

ON THE GENERIC LIMITS OF ERIOPHYLLUM  
(COMPOSITAE) AND RELATED GENERA

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While recent authors largely agree in definitions of species referable to the genus *Eriophyllum* (Compositae, tribe Helenieae) or its neighboring genera, the generic disposition of these synonymy-laden species has been less satisfactory. The genera studied here correspond to those grouped by Rydberg (1915) in the subtribe Eriophyllanae. Since species of all of these genera have been subject to repeated reassignment, all of the taxa required examination before any resolution could be attempted.

The high degree of disagreement seems to stem from the small number of characters by which these genera may be recognized. In the instance of these, and many other highly reduced members of the Compositae, it may well be that relationships will never be properly understood, owing to the fact that only a limited number of characters has been left by evolution for the taxonomist to use. These characters have been taxed to the utmost by the systematist, and decisions have necessarily been arbitrary to a large extent. For this reason, the addition of a cytological character, chromosome number, and a review of morphological characters, particularly in the anatomical details which underlie them, seemed highly desirable.

## HISTORICAL SURVEY

A glance at the historical record will show that this subtribe is a particularly poorly understood one. The genus *Eriophyllum*, created by Lagasca for a perennial species, *E. staechadisfolium*, was adopted by Gray (1884) to include all the perennial species, though he first referred these species to *Bahia* (1876). Subsequent authors have placed all perennial species in *Eriophyllum*. The chief problem, then, was whether or not to refer annuals similar in aspect to the same generic concept. The genus *Actinolepis* had been set up by de Candolle to receive annuals possessing pappus (including species of *Baeria*), while he had erected the genus *Monolopia* for the epappose species. From the time of Gray on, however, persuasive similarities in aspect of some of the annuals to some of the perennials led to their inclusion in *Eriophyllum*, rather than *Actinolepis* or *Monolopia*, with the result of converting *Eriophyllum* into a capriciously heterogeneous assemblage poorly differentiated from incoherent groups of annual species left as outliers. Typical of the attitudes involved in this segregation is the description by Greene (1897) of *Eriophyllum* (now a *Pseudobahia*) *Heermanni* as "wholly an *Eriophyllum*, not only as to habit, but as to the character of the involucre and achenes," while two species of *Eriophyllum* later, he finds *E. ambiguum* (considered here as close to the perennials) "A plant with more the habit of a *Monolopia* than any of the foregoing."

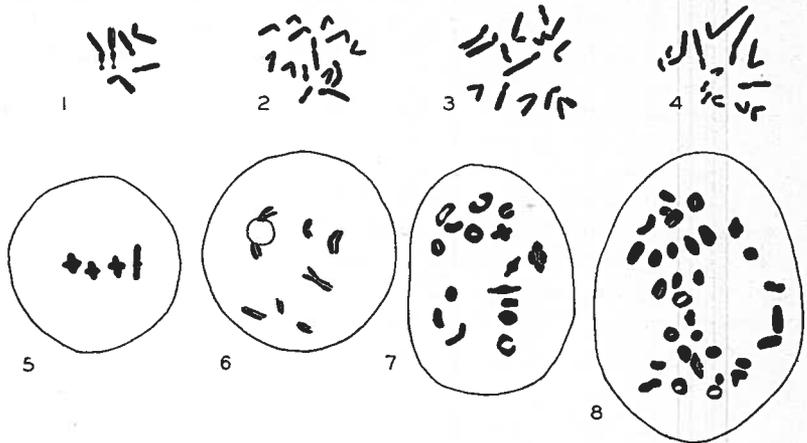
ERIOPHYLLUM. Gray (1884) added the species *ambiguum* to the perennials forming *Eriophyllum*, denoting all of these as "section *Trichophyllum*." Once this species had been allowed in *Eriophyllum*, however, logic demanded the admission of others, and he appended a "section *Actinolepis*" consisting of the entities *Eriophyllum nubigenum*, *E. multicaule*, *E. Pringlei*, *E. lanosum*, and *E. Wallacei*. Greene (1897) restored *Actinolepis* as a genus, but to the perennials of *Eriophyllum* he added *E. bahiaefolium* and *E. Heermannii*, formerly considered by Gray under *Monolopia*. Rydberg (1915) subtracted these last two species, but added *Eriophyllum nubigenum* (formerly in *Actinolepis*), *E. Congdonii*, a recently named species close to both *E. ambiguum* and *E. nubigenum*, and *E. minus*. This last species, known only from the type specimen, was formerly treated as *Monolopia minor*, though it is actually a *Baeria* (see below). Jepson (1925) restored the full complement of species used by Gray, without sectional distinctions, adding, however, *Eriophyllum Heermannii*, and a species for which Johnston (1923) created the monotypic genus *Eremonanus*, *E. mohavense*. Constance (1937) treated the genus similarly to Jepson, removing *Eriophyllum Heermannii* to *Monolopia* and recognizing *Eremonanus mohavense*.

ACTINOLEPIS. While Gray treated this group of pappose annuals as a genus in 1876, he considered it a section of *Eriophyllum* in 1884. Greene, reviving it as a genus, included *A. nubigena*, like Gray, though this species is close to *Eriophyllum ambiguum*, which both regarded as an *Eriophyllum*. Greene's *Actinolepis* agrees with Gray's. Rydberg performed a maximum of segregation among the annuals, leaving the contents of Gray's *Actinolepis* not included in *Eriophyllum* to be distributed among *Actinolepis* and a new genus, *Antheropeas*.

*Actinolepis* contained only *A. multicaulis* and *A. Pringlei*, while *Antheropeas* was created for a close pair of species, *A. lanosum* and *A. Wallacei*. Dubious of the segregation of numerous small genera, Jepson (1925) and Constance (1937) restored all the *Actinolepis* and *Antheropeas* species to *Eriophyllum* without sectional distinctions.

MONOLOPIA; PSEUDOBALIA. Gray, subsequent to his original treatment of *Monolopia* (1876) soon recognized (1884) that the contents of this epappose genus could be split into two sections. The tall, virgate species with subtire leaves, *M. major* and *M. gracilens*, became "section *Monolopia*," while the low, Eriophyllum-like plants with pinnatifid leaves, *M. bahiaefolium* and *M. Heermannii*, were "section *Pseudo-Bahia*." Influenced by the Eriophyllum-like qualities of the latter, Greene placed them in *Eriophyllum*, while Rydberg created a new genus, *Pseudobahia*, for them; both authors retained the remaining species in *Monolopia*. Jepson's treatment agrees with Greene's except for placing *Eriophyllum bahiaefolium* of Greene in *Monolopia* (without sections). Constance, though not dealing with this group directly, accepted Gray's treatment provisionally. It remained for Crum (1940) to offer a careful and detailed revision of

*Monolopia* (excluding *Pseudobahia*). The writer follows her treatment. Crum suggested that *Monolopia minor*, a species the type and only collection of which had apparently been seen by none of the authors mentioned, was actually a *Baeria*. Evidence accumulated by Mrs. Roxana S. Ferris confirms Miss Crum's opinion and in a recent paper (Ferris, 1955) she has made the necessary nomenclatural changes.



FIGS. 1-4. Metaphase of somatic divisions in root tips. 1, *Pseudobahia Heermannii*, Carlquist 302; 2, *Eriophyllum multicaule*, Carlquist 293; 3, *Eriophyllum ambiguum*, Carlquist 312; 4, *Eriophyllum lanatum* var. *arachnoideum*, Carlquist 336. FIGS. 5-8. Meiotic divisions of pollen mother cells. 5, first metaphase, *Pseudobahia bahiaefolia*, Bacigalupi & Carlquist 4014; 6, diakinesis, *Eriophyllum confertiflorum*, Carlquist 330; 7, first metaphase, *Eriophyllum confertiflorum*, Carlquist 325; 8, first metaphase, *Eriophyllum confertiflorum* var. *tanacetiflorum*, Carlquist 327. All  $\times 1200$ .

**SYNTRICHOPAPPUS.** The distinctive pappus of *S. Fremontii* prevented it from being confused with any of the other annuals, though Gray, who named it, realized it was closely related to them. Soon effacing his error of placing a new species, *S. Lemmonii* (thought epappose until now) in *Actinolepis*, Gray (1884), with remarkable intuition, designated it as the second species of *Syntrichopappus*. All subsequent authors have accepted this treatment.

The writer's disposition of these taxa is seen in the table of chromosome numbers, with the exception of *Eriophyllum mohavense*, which he regards as coordinate with *E. Pringlei*, and *E. nubigenum*, which is to be placed beside *E. ambiguum* and *E. Congdonii*.

#### METHODS

To obtain chromosome numbers, young heads, or root tips of plants grown from seed, were fixed in a Carnoy's solution (3 parts absolute ethyl alcohol: 1 part glacial acetic acid). To assure quick penetration, it

was necessary to break open the heads before placing them in the fluid, or aspirate them with a vacuum pump directly after immersion. The usual acetocarmine squash technique was employed for both pollen mother cells and root-tips. The designation "2n" indicates that the number was derived from a somatic division, while "n" denotes a count made from meiotic material. Voucher specimens were made at the same time buds were fixed, or, if plants grown from seed were used, specimens of these were prepared. A set of these specimens has been deposited in the Herbarium of the University of California at Berkeley, and replicates of most of these have been distributed to other herbaria.

Anatomical information was derived from both cleared and sectioned material. Mature flowers from the writer's collections preserved in Carnoy's fluid or from numerous herbarium specimens were cleared in 2.5 per cent aqueous NaOH, dehydrated, and stained in safranin. Heads of plants in the writer's collections fixed in Carnoy's fluid were also dehydrated by means of Johansen's tertiary butyl alcohol series, embedded in paraffin, sectioned, and stained with a safranin-fast green combination.

The writer wishes to express especial appreciation to Dr. Lincoln Constance, at whose suggestion the problem was undertaken, for valuable comment and advice. Thanks are due to him and to Dr. Herbert L. Mason, Dr. G. Ledyard Stebbins, Jr., and Miss Annetta Carter for reading the manuscript and offering suggestions. Acknowledgment is also extended to those who provided fixed material and specimens, and whose names appear among the collections listed in Table 1.

#### CYTOLOGY

The accompanying table shows that distinctive chromosome numbers characterize the various taxa. *Eriophyllum* sect. *Eriophyllum* contains diploids having  $n = 8$  as well as polyploid derivatives. While no diploids were found in *E. Jepsonii*, *E. latilobum*, *E. Nevinii*, or *E. staechadifolium*, both *E. confertiflorum* and *E. lanatum* contain diploids and tetraploids (figs. 4, 6, 7). No correlation was found in the relative size of parts of diploid versus polyploid plants. In fact, the polyploids showed more diminutive parts in most instances. Pollen-size differences likewise were negligible. A strong exception is the extremely robust octoploid *E. confertiflorum* var. *tanacetiflorum* (fig. 8).

The meagre coverage of the large *E. lanatum* complex suggests that both diploids and tetraploids may be found independently in at least two of the varieties. Since a better coverage of this group did not seem necessary for the purposes of generic definition, the nature and distribution of diploid and polyploid plants presents an interesting subject for further investigation. Likewise, the relative frequency of diploids and polyploids in *E. confertiflorum* remains to be studied.

The annuals of *Eriophyllum*, considered here as a section, *Actinolepis*, are characterized by a haploid chromosome number of 7 (figs. 2, 3). The

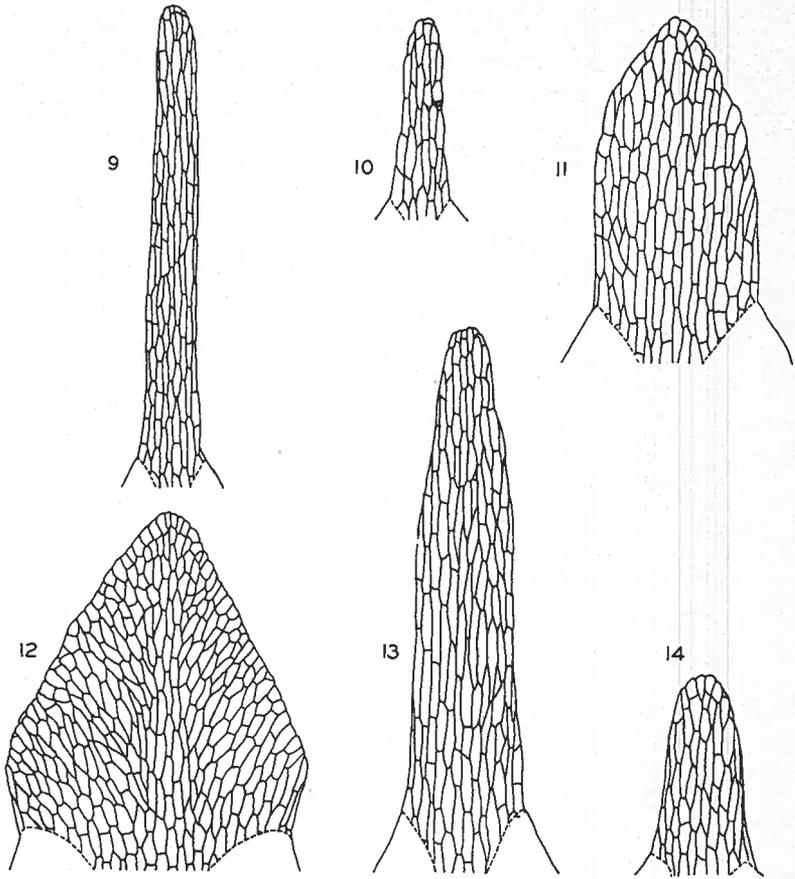
TABLE 1. CHROMOSOME NUMBERS

SPECIES	COLLECTION	APPROXIMATE LOCALITY	NUMBER
<i>Eriophyllum</i> Lagasca section <i>Eriophyllum</i> , sect. nov. (perennials)			
<i>E. confertiflorum</i> (DC.) Gray	<i>Carlquist 330</i>	Fort Tejon, Kern County*	n = 8
	<i>Carlquist 338</i>	Pasadena, Los Angeles County	n = 8
	<i>Carlquist 316</i>	Avalon, Los Angeles County	n = 16
	<i>Carlquist 318</i>	Arroyo del Puerto, Stanislaus County	n = 16
	<i>Carlquist 325</i>	Coulterville, Mariposa County	n = 16
	<i>Carlquist 334</i>	Midpines, Mariposa County	n = 16
<i>E. confertiflorum</i> (DC.) Gray var. <i>tanacetiflorum</i> (Greene) Jepson	<i>Carlquist 327</i>	Coulterville, Mariposa County	n = 32
<i>E. Jepsonii</i> Greene	<i>Carlquist 317</i>	Arroyo del Puerto, Stanislaus County	n = 16
<i>E. lanatum</i> (Pursh) Forbes var. <i>achillaeoides</i> (DC.) Jepson	<i>Chisaki 565</i>	Black Oak Villa, Lake County	n = 8
	<i>Post 105</i>	Alder Point, Mendocino County	n = 8
	<i>Balls &amp; Everett</i> 11 October 1952	Lava Beds, Modoc County	2n = 32
	<i>Gillett 266</i>	Lassen National Park, Shasta County	n = 16
	<i>Sweeney</i> 8 May 1953	Black Oak Villa, Lake County	n = 16
<i>E. lanatum</i> (Pursh) Forbes var. <i>arachnoideum</i> (F. & L.) Jepson	<i>Carlquist 336</i>	Little River, Mendocino County	2n = 16
	<i>Carlquist 324</i>	Coulterville, Mariposa County	n = 8
<i>E. lanatum</i> (Pursh) Forbes var. <i>grandiflorum</i> (Gray) Jepson	<i>Heckard &amp;</i> <i>Sweeney 341a</i>	Oroville, Butte County	n = 16
	<i>Carlquist 305</i>	San Mateo, San Mateo County	n = 16
<i>E. Nevini</i> Gray	<i>Carlquist 315</i>	Avalon, Los Angeles County	n = 16
<i>E. staechadifolium</i> Lagasca	<i>Carlquist 307</i>	Castroville, Monterey County	n = 16
	<i>Carlquist 309</i>	Piedras Blancas, San Luis Obispo County	n = 16
	<i>Carlquist 335</i>	Asilomar, Monterey County	n = 16

TABLE 1. CHROMOSOME NUMBERS (continued)

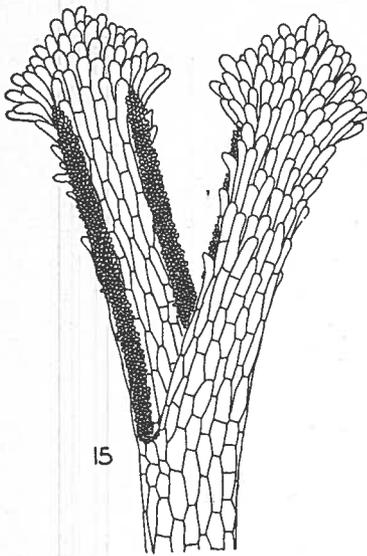
<i>Eriophyllum</i> Lagasca section <i>Actinolepis</i> Gray (annuals)			
<i>E. ambiguum</i> Gray	<i>Carlquist</i> 312	Hobo Hot Springs, Kern County	n = 7 2n = 14
	<i>Carlquist</i> 313	Red Rock Canyon, Kern County	n = 7
	<i>Carlquist</i> 329	Fort Tejon, Kern County	n = 7
	<i>Gillett</i> 411	Edison, Kern County	n = 7
	<i>Gillett</i> 417	Mt. Breckenridge, Kern County	n = 7
<i>E. Congdonii</i> Brandegee	<i>Carlquist</i> 333	El Portal, Mariposa County	n = 7
<i>E. multicaule</i> Gray	<i>Bacigalupi</i> 4117	Gonzales, San Benito County	n = 7
	<i>Carlquist</i> 293	Oceano, San Luis Obispo County	n = 7
<i>E. Pringlei</i> Gray	<i>Carlquist</i> 296	Boron, Kern County	n = 7
<i>Antheropeas</i> Rydberg			
<i>A. lanosum</i> (Gray) Rydberg	<i>Carlquist</i> 337	Las Vegas, Clark County, Nevada	n = 4
<i>Monolopia</i> DC.			
<i>M. gracilens</i> Gray	<i>Carlquist</i> 306	Hecker Pass, Santa Cruz County	n = 12
<i>M. lanceolata</i> Nutt.	<i>Carlquist</i> 289	Lost Hills, Kern County	n = 10
<i>M. major</i> DC.	<i>Carlquist</i> 285	Tracy, San Joaquin County	n = 12
<i>M. stricta</i> Crum	<i>Carlquist</i> 288	Lost Hills, Kern County	n = 10
<i>Pseudobahia</i> Rydberg			
<i>P. bahiaefolia</i> (Benth.) Rydberg	<i>Bacigalupi</i> & <i>Carlquist</i> 4014	North of Friant, Madera County	n = 4 n = 3
	<i>P. Heermannii</i> (Dur.) Rydberg	<i>Carlquist</i> 302	Coulterville, Mariposa County
<i>Carlquist</i> 304		Bagby, Mariposa County	n = 3
<i>P. Peirsonii</i> Munz	<i>Carlquist</i> 287	Ducor, Kern County	n = 8
<i>Syntrichopappus</i> Gray			
<i>S. Fremontii</i> Gray	<i>Carlquist</i> 301	Stoddard's Well, Kern County	n = 6
<i>S. Lemmonii</i> Gray	<i>Carlquist</i> 314	Cajon Pass, San Bernardino County	n = 7

\* Unless otherwise noted, all localities are in California.

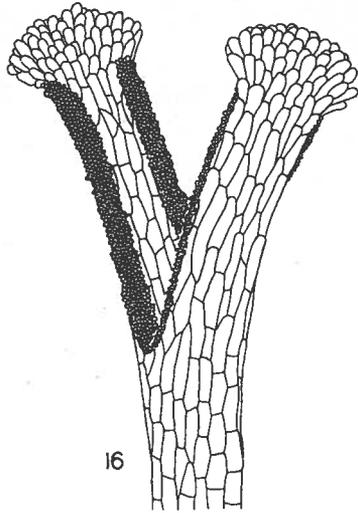


FIGS. 9-14. Stamen tips. 9, *Antheropeas lanosum*, Carlquist 337; 10, *Antheropeas Wallacei*, Carlquist 295; 11, *Eriophyllum Pringlei*, Carlquist 296; 12, *Pseudobahia Heermannii*, Carlquist 304; 13, *Syntrichopappus Fremontii*, Carlquist 301; 14, *Syntrichopappus Lemmonii*, Carlquist 314. All  $\times 90$ .

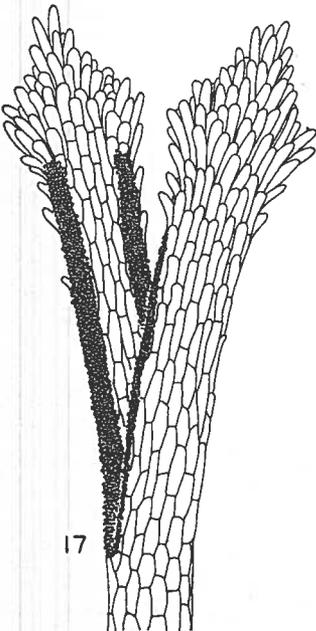
two species of *Antheropeas* show numbers of 5 and 4 respectively. Though similar in habit to the seven-paired *Eriophyllum ambiguum*, both *Pseudobahia bahiaefolia* and *P. Heermannii* have the distinctive numbers  $n = 4$  and  $n = 3$  respectively (figs. 1, 5). *Pseudobahia Peirsonii*, a robust weedy plant, is seen to have  $n = 8$ , which may be tetraploid in relation to the  $n = 4$  of this genus. The species of *Monolopia*, similar to *Pseudobahia Peirsonii* in habit, may also be polyploid, since their high chromosome numbers of ten and twelve suggest a derivative rather than a basic set. Further evidence would be needed to affirm this suggestion. The two species of the well-differentiated genus *Syntrichopappus* show  $n = 7$  and  $n = 6$  respectively.



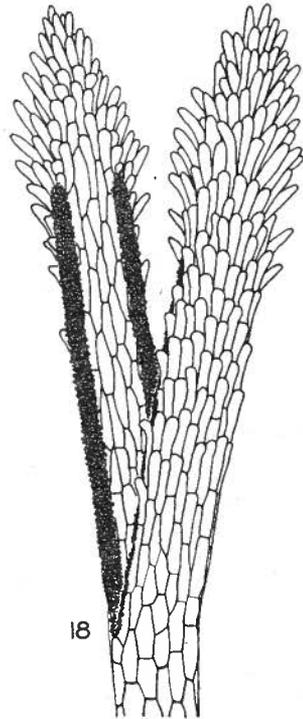
15



16



17



18

FIGS. 15-18. Upper portions of styles. 15, *Eriophyllum staechadifolium*, Carlquist 309; 16, *Eriophyllum multicaule*, Carlquist 293; 17, *Anthropeas Wallacei*, Carlquist 295; 18, *Syntrichopappus Fremontii*, Carlquist 301. All  $\times 85$ .

## MORPHOLOGICAL AND ANATOMICAL CHARACTERS

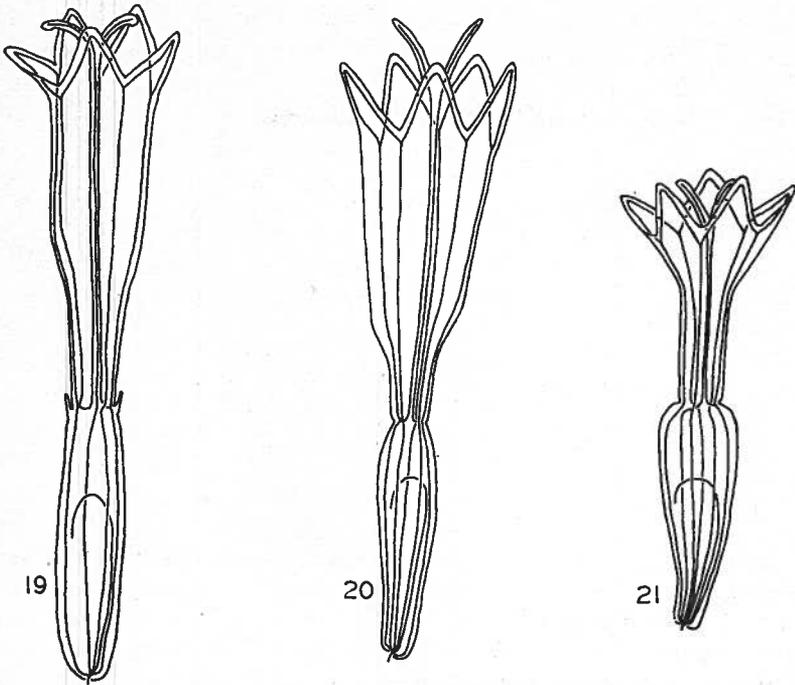
**STAMEN TIPS.** The terminal projection of the anther connective takes markedly different forms in the taxa considered here. The deltoid shape, widened above the base (fig. 12) is characteristic of many Helenieae, and is found throughout *Eriophyllum* sect. *Eriophyllum*, *Pseudobahia*, and *Monolopia*. Occasional specimens of *Eriophyllum* sect. *Eriophyllum* may exhibit deltoid tips tapered from the base. In *Eriophyllum* sect. *Actinolepis*, however, deltoid tips widened above the base may be found only in *E. ambiguum*, *E. Congdonii*, and *E. nubigenum*. In these three species, tips tapered from the base may also be found. In the remaining species of sect. *Actinolepis*, *E. multicaule*, *E. Pringlei*, and *E. mohavense*, tips tapered from the base are characteristic (fig. 11). These tips are relatively narrow and cuneate in some specimens of *E. multicaule*.

*Antheropeas*, on the contrary, shows conspicuously narrower subulate tips (figs. 9, 10), extremely long in *A. lanosum*. In a similar way, the species of *Syntrichopappus* exhibit quite attenuate stamen tips, varying from cuneate in *S. Lemmonii* (fig. 14) to lanceolate in *S. Fremontii* (fig. 13).

**STYLE TIPS.** The tips of the style-halves, frequently termed "style appendages," have long been recognized of diagnostic value. The predominant shape in the Helenieae is deltoid, tapering abruptly above a fringe of elongate hairs (fig. 15). Within both sections of *Eriophyllum* this shape is found to be characteristic, though some species show a very much blunted form. *E. multicaule* has nearly flattened tips (fig. 16), and is the most extreme expression of a blunted tip. *Pseudobahia* and *Monolopia* are found to have a deltoid tip such as shown in fig. 15. *Antheropeas*, on the other hand, has an appreciably more elongate tip, varying from narrowly deltoid to cuneate. Many style-tips of *A. lanosum* and *A. Wallacei* are much more attenuate than the one shown in fig. 17. In addition, in both species of *Antheropeas*, prominent elongate hairs terminate the style tips. The genus *Syntrichopappus* shows the most striking difference from the type found in *Eriophyllum*, the style tips being very much prolonged into a lanceolate form (fig. 18).

**FLORAL VENATION.** Though the floral vasculature of composites is highly stereotyped, certain differences may be found. The disk flowers alone serve for comparison here, since in the taxa studied, wide variation within a single population occurs in ray-flower venation. In the ray corolla, a series of veins runs the length of the corolla, forming interconnections at the tip. While characteristic patterns may be found, these are profoundly altered in depauperate or extremely robust plants. Some species, however, such as *Eriophyllum multicaule*, *E. nubigenum*, *E. Nevinii*, *Antheropeas lanosum* and *A. Wallacei*, show few if any interconnections between the veins at the tip of the ray.

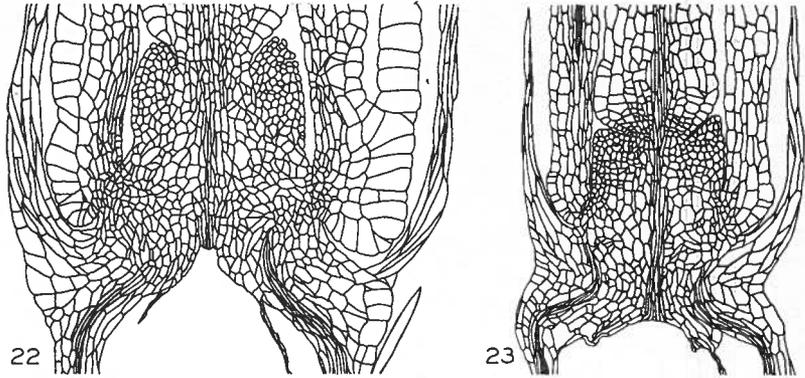
Disk flowers in the genera studied show an identical venation in the corolla, and either four, five, or six veins in the achene (figs. 19-21). An



FIGS. 19–21. Disk flowers, showing venation. 19, *Eriophyllum lanatum* var. *grandiflorum*, Carlquist 324; 20, *Syntrichopappus Lemmonii*, Carlquist 314; 21, *Eriophyllum mohavense*, Jepsen 17130a. All  $\times 14$ .

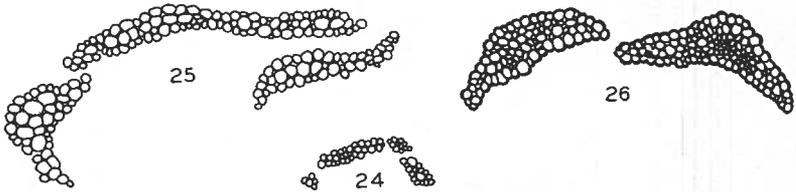
ovule trace and two style traces are always present; stamen traces, slightly better developed in the perennials of *Eriophyllum*, are usually rudimentary or absent. The species of *Eriophyllum* sect. *Eriophyllum* are characterized by four, sometimes five, achene-wall bundles (fig. 19), as are the members of the genus *Pseudobahia*. *Monolopia* and *Antheropeas* have four achene-wall bundles, while *Syntrichopappus* has five (fig. 20). In *Eriophyllum* sect. *Actinolepis*, *E. ambiguum*, *E. Congdonii*, *E. nubigenum*, and *E. multicaule* have four achene-wall bundles, while *E. Pringlei* and *mohavense* have five; occasionally six bundles appear in achenes of *E. mohavense* (fig. 21). The patterns of bundle interconnections are always the same in flowers having four, five, or six achene bundles respectively as shown (figs 19–21).

PAPPUS. Particular interest was focussed on finding if any constant characters besides annual versus perennial habit and 7 versus 8 (16, 32) chromosomes distinguish the annuals, sect. *Actinolepis*, of *Eriophyllum*, from the perennials, sect. *Eriophyllum*. Though differences largely of degree rather than of character may be found, such as the generally more indurate involucre bracts of the perennials, pappus structure offers a



FIGS. 22-23. Portions of longitudinal sections of achenes, showing pappus and basal portions of style and corolla in section; 22, *Eriophyllum Jepsonii*, Carlquist 317, palea at left seen in median section; 23, *Eriophyllum ambiguum*, Carlquist 313. Both  $\times 80$ .

more nearly discrete distinction. In longitudinal section, the pappus base is wider in the perennials (fig. 22), the outer epidermis of the pappus forming a nearly continuous line with that of the achene wall. In the annuals, the achene top is more constricted at the pappus base (fig. 23). This is probably associated with the tendency of the pappus to reflex more widely at maturity in the annuals. Difference may also be seen in the structure of pappus as seen in transection. The paleae of the pappus of annuals vary from simple (fig. 24) to moderately thick (fig. 25), the extremes being represented in these two figures. While pappus paleae such as shown in fig. 25 may also occur in the perennials, paleae with more numerous layers of cells, some of the internal cells smaller, can be found only in the perennial species (fig. 26).



FIGS. 24-26. Transections of pappus paleae. 24, *Eriophyllum multicaule*, Carlquist 293; 25, *Eriophyllum Congdonii*, Carlquist 333; 26, *Eriophyllum Jepsonii*, Carlquist 317. All  $\times 100$ .

The traditional differences in external structure of pappus are quite useful in differentiating the smaller genera. While at least a short crown of pappus or pappus-vestige is present in *Eriophyllum*, the genera *Mono-lopia* and *Pseudobahia* lack any such structure. *Syntrichopappus*, as the name implies, is characterized by a circle of numerous setae united at the

TABLE 2. COMPARISON OF ERIOPHYLLUM AND CLOSELY RELATED GENERA

	<i>Eriophyllum</i> section <i>Eriophyllum</i>	<i>Eriophyllum</i> section <i>Actimolepis</i>	<i>Antheropeas</i>	<i>Monolopia</i>	<i>Pseudobakia</i>	<i>Syntrichopappus</i>
Habit	perennial	annual	annual	annual	annual	annual
Leaves	pinnatifid to nearly entire	lobed (entire in a few plants)	entire to toothed	entire to toothed	pinnatifid, bipinnatifid	lobed or entire
Chromosome no.	n = 8, 16, 32	n = 7	n = 5, 4	n = 12, 10	n = 4, 3, 8	n = 7, 6
Stamen tips	deltoid, widened above base	deltoid, widened above or tapering from base	subulate	deltoid, widened above base	deltoid, widened above base	cuneate to lanceolate
Style tips	deltoid to blunt	deltoid to blunt	cuneate	deltoid	deltoid	lanceolate
Bundles in disk achene	4, 5	4, 5, 6 (depending on species)	4	4	4, 5	5
Pappus	short paleae	short paleae to a crown	paleae	entirely absent	entirely absent	ring of many setae or absent
Corolla hairs	glandular, scattered along tube and throat	glandular, scattered along tube and throat	glandular, scattered along tube and throat	glandular, scattered, plus non-glandular hairs at lobe-tips	glandular, grouped in a ring at base of throat	glandular, scattered along tube and throat

base. While all authors have considered *S. Lemmonii* epappose, populations of this plant contain a few individuals bearing the pappus typical of *S. Fremontii*, though the bristles are shorter and less numerous than in *S. Fremontii*. Despite the prolongation of four or five of the pappus paleae of *Antheropeas lanosum* into setae, there is no fundamental difference between the genus *Antheropeas* and the annuals of *Eriophyllum* in pappus structure.

#### DISCUSSION

The various features already discussed as well as some additional points are summarized in Table 2. It will be seen that in addition to the chromosome number, other differences may be found to support the division of genera which is proposed here. Though the chromosomes of *Eriophyllum mohavense* and *E. nubigenum* have not been seen, other features of these rarities, which may now be extinct, make certain their placement in *Eriophyllum* sect. *Actinolepis*. *Eriophyllum nubigenum* appears to be an alpine extreme closely connected with *E. ambiguum* and *E. Congdonii*. *Eriophyllum mohavense*, despite its distinctive heads consisting of four (or three) flowers grouped around a short central projection of the receptacle, is closely related to *E. Pringlei*. These two species agree in their discoid heads, the numerous short pappus paleae, the short, broadly funnelform corolla, morphology of stamen and style tips, etc. The writer does not agree with Johnston (1923) that *Eriophyllum (Eremonanus) mohavense* must be considered in conjunction with the monotypic genus *Dimeresia* Gray. *Dimeresia* seems only superficially similar by virtue of its two-flowered heads, while the larger flowers (larger than any of the above, with the exception of a few perennials of *Eriophyllum*), the prominent setose pappus, curiously involute at the base, the essentially opposite leaves, lacking any indications of lobes or teeth, all seem to remove it from consideration with any of the Eriophyllanae, including *Syntrichopappus*. Although Gray originally placed *Dimeresia* in the Inuleae, the treatment of Cronquist (1955), who includes this genus in the Senecioneae, seems the most acceptable.

The annuals of *Eriophyllum*, despite their differences from the perennials in chromosome number, are structurally close to them in such species as *E. Congdonii*, so that it has not seemed feasible to segregate the diverse contents of this group into still another genus. Consequently, recognition of them as a section of *Eriophyllum* seems most logical. *Antheropeas*, however, which is often accepted as part of *Eriophyllum*, seems to merit separation from the annuals by virtue of its lower chromosome numbers and notably different stamen-apex and style-tip structures. Likewise, the anomalous chromosome numbers of *Pseudobahia* reinforce the lack of pappus and aggregation of corolla hairs in distinguishing it from *Eriophyllum*. Chromosome numbers, habit, leaf characters, and corolla hairs in turn separate *Pseudobahia* from *Monolopia*.

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## LITERATURE CITED

- CONSTANCE, L. 1937. A systematic study of the genus *Eriophyllum* Lag. Univ. Calif. Publ. Bot. 18:69-136.
- CRONQUIST, A. 1955. Phylogeny and taxonomy of the Compositae. Am. Midl. Nat. 53:478-511.
- CRUM, ETHEL. 1940. A revision of the genus *Monolopia*. Madroño 5:250-270.
- FERRIS, ROXANA. 1955. The identity of *Monolopia minor* DC. Contr. Dudley Herb. 4:331-334.
- GRAY, A. 1884. Synoptical Flora of North America. Vol. I, Part II. New York.
- GREENE, E. L. 1897. Flora Franciscana, Vol. IV. San Francisco.
- JEPSON, W. L. 1925. A manual of the flowering plants of California. Berkeley.
- JOHNSTON, I. M. 1923. Diagnoses and notes relating to the spermatophytes, chiefly of North America. Contr. Gray Herb. 68:80-104.
- MUNZ, P. A. 1949. California miscellany—I. El Aliso 2:77-86.
- RYDBERG, P. A. 1915. Eriophyllanae, in North American Flora 34:81-100 (*Monolopia* by H. M. Hall).