The Pollen-presentation Mechanism in the Compositae.

BY

JAMES SMALL, B.Sc. (Lond.), PH.C.,

Demonstrator in Botany, Armstrong College, Durham University.

With seven Figures and two Tables in the Text.

INTRODUCTION.

WHEN it is remembered that this order includes over 13,000 species, the very voluminous literature does not come as a surprise, but in spite of the numerous contributions to our knowledge of the Compositae, very few attempts have been made towards the elucidation of the evolution of even the main divisions of the order. Cassini (3), in 1826, made one of the first attempts to express the affinities of the tribe. He did so by placing the nineteen tribes, into which he divided the order, in an ellipse with the Vernoniées and Lactucées at one end and the Hélianthés at the other, with twelve lines crossing the enclosed space to indicate the presence of some common characteristic in tribes which he considered to be otherwise unrelated. In 1871 Delpino (5) gave a phylogenetic table for the Artemisiaceae showing the Compositae derived from the Campanulaceae through the Lobeliaceae and the Artemisiaceae derived from the Senecionidae, but since the Senecionidae, to which reference is made here, included many of the genera now in the Heliantheae, Helenieae, and Anthemideae, the value of this speculation, for it was little more, is seen to be negligible.

Bentham (1), in 1873, followed Cassini in his method of expressing the inter-relationships of the tribes with very little change, except in the reduction of the number of divisions to thirteen and the placing of the Senecionideae between the Anthemideae and Calendulaceae instead of next the Astereae, as Cassini had it. In considering the affinities, Cassini does not seem to have thought of one tribe or its ancestors having given rise to any other tribe, as is shown by the form of his diagram and the numerous cross-connexions introduced, but of course he thought in pre-Darwinian terms. Bentham took geographical distribution as his chief guide to the evolution of the different groups, and considered that the order could be detected at its earliest recognizable stage in Africa, Western America, and possibly

Australia. He regarded the Helianthoideae as nearest the primitive type, and evidenced the free anthers in the female flowers of a sub-tribe, Petrobieae, in addition to the presence of paleae on the receptacle and the paleaceous pappus of the tribe, in favour of this view. The capitula of the Petrobieae are, however, dioecious, and this sub-tribe of four species seems in several other characters to be far from primitive. From his remarks on the comparative antiquity of the tribes, one gathers that he considered there had been three main lines of development, the first giving the Eupatoriaceae, Vernoniaceae, Cynaroideae, and Mutiseae; the second giving the Helianthoideae, Helenioideae, Anthemideae, Asteroideae, Senecionideae, and Inuloideae; the third giving the Cichoriaceae.

There has been a number of efforts made to elucidate the phylogeny of the Cichorieae, mostly by French anatomists. Vuillemin (20), in 1884, after his elaborate research, concluded that anatomy was of very little use in the classification of this order. Col (4), in 1899, from his researches on the secretory canals and laticiferous tissue in the Compositae, concluded that the Liguliflorae were derived through the Arctotideae and Calenduleae from the 'Radiées'. Lavialle (11), in 1912, from his study of the development of the fruit, and in particular the structure of the mature pericarp, related the Liguliflorae to the Cynareae, on the one hand, through *Cichorium*, *Catananche*, and *Scolymus*, and to the Mutiseae through *Moscharia* on the other. Dufour (6), in 1907, and Lebard (12), in 1913, after studying the cotyledons of many seedling Cichorieae, applied their researches to the phylogeny of the genera in that tribe.

The classification of the family suffered many changes before the publication of the 'Genera Plantarum' (2), but since then Hoffmann (10), in the 'Pflanzenfamilien', has adopted Bentham's classification in all the chief points, and Wettstein (21) follows Hoffmann entirely. Small (19) raises the family to the rank of an order, which he names the *Carduales* and divides into three families—Ambrosiaceae, Carduaceae, and Cichoriaceae. The separation of the few abnormal genera included in the Ambrosiaceae seems rather unnecessary, and Hoffmann's classification is adopted in the following analysis of the variations in the characters of the essential floral organs, which forms the first of a series of studies undertaken with the purpose of elucidating the inter-relationships of the tribes.

POLLEN-PRESENTATION MECHANISM.

In order to arrive at a natural classification of this very homogeneous family, many attempts have been made to utilize characters which in more varied families are regarded as negligible. Even the achenial hairs have been studied for this purpose (15), but although the structure of the hairs of an order may prove valuable sometimes, as in the Cruciferae, in most cases

this is a very uncertain guide to relationship ; for example, the present writer (18) and also Schmidt (16) and Hoch (9) have studied the hairs of the families of the Tubiflorae, and it is found that, while some allied species or even genera may show very similar hairs in many cases, allied species may have hairs which are quite dissimilar. The study of the achenial hairs of Compositae leads to the same conclusion. Vuillemin (20) showed that anatomy was no certain guide to affinity, and later papers (8 and others) confirm his conclusions that anatomical characters are reliable only in certain special and very limited groups. The floral characters, therefore, become of supreme importance, and as they are so uniform throughout the order, the value of details in their structure must be considered carefully. Linnaeus naturally classified the group according to the condition of sexuality in the florets, but the first systematist to consider the matter in detail (i. e. Cassini (3)) saw at once that the dominating character was the pollen-presentation mechanism, and he accordingly gave the greatest value to the characters of the styles and stamens. Lessing (13) followed Cassini, but laid more stress upon the characters of the style in the delimitation of the larger groups, and in this he is followed by Bentham (2). For generic distinctions the venation of the corolla was used to some extent by Don, and the form of the achene by Schultz Bipontinus (17).

Although the value of the details of structure of the styles and stamens has thus been recognized for purposes of classification, the significance of these details to the plants themselves has been considered negligible. Of all recent synantherologists, Bentham gave the highest value to the variation in the appendages of the stamen, but he writes (1) : ‘ The anthers, however, are sometimes provided with certain appendages apparently of little or no functional or homological importance, but which, nevertheless, from the remarkable constancy of their presence or absence in whole tribes, supply one of the most valuable characters in Compositae if applied with proper caution.’

Since the highest development of these appendages is found in the same groups with the highest complexity in the structure of the style, it becomes highly probable that the appendages have quite a definite function, and a consideration of the facts shows that here, as in the rest of the characters, economy is the dominant factor. Economy of corolla material leads to the aggregation of the flowers into a capitulum ; economy of calyx material leads to the entire disappearance of that part of the flower or to its modification into a pappus ; economy of stamen material leads to reduction in number of the stamens to the minimum compatible with the efficiency of the pollen-presentation mechanism ; economy of carpel material leads to reduction in the number of carpels to two, and of ovules to one. From this it will be seen that the polliniferous tissue is the only

part of the flower in which the tendency to economy has not previously been recognized.

Considering the appendages of the styles and stamens in the light of the idea that economy of pollen is a factor in the success of the Compositae, the value of the hairs on the exterior of the style branches and the appendages of the style branches becomes apparent at once. Cassini recognized the value of these hairs in sweeping out all the pollen from the dehiscent sacs, but a new emphasis is given to their efficiency, and an explanation is afforded of the development of rings of long hairs at or below the point of branching, as in types X and XI, Fig. 2, the spreading hairs at the apex of the style branches in types IV and V, and at the base of the appendages in types VII and VIII. The functions of the staminal appendages, hitherto obscure, become more obvious, for with the corolla-tube of a given length and the stamens in proportion, the amount of pollen produced can be reduced and the staminal tube remain the same length by the production of a membranous prolongation at the apex of each anther. This is a very simple method of reducing the polliniferous tissue while preserving the efficiency of the staminal tube in the pollen-presentation mechanism. The function of the basal appendages is also made clear, since a tube terminating in ten more or less hemispherical lobes, as in type 3, Fig. 1, could not be closed entirely by the style unless that organ actually entered the tube for some distance, in which case the pollen in that part of the sac past which the style had grown would be more or less lost for pollination purposes, unless it were swept up the tube by hairs situated lower down on the style. If the apex of the style merely reached to the lobes when the anthers dehiscent, some of the pollen would fall through the interstices to the bottom of the corolla-tube and thus be lost. If, however, the hemispherical lobes were prolonged into flattened auricles, or ciliate tails, or more elaborate appendages, the style with or without appendages could close the lower end of the staminal tube completely without encroaching on the polliniferous region, and thus no pollen would be wasted so far as the pollen-presentation mechanism was concerned.

The question immediately arises whether these conditions actually occur at the time of the dehiscence of the anthers. A considerable number of species has been examined, and nothing has been found which is incompatible with the above explanation of the functions of the appendages. Each case, however, must be considered separately because a conical style appendage of type VIII may be quite efficient in the absence of basal appendages to the stamens, and the figures in the tables bear this out in a very striking way for the *Astereae*, *Heliantheae*, and *Helenieae*. Much exact work remains to be done on this point, and it is purposed to make this and other problems subjects for further instalments of these studies.

The hypothesis that the appendages of the style branches and the

apical and basal appendages of the stamens are the expression of a tendency to economy of pollen, which is limited only by the biological necessity of providing sufficient pollen to ensure fertilization, implies that these appendages will show correlative development, and Tables I and II are an attempt to analyse the development of these structures throughout the order.

In such tables it is very difficult to assign the correct value to each genus, since a small genus may represent a large, almost extinct group, while a large genus may be composed of numerous small variations about a single type. It is obvious that a higher value should be given to one species of the former genus than to one of the latter. Likewise, if the genus is large and variable, it is proper that it should receive a proportionate value. Since the task of tabulating the characters of 13,000 species is out of the question, the genera have been analysed in the following way: If a genus shows one type of style or stamen it has been counted 1; if it shows two types, then each type has been counted $\frac{1}{2}$; and if, as in some large genera, it shows three types, then each type has been counted $\frac{1}{3}$, so that a large and varied genus has the value $1\frac{1}{3}$ in the tables. It was thought inadvisable to give a genus showing two types a value greater than unity in order to keep the numbers approximately those of the genera in each tribe.

DESCRIPTION OF STAMENS AND STYLES.

The types given here are in most cases of a synthetic character, as many of the intermediate stages between one definite type and the others occur. In all the types of stamens except types 1 and 4^a the apical appendage is present. It is a more or less flattened outgrowth and nearly always simple in outline, very rarely bifid. In certain types this appendage becomes more elongated (types 6^a, 11, 15, and 16), or, as in *Sclerolepis* (Fig. 5), it may become truncate, or it may have the apex inflexed, as in the Ambrosinae. Type 1, in which the apical appendage is absent, occurs only in the Piquerinae, a sub-tribe of the Eupatorieae; 4^a is a rare type which occurs only in *Eleutheranthera*: it is type 4 without the apical appendage. Type 6^a is interesting as occurring in a discoid genus of Senecioneae, *Culcitium*. This type and type 11, which occurs in the Mutiseae (*Leuceria*), are to be compared with the elongated apical appendages of types 15 and 16, which are the typical forms for the Cynareae.

The basal appendages show more variation. They are absent entirely from types 1, 2, and 3. In the other types the polliniferous region is shaded so that the appendages may be clearly distinguished. Type 4 shows a sagittate stamen with very small auricles; types 5 and 6 show these auricles enlarged: in the former they are obtuse, in the latter acute. Type 6^b occurs very seldom: the auricles here are enlarged. Type 7 is a sagittate stamen with the auricles connate; type 8 shows the beginning of the

so-called tails, the auricles being mucronate; type 9 is similar, but the auricles are connate and mucronate; types 10, 11, and 12 show stages in

FIG. 1. Types of Stamens in the Compositae (for explanation see text, pp. 461-4).

the elongation of these tails, which remain simple and undivided; in type 12 the tails of the contiguous auricles are united; types 13 and 14 show further

elaboration of these appendages, the former being branched and the latter more or less lacerate or fringed with hairs; type 15 is similar to 14, but the tails of contiguous anthers are united. Type 16 includes two forms of

FIG. 2. Types of Styles in the Compositae (for explanation see text, pp. 464-5).

lacerate or more or less elaborate tails; the first form has the adjoining tails free and the other has them united; both these forms occur in many genera of the Cynareae. Fig. 7 represents an example of this type which should be compared with the forms shown in Figs. 3-6. As a final stage in

the fusion of the basal appendages, there is the form which occurs in *Tricholepis*, type 16^a, where the appendages of each stamen are fused and those of neighbouring stamens connate, so that there is a continuous sheath of non-polliniferous tissue at the base of the staminal tube.

The very various style forms can be reduced to thirteen mean types, around which the numerous variations can be grouped. Type I is characteristic of the Cichorieae, and the female florets of most of the other tribes. The region of the stigmatic papillae is indicated by the dark line and extends from the apex almost to the point of branching. The external surface of the style branches is more or less hairy. Type II is characteristic of the Eupatorieae; the apex of the style branches is more or less clavate, the branches vary considerably in length, as they do in most of the types, and may be reduced to such a form as is shown by *Ophyrosporus*, type II^a. Type III is characteristic of the Vernoniaceae; the style branches are more or less rounded and hirsute, with an obtuse apex. Type IV, as will be seen from Table II, is the most common form of style in the hermaphrodite florets. The style branches are flattened or more or less rounded, and may be longer or shorter than in the mean type; the stigmatic papillae are marginal and reach to the apex, which is truncate or rounded and more or less hairy. This type, when it occurs in the male flowers of the disc, usually remains closed and unbranched; this condition is represented in type V. Type VI is characteristic of the male disc florets in Calenduleae; it has the style branches very short and no stigmatic papillae.

Type VII is a form similar to type IV, but with the apex prolonged into a hairy, more or less conical or rounded appendage; the stigmatic papillae cease at the base of the appendage. This type may have the branches so short that a form arises like that of *Bellis*, type VII^a. Type VIII is similar, with the appendage more elongated.

FIGS. 3-7. 3. *Piqueria serrata*. $\times 18$. 4. *Adenostemma viscosum*. $\times 42$. 5. *Sclerolepis verticillata*. $\times 10$. 6. *Eupatorium cannabinum*. $\times 18$. 7. *Centaurea scabiosa*. $\times 18$.

Type IX is characteristic of the Mutiseae and resembles type XI, without the ring of long hairs; here, as in the former type, fusion of the branches may be more or less complete, so that the stigmatic region is limited to a hollow, rounded region at the apex. Types X and XI are characteristic of the Cynareae, and are distinguished by the ring of long hairs situated at (type X) or below (type XI) the point of branching: in the former the stigmatic papillae extend from the point of branching to the apex; in the latter there is a very short zone of stigmatic papillae, but numerous intermediate stages are found in the fusion of the two branches above the ring of hairs. Type X^a is the form of style which occurs in the female florets of many Cynareae; here the point of branching is below the zone of hairs and the stigmatic papillae extend from this ring to the apex. Type XII is characteristic of the Inuleae and has no appendages, the style branches being rounded and glabrous or slightly hairy externally, with the stigmatic papillae marginal and extending to the apex. Type XIII is an unbranched, club-shaped, hirsute form, common in the male disc florets of several tribes; it has no stigmatic papillae, and acts solely as a pollen-presenter.

DISCUSSION OF TABLES.

The types of stamens have been arranged so that the complexity increases from I to 16, and the order in which the tribes are given by Hoffmann has been altered so that the affinities may be rendered more diagrammatically clear. The chief alterations are the interchanging of the Vernoneae and Eupatorieae, the Mutiseae and Cynareae, and the placing of the Inuleae and Cichorieae nearer the Senecioneae.

The Eupatorieae are placed first because it is in the Piquerinae, a sub-tribe of this group, that the simplest type of anther occurs. The Piquerinae, which has the typical style of the Eupatorieae, is a group of eight essentially American genera. *Adenostemma*, however, has several Old World species, *A. viscosum* being very cosmopolitan. An interesting modification of the stamen of this sub-tribe occurs sometimes in *Adenostemma*. At a period when all the pollen grains have disappeared from the dehiscent anthers, the line of dehiscence is found to extend to a point a little below the apex (Fig. 4). This is a variation which, by preventing the untimely overflow of pollen from the staminal tube, would carry out the same function as a terminal, non-polleniferous appendage. In this connexion it should be noted that Bentham places this genus next to *Sclerolepis*, which he makes the first genus in the Ageratae, and *Sclerolepis* shows an abnormal truncate form of apical appendage (Fig. 5) which has all the appearance of a reduced type. The other genera of the Eupatorieae have the type of appendage shown in Fig. 6. The Vernoneae show a greater variety and have higher types of stamens, but this can be correlated with

TRIBES	TABLE I ——— TYPES OF STAMENS															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
EUPATORIÆ	7	1	30													
VERNONIÆ					26	3	4			14½				1		
ASTEREÆ		6½	85½	2½	½					1						
MELIANTHÆ		10	72½	40	6½	1										
MELENIÆ		2½	35	14½	2	2										
INULEÆ			3½	1½					1	74		29½	22½	12		
ANTHEMIDEÆ	2	40	2½				1									
SENECIONEÆ	2	27	10½													
CALENDULEÆ			2	½				½	1	13		1				
CICHORIEÆ			½		½	25½		33½								
ARCTOTIDEÆ			1½	2	3	2	½	½		2						
MUTISIEÆ			1½	½						2	22½	2	2½	23½	1½	1
CYNAREÆ									5½	½		5		1	9½	12½

TRIBES	TABLE II ——— TYPES OF STYLES												
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII
EUPATORIÆ		36½											
VERNONIÆ			40										
ASTEREÆ			14	11				29½	45			1	5
MELIANTHÆ			7½	17	8			40½	26			½	31½
MELENIÆ			1	24½	1			19½	12			1½	
INULEÆ			½	73	2							152½	18
ANTHEMIDEÆ				42	4								
SENECIONEÆ			8	29	2		7	2					2
CALENDULEÆ				2		15		½					½
CICHORIEÆ	61												
ARCTOTIDEÆ				8						12			
MUTISIEÆ				32			1½		24½		1		
CYNAREÆ										12	20		53

TABLES I and II.

the simple form of the style, whereas the Eupatorieae have both stamens and style simple.

In the remaining groups it will be seen that the stamen with an apical appendage but no basal appendage, type 3, is the most common form. This form is undoubtedly the fundamental type of stamen for the Compositae, types 1 and 2 being reductions and the others amplifications of it. The Astereae show this simple stamen in the large majority of the genera, but this tribe, while showing the simplest type of auricle in three¹ genera, also shows the truncate type, which is taken as a reduction form in twelve genera. The Astereae, therefore, are the antepenultimate step in the reduction series which ends in the Piquerinae. This type of anther occurs in a considerable proportion of the Heliantheae, but this tribe also shows a large percentage of higher forms. The Helenieae are very similar to the Heliantheae, while the majority of the Anthemideae have anthers of type 3. The Inuleae are notable on account of the majority of the genera showing anthers with relatively complex basal appendages, but this is to be correlated, as in the Vernonieae, with the simple style. The majority of the genera in Senecioneae remain relatively simple in their stamens. The Calenduleae, a small and specialized group in many ways, show a considerable proportion of genera with stamens of the higher types. With few exceptions the Cichorieae have stamens of type 6 or 8, both types occurring in most of the genera. The Arctotideae are very similar to the Senecioneae, but show type 10 in three genera, and thus form an intermediate stage between the Senecioneae and the Mutiseae, which latter tribe is very similar to the Inuleae in the degree of complexity reached by the anther appendages. The Mutiseae show types 15 and 16 in three genera, thus forming a transition to the Cynareae, the majority of which show one or other of these two complex types.

Considering the probable lines of development and omitting as negligible those cases where the number in the tables is less than two,² we find that the Senecioneae form a group from which radiate five lines thus: two short lines, one to the Anthemideae and the other to the Cichorieae; two main lines, the first leading to the Eupatorieae and giving off branches to the Helenieae, Heliantheae, Astereae, and Vernonieae, the second leading to the Cynareae and giving off branches to the Calenduleae, Arctotideae, and Mutiseae; the fifth leading to the Inuleae through the higher types in the Senecioneae.

Keeping these lines of probable development in mind, consider the figures of Table II, neglecting as before figures below two. The columns

¹ See explanation of tables, p. 461.

² Except in the Astereae, where parts of two large genera, *Olearia* and *Celmisia*, are included in the 1, and in Calenduleae, where parts of the largest two genera, *Osteospermum* and *Tripteris*, are included in the 1 of the table.

under types V and XIII may be omitted, as these types of styles occur wherever there is the necessary form of floret, as does also type I. The Eupatorieae and Vernonieae have simple styles. It will be seen at a glance that type IV is the form of most common occurrence, and this type is undoubtedly the fundamental type of style for the Compositae. The majority of the Astereae show styles with appendages more or less complex, and with this is to be correlated the great preponderance of simple stamens in this tribe. The Heliantheae show a very similar stage of development, but the Helenieae have a distinctly larger proportion of genera of the simple type IV.

In the Anthemideae the great majority of genera have this type of style. The Inuleae are again anomalous in having a peculiar style, type XII, which is almost, if not quite, as simple as type IV, and is to be correlated with the preponderance of the higher types of stamens in this tribe. The Senecioneae, while showing a considerable range of structure in the style, have a large proportion of type IV. Indeed, Bentham describes type IV as the characteristic style of the Senecioneae. The Calenduleae have quite a special type of style, type VI. The Cichorieae, without exception, have the style of type I, which is the type for the ray florets in many other tribes. As with the stamens, the Arctotideae show a considerable percentage of simple styles with some of the higher types, forming a transition to the Mutiseae, and the latter tribe forms an ideal intermediate stage between the Arctotideae and the Cynareae, which have the highest form of style, types X and XI.

Neglecting columns V and XIII for the above-mentioned reasons, and taking type IV as a base, we find that lines of development are to be found almost diagrammatically similar to those in Table I. As before, there are two short lines, one to the Anthemideae and the other to the Cichorieae; two main lines, the first leading to the Eupatorieae and giving off branches to the Helenieae, Heliantheae, Astereae, and Vernonieae, the other leading to the Cynareae and giving off branches to the Arctotideae and Mutiseae; and a fifth leading to the Inuleae. The only difference is that a sixth line leads to the Calenduleae, the style of which cannot be considered a transition stage to that of type IX.

Thus from these tables alone we get two phylogenetic diagrams almost identical. This is only to be expected if the pollen-presentation mechanism has undergone progressive or retrogressive development, and economy of pollen seems to be the simplest explanation of this progressive elaboration of those parts which deal with the problem of delivering to each insect visitor a sufficient, but also a minimum, amount of pollen.¹

¹ To those who have watched the miserly way in which the pollen-presentation mechanism of *Centaurea* supplies pollen to the bees the idea of economy is sure to have suggested itself, but, of course, there is in this case the additional mechanism of sensitive stamens.

The pollen-presentation mechanism is not the only character which shows progressive variation in the Compositae, and any phylogenetic scheme must take into account the form, development, and colour of the corolla, the form of the pappus, the composition of the capitulum, and the geographical and geological distribution of the main divisions of the order; the available data concerning these characteristics must be increased before a satisfactory discussion of the inter-relationships of the tribes can be attained.

CONCLUSION.

In dealing with so recent an order, and one which, as a whole, is herbaceous, the fossil evidence is scanty and conflicting. Such being the case, the somewhat scattered fossil literature of the order awaits critical study.

That the cytological phenomena might be of value occurred to the writer early in 1913, and material was afterwards prepared for cytological investigation. Since that time the question of correlation between chromosome dimensions and phylogeny has been the subject of several papers (14 and 7) which have dealt with the problem in relation to the larger groups of the animal and plant kingdoms, and the results already obtained are being held over, pending a critical study of a considerable number of closely related species. The characteristic more or less spherical forms of the chromosomes in most Compositae may be mentioned as one interesting fact, in view of the controversial condition of the subject at present.

In addition to the data which have already been collected concerning the floral organs, a number of isolated but relevant observations have come under my notice during the four years which I have been working at this problem, and although these cannot be introduced readily into such a brief and tentative account as the foregoing, all the known facts are quite compatible with the origin of the tribes which is suggested as a result of the analysis of the staminal and stylar forms.

Acknowledgements are due to the Regius Keeper of the Royal Botanic Garden of Edinburgh for permission to study in the herbarium and for fresh material of many species of *Senecio*; to Professor M. C. Potter, for access to books and periodicals; to Professor A. C. Seward, for help with the fossil literature; to Professor A. H. Trow, Mr. W. Hales, A.L.S., Chelsea Physic Garden, and Mr. R. Irwyn Lynch, M.A., University Botanic Garden, Cambridge, for material.

SUMMARY.

1. The hypothesis that the appendages of the style branches and the apical and basal appendages of the anthers are the expression of a tendency

to economy of pollen, which is limited only by the biological necessity of providing sufficient pollen to ensure fertilization, is supported by evidence of correlative development of these appendages.

2. Tables are given showing the relative frequency of occurrence of the different types of styles and stamens in the various tribes, and these tables are also used to show lines of development and specialization in the pollen-presentation mechanism.

LITERATURE CITED.

1. BENTHAM, G.: Notes on the Classification, History, and Geographical Distribution of Compositae. Journ. Linn. Soc. (Bot.), vol. xiii, 1873.
2. BENTHAM, G., and HOOKER, J. D.: Genera Plantarum, vol. ii, Pt. I, London, 1874.
3. CASSINI, H.: Opusculs phytologiques. Paris, 1826.
4. COL, M.: Quelques recherches sur l'Appareil sécréteur des Composées. Journ. de Botanique, vol. iii, 1899.
5. DELPINO, F.: Studi sopra un lignaggio anemofilo delle Composte. Firenze, 1871.
6. DUFOUR, L.: Observations sur les affinités et l'évolution des Chicoracées. Compt. Rend., vol. cxlv, 1907.
7. FARMER, J. B., and DIGBY, L.: On Dimensions of Chromosomes considered in Relation to Phylogeny. Phil. Trans. Roy. Soc., B., 205, 1914.
8. HILDEBRAND, F.: Beiträge zur vergleichenden Anatomie der Ambrosiaceen und Senecionideen. Marburg, 1887.
9. HOCH, F.: Vergleichende Untersuchungen über die Behaarung unserer Labiaten, Scrophularineen und Solaneen. Freiburg i. B., 1885.
10. HOFFMANN, O.: Engler und Prantl's Die natürlichen Pflanzenfamilien, Teil IV, Abt. 5. Leipzig, 1897.
11. LAVIALLE, P.: Recherches sur le développement de l'ovaire en fruit chez les Composées. Ann. d. Sci. nat., Bot., 9^e sér., t. xiv, 1912.
12. LEBARD, P.: Remarques sur les affinités des principaux genres du groupe des Liguliflores. Compt. Rend., clvii, 1913.
13. LESSING, C. F.: Synopsis Generum Compositarum. Berolini, 1832.
14. MEEK, C. F. U.: A Metrical Analysis of Chromosome Complexes. Phil. Trans. Roy. Soc., B., 203, 1913.
15. NICHOLS, M. A.: Achenial Hairs of Compositae. Bot. Gaz., vol. xviii, 1893.
16. SCHMIDT, C.: Vergleichende Untersuchungen über die Behaarung der Labiaten und Boragineen. Rybnik, 1888.
17. SCHULTZ BIPONTINUS: Cassiniaceae. Flora, 1852, &c.
18. SMALL, J.: The Identification Value of Hairs. Pharm. Journ., Ser. iv, vol. xxxvi.
19. SMALL, J. K.: Flora of South-eastern United States. New York, 1903.
20. VUILLEMIN, P.: Tiges des Composées. Paris, 1884.
21. WETTSTEIN, R. V.: Handbuch der systematischen Botanik. 1903.

Small, James. 1915. "The pollen-presentation mechanism in the Compositae." *Annals of botany* 29, 457–470.

<https://doi.org/10.1093/oxfordjournals.aob.a089559>.

View This Item Online: <https://www.biodiversitylibrary.org/item/243629>

DOI: <https://doi.org/10.1093/oxfordjournals.aob.a089559>

Permalink: <https://www.biodiversitylibrary.org/partpdf/320076>

Holding Institution

Smithsonian Libraries

Sponsored by

Biodiversity Heritage Library

Copyright & Reuse

Copyright Status: Not in copyright. The BHL knows of no copyright restrictions on this item.

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.