REPRODUCTIVE PROCESSES AFFECTING THE TAXONOMY OF SOME MEXICAN AND CENTRAL AMERICAN SPECIES OF EUPATORIUM

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ABSTRACT

REPRODUCTIVE PROCESSES AFFECTING THE TAXONOMY OF SOME MEXICAN AND CENTRAL AMERICAN SPECIES OF EUPATORIUM

By

Jerold Lee Grashoff

Eupatorium is one of the two largest genera in the Compositae. It consists of an estimated 1200 herbs, shrubs, vines, and trees which are distributed chiefly in the American tropics. The genus has not been treated systematically for over one hundred years and is often considered to be taxonomically difficult. The four parts of this thesis may ultimately contribute to a systematic treatment of the genus.

Cytological and histological studies were made on young ovules of *Eupatorium muelleri* Sch. Bip ex Klatt, section *Eximbricata*, and *E. macrophyllum* L. f., section *Subimbricata*. The former is a tetraploid, obligate apomict. Agamospermy in this species was observed to be that of diplospory by somatic division. Sizeable embryos are formed before anthesis begins. The latter, a diploid, sexual species was observed to have normal meiosis resulting in a linear tetrad, the chalasal cell of which usually develops into the mature gametophyte. Antipodal cells and nuclei in *E. macrophyllum* are variable in number.

An investigation of the contents of anthers of preanthesis florets of 1,048 specimens representing 192 species was made to provide an estimate of the extent of apomixis in Mexican and Central American species of *Eupatorium*. On the basis of this examination apomixis is thought to occur in 35 (18.2 per cent) of the species studied. Three sections of the genus contain possible apomicts. It is hypothesized that apomixis has developed independently in each of these sections.

Concentrated systematic effort in a genus in which apomixis occurs has often resulted in taxonomic confusion. Much of the taxonomic confusion in Mexican and Central American *Eupatoria* may be the result of an inadequate understanding of the extent of apomixis in the genus. Some suggested guidelines are given for the monographic treatment of apomictic species in a genus such as *Eupatorium*.

Wind pollination in the Compositae has heretofore been known to occur only in the tribe Anthemideae and the subtribe Ambrosinae of the Heliantheae. Eight species of *Eupatorium* were observed to have morphological adaptations thought to be indicative of anemophily. These species generally have copious, small, relatively smooth pollen, elongated inflorescences, increased stigmatic surfaces on the style branches, and reduced apical anther appendages. On the basis of morphological evidence it is concluded that anemophily has developed in the Eupatorieae independently from that of the other tribes and that, as exhibited by these eight species, the adaptation to anemophily in Eupatorium is in its incipient stages.

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By

Jerold Lee Grashoff

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A collecting expedition to Mexico and Central America was sponsored by the Institute of International Agriculture and Nutrition.

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GENERAL INTRODUCTION

Eupatorium is one of the two largest genera in the Compositae. It contains an estimated 1200 species of herbs, shrubs, vines, and trees which are distributed chiefly in the American tropics but range from southern Canada to Patagonia. The greatest diversity appears to be in South America. About 300-400 species occur in Mexico and Central America; 50-75 are found in the United States and Canada; approximately 100 are located in the West Indies. Four species are native to Europe, one to Africa, and several to Asia.

Eupatorium is economically important as the result of some undesirable attributes of several species. Livestock have been poisoned by *Eupatorium rugosum* (see Kingsbury, 1964) and humans have died from the ingestion of the milk of the sick cattle. Milksickness, as the disease is called in humans, was a major problem during the settlement of the mid-western states of the United States where it often reached epidemic proportions. The disease is said to have been the cause of death of Abraham Lincoln's mother. Eupatorium wrightii of the southwestern United States and northern Mexico is said to kill cattle quickly and without any visible symptoms. Research concerning the poisonous properties of some species of Eupatorium is summarized by Kingsbury (1964). Several species of Mexican origin have become distributed throughout the tropics where they have become pernicious weeds and are now a significant problem to tropical agriculture to the extent that eradication programs have been initiated in several countries.

No comprehensive taxonomic work has been done in Eupatorium since De Candolle (1836). He divided the genus into three series: Imbricata (with four sections), Subimbricata, and Eximbricata. The series were distinguished by the number of rows of phyllaries and their degree of imbrication. Bentham and Hooker (1876) expanded Eupatorium with the inclusion of twelve previously described genera. Hoffmann (1889) described the eight sections of the genus which are in current usage, again basing the sections largely on characteristics of the involucre. Several of the sections are, however, poorly defined and are in need of reinvestigation. Six of the eight sections are represented in Mexico and Central America. The greatest amount of information on the tropical species was published by B. L. Robinson who, between the years of 1893 and 1934, approximately doubled the number of described species of Eupatorium.

Three factors confound investigation in Eupatorium: hybridization, apomixis, and morphological or phenotypic plasticity. Hybridization has been documented in species of Eupatorium from the southeastern United States (Fryar, 1964) and is currently being investigated by Dr. R. K. Godfrey. Hybridization probably also occurs in the tropical species but these have not been adequately studied because the great number of relatively obscure species make hybridization difficult to detect. Conversely, apomixis is known from the tropical species (Holmgren, 1919; Sparvoli, 1960) but is only suspected in some temperate species from the southeastern United States (Grant, 1953). Morphological plasticity is reported by Baker (1965, 1967) in several self-compatible weedy species from Mexico and Central America. An even greater amount of phenotypic plasticity is displayed in some presumably apomictic Mexican species but this is in need of further investigation.

Any comprehensive work on the tropical species of Eupatorium awaits a thorough systematic treatment of the genus. It is imperative, however, that the systematist be aware of the biological phenomena which tend to confuse the species boundaries. This paper is meant to illustrate several reproductive processes which have evolved in Mexican and Central American Eupatoria. It is expected that a better understanding of the reproductive processes will permit a more accurate taxonomic treatment of the genus. The following observation by Ornduff (1969) seems especially relevant to the taxonomy of Eupatorium.

> Many of the diverse floral characteristics used by taxonomists in assessing relationships among taxa represent adaptations to specific pollinators or pollinating methods. Therefore, the diversity of reproductive methods that occurs within a phylad has a strong influence on the number of taxa that are generally recognized in the phylad. . . . It is suggested that taxonomists should make an attempt to understand the reproductive methods of the plants with which they work, since such an understanding will strengthen the foundation upon which taxonomic judgments are made.

The thesis is in four parts, each of which contains its own introduction and literature review. The individual parts may ultimately contribute to a systematic treatment of the genus, which is beyond the scope of the present study.

CYTOLOGICAL AND EMBRYOLOGICAL OBSERVATIONS

Introduction

Cytological investigation in *Eupatorium* has been, for the most part, restricted to studies of apomictic species and to chromosome counts. At present, chromosome numbers have been reported for over 100 species of the genus. Several counts have not been reported in the literature but are indicated on voucher specimens only. The meiotic number of *n* = 4 has been reported in *E. sinclairii* and *E. microstemon*. This number is considered by Baker (1967) to be derived from the more common condition of *n* = 10. Crosses between plants with *n* = 4 and *n* = 10 produce highly fertile and vigorous offspring. The number *n* = 17 is common in section *Eximbricata* (as is *n* = 10) but the higher base number is apparently restricted to this section. Over 25 per cent of the species thus far counted are polyploids or contain polyploid populations. Most common are triploids (17 spp.) and tetraploids (10 spp.) with a few others: hexaploids (4 spp.), octaploids (1 sp.) and four species at an undetermined ploidy level. Synapsis is never seen in the triploids and may or may not occur in the tetraploids. Information is not available concerning synapsis in the higher polyploids.

Apomixis consists of two basic methods of asexual reproduction. Vegetative reproduction, or asexual reproduction by vegetative propagules, occurs commonly in both sexual and asexual plants. Vegetative reproduction may be a natural process of the plant or it may be induced by various horticultural practices. Agamospermy, or asexual reproduction by seeds, was not discovered until the mid-nineteenth century (J. Smith, 1841), and since that time agamospermy has been demonstrated in a wide array of vascular and non-vascular plants.

Agamospermy can be divided into two subcategories. In adventitious embryogeny the embryos arise in the ovule from nucellar or integumental outgrowths, omitting the gametophyte from the life cycle altogether. The other subcategory is that in which gametophytes develop. This subcategory, in turn, is divisible into diplospory, in which the gametophyte arises directly from a megaspore mother cell (EMC); and apospory, in which the gametophyte develops from some cell other than the EMC. Three types of diplospory are recognized.

Diplospory by means of a restitution nucleus is a process in which the chromosomes never pair. The first division of meiosis is arrested at anaphase and a nuclear membrane envelops the entire mass of chromosomes. The restitution nucleus is characteristically elongated. At metaphase of the second division all the chromosomes are gathered on a common plate. After telophase II daughter nuclei contribute to the binucleate embryo sac. This type of diplospory is not known in _Eupatorium_.

Diplospory by means of a pseudohomeotypic division is a process in which the EMC nucleus has the appearance of a pre-meiotic nucleus. The chromosomes remain unpaired at diakinesis and are scattered in the cell. The metaphase univalents collect at the equatorial plane, divide longitudially and separate, forming two nuclei each with the unreduced chromosome number. The resulting dyad may or may not undergo a somatic division before one of the cells becomes dominant and forms an embryo sac at the expense of the others. This type of diplospory has been observed by Sparvoli to occur occasionally in _Eupatorium riparium_.

Diplospory by means of a somatic division is a process in which the EMC never assumes the characteristic aspect of a pre-meiotic cell. Except for its great size, the nucleus of the megaspore mother cell resembles nuclei of surrounding somatic cells. Division is typically mitotic, resembling that of any somatic cell. This type of diplospory is the rule in _E_. _adenophorum_ and _E_. _riparium_.

There is some doubt (cf. Beaman, 1957) whether the first two types of diplospory, noted above, are distinct from one another. No information concerning this question was obtained in the present study.

Apomixis in _Eupatorium_ was first reported by Holmgren (1916, 1919). He investigated 8 sexual species and

E. adenophorum (reported as *E. glandulosum*), a triploid, obligate apomict (2*n* = 51). In *E. adenophorum* an embryo sac develops by diplospory with the division of the EMC resembling a somatic division. The unreduced egg develops into the 2*n* embryo and the polar nuclei unite and develop into the 4*x* cellular endosperm. A similar case was reported by Sparvoli (1958, 1960) in another triploid, obligate apomict, *E. riparium* (2*n* = 48). In addition to somatic diplospory, Sparvoli observed occasional diplospory by means of a pseudohomeotypic division of the megaspore mother cell.

Eupatorium muelleri

Eupatorium muelleri Sch. Bip. ex Klatt (section *Eximbricata*) is a tetraploid with 68 univalents and is closely related to at least ten other wholly or partially apomictic species. It is an herb of low stature with an erect or ascending stem one meter or less in length. The foliage is confined to the lower portion of the plant and the inflorescence is a few-headed open panicle with heads of 80 or more white florets. No sexual populations of the species are known. Unlike the two apomicts studied by previous investigators, *E. muelleri* is not weedy. It has instead a rather limited habitat preference, being restricted to pine or oak-covered slopes from central Mexico to Honduras. It is usually found in semi-shady areas.

Microsporogenesis

Seeds were obtained from a herbarium specimen (McVaugh 21246, MICH) and were germinated on moist filter paper in petri dishes. The plants were grown to maturity, at first in a growth chamber, later in the garden, and then in the greenhouse. Flowering was delayed due to cool autumn weather but the plants flowered shortly after they were placed in a greenhouse. Flowering occurred nearly a year after germination. Probably as a result of the delayed flowering the plants became atypically shrubby and grew unusually tall. Buds were fixed for 24 hours in Carnoy's solution of 6 parts 100% ethanol, 3 parts chloroform and 1 part glacial acetic acid. They were maintained at ca. 40^{o} F in 70 percent ethanol until used. Anthers were crushed in aceto-carmine for chromosome analysis. Microspore mother cells at diakinesis were observed to have 68 univalent chromosomes (Figure 1). This number was observed repeatedly in cells from several florets. A voucher specimen is filed in the Michigan State University Herbarium (MSC). After flowering, the plants died back and the areal shoots were cut off. Some of the plants died at this point while others sent up new but weak shoots from the base of the stem. These also eventually died before reaching flowering stage.

Plants were also grown from seeds obtained from Grashoff 188 and 236 from Jalisco and Chiapas, respectively. The florets were prepared primarily for investigation of the

Figure 1. *Eupatorium muelleri*. Microsporocytes with 68 univalents (ca. x 9500).

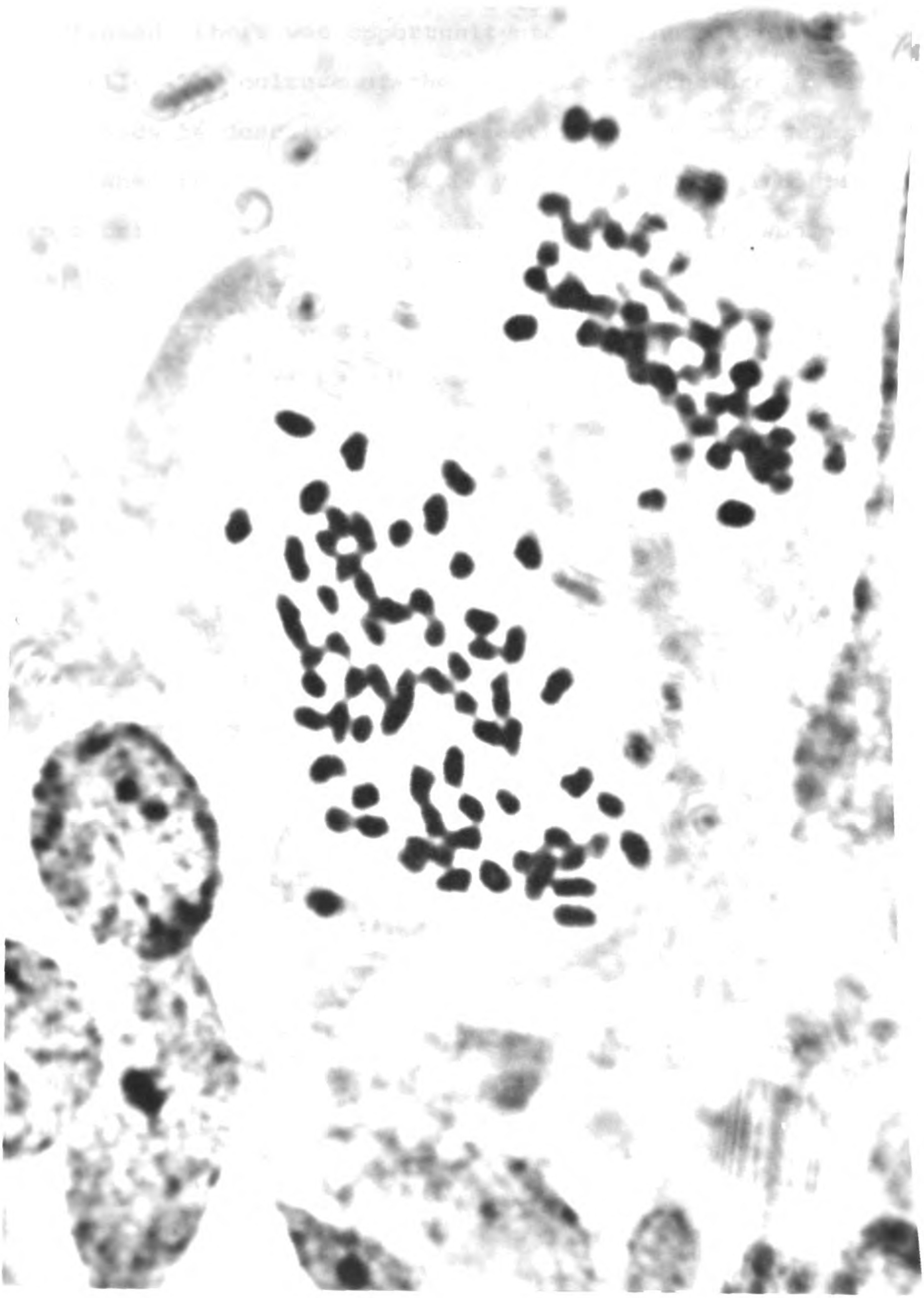


Figure 1

megagametophyte but since the whole floret was usually sectioned, there was opportunity to examine microsporogenesis as well. The culture of these plants and the preparation of the heads is described in the section on megasporogenesis.

When the megasporocyte is young and nearly indistinguishable from the other cells in the ovule, the microsporocytes have already enlarged and distorted the tapetal layer. The microsporocytes have the appearance of large somatic cells. The first division of meiosis occurs soon afterward, and, although some cells appear normal at metaphase I, others contain lagging chromosomes. After the first division the two halves of the dyad often separate and become spherical. Many cells abort at this point, some form pollen walls, and the rest enter the second stage of meiosis. Nuclei at this time all look very unorganized with numerous dark-staining bodies which appear tangled. The second metaphase is more abnormal than the first. Often so many lagging chromosomes are present that there is no well-formed metaphase plate. Telophase, if it is reached before abortion, is characterized by unequal groups of chromosomes forming the daughter nuclei. Micronuclei occur occasionally. The four resulting nuclei (occasionally there appear to be but three) never form walls about them but begin to disintegrate almost immediately. The cells may abort at any stage of meiosis. Those cells which form pollen walls lose them later in a process of resorption. All the products of microsporogenesis begin to disintegrate before the first division of the EMC nucleus. The only remnants of the process are bodies of variable diameter which are clear and oil-like when seen in fresh condition. They are often preserved in the anthers of dried specimens and can usually be regarded as an indication of apomixis.

Megasporogenesis

Material for the investigation of megasporogenesis was obtained in Mexico (<u>Grashoff</u> <u>188</u> and <u>236</u>). Seeds were germinated in petri dishes and the seedlings were removed to flower pots shortly after germination, which occurred in a period from 3 days to 3 weeks after sowing. The young plants were kept near a window at first and after a few weeks were transferred to a growth chamber. The plants appeared to grow slowly until the temperature was increased to 90° F by day and 70° F by night. After the temperature was raised, the plants grew rapidly; however, difficulty in maintaining a moisture supply was corrected by lowering the day temperature to 80° F. Under these conditions and with a ten-hour day length the plants began flowering about 5 months after germination. Heads were killed and fixed in Navashin's solution of 10 parts 1% chromic acid, 7 parts 10% acetic acid and 3 parts commercial formaldehyde. They were kept in this solution at ambient temperature until use. The heads were then washed in water, the florets removed, and the involucre and receptable discarded. Sections were cut on a rotary microtome at a thickness of 10 microns. The sections were stained according to a haematoxylin-safranin staining procedure adapted from Esau (1944) and were mounted in Canada balsam. The slides are in the possession of the author. Voucher specimens are filed in the Michigan State University Herbarium.

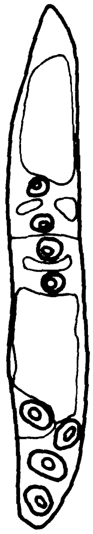
Diplospory by means of somatic division was the only type observed in ovules of Eupatorium muelleri, and the process is essentially identical with that described by Holmgren (1919) and Sparvoli (1960). When the ovule is young, the megaspore is nearly indistinguishable from the surrounding tissue (Figure 2). At length the larger size and the central position of the megaspore clearly distinguish it from the rest of the cells (Figure 3). The megaspore continues to enlarge at the expense of the nucellus. At this point it can be considered a one-nucleate embryo sac. Associated with this increase in size is the vacuolization of the embryo sac. The uninucleate stage is one of long duration, often lasting until shortly before anthesis. The normal duration of the one-nucleate stage corresponds roughly to the time in which sexual species would undergo meiosis, form tetrads and, at length, develop a one-nucleate embryo sac (see discussion of E. macrophyllum, below). Two divisions occur rapidly to give a four-nucleate embryo sac (Figures 4-7). A final division results in an eight-nucleate embryo sac

Figures 2-7. *Eupatorium meulleri*. Embryo sac development. 2 and 3, Megasporocyte stage; 4, Uninucleate stage resulting from the enlargement of the megasporocyte. The nucellus is disintegrating. 5 and 6, Binucleate stage; 7, 4-nucleate stage (all ca. x 1500).

which, at first, has the nuclei arranged in groups of four at each end of the sac (Figure 8). One nucleus from the micropylar end and one from the chalazal end migrate toward the center of the embryo sac to become the polar nuclei. Unlike the sexual species studied, in which the polar nuclei unite shortly after migration to the center of the embryo sac, the polar nuclei in _E_. _muelleri_ do not unite until after division of the diploid egg. At length the egg cell is differentiated, the antipodals begin to degenerate, and the synergids become less conspicuous. Division of the diploid egg begins before anthesis and a sizeable embryo can be found in unopened florets (Figure 13). The embryo which is formed is unquestionably the result of apomixis. No viable pollen is ever produced, no pollen tubes can therefore reach the egg (none were ever seen), yet embryos are developed in pre-anthesis florets. The polar nuclei unite at a common metaphase plate by the time the embryo consists of a few cells (Figure 11). The endosperm cells are very large and, for a time, divide in synchrony with the cells of the embryo. Cells of both endosperm and embryo can contain two nuclei each (Figure 12), cell wall formation apparently coming later.

Abortion of the embryo sac is observed occasionally. This apparently can happen at any stage of development but the highest frequency of abortion seems to be during the uninucleate stage.

Figures 8-13. Eupatorium muelleri. Embryo sac development (continued) and early embryogenesis. 8, Early 8-nucleate stage; 9, Later 8-nucleate stage showing 3 antpodal cells, 2 polar nuclei, egg (nucleolus not shown), and 2 synergid nuclei; 10, Deliniation of egg cell, synergids somewhat obscured; 11, Embro sac containing 4-nucleate embryo, polar nucleus is dividing; 12, Young embryo and surrounding endosperm; some cells are binucleate; 13, Embryo and endosperm shortly before anthesis (all ca. x 600).



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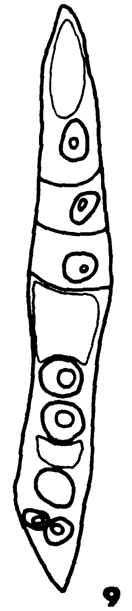

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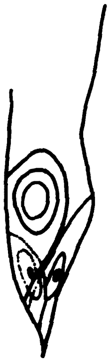

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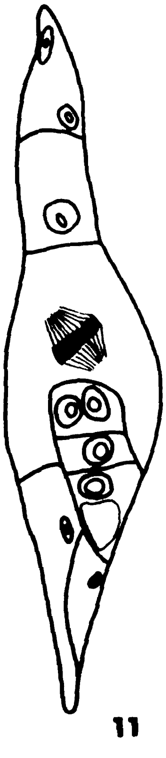

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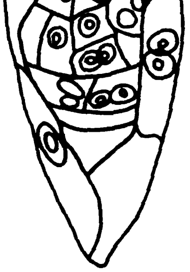

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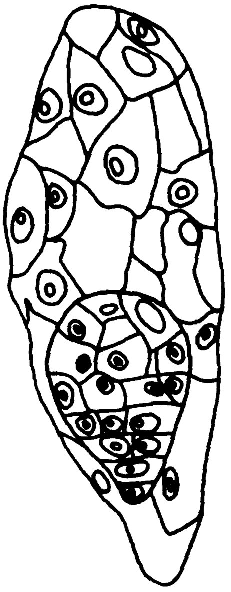

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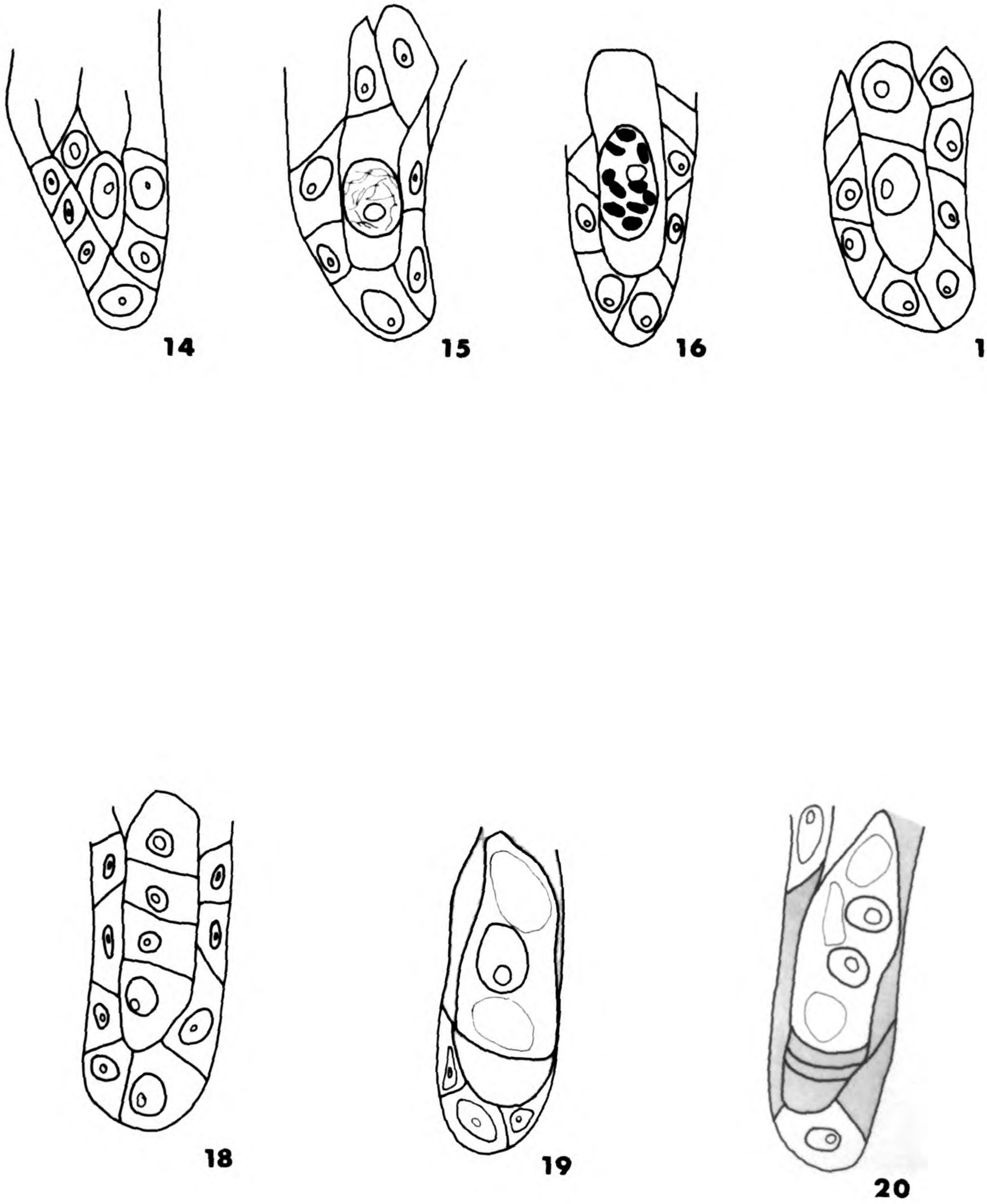
Figures 8-13

Megagametogenesis in Eupatorium macrophyllum

Eupatorium macrophyllum L. f. (section Subimbricata) is a moderately large herb occurring from Mexico to Brazil. It is generally found in areas of high rainfall. It appears to reproduce only sexually throughout its range, and has the chromosome number of n = 10. Material was obtained from seeds of specimens collected in southwestern Costa Rica near San Vito de Java (Grashoff 105). The plants were grown, fixed, sectioned, and prepared like those used for megagametophyte studies in E. muelleri. Only pre-anthesis florets were used.

The development of the female gametophyte in E. macrophyllum is comparable to that of most other Compositae. The megasporocyte, when first distinguishable from surrounding cells, is seen in leptotene (Figure 15). As the stages of prophase progress the megaspore increases slightly in size and at diakinesis 10 chromosomes are visible (Figure 16). The first division of meiosis is rapidly followed by the second and dyads are rarely found (Figures 17 and 18). The result of meiosis is a linear tetrad, the chalazal cell of which generally (but, apparently, not exclusively) becomes the one-uninucleate embryo sac (Figure 19). A series of three mitotic divisions forms the eight-nucleate embryo sac. The antipolal cells are separated by cell walls from the remainder of the gametophyte. Two polar nuclei, one from each end of the embryo sac, migrate toward the center and

Figures 14-20. Eupatorium macrophyllum. Megagametogenesis. 14, Megasporocyte and surrounding tissue before meiosis; 15, Megasporocyte at leptotene; 16, Megasporocyte at diakinesis, *n* = 10; 17, Dyad; 18, Tetrad; 19, Uninucleate embryo sac, nucellus and 3 of the megaspores degenerating; 20, Binucleate embryo sac, nucellus and 3 megaspores degenerating (all ca. x 1400).



Figures 14-20

Figures 21-24. *Eupatorium macrophyllum*. Megagametogenesis (continued). 21, 4-Nucleate embryo sac; 22, Early 8-nucleate stage; 23, Later 8-nucleate stage showing 3 antipodal nuclei, 2 polar nuclei, egg and 2 synergids; 24, Mature embryo sac, antipodals are beginning to degenerate; polar nuclei have fused; egg cell has enlarged and obscured the 2 synergids (all ca. x 1500).

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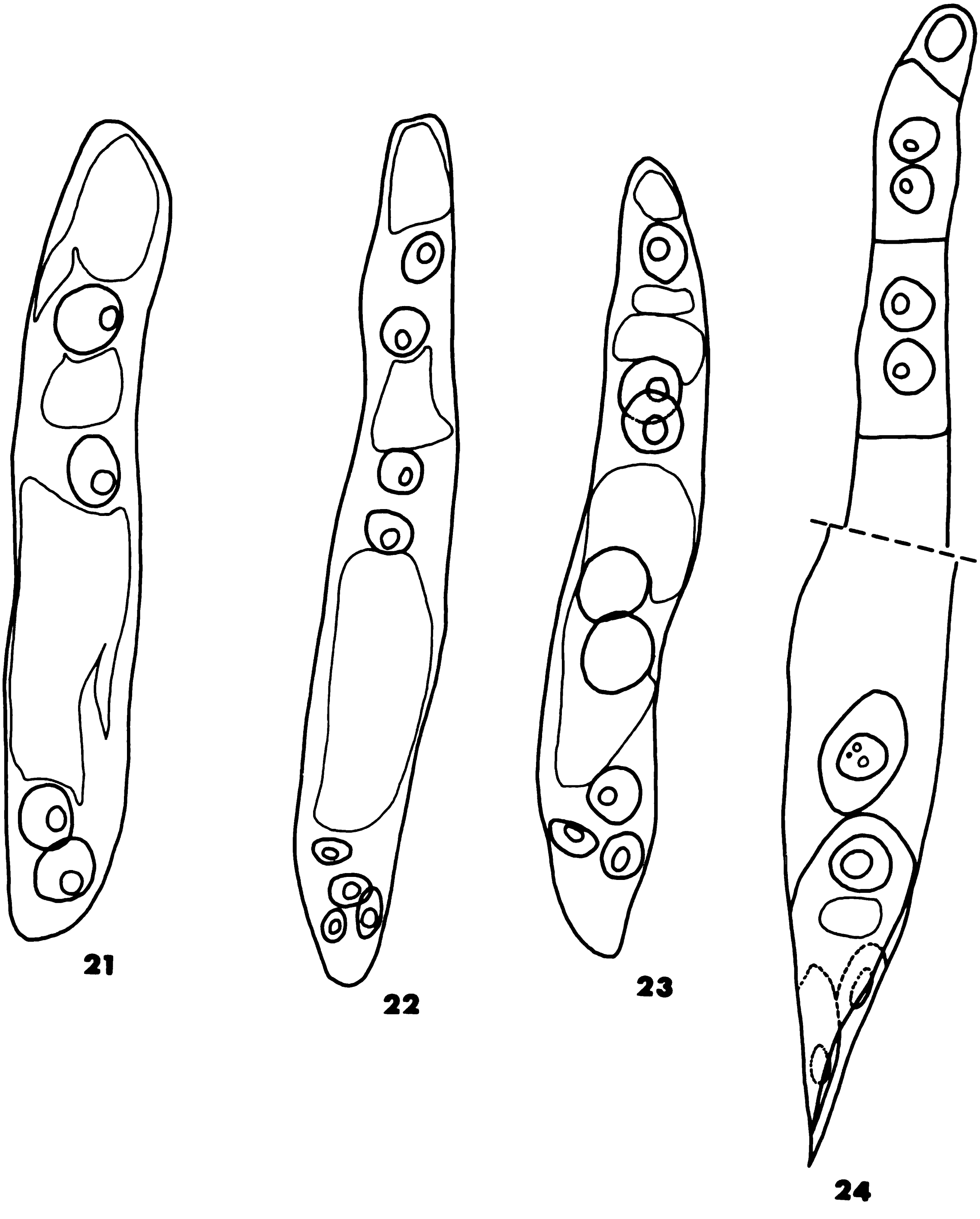
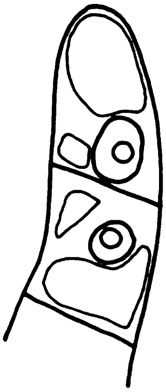


Figures 21-24

Figures 25-29. _Eupatorium macrophyllum_. Chalazal portion of embryo sacs showing variation in the number of antipodal cells and nuclei (all ca. x 1500).



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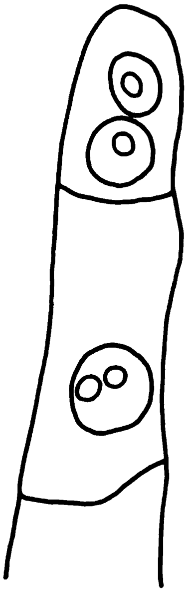

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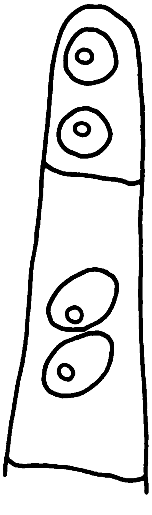

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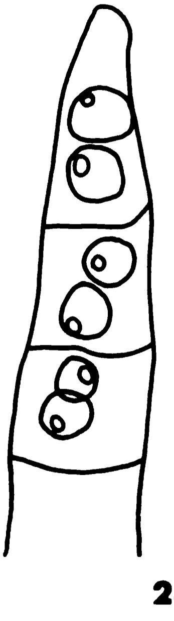

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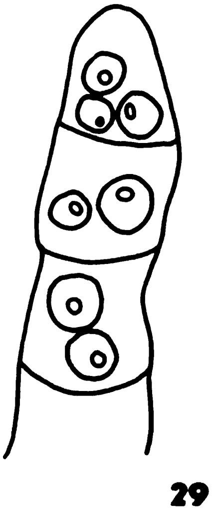

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Figures 25-29

fuse. The egg cell then enlarges and becomes vacuolized. In later stages of development the synergids are somewhat obscured by the egg cell and the antipodals begin to degenerate (Figure 24). The number of antipodal nuclei and cells is apparently loosely governed for they often proliferate. The usual case is to have two antipodal cells, one with two nuclei, the other with but a single nucleus. However, variations are frequent and range from two cells each with a single nucleus to three cells each with two or three nuclei (Figures 24-29).

Shortly before fusion of the two polar nuclei, ten dark bodies (prochromosomes?) are visible. The resultant polar nucleus has a larger size and often shows light portions in its nucleolus (Figure 24).

A SURVEY OF THE CONTENTS OF ANTHERS OF MEXICAN AND CENTRAL AMERICAN EUPATORIA

Introduction

Proof of agamospermy usually has rested upon breeding experiments or intensive cytological study of the megagametophyte. Both methods of investigation are time-consuming and neither can be adapted to accommodate a large amount of material in a limited time. To support my hypothesis that apomixis is a major factor contributing to taxonomic confusion in Eupatorium, a method was utilized in which large numbers of species could be examined with reference to breeding behavior.

Agamospermous plants often have abnormalities in microsporogenesis resulting in production of little or no viable pollen. No pollen is produced by the three apomictic species of Eupatorium thus far studied. Abortive pollen of irregular size and shape is produced by apomicts of Townsendia (Beaman, 1957) and Erigeron (Holmgren, 1919). An examination of pollen was therefore conducted to provide an indication of the possible presence of agamospermy in Mexican and Central American species of Eupatorium. Pre-anthesis florets from specimens of the Field Museum (F), the University of Michigan Herbarium (MICH), and the Michigan State University Herbarium (MSC) were used in the survey.

Materials and Methods

Florets from 1,048 specimens representing 192 species were macerated in drops of aceto-carmine to liberate the pollen. The preparations were examined directly with a compound microscope at 150-420 x magnification. Normal pollen grains are uniform in shape and size and stain reddish in aceto-carmine. After several minutes, the nuclei stain dark red but they are often obscured by the highly sculptured pollen wall. Two kinds of abnormal pollen are observed in *Eupatorium*. In specimens of section *Cylindrocephala* the grains are frequently of two sizes, the larger stained, the smaller usually clear. The other type of abnormality is found most frequently in specimens of section *Eximbricata*. In these specimens, the pollen is more or less uniform in size but the grains appear empty and collapsed or distorted. The extreme condition is one in which no grains are formed at all and, in a few specimens, even the spherical residue bodies are missing, the anthers being empty.

Many precautions must be taken when judging the condition of the pollen because other factors than meiotic abnormalities may cause pollen grains to look abnormal. First, the florets must be of the proper stage of development, preferably immediately before anthesis. Anthers which are too young have immature grains which do not stain well. Post-anthesis florets often have lost too many grains to permit an accurate analysis. Examination of immature or post-anthesis florets is therefore not useful. Second, while most specimens are useable regardless of age, some, possibly due to slow drying, have grains which appear to have fermented. In one instance the contents of the anthers were found to be fungal spores. Third, some pollen abortion is normal even in sexual plants and the amount of abortion often increases with higher levels of ploidy. Fourth, interspecific hybrids, if they exist, can be expected to show a high degree of pollen sterility. Fifth, plant collectors often select unusual examples from a population resulting in perhaps a higher proportion of abnormal specimens in herbaria than actually exist at any one time in nature. Sixth, environmental factors such as drought, insect damage, disease, or herbicides can cause the production of abnormal pollen grains.

Pollen quality was judged "bad" (Table I) when over 50 percent of the grains were unstained, when great irregularity in size and shape occurred, or when few or no grains were produced. Pollen quality was judged "?" when about 30 to 50 percent of the grains were unstained. Pollen quality was judged "good" if the grains, though unstained, were regular in size and shape. This was frequently the case with specimens which appeared to have fermented.

From one to 60 specimens were examined for each species. Lack of adequate material often limited the number of specimens which could be observed. Generally, judgments concerning the probable presence of agamospermy in a species were only made on those species for which five or more specimens were observed. However, some species which are closely related to suspected apomicts and which showed pollen abnormality were also judged likely to be apomictic even if fewer than five specimens were used.

When the survey was initiated, two florets selected from each specimen were examined separately. As the study progressed it became evident, however, that the degree of pollen normality varied little, if at all, from floret to floret. It was felt that the uniformity of the anther contents and the nature of the survey did not require duplication of observations but that by limiting the number of observations per specimen to one, a greater number of specimens could be examined. Often if the contents of the anthers appeared dubiously good or dubiously bad a second floret was prepared, but in the majority of cases, the preparation of the second floret appeared identical to the first.

Table 1 summarizes the survey and the judgments made on each species. The Appendix lists the specimens examined and the conclusions on each specimen.

TABLE 1. Summary of pollen quality in Mexican and Central American species of *Eupatorium*

Eupatorium species	No. of specimens examined				Judgment concerning species	Section (putative apomicts only)	Remarks
		Pollen quality					
	Total	Good	?	Bad			
1. adenachaenium	2	2	0	0	c1		
2. adenophorum	11	5	0	6	b	E	2n = 51 (Holmgren, 1919)
3. adenospermum	5	4	1	0	a		
4. albicaule	18	17	1	0	a		
5. amblyolepis	3	1	0	2	c2	E	
6. amestinum	1	0	0	1	c2	C	
7. amygdalinum	7	7	0	0	a		
8. anchisteum	11	0	0	11	b	E	
9. angulifolium	3	3	0	0	a		
10. angulare	12	12	0	0	a		n = 25 II (Turner and King, 1964)
11. anisochromum	12	12	0	0	a		n = ca 17 (Turner and King, 1964)
12. antiquorum	1	1	0	0	c		
13. aralaefolium	8	8	0	0	a		
14. areolare	10	10	0	0	a		
15. arthrodes	2	2	0	0	a		
16. aschenbornianum	60	22	1	37	b	E	n = 20+ frags. (Turner et al., 1962)
17. azureum	9	9	0	0	a		
18. bartlettii	7	7	0	0	a		
19. bellidifolium	18	0	0	18	b	E	n = 67-68 II (unpublished)
20. bertholdii	7	6	0	1	b	C	
21. betonicum	13	13	0	0	a		n = 10 (Turner and King, 1964)
22. biglovii	8	2	3	3	b	C	
23. bilbergianum	2	2	0	0	c		
24. bimatrum	8	7	1	0	a		
25. blakei	2	2	0	0	c		
26. brandigeanum	1	1	0	0	c		
27. brenesii	1	1	0	0	c		
28. brevipes	21	18	3	0	a		
29. caecilae	2	2	0	0	c		
30. calaminthaefolium	9	9	0	0	a		
31. calophyllum	8	8	0	0	a		
32. campechense	3	3	0	0	c1		
33. capillifolium	3	3	0	0	c1		
34. cardiophyllum	7	7	0	0	a		2n = 20 (Grant, 1955)
35. carltonii	3	3	0	0	c1		
36. chapalense	5	5	0	0	a		
37. chiapense	7	6	1	0	a		n = 17 II (unpublished)
38. choricephalum	14	2	0	12	b	E	
39. chrysostyloides	3	3	0	0	c1		
40. chrysostylum	2	2	0	0	c1		

continued

TABLE 1 - continued

Eupatorium species	No. of specimens examined				Judgment concerning species	Section (putative apomicts only)	Remarks
		Pollen quality					
	Total	Good	?	Bad			
41. collinum	15	10	1	4	b	S	
42. collodes	2	2	0	0	c		
43. conspicuum	7	3	0	4	b	E	
44. constipatiflorum	2	1	1	0	c		
45. conzattii	2	2	0	0	c		
46. coulteri	11	5	4	2	b	E	
47. crassirameum	6	6	0	0	a		
48. cremastrum	2	1	1	0	c		
49. crocodilium	2	2	0	0	c1		
50. daleoides	18	16	2	0	a		2<u>n</u> = 20 (Grant, 1953)
51. deltoideum	8	8	0	0	a		
52. dryophyllum	2	2	0	0	c		
53. durandii	6	6	0	0	a		
54. ehrenbergii	1	1	0	0	c		
55. elatum	6	6	0	0	a		
56. eriocarpum	1	1	0	0	c		
57. erythropappum	9	9	0	0	a		<u>n</u> = 50-51 II (unpublished)
58. espinosarum	10	10	0	0	a		
59. galleotii	1	1	0	0	c		
60. glaberrimum	1	1	0	0	c		
61. glabratum	22	21	1	0	a		<u>n</u> = 17 (Turner et al., 1961a)
62. glaucum	2	2	0	0	c		
63. glischrum	1	1	0	0	c		
64. gonzalezii	1	1	0	0	c		
65. gracicaule	1	1	0	0	c		<u>n</u> = 10 (Powell and Turner, 1963)
66. greggii	13	13	0	0	a		<u>n</u> = 10 (Turner et al., 1961b)
67. griseum	9	8	0	1	a		
68. haenkianum	4	4	0	0	a		
69. hastile	7	7	0	0	a		
70. havanense	9	9	0	0	a		
71. hebebotryum	6	6	0	0	a		
72. hederaefolium	1	1	0	0	c		
73. hemipteropodum	1	0	0	1	c		
74. heydaenum	4	4	0	0	a		
75. hidalgense	5	5	0	0	a		
76. holwayanum	2	2	0	0	c		
77. hondurense	4	4	0	0	a		
78. hospitale	5	5	0	0	a		
79. heuheutecum	2	0	0	2	c2	E	
80. hylonum	3	2	1	0	c		

continued

TABLE 1 - continued

Eupatorium species	No. of specimens examined				Judgment concerning species	Section (putative apomicts only)	Remarks
		Pollen quality					
	Total	Good	?	Bad			
81. hymenolepis	4	4	0	0	a		
82. hypodictyon	1	0	0	1	c		
83. hypomalacum	2	1	0	1	c		
84. hyssopifolium	1	1	0	0	c2	S	2n = 20, 2n = 30 (Grant, 1953)
85. hyssopinum	8	7	1	0	a		
86. imitans	8	8	0	0	a		n = 29 II (unpublished)
87. incarnatum	1	1	0	0	c		
88. incomptum	5	5	0	0	a		
89. iresnoides	1	1	0	0	c		
90. irrasum	1	1	0	0	c		
91. isolepis	1	0	0	1	c2	E	
92. ivaefolium	7	0	0	7	b	C	
93. ixiocladon	2	2	0	0	c		
94. jejunum	5	5	0	0	a		
95. karwinskianum	2	2	0	0	c		
96. kupperi	1	1	0	0	c		
97. laevigatum	5	0	0	5	b	C	n = 20 (Turner et al., 1961a)
98. lanicaule	2	2	0	0	c		
99. lemmonii	3	1	0	2	c2	E	
100. leptodictyon	2	2	0	0	c		
101. leucocephalum	4	4	0	0	c1		
102. liebmannii	4	4	0	0	c1		
103. ligustrinum	17	17	0	0	a		n = 10 (Turner et al., 1961b) n = 17 (unpublished)
104. loesnerii	3	3	0	0	c		
105. longifolium	1	1	0	0	c		
106. lozanoanum	6	6	0	0	a		
107. lucidum	7	6	1	0	a		
108. luxii	6	6	0	0	a		
109. macrocephalum	3	1	2	0	c		
110. macrophyllum	5	5	0	0	a		n = 10 (Coleman, 1968)
111. macrum	7	7	0	0	a		
112. mairetianum	7	7	0	0	a		
113. malacolepis	6	5	0	1	b	E	
114. malvaefolium	1	1	0	0	c		
115. mariarum	2	1	0	1	c2	E	
116. mendezii	2	0	1	1	c2	S	
117. microdon	1	1	0	0	c		
118. microstemon	12	[illegible]	4	1	a*		2n = 8 (Mangenot & Mangenot, 1962)
119. mimicum	2	2	0	0	c		

continued

TABLE 1 - continued

Eupatorium species	No. of specimens examined Total	Pollen quality Good	?	Bad	Judgment concerning species	Section (putative apomicts only)	Remarks
120. minarum	3	3	0	0	c		
121. monanthum	5	5	0	0	a		
122. morifolium	5	5	0	0	a		
123. meulleri	10	0	0	10	b	E	n = 68 I (Author)
124. multiserratum	2	1	1	0	c		
125. nelsonii	1	1	0	0	c		
126. nemorosum	3	2	1	0	c		n = 10 (Turner et al., 1961a)
127. nubecularum	1	0	0	1	c2	E	n = 12±1 (Turner and King, 1964)
128. nubigenum	4	4	0	0	c1		
129. occidentale	1	1	0	0	c		
130. odoratum	15	9	0	6	b	C	2n = 54, 56, 58 (Ghosh, 1961) 2n = 64 (Mangenot & Mangenot, 1962) 2n = 62, n = 20+ frag.''(unpublished)
131. oerstedianum	9	9	0	0	a		
132. oligocephalum	5	0	0	5	b	E	
133. oreithales	5	0	0	5	b	E	
134. oresbioides	7	7	0	0	a		
135. oresbium	1	1	0	0	c		
136. ortegae	8	6	0	2	b	S	
137. ovaliflorum	5	5	0	0	a		
138. pansamalense	1	1	0	0	c		
139. parryi	5	5	0	0	a		
140. pauciflorum	1	1	0	0	c		
141. pazcuarense	29	11	0	18	b	E	n = 25 II (Turner et al., 1961a)
142. peninsulare	1	1	0	0	c		
143. petiolare	8	8	0	0	a		
144. phoenicolepis	5	5	0	0	a		n = 17 (Turner et al., 1962) n = 17 (unpublished)
145. photinum	1	0	0	1	c		
146. platyphyllum	1	1	0	0	c		
147. plectranthifolium	1	1	0	0	c		
148. porriginosum	1	1	0	0	c		
149. pringlei	4	4	0	0	a		
150. prunellaefolium	13	1	1	11	b	E	n = 17 II (unpublished) n = 50 I (Turner et al., 1961a)
151. pulchellum	5	0	0	5	b	C	n = 52 II(Turner et al., 1961b)
152. purpusii	5	5	0	0	a		
153. pycnocephaloides	1	1	0	0	c		2n = 34 (Grant, 1953)
154. pycnocephalum	22	20	2	0	a		n = 10 (Powell and King, 1969) n = 10,20 (Turner et al., 1962)
155. quadrangulare	7	7	0	0	a		n = 30 II (unpublished)
156. rafaelense	5	5	0	0	a		n = 10 (Turner et al., 1962)

continued

TABLE 1 - continued

Eupatorium species	No. of specimens examined				Judgment concerning species	Section (putative apomicts only)	Remarks
		Pollen quality					
	Total	Good	?	Bad			
157. rapunculoides	6	5	1	0	a		
158. rhodoclamedeum	2	2	0	0	c		
159. rhomboideum	7	6	1	0	a		
160. riparium	1	0	0	1	b	E	2n = 48 (Sparvoli, 1958)
161. rivale	1	1	0	0	c		
162. rothrockii	4	0	0	4	b	E	2n = 51 (Grant, 1964) 2n = +80 (Grant, 1953)
163. rubricaule	4	4	0	0	a		
164. rupicola	1	0	1	0	c		
165. sagittatum	5	5	0	0	a		
166. saltilense	2	2	0	0	c		
167. schaffneri	5	0	1	4	b	E	
168. schultzii	5	5	0	0	a		
169. scorodonioides	13	9	2	2	b	E	n = 17 (Turner et al., 1961a)
170. serotinum	1	1	0	0	c		2n = 20 (Grant, 1953)
171. sinclairii	2	2	0	0	c		n = 4 (Turner and King, 1964)
172. skutchii	8	2	0	6	b	E	n = 17 (unpublished)***
173. solidaginifolium	5	5	0	0	a		2n = 20 (Grant, 1953)
174. solidaginoides	7	5	1	1	a		
175. sordidum	7	6	1	0	a		
176. strictum	2	1	1	0	C		2n = 20 (Holmgren, 1919)
177. subcordatum	2	2	0	0	c		
178. subintegrum	2	2	0	0	c		
179. subpenninervium	2	2	0	0	c		
180. tetragonum	2	2	0	0	c		
181. thyrsiflorum	4	4	0	0	a		
182. tomentellum	4	4	0	0	a		
183. trinervium	7	7	0	0	a		
184. tuerckheimeri	5	5	0	0	a		
185. turbinatum	1	1	0	0	a		n = 16 II (unpublished)
186. vernale	3	3	0	0	c1		
187. viburnoides	4	4	0	0	c1		
188. vitalbae	2	2	0	0	c		
189. vitifolium	5	3	2	0	c1		
190. vulcanicum	1	1	0	0	c		
191. wrightii	4	4	0	0	c1		
192. ymalense	5	5	0	0	a		2n = 34 (Grant, 1964)

[a] Species probably sexual; [b] Species probably containing agamospermous members; [c] Species not adequately represented; [c1] Species not adequately represented--probably sexual; [c2] Species not adequately represented--probably agamospermous, at least in part; *Specimens with unusually high pollen abortion may be hybrids (see Baker 1967); **Voucher specimen for count of n = 20+frag. had well formed pollen; voucher specimen for count of 2n = 62 had [illegible]0-80% aborted grains; ***Voucher specimen for chromosome count had well-formed pollen; [C] Section *Cylindrocephala*; [E] Section *Eximbricata*; [S] Section *Subimbricata*.

Remarks

It must be emphasized that no taxonomic decision is implied either in Table 1 nor the Appendix. Every attempt was made to be taxonomically accurate but the inclusion of a species name in Table 1 does not indicate its acceptance as a taxonomic entity. Nor does the inclusion of a specimen in the Appendix imply that it has been properly identified. The majority of specimens are listed under the species name to which they were assigned in the various herbaria. In a few cases a collection number can appear under more than one species name, although misdeterminations were corrected insofar as possible. The degree of inaccuracy in the determinations probably is not great enough to seriously alter the conclusions which have been drawn.

Of the 192 species examined, 35 (18.2 per cent) were observed to have pollen abnormalities thought to be indicative of agamospermy. Twenty-four of the presumed apomicts are in section _Eximbricata_, 7 in section _Cylindrocephala_, and 4 in section _Subimbricata_. Because of the limited number of specimens examined, no attempt has been made at this time to relate apomixis to phytogeography or ecology. More specimens covering the total range of each of the suspected apomictic species need to be observed before conclusions concerning phytogeography and ecology can be made.

The survey of pollen quality in Eupatorium is not intended to replace the study of living material. Proof of reproductive behavior must still be obtained by intensive cytological investigation and breeding experiments. The survey would not be useful in detecting species which are pseudogamous because in pseudogamous species, the pollen is functional. Nonetheless, the survey has provided an indication of the approximate extent of apomixis in Mexican and Central American species Eupatorium. Furthermore, during the course of the survey, several species were found to have unusually small and smooth pollen grains. This led to a discovery of possible anemophily (see below) which is a method of reproduction never before reported in the genus. The investigation of pollen quality in herbarium specimens provides a tool whereby the investigator can ascertain which species need more intensive study.

PROBLEMS IN THE TAXONOMIC TREATMENT OF APOMICTS IN *EUPATORIUM*

Introduction

Taxonomic confusion has often been the result of concentrated systematic effort in a genus in which apomixis occurs. Studies in *Crataegus*, *Hieracium*, and *Rubus*, for example, have led to the description of an enormous number of microspecies. The microspecies usually represent units of variation which in sexual species would be no greater than the degree of variation between individuals. In apomictic groups, however, there is replication of variants into sizable clones. Hundreds of apomictic biotypes have been given formal taxonomic recognition in these genera.

The description of numerous clones in an apomictic complex is hardly the taxonomic solution required by the biological community. The necessity for dealing with an unwieldly number of taxa may tend to discourage further investigation in a genus. If taxonomic studies are to serve as the foundation for other kinds of investigation, the recognition of vast numbers of poorly defined microspecies may, in fact, defeat the purpose of the classification.

Furthermore, meaningful evolutionary relationships are often obscured when a genus is so subdivided. By giving formal recognition to clones, one risks grouping morphologically similar organisms which have developed independently. This has happened in *Festuca vivipera* (Löve and Löve, 1956).

A great many opinions concerning the classification of apomicts have been published without any particular one gaining general widespread acceptance. Davis and Heywood (1963) provide a discussion of these theories. In *Eupatorium* there are species which are known entirely from apomictic material and species which contain both sexual and agamospermous individuals. Apomixis may be obligate, as in *E. muelleri*, or facultative.

Some species which are totally apomictic have relatively little variability. Species such as *E. muelleri*, *E. bellidfolium*, and *E. anchisteum* are distinct, morphologically well-defined apomictic species which present no unusual taxonomic problems.

Some totally apomictic species exhibit a high degree of variation. *Eupatorium choricephalum* is one of these.[1] The plants appear to respond to environmental factors with a great deal of phenotypic plasticity. In such cases as this the monographer should determine what variation is the effect of environment and what results from genetic differences.

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[1] The determinations are doubtful of the two specimens of *E. choricephalum* with "good" pollen noted in Table 1.

He would also have to judge the taxonomic significance of any genetic difference he detected. This type of information is not readily available from herbarium specimens.

Species containing both sexual and apomictic individuals and species which are facultatively apomictic are frequently taxonomically difficult. Sexuality permits incorporation of new gene combinations through hybridization, mutation and segregation while apomixis permits new gene combinations to be replicated. Often the result of facultative apomixis is the formation of a highly polymorphic group of plants which is difficult to define. Furthermore, hybridization is believed to be a factor contributing to the development of apomixis (Stebbins, 1950). Powers (1945) has illustrated how hybridization could lead to the initiation of apomixis.

Certain species of *Eupatorium* (e.g., *E. aschenbornianum*, *E. odoratum*, *E. pazcuarense*, *E. prunellaefolium*) appear, on the basis of the foregoing survey, to contain both sexual and asexual plants. The range of variability is great in these species and it is not unlikely that more than one species is present under any one of these names. This may certainly be the case in *Eupatorium aschenbornianum*. At least three partially sympatric, morphologically dissimilar groups are currently represented by herbarium specimens so named. One such group occurs in southern Mexico and southward through Central America. Originally described as *E. donnell-smithii*, it has since been treated (Robinson, 1928) as a synonym of

E. *aschenbornianum*. Two other groups exist in Mexico, one on the east coast, centered in Veracruz, and the other covering many of the western states. These groups would deserve recognition as separate species were it not for the apparent hybridization between them. The putative hybrids are more than ephemeral entities for they seem to reproduce by agamospermy. This results in one large complex which has its true nature obscured in part by the application of the single name *Eupatorium aschenbornianum*.

In a situation such as that of *E*. *aschenbornianum* a workable classification can be achieved only through experimentation. However, given the use of cytology, chemotaxonomy, and breeding experiments, the monographer should be able to resolve these problems satisfactorily.

Suggestions Concerning the Taxonomy of Apomicts

When monographing a genus in which apomixis occurs, there are several suggestions which might be followed in order to achieve a more practical and accurate treatment of the apomicts:

1. One should indicate which species are known or suspected to be apomictic and to what extent. If possible, phytogeographical data concerning the distribution of the apomictic biotypes and the sexual biotypes (if any) and information concerning the kind of apomixis involved should be included.

2. One should try to relate apomictic groups to their probable sexual precursors. In many instances the apomicts may be triploid (or otherwise polyploid) derivatives of a sexual species (cf. Grant, 1953). In other instances the relationships may be more obscure due to allopolyploidy or disappearance of the immediate sexual precursors.

3. In such instances where hybridization and subsequent apomixis have obscured specific limits, it may be advantageous to use the concept of the species complex or aggregate species. The species complex may be regarded as a super-specific taxonomic category which is used more for the sake of convenience than accuracy. In using a monograph which incorporates the species complex one could first key a specimen to the appropriate species complex. This may be as accurate a determination as the user requires and he would stop at this point. If a more accurate determination is required the user would then turn to the citation of the species complex in the text where he would find a description of the complex and a key to the included taxa. It is possible that the key would fail to differentiate many of the intermediates but this is to be expected.

4. With apomixis many hybrid intermediates of two sexual taxa may be replicated until they comprise a

sizeable portion of the flora. It may, therefore, be expedient to recognize formally some of the more conspicuous biotypes. However, care should be taken not to obscure the relationships between the members of the complex.

5. Certain biological phenomena may need to be regarded differently if they occur in apomictic species than if they occur in sexual species. The naming of new species on the basis of different chromosome numbers is inadvisable in apomictic groups where polyploidy and aneuploidy are frequently encountered. Species are frequently described solely from herbarium specimens and dried specimens usually do not permit an accurate appraisal of the degree of phenotypic plasticity in a species. Consequently, especially when few specimens are available, it is possible to describe two or more "species" which are, in fact, each a different phenotypic expression of the same species. The greater the phenotypic plasticity of a species, the greater is the chance that it could be divided into several taxa by the unsuspecting taxonomist. Clausen, Keck, and Heisey (1947) reported that the phenotypic plasticity of hybrids is frequently greater than that of either parent. The same is probably true for apomicts which contain genetic compliments of two or more species of differing habitat requirements. Thus the systematist should

determine experimentally the extent of phenotypic plasticity in members of an apomictic complex.

APPARENT WIND POLLINATION IN EUPATORIUM

Introduction

Three types of pollination have been observed in the Compositae; ornithophily (Fries, 1903), entomophily, and anemophily. Entomophilous species constitute the vast majority while anemophilous species have heretofore been known only in the Anthemideae and the subtribe Ambrosinae of the Heliantheae. The occurrence of wind pollination in *Eupatorium*, which apparently has not been recognized previously, illustrates the independent evolution of a presumably adaptive trait in what is considered (Cronquist, 1955) to be a distantly related segment of the family.

Pollination studies on two species of *Eupatorium* were undertaken by Cross (1897) who concluded, on the basis of floral morphology and fruit set, that the species were insect pollinated although pollen not removed by insects was eventually blown away by the wind. Her studies showed that while wind pollination was possible, it did not occur in the two species studied.

Description of Putative Anemophilous Species

In the course of the survey of pollen characteristics in *Eupatorium*, several species were found with short-spined pollen grains. Eleven species of 192 examined thus far show this characteristic. Some of these species obviously represent relatively unrelated segments of the genus, but three species, *E. solidaginifolium* Gray, *E. solidaginoides* H.B.K., and *E. monanthum* Sch. Bip., have many features in common. Although some of these similarities are not obviously correlated with particular adaptive traits, several of their common characters appear to be specializations for wind pollination.

Eupatorium solidaginifolium ranges from Arizona and western Texas to Michoacan and Colima in Mexico. It is a calciphile found at elevations from sea level to 1300 meters in tropical deciduous forests, usually in association with *Quercus* or *Bursera*. The species has often been reported as locally abundant and with flowers ranging in color from white to green to reddish brown or cream. It blooms from October to February.

Eupatorium solidaginoides is a widespread, semi-woody species occurring in South and Central America and as far north in Mexico as San Luis Potosi. It is a calciphile and has a tendency to climb. In Mexico it occurs from 1000 to 2000 meters, blooming from December to February with white to green flowers.

Eupatorium monanthum is known from Sinaloa to Oaxaca, occurring at altitudes ranging from 150-1500 meters. It is reported as locally abundant in tropical deciduous forests often with Quercus or Bursera. The species has been variously described as an arching or scandent shrub or as a vine. The flowers are fragrant, greenish white or greenish yellow and the heads may have reddish involucres. It blooms from February to April.

Robinson (1926) placed E. solidaginifolium and E. monanthum in section Subimbricata and E. solidaginoides in section Eximbricata. His key, however, provides for identification of E. solidaginifolium also with section Eximbricata. A comprehensive reappraisal of Eupatorium will be necessary before the sectional boundaries are clarified, but for the present it appears that these species are more closely related than Robinson's treatment would suggest. In any case, they seem somewhat transitional between sections Subimbricata and Eximbricata as presently understood.

Morphological Evidence

In the trend toward anemophily in these species, E. solidaginifolium appears to be least specialized, E. solidaginoides intermediate and E. monanthum most specialized. Faegri and van der Pijl (1966) and Whitehead (1969) have noted (1) ecological and phytogeographical conditions which favor anemophilous plants and (2) morphological modifications of anemophilous plants. The species of Eupatorium fit the patterns of ecological requirements and morphological adaptations typical of anemphilous species as described by these authors. Furthermore, Payne (1963) has described a number of modifications of the inflorescence of Ambrosia which appear to be correlated with increasing degrees of specialization for anemophily. Some of these, notably an elongation of the flowering axis and placement of the heads in an outward or downward position are paralleled in Eupatorium.

Eupatorium solidaginifolium has the largest heads of the three species, with 10-13 florets, and thickest inflorescence branches. Its florets are also largest, being 6 mm from the base of the achene to the tip of the corolla. The heads are aggregated into secondary glomerules such that the heads fan outward and the entire inflorescence is shorter and more dense than those of the other two species. Eupatorium solidaginoides has heads with 9-11 florets which are 5 mm long. In this species the heads are not aggregated but are borne on extremely slender pedicels about 5 mm long. The inflorescence is about twice as long as that of E. solidaginifolium and the main branches of the inflorescence are well separated, giving the thyrse a more open aspect. Eupatorium monanthum has the least number of florets per head (1 or, occasionally, 2) and the heads are closely aggregated into spherical glomerules such that they all radiate from a common point of attachment. Its florets are about 4.5 mm long, but the inflorescence is the longest of the three species, with clusters of heads on the secondary branches as well as the secondary branches themselves well separated from one another. Separation is further increased by the occasional change from opposite inflorescence branches to an alternate arrangement.

The anther appendages of these species deviate from the majority of Eupatoria. The more "typical" condition is illustrated by E. calophyllum Robins (Figure 30, a), an apparently insect-pollinated species. Eupatorium solidaginifolium (Figure 30, b) has anther appendages about one-half the size of E. calophyllum and they are not as well differentiated from the rest of the anther. Eupatorium solidaginoides (Figure 30, c) has anther appendages which are truncated and have a thickened margin of stronger texture. These anther appendages turn outward, a condition, to my knowledge, not reported in other members of the Eupatorieae. They seem to function in keeping the uncommonly wide corolla from collapsing. In E. monanthum (Figure 30, d) the appendages have been lost altogether except for a small rim of cells.

The style branches of E. solidaginoides (Figure 31, b) are clavate, different in shape than E. calophyllum (Figure 31, a) but not unlike those of many other species of Eupatorium. The apical half of the style branches of E. solidaginifolium are thickened and with a smooth surface; sweeping hairs are absent. The remainder of the style branch is

Figure 30. Apical anther appendages: *a*, *Eupatorium calophyllum*, *Rzedowski 8443* (MSC); *b*, *E*. *solidaginifolium*, *Pringle 942* (MSC); *c*, *E*. *solidaginoides*, *Pringle 3956* (MSC); *d*, *E*. *monanthum*, *Rzedowski 21947* (MSC). (All ca. x 100).

Figure 31. Apical portion of style branches: *a*, *Eupatorium calophyllum*; *b*, *E*. *solidaginifolium*; *c*, *E*. *solidaginoides*; *d*, *E*. *monanthum*. Stippled area represents non-stigmatic portion. Voucher specimens as in Figure 1. (All ca. x 100).

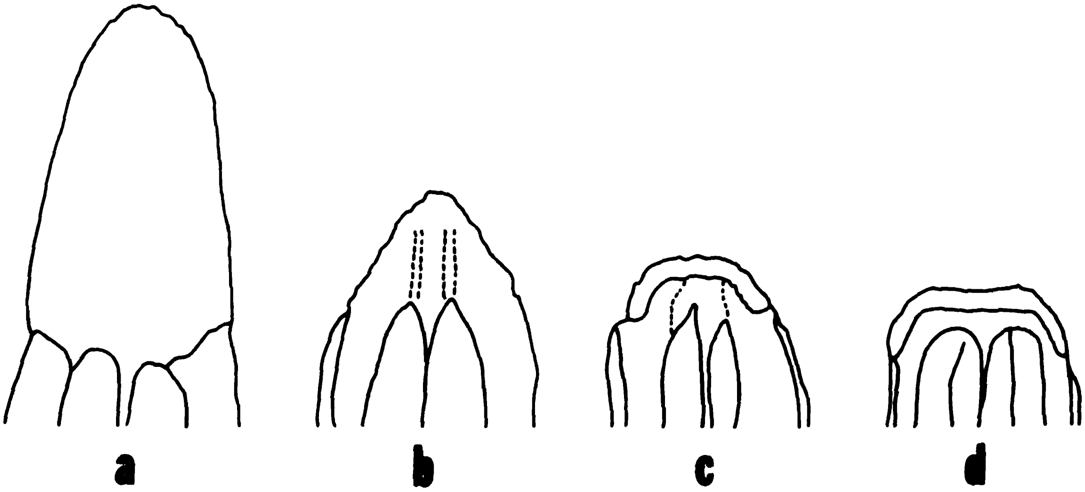

Figure 30

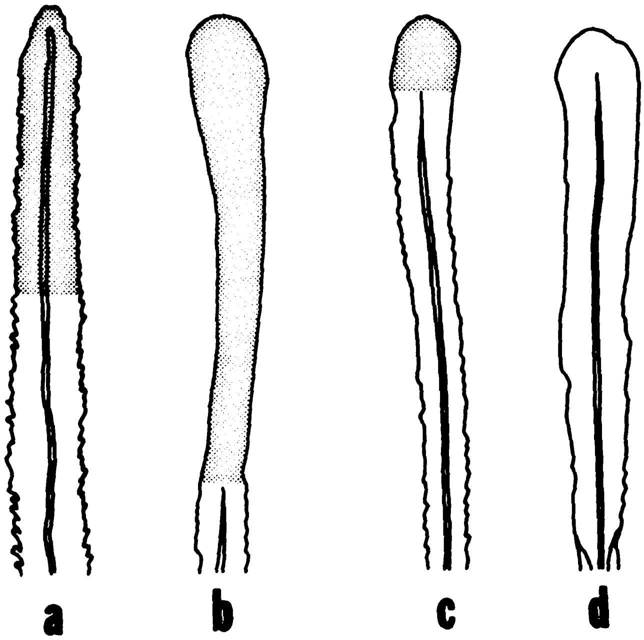

Figure 31

ribbon-like and covered with papillae. In E. solidaginoides (Figure 31, c) the receptive area extends further along the style branch to the extent that only the tip is nonstigmatic. This type of style has been found also in E. coelestinum (Cross, op. cit.). It appears that the proximal portion is more able to retain pollen grains than the sub-apical portion, judging from adhering pollen grains. In E. monanthum the entire length of the style branch appears to be stigmatic (Figure 31, d). The clavate nature of the styles is partially obscured by the increase in width of the greater portion of the style branch. In the dried condition, however, the edges of the branches tend to curl inward revealing the underlying clavate shape.

Most pollen grains in the Compositae are equipped with a more or less elaborate development of the exine into spines or spiny ridges. Spineless pollen has arisen (presumably independently) in several tribes or subtribes, i.e., Mutisieae, Cynareae, Anthemideae, and Ambrosinae. Although lack of spines is not necessarily correlated with wind pollination, the "reduction of spinyness is entirely in keeping with the anemophilous habit" (Wodehouse, 1926).

Pollen from all three presumably wind-pollinated species as well as that from two presumably entomophilous species of Eupatorium were examined with a scanning electron microscope. Pollen grains of ragweed (Ambrosia artemesiifolia L.) were also examined for comparison with a well-known anemophilous species. When so examined, the pollen grains of *Eupatorium solidaginifolium*, *E. solidaginoides*, and *E. monanthum* are not unlike one another nor are the surfaces very different from that of the *Ambrosia* pollen. *Eupatorium solidaginifolium* and *E. monanthum* (Figure 32, a) have grains which measure 15µ in diameter. *Eupatorium solidaginoides* and *Ambrosia artemesiifolia* (Figure 32, e) have grains 20µ in diameter, and *E. calophyllum* (Figure 32, c) and *E. calaminthaefolium* have grains about 30µ in diameter. The florets of *Eupatorium monanthum*, which are one-half the size of those of *E. calophyllum*, produce more pollen than the latter.

The spines of *E. monanthum* (Figure 32, b) are about 0.5µ high and 1.5µ in basal diameter. Those of *Ambrosia artemesiifolia* (Figure 32, g) are 1.5µ high and 2µ in basal diameter. Those of *E. calophyllum* (Figure 32, d) are 3.5µ high and 4µ in basal diameter and are often curved or hooked.

The pollen of the presumably wind-pollinated *Eupatoria* is abundant, powdery, relatively smooth and small and thus it is similar to the pollen typical of most anemophilous plants (cf. Whitehead, 1969); however, the diameter of the pollen of *E. monanthum* and *E. solidaginifolium* (15µ) is just slightly less than that of the "typical" anemophilous plant (20-40µ). When the pollen of the *Eupatorium* species is dry it is elipsoidal in shape (Figure 32, a) but in humid air the grains swell and expand in the region of the colpi to become spherical.

Figure 32. Representative pollen grains photographed with a scanning electron microscope. _a_, _b_, _E_. _monanthum_, _Rzedowski_ _21947_ (MSC) (presumed wind-pollinated species); _c_, _d_, _E_. _calophyllum_, _Rzedowski_ _8443_ (MSC) (insect pollinated); _e_, _f_, _Ambrosia_ _artemesiifolia_, _Beauvais_ _270_ (MSC) (wind pollinated); a, e, ca. x 3030; b,d,f, ca. x 6060; c, ca. x 1200.

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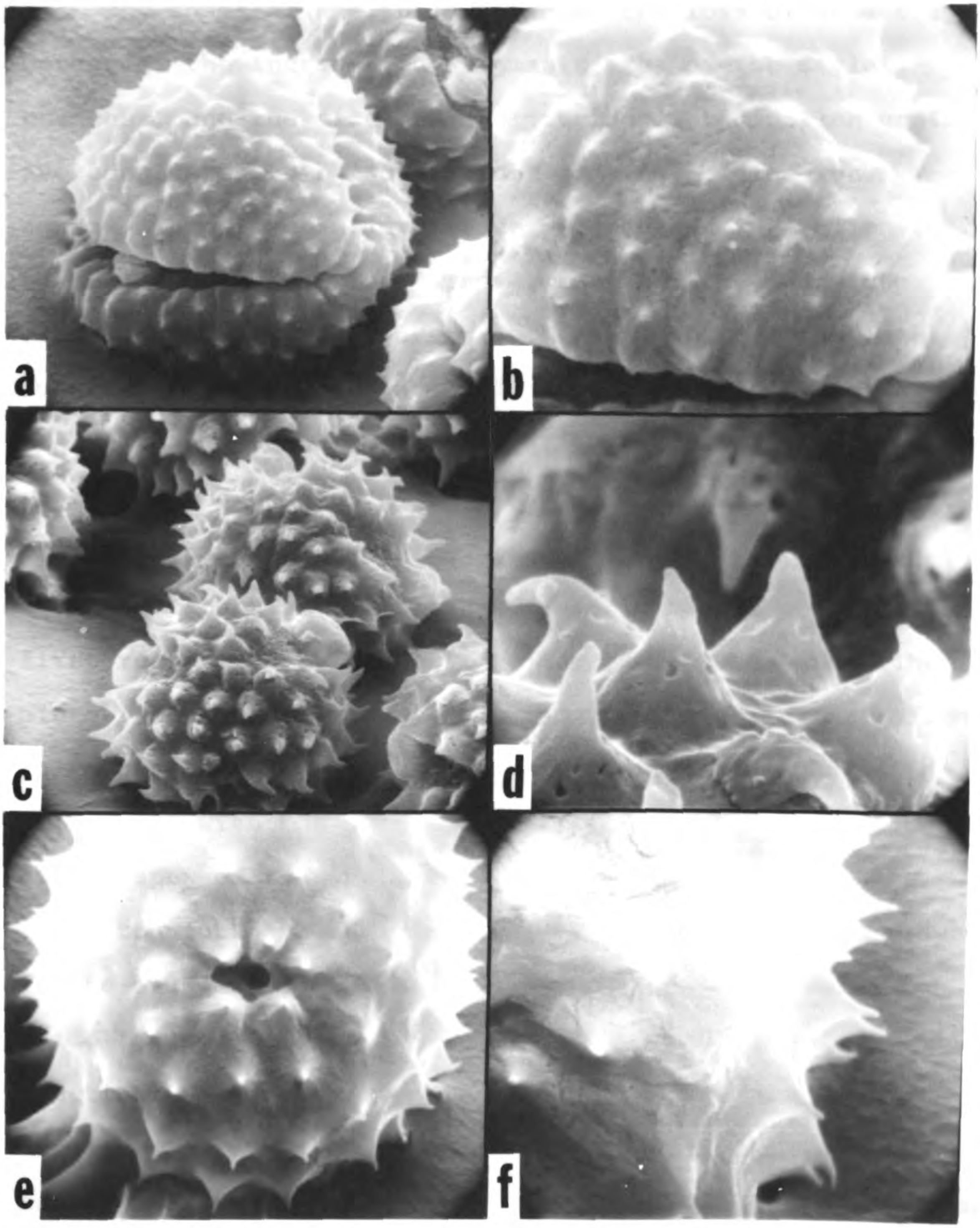

Figure 32

Discussion

The shape of the inflorescence, the loss of anther appendages, the increase in stigmatic area of the style branches, and the size and sculpturing of the pollen grains are considered to be adaptations to wind pollination. The narrow, whip-like inflorescence would cause the pollen to be released in the wind. The aggregation of heads into clusters orients the florets such that the corollas face outward and the styles are well separated. In _E_. _solidaginoides_ the filamentary pedicels would allow the heads to hang pendent in the breeze thus shedding the pollen and allowing the style branches to swing freely back and forth.

The mechanism of pollen release in the Compositae was first recognized by Cassini and has since been termed the plunger mechanism. As a floret reaches anthesis the pollen is released introrsely and the elongating style pushes the pollen out with the sweeping hairs which are usually located at the apex of the style branches. Small (1915) was the first to elucidate the function the anther appendages played in the plunger mechanism. The apical appendages serve to guide the pollen out of the corolla while the basal appendages function in keeping it from falling to the bottom of the corolla. In the common ragweed (Bianchi et al., 1959), the anther appendages are well developed and the pistillodium has an expanded ring of hairs at the apex. In this species, the pollen is expelled in clusters, falls to the foliage below and is later separated and blown away in the wind. In the presumably anemophilous *Eupatoria* noted above, the reduction of the apical appendage would allow the gradual release of pollen grains. This condition would be advantageous for a wind-pollinated plant and, in fact, occurs in anemophilous species of other families. Observations of post-anthesis florets of *Eupatorium* indicate that the pollen is released gradually in the presumably anemophilous species. Species which are insect pollinated seldom have residual pollen in the corolla or anthers of post-anthesis florets and the few grains which remain are aborted. The three species noted above, however, have a large number of grains remaining which are not aborted. Anther appendages are thought (Small, *op*. *cit*.) to represent a sterilization of sporogenous tissue brought about by the economizing of pollen production which entomophily permits. The correlated trend in reduction of the anther appendages in the anemophilous species of *Eupatorium* is a feature which suggests that anemophily is a derived condition in the genus.

The style branches of the presumed anemophilous species of *Eupatorium* are devoid of sweeping hairs but the clavate tips may function in this capacity. The increase in stigmatic surface area of the style branches is thought to represent another adaptation to anemophily. While the length of the style is not unusual in these species, the effective pollen trapping area is considerably increased.

I have not had the opportunity to observe these species of Eupatorium in their native habitats and thus the evidence for anemophily is indirect. Unfortunately, data on their breeding systems is also unavailable. The possibility of occasional insect visitation cannot be ruled out. The retention of apparently well-developed nectaries might suggest occasional insect pollination, but the nectaries are also well-developed in some obligately apomictic species of Eupatorium. Species in several families are known to be entomophilous at one time in their life-cycle and anemophilous at another (cf. Knuth, 1906-09, Vol. I: p. 71). It would appear that the adoption of the anemophilous habit is gradual, and, during the incipient stages, both anemophily and entomophily are operative to some extent.

Thus far only three species of Eupatorium have been studied in detail in relation to possible anemophily. Five other species may also have this method of reproduction. These are E. eriocarpum, E. hebebotryum, E. incomptum, E. morifolium and E. quadrangulare. With the exception of E. morifolium all the species have elongated inflorescences. All have a copious supply of relatively short-spined, powdery pollen. Eupatorium incomptum is in section Hebeclinum; the other species are in section Subimbricata. Chromosome counts of n = 10 are reported for three of the species (see Table 1).

Great importance has been placed on the anther appendage by B. L. Robinson. Species with vestigial appendages were often considered by him to be generically distinct from those with well-developed appendages. The eight presumably anemophilous species of Mexican and Central American Eupatorium show a gradation from fairly well-developed anther appendages to nearly no appendages. Most of these species are closely related and one must therefore question the soundness of any taxonomic decision based on the nature of the anther appendages alone.

GENERAL DISCUSSION

The first hypothesis relating hybridization to apomixis was postulated by Ernst (1918). He observed that meiosis is disturbed in apomicts much the same way as it is in some hybrids; polymorphism and accompanying diffusion of species limits are similar in groups with predominant hybridization as well as in groups with predominant apomixis. Ernst's theory has now become accepted as fact although experiments attempting to produce apomixis by means of hybridization have failed.

Hybridization causes new gene combinations which, through apomixis, can be perpetuated, resulting in large "populations" of individuals each of which contains the hybrid vigor of the original hybrid individual. These perpetual hybrids are frequently capable of a greater degree of tolerance to ecological conditions than the sexual parental species (cf. Stebbins, 1950, p. 393).

Variability can exist in agamic complexes either as a result of variability which was originally incorporated into the complex at its inception or as a result of genetic changes after the establishment of apomixis. Agamic complexes often contain as many biotypes and as much variation as is found in outcrossing species (Clausen, 1960, Valentine, 1960). This is true for both facultative and obligate complexes because obligate apomicts were probably derived from facultative apomicts rather than directly from sexual progenitors (Babcock and Stebbins, 1938, Stebbins, 1941). Aneuploidy (the loss or gain of one or more chromosomes or parts of chromosomes) can produce new biotypes (Sörensen, 1958). Aneuploidy often causes severe weakness and/or sterility in sexual plants; however, apomicts are nearly always polyploid (Gustafsson, 1946), thus the overall deleterious effect of aneuploidy is lessened, and they are capable of overcoming the sterility barrier through agamic reproduction. Mutation and autosegregation occur occasionally (Turesson, 1956). New biotypes may be formed by spontaneous production of polyploid offspring (Kappert, 1956). The production of haploid offspring can be induced in some highly polyploid apomicts (Gustafsson, 1947) but it is not known to occur naturally.

Three conditions have been suggested as contributing to the success of apomicts in arctic and alpine regions (Davis and Heywood, 1963, p. 374).

1. Apomixis facilitates the duplication of favorable gene combinations and thus allows for the rapid spread of asexual plants with favorable genotypes into recently disturbed habitats.

2. Apomixis sometimes allows for more rapid maturation of seeds (embryos often form before anthesis)

and this permits the occupation of areas having short growing seasons.

3. Apomixis is one adaptation to a shortage of pollinating insects.

None of these three conditions are restricted to high altitudes or high latitudes. It should, therefore, not be surprising to find apomicts in other parts of the world where one or more of these conditions exist.

In Mexico and Central America apparently all three conditions occur. Man has altered vast expanses of the natural countryside making available newly disturbed habitats suitable for colonization of plants with the proper genotype. The dry season effectively terminates the lives of many plants or at least limits their growing season. A shortage of insect pollinators, while not proven empirically, is suggested by the several trends toward life cycles independent of insect pollinators (see below).

In Mexico and Central America, species in two sections of *Eupatorium* have a high frequency of pollen abnormality. The contents of anthers of species in section *Cylindrocephala* usually have a different appearance than the anther contents of species in section *Eximbricata*. In section *Cylindrocephala* pollen grains are highly variable in size, ranging from about twice the size of normal grains to about one-third the size of normal grains. The larger grains often stain with aceto-carmine but the smaller ones nearly always appear vacant. In section *Eximbricata* the abnormal pollen grains are not as variable in size as those of section *Cylindrocephala* and they seldom stain. Microsporogenesis is frequently disrupted resulting in the complete failure of pollen production.

On the basis of the appearance of the pollen in these two sections, it appears that apomixis may have arisen independently in each section. Cytological investigation of megasporogenesis in species of section *Cylindrocephala* are needed to support this view.

Eight triploids ($2n = 30$) in section *Subimbricata* were reported by Grant (1953). These species from the southeastern United States may be the result of yet a third independent derivation of apomixis in *Eupatorium*. Three species of Mexican *Subimbricata* occasionally have abnormal pollen: *E. collinum*, *E. mendezii*, and *E. ortegae*. These shrubby species are very closely related to one another but they do not appear closely related to the triploids (all herbaceous) reported by Grant.

No abnormal pollen was found in species of sections *Chromoleana*, *Conoclinum* and *Hebeclinum*.

Eupatorium odoratum (section *Cylindrocephala*), on the basis of the foregoing survey, has both sexual and apomictic plants. Four chromosome numbers have been reported for the species (see Table 1) and each count is different. Voucher specimens of two of the counts were examined in this study.

The count of *n* = 20 + fragment (unpublished) was made in a collection (*King & Soderstrom 4814*) in which pollen appeared normal. The count of 2*n* = 62 (unpublished) was made in a collection (*Breedlove 8837*) in which the pollen was irregular in shape and size and frequently aborted. Of all the species studied, *E. odoratum* is perhaps the most widespread and the most variable in both vegetative and floral structures. The extreme morphological diversity and the various chromosome numbers suggest that *Eupatorium odoratum* may be facultatively apomictic (cf. Davis and Haywood, 1963, p. 365). No experimental studies have yet been done to test this hypothesis.

Inbreeding has become established in species which are related to *Eupatorium pycnocephalum* (section *Subimbricata*) through the development of self-compatibility (Baker, 1965, 1967). In the species studied, self-compatibility is correlated with a reduction of chromosome number and a capacity for weediness. The only known completely self-compatible species is *E. microstemon* which produces 20-40 pollen grains per anther lobe. This is a reduction from the 160-200 grains per lobe produced by the self-incompatible *E. pycnocephalum*. During the study of pollen quality I noted other related, minute-flowered species (*E. jejunum*, *E. macrum*, and *E. minarum*) which also had an unusually low number of pollen grains. No quantitative data on the number of pollen grains per floret were obtained at that time, however. It is possible that these species are also self-compatible.

Because apomixis, anemophily, and autogamy all occur in species of Eupatorium from the same geographical area, it appears that these reproductive adaptations may be responses to the same stimulus. One such stimulus might possibly be a decrease in the number of insect pollinators resulting from widespread post-Pleistocene drying in Mexico and Central America.

Another possible, although currently uninvestigated, adaptation paralleling the three noted above may be non-selectivity of pollinators. Entomophilous species must attract sufficient numbers of insect pollinators in order to maintain the plant population. Such species may respond to a shortage of efficient pollinators by producing substances capable of attracting a greater number and variety of insects. Although many of the insects thus attracted may be inefficient pollinators, the greater numbers of attracted insects may offset any disadvantage caused by their inefficiency. Many species of Eupatorium have brightly colored flowers and very odoriferous glandular secretions in both floral and vegetative structures. Insects of many kinds are attracted to the plants readily. I have observed plants of Eupatorium odoratum surrounded by myriad insects including beetles, wasps, bees, butterflies, and moths. Knuth (1907-9, Vol. 2, pp. 572-3) lists insects of the following orders which were observed to frequent Eupatorium species: Diptera, Hymenoptera, Lepidoptera, Neuroptera, Coleoptera. Breeland and Pickard

(1961) reported mosquitoes feeding on Eupatorium, but these insects most likely play little, if any, role in pollination.

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APPENDIX

APPENDIX

SPECIMENS USED AND POLLEN QUALITY OBSERVED IN THE INVESTIGATION OF POLLEN QUALITY OF MEXICAN AND CENTRAL AMERICAN SPECIES OF *EUPATORIUM*

Listed below are the specimens which were used in the investigation of pollen quality with the evaluation of the quality of pollen observed in each specimen. See text for an explanation of the terms employed.

Eupatorium species, collector and number	F	MICH	MSC	Good	?	Bad	
adenachaenium							
Hernandez s.n.			x	x			
Rzedowski 19332			x	x			
adenophorum							
Bourgeau 172	x					x	
de Harre s.n.	x			x			
McVaugh 22684		x				x	
Palmer 1310-1891		x		x			
Paray 1115bis		x	x			x	
Pringle 2495			x	x			
Pringle 6836			x			x	
de Puga 171			x	x			
Quijano s.n.			x			x	
Rzedowski 19332			x	x			a
adenospermum							
Feddema 2444		x			x		
de Harre s.n.	x			x			
Hinton 3110	x			x			
Langlassé 882		x		x			
McVaugh 14163		x		x			

<u>Eupatorium</u> species, collector and number	F	MICH	MSC	Good	?	Bad
albicaule						
Aguilar 17		x		x		
Gentle 288 (2 spec.)		x		x	x	
Gentle 575		x		x		
Gentle 809		x		x		
Kenoyer A131		x		x		
King 3037		x		x		
Lundell 2791		x		x		
Lundell 4011		x		x		
Lundell 4016		x		x		
Matuda 1466		x		x		
Matuda 3529		x		x		
Palmer 236-1902			x	x		
Pringle 3103			x	x		
Steere 1056		x		x		
Steere 1663		x		x		
Steere 1979		x		x		
Yuncker 4921		x		x		
amblyolepis						
Pringle 8034			x			x
Pringle 9900	x					x
Pringle 9900		x		x		
amestinum						
Tate s.n.	x					x
amygdalinum						
Allen 1278	x			x		
Dodge et al. 16841	x			x		
Kellerman 7605	x			x		
Skutch 2460		x		x		
Standley 55856	x			x		
Standley 56049	x			x		
Williams & Merrill 17150	x			x		
anchisteum						
Johnston 356	x					x
Molina 18534	x					x
Molina 21084	x					x
Morales 1222	x					x
Rodriguez 1458	x					x
Standley 377	x					x
Standley 27320	x					x
Standley 76538	x					x
Standley 77248	x					x

Eupatorium species, collector and number	F	MICH	MSC	Good	?	Bad	
anchisteum (cont.)							
Steyermark 30650	x					x	
Williams et al. 22552	x					x	
angulifolium							
Matuda 3948		x		x			
Standley 58139	x			x			
Standley 58265	x			x			
angulare							
Brenes 3723	x			x			
Brenes 4028	x			x			
Cruz 34	x			x			
Crysler & Roever 5022		x		x			
Dodge & Allen 5670	x			x			
Grashoff 111			x	x			
aschenbornianum							
Bourgeau 1927			x			x	
Breedlove 9314		x				x	
Carlson 703	x			x			
Carlson 777	x			x			
Carlson 990	x				x		
Conzatti 5208		x				x	
Donnell-Smith 1602	x			x			
Donnell-Smith 2365	x					x	
Grashoff 77			x	x			
Heyde & Lux 3408	x			x			
Heyde & Lux 4528	x			x			
King 4225 (2 spec.)		x		x			
McVaugh 11611		x				x	
McVaugh 22666		x		x			
McVaugh - Koelz 413		x				x	
Molina 6223	x					x	
Molina 11285	x					x	
Molina 11289	x					x	
Molina 11370	x					x	
Molina 11503	x			x			
Molina 11518	x			x			
Molina 12705	x					x	b
Molina 13644	x			x			
Molina 13740	x					x	a
Molina et al. 12033	x					x	
Molina et al. 16458	x					x	
Molina et al. 16878	x			x			a
Molina et al. 25985	x			x			

Eupatorium species, collector and number	F	MICH	MSC	Good	?	Bad
aschenbornianum (cont.)						
Paray 3381		x				x
Pringle 8110		x	x			x
Pringle 10098		x	x			x
Purpus 2992	x					x
Puga s.n.		x		x		
Puga s.n.		x				x
Rzedowski 10042			x	x		
Rzedowski 19577			x			x
Standley 65991	x					x
Standley 66067	x	x				x
Standley 66392a	x					x
Standley 66395	x					x
Standley 66404	x			x		
Standley 67207	x					x
Standley 67554	x					x
Standley 68394	x			x		
Standley & Cacón 6840	x					x
Standley & Molina 4453	x					x
Standley et al. 4733	x					x
Steyermark 37131	x					x
Terry 1319	x			x		
Tucker 985	x			x		
Türkheim 927	x			x		
Williams et al. 25904	x					x
Williams et al. 14019	x					x
Williams et al. 22836	x					x
Williams et al. 28558	x			x		
Williams & Molina 11984	x					x
azureum						
Barkley 14357		x		x		
Berlandier 1380	x			x		
Crutchfield & Johnston 5013		x		x		
Johnson & Barkley 11411	x			x		
LaSeur 498	x			x		
Palmer 9-1907	x			x		
Pringle 2481			x	x		
Rzedowski 8607			x	x		
bartlettii						
Elmore L19		x		x		
Lundell 2775		x		x		
Lundell 6254 (2 spec.)	x	x		x		
Lundell 6400	x			x		
Lundell 6481		x		x		
Türckheim II 1912	x			x		

Eupatorium species, collector and number	F	MICH	MSC	Good	?	Bad
bellidifolium						
Anderson & Laskowski 4345		x				x
Breedlove 8005	x					x
Feddema 2879		x				x
Hinton et al. 8688	x					x
Hinton et al. 13555		x				x
Hinton et al. 14945		x				x
McVaugh & Koelz 1284		x				x
Molina 16311	x					x
Paray 3353		x				x
Pringle 1897 (2 spec.)		x				x
Pringle 6065			x			x
Rzedowski 18089		x				x
Rzedowski 23633 (2 spec.)			x			x
Rzedowski 23633		x				x
C. L. Smith 367	x					x
Williams et al. 23215	x					x
bertholdii						
Drouet et al. 3647	x			x		
Gentry 1135	x			x		
Mexia 1473	x			x		
Palmer 1968-1892	x			x		
Pringle 2741	x					x
Pringle 9902	x		x	x		
betonicum						
Barlow s.n.		x		x		
Chare 7639		x		x		
King 2925		x		x		
McVaugh 20737		x		x		
Palmer 425-1880		x		x		
Pennell 18050		x		x		
Pringle 1897		x		x		
Stanford et al. 2266		x		x		
Steere 1890		x		x		
Waterfall 12493		x		x		
White 1732		x		x		
White 1922		x		x		
White & Chatters 194		x		x		
biglovii						
Pringle 10079	x			x		
Pringle 10079		x			x	
Pringle 10079			x			x
Pringle 10208		x			x	
Purpus 4801	x			x		

Eupatorium species, collector and number	F	MICH	MSC	Good	?	Bad
biglovii (cont.)						
Rzedowski 8236		x				x
Wynd & Mueller 459		x	x			
bilbergianum						
Brown 177	x			x		
A. Smith H19	x			x		
bimatrum						
Standley 12472	x			x		
Standley 17482	x			x		
Standley 22114	x			x		
Standley 24105	x			x		
Standley 24647	x	x		x		
Standley 24881	x			x		
Williams 16925	x				x	
blakei						
Bartlett 11462	x	x		x		
brandigeanum						
Purpus 4822	x			x		
brenesii						
Standley & Valerio 50067	x			x		
brevipes						
Cronquist 9756		x	x	x		
Feddema 2270		x		x		
Feddema 2304		x		x		
Feddema 2311		x		x		
Feddema 2437		x		x		
Gentry 6973		x		x		
Gentry 8556		x		x		
Gonzalez 3156		x		x		
McVaugh 13621		x		x		
McVaugh 20605		x		x		
McVaugh & Koelz 2		x			x	
McVaugh & Koelz 3		x			x	
Pringle 1743			x	x		
Pringle 13272			x	x		
Rzedowski 5235		x		x		
Rzedowski 17538		x		x		
Rzedowski 23302			x	x		
Rzedowski 23302		x			x	
Rzedowski 25114		x	x	x		

Eupatorium species, collector and number	F	MICH	MSC	Good	?	Bad	
caciliae							
Molina 21265	x			x			
Williams et al. 27337	x			x			
calaminthaefolium							
Bourgeau 1102			x	x			
Castorena 40			x	x			
DeJong 1544			x	x			
Gonzalez 3206			x	x			
Pringle 8688			x	x			
Pringle 13551			x	x			
Rzedowski 19357			x	x			
Rzedowski 20044			x	x			
Rzedowski s.n.			x	x			
calophyllum							
Fuentes s.n.		x		x			
McVaugh 17038		x		x			
McVaugh 17101		x		x			
Palmer 303-1902			x	x			
Palmer 303½-1902			x	x			
Palmer 304-1902			x	x			
Rzedowski 6879		x		x			
Rzedowski 8443			x	x			
campechense							
Lundell 111	x			x			
Lundell 963	x	x		x			
capillifolium							
Garnier 20	x			x			
Grant 7338	x			x			
Sessé & Mociño 2731	x			x			
cardiophyllum							
Cronquist 9799			x	x			
Hinton et al. 9237		x		x			
McVaugh 13557		x		x			
Pringle 2343			x	x			
Pringle 11515	x			x			
Rzedowski 14582		x		x			
Rzedowski 17535			x	x			a
carltonii							
Steyermark 42223	x			x			
Yuncker et al. 8729	x	x		x			

Eupatorium species, collector and number	F	MICH	MSC	Good	?	Bad	
chapalense							
Gentry 5873		x		x			
Gentry 8062		x		x			
Gentry 8124		x		x			
Mexia 1634	x			x			
Mexia 1859	x			x			
chiapense							
Breedlove 9054	x			x			
Carlson 1628	x			x			
Molina et al. 16457	x			x			
Rzedowski & McVaugh 74			x	x			a
Steyermark 3680	x			x			
Steyermark 37726	x			x			
Steyermark 48533	x			x			
choricephalum							
Bourgeau 1215	x					x	
Cronquist 9126		x		x			a
Ortega 6885	x			x			a
Palmer 712-1886			x			x	
Palmer 851-1896	x					x	
Palmer 857-1896			x			x	
Pringle 747	x		x			x	
Pringle 10099	x		x			x	
Pringle 11824			x			x	
Rzedowski 17316			x			x	
Rzedowski 17446			x			x	
Rzedowski 21494			x			x	
chrysostyloides							
Pringle 10231			x	x			
Pringle 15615		x	x	x			
chrysostylum							
LeSeur 963	x			x			
Palmer 40-1908	x			x			
collinum							
Anderson & Laskowski 4398		x		x			
Cronquist 9743			x	x			
Palmer 152-1894/5			x			x	
Pringle 2733			x		x		
Pringle 4628			x	x			
Pringle 7849		x				x	
Pringle 11516			x	x			
Pringle s.n.		x	x			x	

Eupatorium species, collector and number	F	MICH	MSC	Good	?	Bad	
collinum (cont.)							
Rosas 121		x		x			
Rzedowski 12128		x	x	x			
Rzedowski 17556			x	x			
Rzedowski 23542		x	x	x			
collodes							
Pringle 4941			x	x			
Smith 624	x			x			
conspicuum							
Breedlove 9800		x				x	
Gonzalez 423			x			x	
Pringle 8050	x					x	
Pringle 8050		x	x	x			
Rzedowski 16393			x			x	a
Rzedowski 18818			x	x			a
constipatiflorum							
Breedlove 9552		x		x			
Ton 786		x			x		
conzattii							
King 4238	x	x		x			
coulteri							
Carlson 475	x			x			
Matuda 5112	x				x		
Standley 69854	x			x			
Steyermark 42397	x			x			
Steyermark 42567	x			x			
Steyermark 43423	x				x		
Steyermark 46617	x			x			
Türckheim II 1664	x					x	
Türckheim II 1664		x			x		
Türckheim 8406	x					x	
Williams et al. 15288	x				x		
crassirameum							
Breedlove 9573	x			x			
Kellerman 7438	x			x			
Pittier 1928	x			x			
Pringle 8271	x			x			
Purpus 8995	x			x			
Williams et al. 24623	x			x			

Eupatorium species, collector and number	F	MICH	MSC	Good	?	Bad
cremastrum						
Rzedowski & McVaugh 79		x			x	
Rzedowski & McVaugh 121		x		x		
crocodilium						
Standley 73099	x			x		
Steyermark 3847	x			x		
daleoides						
Armour 5	x			x		
Brenes 369(505)	x			x		
Brenes 6643	x			x		
Brölley 45	x			x		
Donnell-Smith 4856	x				x	
Gonzalez 2223			x	x		
Kerber 356	x			x		
Millspaugh 1510	x				x	
Molina 634	x			x		
Rodriguez 3671 (2 spec.)	x			x		
Standley 15485	x			x		
Stork 1102	x			x		
Williams 11235	x			x		
Williams 15645	x			x		
Williams 23810	x			x		
Williams 25666	x			x		
Williams et al. 11538	x			x		
deltoideum						
Bourgeau 947	x		x	x		
DeJong 1527			x	x		
Krauss 1066			x	x		
Pringle 3660	x			x		
Pringle 4327			x	x		
Pringle 9067	x			x		
Rzedowski 25113			x	x		
dryophyllum						
Barnes et al. 174	x			x		
Pringle 2323			x	x		
durandii						
Ferry s.n.	x			x		
Stork H368	x			x		
Stork 2349	x	x		x		
Stork 2841	x			x		
Stork 3359	x			x		

Eupatorium species, collector and number	F	MICH	MSC	Good	?	Bad
ehrenbergii						
Ehrenberg s.n.		x		x		
elatum						
Dunlap 455a	x			x		
Shattuck 852	x			x		
Skutch 2555		x		x		
Skutch 4729	x			x		
Stern et al. 1781		x		x		
Woodworth et al. 600	x			x		
eriocarpum						
Pringle 6112			x	x		
erythropappum						
Balls 5462		x		x		
Breedlove 7130	x			x		
Breedlove 7797	x	x		x		
Dodds 77		x		x		
Pringle 8957		x	x	x		
Pringle 15004	x	x		x		
espinosarum						
Beaman 2730			x	x		
Beaman 3618			x	x		
Bourgeau 1416			x	x		
Gonzalez 3114			x	x		
Gonzalez 3207			x	x		
Gonzalez 3242			x	x		
Lagunas & Castillo s.n.			x	x		
Pringle 6611			x	x		
Pringle 9906			x	x		
Pringle 13048			x	x		
glaberrimum						
McVaugh & Koelz 687		x		x		
galleotii						
Skutch 1983		x		x		
glabratum						
Arsène 8519	x			x		
Bourgeau 952			x	x		
Föderström et al. 607	x			x		
Garcia s.n.			x	x		
Gilly et al. 2			x	x		
Gonzalez 2100			x	x		

Eupatorium species, collector and number	F	MICH	MSC	Good	?	Bad
glabratum (cont.)						
Gonzalez 2169			x		x	
Hernandez s.n.			x	x		
Holguin s.n.			x	x		
Kenoyer A162	x			x		
Powell 522	x			x		
Pringle 2578	x		x	x		
Pringle 7543	x		x	x		
Pringle 7719	x		x	x		
Pringle 13049	x			x		
Purpus 1831	x			x		
Purpus 2417	x			x		
Rzedowski 6312			x	x		
Rzedowski 11512			x	x		
glaucum						
Cronquist 9647		x		x		
Liebmann 80	x			x		
glischrum						
Purpus 4655	x			x		
gonzalezii						
Conzatti 5260		x		x		
gracicaule						
Virlet 273	x			x		
greggii						
DeJong & Longpre 951			x	x		
Hinton et al. 5453	x			x		
LeSeur MEX366	x			x		
Marsh 209	x			x		
Marsh 691	x			x		
McGreggor et al. 500			x	x		
Palmer 245-1898	x			x		
Powell et al. 522	x			x		
Pringle 247	x			x		
Pringle 913	x		x	x		
Pringle 4692	x			x		
Wilkinson s.n.	x			x		
griseum						
Molina 635	x			x		
Molina 10198	x			x		
Molina 11178	x			x		
Molina 18753	x			x		
Pittier 1832a	x			x		

Eupatorium species, collector and number	F	MICH	MSC	Good	?	Bad
griseum (cont.)						
Standley et al. 914	x			x		
Steyermark 31299	x			x		
Steyermark 33030	x			x		
Williams 11506	x					x
haenkianum						
Langlasse 622		x		x		
McVaugh & Koelz 1593		x		x		
McVaugh & Koelz 1709		x		x		
Palmer 889-1890		x		x		
hastile						
Palmer 240-1902	x		x	x		
Palmer 416-1907	x			x		
Pennell 17911		x		x		
Pringle 3275	x		x	x		
Purpus 4795	x			x		
havanense						
Kenoyer 613A	x			x		
Marsh 1858	x			x		
McGreggor et al. 27			x	x		
Palmer 508-1898			x	x		
Pringle 3072	x		x	x		
Pringle 10811	x		x	x		
Rozynski 243	x			x		
hebebotryum						
Cronquist 9776		x		x		
Hinton et al. 14851		x		x		
McVaugh 20078		x		x		
Purpus 2941	x			x		
Rzedowski 23595			x	x		
Valerio 1039	x			x		
hederaefolium						
Parry & Palmer 348-1878	x			x		
hemipteropodum						
Gaumer s.n.	x					x
heydeanum						
Heyde & Lux 3427	x			x		
Matuda 2656		x		x		
Standley 84976	x			x		
Williams et al. 26893	x			x		

<u>Eupatorium</u> species, collector and number	F	MICH	MSC	Good	?	Bad
hidalgense						
Edwards 843	x			x		
Gonzalez 3264		x		x		
Pringle 9903	x			x		
Purpus 1490	x			x		
Rzedowski 17046		x		x		
holwayanum						
Hinton 2815	x			x		
Hinton 5243	x			x		
hondurense						
Molina 13079	x			x		
Standley 14839	x			x		
Standley 14967	x			x		
Williams et al. 11065	x			x		
hospitale						
Aguilar 948	x			x		
Breedlove 8865	x			x		
Gonzalez 3508			x	x		
Steyermark 43560	x			x		
Tonduz 7314	x			x		
huehuetecum						
Standley 82766	x					x
Standley 84307	x					x
hylonum						
Brenes(213)4201	x			x		
Williams et al. 28986	x				x	
Williams et al. 29123	x			x		
hymenolepis						
Williams 29061	x			x		
Williams 29093	x			x		
Williams et al. 28590	x			x		
Williams et al. 28601	x			x		
hypodictyon						
Nelson 3517	x					x
hypomalacum						
Heyde & Lux 6157	x					x
Skutch 2415		x		x		
hyssopifolium						
Schaffner 299		x		x		

Eupatorium species, collector and number	F	MICH	MSC	Good	?	Bad
hyssopinum						
Gentry 2703	x			x		
LeSeur MEX93	x				x	
Muller 3540	x	x		x		
Palmer 363-1906	x			x		
Pringle 1262		x		x		
Schaffner 299(729)	x			x		
White 3042		x		x		
imitans						
Breedlove 8803		x		x		
Kellerman 5304	x			x		
Raven & Breedlove 19773		x		x		
Standley 15804	x			x		
Standley 82418	x			x		
Standley 88257	x			x		
Steyermark 42153	x			x		
Tucker 582		x		x		
incarnatum						
Johnston 4646		x		x		
incomptum						
Molina 21348	x			x		
Pringle 2469			x	x		
Pringle 11520			x	x		
Standley 58002	x			x		
Steyermark 30642	x			x		
iresnoides						
Allen 1305	x			x		
irrasum						
Rzedowski 19115		x		x		
isolepis						
Hernandez s.n.			x			x
ivaefolium						
Heyde & Lux 6156	x					x
Pringle 3914			x			x
Standley 13872	x					x
Standley 16031	x					x
Standley 28646	x					x
Standley 29180	x					x
Williams et al. 14711	x					x

Eupatorium species, collector and number	F	MICH	MSC	Good	?	Bad
ixiocladon						
Brenes 13426a	x			x		
Brenes 13564	x			x		
jejunum						
Heyde & Lux 4206	x			x		
Standley 75299	x			x		
Standley 76260	x			x		
Standley 77714	x			x		
karwinskianum						
Pringle 8164	x	x		x		
kupperi						
Williams 20070	x			x		
laevigatum						
Allen 1554	x					x
Calderón 2452	x					x
Standley 27874	x					x
Steyermark 42258	x					x
Rodriguez 3680	x					x
lanicaule						
H. Johnson 1256	x			x		
Schipp 1096	x			x		
lemmonii						
Cronquist 9569		x				x
Cronquist 9805		x				x
McVaugh 14405		x		x		x
leptodictyon						
DeJong 1695			x	x		
Rzedowski 20264			x	x		
leucocephalum						
Breedlove 9375		x		x		
Breedlove 9684		x		x		
Matuda 2652		x		x		
Morton & Makrinius 2521		x		x		
liebmannii						
Gilly 111		x		x		
Pringle 6046		x	x	x		
Rzedowski 19206		x		x		

Eupatorium species, collector and number	F	MICH	MSC	Good	?	Bad
ligustrinum						
DeJong 1784			x	x		
Dodds 77			x	x		
Fuentes s.n. (2 spec.)			x	x		
Gonzales 3264			x	x		
Palmer 194-1902			x	x		
Palmer 200-1902			x	x		
Pringle 8957			x	x		
Pringle 10404			x	x		
Pringle 15004			x	x		
Rzedowski 8385 (2 spec.)			x	x		
Rzedowski 16396 (2 spec.)			x	x		
Rzedowski 23443			x	x		
Ton 613			x	x		
loesnerii						
Conzatti 2070	x			x		
Conzatti 2315	x			x		
Pringle 6022	x			x		
longifolium						
Purpus 14062	x			x		
lozanoanum						
Hitchcock 7280	x			x		
Pringle 8942	x		x	x		
Pringle 13552	x	x	x	x		
lucidum						
MacDanials 79	x			x		
Paray 1110			x	x		
Pringle 8475	x		x	x		
Purpus 1577	x			x		
Rzedowski 24184			x		x	
Sessé & Mociño 2739	x			x		
luxii						
Carlson 715	x			x		
Skutch 289		x		x		
Standley 67454	x			x		
Steyermark 43703	x			x		
Tucker 1102		x		x		
Williams et al. 26843	x			x		
macrocephalum						
Matuda 3816		x			x	
Pringle 3200	x			x		
Pringle 3200			x		x	

Eupatorium species, collector and number	F	MICH	MSC	Good	?	Bad
macrophyllum						
Grashoff 63			x	x		
Grashoff 92			x	x		
Grashoff 105			x	x		
Martinez & Calderon 608		x		x		
Yuncker 4633		x		x		
macrum						
Molina 1689	x			x		
Standley 2292	x			x		
Standley 2334	x			x		
Standley 12637	x			x		
Standley 28910	x			x		
Williams 11172	x			x		
Williams et al. 23251	x			x		
mairetianum						
DeJong 1450			x	x		
DeJong 1714			x	x		
Gilly & Simpson 16			x	x		
Paray 1136			x	x		
Rzedowski 16458			x	x		
Rzedowski 19630			x	x		
Rzedowski 22031			x	x		
malacolepis						
Carter & Chiaski 1223		x		x		
Gentry 5819		x		x		
Gentry 7206		x				x
McVaugh 23575		x		x		
Mexia 1777		x		x		
Palmer 90-1906	x			x		
malvaefolium						
Purpus 2372	x			x		
mariarum						
Gentry 7303		x				x
Nelson 4244	x			x		
mendezii						
Parry & Palmer 340-1878	x					x
Rzedowski 8385			x		x	
microdon						
Steyermark 43586a	x			x		

Eupatorium species, collector and number	F	MICH	MSC	Good	?	Bad
microstemon						
Grashoff 62A			x	x		
Hinter & Allen 29	x			x		
Hinter & Allen 215	x				x	
Standley 65429	x			x		
Standley 80655	x				x	
Standley 83691	x				x	
Standley 85956	x				x	
Williams 23079	x			x		
Williams 23101	x			x		
Williams 28564	x			x		
Williams et al. 23101	x			x		
Williams et al. 26947	x					x
mimicum						
Standley 83728	x			x		
Williams et al. 26253	x			x		
minarum						
Carlson 2465	x	x		x		
Williams et al. 25720	x			x		
monanthum						
Mexia 1879	x			x		
Morton et al. 2361	x			x		
Palmer 515-1894/5			x	x		
Pringle 10348	x			x		
Rzedowski 21947			x	x		
morifolium						
Baker 2274			x	x		
Bourgeau 2037			x	x		
Gentle 1593		x		x		
Pringle 4105			x	x		
Rzedowski 7402		x		x		
muelleri						
Grashoff 188			x			x
Grashoff 236			x			x
Hinton 2710	x					x
Pringle 6065			x			x
Pringle 10121	x		x			x
Standley 77626	x					x
Steyermark 30641	x					x
Williams 21775	x					x
Williams 22056	x					x

Eupatorium species, collector and number	F	MICH	MSC	Good	?	Bad	
multiserratum							
Mexia 1534		x		x			
Mexia 1859		x			x		
nelsonii							
King 2379		x		x			a
nemorosum							
Grashoff 139			x	x			
King 5374		x		x			
King 5402		x			x		
nubecularum							
Williams et al. 13718	x					x	
nubigenum							
Johnston 1124	x			x			
Standley 67586	x			x			
Standley 89769	x			x			
Steyermark 34690	x			x			
occidentale							
Pringle 4353			x	x			
odoratum							
Allen et al. 6134		x		x			
Baker 2415			x			x	
Breedlove 8837		x				x	
Breedlove 9430		x				x	
Cronquist 9736			x	x			
Davis s.n.			x	x			
Gillis 6294			x			x	
Gilly et al. 18		x				x	
Gonzalez 2216		x	x				
Gonzalez 3407		x	x				
Janzen s.n.		x	x				
King & Soderstrom 4814	x		x				
Lamb 488		x	x				
McGreggor 16462		x	x				
Purpus 3652	x		x				
oerstedianum							
Deam 6062	x			x			
Dodge 6240	x			x			
Edwards 744	x			x			
Molina 1715 (1717?)	x			x			
Standley 18322	x			x			

Eupatorium species, collector and number	F	MICH	MSC	Good	?	Bad	
oerstedianum (cont.)							
Standley 77020	x			x			
Rodriguez 1621	x			x			
Williams 11516	x			x			
Williams et al. 10911	x			x			
oligocephalum							
Holguin s.n.			x			x	
Martinez s.n.			x			x	
Rzedowski 15581			x			x	
Rzedowski 19428			x			x	
Rzedowski 21979			x			x	
oreithales							
Beaman 3655			x			x	
Beaman 3746			x			x	
Pringle 6563			x			x	
Rzedowski 20452			x			x	
Rzedowski 23066			x			x	
oresbioides							
Breedlove 8093	x			x			
Kellerman 6288	x			x			
Standley 60054	x			x			
Standley 86313	x			x			
Steyermark 35747	x			x			
Williams 26850	x			x			
Williams et al. 27204	x			x			
oresbium							
Pringle 8300			x	x			
ortegae							
Feddema 2529		x		x			
Feddema 2600		x				x	
McVaugh 20328		x		x			
McVaugh & Koelz 512		x		x			
McVaugh - Koelz 715		x				x	
Mexia 1121		x		x			
Rzedowski 8377			x	x			a
Rzedowski 17760		x		x			
ovaliflorum							
Mexia 1473		x		x			
Palmer 1968-1892		x		x			
Palmer 2010-1892		x		x			
Pringle 9902		x		x			
Puga 1043		x		x			

Eupatorium species, collector and number	F	MICH	MSC	Good	?	Bad
pansamalense						
Türckheim II 2143		x		x		
parryi						
Pringle 135		x		x		
Pringle 1595		x	x	x		
Wynd & Mueller 254		x	x	x		
pauciflorum						
Bourgeau 1100			x	x		
pazcuarense						
DeJong 1794			x	x		
Gentry 1943	x			x		
Gunzman GH1138			x			x
Hinton et al. 15637		x				x
Knoblock 5449	x		x			x
Krauss 1067 (2 spec.)			x			x
Krauss 1071			x	x		
McGreggor et al. 264			x	x		
McVaugh 14024		x		x		
McVaugh 20600		x				x
McVaugh 20611		x				x
McVaugh 22792		x				x
McVaugh 23071		x				x
McVaugh 23428		x				x
Mendellin 287			x	x		
Pringle 1265	x					x
Pringle 6562			x	x		
Pringle 8027			x			x
Pringle 8028			x			x
Pringle 11523		x		x		
Rzedowski 8164			x			x
Rzedowski 9725 (2 spec.)			x			x
Rzedowski 18799			x	x		
Rzedowski 21410			x			x
Rzedowski 21426			x	x		
Rzedowski 23069			x	x		
peninsulare						
Pringle 135		x		x		
petiolare						
Gilly & Simpson 16A			x	x		
Gonzalez 421			x	x		
Gonzalez 2040			x	x		
Gonzalez 2065			x	x		

Eupatorium species, collector and number	F	MICH	MSC	Good	?	Bad
petiolare (cont.)						
Gonzalez 2087			x	x		
Gonzalez 2129			x	x		
Gonzalez 2159			x	x		
Schnee s.n.			x	x		
phoenicolepis						
Breedlove 7315		x		x		
Breedlove 7918		x		x		
Breedlove 8017		x		x		
Breedlove 14024			x	x		
Ton 1496		x		x		
photinum						
Pringle 8029			x			x
platyphyllum						
Skutch 2561		x		x		
plectranthifolium						
Rodriguez 306		x		x		
porriginosum						
Pringle 6552			x	x		
pringlei						
Breedlove 7987		x		x		
Breedlove 9214		x		x		
Pringle 6118			x	x		
Ton 670		x		x		
prunellaefolium						
Beaman 2438			x			x
Beaman 2526			x			x
Beaman 2799			x			x
Beaman 2860			x	x		
Beaman 2903			x			x
Beaman 2952			x			x
Beaman 4049			x			x
Beaman 4114			x			x
Beaman 4290			x			x
Pringle 4286			x			x
Rzedowski 20492			x			x
Rzedowski 20517			x		x	
Rzedowski 23876			x			x

Eupatorium species, collector and number	F	MICH	MSC	Good	?	Bad
pulchellum						
Bourgeau 948			x			x
Detling 8724		x				x
Gilly 103			x			x
Pringle 2579			x			x
Rzedowski 25134			x			x
purpusii						
Feddema 2893A		x		x		
Gentry 7169		x		x		
McVaugh 9954		x		x		
McVaugh 22790		x		x		
Rzedowski 18118		x		x		
pycnocephaloides						
Standley 66328		x		x		
pycnocephalum						
Bourgeau 1098			x	x		
Bourgeau 1232			x	x		
DeJong 1434			x	x		
DeJong 1463			x	x		
Gonzalez 3192			x	x		
Grashoff 78			x	x		
Grashoff 86			x	x		
McGreggor 16371			x		x	
Montgomery & Root 8617c			x	x		
Palmer 835-1894/5			x	x		
Palmer 243-1902			x	x		
Palmer 300-1902			x	x		
Pringle 8077			x	x		
Romero 15			x	x		
Rzedowski 5357			x	x		
Rzedowski 8301			x	x		
Rzedowski 9726			x		x	
Rzedowski 10091			x	x		
Rzedowski 19203			x	x		
Rzedowski 19579			x	x		
Rzedowski 21472			x	x		
Rzedowski 23297			x	x		
quadrangulare						
Baker 2302			x	x		
King 2448		x		x		
King 3853		x		x		
King 3964		x		x		
McVaugh 22440		x		x		

Eupatorium species, collector and number	F	MICH	MSC	Good	?	Bad
quadrangulare						
Pringle 2669			x	x		
Wright 1355			x	x		
rafaelense						
Conzatti 5247		x		x		
Laughlin 501		x		x		
Pringle 8031			x	x		
Pringle 8040			x	x		
Pringle 8056			x	x		
rapunculoides						
McVaugh 13280		x			x	
McVaugh 17450		x		x		
McVaugh 18180		x		x		
Palmer 545-1886		x		x		
Pringle 2312			x	x		
Pringle 11517	x			x		
rhodochlamedeum						
Pringle 3370		x		x		
Rzedowski 8320			x	x		
rhomboideum						
McVaugh 13398		x		x		
Pringle 6561			x	x		
Pringle 13795		x	x	x		
Rzedowski 19357		x			x	
Rzedowski 19357			x	x		
Rzedowski 21638			x	x		
riparium						
Bourgeau 1928			x	x		
rivale						
McVaugh 9986		x		x		
rothrockii						
Pennell 19124		x				x
Pringle 1265		x				x
Townsend & Barber 325		x				x
White 4407		x				x
rubricaule						
Hinton et al. 8772		x		x		
Pringle 2878	x			x		
Pringle 4272		x	x	x		

Eupatorium species, collector and number	F	MICH	MSC	Good	?	Bad	
rupicola							
Pringle 4970			x		x		
sagittatum							
Carter et al. 3455		x		x			
Carter & Chisaki 3463		x		x			
Gentry 4712		x		x			
Gentry 4848		x		x			
Wiggins & Rollins 262		x		x			
saltilense							
Muller 2802		x		x			a
Rozynski 193		x		x			a
schaffneri							
McVaugh 13571		x				x	
McVaugh 20546		x				x	
Pringle 13052		x				x	
Pringle 13997		x				x	
Pringle 13997			x	x			
schultzii							
Bourgeau 1923			x	x			
Breedlove 8822		x		x			
Matuda 0732		x		x			
Matuda 0774		x		x			
Matuda 0799		x		x			
scorodonioides							
DeJong 1518			x	x			
Diaz 5			x	x			
Gonzalez 1391			x			x	
Gonzalez 2944			x			x	
Gonzalez 3078			x	x			
Gonzalez 3113		x	x		x		
Gonzalez 3128			x	x			
Lagunas & Castillo s.n.		x	x	x			
Pringle 8244			x	x			
Rzedowski 20044		x		x			
Shreve 9398		x		x			
serotinum							
Palmer 424-1880		x		x			
sinclairii							
King 5343		x		x			
Tucker 439		x		x			

Eupatorium species, collector and number	F	MICH	MSC	Good	?	Bad
skutchii						
Breedlove 6725		x		x		
Breedlove 9267		x				x
Breedlove 9308		x				x
Breedlove 11597		x		x		
Rzedowski 16371		x				x
Standley 66352		x				x
Ton 719		x				x
Ton 738		x				x
solidaginifolium						
McVaugh & Koelz 1673		x		x		
Pringle 942			x	x		
Shreve 6639		x		x		
White 4438		x		x		
Wilkinson s.n.		x		x		
solidaginoides						
Bartlett 11462		x		x		
Pringle 3956			x			x
Purpus 14233			x	x		
Rozynski 641	x			x		
Rzedowski & McVaugh 94		x		x		
Standley 60112		x		x		
Standley 60832		x		x		
sordidum						
Breedlove 9408		x		x		
Dodds & Simpson 17		x		x		
Matuda 1137		x		x		
Pringle 8048		x	x	x		
Rosas 187		x		x		
Rzedowski 11089		x			x	
strictum						
Gentry 644M		x			x	
McVaugh 21703		x		x		
subcordatum						
Rodriguez 316		x		x		
Stork 2388		x		x		
subintegrum						
Pringle 3311			x	x		
Rzedowski 17760			x	x		

Eupatorium species, collector and number	F	MICH	MSC	Good	?	Bad	
subpenninervium							
Matuda 0854		x		x			
Pringle 6275			x	x			
tetragonum							
Rzedowski 23290		x	x	x			a
thyrsiflorum							
Cronquist 9824			x	x			
McVaugh 21771		x		x			
Ortega 4444		x		x			
Pringle 11521		x		x			
tomentellum							
Breedlove 7921		x		x			
Breedlove 14019		x		x			
Cronquist 9695		x		x			
Pringle 4959			x	x			
trinervium							
McVaugh 21229		x		x			
McVaugh & Koelz 784		x		x			
Palmer 563-1886		x		x			
Pringle 1789		x	x	x			
Pringle 11527		x	x	x			
tuerckheimii							
Breedlove 881		x		x			
Breedlove & Raven 8242		x		x			
Carlson 2464		x		x			
Raven & Breedlove 19794		x		x			
Türckheim 77		x		x			
turbinatum							
Rzedowski 5580		x		x			c
vernale							
Breedlove 7998		x		x			
McClintock s.n.		x		x			
Skutch 293		x		x			
viburnoides							
Gonzalez 3286		x	x	x			
Pringle 10366			x	x			
Pringle 15597		x		x			

Eupatorium species, collector and number	F	MICH	MSC	Good	?	Bad	
vitalbae							
Skütch 2482		x		x			
Smith P2531		x		x			
vitifolium							
Anderson & Laskowski 3679		x		x			
King & Soderstrom 4836		x			x		
McVaugh 19391		x		x			
Rzedowski 14716		x			x		
Rzedowski 14716			x	x			
vulcanicum							
Grashoff 141			x	x			a
wrightii							
Fuentes s.n.		x		x			
Gentry 6963		x		x			
Pringle 912			x	x			
Shreve & Dinkham 9727		x		x			
ymalense							
Elmore 1A6		x		x			
McVaugh 11860		x		x			
McVaugh 15923		x		x			
McVaugh & Koelz 1659		x		x			
Turner 2026		x		x			

[a] Determination questionable

[b] Anthers empty

[c] Grains large, tetracolpate