The morphology of Iva xanthiifolia, Nutt

Clifford Harrison Farr
State University of Iowa

This work has been identified with a Creative Commons Public Domain Mark 1.0. Material in the public domain. No restrictions on use.

This thesis is available at Iowa Research Online: https://ir.uiowa.edu/etd/3576

Recommended Citation

Follow this and additional works at: https://ir.uiowa.edu/etd
THE MORPHOLOGY OF *IVA XANTHIFOLIA*, NUTT.

by

Clifford H. Farr.
OUTLINE

Introduction --------------------------------------------------------------- Page. 1.
Distribution and habitat---------------------------------------------------- " 2.
Preparation of material--------------------------------------------------- " 2.
Vegetative Structure------------------------------------------------------- " 3.
I. Inflorescence------------------------------------------------------------- " 4.
Arrangement of flowers in head -------------------------------------------- " 4.
Floral bracts--------------------------------------------------------------- " 4.
Vascular system------------------------------------------------------------- " 5.
II. Floral Development----------------------------------------------------- " 7.
Development of Capitula---------------------------------------------------- " 7.
Involucral bracts----------------------------------------------------------- " 7.
Receptacle--------------------------------------------------------------------- " 8.
The Staminate Flower-------------------------------------------------------- " 8.
-the stamens---------------------------------------------------------------- " 9.
-the nectaries---------------------------------------------------------------- " 10.
-rudimentary pistil--------------------------------------------------------- " 11.
The Pistillate Flower-------------------------------------------------------- " 13.
-order of development------------------------------------------------------ " 13.
-the ovule---------------------------------------------------------------- " 13.
-the stigma---------------------------------------------------------------- " 14.
Anomalous Flowers---------------------------------------------------------- " 14.
-significance---------------------------------------------------------------- " 15.

94479
Discussion

- absence of floral bracts in outer whorl of staminate flowers

Page. 16.

- origin of capitula

" 16.

- origin of pistillate and staminate flowers

" 17.

- cause of abortion of pistil

" 17.

- cause of abortion of stamens

" 19.

III. The Female Gametophyte

- the primary archesporial cell

" 20.

- synapsis

" 20.

- megaspores

" 21.

- mature embryo sac

" 21.

- embryo

" 22.

IV. The Development of Male Gametophyte

- the generative cell

" 24.

Germination of Pollen

" 26.

The Sperms

" 26.

Division of nucleus of generative cell

" 27.

Male nuclei

" 28.

Discussion

" 29.

V. Summary and Conclusions

" 32.

Literature Cited

" 37.

Explanation of Plates

" 40.
The Compositae have long been considered the highest group of flowering plants. The sympetaly and epigyny of the flowers with the diverse modifications of the calyx and corolla, places them at the summit of long lines of evolution in these respects. While the association of flowers together in compact and specialized heads, in which they may be perfect or differentiated into fertile, sterile, or neutral flowers, presents the most highly developed inflorescence of the plant kingdom. It is not surprising that critical morphology, has dealt extensively with more primitive forms and has left this group without thorough investigation. The time has come, however, when more should be known regarding the intimate structure of all plants, specialized as well as primitive. The present study was hence undertaken in the hope of contributing something to the knowledge of this culminating group. The species suggested for investigation was *Iva Xanthiifolia*, Nutt., a form that has special interest on account of its monosporangiate flowers.

The genus, to which this species belongs, is closely related to *Ambrosia*, *Xanthium*, and *Gaertneria*, constituting, according to Britton (1), with these genera a distinct family. It contains many species, five of which are prominent in the United States. One species, *Iva frutescens*, is common in the salt marshes of the Atlantic Coast, while *Iva imbricata* abounds on the sandy shores of the same
region. *Iva axillaris* is a distinctly western species, and the other two, *ciliata* and *Xanthiifolia*, occur in portions of the central states.

The species under investigation differ from the other American forms in that the corolla of the pistillate flower is "a mere rudiment". It was named in 1818 by Nuttall (24) from specimens collected "near Fort Mandan etc, on the banks of the Missouri." It has since been reported as far south as New Mexico, east into Ontario, and west to Utah. Not only has it a rather extensive geographical distribution, but within its range, it is found growing in a wide variety of habitat. Within a few acres near Lake Okoboji, individuals of this species have been observed growing in shady ravines, in small clearings in woods, in the open beside running brooks, on the slopes of treeless hills and in cultivated gardens. They seem, however, to find their best expression in moist soil, where they flourish in dense clusters and patches. In no case did the writer find them thriving under extremely xerophytic conditions, or in densely shaded woods. So that from a study of the conditions under which it lives this species would seem to be neither a typical mesophyte nor an extreme xerophyte.

The material for this investigation was collected in the vicinity of the Iowa Lakeside Laboratory, Dickinson Co., Iowa, during the months of July and August, 1911. A solution of one per cent chronic acetic acid was used in fixation after which the material was imbedded in paraffin and sectioned from three to twelve micra in thickness. Preparations were stained most successfully in Flemming's Safranin-Gentian Violet-Orange G, in Iron alum-Haemotoxylin,
and in Delafield's Haematoxylin. Each of these stains was used singly, as was Eosin and Fuchsin, but with unsatisfactory results. The use of lime water in the 95% alcohol seemed to aid considerably in the clearing of preparations stained in Safranin.

The work was carried on under the supervision of Professor R. B. Wylie, whose many helpful suggestions and kind assistance is thoroughly appreciated. Thanks are also due Professors Macbride and Shimek for assistance in the securing of material and the consultation of literature.

Individuals of this species vary from one to eight feet in height, being smaller when alone and in drier soil. The leaves are from four to six inches in diameter and the epidermal cells are not highly cutinized, adding to the necessity of a large supply of water. On the other hand the leaves are covered with a dense coat of trichomes of two kinds. The slender filamentous hairs of four or eight cells terminate in a long hard spine. These hairs do not ordinarily stand erect but bend over forming a weft, which doubtless prevents the currents of air from reaching the surface of the leaf. Between these are the low globose glandular hairs each made up of two rows of five or six cells. The end is covered by a somewhat disc-shaped glandular cell. These trichomes protect the leaf and favor the growth of the plant in exposed places.
1. ORGANOGRAPHY OF THE FLOWERS.

In common with other Compositae the flowers of *Iva xanthiifolia* are produced in compact heads or capitula. The capitula are associated in "ample, erect, terminal or axillary, spikes." (1). Each head consists of sixteen to twenty-eight individual flowers, of which the five marginal ones are fertile and the remainder are sterile. Britton (1) places the number of staminate flowers at 10-15, which is rather low for the material examined in this investigation.

The arrangement of flowers in cycles in the head is peculiar and is not known to have been previously reported for any of the Compositae. The head is surrounded by a whorl of five involucral bracts which are equally spaced. In the axils of these appear the five pistillate flowers, likewise in a whorl. This arrangement of the members in whorls of five is further extended to the staminate flowers. The innermost whorl of these, however, may be incomplete, consisting of one to four flowers. The individuals of successive whorls alternate. Danforth (6) and others have demonstrated that some Compositae have flowers arranged in spirals arising from the center of the head. It is possible that the cyclic arrangement may have been derived from such a spiral, there being five spirals with one flower of each cycle in each spiral.

Each flower, with the exception of the outer whorl of staminate flowers, develops a floral bract on its outer side. The bracts of the staminate flowers are about three-fourths as long as the mature flower (fig. 12). They are very slender being not more than twice as broad as thick (fig. 26), and fill the interstices between the flowers.
The five pistillate flowers have very large floral bracts (fig. 23), which conform to the inner surface of the involucral bracts. Britton (1) suggests that they constitute an inner whorl of involucral bracts. It will be subsequently shown that these bracts are intimately associated with the pistillate flowers during their development, due to their marginal position. It is easy to understand how such a condition might have arisen phylogenetically.

The anatomy of the vascular supply of the head is of interest in considering the relations of the flowers. Normally five vascular bundles enter the center of the head from the peduncle. One of these proceeds to each of the involucral bracts. A branch is given off from each of these strands just above the peduncle. This branch, being on the inner side, turns and proceeds parallel to the vascular strand of the involucral bract, entering the floral bract of the pistillate flower. It, however, gives off a branch just beneath the base of this bract, which supplies the fertile flower itself. The members of the outer whorl of staminate flowers are supplied by secondary branches which arise from the bundles supplying the floral bracts of the pistillate flowers. The vascular bundles of the flowers of the second whorl of staminate flowers are branches from the bundles supplying the flowers of the first whorl. The bundles of the members of the third whorl are branches from the bundles of the members of the second whorl, and so on. The examination of a number of heads showed that this arrangement of bundles is not entirely constant; but that the bundles supplying the members of the third whorl may be branches from those of the first whorl, instead of the
second, etc. It would seem then, that the vascular system in the head of *Iva Xanthiifolia* does not necessarily follow any predetermined path, but that it is dependent for its form on the order of development of the flowers. It will be seen that since the members of successive whorls alternate (fig. 23), the distance from those of the third whorl to the vascular strand of the first may not be greater than to the vascular strand of the second whorl. So that, it seems probable that the vascular bundle of a flower is formed along the line which marks the shortest distance to a strand already formed.
2. FLORAL DEVELOPMENT.

The Head.

The order of the development of the heads in the spike is very irregular and apparently possesses no constant sequence. The spike originally consists of a central axis with minute branches arising laterally. The heads appear at first sessile along these branches and upon the main axis. As the axis and branches elongate other heads arise at the bases of those already developing. From this time on new heads continue to appear wherever a portion of the spike becomes exposed.

The first indication of a head consists of a little papilla on the surface of the stem. Two layers of cells are lifted up by the swelling and multiplication of cells within the axis. This is accompanied by an anticlinal division of the epidermal cells, to compensate for the tension due to internal growth.

The involucral bracts appear as the papilla presents some suggestion of a peduncle or stalk at its base (fig. 1). Five lobes (fig. 23.) push out from the rim. These bracts are distinct nearly to their bases, and continue to grow until they meet or even overlap above the center of the head (fig. 3). On their outer surfaces the glandular and filamentous hairs furnish an efficient protection, the latter interlocking above the center of the head. Near maturity the apex of the bract is transformed into a long hard spine, which persists throughout the subsequent existence of the head. Eichler (9) calls attention to the same phenomenon in the fertile heads of Xanthium and Ambrosia, and it would seem that this may be associated with the pistillate flowers which in Iva occur in the axils of these bracts (fig. 23).
The receptacle is at first smooth (fig. 2), but as the bracts meet above, it becomes more or less undulate (fig. 3). These undulations become more and more pronounced until they mould themselves into distinct papillae. Rapid cell division goes on beneath these papillae, giving rise to globose structures, the flowers. The receptacle becomes highly convex, although the marginal flowers develop more rapidly than the central. For some time new flowers continue to appear in the center of the head. The number of flowers developed is probably directly related to local conditions during the growth period. An abundant supply of food and water, sufficient protection, and at the same time space in which to expand would doubtless favor the production of many flowered heads.

The Staminate Flower.

Up to this point it is not possible to distinguish between the pistillate and staminate flowers. Presently, however, each flower in the central part of the head grows rapidly in its center and about the margin, resulting in the formation of a ringlike depression on its surface (fig. 4). This marks the line of separation between the corolla and the stamens and is the distinguishing feature of the staminate flower at this stage. The region outside of this indentation does not remain a continuous rim, but becomes segmented into five lobes which are very distinct in cross section (fig. 5). Later five papillae also appear on the inner side of the ring, which mark the origin of the five stamens. These alternate with the five lobes of the corolla (fig. 6). This order of development is the same
as that described for Silphium (21) and Aster and Solidago (20). But in these the appearance of the stamens is followed by the advent of the pappus, while in *Iva Xanthiifolia*, no calyx or structure comparable with a calyx is produced. It is evident that the floral bracts cannot be considered as rudiments of a calyx, since not more than one is associated with each flower and since these bracts occur in other Compositae (9) in which pappus is also developed.

The stamens early appear more or less globose (fig. 8); but later, elongate and become concave on their inner surface (fig. 10), and narrow below, suggesting the appearance of filaments. The four microsporangia of each stamen are similar in size and form in the early stages, but later the outer two show a greater development (fig. 27). This is probably a mechanical adaptation to the space available for growth being restricted by the tubular corolla. The stamens, in fact, enlarge until they touch and the walls of the adjacent stamens appear fastened together, though the epidermal cells remain unmodified. Eichler (9) in describing the Compositae says, "die Antheren jedoch zu einer Rohre verklebt (nicht wirklich verwachsen)". Martin (20), however, in speaking of the condition in Aster and Solidago, states the following, "The anthers do not simply cohere but unite, for cross sections show the blending of epidermal tissue; this makes the union complete". It is doubtless true that some plants show a more marked union of their anthers than others. While the situation in *Iva* is hardly as marked as would seem to be the case in Aster and Solidago, yet it would certainly fall within the description given by Eichler.
for the Compositae. It is therefore very doubtful if this character is sufficiently constant and marked to become the basis of excluding the species from the Compositae, as Britton has done. The results of this investigation would therefore support the classification of Gray (12) and indicates in many ways their close resemblance to the typical Compositae.

The first suggestion of dehiscence is found in the breaking of the walls between the adjacent inner and outer microsporangia, resulting in the formation of two pollen sacs in each stamen. Schneider (29) has suggested that this rupturing of the walls of the microsporangia is due to the growth of the pollen mass. In *Iva Xanthiiifolia* the pollen grains do enlarge just before maturity (fig. 57). It would therefore seem that the breaking together of the microsporangia may be attributed in part at least, to such a growth.

The lateral pollen sacs of adjacent stamens also become confluent in this species. This is accomplished by the breaking down of the central portion of the lateral walls of each stamen. The outer edges of the lateral walls however remain coherent, so that each chamber resulting from the congluence of the contiguous pollen sacs of adjacent stamens is enveloped by an intact wall. In this way, there is present at maturity in each flower five large pollen chambers arranged in a whorl.

Inside the base of the filaments five small structures, (fig. 12) appear which are alternate with the stamens, and, if they function at all, may serve as nectaries. They never become more than one hundredth the length of the mature stamen and are scarcely noticeable even in sections. Goebel (13) describes similar structures as "a fleshy
cushion forming a disk." He (14) presents strong evidence that nectaries arise by the transformation and modification of other morphological structure. He shows how stipules become nectariferous in *Vicia* and *Sambucus*; how "petals or stamens may be transformed into nectaries in many flowers, for instance, in the Ranunculaceae", and that "the outer stamens are transformed into nectaries in *Anemone pulsatilla*". Parkin (26) found nectaries formed from bud scales in *Hevea*. Martin (20) in working with two of the Compositae also regards the structures in question as nectaries and says that they are supposed to represent an inner row of imperfectly formed stamens. Merrell (21) stands apparently alone in opposing this general consensus of opinion. He suggests that, "It is much more reasonable to regard the nectary as an organ of independent origin". The evidence which he presents in support of this view is not entirely convincing and may perhaps admit of other interpretation; of course, it cannot be proven that either is the correct view; and it is quite possible that nectaries may arise in either way. It is however, the attitude of science at the present to explain the existence of structure by their derivation from possible antecedent structures rather than postulating their origin de novo. The number of possible nectaries in *Iva Xanthiifolia* and their position in the flower strongly suggest that they may be the rudiments of an inner whorl of stamens, such as occurs in certain of the Saxifragaceae, Caryophyllaceae, Leguminoseae, Geraniaceae, Simarulaceae, and Euphorbiaceae.

The development of the pistil of the staminate flower is peculiar and is very unlike that of the pistillate flower. The center of the head, which is at first concave, (fig. 6) becomes flat (fig. 7)
and the vertical cell wall at the exact central point appears very much thickened. This thickening develops into a notch (fig. 8) by the elevation of tissue on either side, and becomes quite marked as development proceeds (fig. 10). Meanwhile the developing pistil grows upward carrying the notch on its broadened summit. The pistil, however, remains shorter than the stamens and near maturity develops a large capitulate disk on its upper surface. This disk is covered by long unicellular hairs, which are longest about the margin, giving the disk a concave appearance (fig. 12). Furthermore they grow over and about the notch in such a way as to practically obliterate it.

When the pollen matures, this modified pistil pushes out from among the stamens, and projects a considerable distance beyond them. The stamens possess on their outer end a mass of tissue (fig. 12) which previous to this time has developed into a hard hooklike spine pointing toward the center of the flower. It is evident that when the stylar thrust, above described, takes place, that considerable tension will be brought to bear on these hooks which curve over the capitulate stigma. It is credible that this tension is sufficient to tear open the pollen chambers which are only kept intact by the cohering margins of the walls of adjacent stamens. It would also seem that the broad capitulate structure spreading out over the flower during pollination would tend to prevent the microspores from being shed en masse, scattering them about rather so as to accomplish cross pollination more readily.

In Silphium (21) Merrell found a similar rudimentary pistil, except that the capitulate structure was not developed. That this is the rudiment of a once functional pistil can scarcely be doubted. Its
position, the presence of stigmatic hairs, the notch suggestive of the development of an ovarian chamber in preceding generations, its tardy appearance, and the stylar thrust all point to its being an aborted pistil.

The Pistillate Flower.

The upper surface of the anlage of the pistillate flower assumes a concave appearance, the upturned rim (fig.14) becoming the developing corolla. On the inner side of this rim the carpels appear as two lobes (fig.15), separated by a marked depression. It is interesting to note that in Silphium (21) the stamens succeed the corolla and precede the carpels. It is probable that the abortion of the stamens has been carried a step farther in Iva and that their appearance has been delayed by the emphasis upon the development of the carpels. This is further suggested by the appearance of the aborted stamens as a ring-like development about the base of the style(fig.20). This becomes more and more pronounced, finally developing into a collar-like structure.

As the carpels reach the level of the developing corolla(fig.16) the ovule appears as a small papilla on the inner side of the base of the ovarian cavity. The ovule enlarges gradually and curves back toward the center of the head (fig.19), finally becoming completely anatropous (fig.20). The vascular supply of the ovule (fig.22) agrees with that of Silphium,(21) in being terminal and in circumtraversing the ovule at a point on the inner side at the level of the embryo sac. There has been much discussion regarding the origin of ovules. Coulter and Chamberlain(5) have divided them into three classes: foliar, ter-
minally cauline, and laterally cauline. All indications point to a laterally cauline ovule in *Iva Xanthiifolia*.

The stigna develops by the elongation of the projecting ends of the carpels (figs.15-22). The style is very short reaching merely to the level of the aborted corolla, which forms a collar-like structure enveloping the aborted stamens. The stigma, on the other hand, is very long equaling the length of the ovary prior to maturity, and later elongating beyond the floral bract and curving over the corolla of the staminate flower of the second whorl. It is covered with short globose stigmatic hairs on its inner and terminal surfaces. Very little pollen was found in contact with these stigmas, although they have every external appearance of being functional.

Anomalous Flowers.

Two unusual fertile flowers appeared amongst the material examined, which may throw some light upon the structure of the normal flowers. In one (fig.26) the only abnormality consisted in the production of a tubular corolla twice as long as the normal aborted corolla. This phenomena would seem to indicate that the pistillate flower at one time possessed a corolla like that of the now staminate flowers. Under that interpretation the instance in question would be a case of reversion. The other case however presented a much more complicated condition. Here (fig.24) a fertile flower, possessing a normal bract, bore on its inner side three well developed stamens. On this side the corolla resembled exactly that of the normal staminate flower, being divided into two lobes at the end. On the other side, however, it became gradually reduced in size, from right to left. It
reached its greatest reduction in the inner left region where it is about the size of the corolla found in the normal pistillate flower. So that at this place there is an abrupt change from the pistillate to the staminate type. A similar situation may be traced in respect to the stamens. The inner left stamen has its outer two microsporangia containing nearly mature pollen. The inner microsporangia have pollen aborted at the microspore nucleus stage. The two other stamens on the right (fig.25) possess pollen aborted at the mother cell stage. On the outer and left sides the stamens are reduced into a collar, higher on the right and gradually decreasing in size toward the left. At this point of sudden transition from the pistillate to the staminate condition an opening occurs in the wall of the ovary between the ovarian chamber and the region between the stamens. It is probably due to the over-development of the inner side and the abortion of the outer side of the flower, resulting in a line of weakness where these two parts meet. The evident reversion of the parts of this flower is even extended to the stigma which is normal for a pistillate flower on its outer side but develops a capitate structure on its inner side beneath the corolla.

These cases of reversion serve to show beyond a doubt that the normal pistillate flowers possess both aborted stamens and aborted corolla, while the staminate flower possesses an aborted pistil. It would further indicate that both flowers may have arisen from epigynous, sympetalous flowers, by the abortion of different parts. In other genera structures comparable to the aborted stamens of the pistillate flower show signs of functioning as nectaries. The evidence herewith presented would suggest that such structures arose by the
abortion of stamens.

Discussion.

The absence of floral bracts in the outer whorl of staminate flowers presents a rather difficult problem. All the other flowers of the head possess floral bracts and furthermore, there is a whorl of so-called involucral bracts the phylogenetic origin of which is obscure. It is perhaps possible that the floral bracts of the pistillate flowers and the involucral bracts may have been derived from the floral bracts of the pistillate flowers and of the outer whorl of staminate flowers by some shift in position. However, such an hypothesis no doubt would offer more difficulties than it would explain. The alternative would be to consider that the floral bracts of the outer whorl of staminate flowers have been completely aborted. It is evident that the excessive lateral development of the bracts of the pistillate flower would tend toward such obliteration since the bracts in question would normally occur between the bracts of the adjacent pistillate flowers. Furthermore, it will be observed that the adjacent involucral bracts overlap in the same region, resulting in a pressure which would act in a similar way. Knupp (17) in explaining the rudimentary sepals of Myriophyllum makes use of a similar hypothesis. It is probable that the abortion has been entirely complete in the case of Iva, where no sign of even a rudiment appears.

The study of floral development in Iva Xanthiifolia affords strong evidence that the capitulum is phylogenetically a contracted spike. The presence of a meristematic region in the center of the head is suggestive of apical development. The existence of floral bracts within the head points to the previous arrangement of the
flowers in the axils of subtending leaves. The vascular system, in so far as it is dependent upon recapitulation for its form, likewise is indicative of an axial organization. So that while other origins may be possible, all the evidence supports the view that many generations ago the ancestors of these plants possessed floral spikes.

But whether or not this hypothesis is accepted, it can scarcely be doubted that this capitulum, however formed, was at first composed of perfect flowers, such as are found in many of the Compositae. The aborted pistil of the sterile flowers, the function of which has been reduced from that of seed bearing to the opening of anthers, is more than suggestive of an antecedent perfect flower. This conclusion is further supported by the aborted stamens of the fertile flower. And it is strongly confirmed by the case of reversion in which stamens and pistil are both found in the same flower.

The search for some cause for the differentiation into pistillate and staminate flowers, has lead to the conclusion that this cause is to be found, in part at least, in the relation of the plant to the drying conditions of its environment. Several observations serve to demonstrate that the flowers of the central part of the head of *Iva Xanthifolia* are more exposed than the marginal flowers. The opening of the involucral bracts exposes the central flowers first and their closing protects them last. Furthermore, while the involucral bracts are open they shield the marginal flowers almost completely from the direct rays of the sun, at the same time being of little service, if any, to the central flowers in this respect. The floral bracts of the central flowers are much smaller than those of the marginal flowers. The convexity of the receptacle results in the mark-
ed elevation of the central flowers. The central flowers appear last and so are perhaps, less protected during their early stages of development. And finally the marginal flowers are much less closely connected to the vascular supply, while the marginal flowers and the bracts which subtend them are in direct communication with the vascular bundles of the main axis. In fact the whole organization of the head is such as to afford a maximum protection to the marginal flowers and a maximum of exposure to the central flowers.

It is apparent that the androecium of a flower is better adapted, both in structure and in function to endure dessication, than is the gynecium. The developing ovule and embryo sac must be kept moist. The pistil at maturity must expose a delicate stigma, and after fertilization the growing embryo must be nourished. On the other hand, the stamens develop rapidly. Dehiscence and wind pollination are both facilitated by dry air and dry stamens. With the shedding of pollen the work of the stamen is complete, while the development of the pistil is only fairly begun.

It would seem then that the differentiation of the flowers of *Iva Xanthiifolia* into pistillate and staminate may have been caused by the exposure of the central flowers to drying conditions through many generations. It has been shown that both in habit and in vegetative structure this plant possesses characters which are intermediate between those of a mesophyte and of a xerophyte. It is entirely possible that this organization into pistillate and staminate flowers may be in some way correlated with the subjection of a mesophyte to xerophytic conditions.
The above suggestion explains the sterility of the central flowers, but does not account for the failure of the marginal flowers to produce functioning stamens. This latter phenomena is doubtless a more recent acquisition as is indicated by the case of reversion and the aberrant development of the aborted pistil. The loss of the stamen-bearing habit by the fertile flowers may be due to the necessity for seed production on their part. It is also to be noted that such stamens, if present, would be crowded by the hard involucral bract on one side and the staminate flowers on the other.
3. THE FEMALE GAMETOPHYTE.

The events in the development of the female gametophyte can be given only in outline, because of the difficulty in obtaining good longitudinal sections of the embryo sac. Each head contains only five pistillate flowers, all oblique to the axis of the head, so that even theoretically but one embryo sac could be cut in sections parallel to the axis. The difficulty is further heightened by the smallness of the flowers, a mature head being only three or four millimeters in diameter.

The primary archesporial cell appears near the end of the axial row of the laterally cauline ovule while this is yet directed toward the stigma. It is distinguishable by its subepidermal position, its size, though its staining reaction is not markedly different from the other cells of the ovule at this time. In harmony with other Sympetalae (5) no primary parietal cell is cut off, but the primary archesporial cell functions as the megaspore mother cell.

The nucleus of the megaspore mother cell continues to enlarge, (fig's 30-31) the number of nucleoli is not constant at this stage, but varies from one to four. This fact has also been noted by Schaffner in Lilium Philadephicum (28), as has also the following fact, that just prior to synapsis (fig. 32) a single large nucleolus is present, having a large vacuole. After further enlargement (fig. 33) the nucleus assumes a definite synaptic appearance with heavy linin threads bearing deeply staining knots at frequent intervals.

The dyad chromosomes appear as the nucleus emerges from
synapsis (fig. 34). Their number could not be definitely determined, because of their being massed in the region of the nucleolus.

Following mitosis the two daughter nuclei are separated by a cell plate (fig. 35). Each nucleus contains at least twelve bodies which give a chromatic reaction to the stain. They are more or less V-shaped and may be prochromosomes showing their dual nature due to premature splitting. Inasmuch as the morphology of these bodies was not determined with certainty, it is not safe to form any conclusions as to their significance. It is however interesting to note their presence in the daughter nuclei of a cell which has passed through synapsis. While the number of chromosomes has not been definitely determined for this species, the sporophyte number in no case seemed as much as twenty-four.

The four megaspores (fig. 36) were found arranged in an axial row surrounded by the nucellus. In one preparation the nuclei of the inner three present a reddish blur when stained in Safranin, and the cytoplasm is considerably shrunken. The outer megaspore, on the other hand, takes a clear stain and is not appreciably plasmolyzed. It would therefore seem that the outer in this instance would have become the junctioning megaspore. According to Coulter and Chamberlain (5) instances of such a procedure are rather rare among the Sympetalae,—it having been reported in only five genera. But one such case, viz: Pyrethrum, has been previously reported for the Compositae, and that is somewhat doubtful.

While the mature embryo sac, with the material at hand, presented some difficulties, nothing abnormal could be demonstrated.
The synergids (fig. 37) are long sac-like structures, each containing a relatively small nucleus. The egg is large and somewhat pyriform, being surrounded by a definite membrane. Its large nucleus contains one or two deeply staining nucleoli. Three antipodals (figs. 37, 38, 39) often appear to be disintegrating in the chalazal end of the embryo-sac. The number and history of the polars was not satisfactorily determined. In some cases (figs. 37, 38) a cell plate across the middle of the embryo sac separated two large multi-nucleolate nuclei. A similar situation is often found after the first division of the primary endosperm nucleus following fertilization. It is not always possible, however, in the case of Iva to find indications of the presence of a pollen tube in these stages. On the other hand the synergids may appear deeply stained and disorganized and an elongate structure has been found present on one side of the egg (fig. 38). When the embryo is partly developed (fig. 40) suggestions of a pollen tube having entered the micropyle may be found. It is therefore quite probable that fertilization is accomplished, but more evidence is necessary before definite conclusions can be reached.

In the mature embryo sac there appears a single layer of partly disintegrated cells, lining the antipodal region (figs. 37, 38). Merrel in Silphium (21) and Martin in Aster and Solidago (20) refer to similar structures as remnants of a displaced nucellus. It would seem that the cells in question would lend themselves quite readily to this interpretation.

After the appearance of an embryo, the embryo sac broadens, and the endosperm develops very rapidly. By the time it reaches the three-celled stage (fig. 40) the endosperm already consists of eight or
more cells, each apparently surrounded by a distinct cytoplasm. The number of endosperm nuclei is doubled by the time the embryo has become four celled. (fig. 41).

On account of the scantiness of material examined upon this phase of the life history, very few conclusions can be drawn regarding it. On the whole the procedure seems normal. The possibility of the outer megaspore functioning is, however, an exception. The existence of so many chromatic bodies in the resting nuclei between heterotypic and homotypic division is suggestive of a failure in reduction. On the other hand, the appearance of the micropylar region of the mature embryo sac strongly indicates that fertilization is accomplished.
4. THE DEVELOPMENT OF THE MALE GAMETOPHYTE.

The reduction divisions of the microspore-mother-cell were not studied carefully, but were found to result in the production of four microspores, having the characteristic tetrad arrangement. These soon break apart and assume a more or less spherical form, retaining so far as could be discerned, no markings indicating their tetrad origin. The microspore which measures 5.75 micra in diameter at this time (fig. 41) is filled with a highly vesicular cytoplasm and is enveloped by a thin membrane. Its nucleus, comprising about one-eighth the volume of the cell, lies always in the center and consists of delicate reticulated linin threads with moderate sized granules at their points of juncture.

After a period of growth during which the structure and relative position of the nucleus and cytoplasm remains apparently unchanged, the pollen grain reaches a size slightly more than twice its former volume. At this time a heavy exine is formed, enveloping the microspore completely, broken only by three slits, each of which extends nearly one-half the distance around the grain, but which remains closed for sometime, probably until growth or swelling of the microspore within, forces it open by internal pressure. The surface of the exine takes the form of low obtuse spines, arranged at regular intervals, about twenty or thirty in one circumference. The exine itself is marked by minute radiating striations, extending nearly from the inner to the outer surface. Though this coat appears very dense, it was usually not so hard as to break in cutting.
The Generative Cell.

As the time of mitosis approaches the nucleus assumes a somewhat eccentric position and takes a much deeper stain, the granules meanwhile enlarging (fig. 42). The chromosomes arrange themselves in an equatorial line near one side of the pollen grain (fig. 43). Their exact shape could not be determined at this stage but their ends seem to be at least much rounded. The spindle next assumes a bipolar arrangement in length about four-fifths the diameter of the microspore, the fibers lying for the most part nearly parallel to the intine, but with one pole nearer the wall than the other. A large vacuole takes up much of the rest of the pollen grain.

When the chromosomes have reached the poles (fig. 4) their elongate shape is more apparent. The two daughter nuclei remain wide apart, at first the spindle fibers between them lying straight and parallel. But as the cell plate is laid down the nuclei approach each other (fig. 45), and the spindle fibers spread out, so that a plate, convex inward is laid down at right angles to the intine. This condition has been reported by Gager for Asclepias (7). At this time there appears in both the tube nucleus and the nucleus of the generative cell, large sized bodies of granular nature. They are particularly evident in preparations stained with Delafield's Haemotoxylin. The cytoplasm of the generative cell gives a reaction to the triple stain, which is quite distinct from that in the pollen grain. When Delafield's Haemotoxylin was used the cytoplasm of the generative cell appeared much less dense (fig. 46). After some time the generative cell becomes free within the cytoplasm of the pollen grain (fig. 47).
It is always fusiform and with the iron alum-haematoxylin stain there is sometimes the suggestion of a nucleolus. The presence of a free fusiform generative cell has been found to occur in many different families of Angio-sperms. It has been reported in Elodea by Wylie (32), in Potomogoton by Wiegand (31), in Symlocarpus by Duggar (8), in Lilium by Chamberlain (4), in Cypripedium by Miss Pace (25), in Salix by Chamberlain (3), in Euphorbia by Miss Lyon (19), in Apocynum by Frye and Blodgett (11), and in Asclepias by Frye (10) and Gager (12).

It is at this stage that the first suggestion of the germination of the pollen grain was noticed. A little oval papilla is formed by the intine pushing through the center of one of the slits in the exine. These tubes are noticeable in all subsequent stages in my preparations as well as in the fresh mature pollen. In their later stages one of these tubes is present in each of the three slits. In one instance a mature pollen grain, still in the pollen sac, bore a pollen tube which was in length twice the diameter of the pollen grain.

The Sperms.

During its existence the generative cell retains its fusiform shape and its nucleus gradually enlarges (fig.48). As the time of mitosis approaches an indistinct spirem is formed, which later appears as chromatin in masses of rather obscure shape arranged in an equatorial line at right angles to the longitudinal axis of the cell (fig.49). In metaphase the spindle fibers do not seem to converge near the poles; but late in anaphase the chromosomes are gathered at the extreme ends of the generative cell (fig.50), where the nuclei are
organized (fig. 51). The chromosomes seem to have much the same form as in the preceding mitosis (fig. 44). A situation similar to that shown in figure 51 was found by Frye in *Asclepias* (10) and by Wylie in *Elodea* (32).

The subsequent history of the generative cell as such, was not followed with complete satisfaction. The difficulty was due to the exceedingly small size of the structures and the failure of the stains to prove strongly differential when preparations were lightly stained. Three cases were found in which what appeared to be a cell plate (fig's 52-53) was thrust across the generative cell as the nuclei become organized after the mitosis just described. In each case there was a strong suggestion of spindle fibers on either side of the plate. Two kinds of procedures have been described by which male cells are formed from a generative cell while still in the pollen grain. Wylie (5) in *Elodea* found that the membrane of the generative cell constricts between the male nuclei and that the two male cells thus formed remain attached to each other for some time. Wiegand (31) in describing the procedure in *Potomogoton* states that a cell plate is formed cutting the generative cell into two parts, but shows no figures of such a situation. Evidence of the former method of formation of male cells was sought for diligently in *Iva Xanthii-folia*, but was entirely lacking. The three instances cited were the only ones found which agree with *Potomogoton*. The scarcity of further evidence of the presence of a cell plate might be explained by the fact that such a plate would only appear in pollen grains.
which were cut in exactly the proper plane. Furthermore the two halves of the generative cell may pull apart very soon after the plate is laid down. While the evidence of previous scientific investigation along this line does not make it improbable that a cell plate is formed, yet the evidence in the material examined is hardly strong enough to establish such a procedure with absolute certainty when dealing with such minute structures.

Throughout the subsequent history of the pollen grain the male nuclei are invested by a membrane other than the nuclear membrane, which is rather distinct (fig's 54-58). Very little structure is evident in the cytoplasm between the nucleus and this membrane, and it is possible that it may be an artifact. However the shape is quite constant being pointed at one end and truncated at the other. Furthermore it does not, except in later stages, conform to the outline of the nucleus (fig's. 54-55). There is therefore good reason for considering these structures male cells.

While the history of the generative cell after the division of its nucleus is not entirely clear, there can be no doubt as to the destiny of the deeply stained nuclei. These at first assume a spherical shape (fig.54) and present a more or less uniform structure. As soon as they begin to elongate, however, (fig.55) there again appears, darkly staining chromatic bodies, resembling very closely those in figure 46. Their exact number could not be determined with certainty. The nucleus continues to elongate until it becomes ten or twelve times as long as broad (fig.56). Its ends are usually rounded and it may assume a twisted shape (fig.58). The darkly staining chromatic bodies now appear more distinct, especially in preparations stained lightly in
Delafield's Haemotoxylin. They are now arranged in a single row and the number was about eight. The chromosome number for this species as above stated was not positively determined, but in all cases where the chromosomes were distinct enough to be estimated, they seem to indicate eight or nine as the gametophyte number.

The pollen grain now passes through a period of growth in which it reaches a size two or three times that of the original microspore (fig. 58). It now reacts very differently to stains. Preparations in which preceding stages were overstained by forty-five seconds in Delafield's Haemotoxylin required almost ten minutes to adequately stain this mature pollen grain. The exine thickens considerably, but the structures on the interior of the pollen grain remain little changed. The tube nucleus often appears somewhat irregular in outline and the male nuclei become more sharply pointed at each end.

With the possible exception of Silphium (21), elongate male nuclei have never been previously reported in pollen grains. However, elongate male nuclei have been found in the embryo sac of Lilium by Navaschin (22), Guignard (16), and Miss Sargent (27), in Caltha by Miss Thomas (20), in Silphium by Land (18), and in Helianthus and Rudbeckia by Navaschin (23).

Discussion.

Although some attention has been given to the reduction divisions of the male gametophyte in the Compositae by Rosenberg and Juel: very little work has been done upon its later development. The only paper relating to this phase of the life history of the Compositae is that of Merrell on Silphium (21) in 1900. In that work the writer
-30-

described and figured pollen grains containing two elongate bodies, the origin of which he was not able to trace and was therefore not certain as to their morphology. He labeled them "male cells" in his plate but in his discussion stated that the "male cells" and "male nuclei", using the terms apparently interchangeably. His drawings show no structure in these bodies that would indicate whether they were nuclei themselves or contain nuclei. His findings differ from those herewith presented in the following respects. He shows no mitotic figures, no cell plate separating the tube nucleus and generative nucleus; no membrane enveloping the generative cell, no membrane investing the male nuclei. His findings agree with those here presented in the presence of vermiform bodies in the mature pollen grain, and in the presence of two spherical male nuclei at an earlier stage. Merrell's methods differed from those used in this investigation in that his sections were cut ten micra thick, while those of Iva were three micra thick. His drawings were made with a "Reichert occular twelve and Bausch and Lomb one-twelfth immersion objective", while those herewith presented were studied with a Zeiss Apochromat 2 mm. Apert 1.30 and X8 Compensating Ocular and with filtered light from a Welsbach lamp.

These conclusions suggest a possible interpretation of the vermiform bodies in the mature pollen grain of Silphium, though they, of course, cannot establish their morphology absolutely. But when based on a plant so closely related and having so much in common with Silphium, they, at least, tend to warrant a reinvestigation of the male gametophyte of that genus with a view to determining the origin and nature of these elongate structures.
Davis (7) in 1909 made the following assertion regarding the permanency of chromosomes throughout the male gametophyte. "The nuclei of the pollen grains show prochromosomes arranged in a single series and it seems probable that they retain this arrangement throughout the gametophyte phase of the life history. It also seems probable that the fertilization of the egg nucleus effects the close association of two such series of chromosomes thus accounting for the pairs of prochromosomes arranged in parallel threads". While in this investigation the chromosomes, as such, were not followed through all stages, yet the presence of chromatic bodies in every resting nucleus and particularly the row of prochromosomes in the mature male nucleus, are, in harmony with Davis's view.

As stated above, the Compositae have long been considered the highest group of Angiosperms. In their inflorescence they show beyond a doubt that they have gone farther than any other group of living plants in specialization. It is significant that this specialization should prove to extend to the internal structures as well. A number of Angiosperms have been shown to elongate their male nuclei after entering the embryo sac; but in Iva Xanthiifolia the male nuclei elongate before leaving the pollen grain, as if in anticipation of fertilization. It may be that this elongation of the nucleus is also related in some way to facilitating its transportation through the pollen tube.
V. SUMMARY AND CONCLUSIONS.

1. The flowers of *Iva Xanthiifolia* are arranged in the head in a varying number of whorls of five flowers each. This cyclic organization of the head may have been derived from the spiral arrangement previously reported for other *Compositae*.

2. Each flower, except those of the outer whorl of sterile flowers, is subtended by a floral bract. The head of *Iva Xanthiifolia*, therefore, seems to have originated by the contraction of a spike bearing flowers in the axils of leaves.

3. The members of the outer whorl of staminate flowers are the only flowers which do not possess floral bracts. This fact may be explained by the proximity of the overlapping involucral bracts and the laterally developed floral bracts of the pistillate flowers.

4. The development of the female gametophyte agrees with that of other *Compositae*, which have thus far been studied, in the following particulars:

   (1) the single ovule is laterally cauline and anatropous.

   (2) the primary archesporial cell functions as the megaspore mother cell.

   (3) the nucellus becomes displaced forming a lining about the antipodal region of the mature embryo sac.

5. The development of the female gametophyte of *Iva* agrees apparently with *Pyrethrum* and differs from other *Compositae* in the functioning of the outer of the four megaspores.

6. The development of the male gametophyte agrees with many *Angiospermae*
in the formation of a distinct free fusiform generative cell and in the division of the nucleus of the generative cell within the pollen grain.

7. The development of the male gametophyte differs from that of any other plant which has been critically studied, in the elongation of the male nuclei within the pollen grain. This vermiform structure may be developed in anticipation of fertilization or may be an accommodation to the transportation of the sperms through the pollen tube.

8. A row of chromatic bodies in the elongated male nucleus indicates a structural preparation for fertilization.

9. The enlargement of the pollen grains just before maturity may aid in the breaking together of the microsporangia to form pollen sacs.

10. The pollen sacs of adjacent stamens become confluent, forming five large pollen chambers within the staminate flower. Each such pollen chamber is enclosed by the cohering walls of the adjacent stamens. Such coherence associates this species with the Compositae and is not in harmony with Britton's classification.

11. The existence of pistillate and staminate flowers is attributable to the modification of perfect flowers. This conclusion is supported by the following evidences that the head was once composed of bisporangiate flowers.

   (1) the rudimentary pistil of the sterile flower.
   (2) the rudimentary stamens of the fertile flower.
   (3) the occasional reversion of the pistillate flower to the stamen-bearing habit.
12. The order of development in the staminate flower differs from that in the pistillate flower in that the stamens precede the carpels in the former, whereas they succeed them in the latter.

13. The aborted pistil of the staminate flower differs from the functioning pistil of the fertile flowers in the following ways:
   (1) it is radially symmetrical, instead of bifid.
   (2) there is no suggestion of an ovule or an ovarian chamber.
   (3) its function is probably to aid in the dehiscence of the anthers and in the dispersal of pollen.

14. The rudimentary androecium of the pistillate flower differs from the functional androecium of the sterile flower in the following ways:
   (1) it consists of a collar, the members being completely fused throughout their length.
   (3) it appears late in the development of the flower.
   (4) they do not normally produce pollen.

15. The following conditions account at least in part, for the loss of the seed bearing habit by the central flowers.
   (1) their indirect connection with the main vascular strands.
   (2) the failure of the involucral bracts to furnish them protection, except when completely closed.
   (3) the great reduction of their floral bracts increases their exposure.
   (4) the convexity of the receptacle results in their elevation and consequent increased dessication.
   (5) they appear last and are hence more exposed during their developmental stages.
16. The following conditions account, in part at least, for the loss of the stamen-bearing habit by the fertile flowers:

(1) the lack of space, due to the development of the central flowers on the inner and upper sides and the hard involucral bracts on the outer and lower sides.
(2) the increased demand upon the fertile flower incident to the necessity of the production of seeds.

17. The presence of the fertile flowers in the most protected position indicates that the differentiation into pistillate and staminate flowers was caused by the operation of dryness through many generations.

18. In conclusion it is of interest to consider what light is thrown upon the origin of the Compositae by the present investigation. While it is not possible as yet to find any group of plants which shows signs of being the ancestors of the Compositae to the exclusion of all others; yet it is to be hoped that further investigation will result in the discovery of a large number of characters, which the ancestral form probably possessed. These characters could be correlated with those of some modern group and in this way the origin of this the highest group might be established. As far as this paper can aid such an effort, it would seem that the following characters must have existed in the ancestral form of Iva Xanthiifolia:

(1) the inflorescence was in the form of a spike.
(2) each flower was subtended by a leaf.
(3) the flowers were perfect.
(4) the flowers were epigynous.
(5) the androecium consisted of one or more whorls of five stamens each.
(6) the stigma was bifid.

Submitted to the Faculty of the Graduate College of the State University of Iowa, June 1, 1912, in partial fulfillment for the degree of Master of Science.

Iowa City, Iowa. June, 1912.
Literature Cited.


Explanation of Plates.

The figures on plates 1-1IV were drawing with a two-thirds Bauch and Lomb objective, and X4 or X8 occular.

Figures on plates V-VII were made with a one-twelfth immersion objective and X8 or X4 occular.

Those on plate IX were made with a Zeiss apochromatic objective, 2 mm. 1.30 apert and Zeiss Compensating Occular X8.
Plate 1.

All drawings--X 240

b ---- involucral bract, s ----- stamens,

r ----- receptacle, a. p.--- aborted pistil,

f ----- flower, mg.--- microsporangia,

f.b.--- floral bract, p.s.--- pollen sac,

c ---- corolla, fi---- filament,

Fig. 1. Early stage in development of head.

Fig. 2. Developing head, showing appearance of trichomes.

Fig. 3. Developing head, showing appearance of flowers.

Fig. 4. Early stage of staminate flower.

Fig. 5. Cross section of staminate flower showing the lobes of the corolla.

Fig. 6. Staminate flower showing appearance of stamens.

Fig. 7. Staminate flower showing appearance of aborted pistil.

Fig. 8. Staminate flower showing globose stamens.

Fig. 9. Staminate flower with corolla meeting above.

Fig.10. Staminate flower with stamens elongated.

Fig.11. Staminate flower showing microsporangia.

Fig.12. Nearly mature staminate flower.
Plate II.

All drawings X 240

f.b.-----floral bract, b.-----involucral bract,
a.c.-----aborted corolla, p.f.---pistillate flower,
a.s.-----aborted stamens, s.f.---staminate flower,
ca.------carpel
oc.------ovule,
st.------stigma,

Fig. 13. Early stage of pistillate flower.
Fig. 14. Early stage of pistillate flower showing appearance of aborted corolla.
Fig. 15. Pistillate flower showing appearance of aborted corolla and carpels.
Fig. 16. Pistillate flower showing development of ovarian chamber.
Fig. 17. Cross section of pistillate flower.
Fig. 18. Pistillate flower showing developing ovule.
Fig. 19. Pistillate flower at the time of differentiation of primary archesporial cell.
Fig. 20. Pistillate flower showing inverted ovule.
Fig. 21. Pistillate flower showing appearance of aborted stamens.
Fig. 22. Nearly mature pistillate flower.
Fig. 23. Diagram of capitula.
Plate III.

Anomalous Flowers.
s.----- stamen with pollen nearly mature,
st.----- stamen with pollen aborted at mother cell stage,
a.s.--- stamens completely aborted,
c. ---- corolla,
a.c.---- aborted corolla,
s.s.--- stigma of staminate type,
p.s.---- stigma of pistillate type,
o.----- ovule,
f.b.---- floral bract,

Fig. 24. Anomalous fertile flower showing one functioning stamen.

Fig. 25. Hypothetical floral diagram of same flower.
note: dotted portion indicates missing sections.

Fig. 26. Anomalous flower showing corolla of an intermediate type.
Plate IV.

Floral Diagrams.

c.----lobe of corolla.  s.s.---- stigma of staminate flower.
f.b.---floral bract.  a.c.----aborted corolla.
s.----stamen.  a.s.----aborted stamens.
n.----nectary.  p.s.----stigma of pistillate flower.

Fig. 27. Floral diagram of normal staminate flower.
Fig. 28. Floral diagram of normal pistillate flower.
Plate V.

Early stages in the Development of the Female Gametophyte.

o.—-ovule,

n.—-nucellus,

m.m.c.—megaspore mother cell,

m.—-functioning megaspore,

Fig. 29. Ovule containing primary archesporial cell.

Fig. 30. Primary archesporial cell with multi-nucleolate nucleus.

Fig. 31. Primary archesporial cell (megaspore mother cell) developing a reticulum.

Fig. 32. Megaspore mother cell with large vacuolate nucleus.

Fig. 33. Megaspore mother cell in early stage of synapsis.

Fig. 34. Megaspore mother cell emerging from synapsis.

Fig. 35. Daughter nuclei of megaspore mother cell.

Fig. 36. Row of four megaspore, the inner three disintegrating.
Plate VI.

s.-----synergids.
e.-----egg.
a.-----antipodals.
m.---- micropyle.

Fig. 37. Embryo sac.
Plate VII.

e.-----egg.
a.---- antipodals.
m.---- micropyle.

Fig. 38. Embryo sac.
Plate VIII.

n.----nucellus.
e.---- endosperm.
em.----embryo.
m.---- micropyle.

Fig. 39. Embryo sac containing four celled embryo.
Fig. 40. Embryo sac containing three celled embryo.
Plate IX.

Development of Male Gametophyte.

m.----microspore nucleus. t.----tube nucleus.

g.----generative cell. m.n.----male nucleus.

Fig. 41.--Microspore just after formation of tetrad.
Fig. 42. Microspore with nucleus preparing for mitosis.
Fig. 43. Microspore containing nucleus in metaphase.
Fig. 44. Microspore containing late anaphase of same mitosis.
Fig. 45. Pollen grain with tube nucleus and generative nucleus
separated by a cell plate.
Fig. 46. Pollen grain with tube nucleus and generative cell.
Fig. 47. Pollen grain showing tube nucleus, free generative cell
and germinating pollen tube.
Fig. 48. Generative cell with nucleus preparing for mitosis.
Fig. 49. Generative cell containing metaphase.
Fig. 50. Generative cell containing late anaphase.
Fig. 51. Generative cell with telophase of same mitosis.
Fig. 52. Pollen grain containing tube nucleus and generative cell
after the division of the generative nucleus.
Fig. 53. Another pollen grain at the same stage.
Fig. 54. Pollen grain containing tube nucleus and spherical male
nuclei evidently separated and each with apparently a dis-
tinct cytoplasm.
Plate IX continued.

Fig. 55. Pollen grain with male nuclei beginning to elongate and showing chromatic bodies.

Fig. 56. Pollen grain with vermiform male nuclei.

Fig. 57. Mature pollen grain containing tube nucleus and two male nuclei each surrounded by an apparently distinct cytoplasm.

Fig. 58. A nearly mature male nuclei with the enveloping cytoplasm, showing eight chromatic bodies arranged in a row.