9-30-1976

A revision of *Eriogonum* (Polygonaceae) subgenus Pterogonum

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A REVISION OF ERIOGONUM (POLYGONACEAE) SUBGENUS PTEROGONUM[1]

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ABSTRACT.— This revision discusses the 10 species of *Eriogonum* assigned to the subgenus Pterogonum. Six of the species are essentially restricted to northern Mexico; two additional species, *E. hemipterum* and *E. nealleyi*, are found primarily in Texas; and the remaining two, *E. hieracifolium* and *E. alatum*, are the most widespread species of the subgenus being found mainly in the United States and just barely entering Mexico. The subgenus is characterized by the broad, often winged or ribbed achenes, and the generally erect habit of the stems of these perennial herbs. Three new species, *E. fimbriatum*, *E. viscanum*, and *E. clivosum*, are described. They are related to *E. ciliatum* and are found in the desert foothills of north central Mexico. Two new varieties of *E. atrorubens* are proposed. One, var. *nemorosum*, is restricted to the high mountains of the Sierra Madre Occidental in northern Durango and southern Chihuahua, while the second, var. *auritulum*, is a plant of the Sierra Madre Oriental of Coahuila and Nuevo León. The subgenus is divided into four sections, two of which, Peregrina and Astra, are new. Cytological information is given for nearly all taxa and shows the majority of species to have a haploid number of 20. *Eriogonum atrorubens* var. *intonsum* is a polyploid with $n=40$, and *E. greggii* is the most unusual with a haploid number of 16. Each species is described in detail, discussed, and illustrated. Distribution maps are given noting the known locations for each taxon.

The genus *Eriogonum* Michx. (Polygonaceae) is comprised of nearly 250 species and, perhaps, 160 varieties. It is found primarily in western North America as far north as Alaska and southward as far as north central Mexico. It occurs in numerous ecological situations, ranging from desert to alpine life zones. The only recent published monograph is Stokes' (1936), and because there are no keys and only brief descriptions, it is impractical to use. One of us (Reveal) has begun a study of the genus at all levels, and this joint effort is a part of that study as well as portions of our respective doctoral dissertations.

During the formative years of this research (1961 to 1969), each of us worked on the subgenus Pterogonum (H. Gross) Reveal with varying degrees of concentration. For Hess (1967), this subgenus represented the subject of his dissertation, in which he devoted most of his efforts on field studies and an evaluation of those species found mainly in the United States. Reveal (1969b) reviewed the entire genus for his dissertation, and in his treatment of Pterogonum, he leaned heavily upon the work of Hess (1967), and, too, worked mainly with the United States species. Since 1971, however, we have worked together on this revision and have concentrated our efforts in northern Mexico. Herbarium studies have been intensively conducted in numerous institutions both in North America and in western Europe. As a result of the present studies, we have seen nearly all entities of the subgenus in the field, have reviewed the vast majority of extant collections, and can now report chromosome numbers for nearly all taxa of Pterogonum.

Herbarium citations which are included in this revision follow the suggested abbreviations for major herbaria as proposed by Holmgren and Keuken (1974).

Our subgenus Pterogonum is here defined to include those species of *Eriogonum* which are upright herbaceous perennials with leaves covered by pilose to strigose hairs, non-jointed stems arising singly from each caudex, with or without cauline leaves or foliaceous bracts, solitary involucres which are often pedunculated, and large, strongly angled or even winged achenes with a straight embryo. We recognize ten species and eight varieties among four sections, the

[1]Submitted, in part, as partial fulfillment for the doctoral degrees from the University of Oklahoma (Hess) and Brigham Young University (Reveal). Support of the current research has been via National Science Foundation grants GB-22645 and BMS75-13063 to Reveal. The publication support has been provided by The Morton Arboretum and the University of Maryland Agriculture Experiment Station (Scientific Article No. A2245, Contribution No. 5235). We are grateful for the assistance and patience given us by our major professors, George J. Goodman and Stanley L. Welsh, and the critical suggestions on this manuscript by Marion T. Hall. Figures 34 and 35 were drawn by the staff artist of The Morton Arboretum, Nancy Hart. All other plant illustrations were drawn by Dolly Barker Woll of Maryland. Lastly, we are grateful for having known and been inspired by the late Lloyd Shinners of Southern Methodist University. This paper is presented in his memory.

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majority of which occur in northern Mexico and southwestern United States.

History and Interpretations

Originally, Bentham (1856) placed the members of *Eriogonum* with winged achenes, *E. alatum* Torr. in Sitgr., *E. hieracifolium* Benth. in DC., and E. *atrorubens* Engelm. in Wisliz., in a section he called Alata. Torrey and Gray (1870) treated these species similarly but, in addition, placed the related species *E. ciliatum* Torr. ex Benth. in DC, in section Pedunculata and *E. greggii* Torr. & Gray in section Pseudo-stipulata. These latter are now interpreted by Reveal (1969a) as part of the subgenus Ganysma (S. Wats.) Greene. Watson (1877) did not recognize section Alata but instead included *E. alatum* and *E. hieracifolium* in his larger section, Eueriogonum, and placed *E. atrorubens* with *E. ciliatum* and *E. greggii* in section Ganysma. Gross (1913) interpreted the Alata group (sensu Bentham) as generically distinct from *Eriogonum* and proposed the new genus *Pterogonum* H. Gross to include them. Stokes (1936) believed that this genus was not that distinct and included *E. alatum*, *E. hieracifolium*, *E. artorubens*, *E. ciliatum*, and *E. greggii* along with *E. rupestre* S. Stokes, *E. hemipterum* (Torr. & Gray) S. Stokes, *E. nealleyi* Coult., and *E. inflatum* Torr. & Frém. as Section 1A of her treatment of *Eriogonum*. Except for *E. inflatum* we consider the species of her Section 1A closely related and include them in our concept of the subgenus Pterogonum.

Gross's generic interpretation of *Eriogonum alatum*, *E. hieracifolium*, and *E. atrorubens* has been endorsed by Roberty and Vautier (1964). Their treatment made no mention of any other species in Stokes's Section 1A except for *E. ciliatum*, which was placed in *Eriogonum* and not *Pterogonum*. They did concede, however, that *E. ciliatum* was closely related to *Pterogonum*. There is litle doubt that *E. ciliatum*, *E. greggii*, *E. hemipterum*, and *E. nealleyi* belong in the subgenus Pterogonum as pointed out by Reveal (1969a), and the close relationship between *E. rupestre* and *E. atrorubens* has been repeatedly expressed by several workers (Johnston 1944; Hess 1967; Reveal 1967a). We believe that Roberty and Vautier, by not examining all the members of Stokes's Section 1A, overlooked the strength of the relationship between the two genera *Eriogonum* and *Pterogonum*.

The major characteristics linking the members of our subgenus Pterogonum are the perennial nature of the plants with a single stem arising from the caudex, pedunculate involucres, non-stipitate flowers, and a straight embryo. The precise delimitation of the sections within the subgenus has been debated between us, and the differences of opinion all have some justification. Reveal (1969a, 1969b) recognized two sections in his early versions, while Hess (1967) felt that at least three were more reasonable. As a result of our field and cytological work, we now propose four sections within the subgenus. Included in section Pterogonum is the subsection Pterogonum, which comprises the type for the subgenus, *Eriogonum atrorubens*, and its several varieties, and the other subsection, Adenogonum Hess & Reveal, with *E. ciliatum*, *E. clivosum* Hess & Reveal, *E. viscanum* Hess & Reveal, and *E. fimbriatum* Hess & Reveal, of which the last three named species are new. After considerable debate, we have placed *E. greggii* in its own section, Peregrina Hess & Reveal, acknowledging its close superficial relationship with members of the subsection Adenogonum. The other newly proposed section, Astra Hess & Reveal, contains *E. hieracifolium*, *E. hemipterum*, and *E. nealleyi*. Only *E. alatum* is included in Bentham's old section, Alata.

Cytological Studies

Cytologically, the genus *Eriogonum* has become better understood as more counts have been made and recorded. Reveal has determined numbers for numerous species, and we now have several counts in nearly all subgenera. Since the first reported counts by Stebbins (1942), a number of papers (far too numerous to cite here) have appeared with chromosome numbers for various species of the genus. The counts found in *Eriogonum* vary as follows: $2n = 18, 22, 24, 32, 34, 36, 38, 40$ and 80. Stokes and Stebbins (1955) suggested the basic chromosome number to be $x = 10$, and the more recent counts have tended to support this. While the base number of 10 has not been found, the many polyploids based on a multiple

of 10 would imply this number. Aneuploidy, which resulted in $n = 9$ or 11 or others, certainly may have occurred. This, in conjunction with other kinds of polyploidy such as autopolyploidy and allopolyploidy, may have resulted in various polyploid chromosome numbers. Stokes and Stebbins indicated that if this interpretation is correct, then hybridization has played an important role in the evolution of the present-day species of *Eriogonum*.

In our studies of Pterogonum, cytological material was obtained from buds collected in the field by the authors either individually or together. Reveal's method of preparing smears has already been reported (Reveal 1968a; Reveal & Styer 1973), and Hess followed the method described in the second of these two papers. The voucher specimens for Reveal's early counts of members of Pterogonum (Reveal 1967b, 1968b) are at Utah State University, while those documenting counts since 1969 (either alone or with Hess) are deposited at the Smithsonian Institution. The vouchers for Hess's counts are at the University of Oklahoma.

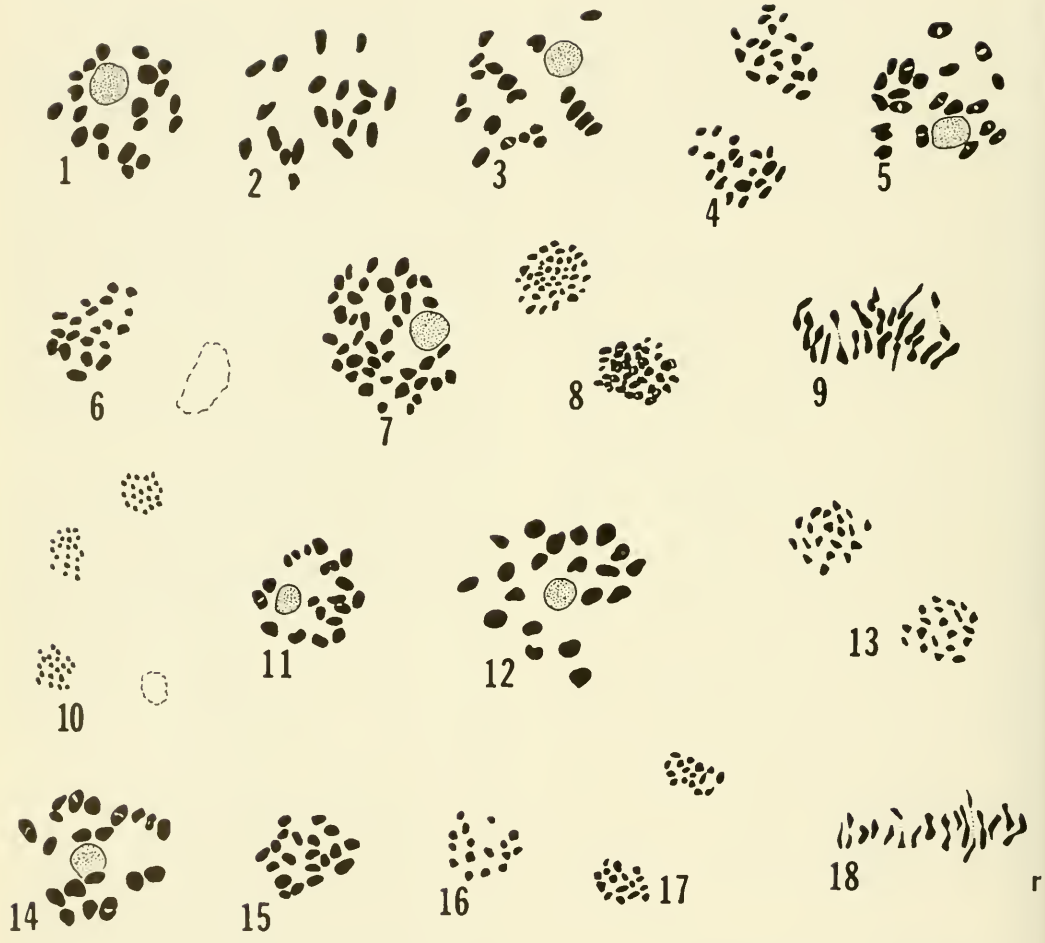
A summary of the chromosome counts and their vouchers is given in Table 1. See Figures 1-33 for illustrations.

In the subsection Pterogonum (H. Gross) Hess & Reveal, all but one variety counted of *Eriogonum atrorubens* have the microsporocytes with $2n = 40$. In var. *intonsum* Reveal, the number is $2n = 80$. In the subsection Adenogonum, no bud material was available for *E. viscanum*, but *E. clivosum*, *E. fimbriatum*, and *E. ciliatum* have meiotic chromosome counts of $2n = 40$. In section Peregrina, its only species, *E. greggii*, has a count of $2n = 32$. In the sections Astra and Alata, all species and varieties showed the usual counts of $2n = 40$, except *E. hemipterum* var. *griseum* I. M. Johnst., for which we had no bud material.

As is evident, all of the species in the subgenus Pterogonum whose chromosomes have been counted show $2n = 40$, with the exception of *Eriogonum atrorubens* var. *intonsum* ($2n = 80$) and *E. greggii*

TABLE 1. Chromosome numbers from microsporocytes and vouchers in *Eriogonum* subg. Pterogonum.

Taxon	Number	Voucher
Sect. *Pterogonum*		
E. atrorubens	20	*Reveal et al. 2757;*
var. *atrorubens*	20	*Reveal et al. 2651; Reveal & Hess 3149.*
var. *auritulum*	20	*Reveal et al. 2697.*
var. *pseudociliatum*	40	*Reveal et al. 2733; Reveal & Hess 3013;*
var. *intonsum*		*Reveal & Hess 3126.*
var. *nemorosum*	20	*Reveal et al. 2737; Reveal & Hess 3105; Reveal & Hess 3124.*
E. ciliatum	20	*Reveal et al. 2612; Reveal et al. 2616.*
E. fimbriatum	20	*Reveal & Hess 3141.*
E. clivosum	20	*Reveal et al. 2664; Reveal & Hess 3143.*
Sect. *Peregrina*		
E. greggii	16	*Reveal et al. 2607; Reveal & Atwood 3382.*
Sect. *Astra*		
E. hieracifolium	20	*Hess 886; Reveal & Davidse 902; Reveal & Davidse 913; Reveal & Davidse 914.*
E. hemipterum		
var. *hemipterum*	20	*Hess 799; Reveal & Davidse 906.*
E. nealleyi	20	*Hess 876; Reveal & Davidse 900; Reveal & Davidse 901.*
Sect. *Alata*		
E. alatum		
var. *alatum*	20	*Holmgren et al. 1961; Holmgren et al. 2070; Hess 353; Reveal & Reveal 2772; Reveal & Reveal 2944.*
var. *mogollense*	20	*Hess 761; Reveal & Reveal 3225; Reveal & Reveal 3229.*
var. *glabriusculum*	20	*Hess 506; Reveal & Davidse 879; Reveal & Davidse 880.*



Figs. 1-18.— Camera lucida drawings of chromosomes from microsporocytes of *Eriogonum* subgenus Pterogonum, sections Petrogonum and Peregrina. Fig. 1. *E. atrorubens* var. *atrorubens*, $n=20$, diakinesis; *Reveal et al. 2757*. Fig. 2 *E. atrorubens* var. *atrorubens*, $n=20$, metaphase I; *Reveal et al. 2757*. Fig. 3. *E. atrorubens* var. *auritulum*, $n=20$, diakinesis; *Reveal et al. 2651*. Fig. 4. *E. atrorubens* var. *auritulum*, $n=20$, anaphase I; *Reveal & Hess 3149*. Fig. 5. *E. atrorubens* var. *pseudociliatum*, $n=20$, diakinesis; *Reveal et al. 2697*. Fig. 6. *E. atrorubens* var. *pseudociliatum*, $n=20$, telophase I, with only one complement shown; *Reveal et al. 2697*. Fig. 7. *E. atrorubens* var. *intonsum*, $n=40$, telophase I; *Reveal & Hess 3013*. Fig. 9. *E. atrorubens* var. *nemorosum*, $n=20$, metaphase I; *Reveal et al. 2737*. Fig. 10. *E. atrorubens* var. *nemorosum*, $n=20$, telophase II, with three of the complements shown; *Reveal et al. 2737*. Fig. 11. *E. ciliatum*, $n=20$, diakinesis; *Reveal et al. 2612*. Fig. 12. *E. ciliatum*, $n=20$, diakinesis; *Reveal et al. 2616*. Fig. 13. *E. fimbriatum*, $n=20$, telophase I; *Reveal & Hess 3111*. Fig. 14. *E. clivosum*, $n=20$, diakinesis; *Reveal et al. 2661*. Fig. 15. *E. clivosum*, $n=20$, metaphase I. *Reveal et al. 2664*. Fig. 16. *E. greggii*, $n=16$, metaphase I; *Reveal et al. 2607*. Fig. 17. *E. greggii*, $n=16$, telophase I; *Reveal et al. 2607*. Fig. 18. *E. greggii*, $n=16$, metaphase I; *Reveal & Atwood 3382*.

Figs. 19-33.— Camera lucida drawings of chromosomes from microsporocytes of *Eriogonum* subgenus Pterogonum, sections Astra and Alata. Fig. 19. *E. hieracifolium*, $n=20$, metaphase I; *Hess 886*. Fig. 20. *E. hieracifolium*, $n=20$, telophase I; *Reveal & Davidse 902*. Fig. 21. *E. hieracifolium*, $n=20$, telophase II; *Reveal & Davidse 914*. Fig. 22. *E. hemipterum* var. *hemipterum*, $n=20$, metaphase I; *Hess 799*. Fig. 23. *E. hempiterum* var. *hemipterum*, $n=20$, diakinesis; *Reveal & Davidse 906*. Fig. 24. *E. nealleyi*, $n=20$, metaphase I; *Hess 876*. Fig. 25. *E. nealleyi*, $n=20$, telophase I; *Reveal & Davidse 900*. Fig. 26. *E. nealleyi*, $n=20$, diakinesis; *Reveal & Davidse 901*. Fig. 27. *E. alatum* var. *alatum*, $n=20$, metaphase I; *Hess 353*. Fig. 28. *E. alatum* var. *alatum*, $n=20$, telophase II; *Reveal & Reveal 2772*. Fig. 29. *E. alatum* var. *mogollense*, $n=20$, metaphase I; *Hess 761*. Fig. 30. *E. alatum* var. *mogollense*, $n=20$, diakinesis; *Reveal & Reveal 3225*. Fig. 31. *E. alatum* var. *mogollense*, $n=20$, telophase I; *Reveal & Reveal 3229*. Fig. 32. *E. alatum* var. *glabriusculum*, $n=20$, metaphase I; *Hess 506*. Fig. 33. *E. alatum* var. *glabriusculum*, $n=20$, telophase II; *Reveal & Davidse 880*.

Map 1. Distribution of *Eriogonum atrorubens* in northern Mexico showing var. *atrorubens* (solid circles); var. *auritulum* (open triangles); var. *pseudociliatum* (solid boxes); var. *intonsum* (open circles); var. *nemorosum* (solid triangles); and var. *rupestre* (open boxes).

($2n = 32$). It is easy to accept the rationale of the octoploid chromosome number for var. *intonsum*, for this variant quite possibly owes its origin to hybridization involving var. *atrorubens* and var. *nemorosum* Hess & Reveal followed by chromosome doubling. However, an explanation for the 32 chromosomes of *E. greggii* is a little more difficult. We feel that *E. greggii* is the most diverged taxon in the subgenus, and this divergence occurred at a relatively early time in the history of the group. We recognize that most authorities would argue that an aberrant chromosome number would generally indicate a recent divergence (Stebbins 1974), but each taxon must be analyzed on its own merits. Characteristics such as growth form, flower color, pubescence, and glandularness indicate to us an early divergence from the main evolutionary line in Pterogonum, and certainly the loss of chromosomes and chromosomal anomalies could occur at any time in the evolution of a species, in this case, *E. greggii*. We will discuss this in more detail in the following section.

Evolutionary relationship of Pterogonum within Eriogonum

Reveal (1969a) has already ventured an opinion on the relationships of the various subgenera within *Eriogonum*. It has been difficult for us to see any firm place of origin for Pterogonum within *Eriogonum*. At one time one of our major professors (Goodman), playing the devil's advocate, had argued for the recognition of Pterogonum as a genus in much the same fashion as we have outlined the group as a subgenus within *Eriogonum*. If only *E. alatum* existed, then some justification for a distinct genus could be made, but the other taxa in Pterogonum tie *E. alatum* firmly to *Eriogonum*. The recent discovery of a new shrubby genus, *Dedeckera* Reveal & Howell (1976), related to *Eriogonum*, called for a fresh review of the genera in the subfamily Eriogonoideae Benth.

We suspect that Pterogonum has its closest relationship with the subgenus Ganysma, a mixture of annuals and perennials with distinctly pedunculate involucres, yellowish to yellowish green flowers in which some approach the flower color of certain members of Pterogonum, as well as maroonish flowers (as in *Eriogonum preclarum* Reveal, a perennial species from Baja California del Sur, Mexico), and erect stems that may or may not be inflated. Upon comparing the two subgenera, we found certain similarities evident.

Eriogonum greggii is cytologically unique in Pterogonum with $n = 16$. This same number appears in section Gomphotheca (Nutt.) Reveal of Ganysma, the subgenus that includes *E. inflatum*, *E. trichopes* Torr., and others (Reveal 1969b). Also in Ganysma is *E. galioides* I. M. Johnst., an endemic from the east coast of Baja California, Mexico, which is superficially similar to *E. greggii*, most notably in its pubescence and flower color. All attempts at chromosome counts for *E. galioides* have failed. The maroonish flowers of *E. preclarum* are vaguely similar to those of *E. ciliatum*, and an unusual collection which we have tentatively identified as *E. hemipterum* (see page 316).

At this point it is pertinent to remind the reader that Torrey and Gray (1870) and Watson (1877) associated a part of Pterogonum with species now placed in Ganysma, and Stokes (1936) placed *E. inflatum*, another member of Ganysma, with the species of Pterogonum.

Still, there are major differences between Pterogonum and Ganysma. Of paramount importance is the straight embryo of Pterogonum versus the curved embryo of Ganysma. The pubescence types seen in Pterogonum are not duplicated in Ganysma, and the peduncles are rather different. In Ganysma they are usually short and slender and commonly much finer than the associated branch system. It is thought that their morphological origin is by a reduction of an entire branching pattern, or by the extension of a branching system by the formation of an involucre-bearing peduncle in the axis of a branch. In Pterogonum the morphological development of the peduncle would seem much less sophisticated. In most species of Pterogonum the peduncles have a similar thickness when compared with the branches, or only slightly less thick. Likewise, the origin of the peduncle seems to be either by the suppression of a branching system in which a single peduncle remains, or as an extension of a bracted axil. Both conditions are evident in *E. atrorubens;* however, the suppression of the branching system seems to be most obvious in *E. ciliatum* and *E. greggii*. In *E. atrorubens* no striking reduction can be seen except in the final branch division, and in its var. *nemorosum*, the inflorescence is as highly branched as any species in Ganysma. Thus, it seems that Pterogonum followed it own line of development, coupling a reduction of branches with a reduction in involucre-bearing peduncles, while probably the opposite is true in Ganysma.

The flower colors in Pterogonum are shades of yellow or yellowish green or maroon. *Eriogonum alatum* best illustrates the yellow green shade with much lighter shades of yellow to even pale white in *E. nealleyi* and *E. clivosum*. A deep lemon yellow flower color is found in *E. hieracifolium*. These shades of yellow are found in a number of species in Ganysma and are not restricted to any natural part of it. The completely maroon flower color so typical of some species of Pterogonum is not found elsewhere in *Eriogonum*,

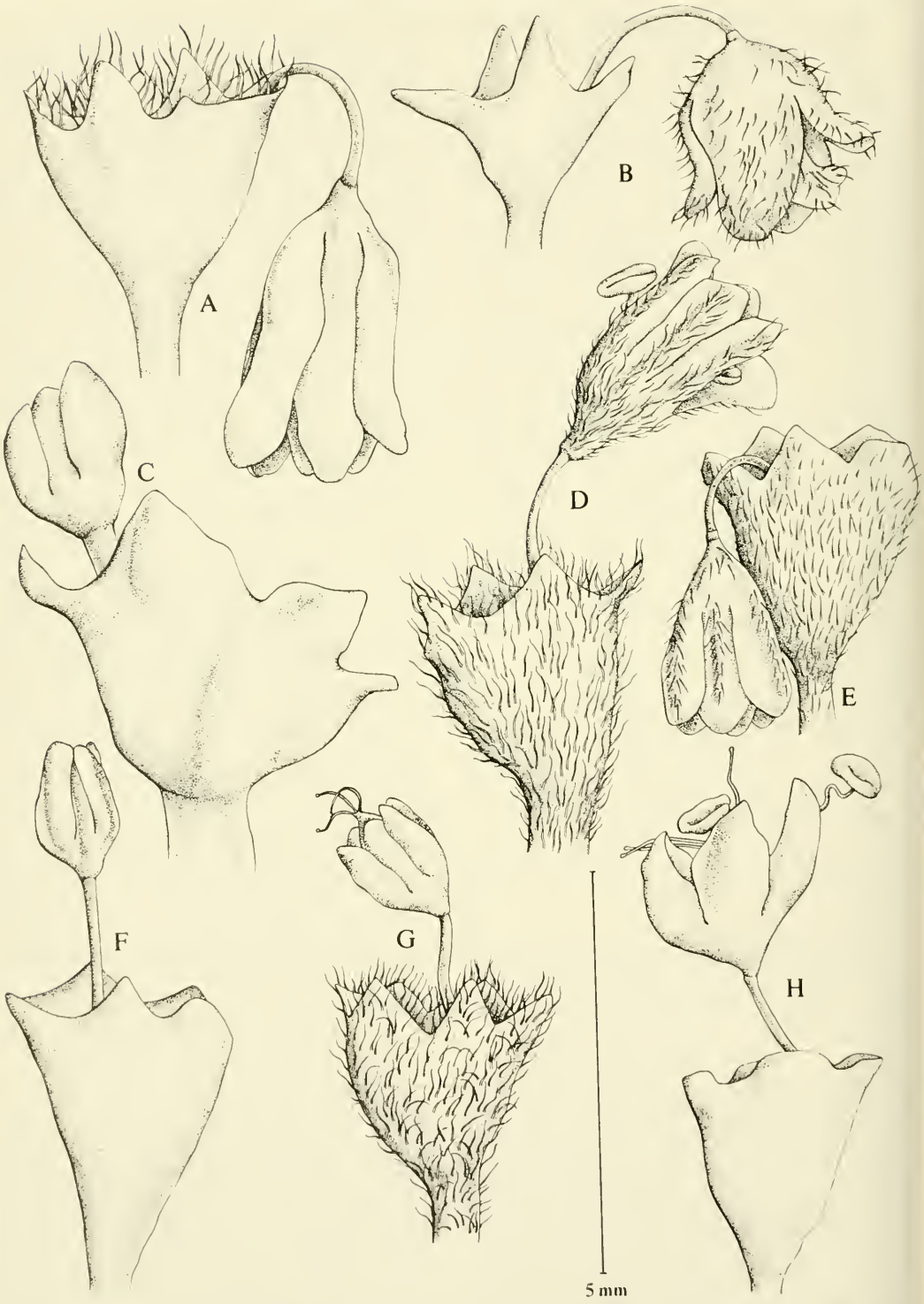


Fig. 34. Involucral and floral parts of *Eriogonum*. A. *E. atrorubens* var. *atrorubens*, *Wislizenus s.n.*; B. *E. atrorubens* var. *rupestre*, *Pringle 285*; C. *E. viscanum*, *Lloyd 116*; D. *E. hieracifolium*, *Hess 886*; E. *E. hemipterum* var. *hemipterum*, *Hess 799*; F. *E. nealleyi*, *Hess 786*; G. *E. alatum* var. *alatum*, *Hess 874*; H. *E. alatum* var. *glabriusculum*, *Hess 507*.

except for the aforementioned *E. preclarum* from Baja California, Mexico. Even in this species the flowers are much lighter and diffused with yellow. The cream-colored flowers characteristic of *E. viscanum* and *E. fimbriatum* are also found in some species of Ganysma.

The flower and involucre shape in the plants of Pterogonum are similar to those found in Ganysma. However, in Pterogonum the flowers and involucres are more consistently alike than in any one group in Ganysma. Figure 34 illustrates some of the involucres and flowers found in Pterogonum. In general, the teeth of the involucres appear less rigid and the flowers are unspecialized with respect to their morphology (which is most unlike the species of Ganysma where some of the most specialized flowers of the genus may be seen). Thus, in Pterogonum, flower and involucre morphology are not important taxonomic characteristics as they are in some of the other groups in *Eriogonum*.

In most of *Eriogonum* the achene morphology is not an important taxonomic characteristic in associating groups of species into higher units of classification. However, some trends may be seen which, when used with other features, may solidify certain relationships. For instance, the achenes of the subgenera Eriogonum and Oliogogonum Nutt. are narrow, somewhat elongated, and variously pubescent, a combination of characters not seen in other subgenera of *Eriogonum*. The achenes of Eucycla (Nutt.) Kuntze, Clastomyelon Cov. & Mort., Ganysma, and Oregonium (S. Wats.) Greene are all essentially identical, except that those of Ganysma have a somewhat more globose base than most, while those of Oregonium are often somewhat narrower than the majority. But in Pterogonum the achenes are unique with morphology totally unlike that found elsewhere in the genus, except for their large size, which is evident in the subgenus Eriogonum and some species of Oligogonum (Fig. 35).

The fruit of *Eriogonum alatum* is the most spectacular in that the entire body of the achene is three winged. This appears to us to be an advanced stage of evo-

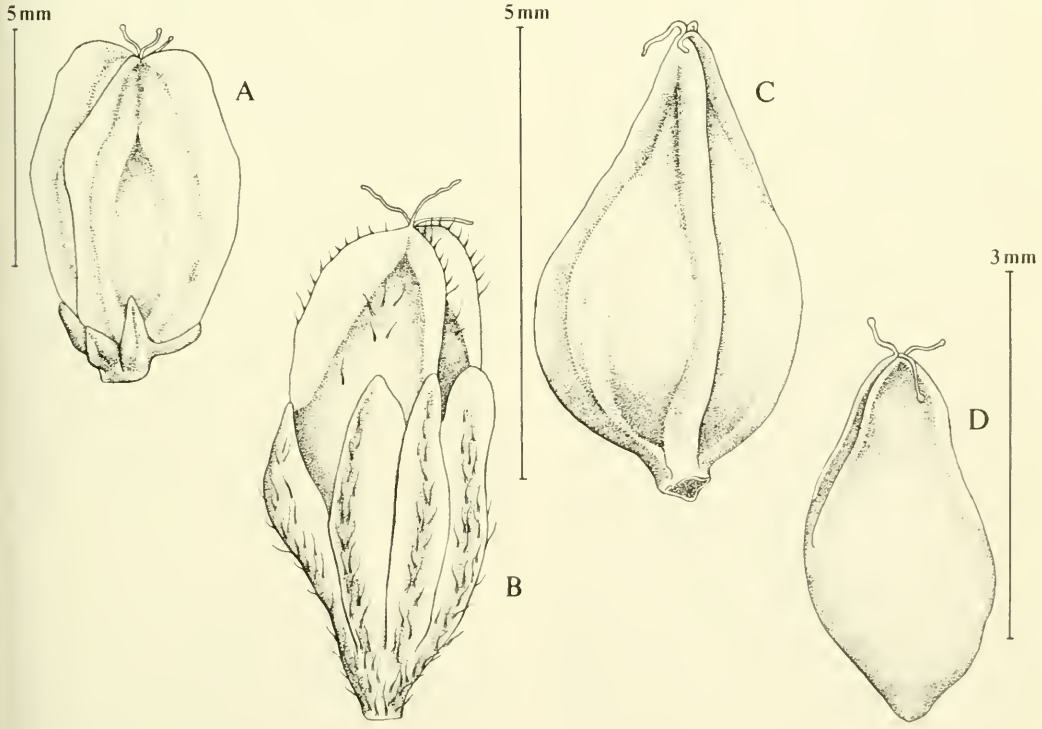


Fig. 35. Achene morphology of *Eriogonum*. A. *E. alatum* var. *alatum*, *Hess 874*; B. *E. hieracifolium*, *Hess 886*; C. *E. atrorubens* var. *atrorubens*, *Muller 3382*; D. *E. viscanum*, *Lloyd 116*.

lutionary development, for, in general, the achenes of Pterogonum are only partially winged or merely strongly ridged or angled. These large, robust fruits are not found in other species of *Eriogonum*, although their large size is approached by *E. tomentosum* Michx., *E. longifolium* Nutt., and in certain taxa related to *E. umbellatum* Torr. In all of these cases, however, the achenes are smooth, narrow, and not at all winged or strongly angled. More than any other feature of Pterogonum, it is the nature of the achenes that is most characteristic of the group.

The significance of the enlarged fruit in the evolutionary development of Pterogonum can only be conjectured. Most likely the reduced number of flowers, involucres, and branches, along with the rather xeric environment common to most of the species of Pterogonum, may have resulted in the formation of a large, endosperm-rich fruit. An abundant endosperm surrounding a large, straight embyro should be environmentally advantageous as a means of survival for plants in which few seeds are produced and precipitation is seasonal and scarce. Whether this feature is "advanced" in *Eriogonum*, we are not so certain, but it is specialized and we think it is adaptively important.

Within *Eriogonum* the trend seems to be toward a reduction in the amount of endosperm present concomitant with a curved embryo and an increase in the number of seeds per plant. Because of these trends, those extant members of Pterogonum have most likely survived a long evolutionary history, and we believe that the external seed morphology represents a specialized development in a group which is otherwise rather primitive.

The winged or ridged condition of the fruit of Pterogonum may function as an aid to seed dispersal, an adaptation important in the survival of the species and the colonization of new localities. As the fruits are relatively heavy, they do not land on the ground much more than a meter away from the plant. Once the fruits have landed, they may be wind-blown for some distances, particularly those with broad wings like *Eriogonum alatum*, tumbling along the ground's surface until they become wedged. The wings also increase the surface area of the fruit without adding much weight, thus enabling them to float more easily. No doubt the intermittent and permanent water courses have provided avenues for a wider distribution of some of these species. It is interesting that there does seem to be a trend in which those species with the broadest winged fruits have a wider distribution than those species with just ridged or angled margins of the fruits. The importance of the ridged or angled fruits in Pterogonum is probably not nearly as great as is the case for those species with the distinctly winged fruits. Most likely these non-winged species have survived better in the xeric condition of northern Mexico because of their greater seed size and endosperm amount and because the competition by other *Eriogonum* species has not been so great.

The basis for our belief that Pterogonum diverged early within the evolutionary history of *Eriogonum* is that there are several features common to members of this taxon and not with any of the other subgenera. Reveal (1969a) has already suggested that it is easy to support the relationship of all subgenera within *Eriogonum* except for two, the subgenera Eriogonum and Pterogonum. These subgenera occur on the peripheral edge of the range of the genus—one to the south (Pterogonum) and one to the east (Eriogonum). In both cases the early divergence occurred from the rest of *Eriogonum* when the fragmentation of the major taxonomic units (and very likely even before some of the related genera) was taking place. Pterogonum has enjoyed a long and successful period of evolution divorced from the majority of *Eriogonum*, and the same is likely true for the subgenus Eriogonum as well. These two subgenera have existed for a long time, separated from the majority of *Eriogonum*, but having retained many of the early characteristics of *Eriogonum*; yet they have specialized with unique and unusual features found only within their own taxa.

Taxonomy

Eriogonum Michx. subgenus *Pterogonum* (H. Gross) Reveal

Eriogonum Michx. subg. *Pterogonum* (H. Gross) Reveal, Sida 3:82. 1967, based on *Pterogonum* H. Gross, Bot. Jahrb. Syst. 49:239. 1913. Lectotype: *P. atrorubens* (Engelm. in Wisliz.) H. Gross = *E. atrorubens* Engelm. in Wisliz., as proposed by Roberty & Vautier, Boissiera 10: 107. 1964.

Tall erect herbaceous perennials mostly with a single stem arising from a deep, often soft, woody, rarely chambered taproot, the plants (0.2) 0.5-2.5 m high; *leaves* basal or basal and whorled or alternate, the basal leaf-blades mostly spathulate to oblanceolate or linear-lanceolate to ovate, glabrous to densely pubescent or glandular-pubescent, especially on the lower surface, or with ciliated leaf margins, the cauline leaf-blades, when present, similar to the basal ones only narrower and shorter, usually sessile; *stems* erect or nearly so, glabrous or glabrate to silky pubescent or glandular-pubsecent, fistulose in some; *bracts* ternate, usually small, scalelike, connate at the base; *inflorescences* mainly elongated, open, long-branched paniculate cymes or di- or trichotomously branched cymes, or cymes with one side suppressed, the branches glabrous to thinly pubescent, fistulose in some; *peduncles* long and slightly curved, often stout; *involucres* turbinate to campanulate, not angled or ribbed, mostly 4-5 (8) lobed, the teeth shallow, erect or slightly spreading, acute to obtuse or truncate; *flowers* astipitate, pubescent or glabrous, white or cream to yellow or red to maroon, the tepals essentially of equal size in most; *achenes* winged or ridged, glabrous or pilose, plump, and usually long exserted above the tepals; *embryo* straight, endosperm copious.

Dry to mesic desert valley grasslands, foothills, and mountain ranges from Wyoming, Nebraska, and Utah southward through western Kansas to western Oklahoma, and in Arizona, New Mexico, and Texas southward into Mexico from Chihuahua to Zacatecas and Coahuila to Nuevo León, from 100 to 3100 meters elevation. Flowering mainly in the late summer and fall of the year.

The center of distribution for the subgenus is most likely northern Mexico, since the greatest number of distinct taxa are found there within the mountains and the dry foothills of the desert ranges. Northward from Mexico the number of taxa decline, but the extent of their distribution increases. The northward migration of the subgenus probably occurred during the madro-tertiary geoflora (Axelrod 1958) or even during the late Pleistocene. Subsequent adaptations from a northward migration might be evidenced by *Eriogonum alatum* with its monocarpic habit and broadly winged achenes.

The section Pterogonum is restricted to the mountains and dry hillsides of northern Mexico and is composed of five species in two subsections. Within the subsection Pterogonum the shortened axis and a complex inflorescence branching pattern is epitomized. Its single species *Eriogonum atrorubens* is found in the greatest ecological diversity, no doubt attributing to a polymorphic condition and resulting in our recognition of five varieties. Throughout its range, however, the much-branched, spreading inflorescence is typical of the plants, and the greatest variation is expressed in the leaves and flowers.

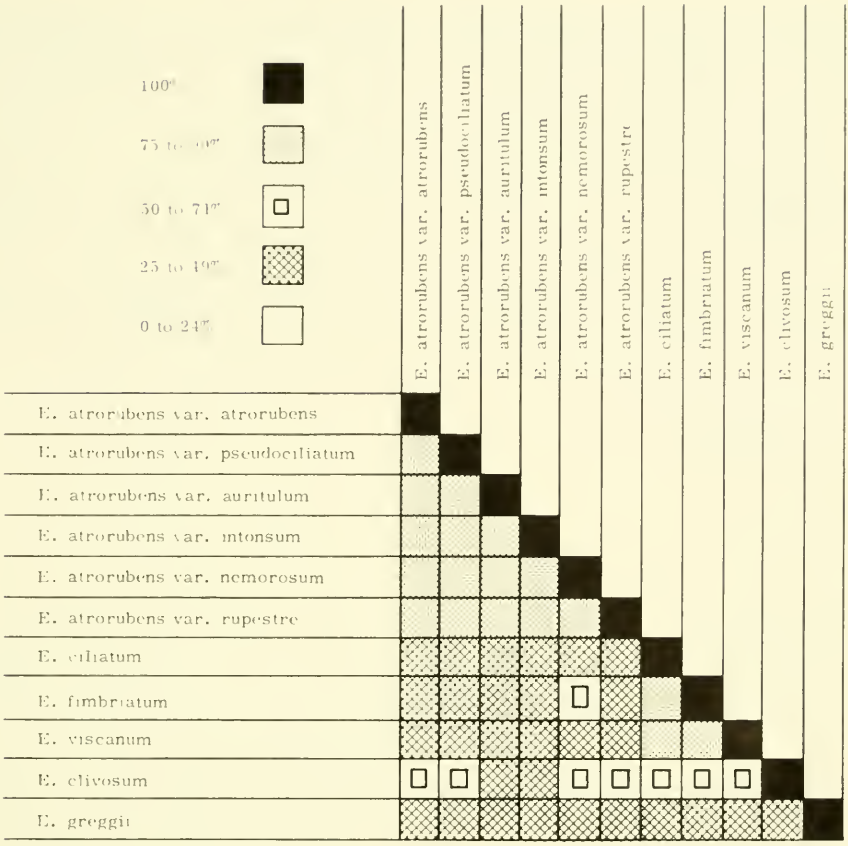
The other four species are placed in the subsection Adenogonum. Three, *Eriogonum clivosum*, *E. viscanum*, and *E. fimbriatum*, form a tightly knit group of low, xerophytic plants found on gypsophilous outcrops at widely scattered locations in northern Mexico. The fourth species, *E. ciliatum*, is easily distinguished from the other by a series of features. Unlike the gypsophilous species of Adenogonum, *E. ciliatum* is found in the lower foothills usually associated with pinyon-juniper woodlands on calcareous soils. The flowers of *E. ciliatum* are maroon like those of *E. atrorubens*, and unlike the cream-colored flowers of the other Adenogonum species. Yet, these flowers have a large, yellowish central portion of the floral tube. Thus, morphologically as well as biologically, the flowers of *E. ciliatum* are more similar to those of Adenogonum than Pterogonum. The inflorescences of Adenogonum may be moderately branched as in *E. clivosum*, or reduced with three to five divisions as in *E. fimbriatum*, or one to three divisions as in *E. ciliatum*. Lastly, as the sectional name implies, the nodes are glandular in all of these species except *E. clivosum*.

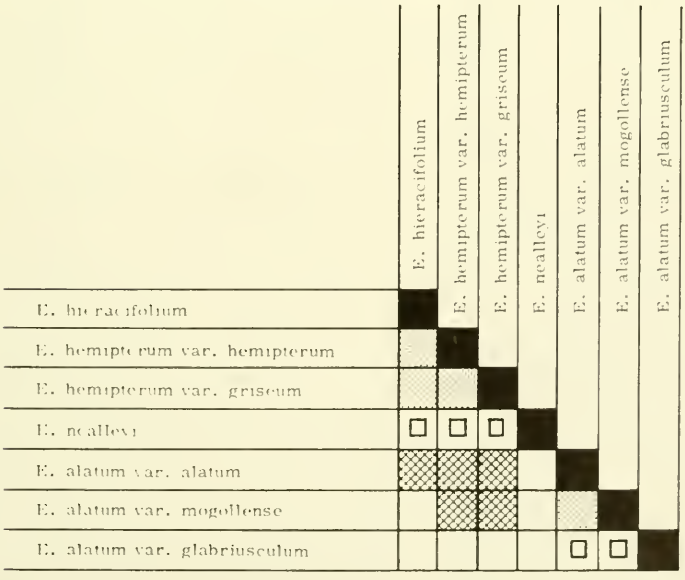
Eriogonum greggii is the only species of the section Peregrina and, except for an outlying population in Hidalgo County, Texas, occurs mainly on the desert ranges and foothills of the Sierra Madre Oriental in northeastern Mexico. This species is readily distinguished in the subgenus by the presence of whorled leaves in the bracts at each node, its dichotomously branched inflorescences which have one side suppressed (monopodial), and its generally glandular-pubescent

Map 2. Distribution in northern Mexico of *Eriogonum ciliatum* (closed circles); *E. fimbriatum* (open box); *E. viscanum* (open circles); *E. clivosum* (solid boxes); and *E. greggii* (triangles).

stems and branches. It is most closely related to members of Adenogonum, as both groups share the broadly laminar petiole of the basal leaves and a greatly reduced inflorescence. However, we believe there is ample justification for the separation of *E. greggii* from the other members of Adenogonum based on the aforementioned morphological distinction and the unique chromosome number of $n = 16$.

We compared the taxa of sections Pterogonum and Peregrina based on the presence or absence of 33 characteristics. From these data we determined the percentage of shared characteristics and charted the results in Figure 36. We duplicated the same procedures with the taxa in sections Astra and Alata, again using 33 characteristics (Fig. 37). We have attempted to illustrate the evolutionary relationships of these taxa in the proposed phylogenetic scheme in which two major lines of development are evident (Fig. 38). In one line of evolution it would appear that subsection Adenogonum and section Peregrina are approximately equidistant from subsection Pterogonum but at different angles. In the other offshoot an early dichotomy resulted in the divergence of section Alata from the other spe-





Figs. 36-37. Percentages of shared characteristics for *Eriogonum*, subgenus Pterogonum. 36. Sections Pterogonum and Peregrina. 37. Sections Astra and Alata.

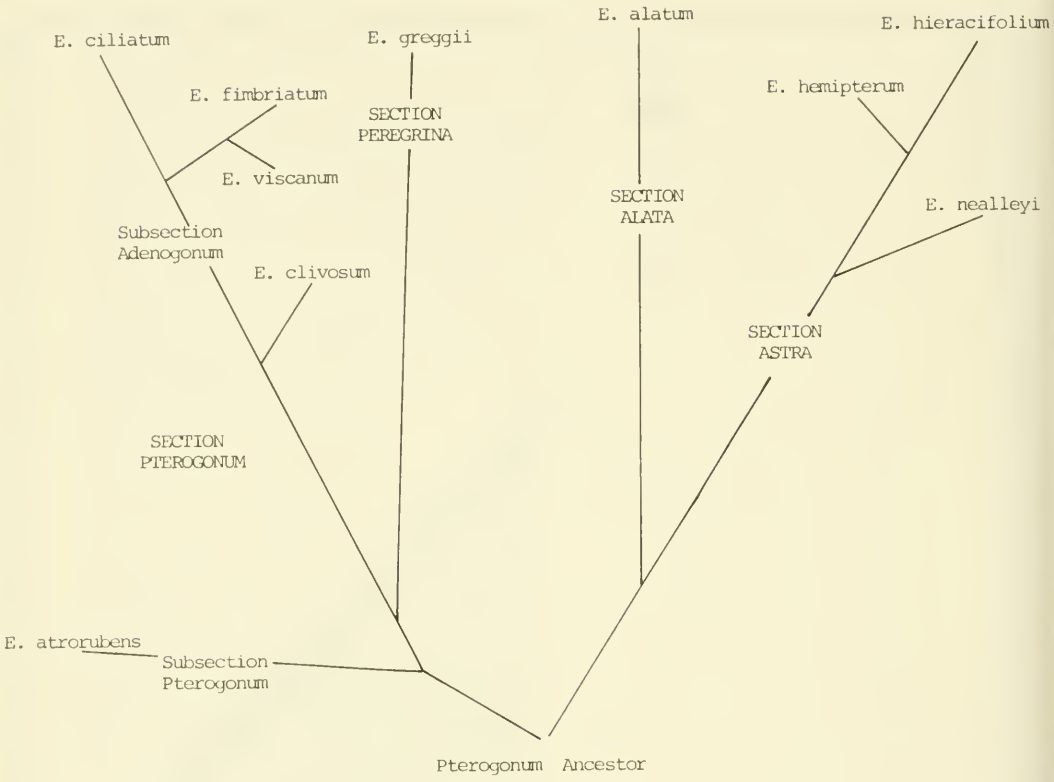


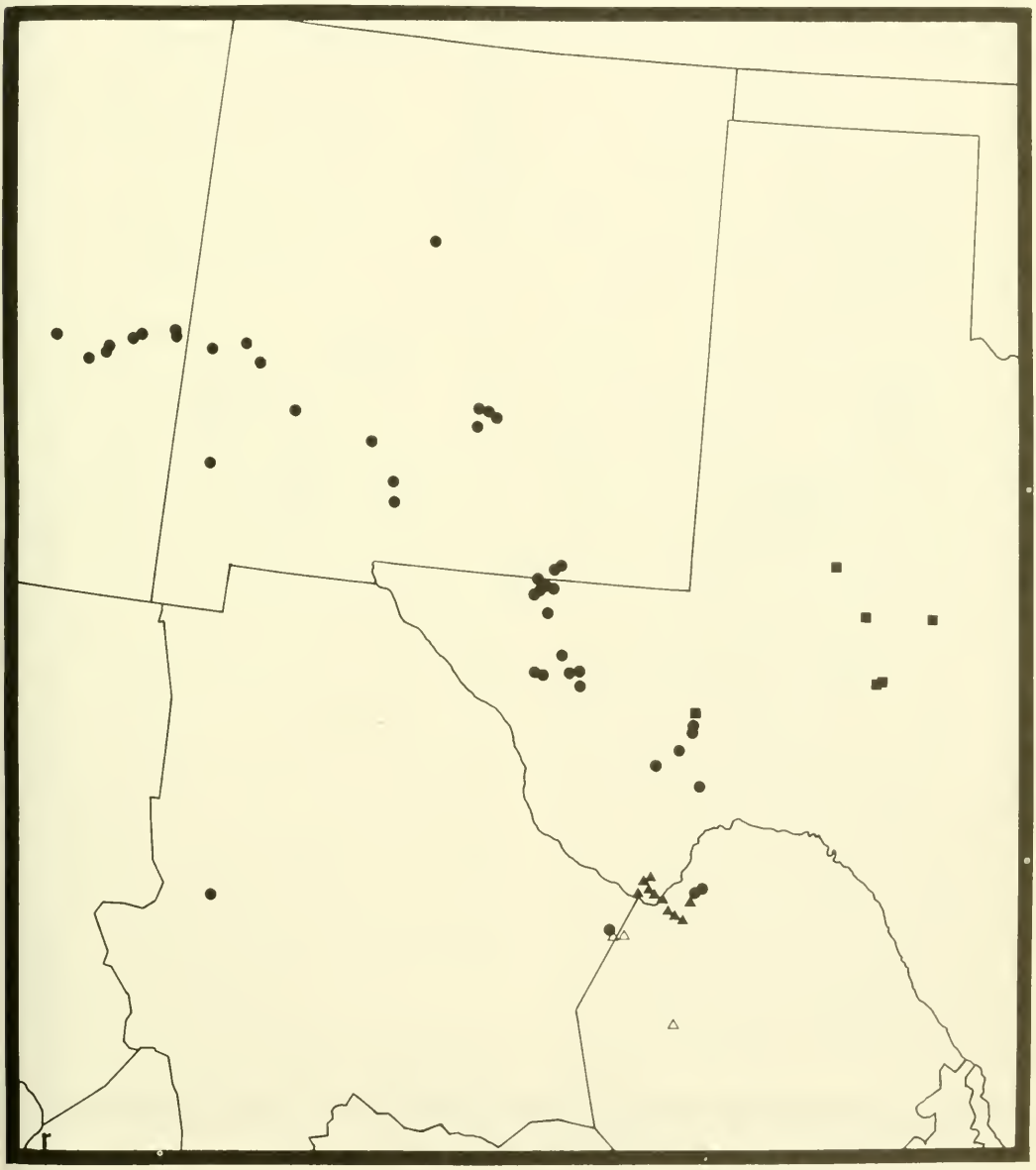
Fig. 38. A phylogenetic scheme for the species within subgenus *Petrogonum*.

cies in section Astra. These last two sections differ from the former ones, primarily in having stems with alternately arranged cauline leaves.

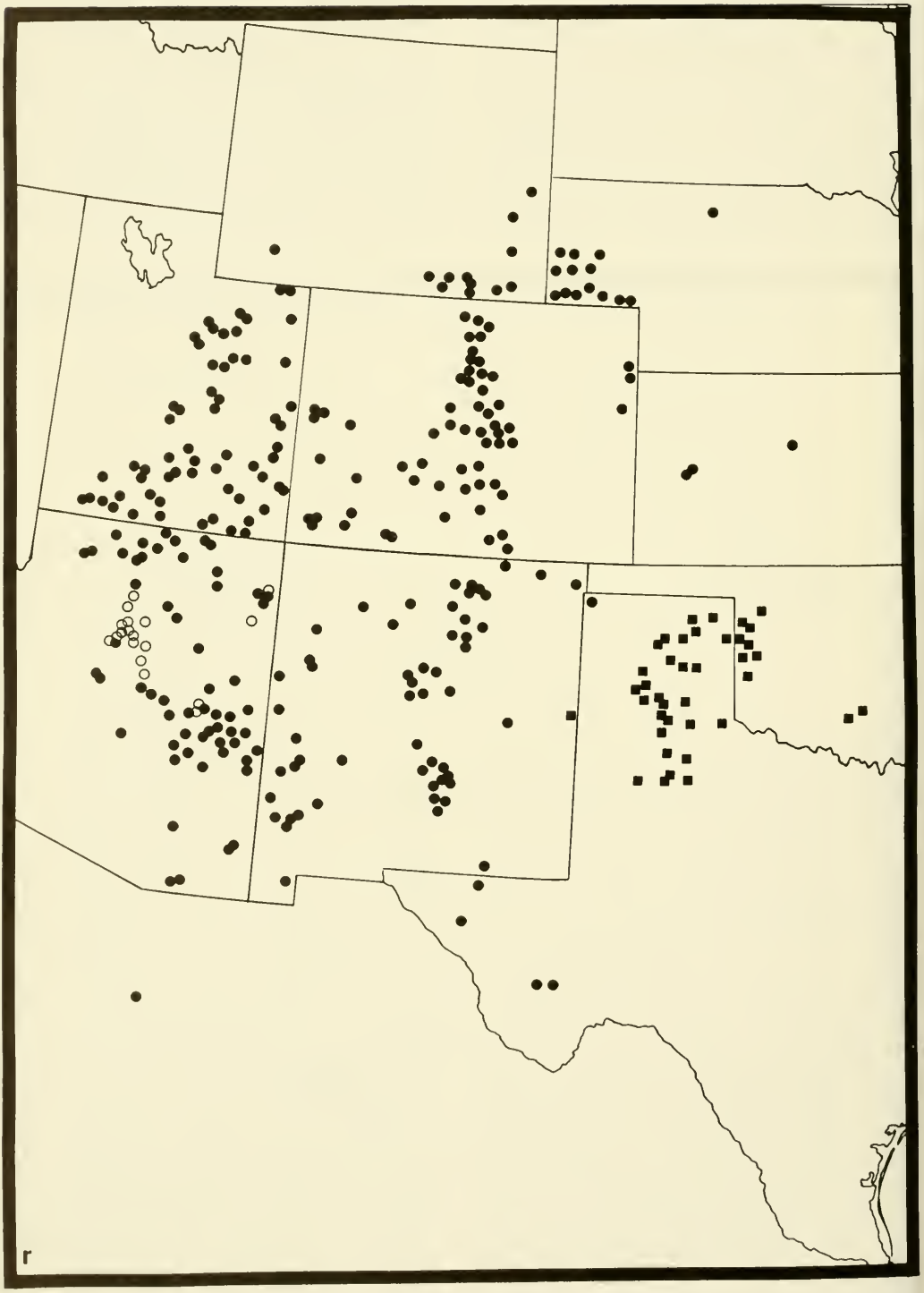
Only the widespread *Eriogonum alatum* is contained within the section Alata. Morphologically, this species is not unique except for two characteristics, monocarpy and distinctly winged fruits. Monocarpy is known nowhere else in the genus *Eriogonum*. It may be appropriate, in the determination of evolutionary relationships, to weigh various characteristics equally; but it is, nevertheless, most difficult for us to keep from emphasizing such a complex characteristic as the monocarpic habit and the occurrence of its many unknown changes. Because of the wide geographic range of *E. alatum*, it would seem that the monocarpic condition occurred early in its evolution, and, perhaps, concomitant with this adaptation it was able to exploit widespread environmental conditions. We believe the large, distinctly winged fruit of *E. alatum* is another unique (and possibly highly specialized) feature. No other members of the subgenus have achenes that are completely winged nor even shaped like those of *E. alatum*, and certainly this feature would be an advanced character over the non-winged character. As is usual, once a species has become established, its evolution proceeds along lines independent of the pressures subjected to the other closely related taxa.

The three species of section Astra are more restricted in distribution and occur in a more xeric habitat than *Eriogonum alatum*. Similar to those species of subsection Adenogonum, these taxa have also evolved into more specialized units, most likely in response to the desert and foothill environments of northern Mexico and Texas (see Axelrod 1958 for a more detailed discussion of this phenomenon). In this section we characterize *E. hieracifolium* as the central line of development, with *E. hemipterum* and *E. nealleyi* as offshoots. Certainly, the more widely ranging distribution of *E. hieracifolium*

in the more mesic regions and its more general morphological characteristics tend to support this suggestion. The restricted range in xeric sites of *E. hemipterum*, its shortened inflorescences, and its smaller maroon (or nearly so) flowers support its divergency from *E. hieracifolium*. *Eriogonum nealleyi* occurs in the most xeric habitat of all the members of Astra and reflects this condition by its convergence in appearance to *E. alatum* var. *glabriusculum* Torr. in Whipple. However, no direct relationship exists with var. *glabriusculum*, and we believe characteristics such as the branched caudex system, flower morphology, and fruit type, which are shared with *E. hieracifolium* and *E. hemipterum*, are more significant. This species is certainly more distinctly unique than the others in Astra and would seem to be early evolved off the *E. hieracifolium* line.



Map 3. Distribution of *Eriogonum hieracifolium* (solid circles); *E. hemipterum* var. *hemipterum* (solid triangles); *E. hemipterum* var. *griseum* (open triangles); and *E. nealleyi* (solid boxes).



Map 4. Distribution of *Eriogonum alatum* showing var. *alatum* (solid circles); var. *mogollense* (open circles); and var. *glabriusculum* (solid boxes).

Key to the Sections

A. Leaves strictly basal, or if appearing to be cauline, then arranged in the axils of bracts; stems often glandular-pubescent at least at the nodes; plants mostly of Mexico.
  B. Leaves strictly basal, not glandular; stems erect, glabrous or glandular only at the nodes; inflorescences open, with elongated branches; flowers maroon to cream colored, glabrous or thinly pubescent ..... I. Sect. Pterogonum
  BB. Leaves basal with whorled cauline leaves arranged in axils of bracts at each node, the leaf-blades glandular as well as pubescent; stems suberect or spreading, densely glandular-pubescent; inflorescences with one side suppressed, not open or with elongated branches; flowers white, densely strigose ..... II. Sect. Peregrina

AA. Leaves basal and alternately arranged on the stem; stems glabrous to strigose, not glandular; plants mostly of the United States.
  B. Plants from branched caudices; achenes distinctly ribbed or winged only along the upper half; flowers deep yellow, cream white, or maroon; long-lived perennials ..... III. Sect. Astra
  BB. Plants from a deep, soft, often chambered taproot; achenes distinctly winged the entire length; flowers greenish yellow; monocarpic perennials ..... IV. Sect. Alata

I. Eriogonum sect. Pterogonum

Eriogonum Michx. subgen. *Pterogonum* (H. Gross) Reveal sect. *Pterogonum*.

Moderately tall, mostly erect perennial herbs, usually but not always with a single stem arising from branched caudices, glabrous and glaucous, or with stipitate glands at or near the nodes; *leaves* basal, oblanceolate to oblong or spathulate, glabrous on both surfaces except for ciliated margins, or thinly strigose on both surfaces, or tomentose below; *bracts* ternate, mostly scalelike, connate at the base; *inflorescences* open, paniculate cymes with few to many di- and trichotomous branches; *peduncles* long and usually stout; *involucres* turbinate to campanulate, the (4) 5 (8) teeth acute to truncate, the bractlets linear-oblanceolate, glabrous or glandular, usually ciliolate, the pedicels glabrous; *flowers* maroon, cream, or white, the tepals glabrous or sparsely pubsecent; *anthers* purple to red or yellowish; *achenes* slightly winged or ridged the entire length, glabrous.

The section Pterogonum is composed of two groups which differ primarily in the type of inflorescence development, vestiture, and habitat. The subsection Pterogonum is monotypic and ranges from the New Mexico-Mexico line southward to Durango mainly in the pine-oak and pinyon-juniper woodlands, with an isolated population in pine woodlands in Zacatecas, and a major center in the high mountains of northeastern Mexico. These plants all have a densely branched inflorescence, glabrous stems and branches, and distinctly petiolate leaf-blades. The second subsection, Adenogonum, contains four species, three of which occur on gypsum outcrops in isolated locations in north central Mexico. The majority of these sites are in broken scrubland communities often dominated by *Larrea*. These plants all have highly reduced inflorescences composed of only a few branches, stems which are either glabrous or glandular at least at or near the nodes, and leaves which have broadly laminar petioles. *Eriogonum ciliatum*, the fourth species of the subsection, is similar in aspect to the others except that it occurs in both pinyon-juniper and grassland communities, and usually on limestone soils, and has maroon instead of cream-colored flowers.

Key to the Subsections

A. Inflorescences of numerous branches, the stems reddish, glabrous, and glaucous; flowers maroon; leaves distinctly petiolate in most; wide-

spread in northern Mexico, mainly in the Sierra Madre Occidental and Oriental ..... A. Subsect. Pterogonum

AA. Inflorescences of few branches, the stems whitish or greenish, or, if reddish, then glandular; flowers white or cream, or, if maroon, then with a bright yellow central portion within; leaves with a broadly laminar petiole; in isolated and scattered places mainly at low elevations in north central Mexico, or in the foothills of Sierra Madre Oriental of northeastern Mexico ..... B. Subsect. Adenogonum

IA. Eriogonum subsect. Pterogonum

Eriogonum Michx. sect. *Pterogonum* (H. Gross) Reveal subsect. *Pterogonum* (H. Gross) Hess & Reveal, stat. nov., based on *Pterogonum* H. Gross, Bot. Jahrb. Syst. 49:239. 1913. Lectotype: *P. atrorubens* (Engelm. in Wisliz.) H. Gross = *E. atrorubens* Engelm. in Wisliz., selected by Roberty & Vautier, Boissiera 10: 107. 1964. This new status is made in accordance with Article 22 of the current International Code of Botanical Nomenclature (Stafleu et al. 1972).

Plants tall, 4-10 (12) dm high; *leaves* oblanceolate to elliptic or linear, 2.5-15 cm long, on distinct petioles in most; *stems* erect, slender and occasionally fistulose, glabrous and glaucous; *inflorescences* open, densely branched in most, glabrous; *flowers* maroon, glabrous or thinly pubescent.

A monotypic group containing only *Eriogonum atrorubens*.

1. *Eriogonum atrorubens* Engelm. in Wisliz.

Figs. 39, 40, & 41.

Tall, erect herbaceous perennials 4-10 (12) dm high from a short, compact, branched, woody caudex; *leaves* basal, the leaf-blades linear, oblanceolate, lanceolate or oblong to elliptic, (2.5) 4-12 (15) cm long, 0.3-3 cm wide, sparsely to densely strigose on both surfaces and greenish above, or densely grayish-tomentose below and strigose and grayish or greenish above, glabrous and greenish on both surfaces in some, the margin and midribs ciliated or sparsely pubescent, the apex mostly acute to slightly obtuse, the base long cuneate in most, tapering gradually to an indistinct petiole only in var. *nemorosum*, the petiole 1-8 (12) cm long, ± winged in some, glabrous to strigose or tomentose, the petiole-base strigose to villous or glabrous without, glabrous within; *stems* erect, often solitary, 1-4.5 dm long, slender and sometimes fistulose at the first node, glabrous and glaucous; *inflorescences* open, cymose, (1.5) 3-8 dm long, the numerous branches mostly spreading, trichotomously branched at the first node, di- or trichotomously branched above, with an involucre-bearing peduncle in the fork of each axis, glabrous and glaucous; *bracts* scalelike, ternate, 1-5 mm long, or linear-lanceolate and 5-10 (15) mm long, becoming strongly reduced in size at the uppermost nodes, sparsely pilose to strigose, especially within and along the margin, infrequently glabrous without, connate at the base; *peduncles* ascending to erect, straight or slightly curved upwardly all along their length, (1) 2-8 (12) cm long, glabrous; *involucres* solitary, turbinate to turbinate-campanulate, (1) 1.5-4 (4.5) mm long, 1-2.5 (3) mm wide, glabrous without, glabrous within except for the sparsely ciliated margin with curled hairs or small glands, the (4) 5 (8) rounded or truncate or acute teeth 0.4-1.5 mm long, the bractlets linear-oblanceolate to oblanceolate, 1-3.5 mm long, glabrous or ciliate and minutely glandular, the pedicels 1.5-5 (6) mm long, glabrous; *flowers* maroon to red or purple, often with a dark green or reddish midrib, (1) 1.5-3 mm long in anthesis, becoming 3-6 mm long in fruit, glabrous or strigose without, essentially glabrous within, the tepals essentially monomorphic, spathulate to obovate or infrequently lanceolate, connate at the base; *stamens* slightly exserted, 1.5-5 mm long, the filaments glabrous, the anthers maroon to reddish purple or yellowish; *achenes* light greenish brown to brown, (2) 3-5.5 mm long, 2-3.5 mm wide, ovate, slightly 3-winged or ridged the entire length.

Infrequent to locally common on exposed meadows, grassland, and plains, or in pinyon-juniper, pine-oak, or pine woodlands, or rarely in desert scrublands, in the Sierra Madre Occidental from extreme northern Chihuahua and Sonora southward to central Durango, and in the Sierra Madre Oriental of southeastern

Coahuila and adjacent Nuevo León, with isolated populations near Chihuahua in central Chihuahua and near Sombrerete in west central Zacatecas, Mexico, from 1500 to 2750 m elevation (Map 1). Flowering mostly from June to October (November).

This species was reviewed by Reveal (1967a) at which time he proposed the subgeneric name Pterogonum and described two varieties of *Eriogonum atrorubens*, var. *pseudociliatum* and var. *intonsum*. Hess (1967) essentially agreed with this treatment except to point out that the material from the Sierra Madre Oriental probably represented another variety (here proposed as var. *auritulum*). Both of us noted the probable reduction of *E. rupestre* to the varietal rank under *E. atrorubens*, and this combination is hereby proposed. In our original studies, we were handicapped by a lack of field experience with *E. atrorubens*. A major part of our joint field effort has gone into a detailed review of this species, and this has resulted in some modification of both our 1967 papers. In addition, we have discovered a new taxon, var. *nemorosum*.

Key to the Varieties of *E. atrorubens*

A. Flowers glabrous.
  B. Leaf-blades oblanceolate, lanceolate, or oblong to elliptic (2.5) 4-8 (10) cm long, (0.5) 1-3 cm wide; involucres 1.5-4 (4.5) mm long.
    C. Leaves glabrous or merely sparsely pubescent on both surfaces.
      D. Leaves pubescent at least on the lower surface, the hairs becoming sparse as the plant matures in some.
        E. Stems usually strongly fistulose; leaves mostly 4-8 (10) cm long; plants of Chihuahua, Sonora, and Zacatecas ..... 1a. var. *atrorubens*
        EE. Stems not fistulose; leaves mostly 2.5-4 (6) cm long; plants of Coahuila and Nuevo León ..... 1b. var. *auritulum*
      DD. Leaves bright green and glabrous on both surfaces except for the ciliated margin and midvein; plants of central Durango ..... 1c. var. *pseudociliatum*
    CC. Leaves densely tomentose below, densely strigose above; plants of extreme northern Durango and adjacent southern Chihuahua ..... 1d. var. *intonsum*
  BB. Leaf-blades lienar, (4) 6-12 (15) cm long, (0.2) 0.3-0.7 (0.9) cm wide; involucres (1) 1.5-2 (2.5) mm long; northern Durango and southern Chihuahua ..... 1e. var. *nemorosum*
AA. Flowers strongly strigose without; plants of low desert ranges east and northeast of Chihuahua, Chihuahua ..... 1f. var. *rupestre*

1a. *Eriogonum atrorubens* var. *atrorubens*

Figs. 39a, b, c, d

Eriogonum atrorubens Engelm. in Wisliz., Mem. Tour North. Mex. 108. 1849.—On the banks of the streamlets at Cusihuiriachic (originally Cosihuiriachi), Chihuahua, Mexico, 19 Sep 1846, *Wislizenus 172*. Holotype: MO! Isotypes: GH, ISC, MO, NY!—*Pterogonum atrorubens* (Engelm. in Wizliz.) H. Gross. Bot. Jahrb. Syst. 49: 239. 1913.

Plants erect, 5-10 (12) dm high; *leaves* lanceolate or oblong to narrowly elliptic, mostly 4-8 (10) cm long, 1-3 cm wide, strigose on both surfaces, often slightly more so below than above, becoming nearly or quite glabrous in fruit; *stems* usually fistulose; *involucres* turbinate to turbinate-campanulate, 1.5-4 (4.5) mm long, 1-2.5 (3) mm wide, the bractlets often hirsutulous and/or glandular; *flowers* glabrous; $n=20$ (Figs. 1, 2).

Locally common in exposed grassy meadows, plains, or scattered pinyon-juniper woodlands on the lower foothills and slopes of the mountains of western Chihuahua from south central Chihuahua northward in the Sierra Madre Occidental to just south of the United States boundary in western Chihuahua and eastern

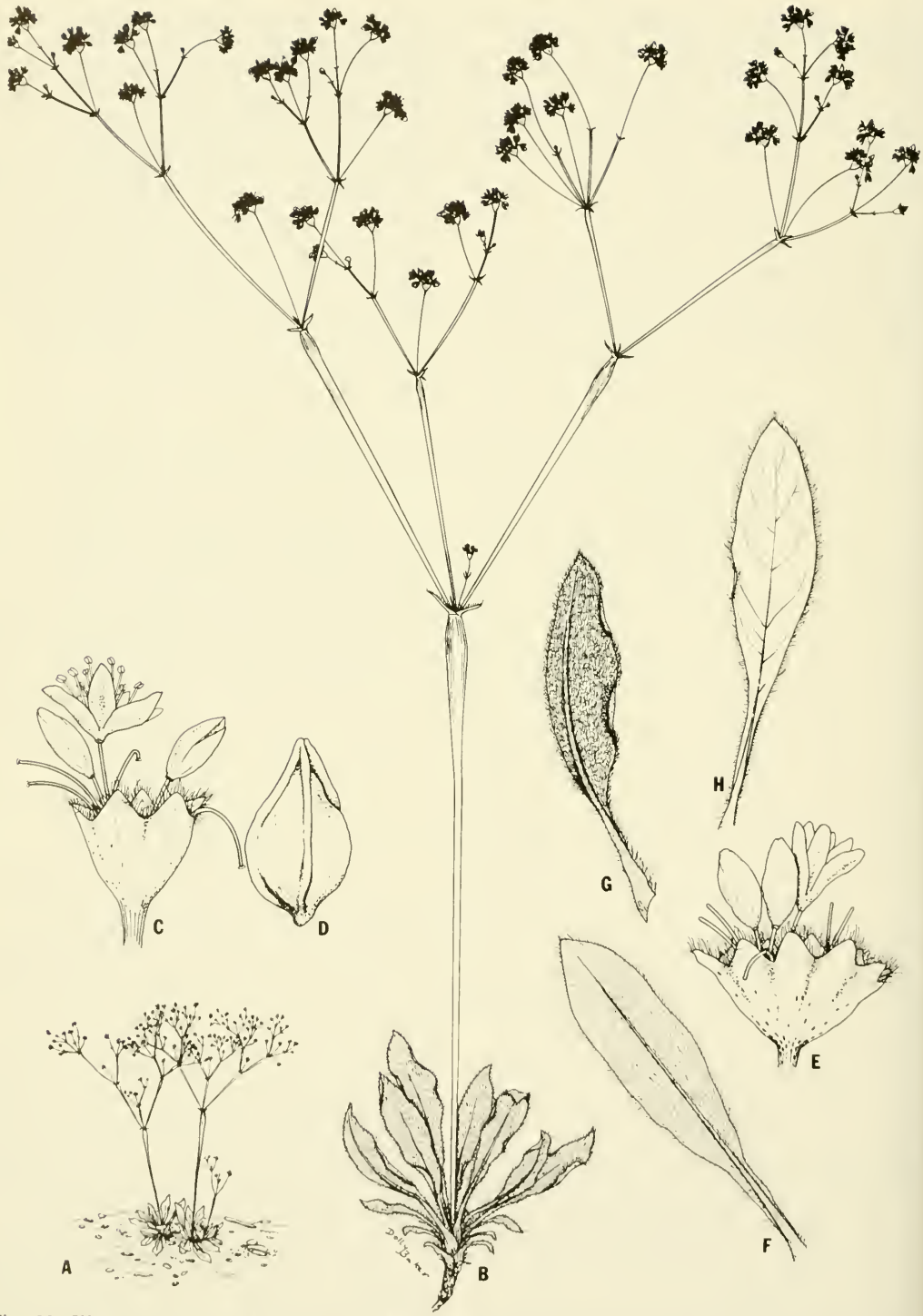


Fig. 39. Illustration of *Eriogonum atrorubens* showing habit of var. *atrorubens* (A), a single plant in detail (B), an involucre and flowers (C), and a mature achene (D). *Eriogonum atrorubens* var. *auritulum* is shown in E (involucre and open flowers) and F (leaf). *Eriogonum atrorubens* var. *intonsum* (G) illustrates the lower surface of the leaf-blade. *Eriogonum atrorubens* var. *pseudociliatum* (H) illustrates the leaf-blade.

Sonora, and in a single location northwest of Sombrerete, Zacatecas, Mexico, mostly below 2150 m elevation. Flowering from June to November.

REPRESENTATIVE COLLECTIONS: MEXICO: Chihuahua: Cajurichi, Río Mayo, 3 Sep 1936, *Gentry 2709* (ARIZ, GH, MO, NY, UC, US); San Diego Canyon, 16 Sep 1903, *M. E. Jones s. n.* (CAS, DS, MIN, MO, NY, POM, US); Sierra Madre, 2 Oct 1887, *Pringle 1357* (GH, ISC, MIN, MO, NDG, NY, UC, US); 10 mi W Cuauhtémoc, 13 Aug 1971, *Reveal et al. 2757* (ARIZ, BRY, CAS, GH, ISC, MEXU, MICH, MO, NY, OKL, RSA, SMU, TEX, UC, UTC, WTU); 12 mi NE Zaragosa, 10 Sep 1972, *Reveal & Hess 2986* (BRY, CAS, GH, MEXU, MO, NY, UC, US, UTC). Sonora: Base of San Luis Mts., 5 Sep 1893, *Mearns 2123* (DS, GH, NY, US). Zacatecas: 9 mi NW Sombrerete, 26 Sep 1948, *Gentry 8484* (AHFH, GH, US).

The var. *atrorubens*, as now defined, includes only those plants of the species which occur principally in grassy areas in the lower foothills of the Sierra Madre Occidental and those which are found in open pinyon-juniper woodlands in adjacent mountain ranges. The plants found in the grassy plains are typical of the species and may be distinguished by their large, strigose leaves and fistulose stems and branches. The plants which occur at a slightly higher elevation and in more xeric sites usually have leaves that are not as pubescent (and in fact may be nearly glabrous in fruit) and stems that are not as obviously inflated.

1b. *Eriogonum atrorubens* var. *auritulum*

Hess & Reveal

Fig. 39e. f

Eriogonum atrorubens Engelm. in Wisliz. var. *auritulum* Hess & Reveal, var. nov.—A var. *atrorubens* foliis strigosis et caulibus gracilibus differt.—Typus: Along Nuevo León Highway 68, 13 mi S Nuevo León Highway 60, 3 mi S Pablillo, on limestone hills associated with *Quercus* and *Pinus* at about 2075 m elevation, Nuevo León, Mexico, 18 Sep 1972, *Reveal & Hess 3149*. Holotype: US! Isotypi: ARIZ, BRY, CAS, GH, K, MEXU, MICH, MO, NY, TEX, UC, UTC!

Plants erect, 5-10 dm high; *leaves* lanceolate to narrowly oblong, mostly 2.5-4 (6) cm long, 1-3 cm wide, strigose on both surfaces, often slightly more so below than above; *stems* not fistulose; *involucres* turbinate, 2-3.5 mm long, 1.5-3 mm wide, the bractlets often hirsutulous and/or minutely glandular; *flowers* essentially glabrous, or rarely with a few scattered, minute, thin, pilose hairs without; $n=20$ (Figs. 3, 4).

Locally infrequent to rather rare in heavily wooded pinyon-juniper and oak woodlands in the mountains of southeastern Coahuila and adjacent Nuevo León, mainly in the Sierra Madre Oriental, from 1,800 to 2,600 m elevation. Flowering from May to October.

REPRESENTATIVE COLLECTIONS: MEXICO: Coahuila: S of Saltillo, 25 Jul-1 Aug 1880, *Palmer 1175* (GH, NY, P, US); Sierra Guadalupe, S of La Cuchilla, 15 Jul 1934, *Pennell 17378* (NY). Nuevo León: Las Canaos on Cerro Potosí, 1 Jul 1935, *Mueller 2184* (ARIZ, CAS, GH, MO, NY, TEX); 1 mi S Pablillo, 6 Aug 1971, *Reveal et al. 2651* (NY, US, UTC).

The var. *auritulum* is morphologically similar to the montane forms of var. *atrorubens*. In general, those plants of var. *atrorubens* have stems that are not strongly inflated and occur in pinyon-juniper woodlands—much like the situation found in var. *auritulum*. However, the latter never has inflated stems and branches, the plants nearly always occur under the forest canopy, and the leaves are always pubescent. These minor features, coupled with the strong geographical separation, has led us to distinguish between the two. The geographical distance between var. *auritulum* and var. *atrorubens*, which Reveal (1967a) assumed might be closed with more fieldwork, has remained distinct.

The flowers of the new variety occasionally have what appear to be minute, sunken, whitish glands. These are usually seen only in fresh material, but occasionally we have noted them on dried specimens. Similar glands have not been seen in the other forms of *Eriogonum atrorubens*. It should be noted, too, that on a few individual plants there are flowers with thin pilose hairs. These hairs are not as prominent nor as abundant as those found in var. *rupestre*.

1c. *Eriogonum atrorubens* var. *pseudociliatum* Reveal

Fig. 39h.

Eriogonum atrorubens Engelm. in Wisliz. var. *pseudociliatum* Reveal, Sida 3:85. 1967. — Otinapa NW of Ciudad Durango, Durango, Mexico, 25 Jul-5 Aug 1906, *Palmer 382*. Holotype: US! Isotypes: GH, K, MO, NY, UC!

Plants erect, 5-8 (10) dm high; *leaves* mostly elliptical, 4-8 (10) cm long, 1-3

cm wide, glabrous and bright green on both surfaces or with a few scattered hairs above, the midvein and margins ciliated; *stems* usually fistulose; *involucres* turbinate-campanulate, 2-4 mm long, 2-3 mm wide, the bractlets glabrous or glandular; *flowers* glabrous; $n=20$. (Figs. 5, 6).

Locally common in grassy meadows and in open pine-oak forests in the Sierra Madre Occidental of central Durango, Mexico, from 2400-2600 m elevation. Flowering from June to September.

Representative collections: MEXICO: Durango: 63 mi W Ciudad Durango, 28 Jun 1950, *Maysilles 7184* (DUKE, NY, TEX, US); El Salto, 12 Jul 1898, *Nelson 4552* (GH, US); 6.5 mi E Llano Grande, 9 Aug 1971, *Reveal et al. 2697* (BRY, CAS, GH, MEXU, MO, NY, RSA, UC, US, UTC); 34 mi W Ciudad Durango, 11 Aug 1956, *Waterfall 12653* (ARIZ, TEX, UC).

As now defined, the var. *pseudociliatum* is restricted to the central Sierra Madre Occidental in Durango. As noted above under var. *atrorubens*, those plants of Chihuahua previously referred to this variety by Reveal (1967a) have been transferred to the typical variant. As now restricted, var. *pseudociliatum* includes only those plants with bright green and usually totally glabrous basal leaves.

1d. *Eriogonum atrorubens* var. *intonsum* Reveal

Fig. 39g.

Eriogonum atrorubens Engelm. in Wisliz. var. *intonsum* Reveal, Sida 3: 86. 1967.—Indé, Durango, Mexico, Aug. 1927, *Reko 5239*. Holotype: US!

Plants erect, 5-10 dm high; *leaves* mostly narrowly elliptic to narrowly oblong, 4-10 (12) cm long, 1-2.5 (3) cm wide, densely grayish-tomentose below, densely strigose above; *stems* usually strongly fistulose; *involucres* turbinate, 1.5-3 mm long, 1-2 mm wide, the bractlets glabrous, hirsute, or glandular; *flowers* glabrous; $n=40$ (Figs. 7, 8).

Locally common on high mountain grassy plains, meadows, and in open pine-oak woodlands in the Sierra Madre Occidental of northern Durango and adjacent southern Chihuahua, Mexico, from 1550 to 2350 m elevation. Flowering from July to October.

Representative collections: MEXICO: Chihuahua: Norogachic, 13-25 Nov 1885, *Palmer JJ* (GH); Pawiciki, 13 Jul 1965, *Pennington 547* (TEX). Durango: 5.5 mi E Ojito, 11 Aug 1971, *Reveal et al. 2733* (ARIZ, BRY, CAS, GH, KANS, KSC, MEXU, MICH, MO, NY, OKL, OSC, RM, RSA, TEX, UC, US, UTC, WTU); 11 mi W Ojito, 16 Sep 1972, *Reveal & Hess 3126* (BRY, NY, US, UTC).

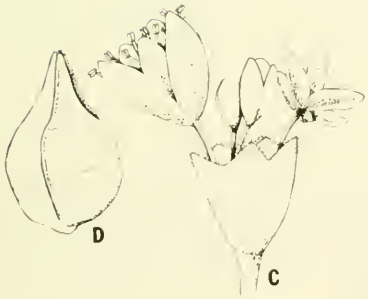
Since this variant was described in 1967, we have seen numerous collections, many of them gathered by ourselves. Not suspected then was the cytological nature of var. *intonsum*. In a routine manner, buds of var. *intonsum* were gathered in 1971, and counts were made during the following winter. With the discovery that var. *intonsum* represented an octoploid ($n=40$), we returned to the Ojito area west of Hidalgo del Parral, and carefully searched for possible parental sources of what we came to suspect was an auto-allopolyploid origin of var. *intonsum*. The dense tomentum associated with the narrow leaves lead us to suspect that one parent was var. *nemorosum* which we had found in 1971, just to the west of var. *intonsum*. A series of populations of both varieties were sampled, and var. *nemorosum* proved to be a consistent tetraploid ($n=20$), and var. *intonsum* an octoploid. No chromosomal irregularities were noted in either taxon. However, populations of what we suspected was the other parent, var. *atrorubens*, could not be found in the immediate area, nor even in the foothills around Parral. Nevertheless, we still feel that var. *intonsum* quite possibly is of a hybrid origin and is now a stable, self-reproducing taxon.

1e. *Eriogonum atrorubens* var. *nemorosum* Hess & Reveal

Fig. 40

Eriogonum atrorubens Engelm. in Wisliz. var. *nemorosum* Hess & Reveal, var. nov.—A var. *atrorubens* foliis linearibus et tomentosis subra et a var. *intoso* foliis angustioribus differt.—Typus: Along the dirt road from Hidalgo del Parral toward El Vergel out of San Francisco del Oro, about 60 mi W Parral and 18.5 mi W Ojito, Sierra Madre Occidental, Durango, Mexico, at about 2450 m elevation, 11 Aug 1971, *Reveal, Hess, & Kiger 2737*. Holotypus: US! Isotypi: ARIZ, ASU, BRY, CAS, COLO, GH, K, KANS, KSC, MEXU, MICH, MO, OKL, OSC, P, RM, RSA, SMU, TEX, UC, UTC, WTU!

Plants erect, 4-6 dm high; *leaves* linear, (4) 6-12 (15) cm long, (0.2) 0.3-0.7 (0.9) cm wide, sparsely strigose and



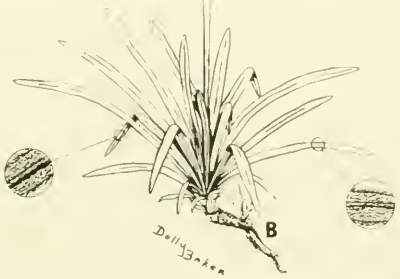


Fig. 40. Illustration of *Eriogonum atrorubens* var. *nemorosum* showing the general habit (A) and a detail of a single plant (B) with close-up detail of the lower leaf surface, an involucre and flowers (C), and a mature achene (D).

greenish above, densely grayish-tomentose below; *stems* weakly fistulose in some; *involucres* turbinate-campanulate, (1) 1.5-2 (2.5) m long, 1-2 (2.5) mm wide, the bractlets slightly hirsutulous and distinctly glandular; *flowers* glabrous; $n=20$ (Figs. 9, 10).

Locally common in pine-oak woodlands on the forest floor or on rocky limestone outcrops, in the Sierra Madre Occidental in northern Durango and extreme southern Chihuahua, Mexico, from 2400 to 2600 m elevation. Flowering from late July to October.

Representative collections: MEXICO: Chihuahua: 69 mi W Parral, 7 Oct 1969, *Correll & Gentry 22885* (ENCB); on road toward Campo Alegre, 6.1 mi W Agua Caliente 15 Sep 1972, *Reveal & Hess 3121* (BRY, MEXU, NY, US, UTC). Durango: 25.1 mi W Ojito, 15 Sep 1972, *Reveal & Hess 3105* (BRY, NY, US, UTC); 17.9 mi W Ojito, 16 Sep 1972, *Reveal & Hess 3124* (ARIZ, BRY, CAS, GH, MEXU, MICH, MO, NY, OKL, RSA, TEX, UC, US, UTC).

The var. *nemorosum* differs from var. *atrorubens* in being a smaller plant with long, slender, linear leaves that are gray-tomentose on the lower surface, and in a number of features relating to the size and shape of the involucre, flowers, and fruits. It occurs in more shaded and mesic locations than does var. *atrorubens*, and generally (although not always) occurs at a higher altitude. It has not been found with, or near, any known population of var. *atrorubens*. The new variety is also similar to var. *intonsum*, differing mainly in leaf shape and the overall size of the plants. Although the two occur in the same general region of Mexico, the var. *intonsum* is found at a lower elevation and on much drier sites. We have noted no overlap in the range of the two varieties.

1f. *Eriogonum atrorubens* var. *rupestre* (S. Stokes) Hess & Reveal

Fig. 41.

Eriogonum atrorubens Engelm. in Wisliz. var. *rupestre* (S. Stokes) Hess & Reveal, stat. & comb. nov., based on *E. rupestre* S. Stokes, Gen. Eriog. 21, 1936.—Rocky limestone slopes near Chihuahua, Chihuahua, Mexico, Aug 1885, *Pringle 285*. Holotype: UC! Isotypes: BM, BRY, DS, E, F, G, GH, ISC, K, MIN, MO, NY, P, PENN, PH, RSA, US, VT!

Plants erect, 4-9 dm high; *leaves* oblong to oblanceolate, 4-10 cm long, 1-2.5 cm wide, densely strigose on both surfaces; *stems* not fistulose; *involucres* turbinate-campanulate, 1.5-2 mm long and wide, the bractlets fringed with scattered hyaline hairs and shorter, capitate, gland-tipped hairs; *flowers* densely strigose without.

Apparently local and infrequent, restricted to low, dry, rocky limestone outcrops in the desert ranges of east central Chihuahua, just northeast and east of Chihuahua, Mexico, from about 1600 to 2000 m elevation. Flowering from June to September.

Representative collections: MEXICO: Chihuahua: Galdeano, E slope of Sierra de Santa Eulalia, 11 Sep 1934, *Pennell 18673* (NY, US); 4 km SE Rancho Encinillas, Sierra de Encinillas, near Fierro, 8-9 Jul 1941, *Stewart 760* (GH, TEX).

We have not seen the var. *rupestre* in the field, although we have explored in the mountains around Chihuahua in search of it. We both observed in our 1967 papers on this species complex that *Eriogonum rupestre* ought to be considered a variant of *E. atrorubens*, echoing an opinion expressed long before us by Johnston (1944). Still, we have been reluctant to reduce the species until we saw the plants in the field. Now we are making the reduction in spite of our lack of first-hand knowledge, feeling that the one major discriminating feature—the pubescent flowers—is not enough to maintain this as a distinct species.

IB. Eriogonum subsect. Adenogonum

Eriogonum Michx. sect. *Pterogonum* subsect. *Adenogonum* Hess & Reveal, subsect. nov.—A subsect. *Pterogono* petiolis late laminaribus et inflorescentiis e non nisi aliquot ramis differt. Typus: *Eriogonum ciliatum* Torr. ex Benth. in DC.

Plants of moderate height, 2-6 dm high; *leaves* oblanceolate to elliptic or spathulate, 1-5 cm long, 0.5-2.5 cm wide, usually on broadly laminar petioles; *stems* erect, slender, glabrous or more frequently glandular at least at the nodes; *inflorescences* open, sparsely branched, glabrous or glandular at the nodes; *flowers* white to cream-colored, or if maroon, then with a bright yellowish center within, glabrous or glandular.

A subsection of four species.

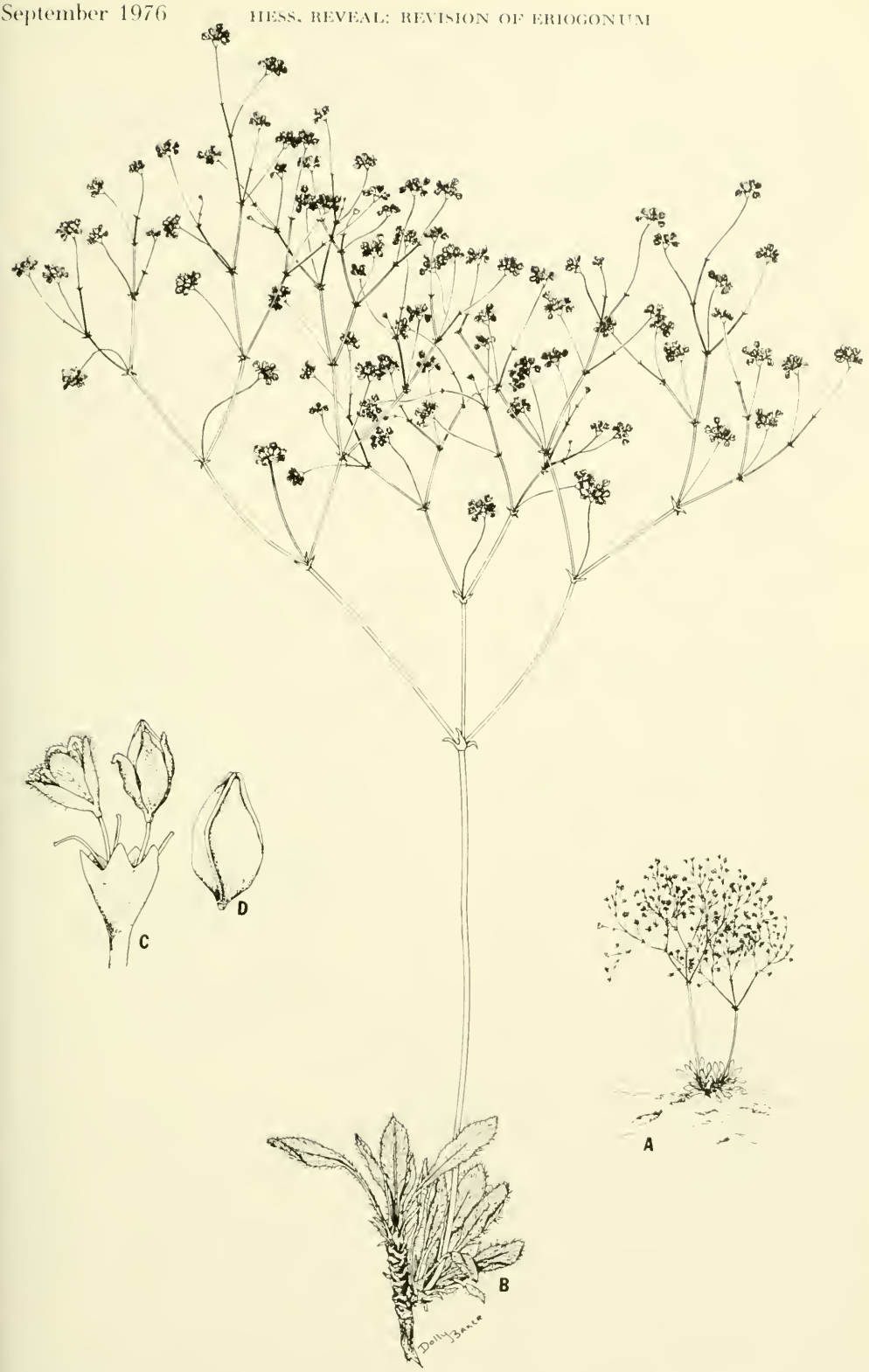


Fig. 41. Illustration of *Eriogonum atrorubens* var. *rupestre* showing the general habit (A) and a detail (B) of a single plant. with an involucre and strigose flowers (C), and a mature achene (D).

Key to the Species of Subsect. Adenogonum

A. Flowers maroon; plants of the foothills along the western slope of the Sierra Madre Oriental and associated desert mountain ranges in Nuevo León, Coahuila, Tamaulipas, and San Luis Potosí, Mexico ..... 2. *E. ciliatum*

AA. Flowers white or cream-colored; plants of low desert ranges in gypsophilous area.

B. Nodes and some branches glandular; tepals minutely glandular; inflorescences of 1-4 divisions.

C. Leaves elliptic, 1-2 cm long, 0.8-1.2 cm wide, glabrous except for the ciliated margins; plants of Nuevo León ..... 3. *E. fimbriatum*

CC. Leaves narrowly oblanceolate to narrowly elliptic, 1.5-4 cm long, 0.3-0.9 cm wide, villous; plants of Zacatecas and San Luis Potosí ..... 3. *E. viscanum*

BB. Nodes and branches glabrous; tepals glabrous; inflorescences of 3-5 divisions; leaves broadly elliptic, (1) 1.5-2.5 (3) cm long, (0.5) 1-1.5 cm wide, glabrous below, villous above; plants of Zacatecas and San Luis Potosí ..... *E. clivosum*

2. *Eriogonum ciliatum* Torr. ex Benth. in DC.

Fig. 42.

Eriogonum ciliatum Torr. ex Benth. in DC., Prodr. 14: 20. 1856.—Camp at Buena Vista, south-southwest of Saltillo, Coahuila, Mexico, 28 Jul 1848. *Edwards s.n.* Lectotype: NY!

Tall, erect herbaceous perennials 2-6 dm high from a short, branched, woody caudex; *leaves* essentially basal, the leaf-blades spathulate, 1-5 cm long, 1-2.5 cm wide, glabrous on both surfaces except for the strigose midvein and margin, the apex obtuse with an apiculate tip, the base abruptly tapering to a broad laminar petiole, the petiole 0.5-4 (5) cm long, winged, ciliated, the petiole-base glabrous on both surfaces or merely strigose without; *stems* erect or nearly so, slender, not fistulose, 2-4 dm long, glabrous except at the nodes where stipitate-glandular in most; *inflorescences* usually open, cymose, mostly with one side suppressed, or dichotomously branched 1-3 times, occasionally reduced to a single, terminal involucre, 1-3 (4) dm long, the main branch bracted, the secondary branch of the dichotomy an elongated peduncle, glabrous except for the stipitate-glandular nodes and lower segments; *bracts* scalelike, ternate, 1-5 mm long, narrowly triangular to linear, usually glandular without, occasionally glabrous, sparsely ciliated on the margin, connate at the base; *peduncles* ascending or erect, straight or slightly curved, the first peduncle 5-20 cm long, the succeeding peduncles (1) 2-7 cm long, glabrous except for the glandular base; *involucres* campanulate, 3-5 mm long, 3-5 (7) mm wide, glabrous within and without, the 5 rounded, shallow teeth 1-1.8 (2) mm long, often ciliate, the bractlets linear-oblanceolate, 1.5-3 (4) mm long, densely hirsutulous with long, whitish cells, the pedicels 2-4 (5) mm long, glabrous; *flowers* maroon with a darker reddish midrib and often a bright, golden-yellow center within, 1.5-2.5 mm long in anthesis, becoming 3-4 mm long in fruit and somewhat greenish red at the base, glabrous, the tepals monomorphic, lanceolate to obovate, connate at the base; *stamens* slightly exserted, 1.5-2.5 mm long, the filaments glabrous, the anthers red; *achenes* greenish brown to light brown, 3-4.5 mm long, ovate, slightly ridged the entire length; $n=20$ (Figs. 11, 12).

Locally common on dry low hills and plains in *Larrea*, pine-oak, or pinyon-juniper woodlands mainly along the foothills of the Sierra Madre Oriental and associated desert ranges, from western Nuevo León and southeastern Coahuila southward through central Tamaulipas to north central San Luis Potosí, Mexico, from 1200 to 2300 m elevation (Map 2). Flowering from May to September.

REPRESENTATIVE SPECIMENS: MEXICO: Coahuila: Near Buena Vista, 22 May 1847, *Gregg 737* (MO); Las Playas, 24 May 1973, *Johnston et al. 11210D* (LL, US); San Lorenzo Canyon, S of Saltillo, 21-23 Sep 1904, *Palmer 385* (MO,

Fig. 42. Illustration of *Eriogonum ciliatum* showing the general habit (A) and a detail (B) of a single plant, with an involucre and flowers (C), and a mature achene (D).

NY, US); Carneros Pass, 4 Sep 1889, *Pringle 2379* (BR, G, MO, NDG, NY, P, US); 0.3 mi E Mex. Hwy 57 along rd to San Lirios, SE of Saltillo, 5 Aug 1971, *Reveal et al. 2612* (ARIZ, BRY, CAS, GH, MEXU, MICH, MO, NY, OKL, RSA, TEX, UC, US, UTC); 0.5 mi S Estacíon Carneros, 5 Aug 1971, *Reveal et al. 2616* (BRY, NY, US, UTC). Nuevo León: Ascensión, Jun 1930, *Viereck 527* (US). San Luis Potosí: Charcas, Jul-Aug 1934, *Lundell 5463* (ARIZ, US); 6 km E Laguna Seca, 10 Sep 1955, *Rzedowski 6515* (MO, TEX). Tamaulipas: 22 km SE Bustamante toward Tula, 20 May 1973, *Johnston et al. 11148* (ILL, US); near Miguihuana, 8 Aug 1941, *Stanford et al. 748* (ARIZ, MO, NY).

Unlike the other members of the subsection Adenogonum that have whitish or cream-colored flowers, *Eriogonum ciliatum* has maroon flowers similar to those of *E. atrorubens* of Pterogonum and *E. hemipterum* of section Astra. However, upon a closer examination one quickly discovers the large, yellowish center of the flower-tube—a feature unique to *E. ciliatum* and not found in the other species in the subgenus. In addition, characteristics such as the laminar petioled leaves, the glandular nodes, and the highly reduced inflorescences are not evident in subsection Pterogonum but are shared with the other members of Adenogonum.

This species is easily recognized in the field by the combination of ciliated, usually spathulate leaf-blades, maroon flowers, and reduced inflorescences. Rarely, whorled leaves may be found in the axils of the ternate bracts at the first node. However, no confusion should occur between *Eriogonum ciliatum* and the species of Astra which have true cauline leaves and no fused ternate bracts below them. In addition, the known ranges of the species of Astra do not overlap the geographical range of *E. ciliatum*, and simply by distribution the two can be separated.

3. *Eriogonum fimbriatum* Hess & Reveal

Fig. 43.

Eriogonum fimbriatum Hess & Reveal, spec. nov.—A *E. ciliato* floribus albis et a *E. viscano* foliis latioribus, a *E. clivoso* caulibus glandulosis differt.—Typus: Along Mexico Highway 57, 11 mi S San Roberto Junction, Nuevo León, Mexico, on low limestone hills at about 1800 m elevation, 19 Sep 1972, *Reveal & Hess 3144*. Holotypus: US! Isotypi: ARIZ, BRY, CAS, COLO, G, GH, K, MEXU, MICH, MO, NY, OKL, P, RSA, US, UTC, WTU!

Erect herbaceous perennials 2-3 dm high from a small, compact, slightly woody caudex; *leaves* basal, the leaf-blades elliptic, 1-2 cm long, 0.8-1.2 cm wide, glabrous and green on both surfaces, the margin ciliated with villous hairs, the apex mostly slightly acuminate, the base abruptly tapering to a winged petiole, the petiole (1) 1.5-2.5 cm long, glabrous, ciliated, the petiole-base glabrous except for the margin; *stems* erect, slender, not fistulose, 0.5-1.5 (2) dm long, glabrous throughout; *inflorescences* open, cymose, divided only once or twice with an ultimate, non-dichotomous node above, (3) 5-8 (10) cm long, glabrous above, glandular below at the node with small, nearly sessile, white, capitate glands; *bracts* scalelike, 1-2.5 mm long, lanceolate, glandular without, essentially glabrous within, connate at the base; *peduncles* slender, erect, straight or slightly curved, the first peduncle up to 6 cm long, the succeeding peduncles up to 3 cm long, both glabrous except for the stipitate-glandular nodes and lower segments; *involucres* campanulate, 2.5-3 mm long, 2.8-3.5 (4) mm wide, glabrous within and without, except for the ciliate margins of the teeth, the 5 broadly acute lobes 0.7-1 mm long, the bractlets linear-oblanceolate, 2.5-3.5 mm long, densely villous with long, non-glandular cells, the pedicels 1.5-2 mm long, glabrous; *flowers* white to yellowish white with a broad brownish red midrib and greenish brown base, (2) 2.5-2.8 mm long in anthesis, becoming 3-3.2 mm long in fruit, glabrous except for the minute glands on the midrib and base, the tepals essentially monomorphic, elliptical, those of the outer whorl slightly broader than those of the inner whorl; *stamens* included, 1.8-2.5 mm long, the filaments glabrous, the anthers yellowish; *achenes* light brown, 3-3.5 mm long, ovate, only the upper ⅓ of the fruit distinctly ridged; $n=20$ (Fig. 13).

Locally common on dry gypsophilous hills and flats associated with *Larrea* south of San Roberto Junction, Nuevo León, Mexico, from 1800 to 1850 m elevation (Map 2). Probably flowering from August to October.

REPRESENTATIVE SPECIMENS: MEXICO: Nuevo León: 11 mi S San Roberto Junction, 5 Sep 1971, *Bacon et al. 1113* (TEX); 14-15 mi S San Roberto Junction, 20 Aug 1973, *Powell & Tomb 2564* (US).

Fig. 43. Illustration of *Eriogonum fimbriatum* showing the general habit (A), and a detail (B) of a single plant, with an involucre and flowers (C), and a mature achene (D).

Currently, *Eriogonum fimbriatum* is known from only one area south of San Roberto Junction in Nuevo León. It is to be expected elsewhere in the area. We assume its distribution will be like that of the related *E. viscanum*—very local, very isolated, and in widely scattered locations. Likewise, we can attest that it and most likely *E. viscanum* are difficult to see in the field, with their small stature, thin stems, inconspicuous flowers, and strictly basal leaves. And when one considers the feeding habits of goats, sheep, horses, burros, and cattle on these species in northern Mexico, it is often a matter of luck that more than a single specimen can be found.

Eriogonum fimbriatum is most closely related to *E. viscanum*. The two differ mainly in the shape and size of the basal leaves, the leaf pubescence, and the arrangement of the glands along the stems. The former occurs to the east of the latter, but in essentially similar habitats. A comparison of the two descriptions will reveal the other subtle differences as well, but on the whole these are the major, macromorphological differences.

4. *Eriogonum viscanum* Hess & Reveal

Fig. 44.

Eriogonum viscanum Hess & Reveal, spec. nov.—A *E. fimbriato* foliis longioribus, laminis villosis (non glabris), pedunculis glandulosis et a *E. clivoso* caulibus glandulosis differt.—Typus: Cedros, Jun-Aug 1908, *Lloyd 116*. Holotypus: MO! Isotypi: UC, US!

Erect herbaceous perennials 2-3 dm high from a small, compact, slightly woody caudex; *leaves* basal, the leaf-blades oblanceolate to narrowly elliptic, 1.5-4 cm long, 0.4-0.9 cm wide, villous on both surfaces or glabrous above except for the villous midvein, the margin ciliated with sparse, villous hairs, the apex acute, the base tapering gradually to a narrowly winged petiole, the petiole 0.5-1 cm long, villous especially along the margin; *stems* erect, slender, not fistulose, 1-1.5 dm long, glabrous throughout; *inflorescences* open, cymose, divided 2-4 times with an ultimate non-dichotomous node above, 5-15 cm long, glabrous on the upper half of each branch, the lower half and each node glandular with small, capitate, reddish glands; *bracts* scalelike, 1-3 mm long, narrowly lanceolate, glandular without, essentially glabrous within or with a few scattered hairs, connate at the base; *peduncles* slender, erect, straight or slightly curved, the first peduncle up to 6 cm long, the succeeding peduncles up to 3 cm long, glandular nearly throughout their length with stipitate-glands; *involucres* campanulate, 1.5-2 mm long, 2.5-3 (3.5) mm wide, glabrous within and without, the 5 broadly acute teeth 0.5-0.7 mm long, ciliate, the bractlets linear-oblanceolate, 1.5-2.5 mm long, densely villous with long non-glandular cells, the pedicels 1-1.5 mm long, glabrous; *flowers* white to cream with a broad brownish red midrib and base, 1.5-2.5 mm long in anthesis, becoming 2.5-3 mm long in fruit, glabrous or minutely glandular without, glabrous within, the tepals essentially monomorphic, elliptical, those of the outer whorl slightly broader than those of the inner whorl; *stamens* included, 1.5-2.5 mm long, the filaments glabrous, the anthers reddish-yellow; *achenes* (when still immature) about 3 mm long, narrowly ovate, only the upper ⅓ of the fruit distinctly ridged.

Rare and local, known only from scattered locations on dry gypsum hills and flats west of Concepción del Oro, Zacatecas, and southwest of Cedral, San Luis Potosí, Mexico, from 2000 to 2200 m elevation (Map 2). Probably flowering from May to September.

REPRESENTATIVE SPECIMENS: MEXICO: San Luis Potosí: 17.5 km SW Cedral, 17 May 1973, *Johnston et al. 11063A* (LL). Zacatecas: 2 km SE Caopa, 17 Jun 1972, *Chiang et al. 7881A* (LL); on hills near Cedros, Aug 1908, *Kirkwood 224* (F).

Eriogonum viscanum is clearly related to *E. fimbriatum*, differing, as noted previously, mainly in leaf characters and pubescence features. At present, the species is known only from four collections, three of which consist of an individual plant. The Kirkwood collection comes from the same area as the type and quite possibly was collected at the same time and place as the type. Lloyd and Kirkwood were employed by the same company at the time of these collections. We have attempted to locate this species in the field without success. Reveal and N. Duane Atwood, then at Brigham Young University, also searched in the Cedros area, but not one plant was found in all our joint or separate efforts. Although the

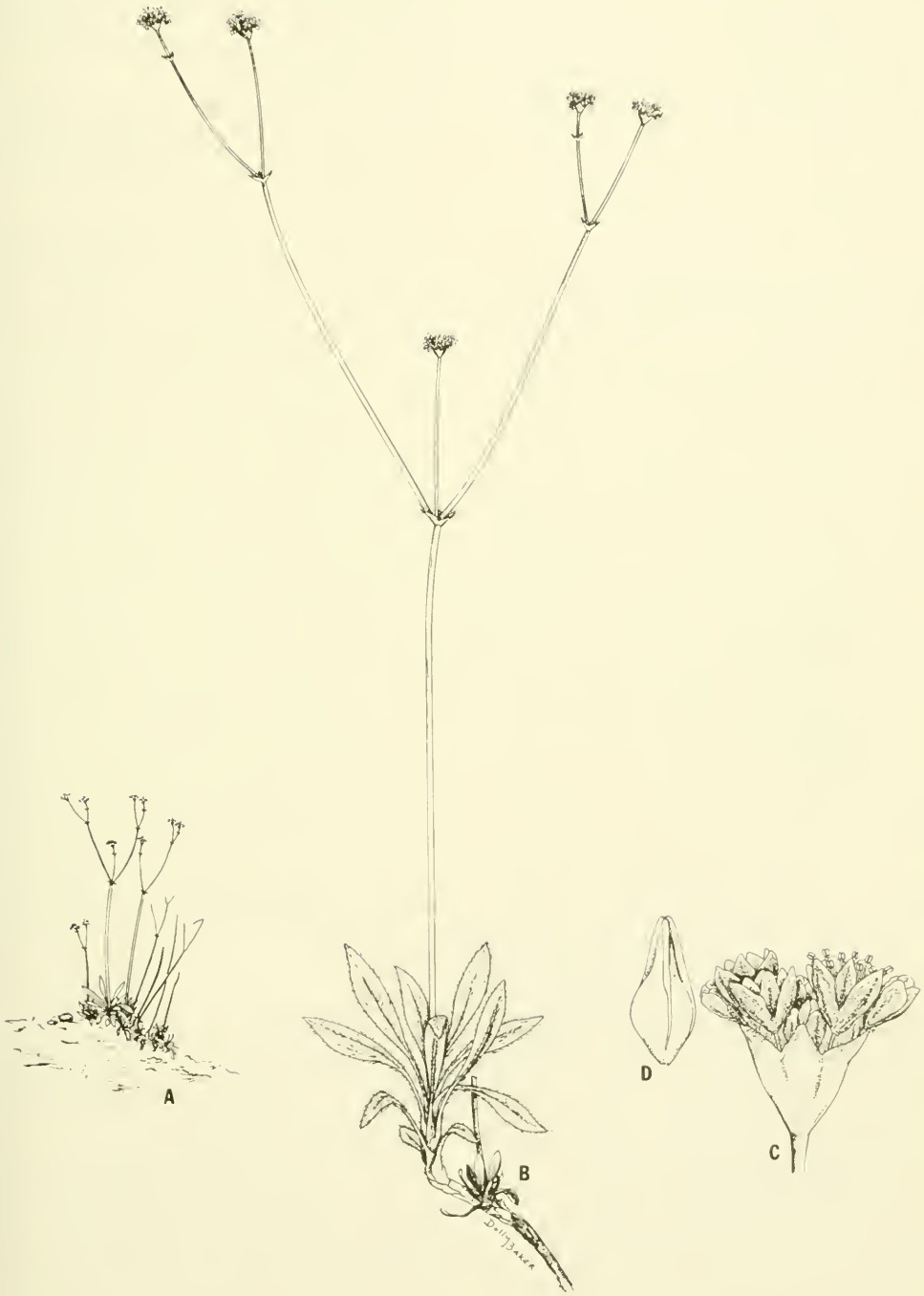


Fig. 44. Illustration of *Eriogonum viscanum* showing the general habit (A) and a detail (B) of a single plant, with an involucre and flowers (C), and an immature achene (D).

description is based on this meager material, we are still convinced that the species is unique.

We have seen two collections which might represent another new species in this group. It is from a gypsum outcrop 1.5 miles southwest of Las Delicias in Coahuila. Hopefully more material of this entity will be collected and the nature of the plants determined.

5. *Eriogonum clivosum* Hess & Reveal

Fig. 45.

Eriogonum clivosum Hess & Reveal, spec. nov.—A *E. fimbriato* et *E. viscano* inflorescentis glabris differt.—Typus: Along Mexico Highway 49, 53 mi E Zacatecas, 5 mi W El Tecomate and 4.5 mi E turnoff to Salinas del Peñon Blanco, on low limestone hills 1 km N of the highway, at 1900 m elevation, San Luis Potosí, Mexico. 18 Sep 1972, *Reveal & Hess 3143*. Holotypus: US! Isotypi: BRY, K, NY, UTC!

Erect herbaceous perennials 2.5-3 dm high from a stout, compact, slightly woody caudex; *leaves* basal, the leaf-blades broadly elliptic, (1) 1.5-2.5 (3) cm long, (0.5) 1-1.5 cm wide, glabrous below, sparsely pubescent above with long villous hairs, the margin ciliated with dense villous hairs, the apex obtuse to mucronate, the base abruptly tapering to a non-winged petiole, the petiole 1-5 cm long, strigose, the petiole-base densely strigose without, sparsely so within; *stems* erect, slender, not fistulose, 1-1.6 dm long, glabrous; *inflorescences* open, cymose, divided 3-6 times, 1-1.5 dm long, the branches and nodes glabrous; *bracts* scalelike, 1-4 mm long, triangular to lanceolate, glabrous without, sparsely pubescent within, connate at the base; *peduncles* slender, erect, straight or slightly curved, 1-5 cm long, glabrous; *involucres* turbinate-campanulate, (2) 2.5-3 mm long and wide, glabrous within and without, the 5 acute teeth 0.7-1 mm long, the bractlets linear-oblanceolate, 2-2.5 mm long, densely glandular, the pedicels 2-4 mm long, glabrous; *flowers* white to cream colored with a faint yellowish hue and with a wide reddish brown midrib and base, (1.5) 2-2.5 mm long in anthesis, becoming 2.5-3 mm long in fruit, glabrous, the tepals monomorphic, lanceolate to oblong; *stamens* slightly exserted, 2-2.5 mm long, the filaments glabrous, the anthers pink to light red; *achenes* light brown, 3 mm long, ovate, ridged nearly the entire length of the fruit; $n=20$ (Figs. 14, 15).

Local and infrequent to rare on dry limestone hills and flats east of Salinas del Peñon Blanco along the Zacatecas-San Luis Potosí state line, Mexico, from 1900 to 2000 m elevation (Map 2). Flowering from July to October.

REPRESENTATIVE SPECIMENS: MEXICO: San Luis Potosí: Known only from the type collection. Zacatecas: 10 mi SE Salinas, 13 Jul 1966, *Moran 13347* (SD); 10 mi SE Salinas, 7 Aug 1971, *Reveal et al. 2664* (NY, US).

It is difficult to interpret the significance of the eglandular nature of *Eriogonum clivosum*, with its more highly branched inflorescence and the lack of a distinctly winged petiole so typical of the other species of the subsection Adenogonum. We have placed *E. clivosum* with *E. viscanum* and *E. fimbriatum* firstly on the basis of flower color—a characteristic we chose not to consider important in the case of *E. ciliatum* and the subsection Pterogonum. This inconsistency is balanced by other characteristics such as the leaf shape and pubescence of *E. clivosum* which are similar to that of *E. ciliatum* and *E. fimbriatum*. The inflorescence of *E. clivosum* is more branched than any other member of *Adenogonum*, but not nearly as much as that seen in *E. atrorubens* of subsection Pterogonum. And lastly, *E. clivosum* occurs in the low, dry desert ranges, similar to those occupied by *E. viscanum* and *E. fimbriatum*, and this ecological feature is not shared by *E. atrorubens* except for var. *rupestre*. On the whole we have felt it best to associate *E. clivosum* with Adenogonum rather than establishing a distinct subsection for it.

II. Eriogonum sect. Peregrina

Eriogonum Michx. subgen. *Pterogonum* (H. Gross) Reveal sect. *Peregrina* Hess & Reveal, sect. nov.—A sect. Pterogono plantis glandulosis et caulibus foliatis differt. Typus: *Eriogonum greggii* Torr. & Gray.

Low, erect perennial herbs with few to several stems arising from branched caudices, glandular throughout; *leaves* basal and cauline in the axils of bracts, spathulate, hispid and stipitate-glandular or rarely glabrous on both surfaces; *bracts* ternate, scalelike to semifoliaceous, connate at the base; *peduncles* long and usually stout; *involucres* campanulate, the

Fig. 45. Illustration of *Eriogonum clivosum* showing the general habit (A) and a detail (B) of a single plant, with an involucre and flowers (C), and a mature achene (D).

5 teeth mostly acute, the bractlets linear-oblanceolate, hirsutulous, the pedicels glandular and hispid; *flowers* yellowish white often with a broad reddish brown to brown midrib, the tepals strigose; *anthers* green or red; *achenes* ridged nearly the entire length of the fruit, glabrous.

The section Peregrina is composed of but one species, *Eriogonum greggii*. It differs from all other species in the subgenus in being densely glandular and hispid, having a suppressed inflorescence, strigose tepals, and a haploid chromosome number of $n=16$. The single species ranges from extreme southern Texas southward into northeastern Mexico, occurring mainly in the limestone ranges and mountains associated with the Sierra Madre Oriental.

We have placed *Eriogonum greggii* in subgenus Pterogonum following Stokes (1936) rather than Watson (1877), who associated the species with the subgenus Ganysma. As discussed previously, we have concluded that this is the only reasonable treatment, but our efforts to satisfactorily place *E. greggii* in Pterogonum have been difficult. It seemed to us that we could not associate it with *E. atrorubens*, and certainly not with *E. alatum* or *E. hieracifolium*. On the basis of the broadly laminar petioles, spathulate leaves, and modified inflorescences, it did not seem to be that closely related to *E. ciliatum*. However, the features of pale yellowish white flowers with the broad reddish midvein and glandular pubescence make it possible to relate it to other members in subsection Adenogonum. But because the plants of *E. greggii* are wholly glandular and hispid, the tepals strongly strigose, and the leaves both cauline and basal, we could only propose a distinct section for it while acknowledging that it is more closely related to Pterogonum than either Astra or Alata.

6. *Eriogonum greggii* Torr. & Gray

Fig. 46.

Eriogonum greggii Torr. & Gray, Proc. Amer. Acad. Arts 8: 187. 1870, based on *E. ciliatum* Torr. ex Benth. in DC. var *foliosum* Torr. in Emory, Rep. U.S. & Mex. Boundary Surv. 175. 1859.—High plains at San Juan de la Vegueria, Coahuila, Mexico, 20 May 1847, *Gregg s.n.* Holotype: NY! Isotypes: GH, MO!

Low, erect herbaceous perennials 1-4 dm high from a short, woody caudex; *leaves* basal and cauline in axils of ternate bracts, the basal leaf-blades broadly spathulate, 2-6 (10) cm long, 0.5-2 (2.5) cm wide, glabrous except for the ciliated margins and midvein, or hispid and uniformly stipitate-glandular on both surfaces, the apex obtuse or infrequently acute, often with an apiculate tip, the base long cuneate and tapering to a ±winged petiole, the petioles 0.5-2 cm long, hispid and glandular, the cauline leaf-blades oblanceolate, obovate, or spathulate, in a whorl of 3-7 at each node, 0.5-4 cm long, 0.2-1.5 (2) cm wide, similar to the basal leaves only more hispid or glabrous except for the margins and midveins, the apex acute to mostly obtuse, the base cuneate, sessile; *stems* erect or nearly so, slender, 5-15 cm long, glandular; *inflorescences* cymose with one side suppressed, branching 3-15 times, 1-3 dm long, the main branch bracted and divided with the lateral branches highly reduced or mostly lacking, the secondary branch of the dichotomy actually an elongated peduncle, glandular throughout; *bracts* scalelike to semifoliaceous, ternate, 3-15 (22) mm long, lanceolate, glandular and hispid with ciliated margins, or merely glabrous and ciliated, connate at the base; *peduncles* ascending to erect, straight or slightly curved, 1-6 (7) cm long, glandular and hispid; *involucres* campanulate, 1.5-3 mm long, 3-5 mm wide, slightly to densely strigose and glandular without, glabrous within except for the ciliated margins, the 5 acute teeth 1-1.5 mm long, the bractlets linear-oblanceolate, 1.5-2 (2.5) mm long, slightly hirsutulous with glandular and non-glandular hairs, the pedicels 2-3 (4) mm long, glandular and hispid; *flowers* yellowish white with a broad and predominant dark reddish brown to brown midrib and base, 1.5-2.5 mm long in anthesis, becoming more reddish and 2.5-3.5 mm long in fruit, strigose without, glabrous within, the tepals monomorphic, lanceolate to oblong; *stamens* slightly exserted, 1.5-2 mm long, the filaments glabrous, the anthers green or red; *achenes* reddish brown, 3-4 mm long, ovate, slightly ridged the entire length of the fruit; $n=16$ (Figs. 16, 17, and 18).

Locally common in open grasslands, dry arid slopes, or pine-oak woodlands on the plains and lower foothills of the desert mountain ranges and Sierra Madre Oriental, from extreme east central and

Fig. 46. Illustration of *Eriogonum greggii* showing the general habit (A) and a detail (B) of a single plant, with an involucre and flowers (C), and a mature achene (D).

southeastern Coahuila and adjacent west central Nuevo León, Mexico, northward to Hidalgo Co., Texas, from 100 to 2300 m elevation (Map 2). Flowering from March to October.

Representative collections: MEXICO: Coahuila: Santa Catarina, 26 Apr 1939, *Frye & Frye 2512* (DS, MO, NY, UC, US, UTC); 1 mi N Rancho de la Gavia, N side Sierra de la Gavia, 18 Mar 1973, *Johnston et al. 10277H* (LL, US); Saltillo, May 1898, *Palmer 166* (MO, NY, S, UC, US); 3.6 mi S Santa Terésa, Sierra de la Muralla, 4 Aug 1971, *Reveal et al. 2607* (BRY, MEXU, NY, US, UTC). Nuevo León: N Dr. Arroyo, 5 Sep 1971, *Bacon et al. 1131* (TEX); 9 km W Villa Garcia toward Icamole, 4 Jul 1973, *Johnston et al. 11601B* (LL, US); 1 mi E Cuesta de Aves, between Saltillo and Monterrey, 22 Sep 1973, *Reveal & Atwood 3382* (ARIZ, BRY, CAS, GH, MEXU, MO, NY, OKL, RSA, TEX, UC, US, UTC).

In all its localized phases, *Eriogonum greggii* may be quickly recognized by its general habit and vestiture. It is rather variable, however, in the amount and distribution of both glands and hairs, as some individual plants may have glabrous leaf-blades (except for the margins and midvein), or merely hispid leaves, or only glandular leaves. In less frequent cases, the stems show a similar degree of variability, but the vestiture of the leaves and stems is not always correlated. No geographic or edaphic restrictiveness is evident concerning this feature and intermediates occur commonly. Some plants may be less erect than others in the same population, while there is a great range in flowering times from individual to individual. While this variation may be seen in the field, the species is easy to distinguish throughout its growth cycle and cannot be confused with other species of the genus.

III. Eriogonum sect. Astra

Eriogonum Michx. subgen. *Pterogonum* (H. Gross) Reveal sect. *Astra* Hess & Reveal, sect. nov.—A sect. Pterogono presentia foliis caulibus atque inflorescentiis paniculatis differt et a sect. Alato herba perennia a ramosus caudice; achaenia alata superioribus tertioribus, pilosa. Typus: *Eriogonum hieracifolium* Benth. in DC.

Tall, erect perennial herbs mostly with a single stem arising from a branched caudex; *leaves* basal and alternate, the leaf-blades spathulate to oblanceolate, strigose to woolly pubescent on both surfaces; *bracts* ternate, scalelike, connate at the base; *inflorescences* open, elongated, paniculate cymes; *peduncles* usually stout; *involucres* turbinate to campanulate, the 5 teeth mostly acute to truncate, the bractlets linear-oblanceolate, glabrous or glandular, sometimes ciliate, the pedicels glabrous or pilose at the base; *flowers* maroon to yellow or cream colored, the tepals glabrous to strigose; *anthers* maroon to yellow; *achenes* winged on the upper third, pilose at the apex.

The species of sections Astra and Alata have leaves that are alternate on the stems, a characteristic not shared by any of the species in sections Pterogonum and Peregrina. The only glandularness present in Astra is that associated with the minute bractlets found within the involucre. The cymose paniculate inflorescence is quite distinct, giving the plants of Astra a totally different appearance from those species previously discussed.

The multiple branched caudices, many of them with flowering stems, distinguish Astra from the monocarpic condition of section Alata. In addition, most of the species of Astra have fruits that are pilose and winged on the upper third as opposed to the plants of Alata which have glabrous fruits that are winged the entire length. The distribution of the members of Astra is primarily in the mountains and arid regions of the southwestern United States and occasional places in the mountains and foothills of extreme northern Coahuila and northeastern Chihuahua in Mexico. Only *Eriogonum hemipterum* var. *griseum* has its distribution solely in Mexico, and then it is restricted to the mountains essentially just south of the Chisos Mountains of Texas. The other taxa, with the exception of *E. hieracifolium*, are found locally in Texas or just over the boundary into northern Coahuila, Mexico. The exception is also locally common, but with a wider distribution, ranging in a narrow band across western Texas through New Mexico into eastern Arizona and northern Mexico.

The maroon flowers of *Eriogonum hemipterum* easily distinguish it from the remaining members in section Astra. As will be discussed later, it was originally considered as a red-flowered variety of the yellow-flowered *E. hieracifolium*. We have on hand a collection from Coahuila, Mexico, of a possible new taxon which has maroon flowers during early anthesis but which become tinged with yellow in

fruit. The significance of this transitional characteristic is not clear with respect to *E. hemipterum* and *E. hieracifolium* and, as yet, neither of us has been able to obtain more plants or investigate this phenomenon in the field.

We feel strongly that the presence of stem leaves and an elongated paniculated cymose inflorescence, plus the pubescent stems, reflect a more exact association of these species than flower color. Likewise, the distribution of the species of Astra, as opposed to that of Pterogonum, strengthens our position as well. The section is well defined, easily recognized, and composed of only three species.

Key to the Species of Sect. Astra

A. Inflorescences strigose to thinly or densely tomentose; flowers yellow to maroon, strigose.
  B. Flowers yellow, sometimes maturing with a reddish tinge; basal leaves usually densely strigose; east central Arizona across central and southern New Mexico to western Texas, and southward to northern Coahuila and Chihuahua, Mexico ..... 7. *E. hieracifolium*
  BB. Flowers maroon; leaves thinly strigose and green on both surfaces, or densely tomentose below and green above; plants of moderate to high elevation in the mountains of Brewster Co., Texas, south to northern Coahuila and northeastern Chihuahua, Mexico ..... 8. *E. hemipterum*

AA. Inflorescences glabrous; flowers cream colored, glabrous to thinly strigose; grassy hills and plains of west central Texas ..... 9. *E. nealleyi*

7. *Eriogonum hieracifolium* Benth. in DC
Fig. 47.

Eriogonum hieracifolium Benth. in DC., Prodr. 14: 6. 1856—Guadalupe Mountains of northwestern Culberson Co., Texas, or perhaps in southwestern Eddy Co., New Mexico, 13-16 Oct 1849. *Wright 616* (*his 1323*). Holotype: GH! Isotypes: GH, K, NY, UC, US!—*Pterogonum hieracifolium* (Benth. in DC.) H. Gross. Bot. Jahrb. Syst. 49: 239. 1913.

Eriogonum panosum Woot. & Standl., Contr. U.S. Natl. Herb. 16: 118. 1913.—Organ Mountains, Doña Ana Co., New Mexico, Aug 1881. *Vasey s.n.* Holotype: US! Isotypes: GH, ISC, K, P, US!—*Eriogonum leucophyllum* Woot. & Standl. ssp. *panosum* (Woot. & Standl.) S. Stokes, Gen. Eriog. 97. 1936.

Erect herbaceous perennials 4-7 dm high from spreading, branched, woody caudices; *leaves* basal and cauline, the basal leaf-blades oblanceolate to spathulate, (3) 5-15 cm long, 0.5-2 cm wide, sparsely to densely woolly on both surfaces, especially so below, the margin ciliated with longer strigose hairs, the apex obtuse or occasionally acute, the base long cuneate to a narrowly winged petiole, the petiole 0.5-5 cm long, strigose, the petiole-base strigose to woolly especially abaxially, the cauline leaf-blades oblanceolate, 0.5-5 cm long, 0.3-1 cm wide, densely strigose below, less so above, the margin ciliated, the apex mostly acute, the base cuneate to the stem; *stems* erect or nearly so, slender, 3.5-5.5 dm long, densely strigose; *inflorescences* open paniculate cymes, the branches restricted to the uppermost part of the plant, 4-15 (18) cm long, strigose throughout; *bracts* scalelike, ternate 2-8 mm long, linear-triangular to linear-lanceolate, the lowermost infrequently lanceolate and up to 15 mm long, strigose on both surfaces and especially along the margin, connate at the base; *peduncles* erect to ascending, straight or curved, 0.5-3 cm long, strigose; *involucres* turbinate-campanulate to campanulate, 2.5-4 mm long, 2.5-5 mm wide, hirsute to strigose without, glabrous within, the 5 triangular teeth 0.5-1.5 mm long, the bractlets linear-lanceolate, 2-3 mm long, glabrous or minutely glandular, the pedicels 2-5 mm long, glabrous; *flowers* yellow with greenish yellow midribs and bases, 1.5-2.5 mm long in anthesis, becoming 3-5 mm long and reddish in fruit, white-strigose along the midribs and bases without, glabrous within except for a few scattered hairs within at the base, the tepals essentially monomorphic, narrowly ovate, connate at the base; *stamens* slightly exserted, 2-3 mm long, infrequently reduced and sterile, the filaments pilose basally, the anthers yellow, 0.5-0.6 mm

Fig. 47. Illustration of *Eriogonum hieracifolium* showing the general habit (A) and a detail (B) of a single plant, with an involucre and flowers (C), and a mature achene (D).

long; *achenes* yellowish green maturing to a light brown, 4.5-6 mm long, 2.5-3.5 mm wide, pandurate, the upper half winged, strigose, exserted; $n=20$ (Figs. 19, 20).

Common in dry open places, mainly in grasslands, pinyon-juniper, and pine woodlands from northern Coahuila and Chihuahua, Mexico, north through western Texas into southern and central New Mexico, and just entering east central Arizona, from 900 to 2600 m elevation (Map 3). Flowering from July to October.

REPRESENTATIVE COLLECTIONS: [1]MEXICO: Chihuahua: Sierra de los Pinos, Dec 1937, *LeSueur 1533* (TEX): above Santo Tomas between Cuidad Guerrero and Madero, 16 Aug 1959, *Kruckeberg 4918* (DS, NY, US). Coahuila: 43 km from La Linda, 8.5 km S Cuatro Palmas on the road to Mina Aguachile, 30 Jul 1973, *Johnston et al. 11939* (LL, US); 20 mi SE La Linda, 1 mi SE Cerro Aguachile, 30 Jul 1973, *Hendrickson 11590* (US). UNITED STATES: ARIZONA: Apache Co.: 1 mi from junction of Big and Little Diamond creeks, Jul 1964, *Applequist 101* (MNA). Gila Co.: 1 mi N Black River, White Mts., 22 Jun 1930, *Goodman & Hitchcock 1288* (BKL, DS, GH, MO, NY, OKL, UC); 10 mi N Salt River, 26 Jun 1944, *Pultz 1006* (KSC, MO, NY, UC). Navajo Co.: Ft. Apache, 26 Jul 1910, *Goodding 683* (GH, NY, US). NEW MEXICO: Bernalillo Co.: Near Tijeras, 9 Oct 1939, *Barneby 2415* (NY). Catron Co.: 9 mi N Aragon, 9 Jul 1965, *Weber & Salamun 12791* (COLO, DAO, ILL, OKL). Doña Ana Co.: Van Paltens, Organ Mts., 25 Jun 1894, *Wooton s.n.* (US). Eddy Co.: Hero Ranch, near Queen, 4 Aug 1909, *Wooton s.n.* (US). Grant Co.: GOS Ranch, 27 Aug-12 Sep 1911, *Holzinger s.n.* (US). Lincoln Co.: Gray, 17 Aug 1898, *Skehan 96* (GH, K, NY, POM, UC, US). Sierra Co.: 3.5 mi W Hwy. 52, N of Winston, 25 Jul 1965, *Hess 310* (OKL, TEX, UC). TEXAS: Brewster Co.: 29.5 mi W Sanderson, 1 Aug 1971, *Reveal et al. 2552* (BRY, NY, US, UTC). Culberson Co.: 9.5 mi NE Pine Springs, 4 Sep 1967, *Reveal & Davidse 914* (ARIZ, BRY, CAS, DS, GH, IDS, ISC, LL, MO, NY, RM, RSA, SMU, TEX, UC, US, UTC); 10 mi W Kent, 7 Aug 1949, *Warnock & Turner 8944* (LL, SMU). Jeff Davis Co.: 2.5 mi S Kent, 3 Sep 1967, *Reveal & Davidse 913* (ARIZ, BRY, CAS, COLO, CS, DAO, DS, GH, IDS, ISC, KSC, LL, MO, NY, RM, RSA, SMU, TEX, UC, US, UTC). Pecos Co.: 25 mi S Ft. Stockton, 5 Nov 1964, *Correll & Correll 30469* (LL).

The precise locality of Wright's collection of *Eriogonum hieracifolium* is unknown. McKelvey (1955) discusses his itinerary as prepared by Ivan M. Johnston, and from this, it appears that he was in Otero County, New Mexico, at the time of its collection. However, she was not positive about his itinerary and even if she were correct, it is still unlikely that *E. hieracifolium* was collected there, particularly since we have seen no collections of this taxon from Otero County. McKelvey stated that Wright crossed the Guadalupe Mountains in Culberson County, Texas, and this would seem to be the most likely area for his collection. Another possibility is that Wright could have wandered into Eddy County, New Mexico, and made his collection there. However, there is no indication that Wright and the small party of United States troops traveled such a route (Geiser 1948), and because Wright was on foot, he likely remained close to the route taken by the troops. Consequently, it is most likely that the type collection of *E. hieracifolium* was made in the Guadalupe Mountains of Texas and not in New Mexico.

The Vasey collection used by Wooton and Standley (1913) in erecting *Eriogonum panosum* was obtained a short distance to the northwest of the Guadalupe Mountains in the Organ Mountains of New Mexico. These two authors suggested that their new species differed from *E. hieracifolium* in its kind of pubescence and smaller size of the leaves, involucres, and perianth parts. However, the variation among the plants, as examined by us both in the field and in the herbarium, has indicated that recognition of *E. panosum* at any taxonomic rank is wholly unwarranted. The curious aspect of this species is its treatment by Stokes (1936). She included *E. panosum* as a subspecies of *E. leucophyllum* Woot. & Standl., and noted that it ". . . is on the borderline between the *lachnogynum* group and the *alatum* group of Section I and geographically it is related to both." This incomprehensible arrangement and highly questionable statement of justification is simply without foundation. Reveal (1969b) has placed *E. leucophyllum* in synonymy under *E. havardii* S. Wats., and he has placed the section Lachnogyna Torr. & Gray in the subgenus Eucycla. We cannot explain the reasoning behind the Stokes arrangement.

The phylogenetic relationship of *Eriogonum hieracifolium* to the other species

[1]In this specie and in *Eriogonum alatum* we are providing only a partial listing of locations. The distribution maps should supply the necessary detailed information regarding exact locations.

within Astra is probably greater with *E. hemipterum* than with *E. nealleyi*. The differences are discussed under each of the last two species respectively; however, all share the pandurate shaped, and often pilose, achenes and the open, paniculate cymose inflorescence. In the subgenus Pterogonum, *E. hieracifolium* is unique with bright yellow flowers. It has a strange distribution pattern in that it is found mainly in the grasslands of the low desert ranges of northern Mexico, western Texas, and southern New Mexico, but occasionally it is found in pine woodlands in central New Mexico and Arizona, and in Chihuahua, Mexico. In this latter respect it is somewhat like *E. alatum*, which occurs in similar habitats over a much larger area of the western United States. Even so, *E. hieracifolium* is essentially uniform throughout its range and is normally not readily confused with other species of Pterogonum.

8. *Eriogonum hemipterum* (Torr. & Gray) S. Stokes

Fig. 48.

Tall, erect herbaceous perennials 2-8 dm high from spreading, branched, woody caudices; *leaves* basal and cauline, the basal leaf-blades oblanceolate to elliptic or spathluate, (2) 4-8 cm long, 0.5-1.5 cm wide, thinly strigose and green on both surfaces or rather densely tomentose and gray below, the margin sparsely ciliated with short strigose hairs, the apex mostly acute, the base long cuneate to a narrowly winged petiole, the petiole 0.5-3 cm long, strigose, the petiole-base sparsely strigose without, glabrous within, the cauline leaf-blades spathulate to oblanceolate, 1.5-5 cm long, 0.2-1 cm wide, thinly strigose on both surfaces or tomentose below, the margin ciliated with long, strigose hairs, the apex acute, the base cuneate to the stem; *stems* erect or nearly so, slender, 1-6 dm long, thinly to densely strigose; *inflorescences* open paniculate cymes, the branches restricted to the upper portions of the plant, 1-3 dm long, strigose throughout; *bracts* scalelike, ternate, 2.5-8 mm long, narrowly triangular to linear-oblanceolate, sparsely strigose on both surfaces and especially so on the margin, connate at the base; *peduncles* erect to ascending, 0.5-8 (12) cm long, strigose; *involucres* turbinate-campanulate to campanulate, 2-4 mm long, (1.5) 2.5-4 mm wide, thinly to densely strigose without, glabrous within, the 5 shallow, triangular teeth 0.5-1 mm long, the bractlets linear to linear-oblanceolate, 2-3 mm long, glabrous or glandular and minutely ciliated, the pedicels 2.5-6 mm long, glabrous; *flowers* maroon, 1.5-2.5 mm long in anthesis, becoming 2.5-3.5 mm long and slightly less reddish in fruit, rarely becoming yellowish red, strigose without especially along the midrib and base, glabrous within except for a few scattered hairs at the base, the tepals essentially monomorphic, narrowly spathulate to obovate, connate at the base; *stamens* slightly exserted, 2-3 mm long, the filaments pilose basally, the anthers reddish purple to maroon, 0.5-0.6 mm long; *achenes* greenish, maturing reddish brown, 3.5-5 mm long, 2-3.5 mm wide, pandurate, the upper third winged, strigose, exserted.

Locally common in the Chisos Mountains of Brewster Co., Texas, and in and near the Sierra del Carmen, Sierra del Jardin, and the Sierra del Pinos of Coahuila, and in the Sierra Diablo of northeastern Chihuahua, Mexico, from 1200 to 2400 m elevation (Map 3). Flowering from June to November.

The two varieties of *Eriogonum hemipterum*, var. *hemipterum* and var. *griseum*, have a distinct and limited distribution in the disjunct mountains of southwestern Texas, northern Coahuila, and adjacent Chihuahua, Mexico. There is no record of both varieties occurring in the same mountain range. This should not be too surprising, since in this area of the Chihuahuan Desert, the mountain ranges are generally separated by dry desert valley floors. These effective barriers allow the small populations to evolve along their separate ways, probably accounting for any of the minor variation exhibited by them.

The close relationship of *Eriogonum hemipterum* with *E. hieracifolium* is quite obvious. They share characteristics such as similarly shaped pubescent fruits with the upper third distinctly winged, distinctly pubescent tepals, up to four or five cauline leaves, similar inflorescences, and similar habits of branched caudices. The maroon flowers, reduced pubescence, and a less robust nature all combine, with other more technical features, to distinguish the

Fig. 48. Illustration of *Eriogonum hemipterum*, showing the general habit (A), detail of a single plant (B), an involucre with flowers (C), and a mature achene (D) of var. *hemipterum*, and a leaf-blade of var. *griseum* (E) showing the more densely pubescent lower surface.

two species. Their distributions are not quite as distinct as we once thought (Hess 1967, Reveal 1969b) with the discovery of *E. hieracifolium* and *E. hemipterum* essentially in the same mountain range in northern Coahuila. Nonetheless, *E. hemipterum* is restricted to the middle and upper elevations of these mountain ranges, whereas *E. hieracifolium* is restricted to the foothills and broad valley floors between the desert mountains.

Eriogonum hemipterum is composed of two distinct variants which may be distinguished by the following key.

Key to the Varieties of *E. hemipterum*

A. Leaves strigose on both surfaces; involucres slightly strigose; bractlets glabrous; peduncles 0.5-8 cm long; plants of Chisos Mts., Texas, and the Sierra del Carmen and Sierra del Jardin, Coahuila, Mexico .. 8a. var. *hemipterum*

AA. Leaves strigose above and tomentose below; involucres densely strigose; bractlets pubescent; peduncles 1-12 cm long; plants of Sierra del Pinos and Sierra del Diablo, Mexico ..... 8b. var. *griseum*

8a. *Eriogonum hemipterum* var. *hemipterum*

Figs. 48a, b, c, d.

Eriogonum hemipterum (Torr. & Gray) S. Stokes, Gen. Eriog. 21. 1936, based on *E. hieracifolium* Benth. in DC. var. *hemipterum* Torr. & Gray, Proc. Amer. Acad. Arts 8: 154. 1870.—Hillsides at Boquillas del Carmen along the Sierra del Carmen, Coahuila, Mexico. 8 Nov 1852. *Parry s.n.* Holotype: NY! Isotypes: ISC, K!

Eriogonum hieracifolium Benth. in DC. f. *atropurpureum* Standl., Field Mus. Nat. Hist., Bot. Ser. 11: 149. 1936.—Chisos Mountains, Brewster Co., Texas, 5 Aug 1931, *Muller 7977*. Holotype: F! Isotypes: BKL, GH, NY, TTC, UC, US!

Plants 2-7 dm high; *leaves* with basal and cauline blades strigose on both surfaces; *peduncles* 0.5-8 cm long; *involucres* slightly strigose without, the bractlets 2 mm long, glabrous; *flowers* 1.5-3 mm long; $n=20$ (Figs. 22, 23).

Locally common in the canyons and mountainsides in the Chisos Mountains of southern Brewster Co., Texas, south to the Sierra del Carmen and Sierra del Jardin, Coahuila, Mexico, from 1200 to 2300 m elevation. Flowering from June to November.

REPRESENTATIVE COLLECTIONS: MEXICO: Coahuila: Sierra del Carmen, 14 Aug 1936, *Marsh 660* (GH, TEX); N side of Pico de Centinela, Sierra del Jardin, 27 Jul 1973, *Johnston et al. 11809* (LL, US). UNITED STATES: TEXAS: Brewster Co.: Chisos Mts.: Oak Creek, near the Window, 23 Aug 1936, *Hinckley 835* (GH, LL, NY); Laguna, 28 Jul 1932, *Muller 46555* (MO, SMU, TAES, TEX, US); along the Laguna Meadow trail to South Rim, 3 Sep 1967, *Reveal & Davidse 906* (ARIZ, BRY, CAS, COLO, CS, GH, ISC, KSC, LL, MO, NY, RM, RSA, SMU, TEX, UC, US, UTC); Oak and Willow creeks canyons, 26 Sep 1936, *Sperry 216* (NEB, TAES, US).

When Torrey first saw the type of this species, he placed the Parry collection in *Eriogonum hieracifolium* (Torrey 1859). At a later date, apparently, he ascribed, without publishing, the herbarium name of "*E. hemipterum*" to the collection, and when Torrey and Gray (1870) proposed the name *E. hieracifolium* var. *hemipterum*, this herbarium name was cited in synonymy. Stokes (1936), believing the entity to be specifically distinct, used the author citation of "Torr. in T. & G." in her monograph, not realizing that the specific combination had never been made. Johnston (1944), in attempting to correct her error, proposed the author citation as "Torr. ex Stokes." Goodman (1945) disagreed, explaining that he believed Stokes intended to raise var. *hemipterum* to the species level, and the citation of authorship should read "(Torr. & Gray) S. Stokes." We concur with Goodman's interpretation.

Until recently (Reveal 1968b, 1970), the name *Eriogonum hemipterum* has been largely obscured by Standley's (1936) name, *E. hieracifolium* f. *atropurpureum*. Although Johnston (1944) was the first to place the Standley name in synonymy under *E. hemipterum*, this change went mostly unnoticed by collectors who obtained the species in Texas. A factor which probably prompted Standley to consider the red-flowered Muller collection (no. 7977) as a forma of *E. hieracifolium* was another collection (*Muller 7978*) from the same locality which fits the description of typical *E. hieracifolium*. Careful fieldwork by both of us (plus numerous collectors before and after) has resulted in

no collections of *E. hieracifolium* from the Chisos Mountains and until recently no collections of *E. hieracifolium* within 100 kilometers of the Chisos Mountains. We are at a loss to explain *Muller 7978*, but with the location of *E. hieracifolium* just across the Rio Grande in the northern mountains of Coahuila, Mexico, a greater possibility exists that it, perhaps, did occur in the Chisos Mountains. Nevertheless, we do not believe that these two species are related at the infraspecific level.

The var. *hemipterum* occurs in the moist canyons and wooded slopes throughout its range. In the Sierras del Jardin and Carmen, the plants may be occasionally found in more open, xeric sites, but always at the higher elevations. In the Chisos Mountains, where we have seen several populations, the plants often occur in or under shrubs, with the inflorescence running through the branches of the shrubs. We have seen some plants occurring with various bunch grasses, and again, the inflorescences can be seen among the grass stems, but the basal leaves and spreading caudices are hidden among the bunches of grass. As we shall note below, we understand that var. *griseum* occurs in open forests quite divorced from other plants, and thus it is found as scattered individuals on the forest floor rather than closely associated with other plants of its kind.

8b. *Eriogonum hemipterum* var. *griseum* I. M. Johnst.

Fig. 48e.

Eriogonum hemipterum (Torr. & Gray) S. Stokes var. *griseum* I. M. Johnst., J. Arnold Arbor. 25: 138. 1944.—Central part of the Sierra del Pinos, about 10 km N La Noria on a dry, western ridge near the head of an old log slide north of great cliffs, Coahuila, Mexico, 22 Aug 1940. *Johnston & Muller 547*. Holotype: GH! Isotype: TEX!

Plants 5-10 dm high; *leaves* with basal and cauline blades strigose above and tomentose below; *peduncles* 1-12 cm long; *involucres* densely strigose without, the bractlets 2-3 mm long, ciliate, glandular; *flowers* (2) 2.5-3.5 mm long.

Apparently local and scattered in open places in pine woodlands of the Sierra del Pinos, northeast Coahuila, and in Sierra del Diablo, northeastern Chihuahua, Mexico, above 2000 m elevation. Flowering from May to November.

REPRESENTATIVE SPECIMENS: MEXICO: Chihuahua: NW end of Sierra del Diablo, 29-30 Jul 1941, *Stewart 968* (GH, TEX). Coahuila: Sierra del Pinos, Dec 1937, *LeSueur 1533* (GH); 25 km N La Noria, Sierra del Pinos, 29 Jul 1941, *Stewart 1249* (GH).

We have not seen var. *griseum* in the field, but we interpret what we know about its habitats from the scant information provided by Johnston (1944) and herbarium labels. The plants seem to occur on disturbed sites in open pine woodlands or grassy meadows. It is incongruous to us that we only know this variety from the same material Johnston based his description on over 30 years ago. We are unaware of any recent collections which would supply us with additional habitat data.

This plant is generally taller and more robust than var. *hemipterum*, and has densely strigose involucres and leaves that are tomentose on the lower surface.

9. *Eriogonum nealleyi* Coult.

Fig. 49.

Eriogonum nealleyi Coult., Contr. U.S. Natl. Herb. 1: 48. 1890.—Near Pecos City, Pecos Co., Texas, 1889, *Nealley 433*. Holotype: US! Isotypes: GH, K!

Tall, erect herbaceous perennials 5-12 dm high from spreading, branched, woody caudices; *leaves* basal and cauline, the basal leaf-blades oblanceolate to spathulate, 4-8 cm long, 0.5-1.6 cm wide, rather evenly strigose and grayish on both surfaces, the margin ciliated with long, strigose hairs, the apex acute or obtuse, the base long cuneate to a narrowly winged petiole, the petiole 1-2.5 cm long, strigose, the petiole-base strigose to glabrous without, glabrous within, the cauline leaf-blades few, (0.5) 1-4 cm long, (2) 3-8 mm wide, sparsely strigose, the apex acute, the base tapering to the petiole-base; *stems* erect, slender, 2-4.5 (5) dm long, glabrous; *inflorescences* open paniculate cymes, the branches restricted to the upper half of the plant, 2-5 (7) dm long; *bracts* scalelike, ternate, 0.5-2.5 mm long, linear-triangular to triangular, glabrous, connate at the base; *peduncles* erect, straight or slightly curved, 1-8 cm long, glabrous; *involucres* turbinate-campanulate to campanulate, 2-3 mm long, 2-4 mm wide, glabrous, the 5 irregularly triangular teeth obtuse to acute, 0.5-1 mm

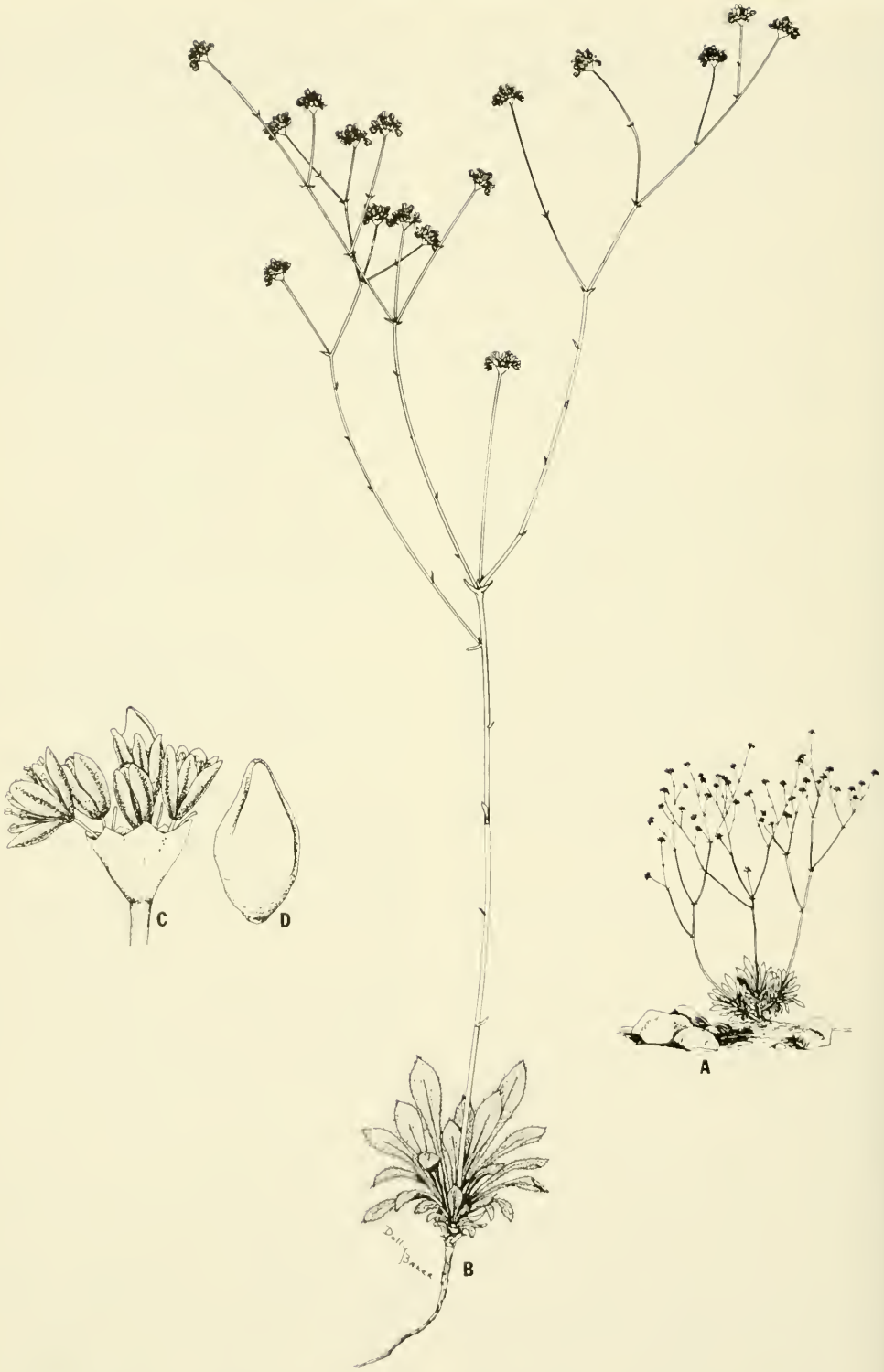


Fig. 49. Illustration of *Eriogonum nealleyi* showing the general habit (A) and a detail (B) of a single plant, an involucre with flowers (C), and a mature achene (D).

long, the bractlets linear-oblanceolate, 1.5-2.5 mm long, minutely glandular, the pedicels 2-6 mm long, glabrous; *flowers* white to greenish white with a green or red midrib and base, 1.5-2 mm long in anthesis, becoming 2.5-3 mm long and pinkish to reddish in fruit, glabrous or sparsely strigose with widely scattered hairs without, essentially glabrous within except for scattered strigose hairs along the midribs, the tepals essentially monomorphic, oblong to narrowly elliptic, connate at the base; *stamens* slightly exserted, 2-3 mm long, the filaments pilose basally, the anthers red to pink, 0.9-1 mm long; *achenes* greenish, maturing reddish brown, 4-6 mm long, 2-3 mm wide, pandurate, the upper half winged, strigose, exserted; $n=20$ (Figs. 24, 25, 26).

Locally common but otherwise rare in dry, open grassland areas and roadsides in west central Texas from eastern Pecos Co., east to Irion Co., and north to Howard Co., from 600 to 900 m elevation (Map 3). Flowering from July to September.

Representative collections: UNITED STATES: TEXAS: Coke Co.: Bronte, 1 Jul 1916, *Palmer 10351* (DS, MO, US). Howard Co.: N of Big Springs, 11 Jun 1900, *Eggert s.n.* (MO). Irion Co.: 3 mo S U.S. Hwy. 67 on Tex. Hwy. 915, 9 Jul 1966, *Hess 786* (OKL); Aug 1890, *Nealley 201* (CS, KSC, NEB); 9 mi W Mertzon, 2 Sep 1967, *Reveal & Davidse 901* (ARIZ, BRY, CAS, COLO, CS, DS, GH, ISC, KSC, LL, MO, NY, RM, RSA, SMU, TEX, UC, US, UTC). Sterling Co.: Hills in Sterling County, 2 Sep 1925, *Tharp 3373* (US).

This species has a very limited distribution and the populations seen by us were very small, consisting usually of only a few hundred individuals. The rareness of this species is also evident by the absence or paucity of specimens in the various herbaria we have visited. The type area is supposedly in Pecos County, Texas, but we have seen no other collections from this part of Texas, and the label data may be in error.

Coulter (1890) stated that *Eriogonum nealleyi* belonged in what we call the subgenus Ganysma and suggested that it was closely related to *E. ciliatum* and *E. atrorubens*—following, no doubt, the practice of Watson (1877) in separating those species associated with *E. atrorubens* from those more closely related to *E. alatum*. However, we believe he erred in this finding as *E. nealleyi* seems more closely related to the members of Alata (sensu Watson) since the inflorescence branching develops in the axils of the upper leaves and not in the axils of the bracts as in the Ganysma (sensu Watson) group.

We have placed *Eriogonum nealleyi* in the section Astra. In certain characteristics this species does resemble *E. alatum* var. *glabriusculum*, especially in the glabrous peduncles and involucres, similar leaf pubescence, and in having seven or more cauline leaves. However, *E. nealleyi* is much more closely related to *E. hieracifolium* in possessing a branched caudex system, pilose filaments of the stamens, and a pandurate achene with scattered strigose hairs. The nearly glabrous condition throughout the stem of *E. nealleyi* quickly distinguishes it from the other species of Astra which have some stem pubescence. The similarity of habit, flowers, and fruits tends to suggest that *E. nealleyi* and *E. hieracifolium* are more closely related to one another than to the Alata complex (Fig. 38).

Of all the species of sections Astra and Alata, *Eriogonum nealleyi* occurs at the lowest elevation (between 600 and 900 m) and in the most xeric conditions. It is easy to speculate that the origin of *E. nealleyi* might be from populations of *E. hieracifolium* in the mountains to the west. After the establishment of *E. nealleyi* and *E. hieracifolium* in the disturbed habitats and along with the varied environmental conditions, convergent evolution could have taken place in which characteristics similar to those in *E. alatum* var. *glabriusculum* developed. In addition to sharing these characteristics with var. *glabriusculum*, they are also somewhat similar in their habitat preference, although var. *glabriusculum* is found a little higher up and consequently in slightly less xeric regions.

IV. Eriogonum sect. Alata

Eriogonum Michx. subgen. *Pterogonum* (H. Gross) Reveal sect. *Alata* Benth. in DC., Prodr. 14: 6. 1856. Species lectotypus: *E. alatum* Torr. in Sitgr., vide Reveal in Gunckel, Curr. Topics Pl. Sci. 243. 1969.—Sect. *Alarium* Kuntze in Post & Kuntze, Gen. Phanerog. 204. 1903.

Tall, erect monocarpic perennial herbs arising from a deep rootstock, glabrous to silky-pubescent; *leaves* basal and cauline, linear-lanceolate to oblanceolate or spathulate, glabrous to densely pubescent; *bracts* ternate, mostly scalelike, connate

at the base; *inflorescences* elongated, open, paniculate cymes; *peduncles* stoutish; *involucres* turbinate to campanulate, the 5 teeth mostly acute to truncate, the bractlets linear-oblanceolate, glabrous or slightly ciliated, the pedicels glabrous; *flowers* yellowish, the tepals glabrous; *anthers* yellow to red; *achenes* winged the entire length of the fruit, glabrous.

The basis for this section is the growth habit of its single species, *Eriogonum alatum*. The plants of this species form a basal rosette of leaves which remain vegetative for two to five or more years before a flowering stem is produced. Once the plant flowers, it dies. These basal rosettes arise from a single, deep taproot, a very different habit from the branched caudices of the species in other sections of Pterogonum. The monocarpic nature, which we speculate to represent a most advanced evolutionary stage within the subgenus, has strongly influenced our evaluation of the section Alata and, consequently, typifies this unique taxon. The section forms a close association with the section Astra in that both groups have cauline leaves, and the ternate bracts are restricted to the inflorescence branches.

The winged achenes of *Eriogonum alatum* are the most pronounced in the subgenus. In the genus overall, the achenes may be angled at the beak, but only in subgenus Pterogonum are the angles accentuated into distinct ridges or wings. Because the margins of the fruit form distinct and nearly membranaceous wings in Alata, we choose to mark this as an evolutionarily advanced condition over the partially winged state of the other species of Pterogonum.

Likewise, the pale yellowish color of the flowers is unique for Pterogonum. So it seems, then, that *Eriogonum alatum* exhibits a series of features which distinguishes it from all others, not only in Pterogonum but in *Eriogonum* as well, and we propose therefore the monotypic section Alata for the species.

10. *Eriogonum alatum* Torr. in Sitgr.
Fig. 50.

Tall, erect monocarpic herbaceous perennials 5-20 (25) dm high from a deep, chambered, soft, woody taproot; *rosettes* basal, of ascending leaves, persisting throughout the growing season and producing a new flush of leaves for an indeterminate number of consecutive years; *leaves* basal and cauline, the basal leaf-blades linear-lanceolate to lanceolate or oblanceolate to spathulate, (3) 5-20 cm long, 0.3-2 cm wide, strigose to glabrous, often slightly more strigose above than below, the margin ciliate, the apex obtuse or acute, the base long cuneate to a slightly winged petiole, the petiole 2-6 cm long, mostly strigose, the petiole-base scattered strigose to densely woolly without, strigose to mostly glabrous within, the cauline leaf-blades alternate, linear-oblanceolate to lanceolate, 1-9 cm long, sparsely strigose to glabrous on both surfaces except for the strigose and ciliate midvein and margin, the apex acute to slightly obtuse, the base tapering to a short, narrowly winged petiole, often with numerous, smaller axillary leaf-blades at the base of the petiole-base; *stems* erect, 2-13 dm high, densely to slightly strigose at the base and becoming scattered strigose to glabrous near the inflorescence; *inflorescences* open paniculate cymes, the branches occurring from the base of the plant upwards, but mostly restricted to the upper half of the plant, 2-10 dm long, sparsely strigose to glabrous; *bracts* foliaceous and scalelike, the foliaceous ones restricted to the base of the secondary branches along the main axis, 2-9 mm long, linear to linear-lanceolate, strigose to glabrous, usually only one per node, the scalelike bracts restricted to the remaining nodes, ternate, 0.8-5 mm long, triangular to linear, strigose to glabrous without, usually glabrous within, connate at the base; *peduncles* erect, slender, straight or curved, 0.5-3.5 cm long, sparsely strigose to glabrous; *involucres* turbinate to campanulate, 2-4 (4.5) mm long and wide, strigose to glabrous without, glabrous within except for the ciliated margins in some, the 5 acute to triangular teeth 1-1.8 mm long, mostly erect or only weakly ascending, the bractlets linear-oblanceolate, 2-3 mm long, glabrous or slightly ciliate, the pedicels 2-6 mm long, glabrous; *flowers* yellow to yellowish green with a dark reddish green or reddish brown midrib and base, 1.5-2.5 mm long in anthesis, becoming 3-6 mm long and reddish in fruit, glabrous without and essentially so within, the tepals essentially monomorphic, mostly lanceolate; *stamens* slightly exserted, 1.5-

Fig. 50. Illustration of *Eriogonum alatum*, showing the general habit (A), a detail of a single plant with a chambered taproot (B), an involucre and flowers (C), and a mature achene (D) of var. *alatum*; and a leaf-blade (E) of var. *mogollense*; plus an involucre with flowers (F) and a mature achene (G) of var. *glabriusculum*.

3 mm long; the filaments glabrous, the anthers yellow to red, 0.4-0.5 mm long; *achenes* yellow to yellowish green maturing reddish brown, short stipitate, 5-9 mm long, 3-6 mm wide, glabrous, distinctly 3-winged the entire length of the fruit, exserted; $n=20$ (Figs. 27-33).

Common in grasslands of the Great Plains and in the pinyon-juniper woodlands and ponderosa pine forests of the Rocky Mountains from northern Chihuahua, Mexico, northward in the Great Plains to Nebraska and Wyoming, and in the Rocky Mountains to Utah and Colorado, from 300 to 3100 m elevation (Map 4). Flowering from June to October.

This polymorphic species, which has resulted in the separation of several infraspecific variants, has a wide range of distribution. We recognize three: var. *alatum*, var. *mogollense*, and var. *glabriusculum*. The two non-typical forms have a restricted distribution, and are easily defined. However, within the concept of var. *alatum*, there are additional forms which have been described and are strikingly different but seem to fail to reflect any particular distribution pattern. In var. *alatum* there are both densely strigose and weakly strigose plants; leaves that are nearly linear and leaves that are much broader; plants which branch from near the base of the stem to the top, and others which branch only on the upper half of the plant. All of these phases are indiscriminately scattered throughout the general range of the typical variant, or they may be found in scattered locations. Because of these field data, we have decided not to further subdivide var. *alatum*.

Key to the Varieties of *E. alatum*

A. Plants strigose throughout or occasionally sparsely strigose on the peduncles with glabrous involucres; inflorescences mostly developed from the basal nodes through the upper nodes; stems and inflorescences 10-17 dm tall; common in the Rocky Mountains and Great Plains southward to northern Mexico.

B. Basal leaves 0.3-1.5 cm wide, linear-lanceolate to lanceolate or oblanceolate; petiole-base strigose; widespread and common throughout the range of the species ..... 10a. var. *alatum*

BB. Basal leaves 1-2 cm wide, spathulate; petiole-base woolly; local in forests around Flagstaff, Arizona ..... 10b. var. *mogollense*

AA. Plants glabrous or slightly strigose in the inflorescence and rarely with strigose peduncles; inflorescences mainly developed in the upper nodes; stems and inflorescences 10-25 dm high; common in the southern Great Plains of north central Texas, and western Oklahoma and rarely northeastern New Mexico ..... 10c. var *glabriusculum*

10a. *Eriogonum alatum* var. *alatum*

Figs. 50a, b, c, d.

Eriogonum alatum Torr. in Sitgr., Rep. Exped. Down Zuñi and Colorado Rivers 168. 1854. —Near Zuñi, McKinley Co.: New Mexico, 25 Sep 1851. *Woodhouse s.n.* Lectotypus NY!—*Pterogonum alatum* (Torr. in Sitgr.) H. Gross, Bot. Jahrb. Syst. 49: 239. 1913.—*Eriogonum alatum* Torr. Sitgr. ssp. *typicum* S. Stokes, Gen. Eriog. 20. 1936.

Eriogonum alatum Torr. in Sitgr. var. *elatum* Geyer ex Benth. in DC., Prodr. 14: 7. 1856. —"On trap rocks, opposite the Red Butter [sic, Buttes], between Platte and Sweet-water Rivers, on banks of deep and ferruginous loam," Natrona Co., Wyoming, Jun or Jul 1843, *Geyer 145*. Holotype: K! Isotypes: BM, E, G!

Eriogonum triste S. Wats., Proc. Amer. Acad. Arts 10: 347. 1875. —Likely from near Kanab, Kane Co., Utah, 1874, *Siler 147*. Holotype: GH! Isotypes: CAS, ISC, K, MO, NY, UC, US! *Eriogonum alatum* Torr. in Sitgr. ssp. *triste* (S. Wats.) S. Stokes, Gen. Eriog. 20. 1936.

Eriogonum alatum Torr. in Sitgr. var. *brevifolium* Gand., Bull. Soc. Roy. Bot. Belgique 42: 186. 1906. —Laramie Hills, Albany Co., Wyoming, 29 Jun 1896, *E. Nelson 1989*. Holotype: LY! Isotypes: BM, CS, KSC, MONT, RM!

Tall, erect perennial herbs 5-13 (17) dm high; *leaves* basal, infrequently cauline, the basal leaf-blades linear-lanceolate to lanceolate or oblanceolate, (3) 5-15 cm long, 0.3-1.5 cm wide, strigose or glabrous except for the strigose midvein and margin, the petiole 2-5 cm long, the petiole-base sparsely strigose to strigose, the cauline leaf-blades 1-6 cm long; *inflorescences* thinly strigose, infrequently glabrous at maturity, 2-10 dm long; *peduncles* stri-

gose or nearly so; *involucres* strigose to rarely glabrous without, the teeth acute or obtuse; *achenes* 5-8 mm long, 3-6 mm wide; $n=20$ (Figs. 27, 28).

Common in sandy to gravelly places in open grasslands or among pinyon-juniper woodland or pine forests of the Rocky Mountains from Utah and Arizona across Colorado and New Mexico into the Great Plains from southwestern Nebraska and adjacent Wyoming to northern Mexico, from 1350 to 3100 m elevation. Flowering from June to October.

REPRESENTATIVE COLLECTIONS: MEXICO: Chihuahua: Guayanopa Canyon, Sierra Madre Occidental, 24 Sep 1903, *M. E. Jones s.n.* (NY). UNITED STATES: ARIZONA: Apache Co.: Luka-Chukae Mts., 9 Aug 1939, *Goodman & Payson 3189* (ISC, MO, NY). Cochise Co.: Mustang Mts., 28 Jun 1884, *Pringle s.n.* (BR, E, G, GH, NY, OKL, P, US). Coconino Co.: Near Jacob Lake, 4 Aug 1967, *Gentry & Davidse 1797* (NY, UC, UTC, WTU). Gila Co.: Near Black River, 28 Jul 1965, *Hess 353* (ARIZ, OKL). Graham Co.: 6 mi W Point of Pines, 24 Jul 1952, *Bohrer 425* (ARIZ). Greenlee Co.: Below Sardine Saddle, 24 Jul 1973, *Lehto et al. 11262* (ASU). Mohave Co.: Toroweap Valley, 10 May 1952, *McClintock 52-517* (ARIZ). Navajo Co.: 19 mi NE Show Low, 29 Jul 1965, *Hess 371* (ARIZ, DUKE, OKL, TEX, UC). Pima Co.: Box Canyon, 15 Sep 1958, *Goodding 488-58* (ARIZ). Yavapai Co.: Near Prescott, 8 Aug 1926, *Peebles et al. 2656* (ARIZ, US). COLORADO: Alamosa Co.: N of Alamosa, 28 Aug 1967, *Lewis s.n.* (ASU). Archuleta Co.: Pagosa Springs, 12 Jul 1899, *Baker 283* (BM, GH, K, MO, NY, US). Boulder Co.: Horse Mesa, 22 Jun 1913, *Ramaley 9600* (COLO). Chaffee Co.: 4-5 m SW Trout Creek Pass, 2 Jul 1959, *Russell 10115* (CS). Clear Creek Co.: Idaho Springs, 17 Aug 1923, *Pammell & Jeffers s.n.* (ISC). Custer Co.: 2 mi E Westcliffe, 3 Aug 1968, *Stephens & Brooks 26693* (KANS). Delta Co.: 4 mi NW Cedaredge, 31 May 1952, *Weber 7575* (COLO). Douglas Co.: Buffalo Creek, 4 Aug 1933, *Goodman 1997* (GH, ISC, MO, NY, OKL, WTU). El Paso Co.: Mantou, 18 Jul 1886, *Bessey s.n.* (NEB). Fremont Co.: 8 mi NE Texas Creek, 5 Jul 1954, *Harrington 7522* (CS). Gilpin Co.: Near Pine Cliff, 13 Jul 1917, *Hall 10404* (UC). Huerfano Co.: 16 mi NW Gardner, 2 Aug 1968, *Stephens & Brooks 26660* (KANS). Jefferson Co.: Morrison, 1877, *Hooker & Gray s.n.* (K). Kit Carson Co.: Without location, Aug 1890, *Harris s.n.* (ILL). La Plata Co.: 5 mi W Durango, 4 Aug 1965, *Hess 469* (ARIZ, OKL). Larimer Co.: 3.5 mi S Estes Park, 21 Aug 1970, *Stephens & Brooks 42769* (KANS). Mesa Co.: 6 mi S Fruita, 22 May 1948, *Weber 3892* (ARIZ, COLO, TEX, WTU). Montezuma Co.: 7 mi E Cortes, 9 Sep 1968, *Howell & True 45005* (CAS). Montrose Co.: 18 mi E Naturita, 15 Jul 1935, *Maguire & Piranian 12439* (UC). Ouray Co.: Ouray, 11 Jun 1969, *Atwood & Higgins 1822* (BRY). Park Co.: Spruce Grove Campground, 5 Aug 1971, *Pinkava 8932* (ASU). Pueblo Co.: Colorado Springs, 25 Jul 1884, *Letterman s.n.* (MO). Sanguache Co.: Junct. of 114 S of U.S. Hwy. 50, 13 Jul 1963, *Dunn & Willey 14556* (UMO). Teller Co.: 2 mi S Florissant, 16 Aug 1961, *Iltis & Iltis 18735* (WIS). KANSAS: Russell Co.: 4 mi N Russell, 6 Jul 1959, *Jackson 139* (KANS). Scott Co.: 14 mi N Scott City, 28 Aug 1957, *McGregor 13643* (KANS). NEBRASKA: Banner Co.: SW Harrisburg, 17 Jul 1968, *Stephens & Brooks 24801* (KANS). Cherry Co.: Near Hackberry Lake, Jun 1912, *Doorak s.n.* (NEB). Cheyenne Co.: 1 mi E, 1 mi N Sunol, 10 Aug 1967, *Stephens & Brooks 16048* (KANS). Deuel Co.: McColligan Canyon, 22 Aug 1891, *Rydberg 330* (ARIZ, NEB, NY). Kimball Co.: 1.5 mi W Dix, 27 Jul 1971, *Stephens 50127* (KANS). Morrill Co.: 4 mi N Broadwater, 12 Jul 1967, *Stephens & Brooks 13914* (KANS). Scotts Bluff Co.: 8.5 mi W Gering, 17 Aug 1970, *Stephens & Brooks 43993* (KANS). NEW MEXICO: Bernalillo Co.: Manzano Mts., 6.2 mi S U.S. Hwy. 66 along N.M. Hwy. 14, 24 Aug 1973, *Holmgren & Holmgren 7379* (BRY, NY, UNM). Catron Co.: 4 mi S Beaverhead Ranger Station, 18 Aug 1966, *Hess 879* (ARIZ, OKL). Colfax Co.: Raton Pass, 27 Jun 1971, *Godfrey 70566* (FSU). DeBaca Co.: 8 mi E Yeso, 12 Aug 1947, *Waterfall 7730* (GH). Eddy Co.: Guadalupe Mts., 19 Oct 1939, *Barneby 2585* (NY). Grant Co.: Near Tyrone, 9 Aug 1968, *Gentry & Jensen 2277* (ASU, CS, DS, IDS, ISC, KSC, NY, OSC, TEX, UTC, WTU). Hidalgo Co.: Indian Cr., Animas Mts., 7 Oct 1967, *Hess 1552* (SMU). Lincoln Co.: 3 mi E Nogal, 25 Jul 1965, *Hess 302* (ARIZ, OKL, TEX). McKinley Co.: Chaco Canyon, May 1937, *Hastings s.n.* (ARIZ). Mora Co.: 1 mi NW Wagon Mound, 30 Jul 1968, *Stephens & Brooks 26171* (KANS). Otero Co.: 12.5 mi S Mescalero, 24 Jul 1965, *Hess 294* (ARIZ, OKL). Rio Arriba Co.: 44 mi N Española along U.S. Hwy. 84, 3 Jul 1970, *Higgins 3584* (BRY, WTS). Sandoval Co.: Sulphur Springs, 17 Aug 1926, *Arsène & Benedict 16440* (ISC). San Miguel Co.: Gallinas River Valley, 11-17 Aug 1945, *Lundell & Lundell 14494* (LL). Santa Fe Co.: Cañoncito, 12 Jul 1926, *Arsène & Benedict 15913* (P). Socorro Co.: Chupadera Mesa, 11 Aug 1948, *Dunn & Lint 4339* (UMO). Taos Co.: Near Tres Ritos, 16 Aug 1946, *Martin 1064* (WTU). Torrance Co.: 2 mi NW Monzano, 4 Aug 1949, *Dunn 6163* (KANS, UMO). Union Co.: 32 mi W Clayton, 24 Aug 1966, *Hess 976* (ARIZ, OKL). Valencia Co.: Mt. Sedgwick, Zuni Mts., 17 Aug 1968, *Riffle 811* (UNM). TEXAS: Brewster Co.: Green Valley, Glass Mts., 23 Jul 1940, *Warnock W5* (ARIZ, ISC, TEX, US). Culberson Co.: Near Frijole, 30 Jul 1930, *Grassl 182* (ARIZ). Dallam Co.: Unknown location, 8 Aug 1891, *Carleton 397* (CS, KSC, OSC). Hudspeth Co.: 0.5 mi N McAdoo Ranch, Sierra Diablo Mts., 29 Aug 1949, *Hinckley & Hinckley 308* (KANS, SMU). UTAH: Carbon Co.: Tavaputs Plateau, 19 Jun 1965, *Holmgren et al. 1961* (ARIZ, BRY, CAS, COLO, CS, DS, GH, ISC, KSC, MO, NCU, NY, OKL, OSC, RENO, RM, RSA, SMU, TEX, UC, US, UT, UTC, WIS, WS, WTU). Daggett Co.: 12 mi S Manila, 16 Aug 1935, *Maguire et al. 12655* (GH, UTC). Duchesne Co.: 18 mi W Duchesne, 5 Jul 1947, *Ferris 11312* (CAS, DS, UTC, WTU). Emery Co.: 27 mi W Green River, 25

May 1961, *Cronquist 9104* (NY). Garfield Co.: 7 mi E Escalante, 2 Jun 1948, *Holmgren 7727* (CAS, UC, UTC, WS, WTU). Grand Co.: Moab, 9 Jul 1913, *M. E. Jones s.n.* (POM). Iron Co.: Near Cedar Breaks Natl. Mon., 2 Sep 1936, *Gierish s.n.* (UTC). Kane Co.: 10 mi N Glendale, 18 Jul 1940, *Maguire 19663* (NY, UTC). San Juan Co.: Comb Reef, 20 Jun 1944, *Holmgren & Hansen 3414* (ARIZ, GH, IDS, NY, OSC, UC, US, UTC, WS). Sevier Co.: 31 mi S Emery, 22 Jun 1961, *Cronquist & Holmgren 9325* (NY, UTC, WS, WTU). Uintah Co.: 46 mi SE Ouray, 27 Jul 1965, *Holmgren et al. 2273* (ARIZ, BRY, CAS, COLO, CS, DS, GH, MO, NY, OKL, OSC, RENO, RM, RSA, TEX, UC, US, UTC, WTU). Utah Co.: P. V. Junction, Aug 1883, *M. E. Jones s.n.* (DS, POM). Washington Co.: Hurricane, 17 Jul 1925, *Kraus s.n.* (WIS). Wasatch Co.: Strawberry Reservoir, 22 Jul 1948, *Ripley & Barneby 9946* (CAS). Wayne Co.: 30 mi N Boulder, 2 Aug 1965, *Hess 423* (ARIZ, OKL). WYOMING: Albany Co.: Sheep Mtn., 2 Sep 1903, *Goodding 2108* (GH, NY, US). Carbon Co.: Platte River, 9 Jul 1894, *Nelson 416* (NY, RM). Goshen Co.: Raw Hide Buttes, 23 Jul 1909, *Cory 378* (US). Laramie Co.: Cheyenne, 11 Aug 1891, *Nelson 18* (GH). Niobrara Co.: 3 mi S Manville on Wyo. Hwy. 270, 11 Aug 1975, *Hess 3542* (MOR). Platte Co.: Guernsey Lake State Park, 11 Jul 1946, *C. L. Porter 4011* (DS, GH, KANS, RM, UC, WTU). Sweetwater Co.: 20 mi W Green River near Little America, 17 Sep 1961, *Mason 4034* (ASU, BRY, OSC).

In the subgenus Pterogonum, the distribution of var. *alatum* is the most extensive. Within this broad geographical range there are numerous minor phases which have, in the past, been noted as distinct. Ecological conditions most likely account for this variation since the plants of var. *alatum* may occur within ponderosa pine forests, grasslands openings within the forests, in the grasslands of the northern latitudes, or in the quite xeric areas on exposed limestone with scattered pinyon-juniper as seen in parts of Utah and northern Arizona. The plants in Wyoming and adjacent western Nebraska have been called var. *elatum* (and later, var. *brevifolium*) and are characterized by short, narrow, basal leaves. The occurrence of this kind of leaf shape, however, is widely scattered, and plants which resemble those of var. *elatum* are found throughout the general range of var. *alatum*. Those plants considered to be *Eriogonum triste* are more restricted, occurring primarily in southern Utah and northern Arizona. They have a tendency toward a glabrous condition, but again this feature can be seen in other populations beyond the range noted above. Even in Utah and Arizona there are individual plants which vary from densely strigose to nearly glabrous even in a single population. We have seen var. *alatum* in the field throughout most of its range and have examined innumerable herbarium specimens. We prefer a more conservative treatment because of the wide morphological variation and lack of any consistent geographical associations found in the various forms aligned with var. *alatum*.

The center of distribution for var. *alatum* would seem to be the southwestern United States, perhaps in the Mogollon Mountains of New Mexico. Here the populations mostly occur in relatively undisturbed areas, whereas farther north the populations are more common along disturbed sites such as road cuts, erosional cuts, and canyon breaks. Its migration would seem to be northward in the mountains and onto the Great Plains via waterways. With such a broad distribution and the diversity of available habitats, certain morphological features (i.e., short leaves, glabrous condition) have become established. However, no discernible patterns have been consistent, and as a result var. *alatum* is quite variable, perhaps with ecotypes in their early stages of evolutionary development.

Plants intermediate between var. *alatum* and var. *glabriusculum* were found in Union County, northeastern New Mexico, on the canyon breaks above Tramperos Canyon (*Hess 976*). This has indicated a possible pathway for the movement of certain members of this species onto the Great Plains. With the following isolation and selection within a more restricted distribution, a polymorphic taxon of *Eriogonum alatum* could result.

10b. *Eriogonum alatum* var. *mogollense* Stokes ex Jones

Fig. 50e.

Eriogonum alatum Torr. in Sitgr. var. *mogollense* Stokes ex Jones, Contr. W. Bot. 11: 15. 1903.—Flagstaff, Coconino Co., Arizona, 7 Aug 1884, *M. E. Jones 3975*. Lectotype: POM! Isolectotypes: ARIZ, BM, BR, CAS, DS, G, GH, NY, P, UC, US, UTC!—*Eriogonum alatum* Torr. in Sitgr. ssp. *mogollense* (Stokes ex Jones) S. Stokes, Gen. Eriog. 20. 1936.

Eriogonum alatum Torr. in Sitgr. var. *macdougalii* Gand., Bull. Soc. Roy. Bot. Belgique 42: 186. 1906.—Near Flagstaff, Coconino Co., Arizona, 8 Jul 1898, *MacDougal 259*. Holotype: LY! Isotypes: BKL, E, G, GH, ISC, NY, P, PH, UC, US!

Tall, erect perennial herbs 8-13 dm high; *leaves* basal and cauline, the basal leaf-blades spathulate, 4-11 cm long, 1-2 cm wide, strigose above, glabrous below except for strigose midvein and margin, the petiole 4-6 cm long, the petiole-base densely brown woolly, the cauline leaf-blades 1-5 cm long; *inflorescences* strigose, 2-6 dm long; *peduncles* strigose; *involucres* strigose without, the teeth mostly acute, the bractlets ciliate; *achenes* 5-8 mm long, (4) 4.5-6 mm wide; $n=20$ (Figs. 29, 30, 31).

Common in open pinyon-juniper and ponderosa pine forests in and around the Flagstaff area of Coconino Co., Arizona, northward to the south rim of the Grand Canyon, and eastward on the Mogollon Plateau to north of Show Low, Navajo Co., Arizona, from 1800 to 2500 m elevation. Flowering from June to September.

Representative collections: ARIZONA: Coconino Co.: Flagstaff: 29 Jul 1910, *Adams s.n.* (WIS); 22 Aug 1941, *Deaver 429* (ASC); 8 Aug 1922, *Hanson A183* (NEB, OSC, TEX); 14 Aug 1920, *Thornber s.n.* (ARIZ, TAES); 28 Jun 1935, *Whiting 756/870* (MINA); 1 mi N of S entrance to Grand Canyon N.P., 25 Jul 1961, *Harrington 9639* (CS); 23 mi N Payson, 23 Aug 1966, *Hess 961* (ARIZ, OKL); NW of Flagstaff, 18 Aug 1973, *Reveal & Reveal 3225* (BRY, NY, US). Navajo Co.: 9 mi N Heber, 4 Jul 1965, *Pinkava 2320* (ASU).

The plants of var. *mogollense* are restricted in distribution to the mountains around Flagstaff, Arizona, and eastward on the Mogollon Rim to southwestern Navajo County. This variant may be characterized by its spathulate basal leaves and woolly petiole-bases. Otherwise, the plants are similar to var. *alatum*. Populational analysis of the plants in the Flagstaff area predominantly shows the spathulate leaf character. It would seem that no or little movement of genes controlling the leaf-shape has occurred in this area; therefore, the spathulate leaf character has been maintained. However, it is difficult to determine if there is a populational change in the frequency of plants with spathulate leaves as opposed to those with lanceolate leaves. Although plants approaching the morphological characteristics of var. *mogollense* occur elsewhere, it seems reasonable to recognize var. *mogollense* due to the constancy of its morphological characteristics associated with its limited range.

10c. *Eriogonum alatum* var. *glabriusculum* Torr. in Whipple

Figs. 50f, g.

Eriogonum alatum Torr. in Sitgr. var. *glabriusculum* Torr. in Whipple, Explor. & Surv. Railroad Route from Mississippi River to Pacific Ocean 4: 131. 1857.—High places near the Canadian River, Roger Mills Co., Oklahoma, 3 Sep 1853, *Bigelow s.n.* Holotype: NY! Isotype: US!

Tall, erect perennial herbs 10-20 (25) dm high; *leaves* basal and cauline, the basal leaf-blades linear-lanceolate to lanceolate, 8-20 cm long, 0.5-1.5 cm wide, slightly strigose or glabrous above, glabrous below except for the strigose midvein and margin, the petiole 2-5 cm long, the petiole-base slightly strigose without, the cauline leaf-blades 1-9 cm long, 0.3-0.9 cm wide; *inflorescences* glabrous, 2-6.5 dm long; *peduncles* glabrous or occasionally slightly strigose; *involucres* glabrous without, the teeth obtuse or truncate, the bractlets glabrous; *achenes* 5.5-9 mm long, 3-5.5 mm wide; $n=20$ (Figs. 32, 33).

Common in the grasslands along canyon breaks from Curry Co., New Mexico, eastward across northern Texas to western Oklahoma, from 300 to 1400 m elevation. Flowering from July to October.

Representative collections: NEW MEXICO: Curry Co.: Along Frio Draw, near Ruth, 27 Jul 1939, *Reynolds 242* (NEB). OKLAHOMA: Beckham Co.: 21 mi N Sayre, 10 Aug 1927, *Stratton 364* (MO). Ellis Co.: Near Shattuck, 11 Oct 1913, *Stevens 2938* (DS, GH, K, MO, NY, OKL, US). Garvin Co.: 2 mi S Purdy, 24 Sep 1966, *Hess & Harrison 984* (ARIZ, OKL). Roger Mills Co.: 6 mi SE Cheyenne, 21 Aug 1950, *Goodman & Kelting 5404* (KANS, NY, OKL, TEX). Stephens Co.: 6 mi W Foster, 24 Sep 1966, *Hess & Harrison 985* (OKL). Woodward Co.: 8 mi SW Woodward, 20 Jul 1934, *Goodman 2180* (ISC, MO, OKL). TEXAS: Armstrong Co.: 15 mi S Claude, 23 Aug 1967, *Reveal & Davidse 879* (ARIZ, BRY, CAS, GH, MO, NY, RM, RSA, UC, US, UTC). Briscoe Co.: Tule Canyon, 24 Aug 1967, *Reveal & Davidse 880* (ARIZ, BRY, CAS, GH, LL, MO, NY, RM, RSA, SMU, TEX, UC, US, UTC). Carson Co.: 3 mi NW Skellytown, 27 Aug 1967, *Stephens & Brooks 17350* (KANS). Childress Co.: Childress, 1 Oct 1932, *Tharp s.n.* (TEX). Crosby Co.: 3 mi E Crosbyton, 29 Jun 1964, *Hanson 479* (LL, TEX, US). Dickens Co.: Between Croton and East Afton, 10 Aug 1972, *Higgins 6092* (BRY, WTS). Donley Co.: Between Clarendon and Brice, 8 Sep 1934, *Reed 4087* (TEX). Floyd Co.: Plainview Road, 23 Aug 1921, *Ferris & Duncan 3366a* (MO, NY). Gray Co.: 15 mi SE Pampa, 3 Aug 1966, *Hess 761* (OKL). Hall Co.: Brice, 8 Sep 1934, "*collector unknown*"

4087 (TTC). Hemphill Co.: 6.7 mi NE Canadian, 28 Sep 1935, *Parks & Cory 16182* (TAES). Hutchinson Co.: 7 mi from Adobe Wall site, 28 Aug 1964, *Correll & Correll 30014* (LL). Lipscomb Co.: 1 mi N Lipscomb, 21 Sep 1958, *Wallis 7956* (SMU, TEX). Lubbock Co.: Lubbock, *s.d.*, *Reed 3106* (US). Motley Co.: Roaring Springs, 26 Sep 1935, *Parks & Cory 15977* (TAES). Ochiltree Co.: 12 mi SE Perryton, 20 Sep 1958, *Wallis 7883-1* (DUKE, SMU, TEX). Randall Co.: Canyon, 3 Oct 1918, *Palmer 14587* (BKL, MO, NY, WIS). Roberts Co.: 27 mi S Perryton, 19 Sep 1958, *Wallis 7843* (TAES, TEX).

The trends in var. *glabriusculum* are easily distinguished when populations are examined. Many plants are over 1.5 m tall, and heights of 2.5 m are known. The basal leaves are generally long and narrow, with less pubescence than those of the other varieties of the species. The inflorescence branching is restricted to the upper nodes of the stem and is not developed from the bottom nodes as is common in var. *alatum* and var. *mogollense*. For the most part, the involucres and peduncles are quite glabrous and the remaining branches of the inflorescence are glabrous or with scattered pubescence. The involucral lobes are not sharply pointed but are often irregular or truncate. These trends in populations of var. *glabriusculum* tend to place it apart from the other varieties.

In Oklahoma and Texas, var. *glabriusculum* is most often found on slightly disturbed ground at the edges of canyons and gullies. The occurrence of this variant on the breaks suggests a pathway of distribution from the Rocky Mountains onto the Great Plains as mentioned before. Incipient speciation may occur with the present isolation if the morphological difference of var. *glabriusculum* and var. *alatum* are genetically controlled. This would be speculation, and since var. *alatum* is quite variable, including some infraspecific characteristics common to var. *glabriusculum*, consideration of the Oklahoma and Texas taxon as a variety seems to be the most reasonable.

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