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POLLINATION AND LIFE HISTORY STUDIES OF LETTUCE (LACTUCA SATIVA L.)

H. A. JONES[1]

INTRODUCTION

The lettuce crop is a very important one in California, and the product is shipped in considerable quantity throughout most of the year. The production of lettuce seed is also an important industry. While the variety New York is the only one produced for shipping fresh, almost all of the important varieties are grown for seed. The growing of lettuce for seed is confined almost entirely to the delta lands of the Sacramento and San Joaquin rivers and to the Santa Clara Valley. Wherever a large number of varieties are grown in close proximity, there arises constantly the question of the danger of cross pollination. Pollination investigations reported herein were initiated because of this question. The morphological studies reported in this paper were commenced to furnish information needed in order to prosecute more successfully other lines of investigation that have been started on lettuce.

MATERIAL AND METHODS

The lettuce seed used for growing the material for the morphological studies herein reported, was planted at the University Farm, Davis, California, in December, 1923. The variety employed was Iceberg. The material for study was killed in formalin-alcohol solution, then dehydrated and embedded in paraffin according to the usual procedure. Most of the sections were stained in Delafield's haematoxylin, or safranin and gential violet.

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DEVELOPMENT OF THE FLOWER

In order to allow the flowering stem to develop normally it is often necessary to quarter the heads or else remove the upper leaves entirely. This operation is usually performed before the head becomes hard and while the stems are short (fig. 1). If quartering is delayed until the stem has become elongated (fig. 2) there is danger of injuring it.

The oldest flower head terminates the main axis (fig. 3). The meristematic region of the receptacle, at first convex (fig. 4), becomes flattened and broadened (fig. 5); after this there arise, simultaneously over the entire surface, the protuberances that give rise to the individual flowers (figs. 3, 6, 9). The protuberances soon become angular in outline and the appearance of a marginal ring on each protuberance indicates the beginning of the corolla tube (figs. 3, 7, 10). Swellings soon appear upon the inside of the corolla tube (figs. 8, 11) and an elevated ring of meristematic tissue which gives rise to the pappus is formed near the base of the corolla tube and on its outer side (figs. 8, 11). The stamens and pappus appear almost simultaneously. These observations coincide with those of Martin[7] on *Aster* and *Solidago*. The carpels are the last organs of the flower to differentiate (figs. 12, 13). By the time the carpels appear, the corolla has started to curl inward over the top of the flower (fig. 12). The cavity of the ovary is soon formed as a result of the upward growth of the carpellary tissue (fig. 13).

OOGENESIS

The ovule arises at the bottom of the ovarian cavity. The hypodermal archesporial cell, which in this case is the megaspore mother cell, is differentiated early in the life of the ovule (fig. 14). It is easily distinguished by its large size and its deeply staining contents, and by its inclusion within a single-layered nucellar tissue. After the appearance of the megaspore mother cell, the single massive integument becomes increasingly evident (figs. 15, 16). The growth of the integument is unilateral and as a result the ovule finally assumes a position of complete anatropy (fig. 19). The nucellar cells divide anticlinally only, thus allowing for the growth of the megaspore mother cell. The nucellus never consists of more than a single layer of cells. The ovule is completely inverted by the time the heterotypic divisions are initiated.

By two successive divisions (figs. 20, 21, 22, 23) the four megaspores are formed. A wall forms between the two daughter nuclei after the completion of the heterotypic division. Walls are again formed at the completion of the homotypic divisions giving a linear series of four megaspores of equal size. The three micropylar megaspores soon degenerate as a result of encroachment upon them by the functioning innermost megaspore (fig. 26). Virtually the same method of megaspore development has been figured by Merrell[8] for *Silphium,* by Small[13] for *Senecio,* and by Martin[7] for *Aster* and *Solidago.* The nucellar cells abutting on the micropyle appear to enlarge slightly for a time (fig. 26). The rapidly growing embryo sac, however, soon crowds the lower cells of the nucellus and the degenerating megaspores into the upper end of the micropyle to form the so-called nucellar cap (fig. 45).

The functioning or fertile megaspore enlarges considerably before the first division of its nucleus (fig. 26). The first nuclear division takes place near the middle of the embryo sac (fig. 27). The daughter nuclei then migrate toward opposite ends (figs. 28, 29) and by two successive divisions form four free nuclei at the extremities of the sac. The polar nuclei move toward the center and finally come to rest just above the egg (fig. 32).

The polar nuclei are rather distant from one another two hours before anthesis (fig. 32) and, so far as has been determined, fusion of the polar nuclei does not take place until the time of fertilization. According to Land,[6] in *Silphium* the polar nuclei fuse long before fertilization, whereas Nawaschin[10] reports their early fusion in *Helianthus.*

Not more than three antipodal cells were ever observed. Sometimes they are in a linear row completely filling the antipodal neck of the embryo sac (fig. 62) while in other cases, the two lower antipodals lie side by side with the third cell forming a sort of summit. The variability in number reported for *Silphium,*[8] *Aster* and *Solidago,*[2] *Senecio,*[9] *Erigeron,*[6] and *Bellis*[1] does not seem to occur in *Lactuca.* Schwere[12] reports only three antipodals for *Taraxacum* and, according to Small,[13] this number seems to be the rule for most of the *Cichoriaceae.*

The occurrence of two ovules in a single ovary is common (fig. 25), and often three ovules were observed. Occasionally an ovule was observed with two developing embryo sacs (fig. 25), but in no case were two embryos observed within the same ovule.

A single layer of inner integumentary cells forms a jacket completely surrounding the embryo sac. This layer is very conspicuous

before the egg apparatus is mature (fig. 25) and does not entirely disappear until the seed is almost ripe. According to Coulter and Chamberlain,[3] this layer of cells is nutritive in function. These authors also mention a large number of genera in which this nutritive jacket has been observed.

SPERMATOGENESIS

When the young stamens have reached the stage of development shown in figures 34 and 35, a single row of hypodermal archesporial cells is already distinguishable. The first periclinal wall cuts off a single row of pollen mother cells on the inside (fig. 36), and an outer layer, which divides to form the tapetum, the middle layer, and the endothecium (fig. 37). The pollen mother cells and their nuclei enlarge considerably before the heterotypic division is initiated (fig. 37).

Gates and Rees[4] made a cytological study of pollen development in three species of *Lactuca: L. sativa* L., *L. scariola* L., and *L. muralis* Frees. In a single loculus of each species, they found from fifteen to twenty pollen mother cells, which in turn produce a total of about sixty pollen grains. According to these authors, the pollen mother cells frequently separate from each other before synapsis. Figure 38 shows the pollen mother cells separated and well rounded off. About the beginning of synizesis, or a little earlier, the tapetal cells become binucleate. This latter stage is well illustrated in figure 37. Later the tapetal cells become quadrinucleate (fig. 39).

According to Gates and Rees[4] there are nine bivalent chromosomes. They state that at the time of diakinesis "the nine bivalent chromosomes form a graded series which can be arranged in a general way in three groups, three of maximum length four or five times as long as broad, three of intermediate length, about two or three times as long as broad, and three very short and almost cubical. Between the stage of diakinesis and the arrangement of the chromosomes on the heterotypic metaphase they are condensed to such a degree that there remains little observable difference in length between them."

In the homotypic metaphase (fig. 41) the spindles extend in opposite planes. According to Coulter and Chamberlain,[3] this method of division is common in the dicotyledons; the two nuclear divisions occur before the walls are formed, then all of the latter are formed simultaneously. The method of cytokinesis in *Lactuca* has been studied in detail by Gates and Rees,[4] who state that "after the

reduction divisions the cytoplasm of the pollen mother cells begins to constrict at four points and these constrictions finally meet at the center, cutting the contents of the cell into four parts. The young pollen grains so formed alter their shape within the mother-cell wall, becoming roughly heptagonal and then secreting a cell wall. The mother-cell wall then breaks down and the wall of the pollen grain ultimately becomes remarkably thickened and sculptured."

The pollen grain germinates within the anther. Samples collected several hours before anthesis (fig. 44) show two filamentous sperms and a vegetative nucleus. The sperms at this time reach about half way around the interior wall of the pollen grain. Filamentous sperms of this general type in the Compositae have been described by Merrell[8] and Land[6] for *Silphium,* and by Nawaschin[10] for *Helianthus.*

Figure 24 shows a transverse section of a flower head, the anthers of which are in the mother-cell stage. This figure shows a large number of individual flowers that have more or fewer stamens than the characteristic number, five. The syngenesious character of the androecium is not well illustrated in this figure.

POLLINATION

About twenty-four hours before anthesis, the bracts subtending the flower head start to open at the summit because of the development of the individual flower buds (fig. 84). The buds make a remarkable elongation during the twenty-four hours before anthesis. The extent of this development can best be seen by comparing figure 84 with figure 87. Figure 84 is taken from the head illustrated in figure 83. Figure 87 shows the flower at time when the floral organs are fully extended and expanded and the brush hairs of the pistil are covered with pollen. Figure 85 shows the flower head two hours before anthesis. In figure 86 the pistil is not fully extended; the brush hairs that are visible are covered with pollen; and the stigmatic lobes have started to expand.

Although the lettuce flower is almost entirely self-pollinated, crossing can take place. When the pistil elongates and pushes its way through the anther tube, the brush hairs on the side of the pistil sweep the pollen grains upward out of the pollen sacs of the dehisced anthers. According to Oliver,[11] the anthers dehisc before the flower head opens and when the unexpanded stigmas appear through the staminal column they are already covered with pollen. When the stigmatic

lobes expand, pollen falls on the stigmatic hairs of the inner surface, insuring self-pollination. Knuth[5] states that when the stigmatic lobes expand, they make a complete revolution backwards and the stigmatic papillae come into contact with the pollen held by the brush hairs of the pistil, thus bringing about self-pollination. It is not known definitely whether or not the pollen grains will germinate elsewhere on the pistil than on the stigmatic papillae.

Oliver[11] suggests that crossing may occur in the field if the pollen has been washed from the stigmas by rain. Foreign pollen may then be brought in by insects. Since rains occur so seldom in California during the lettuce blooming season, the danger from this source is almost negligible. If self-pollination is brought about, in the manner described by Knuth,[5] there is danger of foreign pollen being brought in by insects before the inner surface of the outward curving stigmatic lobes have come into contact with the pollen held by the brush hairs of the pistil of the same flower. There is also the possibility of differential pollen-tube growth between foreign pollen and that of self-pollen.

Observations were made on methods of natural pollination in the White Paris Cos variety of lettuce in June, 1926, at Davis, California. A number of flower heads were protected against insect visitation. When the stigmatic lobes were fully expanded the pollen grains that had fallen on the inner surface of the stigmatic lobes of each flower were counted. Seventy flowers were observed. Of these 58 did not have any pollen grains on the inner stigmatic surfaces. The number of pollen grains on the inner stigmatic surfaces of the other 12 flowers ranged from 1 to 7. The edges of the stigmatic lobes were always covered with pollen, however, as well as the backs of the lobes. It was also observed that only occasionally do the stigmatic lobes make a complete revolution backwards.

Even though the anthers dehisc and the pollen grains are in contact with the stigmatic lobes and upper portion of the style before the latter is extended through the staminal column, Oliver[11] states he was able to completely depollinate the lettuce flowers by washing off the pollen with a fine stream of water from the fully extended pistils. This method of depollination has been used by a number of investigators.

With reference to pollination by insects, Knuth[5] reports different species of flies visiting the flowers. Flies have also been observed visiting the flowers in various lettuce seed fields in California. At Davis, California, a brilliant green bee, *Agapostemon texanus* Cresson[2] was

[2] Identified by Professor T. D. A. Cockerell.

found to be the most frequent insect visitor. Several species of *Halictus*[3] have also been observed visiting the flowers. The bees that visit the lettuce flowers are probably pollen collectors, only. In June, 1926, a count was made of the number of pollen grains on the surface of the stigmatic lobes of flowers that were insect visited. All of the seventy flowers observed had pollen grains on the inner stigmatic lobes. These ranged in number from 4 to 51. One plant observed had 169 flower heads open on June 26. During the short time that these were open 88 were visited at least once by insects and some were visited a number of times. On the same day another plant had 82 flower heads open and 60 of these were visited by insects.

As a protection against insect visitation and to avoid the danger of introduction of foreign pollen, some seedsmen enclose the selected plants in cloth bags during the entire flowering period. These bags may be left on the plants until the seed is harvested.

The stigmatic papillae develop from large rectangular cells that are very early differentiated. At an early stage of development, these cells stain very deeply and possess exceptionally large nuclei. In figure 33, these large cells are seen abutting on the nutritive cells below. These nutritive layers coalesce below the style branches and form a single tissue through the style. A single vascular bundle is found in each lobe of the stigma. At the stage shown in figure 33, the microspores have already escaped from the wall of the pollen mother cell and the outer sculpturing is beginning to form. Figure 31 shows the stigmatic papillae somewhat elongated. At this stage the embryo sac is two-nucleate, as shown in figure 29.

ANTHESIS

In 1925, studies were made of a number of lettuce plants in order to determine the waves of anthesis occurring during the season and the length of time required for the seeds to ripen. Seed of the Iceberg variety was planted in November, 1924. In the early spring of 1925, when the plants were about two inches high, they were thinned so that they were twelve inches apart in the row. The heads were quartered while still soft so as to allow the emergence of the seed stem. Ten plants that had flowers in bloom for the first time on June 11 were selected for study. Table 1 gives the number of flowers in bloom each day on the different plants from June 11 to July 30. The taking of

[3] Miss Grace Sandhouse of the U. S. National Museum identified one species of *Halictus* as *H. titusi* Crawford.

records was discontinued after July 30. The flower heads were counted each morning at the time of anthesis.

Lettuce plants show definite flowering peaks. The data in table 1 show that almost all the plants reached a flowering peak in the latter part of June. Then a drop to zero occurred in some cases, continuing for several days, and then another peak of less magnitude occurred in July. The general flowering curve and its minor irregularities due mainly to fluctuations in temperature can best be studied when individual plants are considered. The morning after a very warm day there is usually a decided rise in the flowering curve; the morning after a cool day, there is usually a pronounced drop. The influence of temperature is more noticeable during the early than the latter part of the flowering period. Although different plants may start flowering at the same time, their flowering curves seldom parallel one another. Some plants also have more definite flowering cycles than others. Those of plants 5 and 7, are not nearly so pronounced as those of plants 1, 2, 3, 6, 8, and 9. In figure 109 the flowering and seed ripening curves are plotted for plant No. 8. The mean temperature for the same period is also given.

RIPENING OF THE ACHENES

The lettuce flowers are open usually an hour or two only. The ligulate corollas then fold tightly together and do not again open (fig. 88, 89). Within two or three days the corollas, dehisced stamens, and withered styles and stigmas are shed in a cluster. The bracts then close tightly about the developing achenes. This is well illustrated in samples collected three days after anthesis (fig. 91). The beak of the young fruit elongates and carries the pappus along in its upward growth. The rate of elongation is fairly rapid, as can be observed in the different aged fruits in figures 89, 90, 92, 93, and 95. These illustrations were made from samples collected 1, 2, 3, 4, and 5 days after anthesis. Within four or five days after anthesis, the pappus begins to appear through the bracts (fig. 94). The growth made by the embryo from ten hours after anthesis to the morning of the eleventh day are shown in figures 96 to 108C. The embryo in each figure has been colored black. The intervals of time between anthesis and collection of the samples used for the illustrations are as follows: figure 96, ten hours; figure 97, fourteen hours; figure 98, twenty-six hours; figure 99, thirty-four hours; figure 100, three days; figure 101, four days; figure 102, five days; figure 103, six days;

TABLE 1

LETTUCE ANTHESIS. 1925

Date	Number of flower heads in bloom										
	Plant No. 1	Plant No. 2	Plant No. 3	Plant No. 4	Plant No. 5	Plant No. 6	Plant No. 7	Plant No. 8	Plant No. 9	Total	Average
June 11	1	1	1	1	1	4	3	2	2	16	1.8
12	9	1	2	3	0	9	5	4	0	33	3.7
13	20	9	8	11	0	19	11	4	3	85	9.4
14	51	8	27	19	3	45	21	13	2	189	21.0
15	59	24	31	68	2	33	30	18	3	268	29.8
16	33	21	27	43	4	16	28	26	4	202	22.4
17	39	33	21	34	10	33	20	64	10	264	29.3
18	48	33	25	24	7	61	23	63	12	296	32.9
19	71	25	41	64	5	86	20	65	24	401	44.6
20	69	21	85	108	16	82	23	95	43	542	60.2
21	55	27	117	101	61	72	21	117	67	638	70.8
22	36	48	91	79	46	49	19	109	48	525	58.4
23	30	43	45	24	33	49	22	85	30	361	40.1
24	27	57	69	42	67	51	34	116	52	515	57.2
25	22	51	53	27	82	53	21	145	107	561	62.4
26	22	85	65	50	109	68	43	196	154	792	88.0
27	61	100	84	47	96	72	52	170	140	822	91.4
28	40	75	91	41	70	62	31	133	74	617	68.5
29	24	77	69	37	47	34	20	80	65	453	50.3
30	14	42	46	19	28	10	26	39	38	262	29.1
July 1	9	28	50	32	38	6	25	14	16	218	24.2
2	5	22	42	23	48	1	32	2	15	190	21.1
3	6	10	9	17	32	1	22	0	6	103	11.4
4	1	4	4	14	34	0	25	0	6	88	9.8
5	0	8	8	16	43	0	22	0	12	109	12.1
6	3	7	10	9	30	0	19	2	8	88	9.8
7	2	7	11	18	36	0	25	1	17	117	13.0
8	3	7	13	24	40	0	19	0	24	130	14.4
9	3	17	6	34	26	2	29	2	23	142	15.8
10	4	25	25	29	31	5	29	11	31	190	21.2
11	5	40	23	49	37	5	25	25	34	243	27.0
12	3	37	31	43	30	13	35	24	31	247	27.5
13	21	51	26	67	27	19	39	28	16	294	32.7
14	27	45	52	72	23	25	49	44	16	353	39.2
15	38	43	58	64	28	38	50	93	41	453	50.3
16	61	58	72	46	46	35	52	121	60	551	61.2
17	55	46	63	25	43	46	53	103	41	475	52.8
18	20	41	50	9	36	47	31	67	38	339	37.6
19	7	57	40	.....	27	54	25	83	62	355	44.4
20	2	44	31	.....	18	52	9	71	35	262	32.7
21	3	49	26	.....	22	35	12	64	41	252	31.5
22	2	28	16	.....	7	26	4	32	21	136	17.0
23	0	31	15	.....	17	16	2	39	33	153	19.1
24	1	46	20	.....	4	11	0	35	16	133	16.6
25	1	37	20	.....	12	20	1	42	12	145	18.1
26	4	43	14	.....	8	12	0	19	18	118	14.8
27	2	37	14	.....	15	8	0	27	21	124	15.5
28	3	26	7	.....	12	10	0	27	11	96	12.0
29	9	35	21	.....	11	21	0	40	19	156	19.5
30	13	50	19	.....	17	37	0	55	27	218	27.0
Total.....	1,044	1,760	1,794	1,433	1,485	1,453	1,107	2,615	1,629	14,320	

figure 104, seven days; figure 105, eight days; figures 106 and 108A, B, and C, eleven days; and figures 107A, B, and C, nine days. On the twelfth day (June 24, 1924) the seeds were ripe. The long filamentous suspensor is very conspicuous in samples collected three and four days after anthesis (figs. 100, 101).

In 1925 seed-ripening studies were made on the same plants that were used for a study of flowering habit.

TABLE 2

SEED-RIPENING DATA. 1925

Date	Seed heads mature on plant No.										
	1	2	3	4	5	6	7	8	9	Total	Average
June 22	0	0	0	0	0	4	0	0	0	4	.4
23	2	3	0	0	1	0	3	0	2	11	1.2
24	11	0	2	2	0	9	5	4	0	33	3.7
25	48	12	12	8	0	33	16	7	3	139	15.4
26	86	24	41	41	4	60	55	32	6	349	38.8
27	37	20	30	49	2	37	25	39	5	244	27.0
28	42	41	33	64	12	6	20	55	13	286	31.8
29	43	21	22	30	3	84	22	48	12	285	31.8
30	13	13	33	32	6	27	6	15	10	155	17.2
July 1	60	21	32	38	4	81	15	55	18	324	36.0
2	66	23	58	33	19	96	21	100	47	463	51.4
3	62	44	60	144	84	91	35	194	83	803	89.2
4	25	24	60	66	19	17	4	23	19	257	28.5
5	29	49	51	45	60	56	34	94	54	472	52.4
6	15	36	37	11	37	28	18	60	35	286	31.8
7	10	37	27	15	72	33	21	62	60	337	37.4
8	20	62	57	41	59	62	24	93	91	509	56.5
9	28	76	69	40	95	65	42	172	130	717	79.8
10	38	64	69	38	67	49	28	195	93	641	71.2
11	47	76	100	40	67	65	46	136	87	664	73.8
12	.....	.....	.....	50	57	39	49	119	92	406	67.6
13	.....	.....	.....	9	17	0	7	7	17	57	9.5
14	.....	.....	.....	18	43	5	30	11	18	125	20.8
15	.....	.....	.....	19	44	1	19	5	14	102	17.0
16	.....	.....	.....	20	40	0	15	4	8	87	14.5
17	.....	.....	.....	27	60	0	50	9	23	169	28.1
18	.....	.....	.....	.....	44	0	27	1	12	84	16.8
19	.....	.....	.....	.....	68	0	37	6	49	160	32.0
20	.....	.....	.....	.....	41	8	28	16	36	129	25.8
21	.....	.....	.....	.....	36	7	45	21	36	145	29.0
22	.....	.....	.....	.....	19	6	17	18	25	85	17.0
23	.....	.....	.....	.....	24	8	29	21	19	101	20.5
24	.....	.....	.....	.....	20	9	35	22	18	104	20.8
25	.....	.....	.....	.....	11	15	22	34	15	97	19.4
26	.....	.....	.....	.....	16	5	44	20	8	93	18.6
27	.....	.....	.....	.....	16	22	12	44	29	123	24.6
28	.....	.....	.....	.....	31	32	43	98	45	249	49.8
29	.....	.....	.....	.....	32	36	47	67	36	218	43.8
Total	682	646	793	880	1,230	1,096	996	1,916	1,274	9,513	

Each day all the seed heads which had ripened their achenes were counted and then removed. The first seed heads were ripe on June 22, as is shown in table 2. Of the nine plants under observation only one ripened seed on this day. Some plants did not ripen seed until June 24. The average number of flower heads open and the average number of seed heads ripe on the different dates from June 11 to July 30 are plotted in figure 110. It is thus seen that the two high peaks in seed ripening occurred twelve days after the flowering peaks. This indicates that the average time from anthesis to fruit maturity is about twelve days, under conditions as they existed at the time. If the temperature remains high, the ripening of the achenes is hastened, and if the average temperature is low, the time from anthesis to fruit maturity is increased.

In counts made on thirty different heads, which were taken from several plants, it was found that the number of flowers varied from 15 to 22, with an average of 18.3. The number of normally developed achenes averaged 16.2 to a head. Either a number of the ovules are not fertilized or the embryos fail to develop.

FERTILIZATION

In June, 1924, a study was made to determine the length of time between pollination and fertilization and also the interval between pollination and fruit maturity, and other attendant phenomena. The study was started the morning of June 12. Table 3 gives a record of temperatures taken in the shade of lettuce plants in the field.

TABLE 3

TEMPERATURES IN THE SHADE. JUNE 12, 1924

Time	Temperature degrees C.	Time	Temperature degrees C.
5 A.M.	12.0	1 P.M.	31.0
6 A.M.	13.5	2 P.M.	31.8
7 A.M.	16.0	3 P.M.	31.4
8 A.M.	21.5	4 P.M.	28.8
9 A.M.	24.0	5 P.M.	27.0
10 A.M.	26.5	6 P.M.	25.0
11 A.M.	28.6	8 P.M.	18.0
Noon	29.4	10 P.M.	14.5

At 5 A.M. and at 6 A.M. the flowers were still closed. At 7 A.M. the corollas were just starting to unfold, and although the stigmas were still enclosed within the staminal column, some of the anthers had

dehisced. The flowers were fully expanded at 8 A.M. and the pistils were fully extended. Eight o'clock is hereafter referred to as the time of pollination in this study.

At 11 o'clock the same morning sperms were first observed in the embryo sac. There were only a very few embryo sacs that contained sperms at this time. At noon a few more of the embryo sacs had sperms in them (fig. 46). By 1 P.M., or five hours after pollination, the majority of the embryo sacs contained sperms. In samples taken at 2 P.M., no fertilization stages were found, but the embryo sacs contained all stages of development from fertilized eggs to two-celled embryos (figs. 47 to 50). The time elapsing between pollination and fertilization in lettuce is, then, extremely short. Considering 8 A.M. as the time of pollination, it was only three hours before the first fertilization stages were observed, and in less than six hours, fertilization had been completed in all the flowers studied. In figure 45, one male cell is lying near the egg nucleus. The polar nuclei are fusing, but the second sperm destined to unite with the two polar nuclei can not be detected. In figure 46, one male cell is in close proximity to the egg nucleus, and the other is in contact with the polar nuclei. It appears that there is approximately simultaneous union of the three nuclei to form the primary endosperm nucleus.

DEVELOPMENT OF THE EMBRYO

The embryo of lettuce follows the general type of development outlined by Carano[1] and Souèges[14] for other members of the Compositae. The term embryo instead of proembryo is used in this discussion.

After fertilization, the zygote develops a definite wall and elongates considerably. The lower or micropylar end is occupied by a large vacuole. The large nucleus usually contains two or three nucleoli (fig. 47). Divisions are initiated very shortly after fertilization. A number of two-celled embryos were found at 2 P.M., three hours after the first sperms were observed in the embryo sacs. The first wall is transverse. This wall cuts off a terminal cell (fig. 50, *a*), from which develop the cotyledons and epicotyl, as well as a lower cell (fig. 50, *b*), which gives rise to the hypocotyledonary parts of the embryo. The upper cell (*a*) is much the smaller. The basal cell (*b*) has a large vacuole occupying the greater portion of the lower two-thirds, thus forcing the nucleus to occupy a terminal position. Both cells of the two-celled embryo divide at very nearly the same time. In figure 51,

both cells are in anaphase, but cell *a* is slightly in advance of cell *b*. In figure 52, cell *a* is in telophase while cell *b* is still in metaphase. While the basal cells of these two figures are in the same stage of development, cell *a* of figure 53 is somewhat in advance of that of figure 52. In figure 54, cell *a* is in telophase and cell *b* is in anaphase. The upper cells of figures 53 and 54 are in approximately the same stage of development, but the basal cell of figure 54 is slightly farther advanced than that of figure 53. In figure 55, there are two cells in tier *a;* cell *b* is still in telophase. Thus, it is seen that the division of cell *b* lags slightly behind that of cell *a*, and as a general rule, the cells at the terminal portion of the embryo develop more rapidly than those of the basal part. In the four-celled embryo, the two cells in tier *a* are formed by a longitudinal wall, while cells *c* and *d,* daughter cells of *b*, are formed by a transverse wall (fig. 56, 57). The embryo shown in figure 56, is as it appears only 6 or 7 hours after fertilization.

Every cell of the four-celled embryo contributes to the formation of the eight-celled embryo. Again, each tier usually divides slightly in advance of the one below it. In figure 58, both cells of tier *a,* and also of cell *c,* are in metaphase, while cell *d* is still in prophase. In figure 59, both cells of tier *a* are in anaphase, one slightly in advance of the other; cell *c* and cell *d* are in prophase. In figure 60, cell *c,* which is in anaphase, is slightly in advance of both cells of tier *a,* which are in metaphase, and of cell *d,* which is in prophase. In figure 61, one cell of tier *a* is in anaphase while the other is in metaphase; cell *c* is in mid-anaphase while cell *d* is in prophase. The eight-celled embryo of figure 63 was observed in samples collected 20 hours after pollination. In this figure, tier *a* has four cells, and tier *c,* two cells; *e* and *f* are daughter cells of *d*. The quadrants of tier *a* are formed by the development of two longitudinal walls at right angles to the initial wall. A longitudinal wall divides tier *c,* but *e* and *f* have been formed from *d* by a transverse wall. Thus the three lower tiers of cells in the eight-celled embryo (fig. 63) have been derived from the basal cell, and the upper tier of four cells has been derived from the terminal cell of the two-celled embryo. While the general plan of development of the young embryo is well established, the relative rates of development of similar cells in the different embryos are not always the same. Doubtless the rates of development and of division of the different cells are considerably influenced by the conditions that surround them.

The sixteen-celled embryo is formed by the division of each cell of the eight-celled embryo. The cells of tier *a* are the first to divide. The wall dividing each of the quadrant cells of tier *a* is united with

the peripheral wall near its middle (fig. 64), and with the lower horizontal wall. Occasionally this wall is attached to the base of the vertical walls (fig. 71). When the octants are formed in tier *a*, the embryo is twelve-celled (fig. 64). No more divisions occur in this layer until all the tiers of cells below it have undergone division. Tier *c* is the next to divide. In figure 64, both cells of tier *c* are in anaphase and cell *e* in prophase. Segmenting walls develop at right angles to the axial wall and divide tier *c* into quadrants forming the fourteen-celled embryo (fig. 65). Cell *e* divides later by a vertical wall forming the fifteen-celled embryo (figs. 66–71). The division of cell *f* lags considerably behind that of cell *e*. In figure 68, cell *f* is in prophase, in figures 69 and 70, it is in metaphase, and in figure 71, it is in telophase. The division of cell *f* by a transverse wall completes the sixteen-celled embryo (fig. 72). In the sixteen-celled embryo, the eight cells of the upper tier are derived from the terminal cell of the two-celled embryo, while the total of eight cells in tiers *c*, *e*, *g*, and *h* have been derived from the basal cell. In the sixteen-celled embryo, then, as many cells have been derived from the basal as from the terminal cell of the two-celled embryo. This stage was found in samples collected 25 hours after pollination. The early development of the embryo is very similar to that described by Soueges for *Senecio*. In figure 73, tangential walls have differentiated the dermatogen, periblem, and plerome. In tier *e*, four cells are formed by the development of vertical walls. Tangential walls then differentiate the dermatogen from four inner cells which are the periblem initials. Transverse walls divide the plerome cells of tier *c* into a two-celled layer (figs. 75, 76). After this a series of longitudinal and transverse cell divisions differentiates the plerome of tier *c*, a four-celled layer (fig. 78). This stage of development is reached three days after anthesis and at the same time that the cotyledonary elevations are first noticeable in tier *a* (fig. 78).

It is rather difficult to determine the sequence of wall formation in tier *g*. In figure 76, the first wall appears to be longitudinal, while in figure 77, it appears to be transverse. In samples collected exactly four days after pollination (fig. 79), transverse and longitudinal wall formation had made of tier *g* a two-celled layer, the upper cells of which are the dermatogen initials, and the lower of which contribute to the formation of the root cap. Thus tier *e* contributes the periblem initials and dermatogen cells to the young embryo, and tier *g* contributes the dermatogen initials and a portion of the root cap.

The root cap is built up by the division of the lower dermatogen cells of tier *c*, and from the dermatogen cells of tiers *e* and *g*. The

cells of the root cap are formed by periclinal division of the cells of the dermatogen. The method of formation and the development of the root cap correspond very closely with that described by Carano[1] for *Bellis*.

Tier *c* contributes the plerome initials, one of which is seen dividing in figure 79A. A definite single cell layer, the pericycle, is already differentiated in figure 79A and from all appearances has its own initials.

The dermatogen, periblem, and plerome tissues of the hypocotyl all arise from different initials. As previously stated, the root cap is built up by periclinal division of the lower dermatogen cells and dermatogen initials. The suspensor is formed from cell *h*, and varies in length and in the number and method of division of its cells.

ENDOSPERM

The divisions of the endosperm nuclei are at first slightly in advance of those of the embryo. When the embryo is four-celled, the free endosperm nuclei have almost completed their fourth division (fig. 80). During the early stages, the divisions of the free nuclei are usually nearly simultaneous. This is shown very well in figure 80, where six of the dividing nuclei are in telophase, while the other two are in late anaphase. This parallelism of division, however, is not always maintained, for in figure 57, a transverse section of an embryo-sac containing an embryo of the same age and stage of development as that in figure 80, one endosperm nucleus is in late anaphase while the other appears to be in a resting condition. By the time the eight-celled embryo is formed, twenty hours after pollination, walls have appeared in the endosperm (fig. 81). The endosperm cells at this time completely fill the embryo-sac; they are few in number, very large and highly vacuolate. The endosperm cells continue to divide. They grow with such rapidity for a considerable time as to continue to occupy the space within the rapidly enlarging embryo sac. Figures 98 to 103, showing endosperm development, were drawn from samples collected 26 and 34 hours, and 3, 4, 5, and 6 days after pollination.

The developing embryo rapidly encroaches upon the endosperm, digesting and absorbing it. The seventh day after pollination (fig. 104), the endosperm tissue is almost entirely destroyed. Figure 82, drawn from a sample collected three days after pollination, shows the outer layers of endosperm cells compressed and flattened against the integument. The walls of the two outer cell layers of the endosperm

become somewhat thickened and are very conspicuous during the late stages of seed development (figs. 104 108C). This membrane is also present in the ripe seed and completely invests the embryo.

The endosperm cells do not contain much reserve food at any stage of their development. They are always highly vacuolate. When the seed is ripe, all of the reserve food is stored within the cells of the embryo, and it is upon this food supply that the growing seedling must draw until it starts to manufacture its own food. The nutritive layer of the integument, which is very conspicuous during the early stages of development of the embryo (figs. 81, 82) is gradually absorbed and disappears entirely by the time the seed is mature.

SUMMARY

(1) In the development of the flower, the first primordial whorl to appear is that of the corolla. The primordia of the stamens and pappus are the next to appear, at approximately the same time, while the primordial tissue of the carpels is the last to develop.

(2) The archesporium is the megaspore mother cell. Four megaspores are formed. The inner enlarges to form the embryo-sac. The nucellus consists of a single layer of cells. The polar nuclei appear to unite at about the time of fertilization. Not more than three antipodal cells were ever observed. A nutritive jacket of integumentary cells completely surrounds the embryo-sac.

(3) The development of the microspore precedes that of the megaspore. Very early there is formed a single row of pollen mother cells, each giving rise to four microspores. The tapetum, middle layer, and endothecium arise from the sister cell of the pollen mother cell. At the time of pollination, in addition to the tube nucleus, two sperms, filamentous in form, reach about half way around the interior wall of the pollen grain.

(4) The lettuce flower is almost entirely self-pollinated. Pollen is shed before the flower head is fully expanded. The pollen is carried from the anther tube by the brush hairs on the outside of the elongating pistil.

(5) Lettuce flowers are open for only a short time. The lettuce plant as a whole usually shows definite flowering peaks. Plants under observation at Davis, California, reached a flowering peak in the latter part of June and another of less magnitude in July. Minor irregularities in the flowering curve are due primarily to fluctuations in the temperature.

(6) Under the conditions of this study, the average time from anthesis to maturity of the achenes was about twelve days.

(7) Studies made on June 12, 1924, show that fertilization is complete in less than six hours after pollination. A few sperms were observed in the embryo sacs three hours after pollination. Five hours after pollination sperms were found in most of the embryo sacs studied.

(8) The zygote divides very soon after fertilization. The first wall is transverse, cutting off a small terminal cell which gives rise to the cotyledonary and plumule parts of the embryo and a large basal vesicular cell, from which develops the hypocotyledonary portions. The upper cell divides by a longitudinal wall and the lower by a transverse wall, forming the four-celled embryo. Every cell of the four-celled embryo, by division, contributes to the formation of the eight-celled embryo. In the sixteen-celled embryo, as many cells have been derived from the basal as from the terminal cell of the two-celled embryo. At this stage there are five tiers of cells. The upper tier of eight cells contributes the cotyledons and plumule. The second tier of four cells gives rise to all the primary tissues of the hypocotyl and plerome initials, the third tier of two cells produces dermatogen cells and periblem initials. The fourth tier (one celled) contributes the dermatogen initials and a portion of the root cap, while the fifth tier or basal cell develops into a many-celled filamentous suspensor. Cells of the root cap are formed by periclinal division of the cells of the dermatogen.

(9) The divisions of the free endosperm nuclei at first precede those of the embryo. By the time the embryo is eight-celled, walls have appeared in the endosperm. A two-celled endosperm layer persists in the lettuce seed; all other endosperm tissue is digested and absorbed by the embryo before the latter matures.

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EXPLANATION OF PLATES

ABBREVIATIONS

m.a., main axis; *t.fl.*, terminal flower head; *r.*, receptacle; *cor.*, corolla; *st.*, stamens; *pa.*, pappus; *carp.*, carpels; *in.*, integument; *nuc.*, nucleus; *m.m.*, megaspore mother cell; *o.c.*, ovarian cavity; *peri.*, pericarp; *m.*, megaspores; *br.*, bracts; *ov.*, ovule; *e.s.*, embryo sac; *micro.*, micropyle; *s.*, style; *anth.*, anther; *p.n.*, polar nuclei; *syn.*, synergids; *n.c.*, nucellar cap; *sp.*, sperms; *v.n.*, vegetative nucleus; *n.j.*, nutritive jacket; *vac.*, vacuole; *t.c.*, tapetal cells; *p.m.c.*, pollen mother cells; *a.c.*, archesporial cells; *epi.*, epidermis; *s.p.*, stigmatic papillae; *te.*, tetrads; *e.n.*, egg nucleus; *der.*, dermatogen; *n.t.*, nutritive tissue; *endo.*, endothecium; *m.l.*, middle layer; *der. i.*, dermatogen initials; *peri.*, periblem; *peri. i.*, periblem initials; *pl.*, plerome; *pl. i.*, plerome initials; *r.c.*, root cap; *peric.*, pericycle; *endo.*, endodermis; *en.*, endosperm; *emb.*, embryo; *susp.*, suspensor.

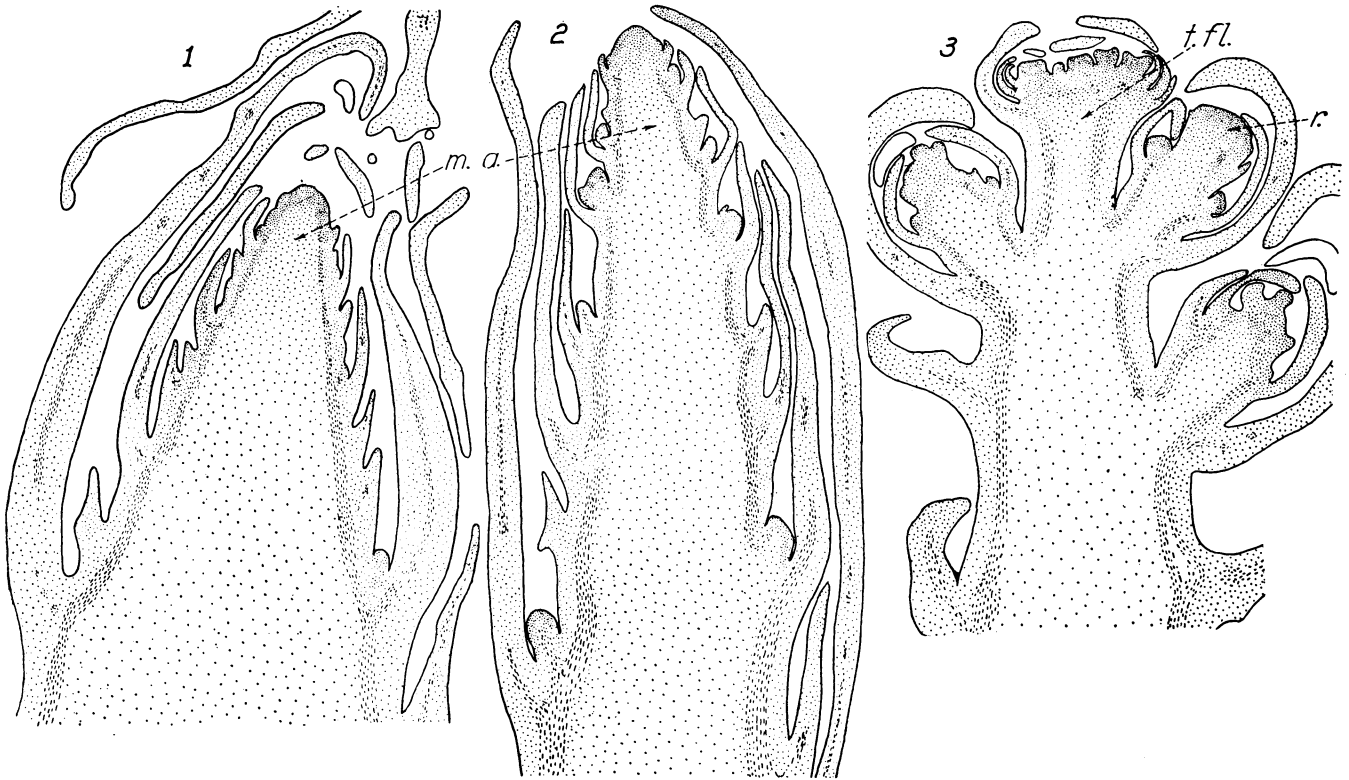
PLATE 1

All figures *ca.* × 30.

Fig. 1. Terminal portion of central axis. Heads soft, in best condition for quartering or removing upper leaves to allow the emergence of seed stalk.

Fig. 2. Terminal portion of central axis. Heads in prime condition for cutting for market.

Fig. 3. Terminal portion of central axis.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2
3
t. fl.
r.

PLATE 2

Figs. 4 and 5. Receptacles, convex in figure 4 and flattened in figure 5. *Ca.* × 65.

Fig. 6. Flower head with protuberances that give rise to the primordia of the floral organs. *Ca.* × 65.

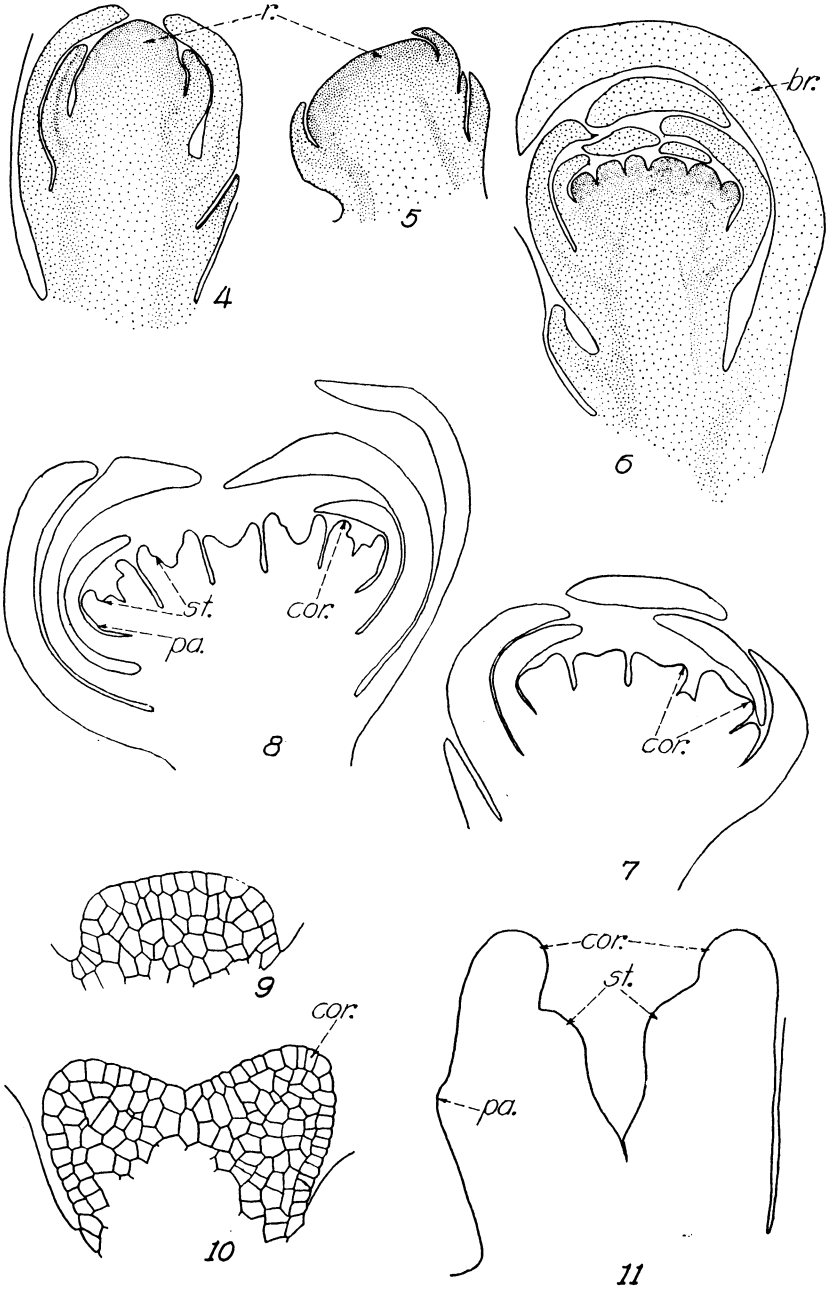
Fig. 7. Flower head showing the appearance of the corolla. *Ca.* × 65.

Fig. 8. Flower head, showing the corolla, stamens, and pappus. *Ca.* × 65.

Fig. 9. Detail of protuberance that later gives rise to flower primordia.

Fig. 10. Detail of early development of corolla.

Fig. 11. Individual flower. *Ca.* × 345.


r.
4
5
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6
st.
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9
cor.
10
cor.
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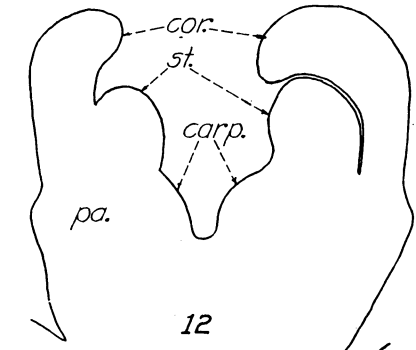
PLATE 3

Figs. 12 and 13. Development of floral organs. *Ca.* × 345.

Figs. 14 to 16. Developing ovule with megaspore mother cell, shaded. *Ca.* × 700.



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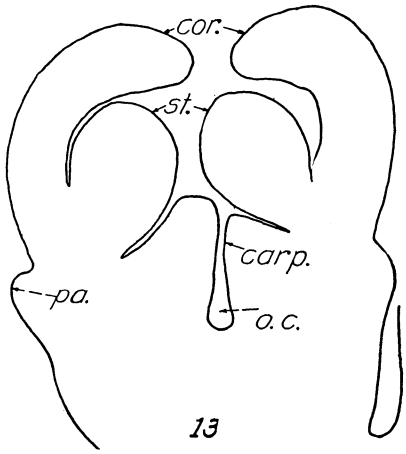

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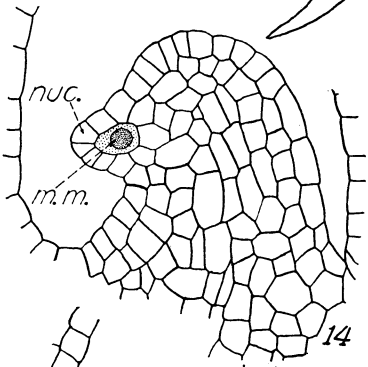

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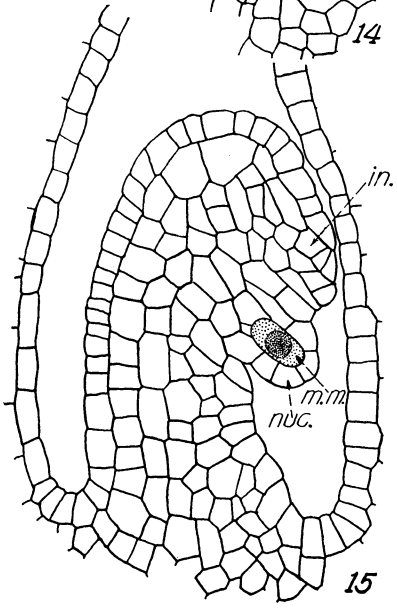

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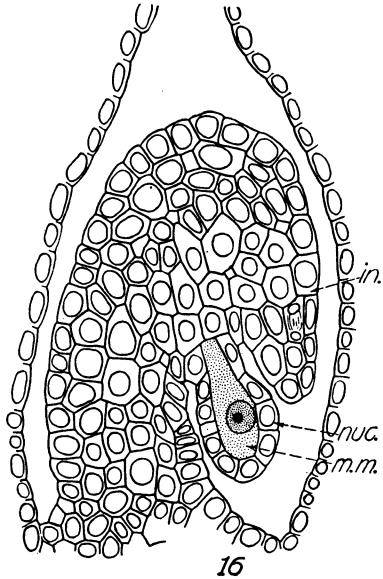

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PLATE 4

Fig. 17. Longitudinal section through flower. Anthers in mother cell stage. Ovule in stage of development shown in figure 14. *Ca.* × 30.

Fig. 18. Transverse section through ovary and ovule. Megaspore mother cell and nucellus shaded. Megaspore mother cell in about the same stage of development as shown in figure 19. *Ca.* × 700.

Fig. 19. Ovule, showing large fleshy integument, the single layered nucellus, and the mature megaspore mother cell. *Ca.* × 700.

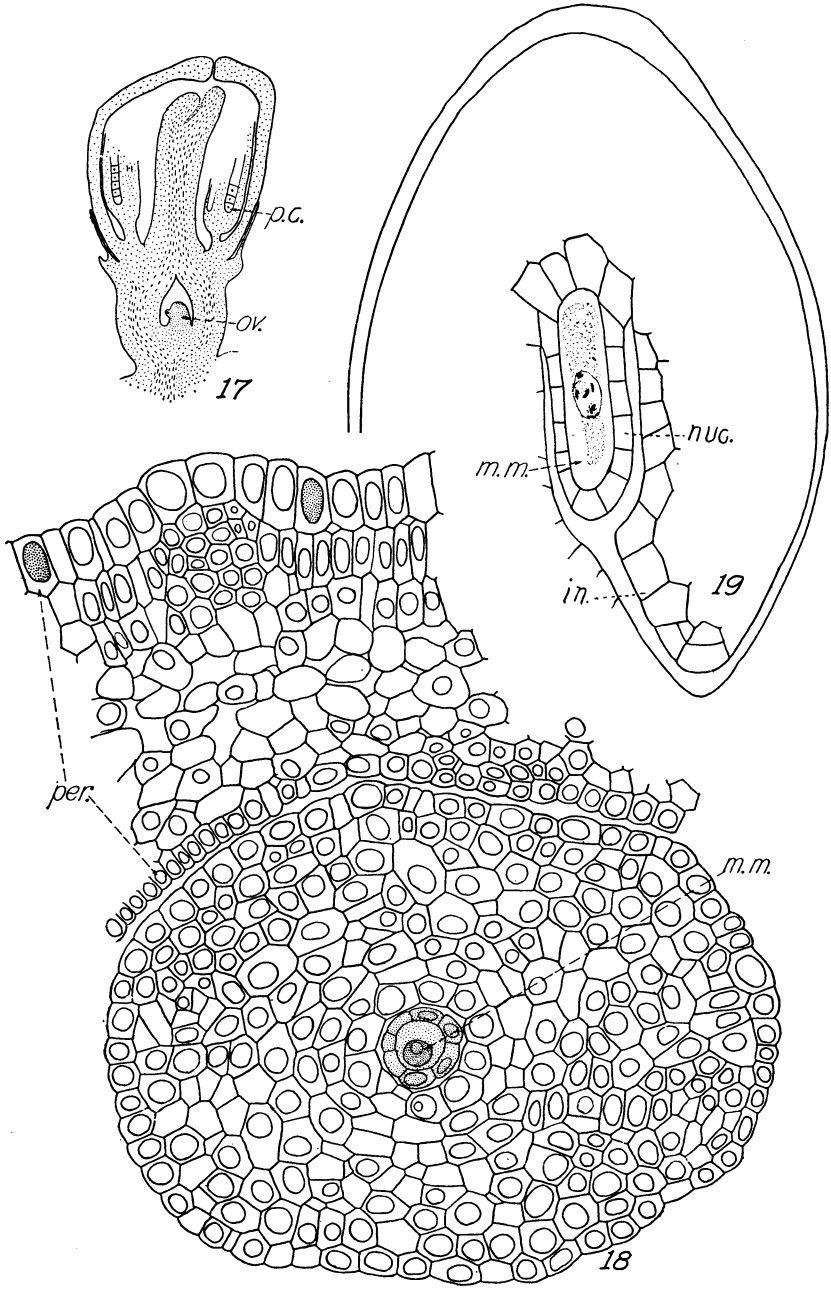
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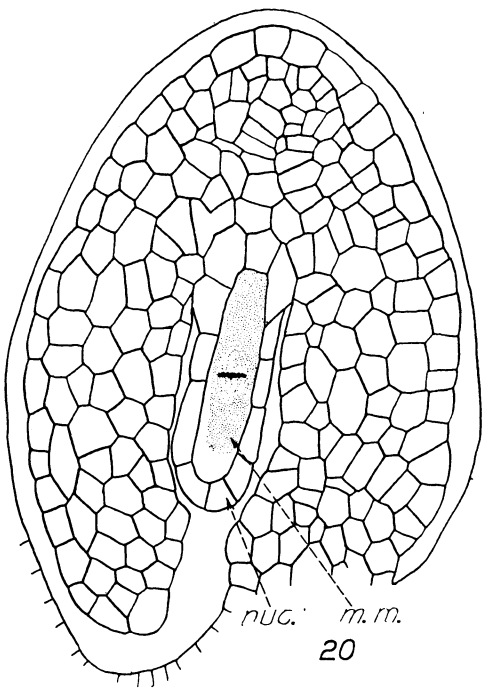
PLATE 5

All figures *ca.* × 700.

Fig. 20. Metaphase of heterotypic division of the megaspore mother cell.

Fig. 21. Metaphase of homotypic division of the daughter cells.



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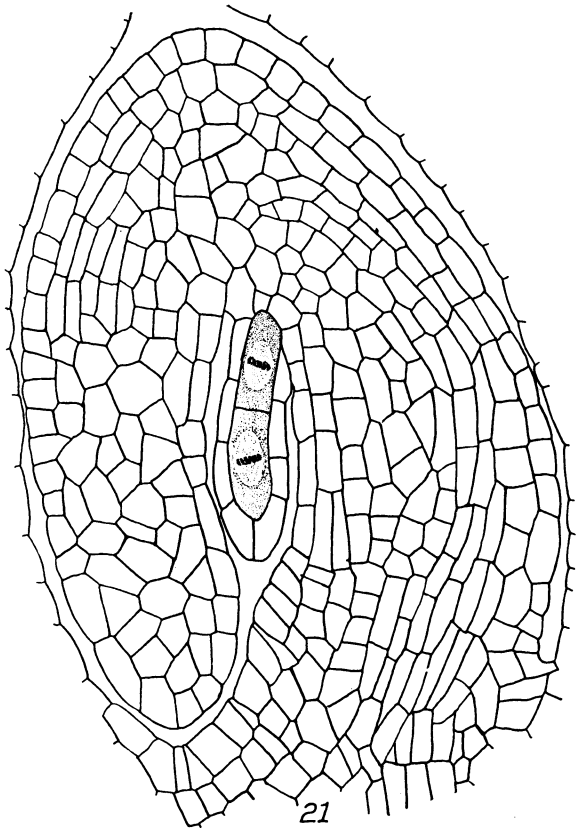

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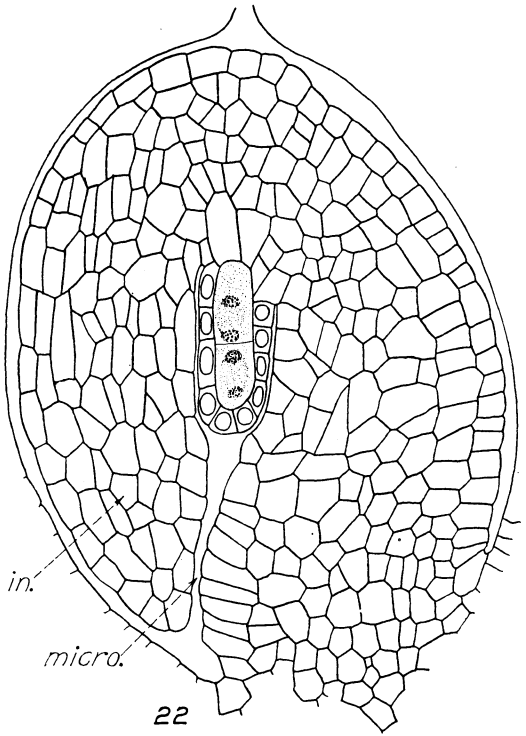
PLATE 6

All figures *ca.* × 700.

Fig. 22. Telophasic division of the two daughter cells.

Fig. 23. Tetrad of megaspores.



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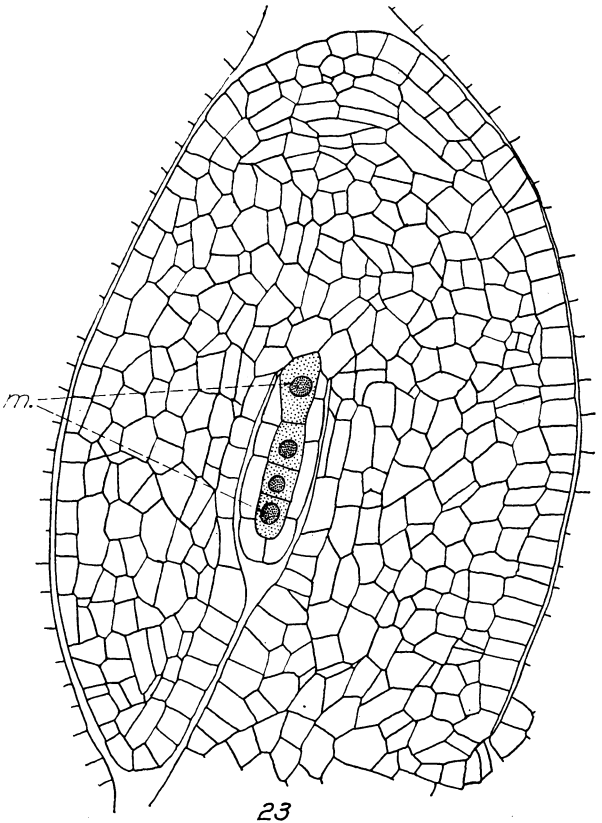

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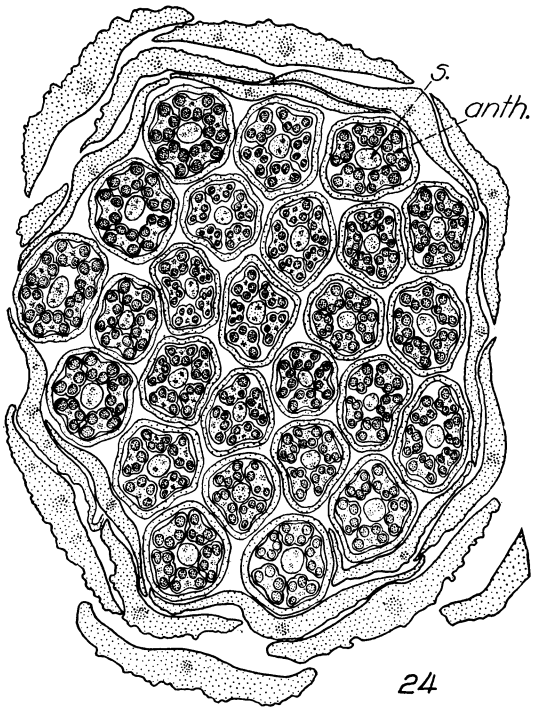
PLATE 7

All figures *ca.* × 30.

Fig. 24. Transverse section through entire flower head. Anthers in pollen mother cell stage.

Fig. 25. Transverse section through flower head. Sample collected 5 A.M., June 12, 1924, three hours before pollination. Note the ovary with two ovules, one of which has two embryo sacs.



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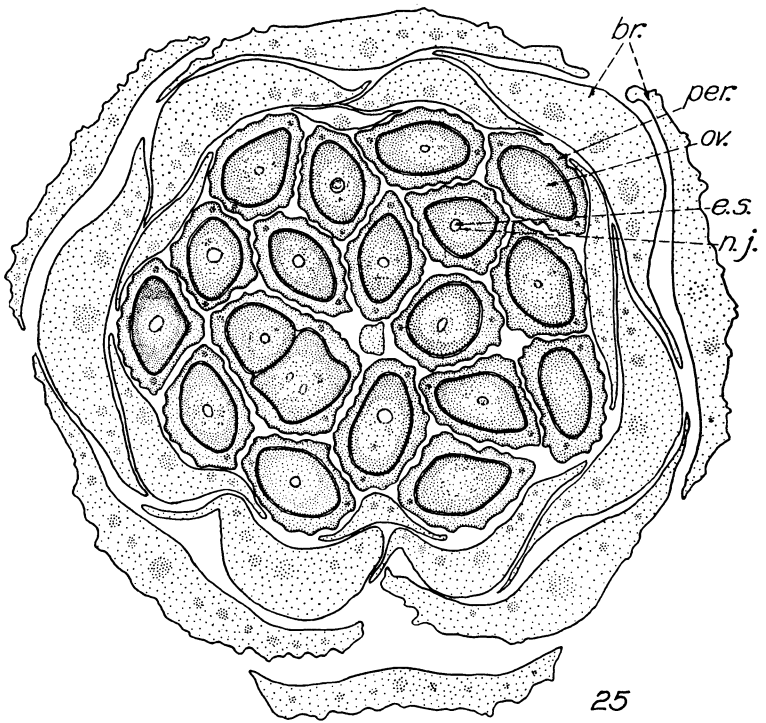

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PLATE 8

Fig. 26. Growth of the functioning megaspore and degeneration of the three lower (micropylar) megaspores. *Ca.* × 700.

Fig. 27. Embryo sac with two nuclei. *Ca.* × 700.

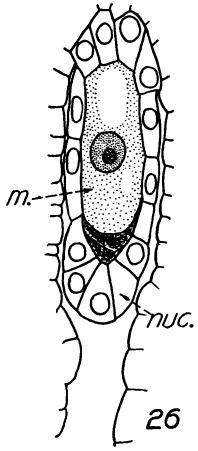
Fig. 28. Embryo sac with two nuclei, the latter migrating toward the poles. *Ca.* × 700.

Fig. 29. Longitudinal section of entire flower with ovule in same stage of development as shown in figure 28. The tetrads have escaped from the wall of the pollen mother cell. *Ca.* × 30.

Fig. 30. Embryo sac with four nuclei. *Ca.* × 700.

Fig. 31. Stigmatic papillae from inner surface of stigmatic lobes in stage of development shown in figure 29. *Ca.* × 700.

Fig. 32. Portion of mature embryo sac. *Ca.* × 700.



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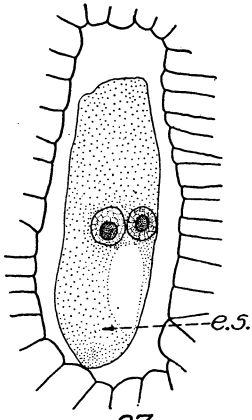

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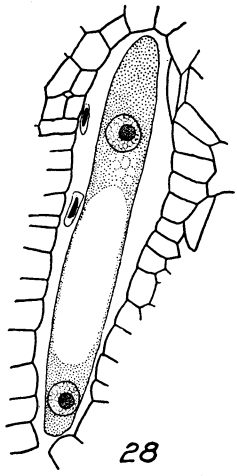

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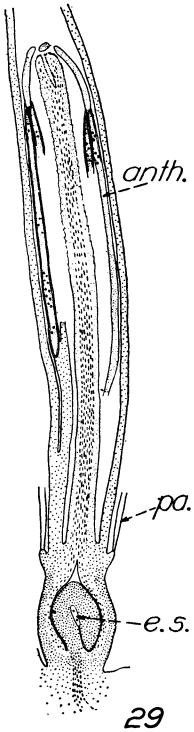

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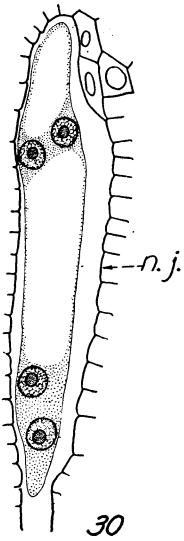

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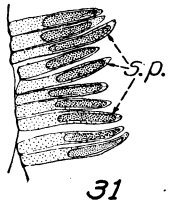

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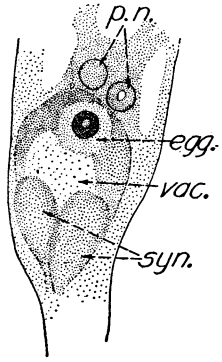


32

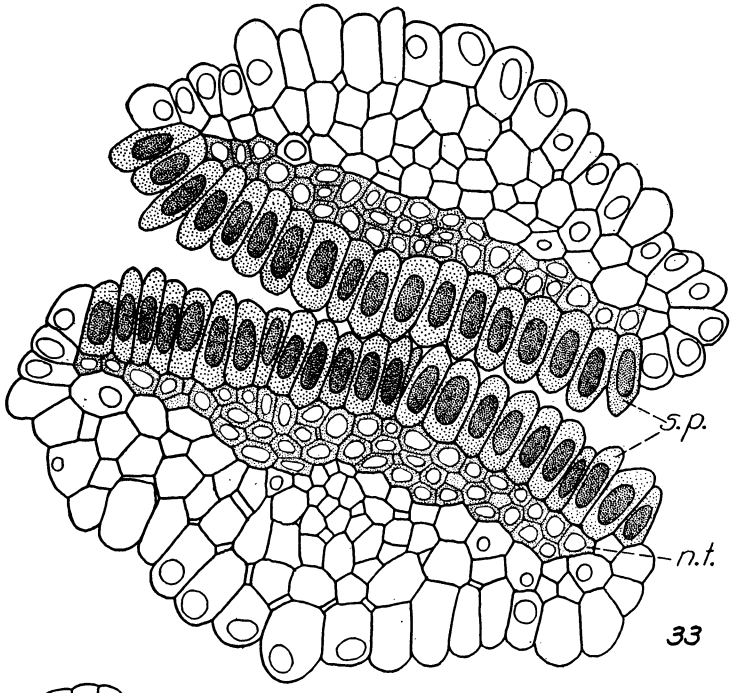
PLATE 9

All figures *ca.* × 700.

Fig. 33. Transverse section through stigmatic lobes. Stigmatic hairs develop from the deeply stained, elongated, large-nucleate cells.

Figs. 34 and 35. Longitudinal sections of young anthers showing single row of archesporial cells.

Fig. 36. Four archesporial cells have divided and cut off pollen mother cells on the inside.



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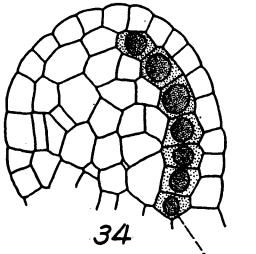

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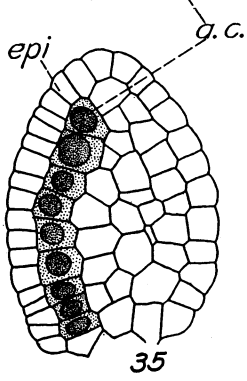

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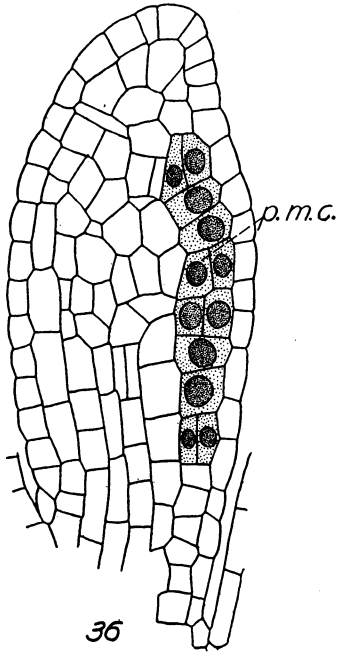


36

PLATE 10

All figures *ca.* × 700.

Fig. 37. Single row of pollen mother cells and two-nucleate tapetal cells.

Fig. 38. Mother cells rounding off.

Fig. 39. Metaphase of heterotypic division of pollen mother cells. Four-nucleate tapetal cells.

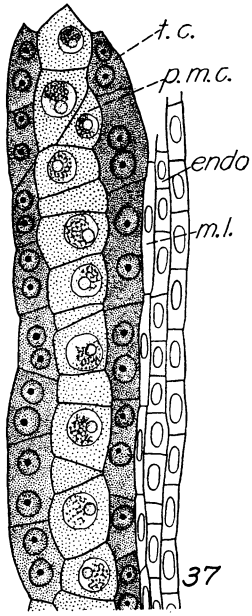
Fig. 40. Late anaphase of heterotypic division of pollen mother cells.

Fig. 41. Metaphase of homotypic division of the daughter cells.

Fig. 42. Transverse section of pollen sac. Tetrads enclosed within the wall of the pollen mother cell.

Fig. 43. Tetrads rounding off.

Fig. 44. Mature pollen grains, showing filamentous sperms and vegetative nucleus. Sample collected at 5 A.M., June 12, 1924, three hours before the time of pollination.



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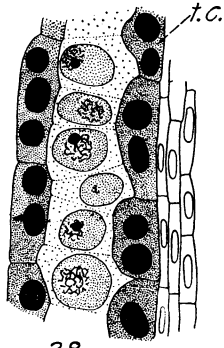

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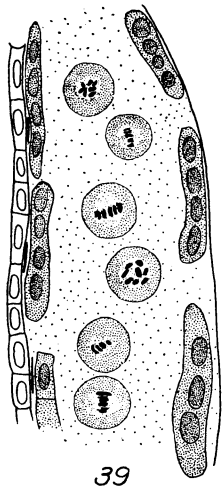
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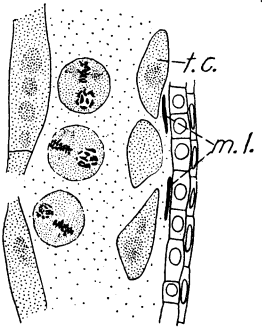

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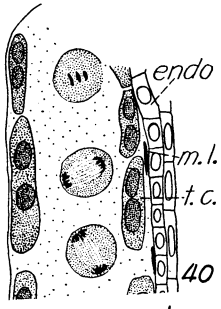

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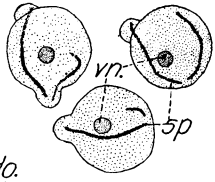

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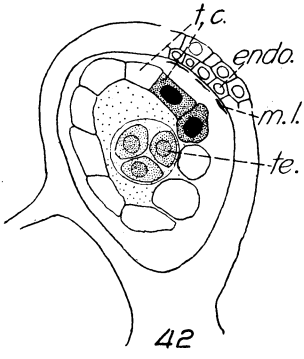

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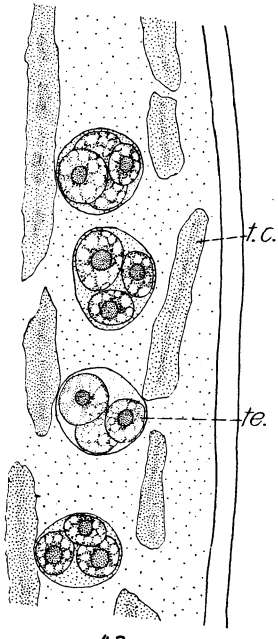

43

PLATE 11

All figures *ca.* × 700.

Fig. 45. Fertilization: sperm nucleus within the egg cell; polar nuclei fusing. One P.M., June 12, 1924, five hours after pollination.

Fig. 46. Fertilization: one sperm nucleus in egg cell, the other in contact with the two polar nuclei, noon, June 12, 1924, four hours after pollination.

Fig. 47. Fertilized egg. Two P.M., June 12, 1924, six hours after pollination.

Fig. 48. First division of the zygote: metaphase. Two P.M., June 12, 1924, six hours after pollination.

Fig. 49. First division of fertilized egg: telophase. Two P.M., June 12, 1924, six hours after pollination.

Fig. 50. Two-celled embryo: *a*, upper; *b*, lower.

Fig. 51. Two-celled embryo: cell *a* and cell *b* in late anaphase. Five P.M., June 12, 1924, nine hours after pollination.

Fig. 52. Two-celled embryo: cell *a* in telophase and cell *b* in metaphase. Five P.M., June 12, 1924, nine hours after pollination.

Fig. 53. Cell wall being formed in cell *a;* cell *b* in metaphase. Five P.M., June 12, 1924, nine hours after pollination.

Fig. 54. Cell *a* in telophase; cell *b* in anaphase. Five P.M., June 12, 1924, nine hours after pollination.

Fig. 55. Three-celled embryo: tier *a* two-celled; cell *b* in telophase. Five P.M., June 12, 1924, nine hours after pollination.

Fig. 56. Four-celled embryo: *c*, and *d*, daughter cells of *b*. Six P.M., June 12, 1924, ten hours after pollination.

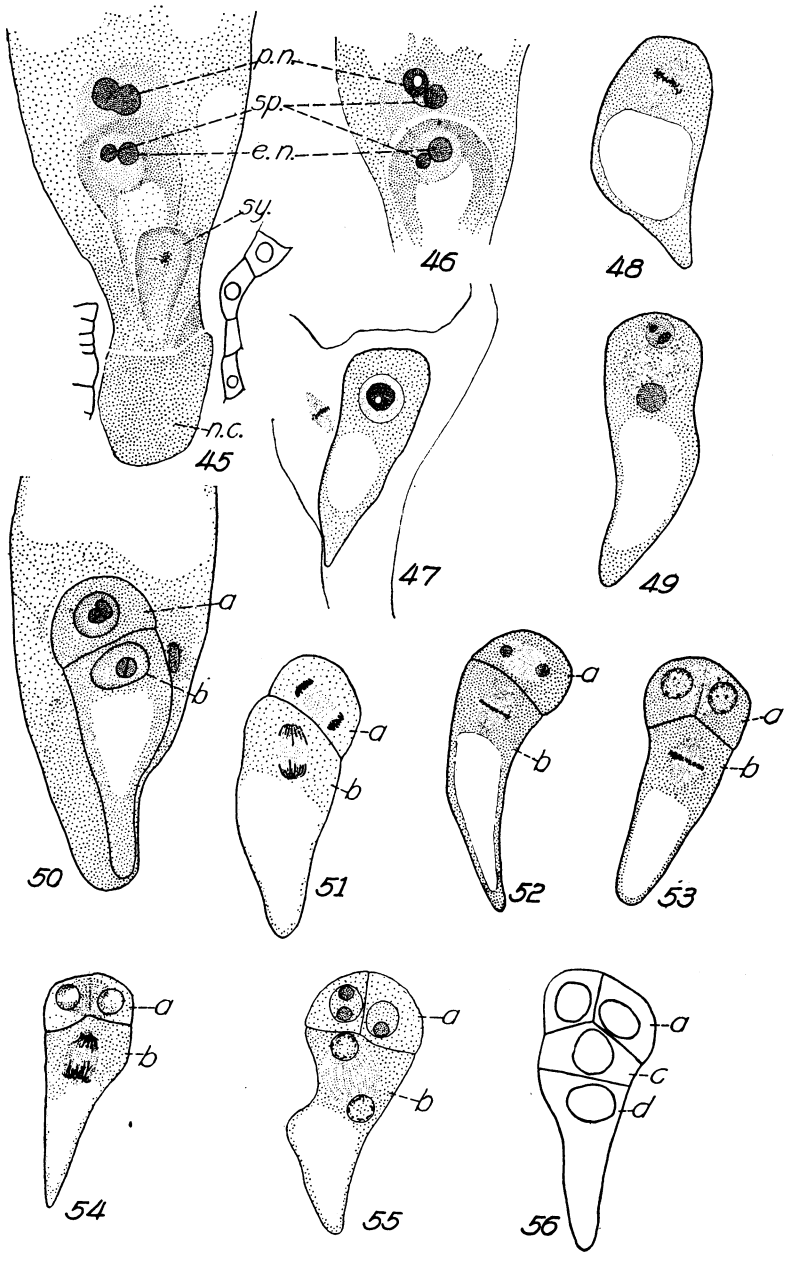
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PLATE 12

All figures *ca.* × 700.

Fig. 57. Four-celled embryo: transverse section through tier *a*. Nuclei of both cells in prophase; one of the endosperm nuclei in anaphase. Eight P.M., June 12, 1924, twelve hours after pollination.

Fig. 58. Four-celled embryo: both cells of tier *a* in prophase, cell *c* in metaphase, and cell *d* in prophase. Eight P.M., June 12, 1924, twelve hours after pollination.

Fig. 59. Four-celled embryo: both cells of tier *a* in anaphase, one slightly in advance of the other; cells *c* and *d* in prophase. Eight P.M., June 12, 1924, twelve hours after pollination.

Fig. 60. Four-celled embryo: both cells of tier *a* in metaphase, cell *c* in anaphase, and cell *d* in prophase. Eight P.M., June 12, 1924, twelve hours after pollination.

Fig. 61. Four-celled embryo: one cell of tier *a* in late anaphase, the other in metaphase; cell *c* in anaphase; and cell *d* in prophase. Ten P.M., June 12, 1924, fourteen hours after pollination.

Fig. 62. Antipodals. Eight P.M., twelve hours after pollination.

Fig. 63. Eight-celled embryo: tier *a*, four-celled; tier *c*, two-celled; *e* and *f*, daughter cells of *d*. Four A.M., June 13, 1924, twenty hours after pollination.

Fig. 64. Twelve-celled embryo: tier *a*, eight-celled; both cells of tier *c* in anaphase; cell *e* in prophase. Ten A.M., June 13, 1924, twenty-six hours after pollination.

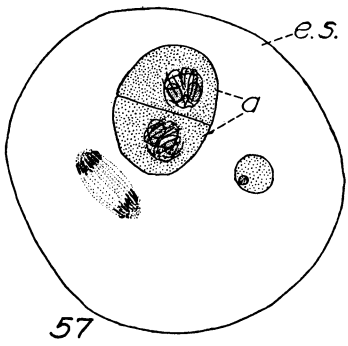
Fig. 65. Fourteen-celled embryo: tier *a* eight-celled; tier *c* four-celled; cell *e* in metaphase. Ten A.M., June 13, 1924, twenty-six hours after pollination.

Figs. 66 and 67. Fifteen-celled embryo: tier *a* eight-celled; tier *c*, four-celled; tier *e*, two-celled. Ten A.M., June 13, 1924, twenty-six hours after pollination.

Fig. 68. Fifteen-celled embryo: cell *f* in prophase. Ten A.M., June 13, 1924, twenty-six hours after pollination.

Figs. 69 and 70. Fifteen-celled embryos: cell *f* in metaphase. Ten A.M., June 13, 1924, twenty-six hours after pollination.

Fig. 71. Fifteen-celled embryo: cell *f* in telophase. Ten A.M., June 13, 1924, twenty-six hours after pollination.



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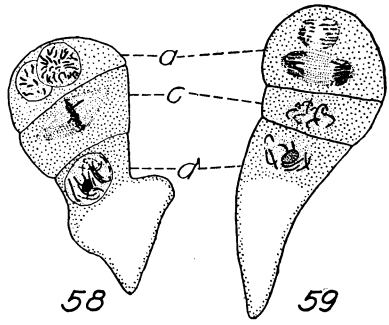

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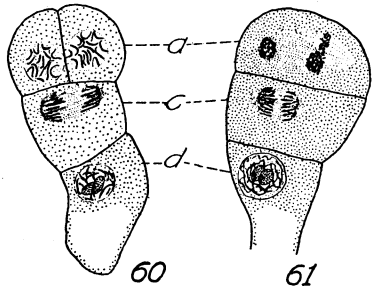

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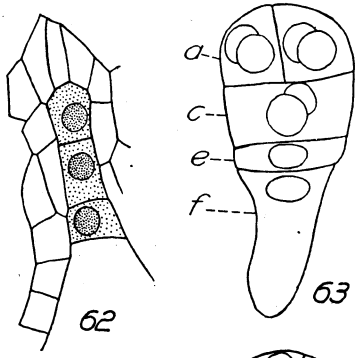

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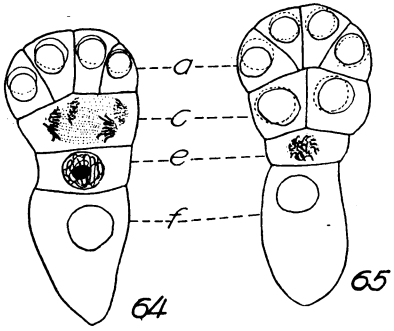

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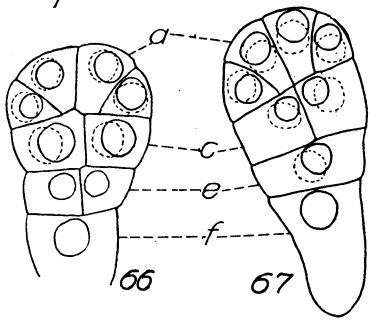

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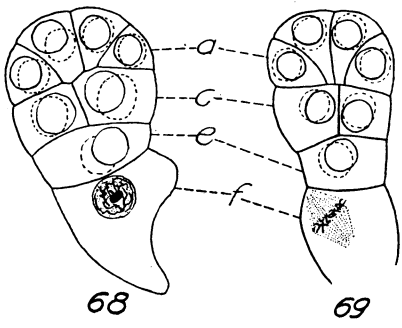

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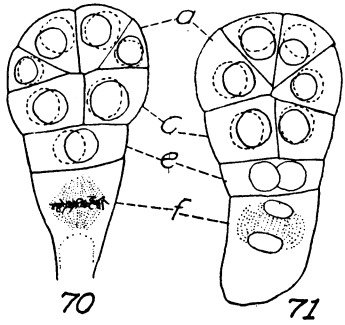

70 71

PLATE 13

All figures *ca.* × 700.

Fig. 72. Sixteen-celled embryo: tier *a*, eight-celled; tier *c*, four-celled; tier *e*. two-celled; *g* and *h*, daughter cells of *f*. Ten A.M., June 13, 1924, twenty-six hours after pollination.

Figs. 73 and 74. In tiers *a* and *c*, dermatogen cells have been cut off; in tier *c*, periblem and plerome cells have been differentiated. Six P.M., June 13, 1924, thirty-four hours after pollination.

Fig. 75. One cell of the plerome in tier *c* has divided transversely. Dermatogen cells and periblem initials have been differentiated in tier *e*. Six A.M., June 14, 1924, forty-six hours after pollination.

Fig. 76. Both plerome cells of tier *c* have been divided into two by transverse walls. Six A.M., June 14, 1924, forty-six hours after pollination.

Fig. 77. Tier *c* has become a 3- to 4-celled layer. Eight A.M., June 15, 1924, three days after pollination.

Fig. 78. Cotyledonary swellings appearing. Eight A.M., June 15, 1924, three days after pollination.

Fig. 79. Lower portion of embryo. Cells of root cap (shaded); dermatogen cells with nuclei shown. Eight A.M., June 16, 1924, four days after pollination.

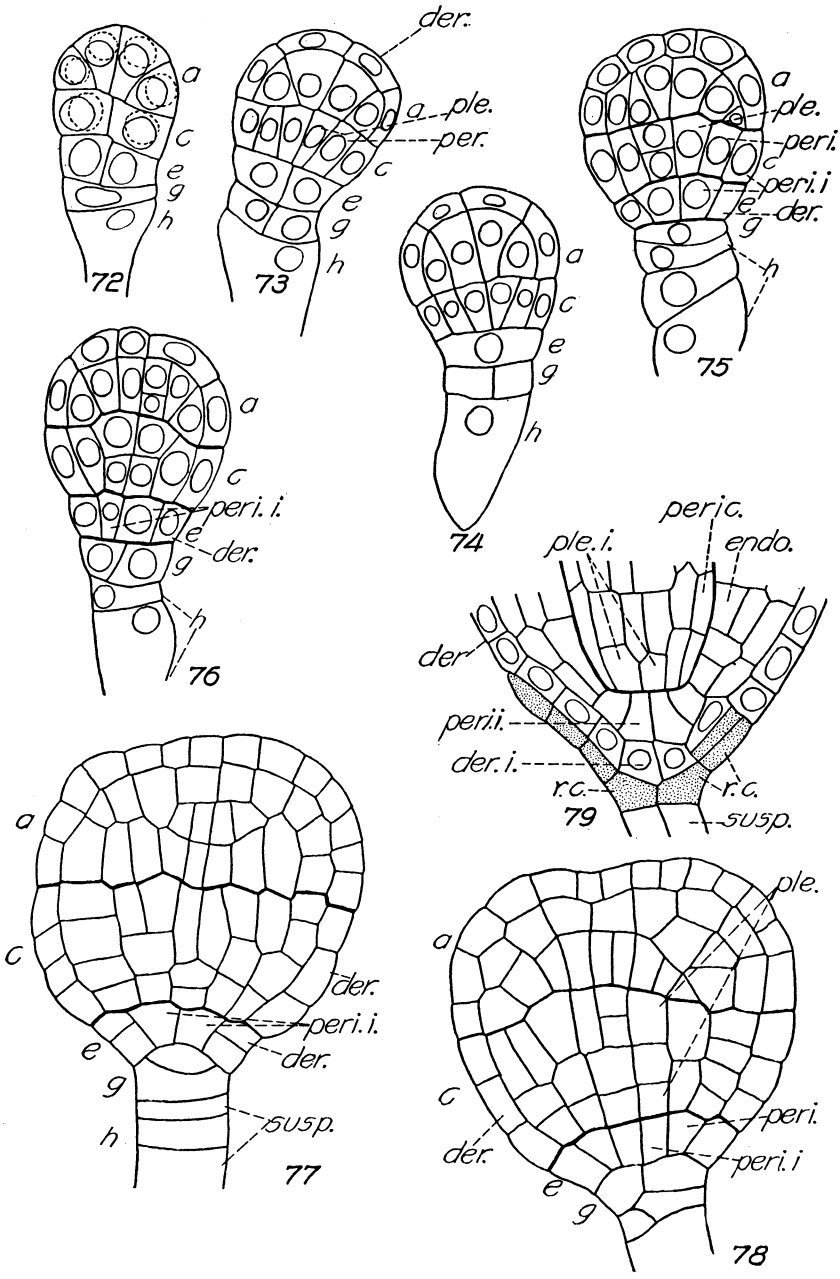
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PLATE 14

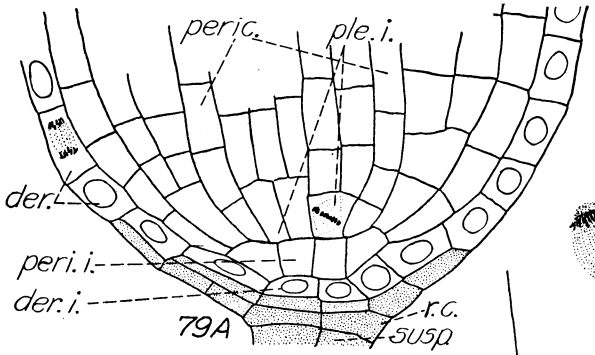
All figures *ca.* × 700.

Fig. 79*a*. Lower portion of embryo. Cells of root cap (shaded), and dermatogen cells with nuclei shown. Eight A.M., June 16, 1924, four days after pollination.

Fig. 80. Four-celled embryo: fourth division of the free endosperm nuclei. Eight P.M., June 12, 1924, twelve hours after pollination.

Fig. 81. Eight-celled embryo: walled endosperm cells. Four A.M., June 13, 1924, twenty hours after pollination.

Fig. 82. Longitudinal section of embryo sac showing endosperm tissue just above the developing embryo. Eight A.M., June 15, 1924, three days after pollination.



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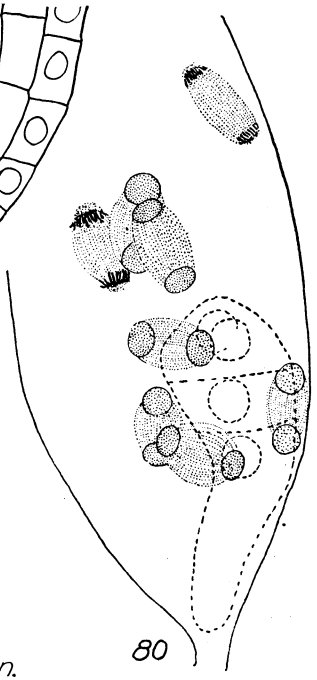

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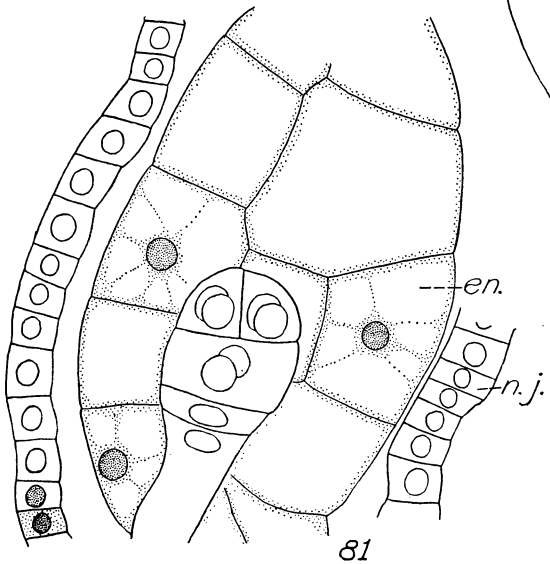

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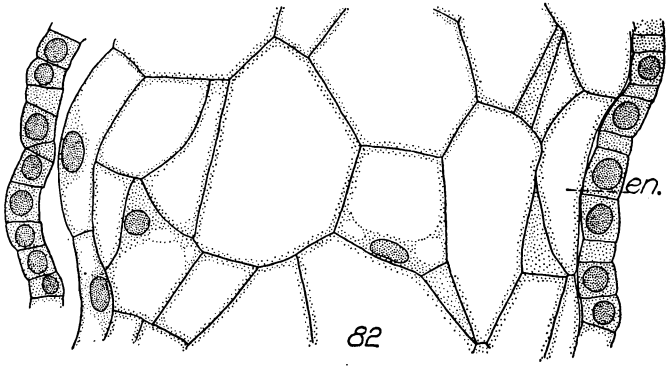


82

PLATE 15

All figures *ca.* × 5.

Fig. 83. Flower head twenty-four hours preceding anthesis.

Fig. 84. Single bud of head shown in figure 83.

Fig. 85. Flower head two hours preceding anthesis.

Fig. 86. Single flower, just before full bloom. Pollen-covered pistil not fully extended.

Fig. 87. Single flower in full bloom. Pistil is fully extended and covered with pollen.

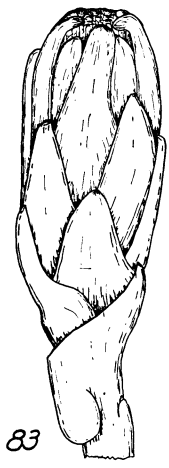
Fig. 88. Twenty-four hours after anthesis. Withered corollas, stamens, and styles still attached.

Fig. 89. Individual flower from head shown in figure 88.

Fig. 90. Developing achenes; forty-eight hours after pollination.

Fig. 91. Seed head three days after pollination.

Fig. 92. Developing achenes from head shown in figure 91.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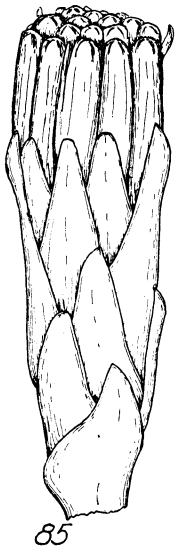
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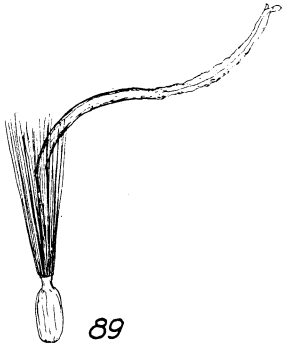
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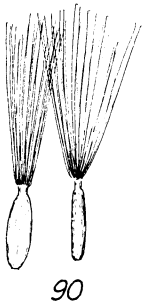
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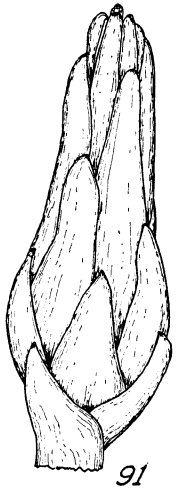
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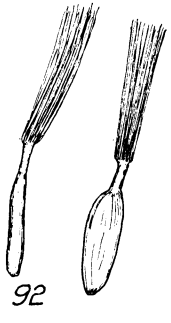

92

PLATE 16

Figs 93 to 95 *ca.* × 5; figs. 96 to 102 *ca.* × 30.

Fig. 93. Developing achene four days after pollination.

Fig. 94. Seed head five days after pollination.

Fig. 95. Developing achene six days after pollination.

Figs. 96 to 102. Longitudinal sections through the developing fruit.

Fig. 96. Six P.M., June 12, 1924, ten hours after pollination.

Fig. 97. Ten P.M., June 13, 1924, fourteen hours after pollination.

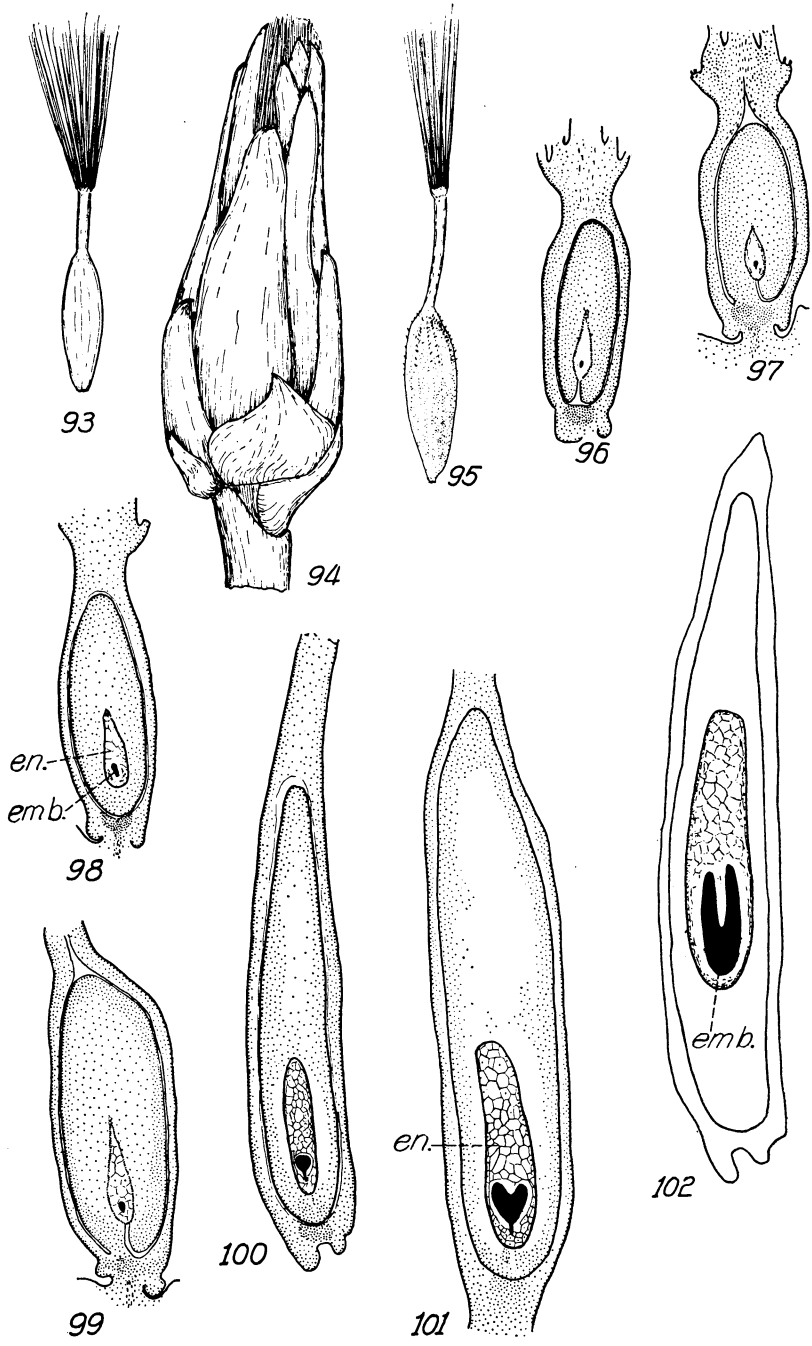
Fig. 98. Ten A.M., June 13, 1924, twenty-six hours after pollination.

Fig. 99. Six P.M., June 13, 1924, thirty-four hours after pollination.

Fig. 100. Six A.M., June 14, 1924, forty-six hours after pollination.

Fig. 101. Eight A.M., June 16, 1924, four days after pollination.

Fig. 102. Eight A.M., June 17, 1924, five days after pollination.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102

PLATE 17

All figures *ca.* × 30.

Fig. 103. Eight A.M., June 18, 1924, six days after pollination.

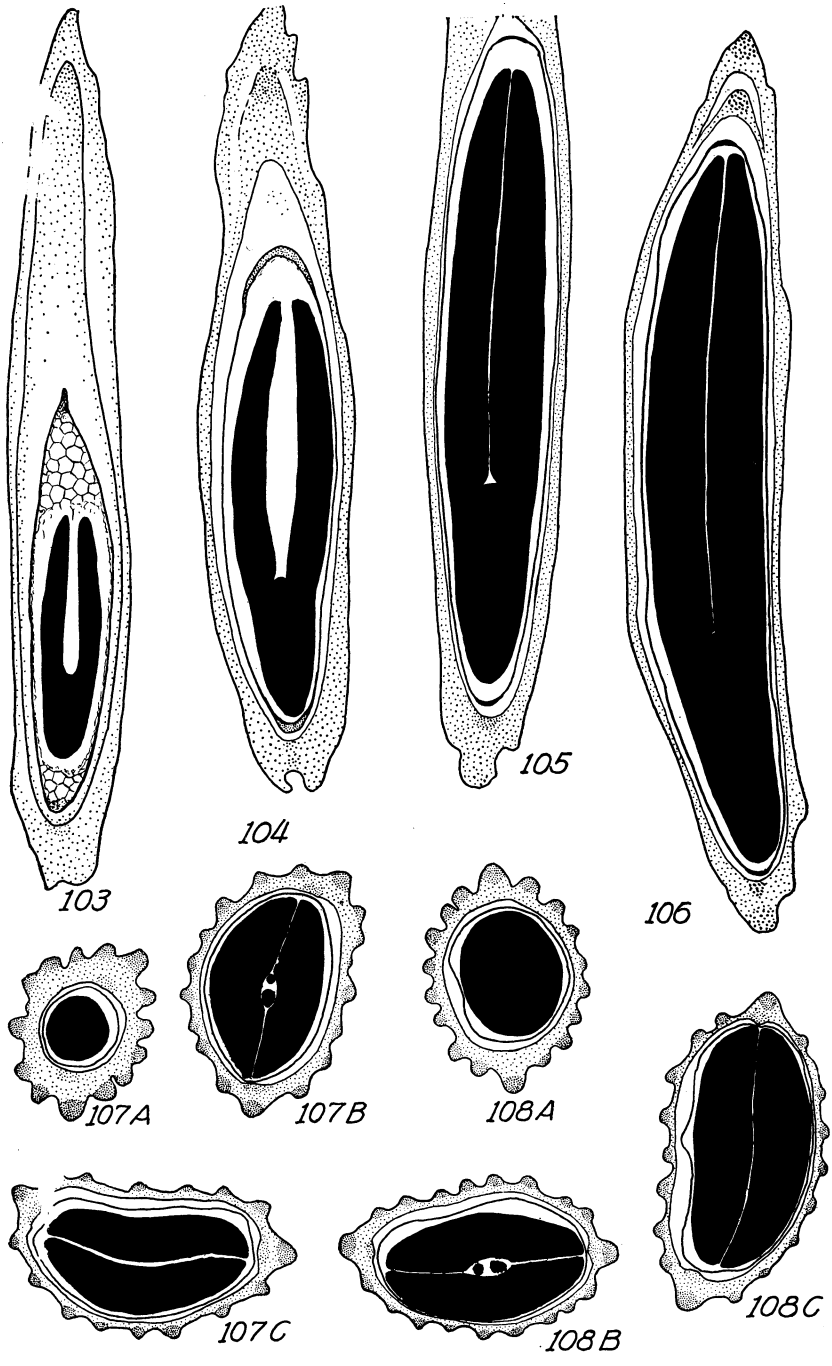
Fig. 104. Eight A.M., June 19, 1924, seven days after pollination.

Fig. 105. Seven A.M., June 20, 1924, eight days after pollination.

Fig. 106. Eight A.M., June 23, 1924, eleven days after pollination. (The following day the achenes of the same age were ripe.)

Fig. 107. Transverse section through developing achenes. Eight A.M., June 21, 1924, nine days after pollination. *A*, radicle; *B*, cotyledons and plumule; *C*, cotyledons.

Fig. 108. Transverse section through developing achene. Eight A.M., June 23, 1924, eleven days after pollination. *A*, radicle; *B*, cotyledons and plumule; *C*, cotyledons.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107A
107B
108A
107C
108B
108C

PLATE 18

Fig. 109. Flowering and seed ripening curves for plant No. 8. Mean temperature is given in degrees Fahrenheit.

Fig. 110. Flowering and seed ripening curves. Average of all plants.

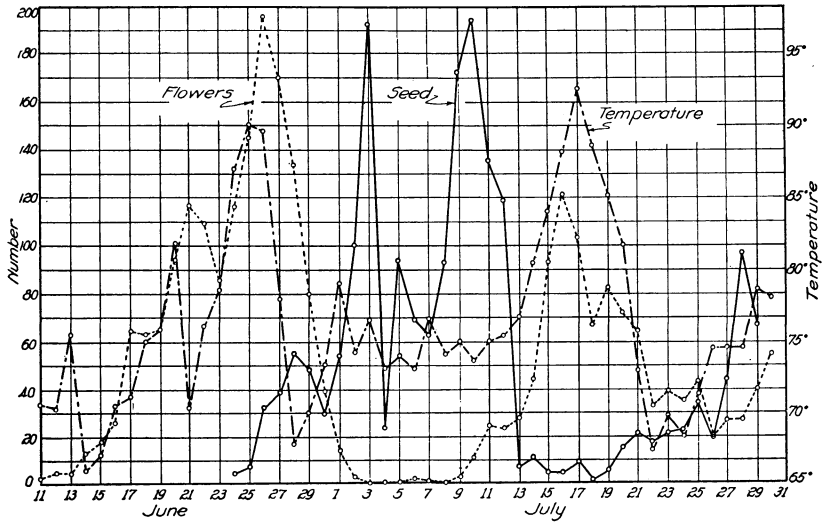

Fig. 109

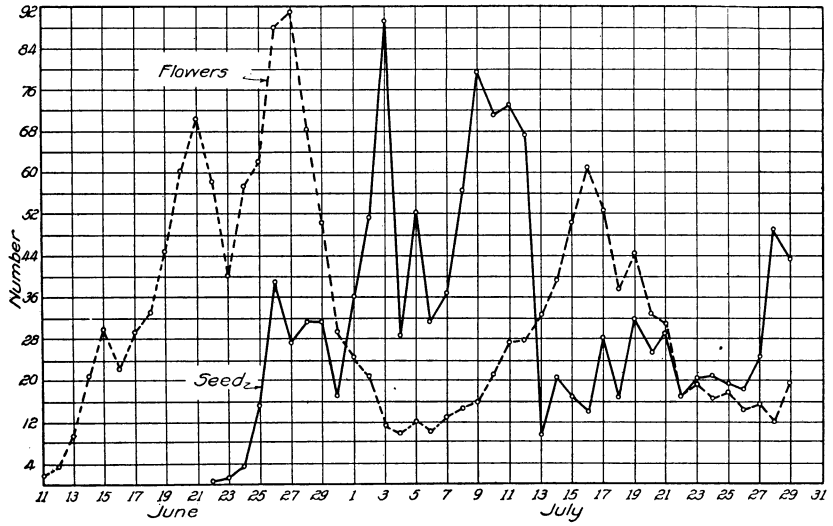

Fig. 110

The titles of the Technical Papers of the California Agricultural Experiment Station, Nos. 1 to 20, which HILGARDIA replaces, and copies of which may be had on application to the Publication Secretary, Agricultural Experiment Station, Berkeley, are as follows:

1. The Removal of Sodium Carbonate from Soils, by Walter P. Kelley and Edward E. Thomas. January, 1923.
3. The Formation of Sodium Carbonate in Soils, by Arthur B. Cummins and Walter P. Kelley. March, 1923.
4. Effect of Sodium Chlorid and Calcium Chlorid upon the Growth and Composition of Young Orange Trees, by H. S. Reed and A. R. C. Haas. April, 1923.
5. Citrus Blast and Black Pit, by H. S. Fawcett, W. T. Horne, and A. F. Camp. May, 1923.
6. A Study of Deciduous Fruit Tree Rootstocks with Special Reference to Their Identification, by Myer J. Heppner. June, 1923.
7. A Study of the Darkening of Apple Tissue, by E. L. Overholser and W. V. Cruess. June, 1923.
8. Effect of Salts on the Intake of Inorganic Elements and on the Buffer System of the Plant, by D. R. Hoagland and J. C. Martin. July, 1923.
9. Experiments on the Reclamation of Alkali Soils by Leaching with Water and Gypsum, by P. L. Hibbard. August, 1923.
10. The Seasonal Variation of the Soil Moisture in a Walnut Grove in Relation to Hygroscopic Coefficient, by L. D. Batchelor and H. S. Reed. September, 1923.
11. Studies on the Effects of Sodium, Potassium, and Calcium on Young Orange Trees, by H. S. Reed and A. R. C. Haas. October, 1923.
12. The Effect of the Plant on the Reaction of the Culture Solution, by D. R. Hoagland. November, 1923.
13. Some Mutual Effects on Soil and Plant Induced by Added Solutes, by John S. Burd and J. C. Martin. December, 1923.
14. The Respiration of Potato Tubers in Relation to the Occurrence of Blackheart, by J. P. Bennett and E. T. Bartholomew. January, 1924.
15. Replaceable Bases in Soils, by Walter P. Kelley and S. Melvin Brown. February, 1924.
16. The Moisture Equivalent as Influenced by the Amount of Soil Used in its Determination, by F. J. Veihmeyer, O. W. Israelsen and J. P. Conrad. September, 1924.
17. Nutrient and Toxic Effects of Certain Ions on Citrus and Walnut Trees with Especial Reference to the Concentration and Ph of the Medium, by H. S. Reed and A. R. C. Haas. October, 1924.
18. Factors Influencing the Rate of Germination of Seed of Asparagus officinalis, by H. A. Borthwick. March, 1925.
19. The Relation of the Subcutaneous Administration of Living Bacterium abortum to the Immunity and Carrier Problem of Bovine Infectious Abortion, by George H. Hart and Jacob Traum. April, 1925.
20. A Study of the Conductive Tissues in Shoots of the Bartlett Pear and the Relationship of Food Movement to Dominance of the Apical Buds, by Frank E. Gardner. April, 1925.