Eupatorium perfoliatum L. : a morphological study

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A Morphological Study.

By
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Introduction.

The Campanales are regarded as the highest order of plants. They are characterized by sympetalous corolla, stamens as many as the corolla lobes, anthers united (in all but a few genera), and ovary inferior. This order includes six families: the Cucurbitaceae, the Campanulaceae, the Goodeniaceae, the Candolleaceae, the Calyceraceae, and the Compositae. The Compositae comprise the highest family and include at least 12,500 species. In addition to the characters named, the Compositae have epigynous flowers, fruit an akene, calyx modified into a pappus, and flowers organized into a head.

The most conspicuous taxonomic feature of the Compositae is the anthodium. Compact inflorescences occur among much lower forms, e.g. the cat-tail, so that this does not necessarily mean high rank. It is worthy of note, however, that the Compositae which show such high development along all the evolutionary tendencies should have adopted this form of inflorescence. Many of them have gone still farther in the division of labor and show a differentiation into ray and disk flowers.

The family is divided into two series: the Tubuliflorae, with the corolla tubular in all the perfect flowers, regularly five-lobed, ligulate only in the ray-flowers which when present are pistillate only or neutral; and the Liguliflorae with the corolla ligulate in all the flowers of the head and all the flowers perfect. The Tubuliflorae is the dominant series with eighty-seven genera described by Gray for eastern and central United States.
The Compositae, altho so large a family, have been little studied on the morphological side. Their high rank as well as the fact that they are the most successful in numbers and in world-wide distribution, especially entitles them to critical investigation. The question arises, have the Compositae developed from a common line of descent, or has their high combination of characters been independently reached through more than one line of development. It was with the hope of throwing some light on this and other questions that this morphological study was undertaken.

Eupatorium perfoliatum L., the object of this study belongs to the Tubuliflorae series of the Compositae and to the second tribe, the Eupatorae. In this group the flowers are all alike, perfect and tubular, never yellow; branches of the style thickened upward or club-shaped, obtuse, very minutely and uniformly pubescent.

The genus Eupatorium is further distinguished by its five-angled akene and pappus made up of a single row of roughish bristles. There are at least four hundred species of Eupatorium, mostly tropical. Many of the species are described from Central America. Gray's manual describes nineteen species with several varieties for eastern and central United States. At least five of these species occur in Iowa.

My thanks are due to Dr. R. B. Wylie, at whose suggestion and under whose direction the work was carried on - also to Professor Macbride for his kindly interest and encouragement.
Methods.

The material for this study was collected near Macbride Lakeside Laboratory on Lake Okoboji during the summer of 1911. It was killed in 1% chromo-acetic acid, run thru alcohol and xylol into paraffin and serial sections 8-15 microns in thickness were cut. For floral development Delafield's Haematoxylin was used and for later stages Iron-alum-Haematoxylin and Flemming's Triple stain.

Floral Development.

_Eupatorium perfoliatum_ l. is a sturdy plant, indigenous to America, common in low grounds. It grows 0.5-1.5m high. The leaves are long and connate perfoliate. The whole plant is covered with abundant trichomes and glandular hairs which are especially abundant around the flowers. The heads are born in crowded, terminal or axillary corymb, from 2500 to 5000 heads to a plant. If the terminal heads are injured the plant sends out new axillary branches bearing flowers. Flowers may arise from the axils of any of the leaves even well down toward the base. The individual head has two, sometimes three rows of narrow imbricated bracts, the outer row shorter than the inner. The flowers, fourteen to twenty-four in a head, are perfect and alike, and show no special arrangement in the head. The plant therefore produces 35,000 to 120,000 flowers in a season. The receptacle, early convex, at maturity becomes flat. There are no foliar bracts.
The flower is about 5mm. long and very slender, with a regular five-lobed white corolla, a whitish pappus made up of a single row of rough bristles, five stamens inserted on the corolla, alternate with its lobes, five nectaries united around the base of the style, and a single carpel with long style and deeply two-cleft hairy stigma, which extends at maturity far beyond the corolla.

The flowering season lasts for at least a month, probably longer. In Iowa the first flowers open the last of June or the first of July. There seem to be latent flower buds not only in the axils of the lower leaves, but even in the axils of the peduncles, for heads frequently appear within a nearly mature cluster of heads.

The terminal head of a system is the first developed. The head first appears as a terminal papilla (Fig. 1, 2.), which rapidly increases in size, becoming very broadly dome-like (Fig. 2). The outer row of bracts is the first to develop. These arise as slender papillae around the outer edge of the receptacle (Fig. 2, 3.) When the outer whorl is well started the inner row appears, and its members alternate with those of the outer. Two or three cases were noted in which a bract seemed to be developing in place of a flower (Fig. 7). These were all in young heads; no foliar bracts were found in mature heads.

The individual flowers arise as papillae upon the broad receptacle, now enclosed by bracts. (Fig. 3-7) The bracts are much more slender than the flowers, and have a rather sharply pointed apex instead of the broadly rounded one shown by the flower (Fig. 4).
The order of development is acropetal. The flowers rapidly elongate; at the same time their bases become separated by the broadening of the receptacle which is now almost flat.

Each individual flower becomes flattened at the apex (Fig. 9). The corolla appears about its margin as a tubular outgrowth. (Fig. 10, 11) As it pushes upward it leaves a cup-like depression. (Fig. 10-15). The lobes of the corolla arise as papillae around the top of the tubular limb and as they develop, turn inward meeting in the center over the other organs.

The calyx appears as a slight swelling around the outside of the flower, when the corolla is well started (Fig. 11), but it grows very slowly for some time. This time of appearance of the calyx does not agree with Coulter and Chamberlain (18) who say "It is also generally known that among the Compositae, in which the sepals are much reduced or modified, their primordia do not appear until after those of the stamens and carpels". Merrill (14) found this statement true for Silphium but Martin (13) says that in Aster and Solidago the pappus appears simultaneously with the stamens. It is true however that the pappus does not greatly elongate until after the carpel appears (Fig. 15-16). It then grows rapidly and attains maturity before any other organ of the flower (Fig. 18).

The androecium appears as a whorl of papillae on the base of the corolla. (Fig. 14) Each stamen is at first very broadly club-shaped but it later becomes long and narrow. The filament
is very short and is a fifth the length of the anther. There are four microsporangia but later the wall between the outer and inner sporangium breaks down making only two pollen sacs. The stamen bears at its summit a long slender crown which breaks off when the pollen is mature. (Fig.19,20,23) It seems that this sterile crown is of service in the dehiscence of the anther, for until the flower opens and the stigma is exerted these stamen tips bend over the stigmas so that the stylar thrust, here due to cell elongation must push them back and tear them off.

The style and stigma are formed by the inward and upward growth of two sides of the flower-cup just below the base of the stamens. As growth continues the ovarian chamber is roofed over. (Fig.16). The stylar canal is early closed.

Last to appear are the five nectaries, each of which has an opening at its top which looks something like a stoma, but is more nearly circular in outline (Fig.27-29). These openings are similar to the water pores or hydathodes found in many plants. (Goeble 19) After fertilization the nectaries shrivel and their united bases remain as a shoulder at the top of the ripe akene. Nectaries of this sort are found in many of the Compositae. Merrill (14) found them in Silphium, Martíníng(13) in Aster and Solidago, and Farr(9) in Iva. They have discussed the question of whether they are aborted stamens or are separate structures. Merrill thinks that they are separate structures. Farr on the other hand believes that they are modified stamens. The strength of his position rests on the fact that he found a flower in which a second cycle of stamens was partially developed in place of the
Abnormalities were very common, at least half the heads studied showing one or more flowers failing to reach maturity. These aborted flowers may occur in any part of the head though they are perhaps more common toward the center than at the periphery. Many cases were found in which only the stamens had aborted, frequently at the end of the homotypic division. This frequent abortion of the stamens when the carpel is not affected seems to indicate a tendency toward the monosporangiate habit. No cases were found in which the carpel only was aborting.

The Megasporangium.

By the time the ovarian chamber is well roofed over, the ovule is apparent as a protuberance at the bottom of the cavity. It is therefore cauline, and is anatropous, with the single massive integument characteristic of the Sympetalae.

The single archesporial cell becomes apparent by its different staining reaction and larger size at about the time the ovule begins to turn. This archesporial cell functions directly as the megaspore-mother-cell. The nucellus is here limited to the axial row terminated by the archesporial cell and to the epidermal layer around this cell. This suppression of the division into primary sporogenous and primary parietal cell seems to be universal among the Sympetalae so far as studied.

Female Gametophyte.

The megaspore mother-cell goes through a long period of growth while the ovule is turning. During this time it increases to about three times its original size (Fig. 33-37). The nucleus
shows the usual synaptic knot (Fig.35) and then the spirem (Fig.36). The chromosomes as seen in anaphase of the heterotypic division (Fig.37) were very long and slender, showing premature splitting for the homotypic division. The chromosome number could not be determined with any certainty, tho it probably does not exceed eight for the gametophyte and may be smaller.

As is commonly found among the sympetalae four megaspores are formed, the inner one functioning. While among the Monocotyledons a number of forms have reached the undividing mother-cell (Coulter and Chamberlain 8) and among the Archichlamidae a row of three megaspores seems to be more common than one of four, the complete tetrad appears with great uniformity among the Sympetalae. A few cases of only three megaspores are reported. There are very few exceptions to the functioning of the inner megaspore. Among the Sympetalae, Trapella (Oliver 17) in which the outer one functions, is the only well established exception. Cases have been noted in which the outer one occasionally functions in a species where ordinarily the inner megaspore functions.

The first division of the megaspore nucleus takes place near the centre of the sac, the daughter nuclei moving to the two ends. No mitotic figures were found in the female gametophyte after the heterotypic division, indicating slow fixation or that the divisions are passed thru rapidly.

There is a very prominent nutritive jacket layer derived from the inner layer of the integument, and the funiculus where that takes the place of the integument. This jacket layer is also conspicuous in Helosis (Chodat and Bernard 7), Sium (Balicka-Iwanowska 1), Campanula (Barnes 2), Styloideae (Burnes 4)
and has been observed by Billings (3) in numerous Sympetalous forms, conspicuous among them Lobelia, Linum, Forsythia, etc. Chamberlain (6) finds it around the embro-sac except at the antipodal end in Aster. In Eupatorium it extends along the sides of the antipodals as well.

One difference between Eupatorium and Silphium (14) is in the behavior of the nucellus. Merrill finds that as the sac enlarges the nucellus is stretched until it ruptures and part of it is carried down on the tip of the growing sac, forming a cap. The same condition is found in Arisaema (Müttier 16) Lemna (Caldwell 5), Liliaceae and many other forms. In Eupatorium the nucellus entirely disappears, leaving no trace. This destruction begins with the growth of the functioning megaspore, and is complete before the eight celled stage is reached.

On reaching the eight celled stage the embryo-sac is about four times as long as before the first division (Fig. 39-42). The two polars move toward each other and at once fuse (Fig. 43). This early fusion occurs also in Silphium (Merrill 14), in Senecio vulgaris (Strasburger 18), and in Aster novae-angliae (Chamberlain 6). The moment of fusion in different forms varies from the time the polars are first formed till fertilization. The fusion in Eupatorium occurs so early that a very large percent of the sacs studied showed them so completely fused as to at first suggest that only one polar was formed.

The fusion nucleus is the largest and most prominent one of the sac (Fig. 44-47). It has a very large nucleolus, and is less regular in shape than the egg nucleus. Merrill found that in Silphium (14) the fusion nucleus is much larger than the egg,
Chamberlain (6) reports the same for Aster, and Mottier (15) and Strasburger (18) for Senecio. This nucleus lies about the middle of the sac and is surrounded by cytoplasmic strands, with a very narrow space between its membrane and that of the egg. Toward the antipodal end the cytoplasm is very vacuolate. Between the time of polar fusion and fertilization the embryo-sac about doubles its length. The width is about one fourth of the length and is greatest near the middle.

The egg apparatus which at the time of fusion occupied only the micropylar quarter now occupies nearly half. This is much more than the space occupied by the egg apparatus in Silphium (Merrill 14). The egg cell is rather broadly tapering at the micropylar end and vacuolate, the opposite end is rounded. The nucleus lies in this wider rounded part, surrounded by rich cytoplasm. It has a deeply staining nucleolus and usually shows dark chromatin granules (Fig. 45446). The long beak-like synergidgids lie beside and above the egg and frequently push out into the micropyle. Their nuclei, usually lying about the middle are small and not conspicuous.

The antipodal end of the embryo-sac grows very little after the eight celled stage is reached (Fig. 42-47). The cytoplasm about the antipodals is distinctly separated from the rest of the sac and is divided into two or three cells. A very common arrangement is for one nucleus to wall itself off at the very end and for the two others to lie in another cell above it. There is no such invasion of neighboring tissue as a haustorium as is found in Antennaria (Juel 12) and in Aster novae-angliae (Chamberlain 6). The number of nuclei varies, occasionally only two were found, and sometimes as many as six. Four was rather
common. This variation in the number of antipodals is common; Senecio (Mottierl5) has two to six, Silphium (Merrill 14) three to eight, Aster Chamberlain 6) three to thirteen, and Taraxicum (Hegelmaier 11) three to five. While the antipodals do not function as aggressive haustoria they usually remain until the embryo- is well developed (Fig.49).

One very peculiar case was observed in which a second massive integument was developed outside of the usual one. In the end of this was an embryo-sac, as long as the ordinary sac, and somewhat wider. The micropylar end was broadly rounded instead of narrowly pointed. The egg apparatus was not so well organized as in the normal sac, for the egg nucleus did not lie in a definite cell but was surrounded by a few irregular strands of cytoplasm that joined it to the two synergids which lay to the side and above the egg. The large fusion nucleus was pear shaped, showing some evidence of a spirem, and with an enormous nucleolus. A few strands of cytoplasm extended out from this nucleus. There was no suggestion of antipodals. In the same flower in the normal position was another sac with two large nuclei at the micropylar end, and a single nucleus walled off at the antipodal end. The other flowers of the head were normal, with the embryo-sacs almost ready for fertilization.

The Micr sporangium.

Little work was done on this phase of the plant owing to unfavorable material. The archesporium is early distinguishable by the larger size and deeper staining reaction of the cells. It consists at first of a single column of cells which divides
and forms three, sometimes only two columns. It is during this time of division of the sporogenous cells that the walls of the anther begin to fuse with those of the adjacent anthers. A tapetum of large deeply staining and frequently binucleate cells is formed around the microspore-mother-cells. Between this and the epidermis is a very thin layer of elongate cells and then a thicker one. (Fig. 50)

As in Silphium (Merrill 14) by the time the pollen-mother cells divide they are nearly spherical and are lying free in the cavity. The heterotypic division was not seen. The spindles of the homotypic division most frequently lay with their poles toward the base and apex of the sporangium.

Immediately after the formation of the tetrad the nuclei showed a number of very deeply staining granules (Fig. 52-54). They were frequently connected by linnin threads. They probably represent the chromosomes for there were from six to eight of them, the probable gametophyte number.

The members of the tetrad soon break apart, and the pollen grains assume the spherical form. The divisions of the male gametophyte occur before shedding. The tube nucleus is large and round. The male nuclei are much smaller, deeply staining and at first spherical, tho later they are elongate and somewhat twisted (Fig. 55). The mature pollen grain 18 microns in diameter, has a very heavy spiny exine, with three openings thru which the intine protrudes (Fig. 55)
Fertilization.

Few pollen tubes were found. These had entered the embryo-sac thru the micropyle. One case showed two pollen tubes, one of which had entered the embryo-sac, and a second one with swollen tip in the micropyle. The pollen tube in entering had destroyed one of the synergids and was deeply stained. The tip of this tube was much swollen and seemed broken at its end which lay opposite the second synergid nucleus. One sperm was in contact with the egg; no sperm was seen in contact with the fusion nucleus.

Altho so few pollen tubes were seen, fertilization probably occurs regularly. Some heads showed unfertilized eggs which gave no sign of farther development while the flowers on either side had well developed embryos, and sometimes showed a trace of a pollen tube.

The endosperm develops very rapidly after fertilization, nearly filling the sac with a loose cellular tissue, by the time the fertilized egg has completed the first division. These divisions of the endosperm occur so rapidly that the spindle fibers are sometimes seen connecting several nuclei. The embryo has a long suspensor cell at its micropylar end. As it grows it completely destroys the endosperm.

Discussion.

The close relationship given the Compositae by taxonomists appears from a comparison of the work done by morphologists on the Compositae, to have a morphological basis. In many points Eupatorium agrees very closely with the other Compositae studied.
In the order of floral development it varies from the generally accepted opinion by developing the pappus before the carpel. In this respect however, *Aster* and *Solidago* at least, vary also. The nutritive jacket around the embryo-sac is found in *Aster*, *Silphium*, *The", "early fusion of the pôlaris is common to *Aster*, *Silphium*, *The", and *Senecio*, and nearly all the morphological investigators of the Compositae speak of the fusion nucleus as being the largest one in the sac. Variation in the number of antipodals is reported for nearly all the Compositae studied. This variation in number, and more especially the development of the antipodals as aggressive haustoria has been used as a strong argument for making the antipodals correspond to the vegetative part of the Gametophyte in lower forms. It would seem therefore that the Compositae are as closely related morphologically as taxonomically. They do not seem to be the culmination of a number of widely different lines of development, each reaching this external form as the one best adapted to their environment.

While *Eupatorium* has not reached the division of labor attained by those forms which have both ray and disk flowers the frequent abortion of stamens may indicate a tendency in that direction.

**Summary.**

1. The floral parts appear in the order corolla, calyx, stamens, carpel, nectaries.
2. Four megaspores are formed, the inner one functioning.
3. There is a prominent jacket layer around the embryo-sac.
4. The polars fuse very early and completely.
5. The egg apparatus at maturity occupies nearly half the sac.
6. The synergids are long and beak-like.

7. The fusion nucleus is the largest and most prominent one in the sac.

8. The number of antipodals varies from two to six.

9. Fertilization takes place.
The abbreviations employed in describing plates are as follows:
a. antipodals.
b. bract.
c. corolla.
cr. carpel
e. egg	em. embryo	en. endosperm
f. flower
fn. fusion nucleus
j. jacket cell
m. male nucleus
n. nectary
o. ovule
p. pappus
pm. pollen-mother-cell
pp. polar
pt. pollen tube
s. stamen
sm. stigma
sp. sperm
st. style
sy. synergids
t. tapetal cell	n. tube nucleus.
Plate I

Figure 1. A group of heads developing.
Figure 2. A group of heads a little more developed than in 1.
Figure 3. A single head showing the bracts.
Figure 4. A head with the flowers well started.
Figure 5, 6, 7, Later stages in the growth of the head.
Plate II.

Figure 9. A single flower

Figure 10. The corolla just beginning

Figure 11. The corolla farther developed, the pappus appearing.

Figures 12, 13, 14, The stamens appearing.
Plate III

Figure 15. A flower in which the carpel is just starting.

Figure 16. The carpel farther advanced, the styles have come together.

Figure 17, 18. The ovule appearing, and the nectaries. The stamens show the crown at the top.
Plate Iv.

Figure 19-20. The pappus is mature, the stamens have reached the tetrad stage and the ovule is going thru the reduction divisions.
Plate V.

Figure 21. Cross section diagram of a single flower.

Figure 22. Cross section diagram of a head.
Plate VI.

Figure 23. A mature flower.
Plate VII.

Figure 24. Leaf of *Eupatorium perfoliatum* L.

Figure 25. Stoma from leaf.

Figure 26. Section of leaf.

Figure 27. Longitudinal section of nectary.

Figure 28. Pore at top of nectary.

Figure 29. Nectary partly shriveled.

Figure 30. Longitudinal section of Glandular hair.

Figure 31. Cross section of glandular hair.

Figure 32. Trichome.
Plate VIII.

Figure 33. Ovule showing archesporial cell.

Figure 34. Ovule a little later, the integument just starting.

Figure 35. Megaspore mother cell - synapsis.

Figure 35. Megaspore mother cell after synapsis, showing spirem.

Figure 37. Anaphase of heterotypic division.

Figure 38. Between heterotypic and homotypic divisions.

Figure 39. The four megaspores, the inner one beginning to grow.

Figure 40. The two celled female gametophyte, destroying the other megaspores.
Plate IX.

Figure 41. Two celled female gametophyte, the nuclei have moved to the ends of the cell.

Figure 42. The eight celled stage before polar fusion.

Figure 43. The two polars fusing.

Figure 44. The polars have fused.

Figure 45. An eight celled stage a little later.
Plate X.

Figure 46. An embryo-sac just before fertilization.

Figure 47. Fertilization, a sperm is in contact with the egg, one pollen tube in the sac and one in the micropyle.
Plate XI

Figures 48-49. The embryo and endosperm developing.
PLATE XI

Diagram showing cellular structures with labels "a," "e.m," and "s."
Plate XII

Figure 50. A lobe of the anther showing the microspore-mother-cells and surrounding tapetum.

Figure 51. The homotypic division.

Figure 52. Early tetrad stage.

Figure 53. Later tetrad stage.

Figure 54. A pollen grain just after the members of the tetrad have broken apart.

Figure 55. A pollen grain showing spiny exine and protruding intine.

Figure 56. A corner of the field where the material used was collect
Literature cited.


