

## DISTRIBUTION AND PHYLOGENY OF ERIOGONOIDEAE (POLYGONACEAE)

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**ABSTRACT.**—Eriogonoideae is a subfamily of the knotweed family, Polygonaceae, endemic to the New World, and is composed of 14 genera and perhaps 320 species. It differs primarily from the other members of Polygonaceae in lacking well-defined sheathing stipules or ochrea. The species of Eriogonoideae vary from tiny, fragile annuals to herbaceous perennials, low subshrubs or shrubs to large and often arborescent shrubs. The seemingly most primitive extant genus of the subfamily is *Eriogonum* (247 species), which is widespread in central North America. A series of genera are closely related to *Eriogonum*, and probably have evolved directly from *Eriogonum*. These genera are *Oxytheca* (9 species) of the western United States, and Chile and Argentina of South America; *Dedeckera* and *Gilmania*, both monotypic genera of the Death Valley region of California; *Stenogonum* (2 species) of the Colorado Plateau and adjacent areas of the Rocky Mountain West; *Goodmania* and *Hollisteria*, 2 monotypic genera of central and southern California; and *Nemacaulis*, a monotypic genus of the southwestern United States and northwestern Mexico. A second major complex of genera also probably evolved from *Eriogonum*. In this group, the most elementary genus is *Chorizanthe* (about 50 species), in which the extant perennial members of the genus are perhaps evolutionarily the oldest taxa of the subfamily. These perennials are restricted to Chile, while in the western United States and northwestern Mexico of North America, only annual species are found. *Mucronea* (2 species) of California and *Centrostegia* (4 species) of the southwestern United States and northwestern Mexico are clearly related to *Chorizanthe*. In a somewhat intermediate position between the *Eriogonum* complex and the *Chorizanthe* complex—but still more closely related to the latter than the former—is the genus *Lastarriaea* (2 species) found in California, Baja California, and Chile. All of these genera belong to the tribe Eriogoneae. A second tribe, Pterostegae, contains only 2 discordant, monotypic genera: the shrubby perennial genus *Harfordia* of Baja California and the more widespread annual, *Pterostegia*, of the western United States. While time and evolution have obscured the relationships between Eriogoneae and Pterostegae, the affiliations among the various genera of the tribes can be ascertained to some degree. The geographical center of origin of the subfamily may have been in a subtropical climate, with the differentiation of modern-day genera occurring in temperate, xeric regions of North America. The origin of *Chorizanthe* was an ancient development, with the migration of the primitive perennial members into South America in the Tertiary. The subsequent development of the annual habit, and migration of annual species of Eriogonoideae into South America has probably occurred in the Quaternary. The intermediate stages of evolutionary development of the genera and species of the subfamily occurred in a habitat similar to the pinyon-juniper woodlands of the Great Basin, while evolution of the more advanced genera and species has occurred in xeric grasslands, chaparral scrub, or xerophytic “hot desert” communities.

### INTRODUCTION

*In considering the action of evolutionary processes ... both extinction and extensive alterations of geographic and ecological distribution patterns must be recognized.* (Stebbins 1974: 37).

Polygonaceae Juss. is a large, temperate or subtropical family of flowering plants found throughout much of the world, but

mainly in the Northern Hemisphere. It contains many important agricultural and horticultural species in addition to many well-known and troublesome weeds. The vast majority of the plants are small, inconspicuous members of the world's vascular plant flora, and they can claim few positive attri-

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butes. The family is composed of about 40 genera and approximately 900 species (Lawrence 1951, Melchior 1964, Airy Shaw 1973), with *Polygonum* L., *Rumex* L., *Eriogonum* Michx., *Coccoloba* P. Br. ex L., *Rheum* L., and *Chorizanthe* R. Br. ex Benth. among the larger genera in terms of species numbers. Domestically, the genus *Fagopyrum* Mill. is the commercial source of buckwheat, and leaf petioles of *Rheum* (rhubarb) are frequently eaten. *Antigonon* Endl. is an elegant ornamental both in the garden and in nature, although it is more often a weed. A few species of *Polygonum*, *Eriogonum*, and *Coccoloba* are grown for their exotic properties.

The family is usually considered as the only member of a monotypic order, Polygonales, which is supposedly related to the Caryophyllales (Takhtajan 1959, 1969, Cronquist 1968, Hutchinson 1969), although some authors still place it with the Caryophyllales (Thorne 1968, Benson 1974). Recently, the relationship with the Caryophyllales has been challenged on the basis of pollen data (Nowicke, pers. comm.), and the Polygonales might be better treated as an isolated taxon with no immediate close relatives.

Polygonaceae has been variously divided into subfamilies (Bentham 1856, Bentham & Hooker 1880, Dammer 1892, Roberty & Vautier 1964), and the differences in opinion cannot be resolved here. The one point of near unanimity among all of these authors, and others who have treated the Polygonaceae, is that Eriogonoideae Benth.<sup>2</sup> is the most distinct subfamily of Polygonaceae and can be readily excluded from the remaining subfamilies. The only serious difference, now largely resolved, has been the relationship of the genus *Koenigia* L. to the western United States genera, *Hollisteria* S. Wats., *Nemacaulis* Nutt., and *Lastarriaea*

Remy in Gay of Eriogoneae Benth., and *Pterostegia* Fisch. & Meyer of the tribe Pterostegae Torr. & Gray. Bentham and Hooker (1880) proposed that *Koenigia* was related to these genera, placing all of them in a tribe termed Koenigaeae. This was directly contrary to Torrey and Gray (1870) who placed *Nemacaulis* and *Lastarriaea* in the tribe Eriogoneae, and *Pterostegia* in Pterostegae; *Koenigia* was not even mentioned by Torrey and Gray. Roberty and Vautier (1964) removed *Koenigia* from Eriogonoideae, and placed this arctic and subarctic genus in the Polygonoideae where it certainly belongs.

All further comments in this paper will be restricted to the subfamily Eriogonoideae.

#### GENERIC COMPOSITION OF ERIOGONOIDEAE

The members of Eriogonoideae are restricted to the xeric regions of the New World, with the vast majority of species confined to the western half of central North America from the Tropic of Cancer northward to the fiftieth parallel. In South America, the few species that are known to be native elements in the flora are found in the deserts of northern Chile and scattered parts of adjacent Argentina. The state of California in the United States harbors more species and genera of the subfamily than any other comparable political area; the state also has more endemic genera (five) than any other area. Both *Eriogonum* and *Chorizanthe* have a large number of species in California (about 40 percent of *Eriogonum* and perhaps 70 percent of *Chorizanthe* are in the state), and of all the genera of the subfamily, only two, *Stenogonum* Nutt. and *Harfordia* Greene & Parry, do not occur in California. Three genera occur in both North and South America. *Chorizanthe*

<sup>2</sup>The authorship of the subfamily name, Eriogonoideae, is here attributed to George Bentham's name "Subordo Eriogoneae" published in deCandolle's *Prodromus* (14: 5. 1856) based upon Article 18 of the present Code (Stafleu et al. 1972), which states "Names intended as names of families, but published with their rank denoted by one of the terms order (*ordo*) or natural order (*ordo naturalis*) instead of family, are treated as having been published as names of families." Unfortunately, in Article 19, which deals with subfamily, no similar provision is stated. For this reason, some may reasonably argue that the correct authorship of the subfamily is Roberty and Vautier (Boissiera 10: 83. 1964).



is strictly an annual group in North America where some 40 of the 50 species of the genus are found, but in South America, all but one (*C. commissuralis* Remy in Gay) of the 10 or so species of the genus are perennials, and no species is common to both continents. The genus *Lastarriaea* is now usually defined to include 2 species (Goodman 1943, Hoover 1966, Munz 1974), *L. chilensis* Remy in Gay of Chile, and *L. coriacea* (Goodman) Hoover of coastal California and northern Baja California, Mexico, although the genus has been considered to be monotypic with two variants (Gross 1913, Goodman 1934) or without any differences (Parry 1884, Abrams 1944, Munz & Keck 1959). The third genus, *Oxytheca* Nutt., has a single species in South America and 8 species are restricted to North America. All of the remaining genera are restricted to North America as are approximately 305 of the 320 species of the subfamily.<sup>3</sup>

Eriogonoideae is composed of fourteen genera unequally divided into two tribes. The large, typical tribe, Eriogoneae, contains twelve genera and about 318 species, with the majority of the species distributed in two genera, *Eriogonum* (247 species) and *Chorizanthe* (about 50 species). The least advanced member of the tribe is the genus *Eriogonum*. Associated with this genus are a series of small, satellite genera which can trace their probable origin to an extant group within *Eriogonum* as it exists today. Likewise, around *Chorizanthe* are related genera which probably owe their origins to *Chorizanthe*, with *Chorizanthe* itself likely evolved from a now extinct portion of *Eriogonum*. The second tribe, Pterostegae, is composed of two monotypic genera which are only superficially related, and whose relationship with Eriogoneae is frankly lost.

*Eriogonum* is widespread in North America, ranging from east central Alaska (Welsh 1974) southward to central Mexico, and

from the offshore islands of California and Baja California eastward to the Appalachian Mountains of Virginia and West Virginia southward to Florida. In spite of its large size in terms of species numbers, *Eriogonum* has only three generic synonyms. *Eucycla* Nutt. (Nuttall 1848a) and *Pterogonum* H. Gross (1913) are now recognized as subgenera of *Eriogonum* (Reveal 1969a, b; Hess & Reveal 1976), while *Sanmartinia* Buchinger (1950), a name proposed for *Eriogonum divaricatum* Hook. (Reveal & Howell 1976) when it was discovered as an introduction into Argentina (Spegazzini 1902, Moreau & Crespo 1969) and thought to represent a distinct species of *Eriogonum* or a valid genus, is now reduced to synonymy completely.

The genus *Eriogonum* is currently being monographed by myself, but past reviews have been presented by Nuttall (1817), Bentham (1836, 1856), Torrey and Gray (1870), Watson (1877), Stokes (1904, 1936), and Reveal (1969a).

Most closely related to *Eriogonum* is *Oxytheca*. This genus of nine species has been reviewed by those who revised the species of *Eriogonum* (except Nuttall [1817], Bentham [1836], and Reveal [1969a]) at least as far as the genus in North America is concerned, with both Stokes (1904, 1936) and, indirectly, Roberty and Vautier (1964) including the species of *Oxytheca* in *Eriogonum*. Critical reviews of the genus have been presented by Jepson (1913), Abrams (1944), and Munz and Keck (1959) in floristic studies of the California species where seven of the eight North American species are found. Barbara J. Ertter, a graduate student at the University of Maryland, is now monographing the genus. One new species has been discovered from California, and, although recognized as unique by Stokes (1904) and by Goodman (in herbaria annotations), this San Bernardino Mountains endemic has not been described. Two generic

<sup>3</sup>See note added in proof at end of paper.



segregates have been proposed for species of *Oxytheca*: *Brisegnoa* Remy in Gay (1851), a name actually proposed by Remy prior to 1848 when Nuttall described *Oxytheca*, but whose publication was delayed, and *Acanthoscyphus* Small (1898) for a California species of *Oxytheca*, *O. parishii* Parry, that differs from most species of the genus in having a multiple-awned, nonlobed involucre. *Oxytheca luteola* Parry is now referred to *Goodmania* Reveal & Ertter, and *O. insignis* (Curran) Goodman is placed in *Centrostegia* Gray ex Benth. in DC. (Goodman 1957). In this latter paper, Goodman informally proposed to divide *Oxytheca* into two new genera and at the same time submerge a part of *Oxytheca* in *Eriogonum*. Based upon herbarium annotations, he would have placed *O. dendroidea* Nutt., *O. watsonii* Torr. & Gray, *O. perfoliata* Torr. & Gray, and *O. parishii* in *Eriogonum*, *O. luteola* in a new genus, and referred *O. caryophylloides* Parry, *O. emarginata* Hall, and *O. trilobata* A. Gray to a second new genus. Goodman did not recognize the South American form of *Oxytheca* as a distinct species as proposed by Miers (1851), but retained it as a variant of the North American species, *O. dendroidea* as suggested by Johnston (1929) who proposed var. *tonsiflora* I. M. Johnst. He and Goodman felt the Chilean and Argentinean plants were a distinct form of *O. dendroidea*, which they believed also occurred in other areas of South America. Goodman never published his proposed revision of *Oxytheca*, and Ertter and I are now investigating the genus.

As noted above, one of the species of *Oxytheca* that Goodman proposed to place in a distinct genus was *O. luteola*. This suggestion has recently been accepted by Reveal and Ertter (1976b), who proposed the genus *Goodmania* for this species. *Goodmania* is restricted to alkaline places, dry lake flats, and similar locations in the southern end of the Central Valley of California and elsewhere in the southern part of the state. This monotypic genus seems to be re-

lated to both *Oxytheca* and *Gilmania* Cov.

Somewhat less closely related to *Eriogonum*, but still clearly derived from that genus (rather than *Chorizanthe*), are a series of highly restricted, endemic, western North American genera. *Dedeckera* Reveal & Howell (1976) is a large perennial shrub restricted to a single known location just outside the northwestern edge of the Death Valley National Monument near Eureka Valley in Inyo County, California. This is the only immediate relative of *Eriogonum* that is perennial.

*Stenogonum* (Nuttall 1848a) is a genus of two species and is restricted to the Colorado Plateau and adjacent regions of Wyoming southward through eastern Utah and adjacent western Colorado into northern Arizona and New Mexico. Until recently, this genus was included in *Eriogonum*, where it had been placed by Hooker (1853) shortly after it was proposed by Nuttall, but it is now considered a valid genus on the basis of its unique involucral construction (Reveal & Howell 1976, Reveal & Ertter 1976a).

*Gilmania* (Coville 1936), another Death Valley region endemic, was originally proposed under the generic name of *Phyllogonum* Cov. (Coville 1893), but as this name proved to be a later homonym, Coville renamed it for a local Death Valley naturalist, M. French Gilman. Stokes (1904, 1936) maintained the genus as distinct from *Eriogonum*, although Jones (1903) reduced it to *Eriogonum* without comment. Roberty and Vautier (1964) placed *Gilmania* in *Eriogonum* too; but, unlike Jones, who retained the species as distinct, they placed the name in synonymy under *Stenogonum salsuginosum* Nutt. (which they placed in *Eriogonum*), an opinion that is totally incomprehensible.

On the Inner Coast Ranges of California is the monotypic genus *Hollisteria* (Watson 1879). Jones (1908) proposed *Chorizanthe floccosa*, which proved to be a synonym of *H. lanata* S. Wats., but it seems unlikely that Jones comprehended the significance of



his proposal and simply felt the plants represented a species of *Chorizanthe*, and did not consider that he was reducing *Hollisteria* to *Chorizanthe*. Roberty and Vautier (1964) placed the taxon in *Eriogonum*, but this concept has not been followed by anyone, and not even Stokes (1904, 1936) felt compelled to reduce *Hollisteria* to *Eriogonum*, although what her opinion might have been regarding its placement in *Chorizanthe* was never expressed in print.

The genus *Nemacaulis* (Nuttall 1848a, b) is rather widespread in the southwestern United States and extreme northwestern Mexico, with the single species, *N. denudata* Nutt., divided into two weakly defined variants. Stokes (1904, 1936) reduced *Nemacaulis* to *Eriogonum*, perhaps following the ideas of Curran (1885), who noted the close relationship between *N. denudata* and *E. gossypinum* Curran. No one except Roberty and Vautier (1964) has followed this reduction.

A second cluster of genera is related to *Chorizanthe*. Unlike those which have just been reviewed, the satellite genera in this section can be traced to extant sections of *Chorizanthe*.

*Chorizanthe* itself is a genus of perhaps 50 species, with about 40 species found in west-central North America, and the remaining 10 or so restricted to northern Chile in South America. All of the species in North America are annuals, while all but one of the South American species are subfruticose perennials. The genus has been monographed only by Bentham (1836, 1856), although the North American species have been revised by Torrey and Gray (1870), Watson (1877), Parry (1884), and Goodman (1934). Remy (1851) and Philippi (1864, 1873, 1895) have added species to the South American component of *Chorizanthe*.

Like *Eriogonum*, the generic concept of *Chorizanthe* has changed over the years, with *Chorizanthe* being defined in both a broad and a strict sense. As the genus is outlined here—and it is done so only in a

tentative fashion—a middle-of-the-road approach is proposed. Several segregate genera have been proposed from members frequently placed in *Chorizanthe*. These genera are *Mucronea* Benth., *Lastarriaea*, *Centrostegia*, *Acanthogonum* Torr., and *Eriogonella* Goodman. In the following treatment, *Mucronea*, *Lastarriaea*, and *Centrostegia* are recognized as distinct from *Chorizanthe*, with *Acanthogonum* and *Eriogonella* retained in *Chorizanthe*.

The genus *Mucronea* (Bentham 1836) was described at the same time that *Chorizanthe* was proposed, and it was retained as a distinct genus by Bentham (1856) in his monograph on Eriogonoideae in deCandolle's *Prodromus*. Torrey and Gray (1870) reduced *Mucronea* to *Chorizanthe*, and their opinion was followed by Bentham and Hooker (1880) a decade later. Goodman (1934) reintroduced *Mucronea* into the literature when he distinguished it from *Chorizanthe* in his monograph on the latter genus. However, even with Goodman's study, the genus remained suppressed (Abrams 1944, Munz & Keck 1959) except for Hoover (1970), who recognized the genus in a local flora. As defined here, the genus is considered to have two species, both of which are restricted to California.

*Lastarriaea* was proposed by Remy in Gay's *Flora Chilena* (1851), but it was not associated with the tribe Eriogoneae (Bentham 1856) until Torrey and Gray (1870) placed the genus in the tribe. Bentham and Hooker (1880) removed it, *Hollisteria*, and *Nemacaulis*, along with *Pterostegia*, and placed them in the tribe Koenigeae. Except for Dammer (1892), this significant departure has not been followed to any degree.

As now defined, *Lastarriaea* contains two species, one in North America and one in South America (Goodman 1943, Hoover 1966).

The genus *Centrostegia* was published for Asa Gray by Bentham (1856) and considered at the time to be a monotypic genus. In 1870, Torrey and Gray added a second species, but in 1877, Watson reduced the



genus to *Chorizanthe*, where it remained until Goodman's revision of *Chorizanthe* in 1934. In 1957, Goodman revised *Centrostegia*, bringing the number of species in the genus to four. One species, *Centrostegia insignis* (Curran) A. A. Heller (1910), was originally described as a species of *Chorizanthe* by Curran (1885) but placed in *Oxytheca* by Goodman (1934) without comment. In short, this single, unusual species has been batted around in three separate genera, and it still seems out of place in *Centrostegia*. As now defined, *Centrostegia* occurs from Arizona and Utah westward to California, where it is found from Monterey and San Luis Obispo counties southward.

Of these three genera, all of which have at one time or another been associated with *Chorizanthe*, data would now seem to indicate that only *Mucronea* is actually all that close to *Chorizanthe*, with *Centrostegia* occupying a position somewhat intermediate between *Eriogonum* (not *Oxytheca*) and *Chorizanthe*, and *Lastarriaea* well isolated from all of the genera but still closer to the *Chorizanthe* complex than the *Eriogonum* complex.

Preliminary studies on the *Chorizanthe* complex have revealed some major areas of investigation for future studies. The most important one is to determine the relationship between the northern annuals and the southern perennials in the genus *Chorizanthe*. The type of the genus is a South American perennial, *C. virgata* Benth., and these perennials differ markedly from the annuals. Current plans call for a detailed study of the South American species, which have not been revised in over 100 years. It is hoped this group of plants will be the subject of a doctoral dissertation. A second area of investigation is whether or not the genus *Acanthogonum* should be recognized and, if so, what members of *Chorizanthe* should be placed in it.

All of the genera discussed to this point belong to the tribe Eriogoneae. The second tribe of the subfamily is Pterostegaeae. This taxon may be characterized by the bisaccate

bracts which become enlarged, scarious, and reticulate in fruit, and the consistently opposite leaves.

The genus *Pterostegia* is a monotypic genus of low, spreading to decumbent annual herbs. Described by Fischer and Meyer (1835) from material gathered by the Russian explorers near Fort Ross in California, the genus can be rapidly distinguished from all other members of Polygonaceae by its floral features and fruiting characteristics. A major problem has been how to interpret the bisaccate bracts. Fischer and Meyer completely misunderstood the relationship of the bracts of *Pterostegia* as they attempted to relate these bracts to those of *Eriogonum*. Bentham (1856) misunderstood the bracts too, attempting to define them as three leaves with a contiguous margin which are expanded into a dorsal wing or crest. Torrey and Gray (1870) stated that the bracts were homologous with the bracts of *Nemacaulis*, but even this seems most unlikely today, although the concept expressed by them was accepted by Bentham and Hooker (1880). The involucre bracts of *Pterostegia* are two-lobed, enlarged in fruit, and are simply unlike anything found in any genus of Eriogoneae.

*Pterostegia* is a rather variable species which ranges from Oregon southward to northern Baja California and eastward into Utah and Arizona. It does not seem to be divisible into infraspecific elements although Nuttall (1848a) suggested some segregates.

The second genus of Pterostegaeae, *Harfordia*, was proposed by Greene and Parry in a paper published by Parry (1886). The year before, Greene (1885) had described *Pterostegia galioides* Greene, and, while he placed the species in *Pterostegia*, it was the first time that good specimens of *P. macrop-tera* Benth. (Bentham 1844) were found. Bentham's descriptions of his species, published both in 1844 and 1856, lacked the fine detail, and he was not even sure whether the plants were annuals or perennials. It is likely that the lack of adequate material accounted for the long delay in as-



certaining the significant differences between the type species of *Pterostegia*, *P. drymarioides* Fisch. & Mey., and *P. macroptera*. Once *Harfordia* was described, it was immediately accepted, and the genus is now well recognized (Shreve & Wiggins 1964). At present, *H. macroptera* (Benth.) Greene & Parry is known only from the west coast of central Baja California, Mexico.

#### ORIGIN OF ERIOGONOIDEAE

The origin of Eriogonoideae is unknown. The subfamily is clearly a member of Polygonaceae, for it shares with the other subfamilies of the family a large number of morphological and biochemical similarities, and the subfamily Eriogonoideae cannot be raised to the familial level as proposed by Meisner (1841) without violence to our understanding of families in the Magnoliophyta. Eriogonoideae has a single, basal, bitegmic, crassinucellate ovule similar to that of *Polygonum* and has the typical trinucleate pollen of the family. Still, these are features which are not only typical of Polygonaceae, but of Plumbaginaceae and nearly all of the families commonly associated with the Caryophyllales (Cronquist 1968). Eriogonoideae also shares with the other subfamilies of Polygonaceae the copiously laden endospermous seeds and the anthocyanins pigmentation. The subfamily does differ from the other subfamilies in lacking the distinctly sheathing stipular ochrea of the leaves (although an ochrea is weakly present in some perennial species of *Chorizanthe*), and the pollen of the subfamily is the least specialized of all subfamilies of Polygonaceae (Nowicke, pers. comm.) suggesting that, as a group, Eriogonoideae may be a rather primitive member of Polygonaceae. Equally important in this regard, it may also mean that Eriogonoideae, as a group, has retained many of the least specialized features of the family due to a lack of modification in organs which have occurred in other taxa.

Although the critical similarities between

the subfamilies certainly associate these taxa of Polygonaceae into a distinct family, the place and mode of development of Eriogonoideae from the rest of Polygonaceae is now obscured by time and compounded by a lack of a fossil record. No one group of genera outside of the Eriogonoideae can be considered the exact point of origin of the subfamily, and for this reason, the subfamily (or tribe) has long been considered unique within Polygonaceae (Bentham 1836, Goodman 1934, Roberty & Vautier 1964). Based on preliminary pollen data from extant taxa now available from the work of Dr. Joan Nowicke at the Smithsonian Institution, it seems clear that Eriogonoideae is clearly differentiated from all but the South American tropical genus *Triplaris* Loefl. This is the only genus which has a similar, unspecialized pollen grain (and thus different even from the related American tropical genus *Ruprechtia* C. A. Meyer), but based on extant data on chromosome numbers, gross morphology, and other anatomical and morphological features (especially in the inflorescence), it seems most unlikely that the tribe Triplarideae C. A. Meyer and the subfamily Eriogonoideae have been connected in any but the most remote fashion.

Roberty and Vautier (1964) placed Triplarideae in the subfamily Calligonoidae Roberty & Vautier which they defined as a group of New and Old World genera. Dammer (1892) referred the tribe to Coccoloboideae Dammer, a basically shrubby or arborescent taxon about equally divided in the New and Old World. Dammer's suggestion seems more reasonable as he defined the Coccoloboideae to include (using current nomenclature) such genera as *Coccoloba*, *Muehlenbeckia* Meisner, and *Triplaris*—all genera with ruminated endosperm. Unfortunately, all genera of Eriogonoideae have a smooth endosperm. Meisner (1856), Bentham and Hooker (1880), and Dammer (1892) all placed Eriogonoideae in a position in their revisions of the Polygonaceae which would imply that Eriogonoideae is the least specialized of the family. Roberty



and Vautier placed the subfamily at the end of their treatment; most certainly Roberty and Vautier are correct in their assessment of the placement of the subfamily in the family, for Eriogonoideae is the most advanced member of the extant subfamilies of Polygonaceae and not the least specialized. In Meisner, Bentham and Hooker, and Dammer, interestingly, the Triplarideae was considered the most advanced member of the subfamily Polygonoideae (Meisner and Bentham and Hooker) or Coccoloboideae (Dammer). If this is indeed the case, then it logically can follow that a possible origin of the Eriogonoideae may have been within an ancient taxon that, by definition, might include the basic expression from which the Triplarideae has evolved or in fact was a part. At no time, however, has *Triplaris* or *Ruprechtia* played a direct role in the origin of any genus within Eriogonoideae.

It is likely that the divergency of Eriogonoideae from the rest of Polygonaceae has been so fundamental, so sudden, and so successful, that the new subfamily has completely swamped those groups (or that group) from which it arose. If this divergency is an ancient one, as I suggested some years ago (Reveal 1969b), and occurred at the beginning or slightly before the start of the Tertiary some 65 million years ago, then the loss of such intermediate stages of evolutionary development is to be expected. However, if the origin of the subfamily has been well within the Tertiary, as now seems much more likely, then the loss of the intermediate forms is a matter of the explosive success and highly competitive nature of the new form (in this case, the earliest members of Eriogonoideae) as opposed to the rather static parental type (see Stebbins [1974] for a detailed discussion of this type of explosive evolution above the generic level).

As just noted, it now seems more reasonable to assume that Eriogonoideae arose during the Tertiary, and probably during the Oligocene or Miocene epochs (7 to 38 million years ago) when there was a general

drying of the climate coupled with the rapid development and increase of herbaceous angiosperms (Gray 1964, Axelrod 1966, Tidwell et al. 1972). Pollen grains, attributable to *Eriogonum*, have been found in the Quaternary, which began some 7 million years ago (Leopold, pers. comm.). If this assumption is correct, then perhaps the subfamily Eriogonoideae had its origin from a subtropical group of New World polygonaceous plants near the beginning of the drying period during the Oligocene, which split off into a tropical complex (something like *Triplaris*) and a northern temperate complex (something like *Eriogonum*). This point of origin has subsequently been lost, with the extinct relatives of *Triplaris* and *Eriogonum* extending and amplifying the differences between the two extremes to a point that now only the mere hint of relationship may be noted in a conservative feature such as pollen morphology. If the theories of Takhtajan (1969) and Stebbins (1974) are correct regarding the differential rates of specialization between tropical and xeric temperate groups, then one may assume that the relatives leading to *Triplaris* have undergone less specialization and differentiation than the relatives leading to *Eriogonum*. This would seem to be the case here, especially when one looks at the reduction of the inflorescence in *Eriogonum* to a cluster of flowers, the reduced stature of *Eriogonum*, and the great proliferation of species in the Eriogonoideae when compared with the Triplarideae.

Over the years I have vainly searched the temperate members of Polygonaceae, and especially those of Asia, for a hint to the origin of *Eriogonum*. None has been found. Stebbins (1974) has cautioned us to realize that in evolutionary events such as the origin of taxa above the species rank extinction and extensive changes in the distribution and ecology of a taxon may occur which can substantially change one's outlook as to the possible site and point of origin for a given group. It now seems reasonable to look to the New World tropics for a



point of origin rather than the Old World steppes. Certainly, the pollen data just recently reported to me by Nowicke has greatly strengthened this preconceived idea. The origins of the Eriogonoideae very likely have revolved around the reduction of the inflorescence from an extended one (such as in *Ruprechtia* or *Triplaris*) to a capitate one, the development of an involucre due to the fusion of subtending bracts on the inflorescence, and the reduction of stature from a shrub or small tree to a subshrub or low shrub. The final step, of course, has been the development of an ability to evolve successfully in a xeric habitat rather than in a mesic, subtropical, or tropical habitat. To my knowledge, none of these steps is extant today.

It was proposed by me (Reveal 1969b) that the probable ecological place of origin for *Eriogonum* was in a xeric site, and that the first forms of the genus were subshrubs or low shrubs. This suggestion has been seconded by Stebbins (1974), and there seems to be little reason to alter this opinion. It is important to note that this statement relates to one genus, *Eriogonum*, and not to the origin of the subfamily. It seems to me that the stages of development leading from the tropical origin of the precursors of the Eriogonoideae to the extant genus *Eriogonum* must have taken many different directions, a great deal of time, and undergone many different attempts before arriving at this modern genus. It is now impossible to close that gap, since the history of the Eriogonoideae during the Tertiary is unknown.

The most generalized form of *Eriogonum* that exists today is a low, rounded shrub with cauline leaves, cymose inflorescences, small smooth achenes, and an unspecialized flower with monomorphic tepals. These shrubs occur in xeric habitats mainly in the pinyon-juniper woodlands of the Great Basin in Utah and Nevada. Even so, these species of *Eriogonum* are highly specialized as all are tetraploids, and no diploid species are known to exist in the genus (Stebbins

1942, Stokes & Stebbins 1955, Reveal 1969b). Therefore, *Eriogonum*, as it exists today, is a highly evolved group, and no species now exists which could point to the initial element(s) which might have evolved from other, more primitive, subtropical taxa of Polygonaceae.

The assumption that *Eriogonum* is the most basic genus of the subfamily seems reasonable on the basis of morphological considerations, especially in the makeup of the inflorescence and involucre. However, I suspect, that the most ancient extant members of the subfamily are the perennial species of *Chorizanthe*. As shall be discussed below, *Chorizanthe* likely evolved from *Eriogonum*, and not the other way around. However, one feature found in these perennial species of *Chorizanthe* seems to hint at their ancientness: they have what can only be considered as weakly defined, fibrous remains of ochrea. If these species of *Chorizanthe* should prove to be diploids, this would reinforce their evolutionary significance. Based upon an examination of the gross morphology of these plants, one must add to the definition of the earliest members of Eriogonoideae the presence of an ochrea.

If the genus *Eriogonum* underwent its early development in a xeric habitat dominated by pinyon-juniper woodlands, then where was such a site in the Miocene or early Pliocene epoches when the genus was undergoing its earliest development?

During the Miocene, the Great Basin was dominated by extensive coniferous forest, with the Sierra Nevada to the west about 1000 m in altitude, and thus an ineffective rainshadow (King 1959). It is important to note that these coniferous forests were temperate in nature, with the subtropical forests of the Oligocene largely pushed to the south. Axelrod (1950) has suggested the existence of two major geofloras, with the Arcto-Tertiary geoflora of hardwood-deciduous and conifer forests dominating the Great Basin region, and the Madro-Tertiary geoflora of small-leaved, drought-resistant



shrubs and trees of the southwestern United States and northwestern Mexico. Axelrod (1958) states that the Madro-Tertiary geoflora moved northward into the Great Basin in Early Pliocene, but did not entirely replace the Arcto-Tertiary geoflora.

It would seem possible that *Eriogonum* may have undergone its early development and differentiation in the Madro-Tertiary geoflora during the Miocene and became well established in the Arcto-Tertiary geoflora in at least two different expressions: one typified by the subgenus *Eucycla* (Nutt.) Kuntze in Post & Kuntze (with such species similar to *E. microthecum* Nutt. or *E. corymbosum* Benth. in DC.) and the other of members typical of the subgenus *Oligogonum* Nutt. (with such species similar to *E. umbellatum* Torr. or *E. flavum* Nutt. in Fras.). Out of the Madro-Tertiary geoflora possibly came such subgenera as *Eriogonum* and *Pterogonum* (H. Gross) Reveal which contain such species as *E. longifolium* Nutt., *E. atrorubens* Engelm. in Wisliz., and *E. alatum* Torr. in Sitgr., or their progenitors (Hess & Reveal 1976). Nonetheless, the basic expression of the genus would have belonged to the subgenus *Eucycla*, which is basically a taxon of xeric, pygmy coniferous forests. It is also likely that *Chorizanthe* evolved during this period of time from the subgenus *Eucycla*, probably when the subgenus was in the Madro-Tertiary geoflora and before the subgenus underwent its modern-day development of species complexes now typically found in the Great Basin.

#### EVOLUTION WITHIN ERIOGONOIDEAE

If the hypothesis is correct that *Eriogonum* is the most primitive extant member of the subfamily Eriogonoideae, then a number of corollaries may be presented.

Within *Eriogonum* itself, if the basic expression of the genus was a low, spreading subshrub or shrub with alternate leaves, cymose inflorescences, and unspecialized tepals, then the subgenus *Eucycla* was the initial expression within the genus. As just

noted at the end of the previous section, it is probable that the differentiation of the subgenera *Eucycla*, *Eriogonum*, *Oligogonum*, and *Pterogonum* occurred during the Late Miocene or Early Pliocene in the Madro-Tertiary geoflora of northern Mexico and the southwestern United States. Three of these subgenera of *Eriogonum* are fairly distinct from one another, with no interconnecting forms. It is felt that while *Eriogonum* and *Pterogonum* evolved from *Eucycla*, these two did not evolve from any extant member of *Eucycla*. As for *Oligogonum*, it is close to *Eriogonum* and more distantly related to *Eucycla*, and thus both *Oligogonum* and *Eriogonum* may have developed from extinct, primitive members of *Eucycla* at approximately the same time. Of the remaining subgenera, *Clastomyelon* Cov. & Morton, *Micrantha* (Benth.) Reveal, *Ganysma* (S. Wats.) Greene, and *Oregonium* (S. Wats.) Greene, all can be traced rather directly to the subgenus *Eucycla* without any major difficulties.

As for *Eucycla*, it has developed every perennial habit expression of the genus *Eriogonum* but one, the monocarpic habit of *E. alatum* of the subgenus *Pterogonum*. The subshrub or low shrub habit is widely seen in the less specialized members of *Eucycla*. Such plants are typically seen in the pinyon-juniper (or pygmy) woodlands throughout the western part of central North America today, or essentially the entire geographical range of the subgenus which extends from the fiftieth parallel southward to the Tropic of Cancer. Also found in the pygmy woodland zone are several different kinds of herbaceous perennial expressions belonging to *Eucycla*. Unlike the shrubs which tend to be species of widespread distribution, the herbaceous perennials tend to be more restricted in their range. Some of these species evolved within the zone and have remained while others have extended themselves beyond the confines of the zone, and still others, in more recent evolutionary times, have entered the zone from other areas. From the pygmy



woodland zone, species of *Eriogonum* have migrated into dry, xeric clay habitats, into grasslands or chaparral habitats, and into alpine zones and off-shore islands. In all cases, the present members of the subgenus are tetraploid, derived species, and while the majority of morphological expressions are found in the pinyon-juniper belt, the majority of explosive evolution within *Eriogonum*, and in all of its related genera (except for the most initial phases of *Chorizanthe*), owe their origins to their survival in ecological life zones other than the pygmy woodlands.

The origins of both of the predominantly annual subgenera, *Ganysma* and *Oregonium*, probably owe their origins to the subgenus *Eucycla* and probably had an initial differentiation in the pinyon-juniper woodlands of the West. Once again the basic expression of these subgenera are generally widespread and found mainly in this habitat. However, unlike portions of *Eucycla*, it seems—especially in *Ganysma*—that much of the initial evolutionary development of these subgenera have been lost over time, because there are widely scattered species of *Ganysma* in other habitats in which the species are obviously primitive but by no means ancient.

The temperate arid regions of the inland portions of North America exhibit the unique combination of selective drought and cold temperatures, conditions which have likely played a major role in the evolution of the shrubby habit from which herbaceous and caespitose perennial species could have evolved (Axelrod 1966). The shrubby and subshrubby species of *Eriogonum* and *Chorizanthe* have certainly been subjected to the selective pressures of seasonal cold, coupled with enough summer moisture to sustain growth, and the ability to occupy habitats that are protected enough to allow for long-term survival in extended periods of stress. By looking at a pygmy woodlands as the original home of *Eriogonum* and its first major dichotomy, *Chorizanthe*, one can understand the variety

of habit and morphological expression in this ecological habitat, and the economy in terms of species diversity in this zone. On the whole, the explosive evolution of the modern-day species of *Eriogonum* and its related genera, and *Chorizanthe* and its related genera, has been areas in of extreme environmental stress outside the protective (such as they are) confines of the pinyon-juniper belt. Without a doubt, the majority of the genera related to *Eriogonum* owe their origin to their successful adaptation to a stress condition, mostly selective drought, accompanied by the occupation of ecological areas on the margins of protective life zones. However, as we shall see, the subgenus *Eucycla* has given rise only to the other subgenera of *Eriogonum*, *Chorizanthe*, and *Dedeckera*, but none of the other genera. *Oxytheca*, *Stenogonum*, *Gilmania*, *Goodmania*, *Nemacaulis*, and perhaps *Holisteria* owe origin to *Eriogonum* subgenus *Ganysma*, while *Mucronea*, *Centrostegia*, and perhaps *Lastarriaea* owe their origin to annual species complexes of *Chorizanthe*. And note, all of these genera (except the primitive members of *Chorizanthe*) are basically taxa of areas of extreme aridity, and basically adapted to the annual habit (all but *Dedeckera*).

The one major adaptation which distinguishes *Chorizanthe* from *Eriogonum* is a combination of the production of an awned involucre and the reduction in the number of flowers per involucre. I believe the production of an awned involucre has occurred several times in the history of the subfamily, much as the total loss or reduction of an involucre has occurred several different times and places in the taxon.

The key to understanding the origin and evolution of *Chorizanthe* lies in the unstudied South American perennial species. An examination of available herbarium material seems to point the origin of these perennials to the subgenus *Eucycla* of *Eriogonum*, a theory which seems reasonable if *Eriogonum* is, as I suspect, the basic element of the subfamily. There are, however, some diffi-



culties which in theory can be excused but need to be mentioned.

If *Chorizanthe* evolved from *Eriogonum* subgenus *Eucycla*, it did not evolve from any extant group of the subgenus. One can account for the subshrubby habit of the perennial *Chorizanthe* as having come from *Eucycla*. Even the hooked, awned condition of the involucre could be traced to the subgenus as several extant species of *Eucycla* have long, sharply acute involucre lobes which, while not awned, could point to a stage in the development of the awned condition. The narrow, essentially basal leaves of *Chorizanthe* can be traced to *Eucycla*, as can the congested, cymose inflorescence. Two major drawbacks exist. One is the straight embryo of *Chorizanthe* (Goodman 1934), whereas all species of *Eucycla* have a curved embryo (Reveal 1969a, b). The second is the six-lobed involucre of *Chorizanthe*, while the majority of species in *Eucycla* are five-lobed.

The critical hint here, I believe, is the presence of the remains of the ochrea in some species of South American *Chorizanthe*. As Grant (1971) has noted, a given character may or may not be selected for or against, and thus, while the direction of the subfamily Eriogonoideae has been to get rid of the ochrea, at sometime in its history of divergency from the rest of Polygonaceae it must have possessed this feature. If, as I suspect, the perennial species of *Chorizanthe* are the most ancient extant members of the subfamily, then it would follow that these plants would exhibit some of the more primitive features of the subfamily and provide helpful keys to its origin. By the same token, while I accept *Eriogonum* as the basic expression of the subfamily, and *Chorizanthe* as a derived element, one need not look further than extant and derived members of *Eriogonum* to find all unique features of the South American perennials except the ochrea. Thus, if *Chorizanthe* evolved as a preliminary expression from *Eucycla*, as did the subgenera *Eriogonum* or *Oligogonum*, then suddenly we find species

of *Eriogonum* with a straight embryo and a six-lobed involucre. The genus *Oxytheca*, which can trace its immediate origin to *Eriogonum* subgenus *Ganysma*, has awned involucre, and the reduction in the number of flowers per involucre can be seen in several different groups of *Eriogonum*, although admittedly this feature is almost entirely restricted to annual species.

The next critical step in this discussion is how did the perennial members of *Chorizanthe* get to South America while *Eriogonum* did not, and if *Chorizanthe* evolved from *Eriogonum* subgenus *Eucycla* in North America, why are there no perennial species of *Chorizanthe* in North America?

The first part of this question can be easily answered. The only members of Eriogonoideae in South America are those which have a distinctly awned, or hooked, involucre lobe. As Stebbins (1974) has pointed out, such an adaptation can be a successful means of long-distance dispersal. Thus *Eriogonum* (with the exception of *E. divaricatum*, an annual species which was found as a waif in eastern Argentina) is perhaps lacking from South America due to the absence of an awned involucre. The second part of this question, why the perennial species of *Chorizanthe* are missing from North America, is much more difficult.

Two options exist about the existence of perennials in South America and their lack in North America, and a third option can be proposed on the basis of either of the first two options if future studies should make such an option necessary from a taxonomic point-of-view.

The first two options are closely intertwined and deal with the actual origin of the perennial species in South America and the annual species in North America. Assuming the idea that *Chorizanthe* evolved as a perennial group from *Eriogonum* in North America, then it had to have migrated to South America as a perennial and become established as a perennial. The South American populations, I believe, have remained essentially unchanged since their (or its) in-



itial introduction with some speciation occurring there within rather limited parameters. One hint that this is so is that all of the perennial *Chorizanthe* species fall within extremely narrow limits morphologically, and, while several species (close to 25) have been described, the actual number of valid species seems to be much less than that. The one annual species in South America is apparently a much more recent introduction than the perennial species because it is closely related to the single most widespread annual species in North America (Goodman 1934).

The first option states that *Chorizanthe* evolved in North America and migrated as a perennial to South America as a single introduction, with the North American perennials gradually being replaced by annual species. In South America, the perennial species were subjected to little direct selection pressure, while in North America the perennial members of *Chorizanthe* were subject to intense pressures from the rapidly evolving and highly competitive, closely related genus *Eriogonum*. In order to survive and compete against *Eriogonum*, which, I feel, was rapidly adopting the annual habit, *Chorizanthe* also had to change if this hypothesis is feasible.

The second option is that the perennial species of *Chorizanthe* in North America became extinct, while the South American species remained. The annual habit then developed in Chile, and only the annual species were introduced into North America. Raven (1963) has noted that, while the majority of species probably migrated north to south, some certainly went from south to north. Once in North America, the annual species underwent active adaptive radiation similar to that observed in such annual groups of *Eriogonum* as the subgenera *Ganysma* and *Oregonium*.

The third option states that the South American perennials represent a genus of plants distinct from the North American (and one South American) annuals. If this is so, then the name *Chorizanthe* would be ap-

plied to the South American perennials, while the annual species would be called *Acanthogonum*, or, if that genus proves distinct, *Eriogonella*. This option takes on added significance if the following scenario should prove correct after careful systematic studies. If indeed *Chorizanthe* evolved as a perennial and migrated southward, and the northern element became extinct, did the annual species evolve prior to the extinction of the perennial group or did the annual species begin from a whole new series of events? In option one, I have accepted the first part of this question, but if the second were the case, then it will be impossible to retain the North American annuals in the genus *Chorizanthe*.

The recently discovered *Dedeckera eurekaensis* probably evolved from the subgenus *Eucycla* of *Eriogonum*, and most likely from the section *Corymbosa*. Its origin is likely most recent. It differs from all other members of the subfamily in having a head of subsessile or sessile flowers, borne on a slender peduncle and subtended by two to five foliaceous bracts, and a single, short-pedicellate axillary flower at the base of each peduncle. It differs from *Eriogonum* in lacking an involucre tube. This monotypic genus is known only from a single site where about 200 individual plants are found. It is likely that the genus evolved in place within recent history and, while its range has expanded and decreased throughout its brief history, it is unlikely that the plant has been beyond the restrictive ecological confines of the Death Valley region of eastern California.

The pubescence of *Dedeckera* is similar to that of *Eriogonum intrafractum* Cov. & Morton, another Death Valley endemic, which is the only representative of the subgenus *Clastomyelon* and a few other members of *Eriogonum*. Of all the subgenera of *Eriogonum*, *Clastomyelon* is the most distinctive on pure morphological grounds in that the stems are broken into a series of ringlike segments, the numerous flowers rupture the involucre tube into irregular



segments, and the bractlets are foliaceous at least in part. While it is possible to trace the origin of *E. intrafractum* to the subgenus *Eucycla*, where *D. eurekaensis* also evolved from, both are amazingly distinct, with *D. eurekaensis* significantly more so than *E. intrafractum*. It is interesting that in the Death Valley area, where speciation has been rather spectacular (Stebbins & Major 1965), Polygonaceae should be blessed with so many different expressions. Much like *Gilmania*, which will be discussed below, *Dedeckera* and *E. intrafractum* have come about in recent times, influenced by the environmentally profound selection pressures of the area.

The remaining satellite genera related to *Eriogonum* evolved from the subgenus *Ganysma*.

*Oxytheca* is being studied currently by Ertter and me to determine the exact make-up of this genus. We have excluded *O. luteola*, placing it in a new genus, *Goodmania*. The remaining nine species, however, may or may not be all related. *Oxytheca dendroidea*, *O. watsonii*, and the South American plants are related to *Eriogonum spergulinum* A. Gray, and, based on this close morphological similarity, Goodman (in herbaria) has placed these plants in *Eriogonum*. *Oxytheca perfoliata* probably belongs to this complex of species (Goodman would have placed the taxon in *Eriogonum*), but it is morphologically distant from the other members. As for *O. parishii* and an undescribed taxon from the San Bernardino Mountains of California, they present a problem. Goodman (in herbaria) would have placed these in *Eriogonum*, but both seem more closely related to *E. apiculatum* S. Wats. and *E. parishii* S. Wats. than *E. spergulinum*. Small (1898) placed *O. parishii* in a monotypic genus, *Acanthoscyphus*. It is possible that *Acanthoscyphus* should be recognized if it can be shown that *O. parishii* and its related taxon are distinct from that group of *Oxytheca* species typified by *O. dendroidea*.

This complex of species (excluding the

*Oxytheca parishii* complex for a moment) seems to have developed in the pygmy woodlands of the Great Basin and, in particular, along the western edge of the Great Basin. This is a complex of volcanic sandy soils that are widely scattered. I suspect the group evolved during the Quaternary (probably the Pleistocene), with the introduction of the South American phase in recent geological time (see Raven 1963).

Goodman (in herbaria) placed *Oxytheca caryophylloides*, *O. emarginata*, and *O. trilobata* in a new genus. Our preliminary studies of these species seem to indicate that they too developed from *Eriogonum apiculatum*, *E. parishii* complex, and perhaps one should consider if these species too ought not to be referred to *Acanthoscyphus*. These three species differ from *O. parishii* and its undescribed relative in having a five-lobed involucre instead of the nonlobed tube with 4 to 30 long bristled awns. All of these plants are found in the granitic mountains of southern California and northern Baja California and occur in approximately the same type of ecological niche.

I have come to look upon *Oxytheca parishii*, *O. caryophylloides*, *O. emarginata*, and *O. trilobata* as a group that has evolved in the Pleistocene in the mountainous region of southern California and adjacent Mexico as the result of sudden and explosive evolutionary changes in the gene makeup of the rapidly developing annual species of both *Eriogonum* and *Chorizanthe*. This is not to say that *Chorizanthe* played a direct role in the development of these species, but one should remember that *Centrostegia* (and in particular *C. insignis*) probably developed at the same time, and this genus is similar to *Chorizanthe*. Thus, I suspect, a whole series of rapid changes were in the process at this time in a small portion of *Eriogonum*, which possibly resulted in this group of *Oxytheca*, *Centrostegia*, and perhaps (if option three is correct) the annual species of *Chorizanthe* as well. If this conclusion should prove correct with regards to the species now placed in *Oxytheca*, then Good-



man would have been proved correct, and these species would have to be placed in a different genus.

*Stenogonum* is a step-child in this group of satellite genera. It is closely related to *Eriogonum*, differing mainly in the construction of the involucre. While in *Eriogonum* the involucre is distinctly tubular, the involucre of *Stenogonum* is composed of two whorls of three lobes. That this condition is possible within a genus clearly and closely related to *Eriogonum* is an important step, because it does demonstrate the potential for a six-lobed or three-lobed involucre as found in the annual species of *Chorizanthe*.

*Stenogonum* evolved from the *Eriogonum inflatum* Torr. & Frém. complex of the subgenus *Ganysma*. It is thought that the origin of this clay-inhabiting genus is relatively recent and has evolved to a point about on the par with the degree of divergence seen in *Oxytheca*. *Stenogonum* is an annual which has evolved from a "hot desert" complex on the Colorado Plateau, which is an area somewhat intermediate between the Mojave Desert and the Great Basin in terms of physiological stress. *Eriogonum inflatum* var. *inflatum* is found on the Plateau, but the more common phase is not the perennial var. *inflatum*, but the annual var. *fusiforme* (Small) Reveal. Likewise, var. *inflatum* is usually found in rocky places above the clay hills and flats, while var. *fusiforme* is typical of the clay sites. Thus it is that the genus *Stenogonum* has evolved by successfully occupying the clay habitat that, for the most part, members of the *E. inflatum* complex cannot enter.

Two genera are difficult to directly associate with *Eriogonum*, and both perhaps have recently evolved in the subfamily. They are *Goodmania* and *Gilmania*. The two seem to be related, as both are prostrate to low-spreading annuals with pubescent yellow flowers, cauline leaves, and small, smooth achenes. *Goodmania* has involucre bracts which subtend each cluster of flowers and act as a protective involucre.

In *Gilmania*, all involucre bracts are lacking, but the three foliaceous leaves, when the plants are immature (but that particular branch is in full flower), are held close together by the shortened internodes so that each cluster of flowers is positioned above the lower whorl of three leaves so that the flowers are protected both by these leaves and the whorl of upper leaves as well. In this condition, the long pedicels extend the ripened flowers beyond the protective confines of the three leaves so that pollination may occur. In this fashion, the flowers of *Gilmania* are better protected from the elements than those of *Goodmania*.

*Goodmania* could possibly be traced to *Oxytheca*, but I think not. True, it has an awned involucre bract, but, in fact, these bracts are just that and they are not arranged into a distinct tube. The individual bracts can be separated from each other without disruption of tissue on an adjacent bract. There is one bract that is longer than the other four bracts which is unlike any species of *Oxytheca*, but is a condition that is seen in some species of annual *Chorizanthe*. The flowers of *G. luteola* are yellow, and no species of *Oxytheca* has yellow flowers, and the plants of this species are glabrous and bright green while those of *Oxytheca* are glandular (at least in part) and usually reddish or grayish in color. As I look about the subfamily, I see a possible close relationship with the subgenus *Oregonium* for this genus and *Gilmania*, and in particular *Eriogonum divaricatum*. The subgenus *Oregonium* underwent a major upheaval in the hot, dry foothills of western California, but *E. divaricatum*, *E. puberulum* S. Wats., and other similar species are more typical of the Great Basin. Thus, while this group of species of *Eriogonum* may hint as a possible place of origin for *Goodmania* and *Gilmania*, the group seems unsatisfactory, and no extant subfamily of *Eriogonum* really reveals a logical place of their origin.

As noted above, these two genera seem to be recently evolved genera. *Goodmania* is



usually found on the plains of old dry lake beds in areas which were covered by water during recent glacial periods. *Gilmania* occurs on the lower rim of Death Valley on alkaline soils near sea level, and thus in areas that were covered by water less than 50,000 years ago. It is likely, therefore, that both genera underwent their evolutionary development at approximately the same time, taking advantage of the same type of opening environment niche.

The origin of *Gilmania* is somewhat more difficult to postulate than that of *Goodmania*. Cauline leaves in *Eriogonum* annuals are infrequent, and when present are rarely arranged in a pattern similar to that of *Gilmania*, nor are they like the leaves of *Goodmania*. In *Goodmania* the leaves are two and opposite, varying from laminar at the lower nodes to acicular at the upper nodes. In *Gilmania*, the leaves are in threes, with two of the leaves opposite, and the third opposite the next branch; all of the blades are laminar. It seems unlikely that both *Gilmania* and *Goodmania* evolved from precisely the same element within *Eriogonum*, but they probably did arise within the same subgenus. I strongly suspect that the selective evolutionary pressures have been much greater on *Gilmania* than *Goodmania*, thus accounting for the great degree of demarcation of *Gilmania*.

Curran (1885) was the first to call attention to the close relationship between *Eriogonum* and *Nemacaulis*. *Nemacaulis* is similar to *E. gossypinum* in that both have copious bractlets and hairs surrounding and protecting the flowers; in *Eriogonum* the tubular involucre is broadly campanulate, but in *Nemacaulis* the involucre is lacking and replaced by subtending bracts. Beyond this, the two taxa are notably distinct. Still, it seems likely that the origin of *Nemacaulis* can be traced to *Eriogonum* subgenus *Ganysma* and, in particular, the section of *Ganysma* which contains *E. gossypinum*.

Looking upon *Nemacaulis* as a recent derivation from *Eriogonum*, it seems to have undergone rapid development in the hot

deserts of southern California and adjacent Mexico, occupying a position on the southern geographical edge of *Eriogonum* section *Ganysma*. I suspect the degree of difference between *Eriogonum* and *Nemacaulis* is on the magnitude of that exhibited by *Eriogonum* and *Oxytheca*.

The genus *Hollisteria* is a most difficult genus to trace back to its possible point of origin. It is a prostrate, spreading annual with two sessile, yellow, woolly flowers subtended by three slightly united involucre bracts. In some respects, *Hollisteria* is intermediate between *Eriogonum* and *Chorizanthe*. It differs from both in lacking a distinct involucre tube, but it is two-flowered and thus similar to *Centrostegia* and has acrose tips on the bracts similar to those on *Goodmania*. It probably did not evolve from an unknown perennial group as proposed by Stebbins (1974) but more likely developed from an annual complex.

I would like to say that *Hollisteria* could have evolved from either *Eriogonum* subgenus *Ganysma* or *Oregonium*, but no extant group in either subgenus can really point the way. I have tried to place the genus near *Chorizanthe*, but still no one group of that genus really is helpful. In some respects, I have tried to fit it into a pigeonhole between what Goodman termed *Eriogonella* (*C. membranacea* Benth.) and *Centrostegia* because here one can find a combination of three-lobed involucres, yellowish flowers, and a spreading annual habit. Still, one compelling bit of evidence that wrenches this entire scene is the nature of the pollen grain. As Nowicke (pers. comm.) has recently shown, the pollen grains of *Hollisteria* and *Lastarriaea* are essentially the same, and unlike any other genus of *Eriogonoideae*. It is possible that both *Hollisteria* and *Lastarriaea* evolved from an extinct, independent complex of annual species. One part of the complex close to *Eriogonum* could have given rise to *Hollisteria* while another part of the complex close to *Chorizanthe* gave rise to *Lastarriaea*.



As one might suspect from the foregoing discussion, the genus *Lastarriaea* is also somewhat intermediate between *Eriogonum* and the annual species of *Chorizanthe*, but closer to the latter than the former. *Lastarriaea* is a low, often spreading annual without a distinctly tubular involucre, acerose bracts, and whitish, glabrous, coriaceous tepals. Unlike all of the genera discussed to this point (with the exception of some species of *Chorizanthe* and *Nema-caulis*), *Lastarriaea* has only three anthers per flower instead of the usual nine. And unlike *Hollisteria*, which is an inland species of the Inner Coast Ranges of California, *Lastarriaea* is a coastal genus found in both North and South America.

Goodman (1934) placed *Lastarriaea* in *Chorizanthe* in the least specialized section of the genus, and, while there are some superficial similarities between the section Suffrutices Benth. and *Lastarriaea* to the point that perhaps it evolved from this section, I doubt that its point of origin can be traced to any extant section of *Chorizanthe*. As noted above, a more likely situation is that *Lastarriaea* developed early in the evolution of the annual species of *Chorizanthe* (or less likely, *Eriogonum*). I strongly suspect that *Lastarriaea* became well established in North America, and that it, the one annual species of *Chorizanthe*, and *Oxytheca* all migrated to South America at approximately the same time as hitchhikers on animals, probably during the Late Pliocene (Raven 1963). The differences between the North and South American elements are not strongly expressed morphologically in these annual species, although a strong difference does not necessarily have to be expressed (Grants 1967).

*Mucronea* is clearly derived from the annual species of *Chorizanthe*. This genus has a distinctly tubular involucre like *Chorizanthe*, but it and *Centrostegia* differ in having three-lobed bracts instead of the typically entire bracts of *Chorizanthe*. The conspicuous bracts of *Mucronea* are united and distinct, and in this feature the genus is sim-

ilar to *Eriogonum* and *Oxytheca*, especially *O. perfoliata*. *Mucronea* is distinct from *Centrostegia* and *Oxytheca* in having straight cotyledons (Goodman 1934), but is similar to *Chorizanthe* in this regard. I suspect that *Mucronea* is a rather recent innovation within the *Chorizanthe* complex.

The genus *Acanthogonum* was recognized as a distinct genus by Goodman (1955), but I am still somewhat reluctant to recognize it. When Torrey (1857) described *Acanthogonum*, he placed a single species, *A. rigidum*, in the genus. In 1858, Torrey questionably added a second species, *A. corrugatum*, noting that this species was "almost intermediate between *Acanthogonum* and *Chorizanthe*." Torrey and Gray (1870) reduced both species to *Chorizanthe* and added to the complex *C. polygonoides* and *C. watsonii*. Goodman (1934) defined *Acanthogonum* to include *A. rigidum* and *A. polygonoides* (Torr. & Gray) Goodman, and these two species were retained in the genus in his 1955 review. Basically Goodman maintained the genus on the basis of the curved cotyledons, but, as I am retaining *Eriogonella* in *Chorizanthe*, which was established (in part) on its curved cotyledons, I cannot very well recognize *Acanthogonum* because of this feature. For now, at least, the relationship between *C. polygonoides* and *C. corrugata*, *C. watsonii*, and *C. orcuttiana* Parry seems too close to allow for a distinct genus to be established.

*Centrostegia* is a most difficult and diverse assemblage of species. As defined by Goodman (1957), the genus consists of four species, three of which, *C. leptoceras* A. Gray, *C. thurberi* Gray ex Benth. in DC., and *C. vortriedei* (Brandeg.) Goodman, form one distinct element within the genus, but *C. insignis* is decidedly aberrant although even *C. vortriedei* is somewhat strange within *Centrostegia*. I am inclined to restrict *Centrostegia* to *C. thurberi* and *C. leptoceras* but am lost when it comes to *C. vortriedei*, and feel *C. insignis* should probably go into a distinct genus. This latter species is certainly most closely related to *Oxytheca*,



where Goodman (1934) placed it at one time. As for *C. thurberi* and *C. leptoceras*, one might look for an origin somewhat intermediate between *Eriogonum* and *Chorizanthe*. Until these species can be carefully studied, especially cytologically, little can be expressed about their relationships. I have little faith in the one unifying character, which is the three-lobed bract, and would like to place more emphasis on the involucre, floral, and vegetative features of these plants.

Up to this point, the discussion has centered on the tribe Eriogoneae, which makes up the vast bulk of Eriogonoideae. The other tribe of the subfamily, Pterostegeae, contains only two monotypic genera. Time and evolution have largely destroyed the interconnecting links between the two tribes so that it is impossible to say what, if any, role Eriogoneae might have played in the evolution of Pterostegeae, or the other way around for that matter. The inflated bracts of the fruiting specimens are unseen in Eriogoneae, and the consistently opposite leaves are rare. I suspect that the two tribes are well separated now by time and events.

Until Parry's (1886) paper in which the genus *Harfordia* was described, the true nature of this narrowly restricted shrub was unknown. Bentham (1844) had placed the perennial in the genus *Pterostegia* not knowing if his species, *P. macroptera*, was a shrub or not. It remained there until 1886. Only Roberty and Vautier (1964) reduced *Harfordia* to *Pterostegia*. In spite of this, there is little reason to closely associate *Harfordia* with *Pterostegia* except in the feature of the fruiting bracts and opposite leaves.

Hutchinson (1926, 1959, 1969) was a firm believer in the concept that certain families of flowering plants were fundamentally herbaceous or woody. Polygonaceae, in his view, was basically a herbaceous group in which the woody, or shrubby, condition was a secondary state. There is something to say about this point, although it may seem contrary to the usual dicta (Bessey 1915). The largest forms of *Eriogonum*, for example,

are highly derived forms from low, sub-shrubby or shrubby groups. *Eriogonum austrinum* (S. Stokes) Reveal is an annual species that will form perennial individuals, and this is a condition that will be seen in other species as well. The reason to bring this controversial subject up is *Harfordia*, the perennial, versus *Pterostegia*, the annual. It is possible that *Harfordia* represents the residue of an ancient series of events in a perennial line of evolution from which, at some time in the past, the ancestral fore-runners of *Pterostegia* evolved. This is the reasonable approach. Another which cannot be totally ignored is that *Harfordia* is a secondarily evolved perennial which developed from an annual group in order to survive in the extreme stress of long-term drought associated with the environment of central Baja California. *Pterostegia* is basically a mesic species, and I do not propose to imply that *Harfordia* evolved from *Pterostegia*, but anatomical and cytological studies may be helpful in unraveling this question.

#### SUMMARY

The subfamily Eriogonoideae is divided into two tribes, Eriogoneae and Pterostegeae, which are somewhat atypical members of the Polygonaceae. The subfamily is restricted to the more xeric areas of central North America and western South America. The basic extant expression in the subfamily is *Eriogonum*, whose ancestral roots can probably be traced to the tropical or subtropical members of the family. *Chorizanthe* was a major side-shoot from *Eriogonum*, and from these two fundamental genera have evolved a series of small, usually closely related genera. *Eriogonum* and the perennial forms of *Chorizanthe* probably developed in the pygmy woodlands of the Madre-Tertiary geoflora, with the related genera evolving mainly in the more xeric, hot deserts at elevations lower than those in which *Eriogonum* is typically found.

The largest and most diverse genus is *Eriogonum*, both in terms of numbers of



species and in expressions. *Chorizanthe* is the next largest, but the degree of morphological divergency in this genus is not as great as in *Eriogonum*. As for the remaining, smaller genera, each attempts to fill an available morphological gap or ecological niche, and for the most part, each is successful.

Much work remains to be done on the subfamily. The South American species of *Chorizanthe* must be studied in the field. The nature of the relationship between the South American perennials and the North American annuals of this genus must be determined, and then, if the two should prove distinct, we must decide by what name the annuals should be called. Field studies are now critically needed so that anatomical and cytological material can be gathered, and perhaps greenhouse investigations made. A series of monographic studies are now in progress, mainly on the genus *Eriogonum* and its immediate relatives. In time, these studies must be expanded beyond the alpha taxonomic level where they are now. This will be a continuing challenge to anyone wishing to travel, study, and investigate one of the world's most unique groups of flowering plants.

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league, Dr. C. Rose Broome, of the University of Maryland, for sharing with me her ideas and thoughts on the complex problems of evolution and speciation as they might apply to Eriogonoideae.

#### NOTE ADDED IN PROOF

Since this manuscript was completed in June 1976, the revision on *Oxytheca* has been completed [ERTTER, B. J. 1977. A revision of the genus *Oxytheca* (Polygonaceae). Unpublished Master's Thesis, University of Maryland Library, College Park] and a number of minor changes must be appended. Ertter found that *Oxytheca* consists of seven (not nine) species, with the "South American form" being merely a subspecies of *O. dendroidea*, and the "new species" from the San Bernardino Mountains of California a variant of *O. parishii*. Ertter concurs that *O. dendroidea* and *O. watsonii* are related to *Eriogonum spergulinum*, and she has shown conclusively that *O. perfoliata* is clearly related to *O. dendroidea*. In fact, *O. watsonii*, a rare species of west-central Nevada, is intermediate between *O. dendroidea* and *O. perfoliata* in many respects according to Ertter.

Ertter also concurs that *Oxytheca parishii* is most closely related to *Eriogonum apiculatum* and *E. parishii*, but in doing so called attention to an error in my own work on *Eriogonum* (Reveal 1969a). In my revision of *Eriogonum* I placed *E. spergulinum* and *E. apiculatum* in widely separated sections of the subgenus *Ganysma*. Ertter has shown that these two species complexes are much more closely related than I had thought. In the present paper I raised the question that if *O. dendroidea* and its allies arose from the *E. spergulinum* complex (in one part of *Ganysma*), and *O. parishii* arose from *E. apiculatum* (in another part of *Ganysma*), then perhaps the genus *Acanthoscyphus* should be recognized. Such a situation now is unnecessary.

The relationship between *Oxytheca parishii* and the remaining members of the



genus in southern California (*O. caryophylloides*, *O. trilobata*, and *O. emarginata*) is still tenuous. Ertter has shown, however, that *O. parishii* is more similar to the *O. dendroidea* complex than it is to the *O. caryophylloides*. She has proposed to place *O. dendroidea*, *O. watsonii*, and *O. perfoliata* in their own typical section, with *O. parishii* in a monotypic section. As for the other three species, these are going into a third section, a taxon somewhat removed from the other sections.

I still believe that the southern California elements evolved as a group in the mountainous regions of southern California during the Pleistocene, but I now feel that this development came not from isolated elements with *Eriogonum* but from a broadly connected group of annual species all belonging to this one genus which were undergoing collectively rapid evolution (see Raven and Axelrod discussed below).

As for the troublesome *Centrostegia insignis*, recent conversations with Goodman confirm the supposition that this species is seriously out of place in *Chorizanthe* (Goodman 1934), *Oxytheca* (Ertter 1977, cited above), and even *Centrostegia* (Goodman, pers. comm.) and that it most likely will have to be placed in its own monotypic genus. This question is now being explored.

Nowicke's pollen work discussed above has now been published [NOWICKE, J. W., AND J. J. SKVARLA. 1977. Pollen morphology and the relationship of the Plumbaginaceae, Polygonaceae, and Primulaceae to the order Centrospermae. *Smithsonian Contr. Bot.* 37: 1-64.].

Lastly, my manuscript has been used by Drs. Peter H. Raven and Daniel I. Axelrod in a book entitled *Origin and Relationships of the California Flora* published by the University of California Press. Based upon my review of their manuscript (which should be published at approximately the same time as this volume), their work will nicely complement the present volume.

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