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STUDIES IN THE KUHNIIINAE (EUPATORIEAE) II *

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With five plates

INTRODUCTION

Liatris and *Brickellia*, the two largest genera of a small subtribe of the *Eupatorieae*, which Robinson (1913) called the *Kuhniiinae*, were examined cytologically and found to have the basic chromosome numbers of 10 and 9 respectively. *Brickellia* with approximately ninety species (Robinson 1917) has its greatest distribution in Mexico and southwestern United States. It extends northward to the Canadian border and southward into Central America and sparingly into Brazil. The range of *Liatris*, with thirty-two species (Gaiser 1946), is confined almost entirely to southern Canada and the United States, though it just crosses the border into Mexico. The remaining seven genera are small. However, their distribution in the American hemisphere is interesting in relation to the two large genera mentioned. *Barroetia* is wholly Mexican and *Kanimia* is found only in South America. Two others, *Trilisa* and *Carphophorus* occur only in southeastern United States while the monotypic genus *Garberia* is limited to Florida. Only the two genera, *Kuhnia* and *Carphochaete* overlap from United States into Mexico.

The comparative growth-form of these genera is also a matter of interest. *Liatris* is a genus of perennial herbs with mostly corm-like rootstocks, though in the series *Punctatae*, deeply penetrating roots occur, and the singular *L. Garberi* of the *Spicatae*, has a tuberous form. By contrast, *Brickellia* consists largely of shrubs or shrubby perennials, of which probably the most woody is *B. argyrolepis*, which attains a height of twelve feet and a stem diameter of two inches (Gaiser 1953). It is difficult to sharply differentiate between herbs and shrubs in this genus, for the stem is often only slightly woody at the base or consists of a woody caudex. Others are perennial herbs with only persistent underground parts which are fusiform, tuberous or more knobby and rhizomatous. Only one species, or possibly two, are annuals. Of the seven species of *Barroetia* (Robinson

* Chromosome Studies in the Kuhniiinae (Eupatorieae). I. *Brickellia*. *Rhodora* 55: 253-267, 269-288, 297-321, 328-345 (1953).

1911b), one is known to be a perennial herb, somewhat woody at the base, and three are recognized as annuals. *Kuhnia* species are comparatively slender herbs with long somewhat conical roots which have been described by Shinnars (1946) as irregularly divided at the top and becoming more or less "soft-woody." Robinson (1911a) described *K. adenolepis* as having a woody caudex. *Carphephorus* and *Trilisa* are true perennial herbs having clustered, thick, almost tuberous roots and leafy rosettes. The single species of *Garberia* is definitely a woody shrub attaining a height of six to eight feet, while the species of *Carphochaete* are generally spoken of as small branching shrubs.

In the cytological studies of *Liatris*, including all the given species except *L. lancifolia*, only the diploid number ($2n = 20$) was found in those of nine series, while polyploidy prevailed in the *Punctatae* (Gaiser 1949, 1950, 1951). In one species only the hexaploid number was found, in a second, only the tetraploid, in a third, the diploid, while both diploid and tetraploid numbers occurred in two others. Further, one of these two latter, *L. punctata* Hook. has the widest distribution of any species in the genus, extending the full north-south range from western Canada, east of the Rocky Mountains, over the Mexican border. In forty-one species of *Brickellia* examined, representing half of the undoubtedly distinct species, and four sections, only the diploid number ($2n = 18$) was found.

On the basis of previous cytological work, it seemed worth while to determine¹ the chromosome numbers in the other genera of this small group of the *Compositae* with the hope that new clues of relationship would become evident. From fossil evidence, the family is believed to be of recent development. With the two largest genera known to differ by one in their chromosome number, questions arose: Was there a smaller basic number? If so would it be found in genera limited to the tropics or to the more woody forms? Would those that were shrubby have the same number as *Brickellia* and the perennial herbs the same as *Liatris*? Or would there be still further variations in number and if so what relationship would this bear to the classification?

There was also the interesting problem of polyploidy, since though lacking in *Brickellia*, it was found in *Liatris*, a genus limited to the temperate zone. There have been contributions which fail to confirm but also some which give support to Hägerup's original hypothesis (1932) that polyploidy developed under rigorous environmental conditions. In Stebbins' (1950) discussion on the topic of the polyploid complex and geographic distribution he stated that no tropical group was known well enough to be included. When undertaking the study of *Brickellia*, it was expected that because of its range into Mexico and Central America it

¹The author gratefully acknowledges a grant from the Canadian Research Council when a beginning was made. Subsequently the project was assisted by a grant from the American Philosophical Society which permitted the collection of species of *Barroetia* and *Kuhnia* as well as *Brickellia* in Mexico, without which this investigation could not have been completed.

would include tropical forms. Field experience in the collection of approximately two dozen species from Mexico and Guatemala impressed upon the author that they were on the plateaus and thus were actually existing in a temperate climate. The annual *B. diffusa* is somewhat exceptional for although it occurs on the plateaus too, it is the only species to be found throughout the Caribbean. All of the species of *Barroetia*, according to Robinson (l.c.) occur on the plateaus in Mexico, and no species has penetrated northward beyond its central zone. There is no monograph of *Kanimia* but the labels on specimens at the Gray Herbarium indicate that they have come from regions in the Andes from the Colombian border to Peru and the province of Minas Gerais, Brazil. Thus there are not included in this subtribe, plants of tropical lowlands such as make up the genus *Anthurium* of the *Araceae*. But we know that polyploidy does appear in five of a total of thirty-nine species of that genus examined (Gaiser 1927). Stebbins (1950) apparently overlooked this when he made the statement cited above. In contrast to one large tropical genus, as *Anthurium*, the *Kuhniiinae* present a challenging succession of related forms which appear to have progressed northward from the tropics in varying degrees.

NOTES ON THE TAXONOMY OF THE GENERA

In his key to the *Eupatorieae*, Robinson (1913) added an additional subtribe to those given by Hoffmann (1890), and changed the name of the *Adenostylinae* to *Kuhniiinae* because the assumed type genus *Adenostyles* did not really belong to the tribe. With its omission from this subtribe, the other nine genera remain the same.

Of them the genus *Kanimia* stands alone in having a definite number of phyllaries. Both in the number of florets and phyllaries it is like *Mikania*, from which Hoffmann (l.c.) had stated it was only separated by its 8–10 ribbed achene. However, *Mikania* is placed at the end of the previous subtribe *Ageratinae*. There is no general treatment of *Kanimia*. Thirteen species have been described from Colombia, Peru, Ecuador, and Brazil. Because it is South American, consists largely of vines or woody forms, as are included in the much larger genus *Mikania* and has a definite number of florets and phyllaries, a strong link is suggested between the two subtribes. Whether the chromosome number would be of any help in adjustment of generic segregation, will have to await the procuring of cytological materials of *Kanimia*.

It is a matter of great satisfaction that of the remainder, the four largest genera had been monographed, and two of them by Robinson, whose specialty was the *Eupatorieae*. Thus we have the excellent treatment of *Brickellia* in 1917, following that of *Barroetia* in 1911, and the key to the whole group in 1913. The genus *Kuhnia* was dealt with by Shinnars in 1946, as had been one series of the genus *Liatris*, the *Scariosae*, in 1943. The latter genus was in the process of being revised by Gaiser at that time and publication followed in 1946. Of the four other genera still

lacking comprehensive treatments, a brief summation of their status is given here.

Carphochaete

Next to the singular *Kanimia*, *Carphochaete* stands apart from the rest of these genera in the nature of its pappus, which is scale-like and dilated at the base, instead of being setose.

There has been no recent treatment of this genus, which was established by Gray (Pl. Fendl. 65, 1849). It was based on a somewhat shrubby herb from northern Mexico, and named *C. Wislizeni* for its collector. In 1852, Gray (Pl. Wright. 89) emended the description of the genus as shrubby or herbaceous but shrubby at the base, when describing two new species, one Mexican, *C. Grahmi*, and the other from the boundary region of Mexico and New Mexico, *C. Bigelovii*. Since then only one other species has been added by Greenman (Proc. Am. Acad. Arts & Sci. 44: 34, 1904). It also is Mexican and was considered as an herbaceous perennial having a ligneous base. As the author's description has distinguished it from the other Mexican species, chiefly by the leaves and phyllaries, it is clear that all four species are similar in their shrubby or near shrubby nature. It was possible to include the American species in this study.

Garberia

Another shrub of this subtribe is found in the genus *Garberia*. When cataloguing a collection of plants that had come from east Florida, Nuttall (Amer. Jour. Sci. 5: 299, 1822) gave a brief Latin description of *Liatris fruticosa*. It was the only species of that genus referred to as fruticose by DeCandolle (Prod. 5: 132, 1836) and became the subdivision *Suffruticose* in Torrey and Gray (Fl. N. Am. 2: 76, 1841). This plant, referred to by Nuttall in 1841 (Trans. Amer. Phil. Soc., ser. 3, 7: 285) as agreeing with the genus *Liatris* in its flowers but not in its habit, was transferred by Gray (Proc. Acad. Nat. Sci. 379, 1879) to the new genus *Garberia*. Thus it appears in more recent floras of the South as *Garberia fruticosa* (Nutt.) Gray. The restudy of William Bartram's plants (Bartr. Trav. 164, 1791; ed. 2 162, 1792) by Merrill (Bartonia 23: 24, 1944) called for a new combination. After Dr. Francis Harper had covered Bartram's routes, he was satisfied that what Bartram had described as *Cacalia heterophylla* was the same shrub. The plant is now known as *Garberia heterophylla* (Bartr.) Merrill & F. Harper. It still is the only representative of the genus.

Carphephorus

The genus *Carphephorus* was established by Cassini (Bull. Soc. Philom. Paris p. 198, Dec., 1816) when naming as *C. pseudo-liatris*, a specimen without locality, seen in the Jussieu herbarium, which for a time was thought to be of Siberian origin. In his Dictionnaire, Cassini (Dict. Nat. Sci. 7: 148, 1817) explained that it belonged to the natural Tribe *Eupatorieae*, "section des *Liatridees*," in which he was placing it, near *Liatris*, the chaffy receptacle being the chief point of difference. Cassini's "sec-

tional" name must be rejected because under the international code a section is of infra generic rank, while Cassini applied this term to a group of genera. Torrey and Gray (1841) found that the character of the receptacle had been overlooked by some in describing other species and rightly recognized *Carphephorus* as an American genus. At that time, three other species were transferred from the genus *Liatris*, *L. bellidifolia* and *L. tomentosa* (Michx. Fl. Bor. 20: 93, 1903) and *L. corymbosa* (Nutt. Gen. 2: 132, 1818). At the same time also the older synonyms were given for these four species, as they were given by Gray (Syn. Fl. 1(2): 1886); hence they have not been repeated here. They still remain the four accepted species of the genus and all have been represented in this study.

Two Californian plants described as *Carphephorus junceus* Benth. (Bot. Sulph. 21, 1844) and *C. atriplicifolia* Gray (Proc. Am. Acad. Arts & Sci. 5: 1591, 1861) were early placed in the *Helanthoideae* instead of the *Eupatorieae*, and assigned to a new genus *Bebbia* by Greene (Bull. Cal. Acad. Sci. 1: 179, 1885). Thus though appearing under the genus *Carphephorus* on page 113 in Gray (Syn. Fl. 1(2) 1886), they are given under *Bebbia* in the supplement of that volume (p. 453). More recently, *B. atriplicifolia* (Gray) Greene has been reduced to varietal rank by I. M. Johnston (Proc. Cal. Acad. Sci., ser. 4, 12: 1197, 1924) so that this genus includes one species, *B. juncea* (Benth.) Greene, its variety *atriplicifolia* (Gray) Johnston, and variety *aspera* Greene (l.c.), all removed from *Carphephorus*.

Other excluded names and species are:

Carphephorus baicalensis Adams in Mem. Soc. Nat. Moscou 5: 115 (1817); DC. Prod. 5: 132 (1836) = *Saussurea pycnocephala* Ledeb. according to Benth. & Hook., Gen. Pl. 2: 249 (1873).

Carphephorus cordifolius DC. Prod. 7: 267 (1838) = *Brickellia cordifolia* Robinson, Proc. Am. Acad. Arts & Sci. 47: 200 (1911).

Carphephorus revolutifolius DC. Prod. 5: 132 (1836) according to Benth. & Hook. Gen. Pl. 2: 249 (1873) "certainly from description, expelled from the genus."

Carphephorus triangularis (DC.) Gray Pl. Wright. 1: 86 (1852), ex Hemsl. Biol. Cent. Am. Bot. 2: 109 (1881); *Bulbostylis triangularis* DC. Prod. 7: 268 (1838) = *Eupatorium vitifolium* (Sch. Bip.) Robinson, Proc. Am. Acad. Arts & Sci. 51: 537-8 (1917), *Hebeclinium vitifolium* Sch. Bip. ex Klatt Leopoldina 20: 90 (1884).

Trilisa

For the genus *Trilisa*, which Cassini (Bull. Soc. Philom. Paris, p. 140, Sep., 1818) established two years after the genus *Carphephorus*, the type was *Liatris odoratissima* Willd. (Sp. Pl. 3: 1637, 1803). Willdenow had taken up this name from Walter's *Anonymos odoratissimus* Walt. (Flor. Carol. 198, 1788), as he had also *A. paniculatus*, these names being declared illegitimate by article 33 of the International Code of Botanical Nomenclature. In his key of the *Eupatorieae*, Cassini (Dict. Sci. Nat. 26: 228, 234, 1823) placed this new genus in his section "*Liatridees*" between *Carphephorus* and *Suprago*, a name which has been retained for the plu-

mose section of *Liatris*. However, Cassini's genus was not accepted at once. DeCandolle (Prod. 5: 131, 1836) used it as a sectional name of the genus *Liatris*, and this was followed by Torrey and Gray (Fl. N. Am. 2: 76, 1841). The latter, however, correctly eliminated unrelated species and limited it to these two, collecting their older flora- and plate-references not included here. Since Bentham and Hooker (Gen. Pl. 2: 248, 1873) referred to the incorrect use of Cassini's generic name for a section, there has been no further confusion of this small genus.

One further species has been added. Small (Bull. Torr. Bot. Club 51: 392, 1924) had described a new plant from Florida under a generic name, an anagram of *Trilisa* which it resembled somewhat in habit, as *Litrisa carnosa*. When Robinson (Contrib. Gray Herb. new ser., 6: 104, p. 49, 1934) closely compared the plant with *Trilisa* and *Carphephorus*, he was led to refer it to the former genus.

MATERIALS AND METHODS

The same methods have been employed as were used in the study of *Brickellia* (Gaiser, l.c.). As some of these materials were collected along with those of *Brickellia*, frequently preparations of both were carried along together so that there might be as little variation in treatment as possible. Whenever seeds were received on herbarium specimens or in packets from other collectors,² they were germinated and eventually treated by the same variety of techniques and stains. In the preparation of figures of the chromosomes, the same photographic and microscopic equipment has been used at the same magnification, with the intention of making adequate comparisons of the size and morphology of the chromosomes with those of *Brickellia*. Thus not only the same terms are used, but with the same connotation of size. The same precautions were taken to study a sufficient number of cells so as to be able to choose similar stages for comparison of the chromosomes of all species of the different genera. Usually comparable stages of each have been photographed, but where the illustrations represent slight variations of condensation, the purpose of the selection has been discussed. In this study, use has been made of the photographic lens to illustrate the trichomes and epidermal figures, both to elucidate and confirm the drawings used for *Brickellia*.

In Table I are given the list of accessions of each species received along with the place and date of collection and the collector's name and number.³ They have been arranged and discussed in the order of a key prepared for the genera (see page 124). As it has been impossible so far to obtain seeds or any cytological material of even a single species of *Kanimia* from South America, that genus is not included in this key.

Following the pattern of the investigation made of *Brickellia*, leaves of the species of these genera were similarly cleared for the study of trichomes.

² The author again expresses deep gratitude to all contributors.

³ Reference to the numbers of collectors will permit examination of a number of specimens in various herbaria. Specimens collected or received by the author will be deposited in the Gray Herbarium.

As stated there, presence or absence of trichomes was not considered important for these studies. Attention was given to their form, as that has been found to change little, if at all, under varying environmental conditions. The terms applied in the descriptions and figures 61 to 88 of *Brickellia*, have again been used here. The same principle was adopted of obtaining leaves at the Gray Herbarium of specimens which had been referred to by authors so that they would approach the typical. As these genera are comparatively small, it was possible to examine one to several leaves of almost all the species and their varieties. It must be pointed out that it does not represent an examination of leaves of numbers of specimens of any species. The difference in upper- and lower-most cauline leaves were illustrated for one species, *Trilisa paniculata*. Changes in the ontogeny of the species were not generally studied in detail.

OBSERVATIONS

I. Seedling growth

Whenever possible, an effort was made to grow some of the germinating seeds for a time at least, in the greenhouse. Attempts to bring the plants into bloom met with varying success. Of three species of *Carphephorus*, two of *Trilisa* and the one *Garberia* none ever produced flowering axes under the same conditions which stimulated flowering of more than a dozen species of *Brickellia*, three species of *Kuhnia*, two of *Barroetia* and one of *Carphochaete*. At least several plants of *Trilisa paniculata* were kept for more than three years, a period longer than normally would be required for a biennial plant to come into flower, and above ground they still had only rosettes of leaves. Time and facilities did not permit further studies along this line.

The plantings attracted attention because of the striking differences of the seedling conditions. As has been described and illustrated for eighteen species of *Liatris* (Gaiser 1950a), during the first season, while the primary root is becoming very much thickened, those seedlings produce only radical leaves. As can be seen in figures 42 to 62, the larger ones with a longer growing period, have formed quite a rosette. Then in the second season, usually a flowering spike is produced. This was also illustrated in the progeny of a natural hybrid (Plate II c, Gaiser 1951). Young plants of *Liatris punctata* were here compared with those of the other genera.

In figures B and C are shown seedlings of *Carphephorus pseudo-liatris* II and *Trilisa paniculata* VIII, of approximately sixteen and eighteen months respectively, in comparison with one of *Liatris punctata* (Fig. A) of approximately two years. The latter is old enough to show the beginning of a forking and the subsequent elongation into the deeply penetrating system which is characteristic of this species. In the *Trilisa*, the modification to the thickened somewhat tuberous roots is already evident and to a lesser extent in the younger *Carphephorus* also. At maturity, a similar thickened fibrous condition would develop, for that is common to all the species of the genus. This photograph happens to illustrate the aptness

TABLE I
Chromosome Numbers in the *Kuhniinae*

Name	Growth Form	Accession				Chromosome Number	
		No.	County	Locality of Collection	Collector, No. & Date	n	2n
<i>Carphochaete Bigelovii</i>	Shrub	II	Pima Co., Ariz.	Santa Catalina Mts.	K. F. Parker 7274, 4/29/50		22
<i>Garberia heterophylla</i>	Shrub	IV	Volusia Co., Fla.	North of Ormond	Mrs. H. Butts, Dec., 1947		20
		V	Highlands Co., Fla.	e. of Sebring, Arbuckle Creek	R. Garrett 11/21/48		20
		VI	Flagler Co., Fla.	Korona	R. B. Miller, 2/16/50		20
		VII	Marion Co., Fla.	Ocala Natl. Forest, near Eureka	Miss L. E. Arnold 2/2/50		20
		VIII	Putnam Co., Fla.	10 mis. s.e. of Interlachen	W. B. Fox, 11/18/51		20
<i>Carphephorus pseudo-liatris</i>	Perennial herb	I	Liberty Co., Fla.	3 mis. e. of Hosford on Hwy. #20	H. Kurz, 11/5/49		20
		II	St. Tammany Parish, La.	1 mi. from Slidell on LaCombe Rd.	L. Ewan 19236, 11/25/49		20
<i>C. bellidifolius</i>	Perennial herb	II	Wake Co., N. C.	2 mis. s. of Fuquay Springs on U.S. #15 A	R. K. Godfrey & W. B. Fox 48679, 10/16/48		20

<i>C. tomentosus</i>	Perennial herb	I	Pender Co., N. C.	10 mis. s. of Harrel's store	R. K. Godfrey 12/22/51		20
<i>C. corymbosus</i>	Perennial herb	I	Alachua Co., Fla.	Gainesville	Miss L. E. Arnold 11/19/46		20
		V	Putnam Co., Fla.	10 mis. s.e. of Interlachen	W. B. Fox, 11/18/51		20
<i>Trilisa paniculata</i>	Perennial herb	II	Volusia Co., Fla.	n. of Ormond	Mrs. H. Butts Dec., 1947		20
		VIII	Leon Co., Fla.	23 mis. w. of Tallahassee	H. Kurz 11/5/49		20
		IX	Leon Co., Fla.	23 mis. w. of Tallahassee	H. Kurz 11/5/49		20
<i>T. odoratissima</i>	Perennial herb	I	Alachua Co., Fla.	Gainesville	Miss L. E. Arnold 11/19/46		20
		IV	Highlands Co., Fla.	Along Jackson Creek, near Sebring	R. Garrett 11/10/48		20
		V	Leon Co., Fla.	23 mis. w. of Tallahassee	H. Kurz 11/5/49		20
		VI	St. Tammany Parish, La.	1 mi. w. of Slidell	L. Ewan 19237 11/25/49		20
<i>T. carnosa</i>	Perennial herb	III	Highlands Co., Fla.	w. of Sebring	R. Garrett 11/11/48		20
		IV	Highlands Co., Fla.	wet pinelands s. of Sebring	R. Garrett 11/4/49		20

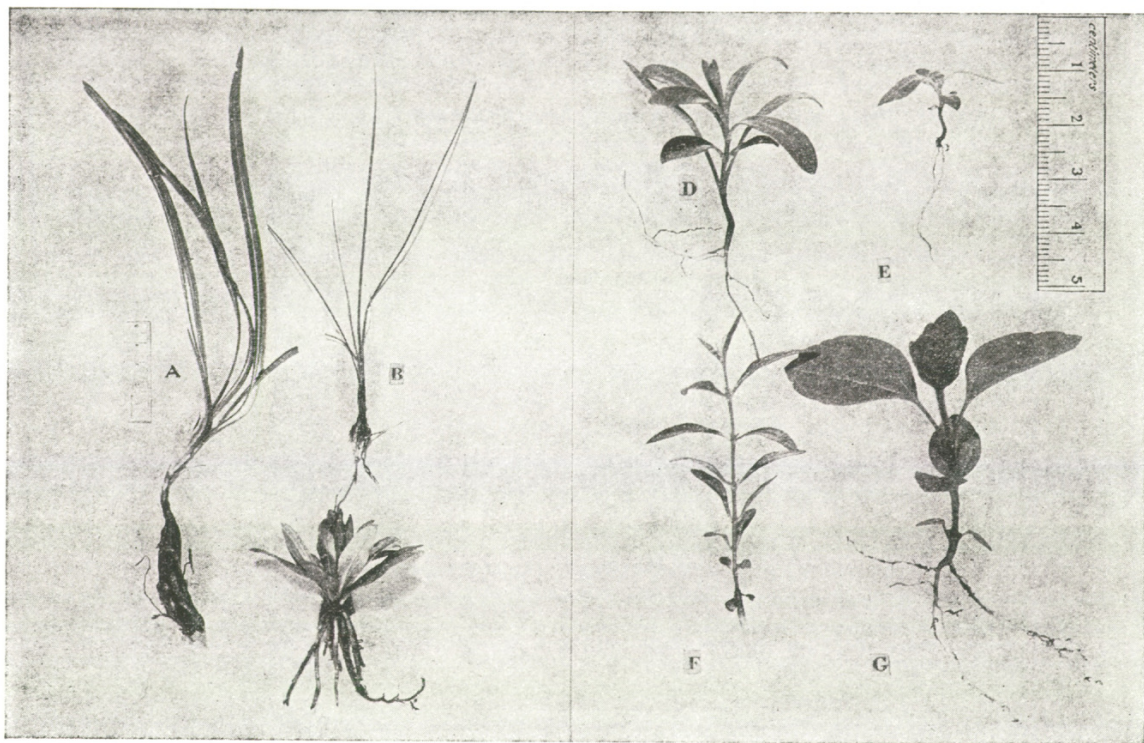
TABLE I—continued
Chromosome Numbers in the *Kuhniinae*

Name	Growth Form	Accession				Chromosome Number	
		No.	County	Locality of Collection	Collector, No. & Date	n	2n
<i>Kuhnia eupatorioides</i> var. <i>pyramidalis</i>	Perennial herb	I	Kalamazoo Co., Mich.	Sect. 29, Schoolcraft Twsp.	C. R. Hanes 9/17/47		18
		II	Clark Co., Ky.	12 mis. e. of Winchester	F. T. McFarland 10/18/47		18
		III	Brazos Co., Texas	5 mis. s. of College Station	H. B. Parks 10/20/47		18
		VII	Kalamazoo Co., Mich.	Along L.S.M.S. Rwy., Schoolcraft Twsp.	C. R. Hanes 1648 10/5/48		18
<i>K. eupatorioides</i> var. <i>texana</i>	Perennial herb	I	Dallas Co., Texas	3100 Block on Rosedale St., University Park, Dallas	L. H. Shinnars 11/11/48	9	18
<i>K. eupatorioides</i> var. <i>corymbulosa</i>	Perennial herb	I	Roosevelt Co., Mont.	10 mis. n.e. of Poplar	M. Ownbey 3229 8/30/49		18
<i>K. Mosieri</i>	Perennial herb	I	Alachua Co., Fla.	Gainesville	R. Garrett 11/3/48	9	18
<i>K. rosmarinifolia</i>	Perennial herb	III	Santa Cruz Co., Ariz.	Shaded canyon, Patagonia	D. H. Darrow & Haskell 2317 10/14/44	9	18
		V	Apache Co., Ariz.	Near cultivated land, St. John's	K. F. Parker 7409 12/3/50		18

<i>K. Schaffneri</i>	Perennial herb	I	Mexico, Mex.	Hills of El Salto, n.w. of Huchuetoca	D. B. Gold & F. Matuda 10/30/51		18
<i>Barroetia subuligera</i> var. <i>latisquama</i>	Perennial herb	I	Jalisco, Mex.	Along rocky cut near top of barranca, Guadalajara	L. O. Gaiser 66 10/27/50	9	18
<i>B. sessilifolia</i>	Annual	I	Puebla, Mex.	Along dry slopes of Cerro Tlacotli 6 kms. s. of Izucar de Matamoros	L. O. Gaiser 75 10/31/50	9	18
		II	Morelos, Mex.	From the limestone mt. at Yautepec	L. O. Gaiser 76 11/3/50		18
		III	Morelos, Mex.	ca. 23 kms. from Cuernavaca on mt. slopes on road to Yautepec	L. O. Gaiser 77 11/3/50	9	18
		IV	Guerrero, Mex.	5 kms. from Taxco, along Mexico to Taxco Hwy.	L. O. Gaiser 88 11/4/50		18

Chromosome Numbers in the Subtribe *Ageratinae*

<i>Mikania scandens</i>	Vine	II	Calvert Co., Maryland	Plum Point	S. F. Blake Autumn 1946		38
		III	Flagler Co., Fla.	Haw Creek Region	Mrs. H. Butts Autumn, 1946		38
		VII	Highlands Co., Fla.	Rich wet soil, Sebring	R. Garrett 11/15/48		38
<i>M. cordifolia</i>	Vine	I	Highlands Co., Fla.	Highlands Hammock, State Park	R. Garrett 11/23/48		38



SEEDLINGS

of the specific name *pseudo-liatris*, given by Cassini to his type species of the genus. While narrower, linear leaves are found in a number of species of *Liatris* other than *L. punctata*, this is the only species of *Carphephorus* possessing them. It is obvious that regardless of the shape and the structure of the root, development of a rosette of leaves is common to all and is of rather prolonged duration. At least under greenhouse conditions, this same *Trilisa* seedling has not varied much in appearance in more than three years.

Figures D to G represent comparatively much younger seedlings of *Carphochaete Bigelovii* II, *Barroetia sessilifolia* I, *Kuhnia rosmarinifolia* V and *Brickellia adenocarpa* III. Only records were kept of the time of sowing the seeds, so that from those dates, the *Carphochaete* is a little more than a month old, the *Barroetia* is less than three months, the *Kuhnia* a little more than two months and the *Brickellia* less than two months. All have developed slender fibrous roots at this time but already show a fast growing stem-axis with a number of nodes and internodes. This similarity in seedlings cannot be attributed to any likenesses of their actual growth-form, for while this species of *Barroetia* is an annual and might be expected to show very rapid growth, that of the *Kuhnia* is an herbaceous perennial, that of the *Brickellia* a shrubby perennial, and the *Carphochaete* a small shrub.

The matter of chief interest was that there were two types into which all of these seedlings can be classified: the rosette and the non-rosette.

II. Chromosome Number and Morphology

CARPHOCHAETE

Cells of *Carphochaete Bigelovii* II were found to have a noticeably greater amount of chromatin than any of the other genera studied. This is due first of all to a larger number of chromosomes ($2n = 22$) but also to the presence among them of a majority of larger ones. While the exact size and form of all the chromosomes is not evident in figure 30, among the thirteen peripherally arranged units can be distinguished some of the long and medium classes.⁴ The V approximately at the center top and the one almost at the center bottom, are designated medium in length (Mm), in contrast to the two long V's along the right (Lm), all of these being medianly constricted. The latter two in turn are distinguished from

⁴The same abbreviations as have been used in Gaiser (1953) are here applied: Using capital letters to express length, long chromosomes with median, submedian and subterminal constrictions are represented as Lm, Lsm, and Lst respectively, chromosomes of median length similarly constricted as Mm, Msm and Mst, and short chromosomes similarly Sm, Ssm and Sst. The short short class became SS; when medianly constricted SSm and when terminally SSst.

EXPLANATION OF FIGURES OF SEEDLINGS

Figures represent seedlings of various accessions of different dates. Figs. A-C photographed 5/9/51. Figs. D-G photographed 4/26/51.

A. *Liatris punctata* 11/22/49. B. *Carphephorus pseudo-liatris* II 1/19/50. C. *Trilisa paniculata* VIII 11/22/49. D. *Carphochaete Bigelovii* II 3/20/51. E. *Barroetia sessilifolia* I 2/26/51. F. *Kuhnia rosmarinifolia* V 2/15/51. G. *Brickellia adenocarpa* III 3/5/51.

two of similar length but having submedian constriction (Lsm), at right and left at the top, and a pair along the left side, in slightly lower focus, which are subterminally constricted (Lst). With the remaining marginal V at the lower left clearly a long chromosome also (Lm), a total of seven of the long class have been counted merely among the peripheral ones. As frequently occurred, toward the center among others, are six shorter units (Sm) of which two can be distinguished at lower left. In a similar cell (Fig. 29) of a Feulgen preparation, only one medium chromosome was left with these six, all of which are short V's and medianly constricted, to fill the center around which fifteen long and medium ones were arranged marginally. There is a sharper break between the six short ones and the remaining sixteen than separates the equal number of long and medium ones into which that number has been divided. In the short ones there was little doubt that the constriction was median. The eight long chromosomes were analyzed as to centromere position with less difficulty, than those of medium length where there was some uncertainty. From the study of material available of one accession the karyotype has been given in Table II as: 2 Lm, 4 Lsm, 2 Lst, 4 Mm, 2 Msm, 2 Mst and 6 Sm.

GARBERIA HETEROPHYLLA

This monotypic species, restricted to Florida, was received through five different collectors from as many different counties. Excellent material was available for study and no variation was found. In a cell (Fig. 28) of accession VI from Flagler County, the number of chromosomes can be counted ($2n = 20$) and their morphology is also clearly recognizable. Thus, by beginning as at twelve, and proceeding clockwise around the dial, the marginal chromosomes represented in succession are as follows: Mst, Lst, Sst, Lsm, Mm, Msm, Lm, Lsm, and Sm. In the cell there are a pair of each of these classes except Mm, and of that there are three pairs. A second cell (Fig. 27) in the same section, shows that two of the shortest units, lower left and right margins, are heterobrachial. This was more convincing in cells particularly favorable for study of accession VII, though not photographed to much better advantage (Fig. 26, 3rd from left at top). By comparison with the cells of *Carphochaete* there is this difference of the fewer (four rather than six) chromosomes of the short class, and in their variation from the uniformly similar isobrachial type. As for the rest, the same classes are present though not to the same numbers. With one pair of long of each of the three constriction types, rather than a total of eight long ones, comes a further reduction in amount of chromatin. This karyotype has the greatest variety: 2 Lm, 2 Lsm, 2 Lst, 6 Mm, 2 Msm, 2 Mst, 2 SM, and 2 Sst.

CARPHEPHORUS

Two of the four species of *Carphephorus* were examined from at least two accessions, while *C. tomentosus* and *C. bellidifolius* were limited to one each. In all, the $2n$ chromosome number was found to be 20.

Of *C. bellidifolius* there were a number of excellent cells for study.

From comparisons made with *Carphochaete Bigelovii* it was observed that the chromosomes were all more nearly equal in length. Two pairs of medium chromosomes one each with medium, Mm, and submedian, Msm, constrictions, were almost as long as the long chromosomes. Also the next to the shortest pair were not sharply different from the medium in length. Frequently when the karyotype was assembled after an analysis of a cell, there were odd numbers for these two classes. The slightly more condensed chromosomes of figure 22 were well spread. Beginning as at seven and proceeding clockwise to four, the marginal ones are: Mst, Mm, Mm, Lst (pale, as slightly below focus), Lsm, Mm, Mm, Mst, Lst, Lm, Msm, and Msm. The two latter and the pair, Mm, directly opposite, closely approach the long ones. In this cell the shortest units are toward the center.

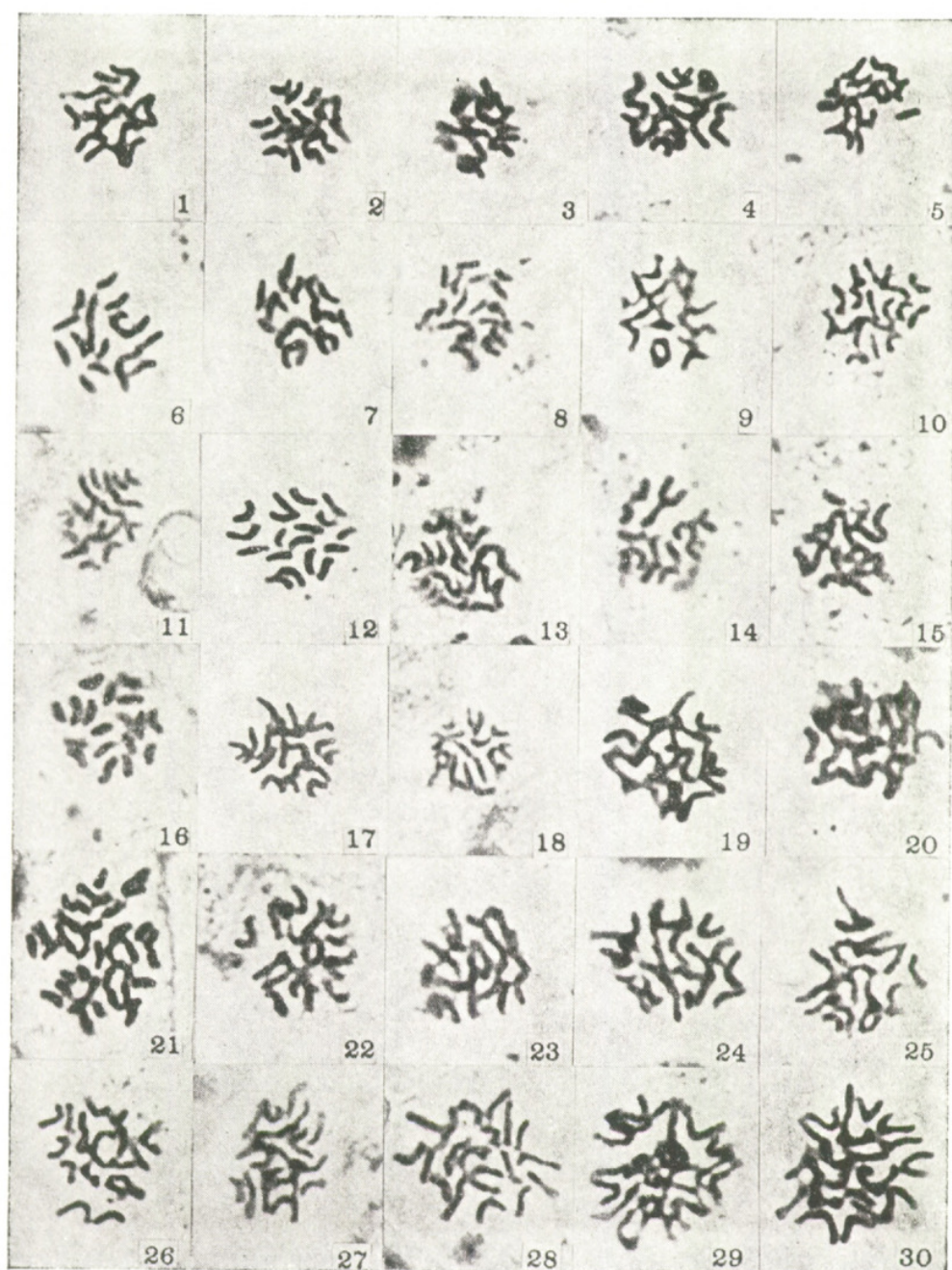
Preparations from seeds of *Carphephorus tomentosus*, which had been received from North Carolina, were more adequate for study than photography. As in the cell of figure 23, the chromosomes may be spatially separated but slight overlapping of the ends confuses the picture. Under the studies of this species the note had been made "remarkably few short chromosomes."

As was customary accompanying the studies of cells, diagrams of *C. corymbosus* V were made and the pairs of chromosomes numbered in succession as to their lengths. With a total of twenty chromosomes, the numbers of the shortest pairs were 9 and 10. While the latter was sure to be of the class Sm, opposite 9 there was frequently placed the question, "short or medium." In figure 24 for example, along the right side two isobrachial chromosomes which are clearly medium in length, alternate with two which are heterobrachial. These latter were numbered 9 and 8 respectively, meaning that while the bottom one was one of the characteristic medium pair with subterminal constriction, Mst, the second from the top was of the questionable class.

Accessions of *C. pseudo-liatris* from Florida and Louisiana were compared. Because tips were available from seedlings (see Fig. B) growing in a pot, as well as from germinating seeds, the most convincing analysis of the morphology of the chromosomes was made of this species. In figure 25, photographed when one each of the two shortest pairs are in focus, a number of the longer chromosomes are foreshortened. Almost at center bottom is a short medianly constricted chromosome, Sm, while the second from the center top is heterobrachial. Frequent analyses left a question concerning the members of this pair, just as had been the case in studies of the other species. Certainly no marked difference was noted for any one. Therefore one karyotype has been given for the four of them: 2 Lm, 2 Lsm, 2 Lst, 6 Mm, 2 Msm, 4 Mst, and 2 Sm. This modification of the two last classes was made with hesitation but allowing for the factor of human error, was accepted on the evidence of the camera.

TRILISA

Of several collections of *Trilisa paniculata*, made in South Carolina in October, germination of seeds was very poor, though it was possible to



CHROMOSOMES
(Caption at bottom of facing page)

obtain the chromosome count, $2n = 20$. More somatic divisions were obtained from two accessions from northern Florida in November and a few seedlings were grown (see Fig. C). While a majority of longer chromosomes in a peripheral arrangement was the more usual, in figure 19 some of the medium and short units are seen in this position. Thus a better idea of the comparative lengths of all the classes of units for this species is obtained. At the top left corner, two medium chromosomes, the one subterminally, Mst, and the other medianly, Mm, constricted, lie respectively below and above a long submedian one. The mate for the former appears at the opposite right hand corner between two radiating long chromosomes of subterminal constriction, Lst. Below these, one each of the longest and shortest medianly constricted chromosomes are sharply contrasted and followed by a similar one medium in length. The latter is one of the medium class which approaches the long. Certainly this medium chromosome and the long one are more nearly equal than it and the short one. In size and form no noticeable variation from the chromosomes of the species of *Carphephorus* was evident. Comparison of this cell with figure 24 of *C. corymbosus* brings the camera's confirmation. The same question arose as to the length of the pair next to the shortest, but they were considered to be heterobrachial and not unlike the class Mst.

Preparations were made from seeds of *Trilisa odoratissima*, known as the Vanilla Plant, from Florida and Louisiana. The long chromosomes were more prevalent and of the same form as in the previous species. Also, there was no evidence that the medium and short ones differed. Because of the abundance of cytoplasmic inclusions in the cells of this species, fewer cells were suitable for photography. When the chromosomes were well spread, globules were often overlying. It would have been better to have made all preparations by the Feulgen technique. Figure 20 is of a cell just back of the meristematic apex and the chromosomes are therefore more crowded. One karyotype is believed to be common to these two species and it has been found to be indistinguishable from that of *Carphephorus*.

EXPLANATION OF FIGURES

Figs. 1-7, 9-30, are from near comparable metaphase plates in root-tips. Fig. 8 is of an early anaphase plate. 1, 2, 3. *Barroetia sessilifolia* I. 4, 5. *B. subuligera* var. *latisquama* I. 6-10. *Kuhnia eupatorioides* var. *pyramidalis*; 6-8. (III from Texas), 9. (II from Kentucky), 10. (VII from Michigan). 11. *K. eupatorioides* var. *texana* I. 12. *K. eupatorioides* var. *corymbulosa* I. 13. *K. Mosieri* I. 14-16. *K. rosmarinifolia*; 14, 15. (of accession III), 16. of V. 17, 18. *K. Schaffneri* I. 19. *Trilisa paniculata* VIII. 20. *T. odoratissima* IV. 21. *Mikania scandens* III. 22. *Carphephorus bellidifolius* II. 23. *C. tomentosus* I. 24. *C. corymbosus* V. 25. *C. pseudo-liatris* I. 26-28. *Garberia heterophylla*; 26. of accession VII, 27, 28. of VI. 29-30. *Carphochaete Bigelovii* II.

Preparations made of root-tips taken from plants, fixed in Belling's at the same time and stained in toto in Feulgen's, Figs. 5, 11, 12, 25, 29. Root-tips of seeds after Belling's and stained in N.G.V., Figs. 16, 24; after Karpechenko's and stained in Feulgen's, Figs. 9, 18, 27, 28. All the rest were of seeds fixed in Karpechenko's and stained in N.G.V. The photomicrographs were taken with the use of a Zeiss microscope and a Homal IV lens. All figures 2300x. Reduced 1650x in reproduction.

The preparation of the plates has been aided by a grant from The Society of Sigma Xi, which the author gratefully acknowledges. It is a pleasure to acknowledge the assistance of Mr. Paul Brown in the photomicrography.

The rarer species, *Trilisa carnos*, limited to Florida, which had been thought to merit new generic rank by Small, was received from the same locality near Sebring, three times from October to November, 1948, and again in November, 1949. The difficulty of germinating seeds of this species was certainly not overcome during the time and with the material available. Only a few seeds ever appeared to begin growth and none developed very far so that an extremely limited number of mitoses were found. The number ($2n = 20$) and approximately the same kinds of chromosomes as found in the other two species were sketched from cells not adequate for photography. However, lacking sufficient material for careful studies, the karyotype of this species cannot be included at this time.

KUHNIA

Three of the four American species given by Shinnars (l.c.) have been available for this study. Accessions had been received of the largest, most widely distributed species, *K. eupatorioides* L. from the states of Michigan, Kentucky, Texas and Montana, which, according to Shinnars (l.c.) would represent all the varieties of that species except *ozarkana* Shinnars. Those from the first three sources were variety *pyramidalis* Raf. and from the last, var. *corymbulosa* T. & G. while Dr. Shinnars himself contributed a packet of seeds of his variety *texana*. A glance at figures 6 to 12 of this polymorphic species, shows a chromosome plate of $2n = 18$, in which there are lacking any of the long chromosomes, so characteristic of the genera here previously discussed.

K. EUPATORIODES variety *PYRAMIDALIS*. From preparations of particular clarity, stained with Newton Gentic Violet five years ago, the sizes of the chromosomes can be shown. At the lower left in figure 6, a parallel pair of the shortest and longest units, both medianly constricted can be compared with a single chromosome of intermediate length, lying almost horizontally above them. The units of this figure are probably all a little more condensed than those in figure 7, which is of a cell in a similar preparation. In the latter, the two longest chromosomes are at outer left and right and are submedianly constricted. From such figures, it is clear that the longest chromosomes would have to be placed in the medium class, according to the scale of sizes here used. One might then expect the shortest chromosomes, since there are units intermediate in length, to be two classes removed and to fall into a short short class, as adopted for some species of *Brickellia* (Gaiser 1953). Considerable effort was made to decide this question by comparison of various stages and of cells of all the accessions. Figure 8 is of an anaphase plate of a recent mitosis as can be judged by the parts of two chromosomes outlying in the cytoplasm at the right, belonging to the other closely overlying plate. The chromosomes are more slender but again they do not cover three distinct classes of length. It is considered that the karyotype includes medium to short chromosomes, and when there are nine pairs of such closely approximating lengths there is difficulty in deciding the boundary between the two classes.

In figure 8, two chromosomes with very small terminal bodies are seen, one at center bottom and the other at center left. More frequently cells were found in which only one such satellite was visible, as is shown at the end of the curved chromosome at upper right of figure 6 and at the inner end of the chromosome stretching toward the center from the left of figure 7. It is believed these chromosomes are next in length to the two longest pairs. By careful analysis of numerous cells of other accessions as well as this, next in succession of length are: 2 Msm and 2 Mm, which more closely approach the aforementioned three pairs than do the other 4 Mm. Whether the latter should be classed as short may be debatable. The four shortest are considered 2 Sm and 2 Sst. In preparations of accession II from Kentucky (Fig. 9) as well as accession VII from Michigan (Fig. 10) this analysis was also favored.

K. EUPATORIODES variety TEXANA. In the second accession from Texas, the figures are very much the same. Cells without any visible satellites were more frequently found than those showing them even delicately as in figure 11 (the second chromosome on the upper left) from a Feulgen preparation.

K. EUPATORIODES variety CORYMBULOSA. The western variety was received from Montana. Well spread chromosomes in the plate of such a cell as shown in figure 12 help to confirm the previous analyses. At the center on the left side is the medium chromosome with a satellite appearing knob-like at its inner tip and close to its centrally placed mate. Above them, occur one each of the longest of Msm and Mm respectively. The curved pair at center bottom are the second pair of so-called Msm while the two overlapping as a V at top are second in length of Mm. It is evident from such a preparation that no sharp line separates the classes of chromosomes. However, on the basis of comparison with those of the other genera the karyotype is believed to be: 8 Mm, 4 Msm, 2 M with sat., 2 Sm, 2 Sst.

Of the two other American species of *Kuhnia* included, the first is a restricted endemic in lower Florida. Two cells of *K. Mosieri* Small, in which the chromosomes were well separated by microscopic adjustment, could be seen in the field of the microscope at one time. Starting with the longest chromosomes, successively those next in size were sketched in different colors and the two cells constantly compared. Unfortunately they did not photograph as well as it was possible to draw them, to add to this interesting exercise. Of course there were points of indecision. However, even before it was recognized that in one of these (Fig. 13, center left) a chromosome with a satellite was represented, its arrangement in the order of consecutive chromosome lengths coincided with that given to such in *K. eupatorioides*. The karyotype of these two species were found indistinguishable. The second species is commonly known as *K. rosmarinifolia* Vent. Shinnars (l.c.) considered this name a "nomen confusum" and put it in synonymy with *K. chlorolepis* Wooton & Standley. Blake (1942) did not consider it necessary to adopt this name in his treatment of the genus for Arizona and so I have not, as both accessions

TABLE II
Karyotypes in Species of Genera of *Kuhniinae*

Name	Accessions Studied	Chromosomes										Remarks
		Total Number	Number of pairs each									
			Lm	Lsm	Lst	Mm	Msm	Mst	M with sat.	Sm	Sst	
<i>Carphochaete Bigelovii</i>	II	22	I	2	I	2	I	I	3		
<i>Garberia heterophylla</i>	IV V VI VII	20	I	I	I	3	I	I	I	I	
<i>Carphephorus pseudo-liatris</i>	I II	20	I	I	I	3	I	2	I	1 Mst = S ?
<i>C. bellidifolius</i>	II	20	I	I	I	3	I	2	I	
<i>C. tomentosus</i>	I	20	I	I	I	3	I	2	I	
<i>C. corymbosus</i>	I V	20	I	I	I	3	I	2	I	
<i>Trilisa paniculata</i>	VIII	20	I	I	I	3	I	2	I	1 Mst = S ?
<i>T. odoratissima</i>	IV V	20	I	I	I	3	I	2	I	
<i>Kuhnia eupatorioides</i> var. <i>pyramidalis</i>	I II III VII	18	4	2	I	I	I	1 Msm and 1 Mm the longest, other Msm and another Mm next in length.
<i>K. eupatorioides</i> var. <i>texana</i>	I	18	4	2	I	I	I	
<i>K. eupatorioides</i> var. <i>corymbulosa</i>	I	18	4	2	I	I	I	
<i>K. Mosieri</i>	I	18	4	2	I	I	I	
<i>K. rosmarinifolia</i>	III V	18	4	2	I	I	I	
<i>K. Schaffneri</i>	I	18	4	2	I	I	I	
<i>Barroetia subuligera</i> var. <i>latisquama</i>	I	18	4	2	I	I	I	Ditto
<i>B. sessilifolia</i>	I III	18	4	2	I	I	I	

here studied came from that state. Of the preparations of *K. rosmarinifolia* III, the same repetition of statements could be made, cells showing a small satellite less frequently seen (Fig. 15, at the center top), than those without them (Fig. 14). Of accession V of this species, a plate of particularly condensed chromosomes was photographed (Fig. 16) to show the narrow gap between the shortest and longest units. Thus, for example, comparison with figures 25 (Gaiser 1953) of *Brickellia microphylla* where the chromosomes were shortened by paradichlorobenzene treatment, or figure 42 of *B. glomerata*, where a similar drastic shortening accidentally happened in one cell of a Feulgen preparation, emphasizes that there is a greater spread in the species of that genus where the karyotype includes long chromosomes.

One of the three species, which do not occur north of Mexico, *K. Schaffneri* Gray, was available for this study. Because the type sheet contains also a root of some legume, Shinnars (l.c.) renamed the species *K. microphylla*, but Blake⁵ considers this unjustifiable.

In a very clear early metaphase plate (Fig. 17) from a Newton Gentian Violet preparation, the range in size of the chromosomes is shown. One of the longest chromosomes, submedianly constricted (Msm) is at the upper right corner and two of the shortest ones, medianly constricted (Sm), can be distinguished as smaller V's among the central group, almost at center top and bottom. At this focus, one arm of several of the marginal V's has been foreshortened. Thus, for example, the chromosome at lower right is the other of the longest pair (Msm) and in succession the other two at center bottom represent medium chromosomes of the next category, Mm and Msm respectively. The straight medium chromosome, which is at a slight angle above the latter, is terminated toward the center by a small knob and is the equivalent of the chromosome with a satellite. The same can be seen in a cell of a Feulgen preparation (Fig. 18) at the tip of the chromosome coming into the small central upper space.

By comparison of figure 17 with that of *K. eupatorioides* var. *corymbulosa* (Fig. 12) of a cell similarly prepared, it might appear that the chromosomes of this species are generally longer, but this is merely so because it is a slightly earlier metaphase stage. It is worthy of note that in both of these cells there is a knob-like body at the end of a pair of the chromosomes. That its appearance cannot be attributed merely to this one kind of preparation is proved by the use of the same kind (e.g., Newton Gentian Violet) in illustrating *K. eupatorioides* var. *pyramidalis* (Figs. 6, 7, 8) and *K. rosmarinifolia* (Fig. 15) where it is seen separated from the chromosome. Yet the same is also visible in Feulgen preparations (see Figs. 11, 18). In summary, in any kind of preparation of all of the species of *Kuhnia* here studied, this very small terminal body, which has been called a satellite, may be found, whereas in similar preparations of the previous genera, no evidences of such has ever been seen. No variation from the

⁵ *In litt.*

karyotype given for *K. eupatorioides* has been found in the three other species studied.

BARROETEA

The one perennial species which is somewhat woody at the base, *B. subuligera* (Schauer) Gray, is known from the northern boundary to Hidalgo, a central state in Mexico. The larger variety *latisquama* Greenman, was described from a specimen collected in Jalisco. A plant of this was collected in the barranca at Guadalajara and from seeds of it, a seedling was grown for a time in the greenhouse. From pollen mother cells as well as root-tips, the chromosome number was found to be the same as in the species of *Kuhnia* studied, $n = 9$ and $2n = 18$.

A comparatively early metaphase of a root-tip cell shows the form of sixteen of the chromosomes, but two short ones which were lying one above the other, resulted in the oval body at the upper right of the figure (Fig. 4). One chromosome of greatest length, submedianly constricted, is seen at lower right and a second in length, medianly constricted, is plainly contrasted at center top with one of the shortest (Sm). By the scale of sizes used for the other genera, neither of the former would exceed the medium class. Thus the karyotype includes medium to short chromosomes only. In this cell a number of the heterobrachial chromosomes are found around the periphery and may appear to be more numerous than in a very comparable stage of a *Kuhnia*, e.g., *Kuhnia Schaffneri* (Fig. 17). However, their number is not greater and in other cells where the chromosomes are a little more condensed (Fig. 5) no confirmation is found of this difference. While no chromosome with a satellite is shown, its equivalent is probably represented in one of medium length, subterminally constricted, for the free terminal body was seen in some other cells.

Of the annual species, *B. sessilifolia* Greenman, seeds were collected from four different localities of three of the central states of Mexico and from root-tips of each, the chromosome number was found to be the same as that of the perennial species, $2n = 18$. It was also possible to grow seedlings (see Fig. E) from two of these accessions and similar meiotic divisions were obtained, $n = 9$.

Figure 1 of *B. sessilifolia* III shows a metaphase stage comparable to that of figure 4 of *B. subuligera* and the sizes of the chromosomes are very similar. On one of the longest chromosomes, at upper left, a satellite is conspicuous. In cells of slightly more condensed chromosomes the same is visible (Figs. 2, 3, lower right). Examination of a number of cells of *B. sessilifolia* I resulted in the same analysis of medium to short chromosomes including one of the former showing a satellite, both in Feulgen and other preparations, either in cells of root-tips taken from the plant or from germinating seeds.

From this study of two species of *Barroetea*, it was found that they were more similar to, than different from, the species of *Kuhnia* seen. The points of likeness consist in having: the same number of chromosomes; chromosomes which range from medium to short across an indefinite

boundary, and, one pair of the medium chromosomes showing a satellite. Certainly no constant difference in the karyotype was detected. It is given as: 8 Mm, 4 Msm, 2 M with satellite, 2 Sm and 2 Sst.

SUMMARY ON CHROMOSOMES

As summarized in Table II.

1. *Carphochaete* is the only genus having 22 chromosomes.
2. All the species of the three genera, *Garberia*, *Carphephorus* and *Trilisa* have 20 chromosomes, in common with a majority of the species of *Liatris*.
3. Four of the seven species studied of *Kuhnia* and two of the species of *Barroetia* have 18 chromosomes, the same number that had been found in all of the examined species of *Brickellia*.
4. Monotypic *Garberia* and the one species studied of *Carphochaete*, are both distinct in their karyotypes. The latter has a greater proportion of long chromosomes with three pairs of isobrachial short chromosomes, while in the former, one of two short pairs are heterobrachial.
5. *Carphephorus* and *Trilisa* could not be distinguished by their karyotypes. Yet they varied from *Garberia* in a closer approach, if not equality, of the shortest heterobrachial pair to the medium class.
6. Long chromosomes are absent in the five species of *Kuhnia* studied, the karyotype consisting of medium to short ones. A pair of medium chromosomes have small satellites.
7. A similar closely graded series of short to medium chromosomes, of which one pair bears satellites, makes up the karyotype in the two species of *Barroetia* studied.

III. Trichomes.

As the type of *B. Pavonii* Gray is in the Boissier Herbarium, only six of the seven species of *Barroetia* could be included in this study of the trichomes of the leaves. Five were found to vary slightly in the abundance of non-glandular trichomes which are uniseriate (Metcalf & Chalk 1950) and of the acuminate type according to the classification of *Brickellia* (Gaiser 1953). The size and the thickness of the wall of the trichome vary very little from species to species. Figure 31 represents that of the annual *B. sessilifolia* and fig. 32, generally a slightly larger form, that of *B. subuligera* var. *latisquama*, the perennial considered somewhat woody at the base. The sixth species *B. glutinosa* Brandege, with leaves described as densely glandular-puberulent, was found to lack this type of trichome but to have the same biseriate glandular form described as being common to a number of species of *Brickellia*. Along the leaf margin these might be found from a few to seven or eight cells high (Fig. 33). If seen edgewise they appeared as a stipitate somewhat globular organ (Fig. 34). When the flat expanse of the leaf was examined, one saw their apices as two typical hemispherical cells (Fig. 35) or by focussing a little lower as rounded cells above the level of the leaf surface. Figure 36 was taken at

a still lower focus where the epidermal pattern, including a stoma, became evident, but the foreshortened trichome was merely a dark blur. Checking leaves of the other species for this type of trichome, it was found only very occasionally on the underside of the midrib near the petiolar attachment. However, the depressed gland, as used also for *Brickellia* (Gaiser, l.c.), and the punctate condition on the lower surface was common to all except *B. glutinosa* where it was lacking on the lower as well as the upper. As in *Brickellia*, this glandular trichome is a longer stalked condition of the short form arising from the epidermal layer in depressions below what is normally seen as the leaf surface. When a species characteristically develops the elevated form, none or very few, if any, are seen remaining sunken below the leaf surface.

No evidence was seen of the smaller uniseriate capitate glandular trichomes in any species of *Barroetia*.

All the species of *Kuhnia*, according to Shinn's classification, were represented and showed a little more variation in trichomes than those of *Barroetia*. On the upper surface of leaves of *K. adenolepis* they were the shortest, consisting of no more than two or three thick-walled cells, arising from a very heavily cutinized epidermis (Fig. 37). Those of *K. Mosieri* were comparatively short, but consisted of thin-walled cells, almost uniform in diameter, so that the trichome tapered very little (Fig. 38). On *K. Schaffneri* (Fig. 39) a more attenuate trichome, of approximately the same length but with heavier walls, showed a tendency towards the moniliform type of rounded bead-like cells. In all those having thick walls this character was prevalent as shown in the uneven-walled form of the scabroid leaf of *K. rosmarinifolia* (Fig. 40). All the succeeding longer ones have been figured at the same magnification (220 \times) just as all the shorter ones had, though they were more enlarged (530 \times). While those of *K. eupatorioides* var. *pyramidalis*, taken from our accession from Kentucky (Fig. 41) resembled that of *K. Mosieri* in the thinner and straight walls, those of varieties *texana*, *ozarkana* and *corymbulosa*, with successively thicker and rougher walls (Figs. 42–44) were attenuate and more moniliform. Those on the scabroid leaves of *K. leptophylla* var. *mexicana* (Fig. 45) and *K. oreithales* (Fig. 46) did not differ much from the latter. In these two species an occasional cell filled with an aggregate crystal was more commonly seen than in any other species. In all of them the apical cell is longer than the rest but would not be recognized as a cap cell, as in some species of *Brickellia*.

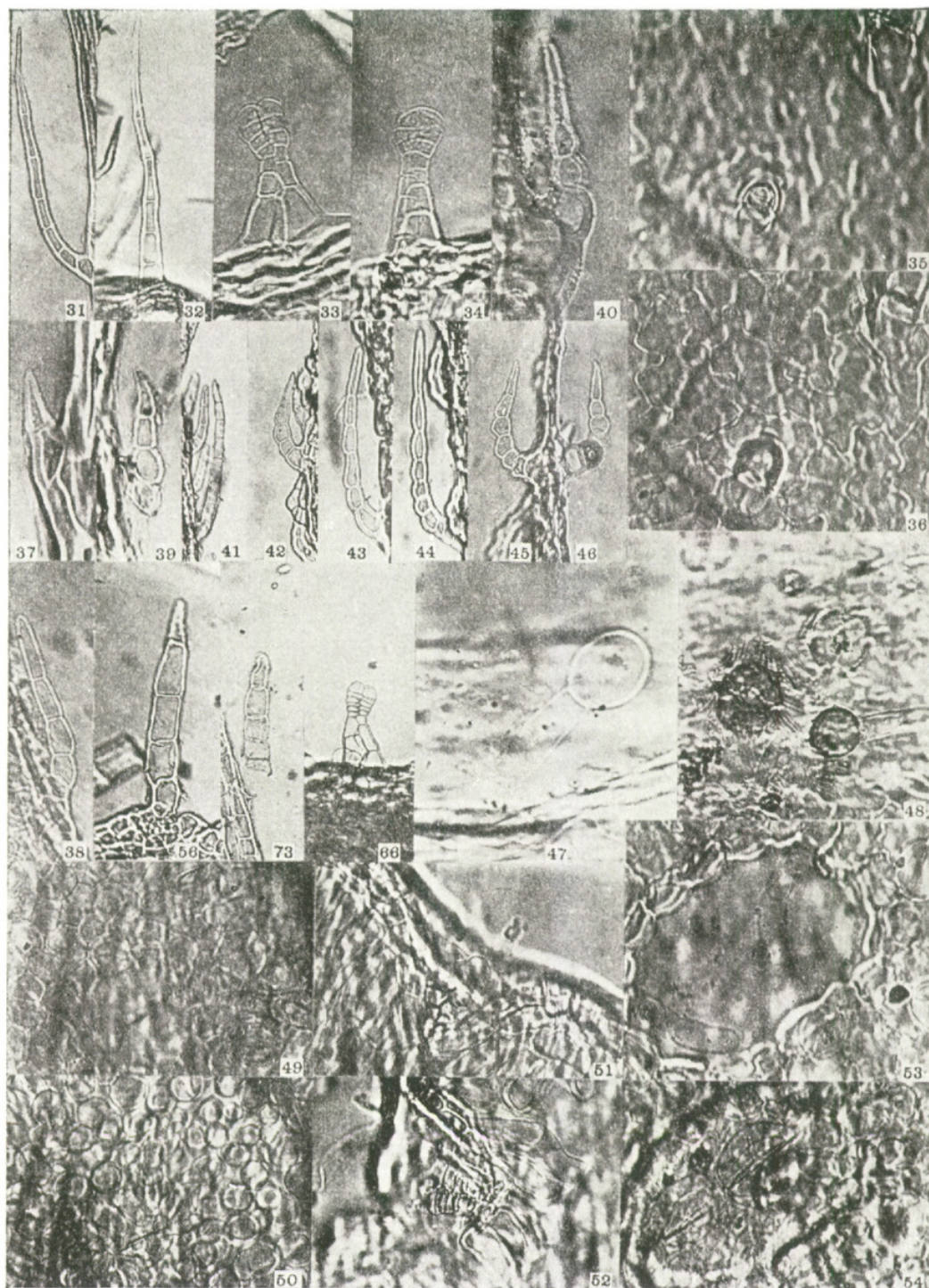
On no leaf preparation examined of any of the species of *Kuhnia* was evidence seen of the biseriate glandular trichome. By contrast the depressed gland and punctate condition was common to all species except *K. adenolepis*, and to both surfaces of the leaf, though generally it was less abundant on the upper.

What in *Brickellia* had been called uniseriate capitate glands, on stalks only a few cells in height, prevailed in all species. Generally they were small as in that genus, requiring a larger magnification for observation as well as photography as shown in Figure 47, 1100 \times , of *K. Mosieri*. An

exception to the general was found in *K. adenolepis*. This species had been distinguished by Robinson (1911b) because of its unique glandular ciliate phyllaries, the glands being described as sessile and black. The leaves had been described as "punctulatis" on both surfaces. Very short trichomes have been described for the upper surface (Fig. 37). Examination of a cleared preparation of the type specimen revealed more abundantly on the lower surface, a gland that is a little larger than the previous (Fig. 48, 530 \times) and distinctive for its dark apical cell when the leaves of all species had been cleared similarly. It is possible that the apical or secretory cell in this species has a different content, as not only was it dark but as shown in the figure some of its secretion had plugged and darkened some of the sunken stomata, from which it had not completely dissolved. From the very evident secretory function of the apical cell of this uniseriate small type of trichome, which is so similar in form to that seen in *Brickellia* (Fig. 87, 88, Gaiser 1953), I have considered them glandular trichomes in these two genera as did also G. Fischer (according to Solereder 1908, original thesis not seen). Vuillemin (1884) had done likewise in *Cynara* and *Echinopus*, though there are no figures of those for comparison. They are quite unlike the bladder-like trichomes observed by Volkens (1887) in *Zollikoferia nudicaulis*, which are considered to be full of cell sap (Solereder 1908, Fig. 103E). In form, they resemble somewhat more the capitate hairs described by Rosenthaler and Stadler (1908, Fig. 28) for *Cnicus benedictus*, consisting of six to twelve cells, with an elongated terminal cell which were said to differ from the non-glandular hairs in having a richer content.

Two genera, *Garberia* and *Carphochaete* had been established as having entire leaves. Neither the single species of the first nor any of the four of the latter had trichomes comparable to those illustrated for the previous genera. They both had a more slender filamentous form somewhat prostrate over the surface of the leaf.

When Bartram first described *Garberia* under the name *Cacalia heterophylla* (see p. 90), he wrote of the fleshy leaves: "of a pale whitish green, both surfaces being covered with a heavy pubescence and vescicular, that when pressed feel clammy and emit an agreeable scent." It was no surprise then when both surfaces gave the familiar appearance of the punctate condition at a focus when stomata were clearly visible (Fig. 49) and of the paired hemispherical cells of the depressed gland (Fig. 50) by sub-surface focusing. In addition, very narrow delicate filaments which tapered slightly if at all, and had cross walls at rather long intervals, lay twisted over the epidermis and proved difficult to follow to their origins. When the margin of this thick, entire leaf was examined it was possible by careful focusing to follow the epidermis as it alternately rose and fell into small pocket-like areas. In each depression was a tiered organ, two cells wide and approximately six cells high (Figs. 51, 52) familiar as the glandular trichome seen upon the leaf-surface of *Barroetia glutinosa* (cf. Fig. 33). In *Garberia* these arose in the epidermal layer from smaller cells which were clearly differentiated by their size. The first cells above

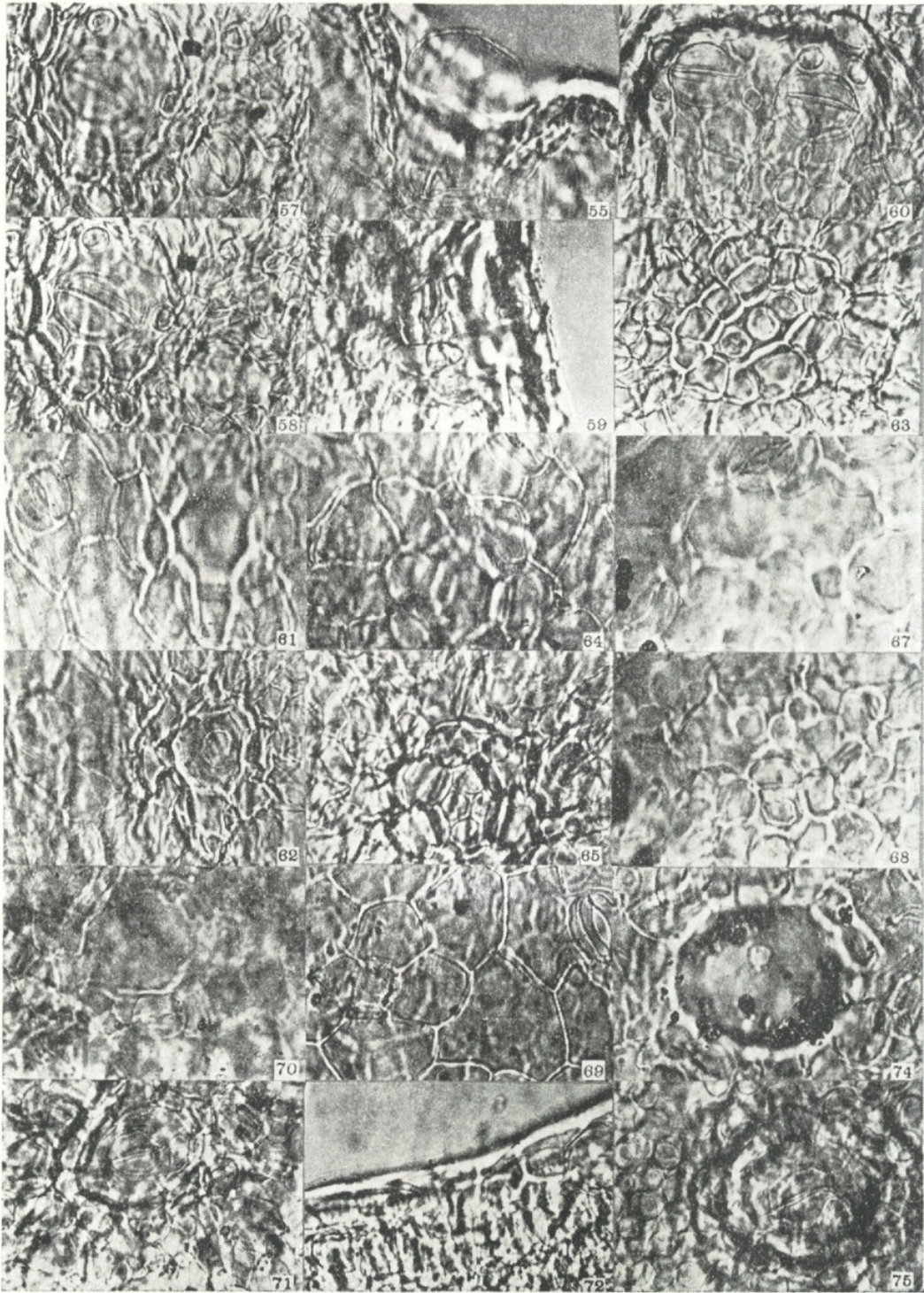


EXPLANATION OF FIGURES OF TRICHOMES

Figs. 31, 32, 37-46, 44-53, 56, 73. Non-glandular trichomes. Figs. 33-36, 66. Glandular biseriate trichomes. Figs. 47, 48. Non-glandular uniseriate trichomes.

31. *Barroetia sessilifolia*. 32. *B. subuligera* var. *latisquama*. 33-36. *B. glutinosa*. 33, 34. Along the leaf margin. 35. Above the epidermal surface. 36. At the epidermal surface. 37. *Kuhnia adenolepis*. 38. *K. Mosieri*. 39. *K. Schaffneri*. 40. *K. rosmarinifolia*. 41-44. *K. eupatorioides*. 41. of variety *pyramidalis*, 42. of var. *texana*, 43. of var. *ozarkana*, 44. of var. *corymbulosa*. 45. *K. leptophylla* var. *mexicana*. 46. *K. oreithales*. 47. *K. Mosieri*. 48. *K. adenolepis*. 56. *Carphephorus corymbosus*. 66. *Trilisa paniculata*. 73. *T. carnosa*.

All these photomicrographs were made from cleared leaves by use of a Zeiss microscope and a Homal IV lens, except Fig. 32, which is 110x. Figs. 38-46, 56, 66, 73, 85x. Figs. 31, 33-37, 48, 200x. Fig. 47, 430x.



EXPLANATION OF FIGURES OF DEPRESSED GLANDULAR TRICHOMES

Figs. 49, 53, 57, 61, 64, 67, 69, 70, 74, by focusing at the epidermal surface. Figs. 50, 54, 58, 60, 62, 63, 65, 68, 71, 75, by focusing below the epidermal surface. Figs. 51, 52, 55, 59, 72, lateral view seen along the margin of the epidermal surface of leaf.

49-52. *Garberia heterophylla*. 53-55. *Carphochaete Bigelovii*. 57-60. *Carphephorus tomentosus*. 63-65. *C. corymbosus*. 61, 62. *C. bellidifolius*. 67, 68. *Trilisa paniculata*. 69. *T. odoratissima*. 70-72. *T. carnosae*. 74, 75. *Liatris punctata*.

All these photomicrographs were made from cleared leaves by use of a Zeiss microscope and a Homal IV lens. x200.

these had thicker walls which generally reflected the light more than the thinner-walled upper cells. Alongside such a trichome frequently a slender filament could be traced until it pushed up to the leaf surface. In Figure 52 part of such a filament is recognizable after it emerged above the leaf, though it is seen less clearly along the right wall of the small depression. Closer microscopic observation of the surface of the leaf then made intelligible what had been baffling in several other genera as well. In addition to the paired hemispheric cells seen when focusing below the surface, an additional small round cell (shown at the bottom in figure 50) accounted for the delicate emerging filament seen on the surface. Thus they are really very delicate uniseriate trichomes of long, narrow, thin-walled cells growing from the sunken epidermal layer alongside the biseriate glandular trichomes.

Volgens (1890) described scattered groups of trichomes consisting of five or six which were uniseriate with whip-like tips, surrounding one central unstalked, biseriate, bladder-like gland (Pl. 8, Fig. 1) on the upper surface of the leaf of a plant labeled "*Baccharis Richardifolia*." A second species of the *Astereae*, *Olearia Hookeri*, was said to be very similar while on the other Compositae that he examined, the uniseriate elements were increasingly fewer. In two genera representing the *Eupatorieae*, *Eupatorium* and *Symphyopappus*, these trichomes might occur occasionally but lacked the characteristic thread at the tip. From his figure 4a, showing two hemispherical cells of *Symphyopappus*, it appears that the biseriate gland was depressed with only the uniseriate emerging above the surface. Thus while the latter (Fig. 4b) appears more torulate, the grouping might be similar to that described here for *Garberia*.

Carphochaete Bigelovii had been described by Gray (see p. 90) as puberulous and resinous punctate. On first examination of the leaf preparation with lower magnification, very numerous depressed areas were seen which were not all equal in size. Closer examination of one of the smaller, revealed besides the two large appressed hemispherical cells, several accompanying small round ones as the one seen in *Garberia*. The delicate filaments, of which the latter are the bases, were not as long and therefore did not appear as abundant over the surface. The larger areas might merely show central cells of a greater diameter but frequently they were the result of the confluence of two pairs (Fig. 54). In this figure there are in addition, the bases of three filaments, two of which are seen at the surface in figure 53. Since the leaves of this species are small but rigid it was possible again by focusing along the margin of a prepared leaf to obtain a lateral view of the gland (Fig. 55). Only the lowermost pair of cells were thick-walled in comparison with the several in *Garberia*. The walls of the cells immediately above were very thin and made it difficult to show that there was but one intermediate pair. It was clear that the uppermost secretory cells were very much expanded, thus contributing to their larger surface-appearance.

Although one of the four known species, *C. Wislizeni*, had been described as "not sprinkled with resinous dots," a leaf of a Pringle specimen

(#765) from the mountains near Chihuahua, where the type was collected, was found to be very similar to *C. Bigelovii*. All four species might differ slightly in the abundance but not in the form and the kind of contents in the depressions.

The species of *Carphephorus* may have the small, upper cauline leaves pubescent when the lower and radicle leaves are nearly glabrous. This is not a character peculiar to the genus, Solereder (1908) having generalized that in many genera only the youngest leaves, branches and leaf petioles are covered with glandular trichomes. Thus much would depend upon the choice of leaf for preparation. Of *Carphephorus*, in common with the other genera, lower larger leaves were examined, leaving to *Trilisa paniculata* the comparison of lower and upper ones.

In form, the non-glandular trichomes on the surfaces and along the margin of the basal leaves of each of the four species of this genus were of near uniform type, of broader cells than seen in species of *Kuhnia*. Though they varied in length and to a minor degree in thickness of wall, being thickest in *C. tomentosus*, the cylindrical shape of the component cells was remarkably constant. One of medium length of *C. corymbosus* is illustrated (Fig. 56).

It was in the punctate condition of the leaf that a greater difference was noted, as is reflected in the descriptions given by Torrey and Gray (1841): *C. tomentosus*, punctate; *C. pseudo-liatris*, sparsely punctate; *C. bellidifolius*, punctate with scattered impressed dots; *C. corymbosus*, sometimes obscurely punctate. From these phrases it was not clear whether the difference was merely one of abundance. Examination of these leaf preparations showed a considerable difference in glandular structures.

On either surface of a lower cauline leaf of *C. tomentosus*, the paired cells characteristic of the depressed gland were seen abundantly when focusing below the surface (Fig. 58) in contrast to the craters seen when stomata are in view (Fig. 57). As described in *Garberia heterophylla*, the two hemispherical cells were accompanied by small marginal circular cells which had been recognized as the median optical view of delicate filaments. Frequently two or three were found and since they appear in figure 57 they obviously reach the surface though none were found spreading over the epidermal cells. Looking along the margin of one of these lower nearly glabrous leaves which is entire, the lateral view of the biseriate trichome with accompanying filaments at the side was seen in the depressed areas (Fig. 59). To this species then, the term punctate, as understood for the previous genera, could certainly be applied. The depressions were conspicuous macroscopically and that may be facilitated by their greater size for it was found that often two glandular trichomes, each with several laterally placed filaments were within the margin of one depression (Fig. 60).

In the preparation of the other three species the surface pattern appeared quite different. In a similar leaf of *C. bellidifolius* there was no sign of the depressed gland of paired cells. Instead, one circular cell,

TABLE III
Types of Trichomes and Glands in the Epidermis of Leaves of Genera of *Kuhniinae*

Name	Elevated above the surface					Depressed (i.e., punctate)								Depressed (but not punctate) secretory, uniseriate upper lower	
	Non-Glandular					Glandular									
	uniseriate, trichomes	uniseriate, capitate		Biseriate		Biseriate		Biseriate uniseriate		uniseriate		uniseriate in groups 1 to 4			
		upper	lower	upper	lower occasional on midrib	upper	lower	upper	lower	upper	lower	upper	lower	upper	lower
<i>Barroetia sessilifolia</i>	acuminate	×
<i>B. subuligera</i> var. <i>latisquama</i>	acuminate	Ditto	..	×
<i>B. laxiflora</i>	acuminate	Ditto	..	×
<i>B. brevipes</i>	acuminate	Ditto	..	×
<i>B. setosa</i>	acuminate	×
<i>B. glutinosa</i>	occasional	×	×	..	×
<i>Kuhnia eupatorioides</i>															
var. <i>pyramidalis</i>	nearly uniform	×	×	×	×
<i>K. eupatorioides</i>	attenuate towards														
var. <i>texana</i>	moniliform	×	×	×	×
<i>K. eupatorioides</i>															
var. <i>ozarkana</i>	ditto	×	×	×	×
<i>K. eupatorioides</i>															
var. <i>corymbulosa</i>	scabroid moniliform	×	×	×	×
<i>K. rosmarinifolia</i>	scabroid moniliform	×	×	×	×
<i>K. Mosieri</i>	nearly uniform	×	×	×	×
	attenuate														
<i>K. Schaffneri</i>	slightly moniliform	×	×	×	×
<i>K. oreithales</i>	scabroid moniliform	×	×	×	×
<i>K. leptophylla</i> var. <i>mexicana</i>	scabroid moniliform	×	×	×	×
<i>K. adenolepis</i>	very short	few	×
<i>Carphochaete Bigelovii</i>								×	×
<i>C. Wislizeni</i>		×	×
<i>C. Grahami</i>		×	×
<i>C. Schaffneri</i>		×	×
<i>Garberia heterophylla</i>		×	×
<i>Carphephorus tomentosus</i>	nearly uniform	×	×
<i>C. corymbosus</i>	nearly uniform	×	×
<i>C. pseudo-liatris</i>		×	×
<i>C. bellidifolius</i>		×	×	..	×	×
<i>Trilisa paniculata</i>		on upper cauline		×	×
<i>T. odoratissima</i>	nearly uniform	×	×
<i>T. carnosa</i>		×	×	occasional	

Types of trichomes as seen by microscopic examination of cleared leaves from annotated herbarium specimens at the Gray Herbarium. × indicates presence of.

larger than those accompanying the gland in *C. tomentosus*, appeared encircled by other leaf cells (Fig. 62). By focusing exactly on the surface, when stomata are visible, there was again a crater-like appearance in its place (Fig. 61). This gave confirmation that we were seeing the punctate equivalent for this species which had been characterized as "compressed dots," likely because they are smaller.

In *C. corymbosus* a similar arrangement of cells was characteristic but the center was usually composed of more cells. Figure 63 shows a frequent linear arrangement of three. When there were four such cells they conformed to the arrangement common to four spheres and the surrounding leaf cells had a circular form (Fig. 65). At the epidermal level with stomata visible, this also had the appearance characteristic of a punctate condition (Fig. 64).

In several preparations of *C. pseudo-liatris* the little evidence seen of glandular punctation indicated similarity to *C. corymbosus*.

Thus all four species are punctate, indicating the presence of a depressed gland or short glandular trichome. In *C. bellidifolius* there was a single or uniseriate condition while in *C. corymbosus* and *C. pseudo-liatris* there might be from one to a group of four of the uniseriate form. In *C. tomentosus* there was the familiar biseriate trichome accompanied by the uniseriate similar to *Garberia*.

From the time of Walter's original descriptions of the two species of *Anonymos* (see p. 91), *Trilisa paniculata* has been distinct from *T. odoratissima* in having a viscidly pubescent stem and upper cauline leaves. For this reason some of the latter as well as the lower glabrous leaves and in addition phyllaries of the inflorescence of this species were cleared. On both the phyllaries and small leaves, typical biseriate glandular trichomes were found (Fig. 66) very comparable to that figured for *Barroetia glutinosa*. Examination of either surface of a basal nearly glabrous leaf showed neither these glandular trichomes nor any trace of the typical depressed gland of two hemispherical cells. Instead rosette-like arrangements around a central cell were seen when viewed at a sub-surface focal level (Fig. 68). This figure does not appear unlike that of *Carphephorus bellidifolius* (see Fig. 62). However, when viewed at the surface the epidermal cells clearly adjoin the specialized cell (Fig. 67). This is confirmed in figure 69 of *T. odoratissima*, photographed at the surface and showing more clearly the secretory droplets. There is no indication of any marked depression in the epidermis of either species. This explains the inclusion of "not punctate with impressed dots" in the description of section *Trilisa* Cass. of *Liatris* by Torrey and Gray (l.c., p. 76) since they included only these two species at that time. At the surface the specialized cell hardly appears to be free from the surrounding cells of the epidermis. However, the fact that a central cell remains in focus from that layer through the next below, which shows distinct encircling cells, indicates that it is a secretory organ with a greater depth than one epidermal cell. None of these distinctive cells was found close to the thin margins of the leaves of these two species and so could not be studied laterally as was possible

in the preparations of *Garberia*, *Carphochaete* and *Carphephorus tomentosus*.

Trilisa odoratissima, commonly named the Vanilla Plant for the fragrance of the crushed leaves, has been used in the tobacco industry and is included in lists of drug plants. Therefore references ⁶ to the study of the structure of its leaves have been found in pharmaceutical journals.

Paschkis (1879) was probably the first to study the leaves microscopically. He described the upper and lower epidermis as including yellow spots, .015 mm. in size, which were surrounded by regular small epidermal cells. From tranverse sections he found these to be glands, in small clefts, consisting of a basal stalk cell wedged in between the two adjacent epidermal cells, and three to four additional ones. These rise just to the level of the other epidermal cells. He makes a point of their close envelopment by the thick cuticle of .008 mm., and as his figures show, the small depression in the epidermis is closely filled. This undoubtedly explains my failure to see any crater-like opening over the gland in surface view. The secretion, which is of such a pleasant odor when expressed, is due to cumarin. The diagram in Higley (1893) is very similar to the above description as is also the figure in Hanausek (1912) who called it a glandular trichome. From the relation to the leaf surface it has its origin as a depressed form. Among the multiple types found in these genera it is here termed uniseriate and not punctate.

In the leaves of the recently added third species, *T. carnosa*, the frequent appearance of a single central cell was again replaced by the two characteristic of the depressed biseriate gland (Fig. 71). By focusing on the surface when stomata are in view, the crater-like appearance of the punctate condition was again shown (Fig. 70). By carefully following around the margin of the leaf for any traces of the gland, only near the apex where it was thicker, a lateral view of one was seen (Fig. 72) giving evidence of at least an occasional uniseriate gland such as found in the previous genera. Certainly when examined microscopically the large basal leaf of *Trilisa carnosa* appears very different from those of its two congeners. However, in a similar way the biseriate glandular condition of one *Carphephorus* species, *C. tomentosus*, distinguished it from the other three.

No non-glandular trichomes were found on the lower leaves of the first two species and only an occasional short one near the petiole of *T. carnosa*. They were very similar to those of *Carphephorus* (Fig. 73).

SUMMARY (RE TRICHOMES)

With the help of table III, the observations on trichomes and glands on basal cauline leaves can be summarized.

1. Non-glandular, uniseriate trichomes are lacking in *Garberia* and *Carphochaete* and show very little variation within three genera, being

⁶ I am indebted to Prof. G. N. Hocking for these references.

acuminate in *Barroetea* and nearly uniform in *Carphephorus* and *Trilisa*. In *Kuhnia*, the largest of these genera, they may vary from being nearly filamentous or uniform to slightly tapering or attenuate. The thicker walled forms of the latter suggested the moniliform.

2. The elevated biseriate glandular trichome, comparable to that forming the indumentum in a number of species of *Brickellia*, was found only in one species of *Barroetea*.

3. The same structure sunken below the leaf surface, the depressed biseriate glandular trichome, was common to all the other species of *Barroetea* and to all species of *Kuhnia* and one of *Trilisa*.

4. In *Garberia* and one species of *Carphephorus* the same biseriate gland was accompanied in the depression by uniseriate but non-capitate glandular trichomes while in all four species of *Carphochaete* the same grouping occurred but the biseriate gland was different in form.

5. In the other species of *Carphephorus* uniseriate glandular trichomes were depressed either singly, in one species, or grouped, in two others.

6. The two other species of *Trilisa* were characterized by compact, depressed, uniseriate, secretory glands.

7. The small uniseriate capitate glands were observed only on species of *Kuhnia*.

8. As the punctate condition results from a depressed gland or glandular trichome it was found in all genera and all species except *Trilisa odoratissima* and *T. paniculata*.

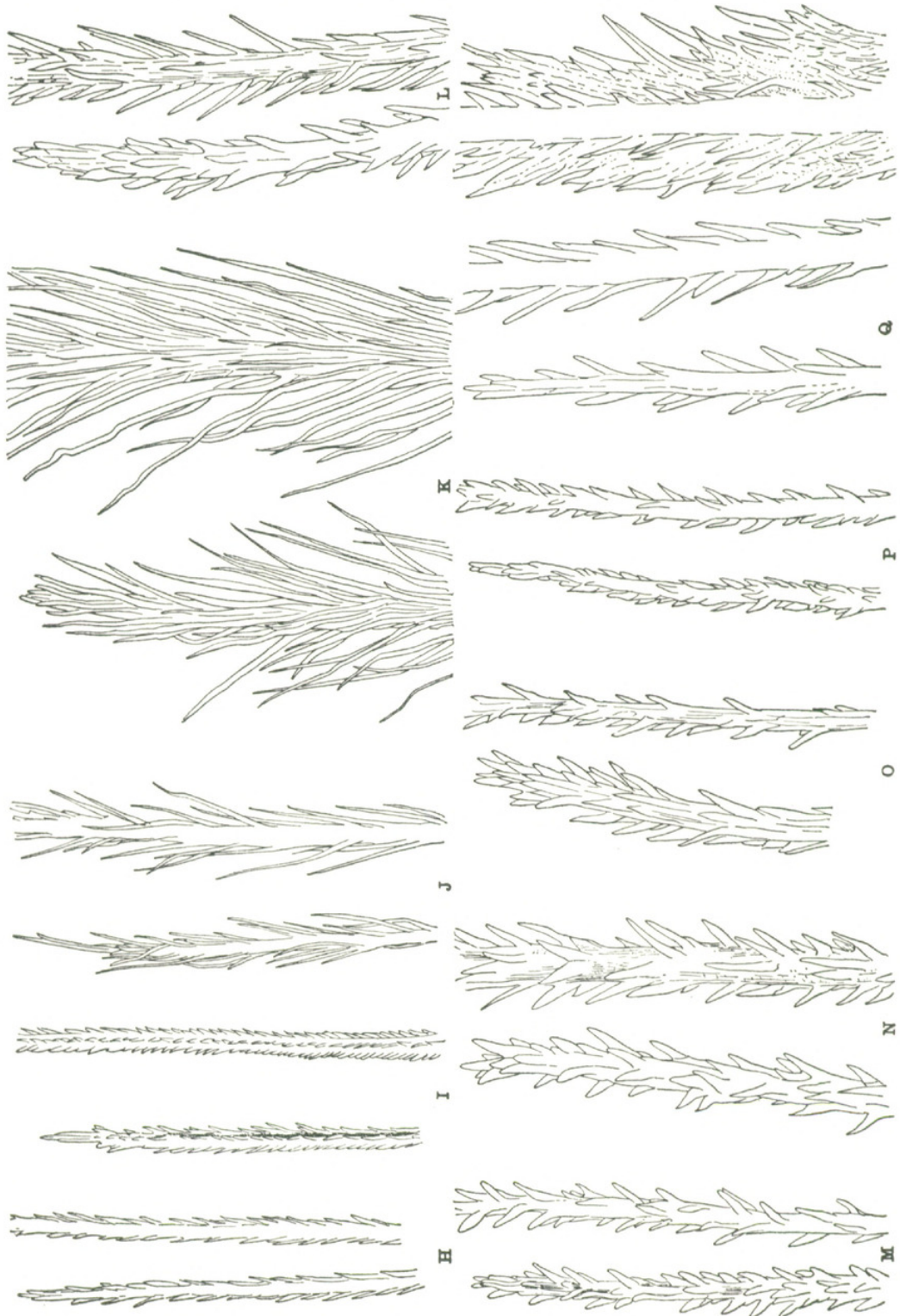
9. While in representatives of each genus, the depression contained the biseriate glandular trichomes, in three species of *Carphephorus* there were uniseriate trichomes singly or in groups. Thus the punctate condition accompanies different glandular contents in these genera.

A very reticulate pattern is evident in the distribution of the glandular trichomes. Though some form is found in every species, the same is not necessarily common to all those of any genus.

IV. Pappus

In the key to his treatment of this group of genera, Hoffmann (1890) made use of differences in the length of barbules of the pappus, besides the singular scale-like nature of that of *Carphochaete*. Thus *Kuhnia* was distinguished by plumose pappus from *Brickellia* and *Barroetea*. Illustrations of *Kuhnia eupatorioides* and *Brickellia californica* A. Gray (Fig. 81 B & C) were drawn to scale and indicate that for these two species, the barbules of the former are at least four times as long as the latter.

Robinson made little use of the pappus in the classification of *Brickellia* because he found that as well as in barbule-length, the number of setae varied widely from species to species. As pointed out (Gaiser 1953), Robinson did include its plumose nature under the sectional heading of *Steviastrum* and elsewhere only in the species-descriptions of *B. brachyphylla* and *B. monocephala*. Lactic acid mounts have confirmed a wide variation in the length of barbules of more than six times from these two



FIGURES OF PAPPI

which are the longest, to the shortest. Generally in any species the barbules become a little longer away from the tip of the seta. However, their arrangement in this genus seemed distinctive from that seen in *Liatris*. The generally flattened appearance along the greater length of the seta in many species resolved itself as a distichous arrangement of the barbules along the axis, as shown for *B. Nelsonii* Robinson (Fig. H). In other species, e.g., *B. Coulteri* where the barbules were only about half as long, their arrangement along the mid-portion of the seta approached the marginal appearance of the serrulate-paleaceous type of Small (1919, fig. 17H). However, the central axis in all the specimens seen did not broaden greatly, showing an increase in diameter of not more than twice with an elongation of barbules of three times or more than that amount. *Brickellia diffusa* and *B. filipes*, the two annuals, appeared exceptional in having the barbules arranged in three rows or tristichously. Always at the apices, the barely emerging barbules came in less regular arrangement and for this reason the illustrations include an apical as well as a median portion of a seta. In some species having short barbules, the irregularity persisted further along the axis.

Comparison of similar mounts of species of all of these genera here studied was therefore included. In contrast to the very large genus *Brickellia*, the smaller genera showed a greater uniformity in the nature of the pappus.

In *Barroetia* the length of the barbules varied little in the six species examined, being about equal to the shortest in *Brickellia*. Their arrangement also was uniform so that the seta had the appearance of a four-angled structure, due apparently to a tetrastichous arrangement of the barbules. In figure I, the row of barbules in the center below were not included. No exact equivalent for this was found in Small's figure 17 of pappus forms in the *Compositae*.

The plumose pappus of species of *Kuhnia* varied distinctly from *Barroetia* not only in the length of the barbules but also in the longer spaces between the points of their emergence from the axis and in their flat, distichous arrangement (Fig. J). In the latter they resembled *Brickellia*. In comparison with the plumose pappus of a species of *Liatris* (Fig. K) the barbules are slightly more slender and appear much less abundant because they do not extend from the mid-axis. Although the tips of emerging cells can be seen over the center region, they do not project laterally.

EXPLANATION OF FIGURES OF PAPPUS

All figures are of pappus from specimens in the Gray Herbarium and will be referred to by the collector's number, except Figs. M and N, *Trilisa paniculata* and *T. carnosa* which were of accessions studied cytologically, from Sebring, Highlands Co., Fla., Ray Garrett, Nov., 1948.

Fig. H. *Brickellia Nelsonii*, Nelson 4449. Fig. I. *Barroetia brevipes*, Nelson 1520. Fig. J. *Kuhnia adenolepis*, Pringle 2933. Fig. K. *Liatris squarrosa* var. *glabrata*, Rydberg 1505. Fig. L. *Liatris ligulistylis*, Nelson 1651. Fig. O. *Carphephorus tomentosus* var. *Walteri*, Fernald and Long 11173. Fig. P. *Garberia heterophylla*, Nuttall. Fig. Q. *Carpochaete Schaffneri*, Schaffner, 241.

The author is greatly indebted to Dr. B. G. L. Swamy for these figures, drawn $\times 45$.

This is indicated in another illustration of *Kuhnia eupatorioides* (Hoffmann 1889, Fig. 60D) where it can also be compared with *Liatris pycnostachya* Michx. (Fig. 60B), which has a barbellate pappus. At least five of the seven species of *Kuhnia* had barbules of approximately the same length, while those of *K. leptophylla* var. *maxima* and *K. adenolepis* were from half to three quarters as long. In length the barbules of this majority are somewhat intermediate between that of *Liatris squarrosa* (L.) Michx. var. *glabrata* (Rydb.) Gaiser, belonging to section *Euliatris* with plumose pappus and *L. ligulistylis* (Nels.) K. Sch., of section *Suprago* in which it is barbellate.

While it is difficult, when the barbules are as long and as abundant as in the plumose pappus of *L. squarrosa* (Fig. K) to illustrate their points of emergence even at the apex, when they are shorter as in the barbellate type of *L. ligulistylis* (Fig. L), their general disposition all around the axis is evident. This is similarly shown in the figure of *L. pycnostachya* of Hoffmann (l.c.). The projecting barbules are not limited to two sides and give no suggestion of a flattened appearance. They emerge somewhat spirally as shown also for this type (Small fig. 17D). This same arrangement was seen in the mounts of species of *Trilisa* (Figs. M & N), *Carphophorus* (Fig. O) and *Garberia* (Fig. P) all of which have barbellate pappi with barbules shorter than those of *Liatris ligulistylis* though equal to those of some other species, e.g., *L. gracilis* Pursh. Except for slight variations in the length of the barbules, the similarity of the pappus from genus to genus, as well as of the species within a genus was too great to allow any differences of classificatory value for *Trilisa*, *Carphophorus* and *Garberia*.

Of course, *Carphochaete* with its paleaceous pappus is quite distinctive from all the others (Fig. Q). It is dilated and scale-like at the bottom and for this reason the figure of this form includes a basal portion in addition to the median and apical. *Carphochaete Schaffneri*, the species illustrated, has the shortest free barbules at the apex of any of the four. The two other Mexican species are very similar to it, while in *C. Bigelovii* they are almost twice as long.

DISCUSSION

This study of six genera indicates a relationship with the two others previously studied, *Brickellia* and *Liatris*. With the exception of *Kanimia*, of which it has been impossible to include cytological examination and therefore discussion has been omitted, there is support for the taxonomic grouping of the subtribe *Kuhninae*. *Kanimia* will have to be compared cytologically with *Mikania*, the genus of the previous subtribe *Ageratinae*, with which it may well be a connecting link because of the several technical characters which the two genera have in common.

Furthermore, some points of relationship within the subtribe have been

added to those noted by earlier authors. These have served as a guide in the preparation of a key (see p. 124) which attempts to more nearly approach a natural classification. It has already been pointed out that when Cassini established each of the two new genera, *Carphephorus* and *Trilisa*, he placed them next to *Liatris*. Also because of the strong similarity of the flowers, Nuttall first described *Garberia* as a shrubby *Liatris*. With the additional evidence gained from the study of seedlings, trichomes, pappi, and chromosome numbers, it is proposed to refer to these four genera as Group I.

Likewise there is sufficient evidence to warrant a second grouping. When Gray (1879) established the genus *Barroetia*, he began the description "Involucrum (15-25) flores *Kuhniae* et *Brickelliae*." Hoffmann (1890) in his introduction to the subtribe also referred to *Barroetia* as approaching *Brickellia* in all else except the nature of the fruit. Robinson, who monographed both these genera, re-emphasized their strong similarity in habit and involucre, giving the flattened achene and sharply toothed leaves as the chief points of difference. To separate *Kuhnia* from *Brickellia*, the same author referred to its less strongly imbricated phyllaries and plumose pappus. For Shinnars (l.c.) these technical characters were not completely satisfactory, as was also an additional one, the nature of the root system. His conclusion was that though separately imperfect they were "strengthened by the obviously close relationship of the species of *Kuhnia* to each other, making a closeknit and recognizably distinct group." The association of these three genera will be continued as Group II.

Even in the seedling stage, at least as they grew in the greenhouse, differences were noted which distinguish the two groups. Those of species representing Group I, had a rosette of leaves which persisted without production of a flowering stem for a longer period than would necessarily be required for a biennial. In seedlings of *Garberia*, the one shrub of the group, this stage did not last as long and then a central leafy stem began to appear though it never flowered. However, species of Group II, including representatives of all three growth-forms, e.g., annual herb, perennial herb, and shrub, produced elongating central axes almost at once and these flowered before the end of a year. The seedlings of *Carphochaete Bigelovii* resembled the members of this latter group.

It was felt by Shinnars that in distinguishing *Kuhnia* undue reliance had been placed on the plumose pappus because it might not be the exclusive type of a genus, e.g., *Liatris*. From an examination of the pappus of these genera by lactic acid mounts, it was found that the arrangement of the barbules differed in these two. Further, though the barbules were longer in *Kuhnia* than in species of *Brickellia*, their lateral arrangement was more nearly like the distichous pattern found in the majority of the species of that genus. In two species of *Brickellia*, the three-sided or tristichous arrangement suggested a mid-way condition between that of the others and that typical of *Barroetia* where it was four-sided or tetra-

A GENERIC KEY TO THE KUHNIAEAE⁷

Anther apex having an ovate or oblong membranaceous appendage, achenes 10–20 (rarely 6–9) ribbed, phyllaries indefinite in number.

- (a) Pappus squamiform, dilated at the base, small shrubs, leaves opposite, young plants without rosettes, corolla rose-colored or white, chromosome number $n = 11$ **Carphochaete.**
- (a) Pappus setose.
 - (b) Phyllaries not conspicuously striate, leaves alternate, young plants with rosettes, corolla rose-colored, rarely white, barbules of pappus indefinitely arranged along the axis, chromosome number $n = 10$ **GROUP I**
 - (c) Woody shrubs, leaves alternate obovate, rosette-form not persisting long, phyllaries herbaceous, pappus barbellate **Garberia.**
 - (c) Perennial herbs, leaves linear to lanceolate, rosette-form persisting.
 - (d) Receptacle chaffy, phyllaries subequal pappus barbellate **Carphephorus.**
 - (d) Receptacle naked.
 - (e) Plants arising from thickened fibrous root-system, phyllaries 2–3 seriate pappus barbellate **Trilisa.**
 - (e) Plants arising from a corm-like or deeply penetrating root-system, phyllaries imbricate, herbaceous or colored or scarious, pappus barbellate or plumose **Liatris.**
 - (b) Phyllaries thin, striate, scarcely herbaceous, leaves alternate or opposite, young plants without rosettes, corolla ochroleucous to yellow, rarely rose-colored, barbules of pappus tend to be in linear arrangement along the axis, chromosome number $n = 9$ **GROUP II**
 - (f) Achenes prismatic or rounded.
 - (g) Phyllaries imbricate in several series, shrubs and perennial, rarely annual, herbs, pappus tends to be arranged distichously, rarely tristichously **Brickellia.**
 - (g) Phyllaries 2–3 seriate, perennial herbs from long conical roots, pappus plumose, barbules arranged distichously **Kuhnia.**
 - (f) Achenes compressed, annual and perennial herbs, barbules of pappus arranged tetrastichously **Barroetia.**

stichous. Thus in the pappus of the two smaller genera, in comparison with *Brickellia*, the arrangement of barbules alone differentiates *Barroetia*, and arrangement in addition to length, *Kuhnia*. While interspecifically *Brickellia* shows considerable variation in length of barbules, the species have the same basic linear arrangement which adds support to the placement of these three genera in one group. Similarly the four genera of Group I resemble one another in a less definite, somewhat spiral arrangement of the short barbules as is shown in figures of setose pappus.

In addition to the characters in prevalent use by taxonomists, it has been noticeable that in the *Eupatorieae*, it was necessary to pay consider-

⁷ Exclusive of *Kanimia*.

able attention to glandular structures. Robinson had established species as well as varieties on the presence of glands on the phyllaries, e.g., *Kuhnia adenolepis*, *Brickellia adenocarpa* var. *glandulipes*, etc. Likewise Brandegee (1908), who described two of the seven species of *Barroetia*, found *B. glutinosa* "differing from the others of the genus" because of the glandular leaves. Also, the common use in manuals, as well as descriptive treatises, of the term punctate and punctulate in some species, left open the question of general application for all of each genus. As explained under *Brickellia*, there was the need for interpretation of the overlapping use of the various terms applied to the depressed glands and the punctate condition. A more detailed comparison than had been possible by macroscopic examination, has helped to clarify.

From the reticulate pattern of glandular trichome distribution in six genera, summarized in Table III, and of *Brickellia* (Table III, Gaiser 1953), it was seen that some form was represented in each species. *Liatris* also can come in this inclusive statement. In the introduction to the treatment of that genus, it was stated that small sunken resinous glands were generally found in the leaves of species. Examination of cleared leaves of at least several species have given confirmation of the presence of the depressed biseriate trichome in connection with the punctate condition, as shown for *L. punctata* (Figs. 74, 75). A closer analysis of these tables gives indication of some intergeneric similarities.

In several species of *Brickellia*, the pubescence consisted almost entirely of the biseriate glandular trichome. That, of all the species of the other five genera examined, only puberulence of one species of *Barroetia* was composed of this form, is another point to add to the number in which that genus strongly resembles *Brickellia*. However, in the thick leaf of *Brickellia glutinosa*, a similar shorter biseriate trichome was shown to make up the depressed gland which gives a surface appearance of only two hemispherical cells as seen in species of *Kuhnia*, as well as the other species of *Barroetia* and *Brickellia*. The conclusion was reached from the range of variation seen in the extent to which the biseriate gland rose above the surface in different species of *Brickellia*, that the superficial glandular trichome was an elevated expression of the depressed gland. With the additional evidence in the fleshy leaves of the other genera of the heights it may attain and still remain macroscopically subsurface, there is no reason to doubt the generality of the statement. It is as understandable that the height of this small organ should vary in leaves of different species as that non-glandular trichomes should vary in length. More important than the variation from a depressed to an elevated condition may be the uniformity of this biseriate glandular organ. While these three genera of Group II have in common this single, similar content in the depressions in the epidermis of the leaf, the four genera of Group I have mixed contents of biseriate and uniseriate, grouped or single uniseriate, or single uniseriate without correlation to the punctate condition.

Examining this apparent diversity, there is a link with the previous three genera in *Garberia* and one species of *Carphephorus* having this

same biseriate form in the grouping along with the uniseriate. To these, the other *Carphephorus* are tied in having only uniseriate trichomes and *Carphochaete*, in having uniseriate with a different form of biseriate trichomes. Likewise in the two species of *Trilisa* the uniseriate trichome, though not accompanied by leaf punctation, appears similar in form to the depressed of *Carphephorus bellidifolius*, while *Trilisa carnososa* has the depressed biseriate resembling those of Group II. Thus while there is greater uniformity in the three genera of Group II, those of the other group seem to have a similitude in intra-generic variations. The particular form of the biseriate depressed gland of *Carphochaete* is individual among them. While its difference sets it apart from the genera of both groups, the true significance of this variation may be better understood when further knowledge is obtained of the forms in the many genera of other subtribes.

Further emphasis on relationships by glandular structures in these genera was found in the fact that there was a smaller, uniseriate, capitate trichome, which would not be readily observed without a microscope, along the veins and under surface of leaves of species of *Brickellia*. The only other genus of the subtribe studied to which it has been found common is *Kuhnia*. A slightly enlarged form apparently became the specialized type of *K. adenolepis*.

From a consideration of the non-glandular trichomes⁸ the largest genus has the widest variety. Comparable preparations of other genera contributed no distinctly new type, though in *Carphephorus*, *Trilisa*, and one species of *Kuhnia*, they were more nearly uniform in diameter and tapered a little less than the attenuate form shown for *Brickellia*. That all the types seen in that genus were not represented in the smaller genera could be explained probably by the smaller total of species. However, in *Brickellia* considerable variation was found in the size of chromosomes and in some subsections a correlation with the types of trichomes.

Cytological evidence has been obtained of some species of each of the genera of the *Kuhniinae* except *Kanimia*. Though incomplete, it supports the conclusions obtained from other sources. The basic number of chromosomes is 10 in the four genera of Group I, 9 in the three genera of Group II and 11 in *Carphochaete*. While no other genus of the subtribe has the same number as *Carphochaete*, the fact that the three basic numbers vary only by one, may be taken as further indication of a fairly close relationship of the members of this subtribe. This seems more significant when the number of species examined for the several genera to which the same number is common, totals forty-seven with $n = 9$, and thirty-nine with $n = 10$. Of course these two chromosome numbers are represented many times in genera of the Compositae as can be seen in Darlington and Ammal (1945, p. 220) where the basic numbers of the tribes of the Compositae are given. When turning to the reports for the tribe *Eupatorieae*, of which there have been few so far, the number 11 does not appear. The recent addition by

⁸ Gaiser (1946) in referring to pubescence as being of little use for species differentiation in *Liatis*, had not made microscopic analyses and there has not been time as yet to do so for that genus.

Grant (1953) of numbers for at least thirty-two species of *Eupatorium* from the temperate zone, give 10 and 17 as the lowest numbers, and 9 for one tropical species of *Vernonia*. The number 11 does not appear. This does present a challenge to investigate *Kanimia*. Also it raises the question of possibly finding the same number in a genus of another subtribe which perhaps may show further intertribal relationships with *Carphochaete*.

Of two species of *Mikania*, the genus of the previous subtribe *Ageratinae*, which has characters in common with *Kanimia*, it was possible to obtain some seeds (see Table I). The somatic chromosome number of three accessions of *Mikania scandens* Willd. and one of *M. cordifolia* (L.) Willd. was found to be $2n = 38$ (Fig. 21), which is quite different from that in any of the *Kuhniinae* investigated. Thus it seems quite probable that cytology might give the deciding evidence for or against the segregation of these two genera within the same subtribe.

No lower basic number was found among these genera than had been found in *Brickellia* and *Liatris*, or had been known previously among the *Eupatorieae*. These numbers, 9 and 10, are higher than have been found in a number of the other tribes of the Compositae, e.g., *Chichorieae* with 3, *Heliantheae* and *Astereae*, with 4, *Inuleae* and *Senecioneae* with 5, etc., but this may find its explanation in the few genera studied. Of the *Kuhniinae*, the genera of Group II with Mexico as their geographic center of distribution, have the lower number 9, while those of Group I, which are to the north of the Mexican boundary have 10. At this time there is no evidence of the origin of these divergent genetic lines. So far, the most northerly genus, *Liatris*, and in that only the *Punctatae* series, remains the only one in which polyploidy has been found. The tetraploid, *L. punctata*, reaches the most northerly latitude of any species of that or any other genus of the subtribe and so exemplifies Hägerup's theory. Since the same species reaches the southern extremity of the range for the genus along the mountains and the diploid is found on the plains in between it also provides an example of the polyploid occupying a wider area than the diploid. Müntzing (1936) believes that the extensive range is the combined result of polyploidy and polymorphism which has enabled adaptation to a wider range of habitats some of which may be unfavorable. Of all the other genera of the *Kuhniinae* few include any species of very extensive range and none which is exactly comparable to *L. punctata*. *Kuhnia eupatroioides* is the only polymorphic species of that genus, occurring in the central states from the northern to the southern boundaries. Michigan to Texas, and from Kentucky to Montana in the west. In his introduction, Robinson referred to *Brickellia grandiflora* and *B. californica* as the two most widely distributed and variable species. Both were found to be diploid in these studies which included a generous representation of thirteen accessions of the latter species. The former species like two others studied, *B. microphylla* and *B. oblongifolia* reach the northern limit for that genus in Washington State, but they also were diploid.

Excepting the species of *Brickellia* in Brazil, the most southerly one from Costa Rica, *B. argyrolepis*, was also a diploid. For the discussion

of the polyploid complex and tropical plants, as pointed out in the introduction, this genus is somewhat exceptional since though within the tropical latitudes the species live on higher altitudes. Of *Barroetia*, which at similar altitudes does not extend north of Mexico, neither of two species were polyploid. Also one species of *Kuhnia* from the southerly limits for that genus was diploid like the three congeners from the United States. The conclusion from this discussion still remains that for these closely related genera, as they have been represented from Central America northward, polyploidy was not prevalent and occurred only in the most northern genus of Group I. However, variation in the size of the chromosomes was noticeable and the karyotypes of the shorter units occurred only in the genera of the more southern group.

This does not mean that we should not expect polyploidy in genera of the tropics. For comparison, in the tropical genus *Anthurium*, of which thirty-seven of four hundred and eighty-six species (Engler 1905) were examined from plants as they grew mostly in the New York Botanical Garden, the situation is quite different. While many additional species have also been added since Engler's monograph of the genus, there is indication that polyploidy is not singular and occurs in species of both limited and wide distribution (Gaiser 1927). With 30 as the lowest somatic number found, at least two other numbers of a polyploid series were represented, two species with ca. 50 and three with ca. 60. The five polyploids were distributed to as many different sections, some nearly monotypic and others, the largest of the genus, e.g., *Urospadix* with ninety-five species. *Anthurium radicans* which belongs to the section, *Chamaerrepium*, comprising two species, is limited to east Brazil, and *A. Wallisii* of section *Polyneurium* of thirty species had been reported as having been collected only once in Colombia. In comparison with tetraploid *A. crassinervium*, from Venezuela, Colombia, Panama, and Tobago Island, nine other diploid species of the second largest section *Pachyneurium* with fifty species were found to be fairly restricted. Two species of section *Urospadix*, very similar to the polyploid *A. digitatum* from Venezuela and Tobago Island, had been collected from comparable areas. However, the fifth, *A. scandens*, is the most variable species in the genus, including five varieties and is known in one of its forms wherever Anthuriums grow. With even but fractional representation studied cytologically, all the complexities of polyploidy in percentage of incidence, different multiples of numbers and correlation of geographic distribution occur in that genus. Also, since Grant (l.c.) found fifteen polyploids (almost fifty percent) among the northern Eupatoriums examined, others might be expected among the many more tropical species of that large genus.

While the studies of *Liatris* were of a different time and were not all accompanied by exactly comparable photographic figures, chromosomes of the series *Spicatae* (Gaiser 1949) were considered to be the longest and to show greater variation than those of the series *Graminifoliae* (ibid. 1950a) and *Punctatae* (ibid. 1950b). Reference to the analysis of the morphology of the chromosomes of *L. pycnostachya* (1949 p. 127) gave

two pairs of long chromosomes in the karyotypes of 2 Lm, 2 Lst, 4 Mm, 4 Msm, 2 Mst, 4 Sm, 2 Sst. In the more recent comparisons the few species of the smaller genera of Group I varied little if at all from species to species. Also, the generally similar karyotypes of *Trilisa* and *Carphephorus*, including three pairs of long chromosomes, were found to vary somewhat from *Garberia* only in the types of the short and medium chromosomes. By comparison, *Carphochaete Bigelovii* was the only species to have a greater number of long chromosomes, four pairs rather than three.

Brickellia with the greatest number of species, had a great variation in chromosome sizes. Of thirty-four species in which the karyotypes were carefully analyzed, nine had only short and medium chromosomes, while in all the others there were also long ones. From the analyses of species of all these genera, only those of *Kuhnia* and *Barroetia* had such a karyotype of the two classes of shorter units. Thus not only have these three genera the same number in common but like a minority of the species of *Brickellia*, the species studied of the two smaller genera, have chromosomes representing an amount of chromatin less than is found in any of the others.

While too few species of *Barroetia* have been examined to draw conclusions regarding that genus, more than half of those of *Kuhnia*, including all but one variety of the polymorphic species *K. eupatorioides* have been included. The great homogeneity in the karyotype as well as chromosome number for all of these, shows a genetic basis for the close relationship of species of *Kuhnia* to each other, pointed out by Shinnars. By contrast the great diversity in chromosome length found in species of *Brickellia* accompanies a diversity of growth from woody shrubs to herbaceous annuals. None of the genera of Group I can compare with this. In *Liatris*, the largest of them, all the species are herbaceous perennials of a fairly similar type.

In the discussion of *Brickellia*, it was pointed out that a minority of the species examined, nine out of thirty-four, had a complement of shorter chromosomes. The species at the opposite extreme having the longest chromosomes, *B. monocephala* and *B. grandiflora*, were considered by reason of their modified underground structure, etc., as belonging to a specialized group of that genus. Others next to them, also having a greater total of chromatin material by reason of longer chromosomes than in the major group, included shrubs and herbs native to Costa Rica, Guatemala and Mexico. With the most woody species from Costa Rica among these, and the one annual examined, in the first group, there was some ground for considering that evolution had gone on in conjunction with reduction in chromatin in that genus. It is of interest therefore that the only other genus including annuals, *Barroetia*, also had short chromosomes in the two species examined. The genus includes no true shrubs and only one perennial variety of a species that has been described as being somewhat woody at the base. *Kuhnia*, too, is a genus consisting entirely of perennials and in it there was found a similar karyotype of the two shorter classes of chromosomes. While it is impossible to trace the steps of evolution from

one genus to another with certainty, it is indicated from the present evidence that the direction at least, was from *Brickellia* to the two other genera through some form, not necessarily extant today, having a complement of shorter chromosomes. Whether this happened in two successive steps or at one time remains a question also. The fact that both genera still include few and, for the most part, less variable species indicates that they are more recent than *Brickellia*. The repeated reference to the close similarity of *Barroetia* and *Brickellia*, especially as seen in both including annual species, suggests that there are possibly blocks of genes common to these two and this could have been one mutation. Also the indecision regarding basic differences between *Kuhnia* and *Brickellia* gives weight to the probability that this might have come as another step. The similarities of each of the two smaller genera to *Brickellia* appear closer than the interdependence of all three. Yet, as has been pointed out, from karyological studies, the six species of *Kuhnia* and two of *Barroetia* had karyotypes consistently represented by a pair of satellite chromosomes. Only in three, of about half of the species of *Brickellia* examined, was this type of chromosome regularly visible. Two of these were xerophytes, *B. incana* and *B. Greenei*, very restricted in distribution and remarkable for their large heads and seeds which are distinctive. The third was *B. Coulteri*, from Baja California, the only species examined of subsection *Brachiatae*. Most of the other seven species have been reported but once and from widely separated regions in Mexico and certainly should be compared cytologically. Without complete representation of a genus, the species not studied may be the ones which withhold the most significant truths. Perhaps the best that can be expected is to gain at least a point of vantage from which to envision the horizons for further efforts in a project.

It is difficult to extrapolate true phylogenetic relationships within Group I. In all four genera the karyotype is made up of more closely approximating units than were seen within the one genus *Brickellia*. Some variation has been reported in the species of five series of the genus *Liatris*⁹ but is not as striking as has been found in *Brickellia*. There was no evidence of marked morphological changes or reduction in size of the chromosomes. Also there is a general similarity of karyotype in the two smaller genera *Trilisa* and *Carphephorus*, including three pairs of long chromosomes. From these, *Garberia* was found to vary only in the medium and short chromosomes. Likewise, except for this one shrub *Garberia*, there is a greater homogeneity in the growth-form represented by each of the three genera. They are herbaceous perennials, provided with excellent modified storage rootstocks, mostly corm-like in *Liatris* and more tuberous in *Trilisa* and *Carphephorus*. From the discussion pertaining to growth-forms in *Brickellia*, just such as these were considered to represent a form of specialization and, these may very well be from a more primitive type now extinct. In the one living species of *Garberia* may lie

⁹ A chromosome list will shortly be forthcoming for species of the other series except the *Squarrosae*, which Dr. Pauline Snure will contribute.

the hint of another more woody progenitor for the other three genera.

The dissimilarity of the karyotype of *Carphochaete Bigelovii* to the species of Group I lay in the fact that it was the only species to have two additional chromosomes, four long chromosomes instead of three and three short ones rather than two. These factors contributed to its having the greatest content of chromatin in any of the genera studied. Comparison of it with the unusually long chromosomes of *Brickellia monocephala* (see Fig. 30, Gaiser 1953) is favorable except for the extra pair of chromosomes. The singularity of its karyotype, supported by the distinct form of the biseriate depressed gland and the individuality of its pappus, is sufficient to set it apart from the genera of both Groups I and II. Yet the prime reason for its inclusion in the subtribe *Kuhniinae*, the similarity of its anther and achenes, also gains weight in a proximal chromosome number and karyotype to that of Group I and in the actual presence of a depressed biseriate gland.

Without examining other genera having paleaceous pappi for comparison with *Carphochaete*, it would be premature to generalize on the evolution of pappus forms. That this small group of related genera may contribute to the overall study is indicated by the variety shown in the barbule-arrangement especially in the three genera of Group II. In *Barroetia* and *Kuhnia* there is near uniformity for the species of each genus, while in the more numerous species of *Brickellia* there is a variety of almost imperceptible changes. The general tendency is for a flattened, lateral arrangement of barbules in two rows. While the significance of their quadrate, linear arrangement in *Barroetia* is not clear, it may be but one of nature's experiments and so also the tristichous disposition in *Brickellia diffusa* and *B. filipes* may be a further shuffling of genes. However, since the latter species are annuals and since *Barroetia* is the only other genus including annual species, it would be in agreement with phylogenetic evidence to assume that the change in *Brickellia* was in the direction away from the flat or distichous arrangement. And if so, the latter referred to as bearing a marginal resemblance to the serrulate-paleaceous, could have been derived from the paleaceous or more foliar by reduction. This would be in agreement with the conception of Babcock and Stebbins (1937) for genera of the *Cichorieae* rather than the alternative hypothesis of Small (1916), that the paleaceous types result from the fusion of the simple scabroid setose which constitute the primitive type.

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