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THE DICLINOUS FLOWERS OF *IVA GANTHIIFOLIA*, NUTT.

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Relatively few of the Compositae have been studied throughout their whole life history. Most investigations have dealt with the varied expressions of a single structure, such as vascular anatomy, style, etc., in various genera of this family. However valuable such research it cannot replace the more intensive study of a single species. Only by this latter method can the different morphological structures be satisfactorily interpreted and relationships established.

Probably no group of Angiosperms displays a wider range of dicliny. In some species all the flowers are perfect; in a few there are pistillate and staminate individuals; while the remaining forms display almost all possible intermediate conditions. Uexkull-Gyllenband (14) and others have called attention to the fact that several forms of dicliny may occur within a single species.

This study was undertaken in the hope of throwing some light upon the organography of the capitulum of the Compositae. *Iva xanthiifolia*, Nutt was selected since it possesses both pistillate and staminate flowers in the same head. The former are always marginal and the latter are always central thus displaying a very stable condition with respect to the differentiation of sex.

The material was collected during the summer of 1911 in the vicinity of the Macbride Lakeside Laboratory on West Okoboji Lake in Iowa. The writer is indebted to Professor R. B. Wylie for many helpful suggestions and for his kindness in directing the work.

INFLORESCENCE.

The flowers of *Iva xanthiifolia*, Nutt. are arranged in the capitulum in concentric cycles of five flowers each (fig. 1), the members of successive whorls alternating. The outer cycle consists of five pistillate flowers, each in the axil of a large involucral bract. The staminate flowers, numbering 11 to 23 in each head, make up the remaining whorls. Development is in acropetal succession, often leaving the youngest inner

cycle incomplete. Britton (1) places the number of staminate flowers at 10 to 15, which is too low for the material examined in this study. Danforth (3) and others have shown that certain of the Compositae have their flowers arranged in spirals. It is possible that in *Iva* the cyclic arrangement of flowers may have been derived from the spiral. The cyclic arrangement of the parts of the angiosperm flower has long been considered as derived from an ancestral spiral arrangement through the shortening of the floral axis. It appears that in the Compositae a similar transition has occurred with respect to the arrangements of flowers in the head, the cyclic being derived from the spiral through the shortening of the spike to form the capitulum.

A floral bract subtends each flower in the head, except the outer whorl of staminate flowers. The slender bracts of all other central flowers are short and stand erect in the interstices between the flowers. The bracts of the marginal pistillate flowers, on the contrary, are very large, taper to a point and conform to the inner surface of the subtending involucral bracts. Britton (1) suggests that these constitute an inner whorl of involucral bracts. This study shows that they are intimately associated with the pistillate flowers (figs. 7, 8, 9, and 10) during their development and are morphologically similar to the floral bracts of the staminate flowers. Furthermore, if Warming's (15) theory of the spicate origin of the capitulum is accepted, it would seem that these structures, subtending the pistillate flowers, should be considered floral bracts.

The abortion of the floral bracts of the outer whorl of staminate flowers is probably due to their peculiar position. It is evident that the excessive lateral development of both the involucral bracts and the bracts of the pistillate flowers would result in crowding and excessive protection in this region. Knupp (7) believes that the development of the sepals of *Myriophyllum* was arrested through excessive protection. Warming (15) attributes the formation of pappus from the typical calyx to the pressure and crowding of flowers in the head. It is possible that these factors may have resulted in *Iva* in the complete abortion of the bracts of the outer whorl of staminate flowers.

A study of the vascular anatomy of the head shows that the marginal flowers are most closely connected with the bundles of the stem. Each of the five strands entering the head proceeds directly to an involucral bract. The pistillate flower is supplied by a branch from this bundle. Normally the flowers of each succeeding cycle receive their vascular supply through branches from the bundles of the next outer cycle. Whatever the determining factors in the arrangement of this system,

the significant fact in the present consideration is that the more nearly central the flower, the farther it is removed from the main vascular supply.

THE STAMINATE FLOWER.

The four microsporangia of each stamens are about equal in size at an early stage, but later the outer become somewhat larger. This may be a mechanical adaptation, since the space available for growth is restricted by the tubular coralla. The stamens enlarge until they touch and the walls of adjacent stamens unite by the fusion of contiguous cutinized layers (fig. 6). It is possible by considerable pressure to separate the anthers of *Iva*. However the fused layers were in no case found to separate, although the cutinized layers sometimes broke loose from the epidermis. Tschirch (12) holds that the anthers of the Compositae remain permanently grown together, "dauernd verwacksen bleibt," since he was unable to separate them either mechanically or by treatment with chemical reagents. Britton (1) has taken the *Ambrosia* tribe out of the Compositae on the ground that their anthers are "not truly syngenesious." It seems that typical Compositae are not alike in this respect, as is shown by Stadler's (12) study of Cnicus in which the walls of adjacent inner microsporangia never fuse. It therefore seems probable that Gray (6) is fully warranted in including *Iva* among the Compositae.

The first sugestion of dehiscence is found in the breaking of the walls between the inner and outer microsporangia. Schneider (11) has suggested that this may be due to a growth of the pollen. In *Iva* the pollen grains do enlarge just before maturity and this probably contributes to the rupturing of the walls.

The lateral pollen sacs of adjacent stamens break together, through the dissolution of the central portion of the lateral wall of each stamen. In this way five large pollen chambers are formed, in the flower, each enveloped by an intact wall and containing the pollen grains of four microsporangia,—the lateral pair of each of the two contiguous stamens (fig. 5).

Five very small structures, having the appearance of nectaries, stand about the base of the pistil and alternate with the filaments (fig. 4). Martin (8) interprets similar structures in *Aster* and *Solidago* as "imperfectly formed stamens." Goebel (5) has presented evidence that certain nectaries arise by the transformation of various morphological structures. Merrell (8) suggests that, "It is much more reasonable to regard the nectary as an organ of independent origin." Of course it

is quite possible that nectaries may arise in either way, but unless evidence to the contrary is shown, it seems better to consider them derived structures. These small structures in Iva may therefore be considered vestiges of an inner whorl of stamens.

The development of the pistil of the staminate flower is very different from that of the fertile flower. No ovarian cavity is formed, but quite early a notch appears in the center of the upper surface of the papilla (fig. 3). This notch is later obliterated by the growth of large hairs which form a broad capitate disc at the apex of the mature style. Although Chamberlain (2) contends that this style "is undivided," it is seen to be somewhat cleft during its development, an indication or derivation from the typical bifid form.

The abortive pistil doubtless aids in the dehiscence of the anthers. As the style elongates it pushes against the hook-like tips ("Anhangseln" 4) of the stamens, which arch over its capitate disc, and in this way probably tears open the pollen chambers. The capitate structure seems to serve a further purpose during pollination in preventing the microspores from being shed *en masse*. Wernham (16) believes that in the Compositae the style "forces its way through the anther tube, sweeping the pollen before it." That this is not the case in *Iva* is shown by the position of the style prior to dehiscence (fig. 4), the brush hairs being above most of the pollen mass.

That this structure in the center of the staminate flowers of *Iva xanthiifolia*, Nutt. is a rudimentary pistil can scarcely be doubted. The position, the tardy appearance, the notch, the brush hairs and the stylar thrust all point to this interpretation.

THE PISTILLATE FLOWER.

The development of the pistillate flower presents only a few peculiarities. The coralla is abortive, never becoming lobed, and does not normally develop to more than one-fifth the length of the mature style (fig. 10). In contrast with Silphium (9) the abortive stamens of the pistillate flower of *Iva* appear after the carpels. Furthermore these rudimentary stamens are not distinct but form a continuous collar-like structure about the base of the style. That this collar is the vestige of a whorl of stamens is further indicated by an abnormal flower which was found in the material examined.

ABNORMAL FLOWERS.

In one of these abnormal pistillate flowers the only irregularity consisted in the lengthening of the abortive coralla, which was better devel-

oped on the inner than on the outer side. In another marginal flower (fig. 11) the parts on the outer side were developed like those of the normal pistillate flower. On the inner side, however, they took the form of the staminate flower, the coralla and stamens being fully formed. This modification even extended to the style which bore brush hairs on the inner (staminate) side. On the lateral side of the flower there was a gradual transition between the two conditions (fig. 12), two stamens aborting at the mother-cell stage. On the other lateral side an abrupt change from the pistillate to the staminate form occurred. At this point there was present an opening in the ovarian wall between the coralla and the base of the style. The abnormal flowers suggest that the normal pistillate flower possesses both abortive stamens and an abortive coralla, and that the staminate flower possesses an abortive pistil, which indicates the derivation of both forms from the perfect flower.

DISCUSSION AND SUMMARY.

The study of floral development in Iva xanthiifolia, Nutt. reveals strong evidence that the capitulum is, as Warning (15) held, phylogenetically a contracted spike. The meristematic region in the center of the head is suggestive of apical growth. The existence of floral bracts within the head points to the previous arrangement of flowers in the axils of subtending leaves. And the vascular system, in so far as it is dependent upon recapitulation for its form, is likewise indicative of axial organization.

Considerable difference of opinion has arisen as to whether the ancestral form of the Compositae possessed perfect or diclinous flowers. Lecoq, Delpino, Dammers and Müller contended that hermaphrodite flowers were derived from the unisexual forms. Spruce, Bentham, Darwin, Hildebrand, Warming and Uexkull-Gyllenband held that perfect flowers represent the primitive condition and that monosporangiate flowers have arisen by the abortion of stamens or pistils. In Iva the abortive pistil which still functions in opening the anthers, indicates the derivation of the staminate flower from the hermaphrodite. In like manner the abortive stamens, which occasionally develop into pollen-bearing members, suggest a similar origin for the pistillate flower. So that the evidence presented in this study favors the view that the unisexual condition is derived.

Assuming, then, that the pistillate and staminate flowers have arisen from the perfect, one seeks an explanation of this differentiation. The conditions surrounding the staminate flowers are in several ways unlike those of the pistillate. The opening of the involucral bracts exposes the

central flowers first and the marginal last. Furthermore, while the involucral bracts are open they shield the marginal flowers almost completely from the direct rays of the sun and from drying currents of air (fig. 2). At the same time the central flowers are subjected to the drying effect of both wind and sun. The marginal flowers are, in addition, protected by their large floral bracts, while with the central flowers these structures are either wanting or else rudimentary. The convexity of the receptacle results in the elevation of the central flowers and hence increases their exposure. The central flowers, moreover, appear last and therefore have a shorter time in which to develop before the buds opens. Nissen (10) found that the vascular bundles which enter the staminate flowers of the Compositae are composed of smaller elements than those entering the pistillate. The water supply of the central flowers is further reduced in *Iva* by their being farther removed from the main vascular supply. In fact, the whole organization of the head is such that the marginal flowers receive a maximum of protection, while the central flowers are subjected to a maximum of exposure. May not the difference in the surroundings of these two kinds of flowers have given rise to the difference in structure?

It is apparent that the androecium of a flower is better adapted, both in structure and function to endure dessication than is the gynoecium. The stamens are relatively short lived and both dehiscence and pollination are facilitated by dryness. With the shedding of pollen the work of the stamen is completed, while the development of the pistil has only fairly begun. The pistil, at maturity, must expose a delicate stigma, and, after fertilization, the growing embryo must be nourished and the seed developed. So that it seems quite probable that the exposure of the central flowers may have resulted in the abortion of their pistils.

The abortion of the stamens in the marginal flowers, is, however, doubtless due to other causes. In an epigynous flower the stamens are necessarily elevated. In the flowers under consideration such a position would bring them into contact with the enlarged ends of the corallas of adjacent staminate flowers on the one hand, and with the apices of convex floral and involucral bracts on the other. It therefore seems that this crowding of the stamens may have prevented their growth.

While decliny has probably become hereditary, the original cause for such differentiation seems to lie in the difference in the conditions surrounding the two kinds of flowers. The existence of a capitulum of this kind necessitates the greater exposure of some flowers and the marked protection of others. Whether this interpretation will hold for other species can only be told after careful investigation of their heads. But

it now seems that dessication will adequately explain the origin of the staminate flower and excessive protection the origin of the pistillate.

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EXPLANATION OF PLATES.

All drawings were made with Spencer camera lucida, except figures 1, 2, 5 and 12. The plates are reduced one-half in reproduction. Figures 3, 4, 7, 8, 9 and 10 were made with Spencer 16 mm. objective and 4 ocular. Figure 6 was made with Bausch and Lomb $^1/_{12}$ immersion objective and 4 ocular. The original magnifications in diameters were

approximately as follows: figure 1, 35; figure 2, 105; figures 3, 4, 7, 8, 9, 10, 11 and 12, 210.

The abbreviations employed in describing figures are as follows: i, involucral bract; f, floral bract; p, pistillate flower; s, staminate flower; c, coralla; l, carpels; y, style; m, stamens; r, abortive stamens; e, epidermis.

Fig. 1. Diagram of capitulum.
Fig. 2. Longitudinal section of one-half of capitulum.
Fig. 3. Young staminate flower in longitudinal section.
Fig. 4. Nearly mature staminate flower in longitudinal section.
Fig. 5. Floral diagram of staminate flower at maturity.
Fig. 6. Fused walls of two adjacent stamens in cross section.
Fig. 7. Young pistillate flower showing appearance of corolla.
Fig. 8. Young pistillate flower showing appearance of carpels.
Fig. 9. Immature pistillate flower showing beginnings of rudimentary stamens.
Fig. 10. Nearly mature pistillate flower in longitudinal section.
Fig. 11. Abnormal flower in longitudinal section.
Fig. 12. Floral diagram of abnormal flower.

Since this paper was presented to the Academy there has appeared in the Transactions and Proceedings of the Botanical Society of Edinburgh for 1913, a paper by Dr. K. von Goebel on "The Inflorescences of the Ambrosiaceae." In this no mention is made of *Iva*, but there is reference to an article on the same subject by S. Rostowzew in Bibliotheca botanica Heft 20. The latter paper is primarily a study of the systematic position of the members of this group, and presents certain of the facts noted above. The author attempts however no interpretation of the rudiments, etc., nor does he discuss the origin of the inflorescence of this form.

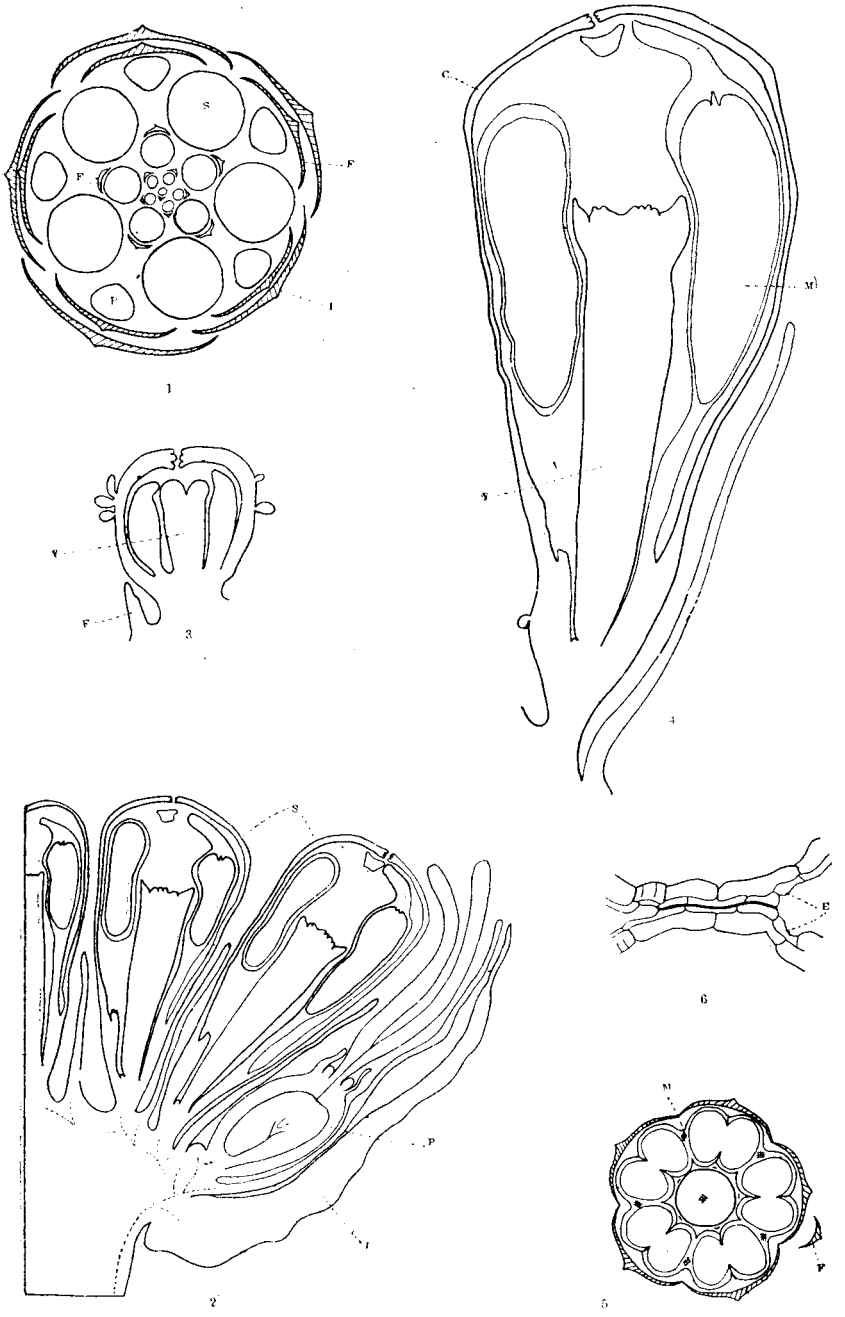

Plate 1.

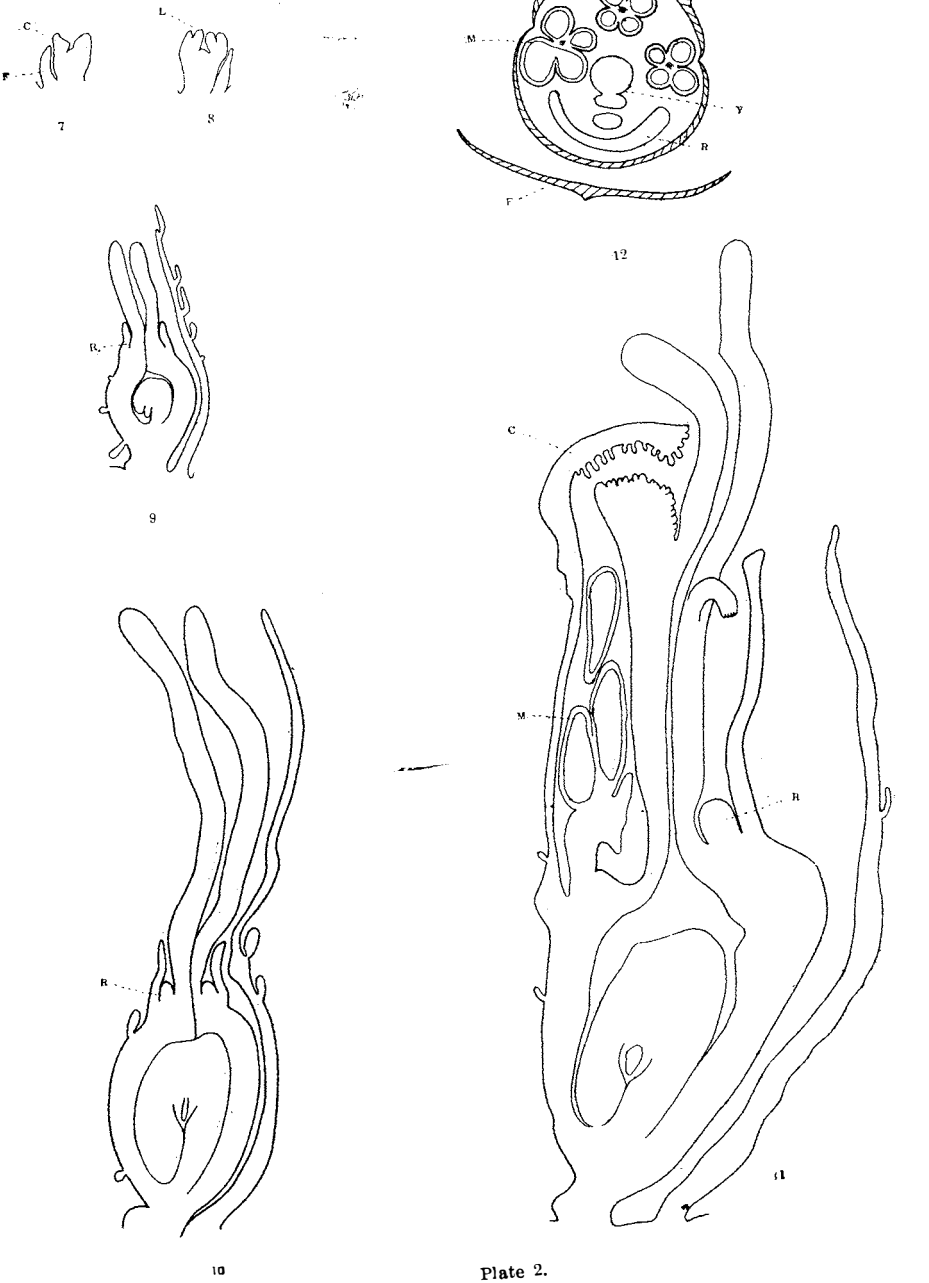

Plate 2.