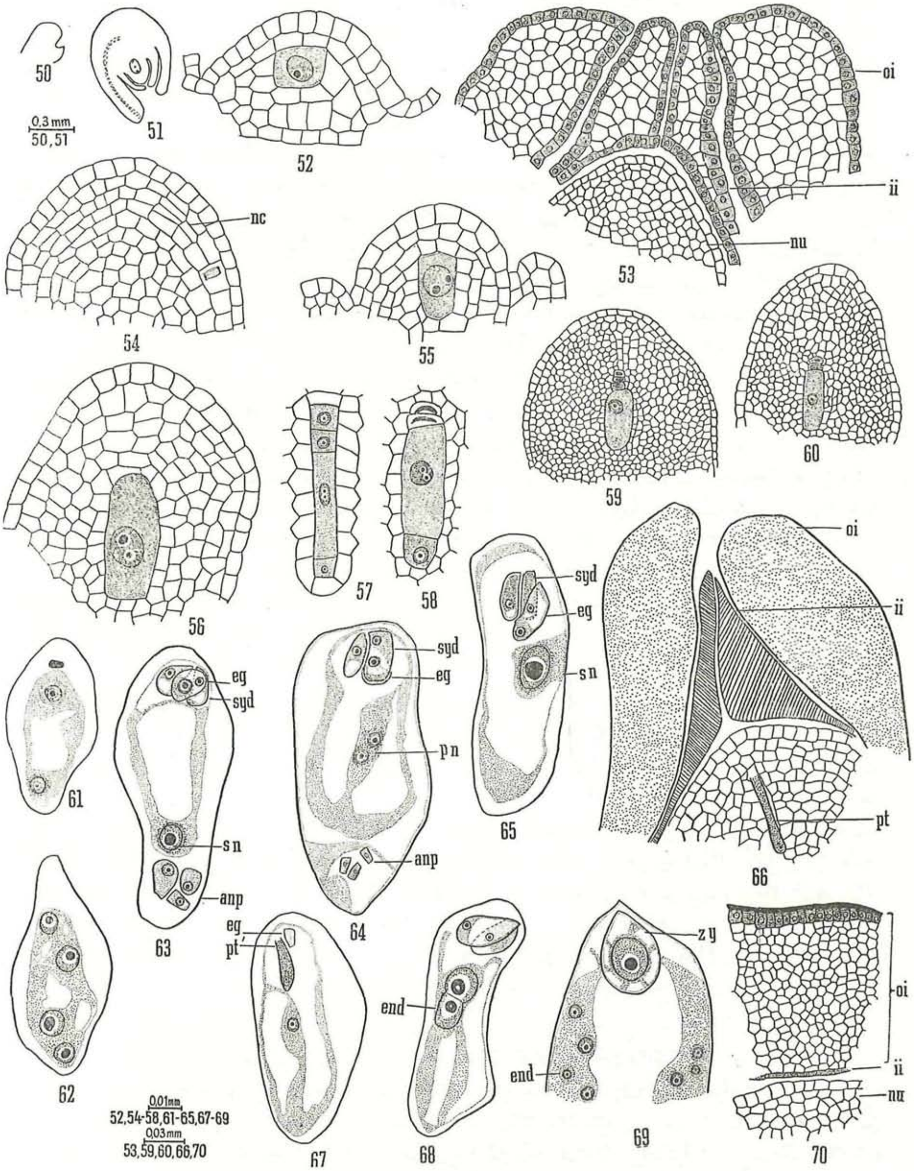
Figs. 50—70, *Melianthus major* (contd.). — Fig. 50, Ovular protuberance. — Fig. 51, Ovule at mature embryo sac stage. — Fig. 52, Parietal cell and sporogenous cell in the young nucellus. — Fig. 53, Part of integument enlarged showing inner integument two-layered at sides and 3-to 5-layered in the micropylar region. — Fig. 54, Nucellar cap formed by the hypodermal layer of the nucellar epidermis. — Fig. 55, Megaspore mother cell. — Fig. 56, Deep seated megaspore mother cell. — Fig. 57, Linear tetrad. — Fig. 58, Two megaspores from the micropylar end degenerating and the third one from micropylar end elongated. Fourth megaspore small in size. — Fig. 59, Chalazal megaspore functioning. — Fig. 60, Two megaspores at the micropylar end degenerated and the third one elongated. No trace of the fourth one. — Fig. 61, Binucleate embryo sac. — Fig. 62, 4-nucleate embryo sac. — Figs. 63—64, Mature embryo sacs. — Fig. 65, Embryo sac, showing no trace of antipodals. — Fig. 66, Portion of the seed at the micropylar region enlarged showing the presence of pollen tube in the nucellus. — Fig. 67, Embryo sac showing degenerating egg, pollen tube with one sperm and a secondary nucleus. — Fig. 68, Primary endosperm nucleus dividing. — Fig. 69, Post-fertilization stage. — Fig. 70, Portion of a seed coat showing cuticle, outer integument many layered, inner integument degenerating and a nucellus.



Figs. 50—70. For explanation see opposite page.

time of dehiscence. At the region of the dehiscence, the epidermal and endothecial cells become small and flattened. A thick cutinised structure is formed by the endothecial layer at the region of dehiscence, which breaks up at maturity to release the pollen grains of each lobe (Figs. 30 and 31). The tapetal cells are uninucleate to begin with, but at the microspore mother cell stage they become two- to three- nucleate (Fig. 27). Later on when the microspores are uninucleate the tapetal cells become highly vacuolated (Fig. 32). Each nucleus of the tapetal cell may contain five to seven nucleoli and sometimes even more than that. Though nucleoli number is no criterion for assuming that the fusion of the nuclei might have taken place in the tapetal cells. This can be concluded from the fact that the size of the nuclei is bigger even more than double in some cases than the other nuclei. After dehiscence the epidermal cells show the signs of the degeneration.

The microspore mother cells undergo the usual two meiotic divisions in a simultaneous manner. The divisions of the microspore mother cells are not synchronous in all the lobes of the same anther. The spindles may be at right angles to each other or parallel to each other, thus giving rise to tetrahedral and isobilateral tetrads, the former ones being more common. Later on the microspores acquire their own walls. Each nucleus in the tetrad may have two to three nucleoli (Figs. 33—37).

The pollen grains are tricolporate and the exine is thick and has ridges and furrows running alternately from pole to pole (Figs. 48 and 49). The intine is thin.

The young microspore has a dense cystoplasm and a centrally placed large nucleus (Fig. 38). Later on a large vacuole appears in the microspore which shifts the nucleus to one side (Figs. 39). This nucleus divides to form two nuclei, which were seen lying close to each other (Figs. 40 and 41), but walls of the generative and vegetative cells were not very clearly made out. Many pollen grains were observed to have three to five nuclei (Figs. 42—44). Sterility is very high in the plant. Right from the first division of the microspore mother cell to the two-celled pollen grains, degeneration is observed. At the tetrad stage, one of the microspore might degenerate and the rest may develop normally (Figs. 45—47).

2.2.3. Megasporogenesis and female gametophyte

The ovules are small, bitegmic, crassinucellate and anatropous. The protuberance destined to become the ovule arises on the placenta as an errect structure lying at the right angles to the placenta (Fig. 50). But it gradually curves down with the differentiation of the hypodermal archesporium and at the megaspore mother cell stage it is almost anatropous (Fig. 51).

The inner integument develops when the hypodermal archesporium is distinguished in the young nucellus (Fig. 52). The outer one also develops soon. The micropyle is formed by the inner integument. The inner integument is two-layered except at the micropylar and where it is three-layered to five-layered. The outer integument is many-layered (Fig. 53). Though MAURITZON 1936 has reported a three-layered inner integument he has not mentioned the exact position where the three layers are found, whether at the micropylar end or down below. A dinstinct nucellar cap with a tapering point is present (Fig. 54). When the pollen grains are formed in the microsporangium, the archesporium is distinguished in the young nucellus.

The hypodermal archesporium divides periclinally to form the parietal cell and sporogenous cell (Fig. 52). The former by the further periclinal divisions, forms the parietal layer thus the megaspore mother cell comes to lie two to three layers below epidermis (Fig. 55). The parietal layers go on increasing by periclinal divisions, later on, the megaspore mother cell is seen lying six to seven layers below the epidermis. At this stage megaspore mother cell is elongated (Fig. 56). Both the divisions of megaspore mother cell are transverse, thus giving rise to a linear tetrad (Fig. 57). According to MAURITZON 1936 two megaspore mother cells were observed lying side by side in some cases. But in the present material only a single megaspore mother cell has been observed. Usually out of the four megaspores of a tetrad the upper two on the micropylar side degenerate along with the one of the chalazal side while the third from the micropylar end functions (Fig. 60). But in some cases the chalazal one is also found functioning (Fig. 57). The functional megaspore lies eight to ten layers below the nucellar epidermis (Fig. 60). The functional megaspore elongates considerably in lenght, and soon divides. The two daugther nuclei move apart towards the two poles. The usual vacuole is present which seperates the chalazal nucleus from the micropylar nucleus (Fig. 61). These nuclei once again divide to form the four-nucleate embryo sac (Fig. 62), and then by the next division the eight-nucleate embryo sac is formed (Fig. 63). The development of the embryo sac conforms to *Polygonum*-type.

The mature embryo sac has a narrow chalazal and broad micropylar end (Fig. 64). The synergids are hooked and the egg hangs down slightly below the synergids. The three antipodal cells are ephemeral and begin to degenerate soon after the fusion of the two polar nuclei (Fig. 65).

3.3.3. Pollination and fertilization

The pollen grains mature earlier than the embryo sac. Therefore, cross pollination may be taking place. The fertilization is porogamous. The pollen tube enters the embryo sac by destroying one of the synergids. The pollen tube is usually ephemeral but it sometimes persists even in the seed where its tip was found to be slightly prominent due to the presence of some dark stained bodies (Fig. 66). These structures may correspond to the x-bodies reported in some plants (See MAHESHWARI 1950). In one case the egg has degenerated leaving its remnants only and the pollen tube is seen approaching the secondary nucleus (Fig. 76). In another case the two-nucleate endosperm with a fertilized egg and a degenerating synergid was observed in an embryo sac (Fig. 68).

3.3.4. Endosperm

The primary endosperm nucleus divides earlier than the zygote and produces two nuclei as mentioned above (Fig. 68). These move apart and soon divide repeatedly to form a large number of free nuclei arranged in the peripheral cytoplasm. Since the early divisions of the endosperm are not followed by cell walls, the endosperm is of the free Nuclear type. In the present material the endosperm is not very clear in the bigger seeds even.

3.3.5. Embryo

In the earlier stages of the formation of the seed a zygote could be made out (Fig. 69), but in the well developed seeds it could not be traced.

3.3.6. Seed

At earlier stages the nucellus remains intact and at this stage the inner integument loses its compactness on the sides except at micropylar canal. The cells of innermost layer of the inner integument at the micropylar region become slightly radially elongated. The outer integument is massive and the cells of the outer epidermis of the outer integument become differentiated from the rest by the deep stain as well as by the prominent nuclei (Fig. 70). Later on the cells become vacuolated. The cells of this layer in the micropylar region of seed become radially elongated and give the appearance of pallisade-like layer.

3.3.7. Pericarp

The ovary at the time of fertilization consists of ten to eleven layers of cells. Later on, the pericarp increases in girth by further divisions of cells.

The develpment of fruit and seed without the development of embryo may appear queer. However, it can be explained on the basis that the stimulus of the fertilization is sufficient to bring about the changes in the walls of the ovule and ovary though no embryo develops in the seed.

4. Discussion

The sepals are five and slightly united. There is an adnation between the supply of sepal and petal whorls and it has been observed that all sepal laterals except the two of the two posterior sepals (one of each sepal) arise fused with petal strands from which they get seperated only in the cortical region. The two lateral sepals arise from the same source from which the two petal strands for the anterior petals and the laterals for the two sepals arise i. e. one lateral sepal and one anterior sepal. Such a complicated type of vasculature in the flower indicates that it might lead to a condition where the sepal dorsal and sepal lateral might arise from one source, since the sepal dorsals and sepal laterals are coming closer and closer to each other.

The disc gets its supply from the combined sepal and petal traces and therefore it may be regarded as the reduced perianth lobe.

The ovary is tetracarpellary and each carpel receives a single dorsal bundle while there is no trace of secondary marginals. The placental strands are formed by the ventrals of the same carpels, and lie opposite the dorsals. The placental strands are inversely oriented. All these facts show that the placentation is axile.

The fibrous thickenings in the endothecium are absent and the pollen grains are released by the cutinisation of the endothecial cells at the region of the dehiscence. This absence of fibrous thickenings in the endothecium has already been on record (See MAHESHWARI 1950). Some remnants of the tapetum were observed in the anther lobes which had evidently released the pollen grains.

The division of the microspore mother cells is a simultaneous and cytokinesis takes place by the centripetal furrowing. Disturbances in the cytology resulting in a lack of proper differentiation of the generative and the vegetative nuclei and supernumerary divisions leading to the formation of pollen grains containing two to five nuclei were observed. Such cases have already been on record (See MAHESHWARI 1950).

The ovules are bitegmic, crassinucellate and anatropous. MAURITZON 1936 did not agree with the observations of GÜRKE 1896 that in *Melianthus major* the ovules are apotrop. According to MAURITZON 1936 the ovules are pleurotrop and epitrop.

The micropyle is formed by the inner integument and. MAURITZON 1936 also reported the same. The vascular strand supplying the ovule goes beyond the chalazal region and traverses it. The nucellar cap is formed by the repeated divisions of the hypodermal layer of the nucellar epidermis.

The three-layered inner integument has been reported in *Melianthus major* GÜRKE 1896 and MAURITZON 1936. In the present studies, the inner integument is observed to be two-layered on the sides but three-to five-layered at the tip. From the description given by MAURITZON 1936 it is not clear, at which portion it is three-layered.

MAURITZON 1936 has reported the occurence of two megaspore mother cells out of which only one develops further while the other lies by the side of the tetrad. The present author has not observed such a thing.

Occasionally, the chalazal megaspore functions, but mostly it is the third one from the micropylar end which is functional. MAURITZON 1936 has however reported that in *Melianthus major*, the chalazal megaspore is functional. According to him "sometimes a wall is not laid down between the nuclei of the upper dyad cell, where from tetrad of three cells is formed of which upper has two nuclei."

Usually the pollen tube is ephemeral but sometimes a pollen tube containing some dark stained bodies was seen persisting even in the seed.

The endosperm was observed getting disorganised at the stage when the zygote was still undivided. The inner integument is almost crushed on the sides except at the micropylar region where its remnants persist for sufficiently long time. Thus the outer integument comes in direct contact with the nucellus.

In conclusion I express my gratitude to Dr. B. N. Mulay for criticism, encouragement and facilities.

5. Summary

Flowers are bisexual and hypogynous. Sepals are five in number and the anterior sepal is sub-saccate. Petals are four. The disc is regarded to be a reduced perianth lobe. The ovary is tetracarpellary, tetraloculed with two alternate rows of ovules in each locule. The placentation is axile.

The development of the floral organs is in the sequence sepals, petals, disc, stamens and carpels.

The anther wall consists of five layers of cells. The fibrous thickenings in the endothecium layer are absent. The tapetum is secretory. The division of the microspore mother cells is simultaneous. Polyspermy has been recorded.

The ovules are bitegmic, crassinucellate and anatropous. Micropyle is formed by the inner integument. The nucellar cap is present. The ovular archesporium is single-celled. The third megaspore from the micropylar end is functional one. The development of the embryo sac conforms to the *Polygonum*-type. The fertilization is porogamous. Endosperm is of a free Nuclear type.

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