A CONTRIBUTION TO THE MORPHOLOGY AND CYTOLOGY OF *CARTHAMUS TINCTORIUS* LINN.

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Carthamus tinctorius, commonly known as 'Safflower', is a crop plant of great economic importance. It is widely cultivated in India both as an oil seed crop, and for the reddish dye in the flowers (*Carthamin*). The dye is found in the florets and these are collected at frequent intervals after the setting of the seeds. The oil extracted from the seeds is known as 'Kusum' oil, and is supposed to have good drying properties. It is grown in India chiefly as a '*Rabi*' crop.

The plant belongs to the tribe Cynareæ of the family Compositæ. An account of the flowering, pollination, natural cross-fertilisation and the isolation and description of 24 unit species has already been given by Howard, Howard and Khan (9). The chromosome number of the plant was first recorded by Gregory (7) who found the diploid number to be 20. Later, Patel and Narayana (15) who worked on Pusa types found the monoploid and diploid numbers to be twelve and twenty-four respectively. This has been confirmed by Gregory (6) for the Pusa types, and he is of opinion that the variation found in the chromosome number was due to his having worked previously with Coimbatore types—which might be distinct karyotypes. Gregory (7) has also worked out the process of somatic mitosis in this plant, and has demonstrated the chromonematic structure of the chromosomes. No other literature on *Carthamus tinctorius*, besides those mentioned above, has been noted by the present writer.

A considerable amount of morphological and cytological work has, however, been done on the family Compositæ. Schnarf (16) and lately Bhargava (1) have summarized the literature and it need not be repeated here. As no reference was found on *Carthamus tinctorius*, it was thought desirable to take up the investigation of which this paper gives an account.

MATERIAL AND METHODS.

The material was collected from plants grown in the University College experimental garden from seeds obtained locally. The cultures were quite uniform and aberrant forms were weeded out. Capitula of various sizes were fixed. Before fixation the involucral bracts were removed and the buds trimmed. In some cases it was necessary to cut the heads into three or four

parts and remove the upper portions of the flowers. Allen's modified Bouin's fluid, Licent's fluid and Nawaschin's fluids were chiefly used for fixation. The first and the last fixative gave good results, but Licent's fluid was found to be better suited for the study of embryology. The material was dehydrated and cleared in the usual way. Sections were cut 6 to 16μ thick depending on the stage required for study. Heidenhain's iron-alum Hæmatoxylin and Newton's Iodine Gentian Violet stain were chiefly used.

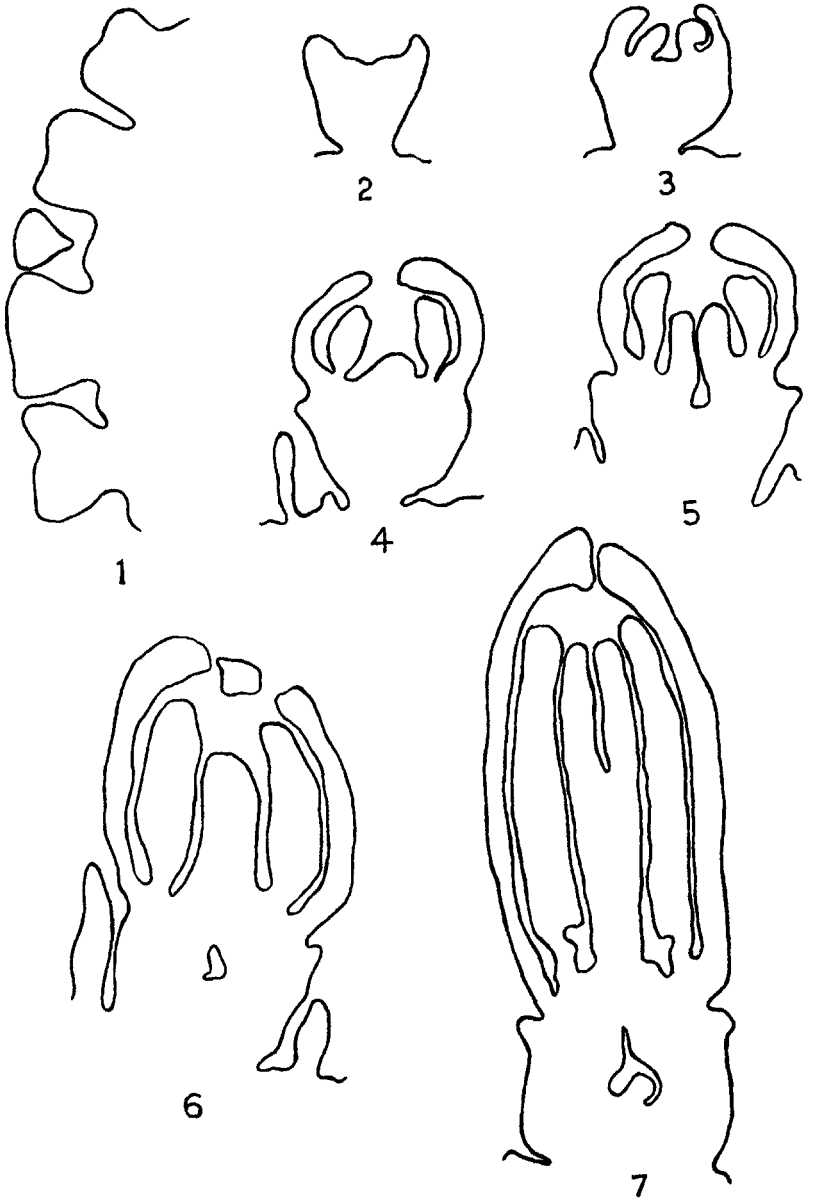
Observations.

(*a*) *The Development of the flower.*—Before the differentiation of the florets the floral axis is convex in outline and is covered by the overlapping bracts. The primordia of the individual florets soon arise in large numbers as minute protuberances of the thalamus and are at first convex in outline. From the edges of the convex papillate processes a number of primordia very soon grow actively and as a result the central region becomes concave in outline (Text-figs. 1 and 2). The outgrowths from the sides, which are five in number (as seen in transverse section), curve inwards particularly at their tips and form an effective covering in the early stages of the development of the flower. These are the petals. The primordia of the stamens are seen next, followed immediately by those of the sepals (Text-figs. 3 and 4). The staminal primordia, which are five in number, grow rapidly and soon the anther lobes become differentiated. The calyx primordia on the other hand remain as mere angular projections and do not develop any further (Text-figs. 4 and 5). The last floral whorl to appear is that of the two carpels which originate on the thalamus close to the inner side of the stamens (Text-fig. 5). They remain free in the early stages of their development but very soon cohere and form the style (Text-fig. 6). At the top, however, they remain free (Text-fig. 7). A flask-shaped cavity is seen at the base of the carpels, where the ovule originates as a minute protuberance (Text-fig. 7).

It has been suggested that in many Compositæ the style is spirally coiled at the base and by its elongation at maturity, it brushes against the anthers and thus secures self-pollination. Careful examination of the present material showed no such arrangement. As stated before, the tip of the style is divided and clothed by unicellular hairs. Pollination is brought about by the sigmatic thrust which is developed on account of an actual increase in the length of the style due to the cell-elongation or growth, as suggested by Merrell (12).

The florets appear to be all of the same type and those at the margin of the capitulum open first. Generally, it takes from four to six days for all the florets of a capitulum to open. The colour of the corolla becomes deeper with the fading of the flowers.

The sequence of development of the floral parts agrees closely with the account presented by Martin (11) for *Aster*, Merrell (12) for *Silphium* and Bhargava (1) for *Eclipta*. Merrell (12) found the calyx to be of the nature of



Text-figures 1–7. *Carthamus tinctorius.* Development of the flower: Figs. 1 and 2. The flower primordia and the appearance of petals; Fig. 3. The origin of stamens; Fig. 4. The first appearance of calyx as angular projections; Fig. 5. Development of the sepals and carpels; Figs. 6 and 7. The further development of the different floral whorls as also the origin of the ovule. ×100.

rudimentary pappus composed of two or three whorls of short hairs. Each hair being composed of about three cells. In *Carthamus* no differentiation of the calyx was noted.

As noted in other species of the Compositæ, the nectary was found to occur in the form of a ring at the base of the style (Text-fig. 7).

(*b*) *Microsporogenesis.*—In the early stages of its development the anther is composed of a mass of homogenous cells which are polygonal in outline and are in an active state of division. The origin of the archesporial cells in the anther could not be definitely traced. It appears that they develop in the hypodermal layer, cut off a parietal layer, and then differentiate as the sporogenous cells. In very young anthers the sporogenous cells have been observed to occur in the third layer; they could be easily made out on account of their larger size, denser cytoplasm, and chromaticity of the nucleus. At first the sporogenous cells are only one layer thick; very soon, however, they divide by oblique walls and become two layered.

Small (18) observed the occurrence of the archesporium to be distinctly hypodermal in *Senecio vulgaris*. Merrell (12) also noted the presence of a single hypodermal cell in *Silphium*, which by division gave rise to the primary parietal and primary sporogenous cells. Longitudinal division of the primary sporogenous cells finally gave rise to a mass of four or five cells in cross section. Bhargava (1) working on *Eclipta erecta* states, 'the archesporial cells are rather late in differentiation and cannot be distinguished from the other cells of the anther till a parietal cell has been formed on the outside'.

The microspore mother cells in the resting stage are mostly polygonal in outline and have dense cytoplasm and conspicuous nuclei. The nuclear membrane is well defined and the nuclear cavity is filled up with a granular substance which is disposed mostly at the periphery (Plate I, fig. 1). With the onset of prophase the nuclear cavity shows the presence of a number of coiled threads which on close examination show the presence of two chromonemata closely intertwined (Plate I, fig. 2). Gregory (8) working on *Elettaria* has observed a similar appearance of the prophasic nucleus. The reticulum gradually contracts away from the nuclear membrane (Plate I, fig. 3) and the contracted knot (synizetic knot) generally lies on one side of the nuclear cavity enclosing the nucleolus in its meshes. The synizetic knot is very tight and it is very difficult to follow the arrangement of the threads inside it. Figure 4 (Plate I) represents a stage of synizesis. In no case was a distinct connection of the nucleolus with the spireme noted, nor was there any evidence to suggest a transference of chromatic matter from the nucleolus to the spireme.

There are different views regarding the appearance of the synizetic knot which are too well known to be repeated. The author concurs with the opinion of Gates and Nandi (4) expressed in a recent paper that, 'synizesis itself probably represents a sensitive condition of the nucleus when the delicate threads are easily compacted together by the entrance of the fixing agent'.

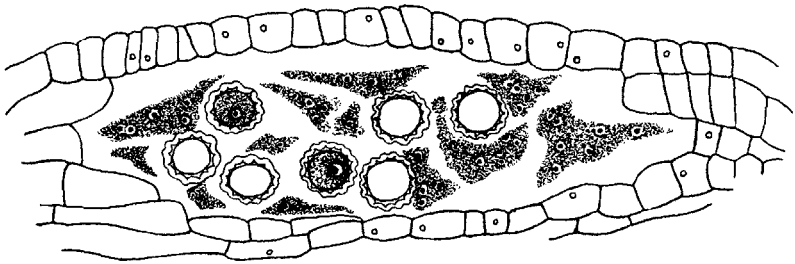
There is distinct evidence as to the growth in size of the nucleus during synizesis and post-synizetic stages. This confirms Gates and Rees' (5) observation on *Lactuca*.

The contracted spireme gradually unravels itself and loops are thrown out from the contracted mass. The spireme emerges as a more or less continuous thread (Plate I, fig. 5) though occasionally free ends may be observed. Parallelism of the threads is not apparent at this stage but at the next stage certain portions of the threads appear to be double in structure. The thread gradually thickens as it fills up the nuclear cavity and appears as a loose coiled rope (Plate I, fig. 6). This is the pachynema stage. No distinct second contraction stage with radiating loops has been observed in this material, though the spireme was observed to be greatly convoluted before segmentation. The segmented bits of spireme show their double nature very clearly (Plate I, fig. 7) and from the nature of the segments, and the absence of the bronchonema stage, it appears that chromosome conjugation is of the parasynaptic type in this plant. The segmented bits of spireme next thicken and shorten to form the typical bivalent chromosomes (Plate I, fig. 8). At this stage the nuclear membrane becomes indistinct and the nucleolus also becomes reduced in volume though its chromaticity remains the same as before. Gradually the bivalent chromosomes reach their maximum condensation and the nucleolus becomes smaller and paler in appearance and finally disappears. At this stage the pollen mother cells separate from one another and round off. In the different species of *Lactuca* studied by Gates and Rees (5) the pollen mother cells frequently separated from one another even before synapsis. Such a condition is, however, rarely met with in plants.

During diakinesis, the gemini which attain their maximum condensation generally lie scattered at the periphery of the nuclear cavity. The two members of a bivalent pair generally lie side by side but some of them show the presence of chiasma. During this stage the nuclear cavity shows the presence of faintly staining delicate fibres from which a multipolar spindle is organized. The multipolar spindle very soon assumes the bipolar form and the chromosomes are arranged in a regular manner in the equatorial region of the spindle (Plate I, fig. 9). Though the chromosomes are very much condensed yet their bivalent nature can be made out while they are oriented on the spindle. A polar view of an equatorial plate at this stage clearly shows 12 bivalent chromosomes (Plate I, fig. 13). The anaphasic separation of the chromosomes appears to be quite regular and no irregularity in the movement or distribution of the chromosomes has been noted. On reaching the poles the chromosomes at first clump together but very soon they separate and assume a filamentous structure in which two closely intertwined threads may be seen. A nuclear membrane is secreted and the whole thing assumes the form of a phragmoplast (Plate I, fig. 10). The spindle fibres at this stage are represented by striations in the cytoplasm. The interkinetic stage is of short duration. During the homotypic division the spindles are arranged

either at right angles, or parallel to each other (Plate I, fig. 11). Polar views of equatorial plates show the presence of 12 chromosomes. The chromosomes are somewhat curved and to a certain extent they resemble the somatic chromosomes. As stated before, Patel and Narayana (15) also found 12 haploid chromosomes in the plants they studied. But Gregory working on Coimbatore types found the $2n$ number to be 20. From the evidence obtained in the present investigation the haploid number of chromosomes in *Carthamus tinctorius* appears to be 12. It is at this stage that the protoplast secretes a mucilaginous substance which completely encases it. As in division I, no irregularity during division II was noted. On the completion of the division four nuclei are organized in which a few chromatic dots and somewhat elongated chromosomes are noted. The four nuclei are, however, seen to be connected to one another by fine striations of the cytoplasm which disappear later. Cytokinesis takes place by the method of furrowing. The furrows originate at the periphery equidistant from one another and gradually cut inwards and meet at the centre. The young microspores at first lie enclosed in the mucilaginous envelope (Plate I, fig. 12), but gradually this envelope disorganizes, and they lie free inside the microsporangium. Each microspore when first liberated has a somewhat shrunken appearance (Plate I, fig. 14) but they become round very soon, and the exine becomes slightly thickened and shows a number of fine spine-like projections. They are uni-nucleate. In optical sections the presence of three furrows is noted on the exine. In surface view these appear as slits on the wall. At this stage the tapetal tissue shows signs of activity. As previously stated the tapetal cells are uni-nucleate, but they become bi-nucleate by mitotic division during the time when the pollen mother cells are in the synizetic stage. Multinucleate tapetal cells have not been observed in this material. The tapetal cells grow inwards, and send out projections in the anther cavity. Very soon, however, the cytoplasms of the different cells fuse and a plasmodium is formed which fills the anther cavity and surrounds the young microspores. The tapetal nuclei lie freely distributed in the plasmodium and some of them are seen to lie close to the young microspores (Text-fig. 8). The nuclei are irregular in shape and contain fine chromatin granules. Juel (10) and Tischler (20) working independently on *Silphium laciniatum* observed that the tapetal cells get in between the pollen grains, but they do not fuse completely. The plasmodium, though it encloses the young microspores, is only in contact with the tips or spinous projections of the microspores in the initial stages. But later, with the disorganization of the plasmodium, it is observed that a certain amount of the plasmodium substance has been incorporated on the exine which now becomes very thick and shows a number of blunt projections (Text-fig. 9). It is interesting to note that Merrell (12) working on *Silphium* observed collection of plasma around the spores which were later encrusted by it in the form of a sheath. The pollen grains though uni-nucleate at this stage show prophasic changes in the nuclei.

The mature pollen grains have three germpores. Three nucleate pollen grains have been noted in *Carduus* and *Centaurea* in the tribe Cynareæ.



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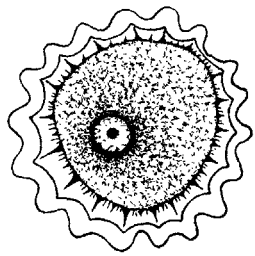

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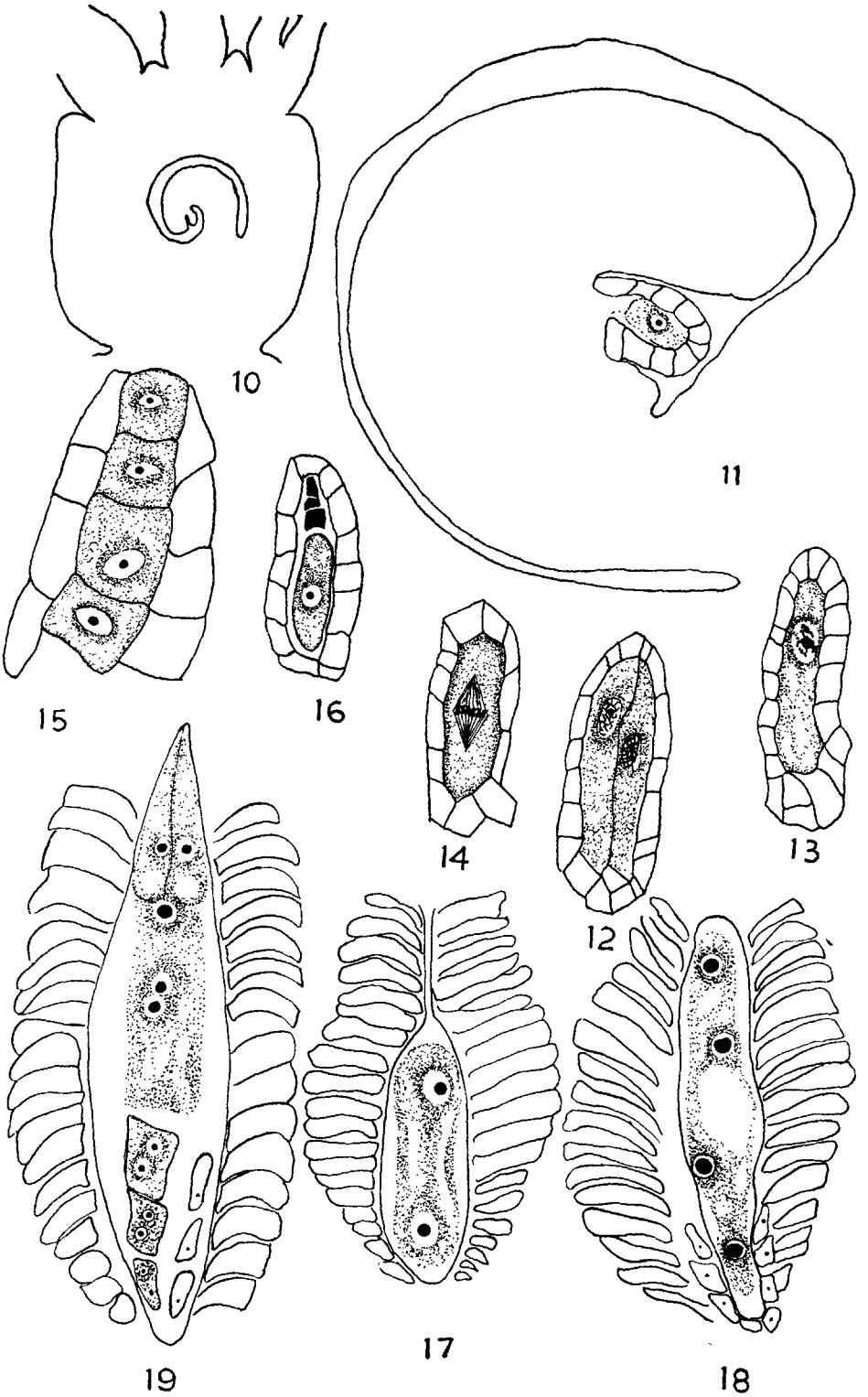
Text-figures 8 and 9. *Carthamus tinctorius.* Fig. 8. Pollen grains surrounded by tapetal plasmodium. ×300; Fig. 9. A pollen grain on the outer surface of which the plasmodial substance has been incorporated. ×1800.

(c) *The Development of the megaspores and the embryo-sac.*—When the microspore mother cells are in the synizetic stage a short blunt hemispherical protuberance is seen in the ovarian cavity. Its position is slightly posterior and it grows obliquely upwards. This is the ovule primordium, which very soon curves inwards and from the centre of this body a tiny protuberance—the nucellus—three cells in thickness, projects out (Text-fig. 10). The integument next becomes differentiated. It grows more rapidly than the nucellus and by its curvature brings about an anatropous condition of the ovule, even before the differentiation of the megaspore mother cell. Very soon a hypodermal cell at the tip of the nucellus becomes differentiated as the archesporial cell and directly functions as the megaspore mother cell (Text-fig. 11). Two megaspore mother cells lying side by side have been noted in some preparations (Text-fig. 12). Schnarf (16) mentions the occurrence of two megaspore mother cells in *Adenostyles alliariæ*. The nucellus at this stage is long and very much reduced and a single layer of epidermal cells enclose it completely. The integument at this stage becomes clearly differentiated as shown in text-figure 11. The megaspore mother cell next increases in size and then passes

through the various stages of reduction division (Text-figs. 13 and 14). On the completion of the homotypic division a linear tetrad of macrospores is produced (Text-fig. 15). No 'T-shaped' tetrad has been observed. The chalazal macrospore alone functions while the rest degenerate (Text-fig. 16). It is interesting to note that in the tribe Calenduleæ the micropylar megaspore usually forms the embryo-sac, while in the tribes Astereæ, Cichorieæ and Senecioneæ either the micropylar or the chalazal megaspore has been found to function. During the linear tetrad stage the epidermal cells covering the nucellus first show signs of degeneration. The functional megaspore soon divides to form the two nucleate embryo-sac. A central vacuole is noted and the nuclei become equally distributed at the two poles (Text-fig. 17). At this stage the cells of the micropylar canal grow out in the form of hairs. Other investigators have noted the presence of such hairs in a number of Compositæ. These hairs are rich in plasma and are always directed towards the egg-apparatus. The quadri-nucleate stage is next reached and the organization of the embryo-sac remains the same as before (Text-fig. 18). At this stage the embryo-sac is considerably elongated and the epidermal cells surrounding the nucellus have degenerated completely, and the integumentary cells immediately surrounding the embryo-sac have become well differentiated and increased considerably in a radial direction. These cells form what is commonly referred to as the 'integumentary jacket' (Text-fig. 17). The eight nucleate stage, which follows soon, shows an increased size of the embryo-sac cavity as well as the vacuole in the centre. The nuclei are distributed equally at the two poles of the embryo-sac. The mature embryo-sac is typical of the angiosperms, but it is somewhat broader in the central region and constricted at the two ends. Due to the disintegration of the nucellar cells capping the embryo-sac, the tips of the synergids project out and lie inside the micropylar cavity (Text-fig. 19). The synergids have very pointed beaks and dense cytoplasm at the distal portion and the nucleus lies just above the vacuole which is placed at the proximal end. The presence of synergid haustoria which has been found by Dahlgreen (2) and others in some plants of this family has, however, not been observed. The egg is suspended between the synergids and has a large vacuole at its upper portion, and its nucleus is larger than that of the synergids. The two polar nuclei lie very close together and in the centre of the embryo sac. Prior to fertilisation they fuse; the fusion nucleus appears to be larger than the egg nucleus, and the nucleolus shows the presence of a large number of vacuoles. This has also been noted by Merrell (12). Opperman (14) working on *Aster* states that in some instances fusion of the polar nuclei may be delayed until the time of fertilisation, but ordinarily the fusion takes place before the pollen tube discharges its contents into the embryo-sac. The antipodal cells, which are three in number, are usually situated one above the other in a row; they lie in the chalazal end of the embryo-sac. The nuclei of the antipodal cells soon divide and very soon two nuclei are seen in most of the antipodal cells. A similar condition of the



Text-figures 10–19. *Carthamus tinctorius.* Fig. 10. The early curvature of the ovule and the origin of the nucellus. ×100; Fig. 11. The differentiation of the megaspore mother cell in the hypodermal layer. ×400; Fig. 12. Two megaspore mother cells lying side by side. ×900; Fig. 13. Megaspore mother cell in early prophase. ×900; Fig. 14. Heterotypic division. ×900; Fig. 15. Linear tetrad of megaspores. ×1600; Fig. 16. Functional megaspore and three degenerated megaspores. ×900; Fig. 17. Binucleate stage of the embryo-sac. ×900; Fig. 18. Quadrinucleate stage of the embryo-sac. ×900; Fig. 19. Mature embryo-sac. ×900.

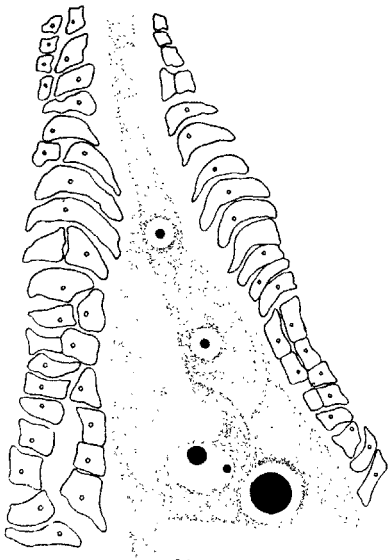
antipodal cells has been recorded in *Dahlia variabilis* and *Tagetes signatus*. Schnarf (16) gives a complete account of the variation in the number and form of the antipodal cells in different tribes of the Compositæ. He, however, states that no information is available as to the nature of the antipodals in Cynareæ. Tackholm (19) has reported as many as forty nuclei in an antipodal cell of *Cosmidium burridgeanum* and Merrell (12) also gives an account of the variations that are commonly noted in antipodal cells.

(*d*) *Fertilisation.*—The ovule, as also the embryo-sac, elongate considerably before the entry of the pollen tube, and the egg also becomes very much elongated. The nucleus lies at the lower portion and a big vacuole lies above it. The secondary nucleus lies close to the egg. At the time of the entry of the pollen tube no trace of the synergids or antipodals are noted in the embryo-sac. Synergids were, however, noted to be present at the time of fertilisation by Mottier (13) in *Senecio*. The pollen tube enters the embryo-sac through the micropyle. Porogamy appears to be the rule in this family, but Doll (3) found two cases of chalazogamy in *Blainvillea rhomboidea*. The tip of the pollen tube appears to be somewhat swollen when inside the embryo-sac cavity (Text-fig. 20). It appears that the vegetative nucleus degenerates before the pollen tube enters the micropyle, as it was not observed in any preparation. On the other hand a number of preparations showed the presence of two small nuclei, one preceding the other and lying very close to the tip of the pollen tube. Such nuclei were also seen in the embryo-sac cavity close to the egg and the secondary nucleus. From these facts, one is inclined to believe that these are the generative nuclei. Actual fusion of the male and the female gametes, or the process of double fertilisation has not been observed.

The form of the generative nuclei in *Carthamus* appears to be spherical. Spherical generative nuclei have also been observed by Mottier (13) and others working on the family Compositæ. Merrell (12) states that the male nuclei when first formed are approximately spherical, but in the later stages they become very much elongated and resolve into a spiral. He further states that preparations showing the nuclei at the tip of the pollen tube indicate that the sex nuclei have assumed a spherical form.

(*e*) *Endosperm and Embryo.*—After fertilisation the egg rests for some time before it commences activity. The definitive nucleus, however, divides very soon. Though the first division of the definitive nucleus has not been observed, yet the presence of a few nuclei at the micropylar end of the embryo-sac and close to the fertilised egg undoubtedly indicates that it divides first. The endosperm is of the nuclear type, and grows by mitotic division. No irregularity in the different stages of division has been observed. Although it has not been possible to count accurately the number of chromosomes in the endosperm nuclei, yet it can safely be stated that it is more than the $2n$ number of the plant. With the increase in size of the embryo-sac cavity the endosperm cells divide rapidly and form a lining layer around the sac. It later fills in

the embryo-sac cavity from the chalazal and micropylar ends. At this stage wall formation of the endosperm cells is noted first at the micropylar end



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Text-fig. 20. *Carthamus tinctorius.* Pollen tube with the generative nuclei. ×800.

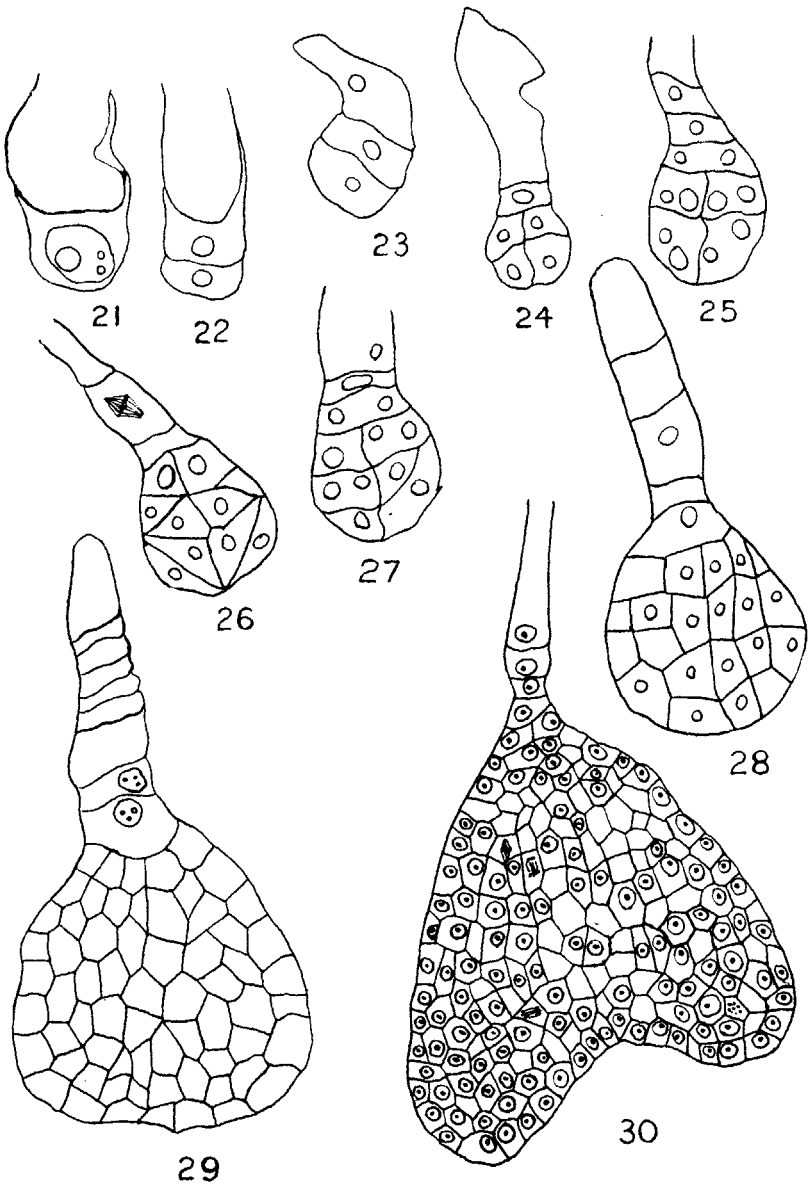
and gradually extends downwards. The nuclei of the endosperm cells contain many nucleoli which, however, differ in size. It is interesting to note that the egg after syngamy increases in size and becomes considerably elongated. It appears as if it was suspended by two cytoplasmic strands from the micropylar end of the embryo-sac (Text-fig. 21). The first division is transverse, resulting in an apical and a basal cell, of which the former is considerably larger than the latter (Text-fig. 22). As observed in many other species of the Compositæ, the basal cell forms the greater part of the embryo, and the apical cell by division forms the suspensor and part of the embryo. The apical cell later divides by a transverse wall and a three-celled pro-embryo is produced (Text-fig. 23). The terminal cell of the pro-embryo next divides by an anticlinical wall, followed very soon by periclinical walls to form the quadrant stage of the embryo (Text-fig. 24). At this stage the embryo becomes globular in outline.

In the octant stage the four superior octants give rise to the cotyledons and the stem tip, while the four inferior octants give rise to the hypocotyl and the primary root. The hypophysis cell, which becomes differentiated at an early stage of the development of the embryo, generally divides when the three histogenic layers are laid down, and contributes to the apex of the root.

The first division of the hypophysis cell in this plant is longitudinal as shown in Text-figs. 25, 26 and 27. Its later divisions have not been traced.

Text-fig. 30 shows the development of the cotyledons. The differentiation of the stem tip has not been observed and it appears to differentiate very late.

The suspensor generally consists of four cells but in certain cases it was found to consist of 8 cells (Text-figs. 28 and 29).



Text-figures 21–30. *Carthamus tinctorius*. Stages in the development of the embryo. ×500.

Text-fig. 30 shows the cotyledon with the three histogenic layers differentiated.

Summary.

The paper gives an account of the development of the flower, pollen grains, and the embryology of *Carthamus tinctorius*.

1. The development of the floral parts occurs in the following succession:—petals, stamens, sepals and carpels. The sepals do not become differentiated but remain as minute angular projections. The opening of the florets takes place from the periphery inwards, and it takes from four to six days for all the florets of the capitulum to open.

2. In the early stages of the development of the microspore mother cells the nucleus shows the presence of a number of coiled threads which appear to be double. The threads contract into a tight knot and on recovery from synizesis the double nature of the spireme is not seen. Chromosome conjugation is of the parasynaptic type. There are twelve diplotene pairs which show the presence of terminal and interstitial chiasma. The haploid number of chromosomes is 12. The chromonematic structure of the chromosomes is apparent at the interkinetic stage. After the II division the microspores are enveloped in a mucilaginous pellicle and show a tetrahedral arrangement.

3. The tapetal cells of the anther develop into a plasmodium which fills the anther loculus completely when the young microspores are formed. Some of the plasmodial substance appear to be incorporated on the spiny exine of the pollen grains which then becomes differentiated as blunt processes. The microspores have three germ pores.

4. The development of the female gametophyte is of the normal type. The megaspore mother cell is hypodermal in origin. Two megaspore mother cells have been noted to occur side by side. A linear tetrad of megaspores is produced. The chalazal megaspore becomes functional and gives rise to an eight nucleate embryo-sac. The mature embryo-sac is of the normal angiospermous type. The antipodals are binucleate. The cells of the integument lining the micropyle grow out in the form of hairs and these are directed towards the egg apparatus.

5. Fertilisation is porogamous. The synergids and the antipodals degenerate completely before the entrance of the pollen tube into the embryo-sac. The secondary nucleus lies very close to the egg at the time of fertilisation. The sperms appear as spherical nuclei.

6. The division of the endosperm nucleus occurs prior to that of the egg and the endosperm is of the nuclear type. The zygote divides first by a transverse wall. The further development of the embryo appears to be that of a *Capsella* type. The suspensor is composed of four to eight cells. The three histogenic layers become differentiated in the embryo before it attains full development.

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