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SYSTEMATICS AND RELATIONSHIPS OF *FALLUGIA* (ROSOIDEAE—ROSACEAE)

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ABSTRACT

The paper presents a systematic monograph of *Fallugia* (Rosoideae, Rosaceae) consisting of one variable species, *Fallugia paradoxa*. Morphological, cytological and molecular data clearly support its relationship with *Geum s.l.* rather than *Purshia-Cowania*, with which it is often allied. The species was named twice independently in 1825 from the specimens and drawings, respectively, assembled by Sessé and Mociño for their proposed *Flora Mexicana*. The paper discusses the nomenclatural history, morphological variation, and the polygamo-dioecious mode of reproduction of the species. No infraspecific taxa are recognized.

Key words: Apache plume, *Fallugia*, Rosaceae, Rosoideae, systematics.

INTRODUCTION

Fallugia paradoxa (D. Don) Endl., the Apache plume, is a common shrub in deserts of the southwestern United States and northern Mexico. The species has long been considered related to *Cowania stansburiana* Torr., the cliffrose now placed in *Purshia* as *Purshia stansburiana* (Torr.) Henrickson (Henrickson 1986). In most phylogenetic treatments dealing with the relationship of rosaceous genera (e.g., Bentham and Hooker 1862; Focke 1894; Rydberg 1913; Schulz-Menz 1964) *Fallugia* is placed with *Cowania* near or between *Dryas* and *Geum* (sensu lato) within the tribe Dryoideae of the subfamily Rosoideae. Likewise, in most southwestern floras using a phylogenetic arrangement of genera, *Fallugia* lies between *Cowania* and *Geum* (Abrams 1944; Kearney and Peebles 1951; Munz 1959). However, recently published cytological data (McArthur et al. 1983) and molecular data (Morgan et al. 1994) give strong evidence for *Fallugia* being closely related to *Geum*, but not *Cowania* and *Cercocarpus*.

While cytological and molecular data have provided strong evidence of the relationship of *Fallugia*, it will be shown that the same conclusion can be obtained from even a cursory examination of morphological and anatomical characteristics.

MATERIALS AND METHODS

This study is based primarily on empirical evidence derived from herbarium and field observations of *Fallugia*, *Purshia* (*Cowania*), *Geum*, and from the literature. Material of *Fallugia* was borrowed from or observed at ARIZ, ASU, A-GH, CSLA, JEPS, MO, NY, RSA-POM, TEX-LL, UC, UNM, and US and observed in the field in eastern California, Arizona, central New Mexico, and throughout the Chihuahuan Desert, particularly in central Coahuila. SEM was done with a Jeol JSM T200 Scanning Electron Microscope at CSLA from dried materials.

RESULTS

Comparative Structure of Fallugia, Purshia *(*Cowania*) and* Geum

Fallugia is often sympatric with *Purshia stansburiana*, and the two share the following characteristics. Both are shrubs in the southwestern deserts, with fibrous bark that separates into many thin, cinnamon-brown layers. Both have a basic vestiture of unicellular hairs along with pinnately divided leaves that are green above, and strongly vestitured beneath with revolute margins that converge towards thickened central veins. In both taxa, the leaves are crowded on long and short shoots, and as in many Rosaceae, the blades abscise above the persistent conjoined leaf bases and stipules. Both produce large flowers. The hypanthia bear 5 large, imbricate sepals, 5 orbicular petals, many stamens with yellow, longiscidal anthers borne on slender filaments, and multiple ovaries with terminal, non-articulating styles that form accrescent, plumose awns on the mature 1-seeded achenes. The seeds have basal radicles and no endosperm. In both, the fruits are wind dispersed.

Fallugia (Fig. 1–19), however, has a large number of distinctive traits. In sandy arroyos, *Fallugia* produces rhizomes and tends to form colonies (Fig. 4, 5). Vegetative portions have a distinctive orange-rust-colored lepidote understory vestiture (Fig. 24) and seedling leaves have scattered uniseriate, multicellular, stipitate glands (Fig. 26; Kyle et al. 1986). Its mature leaves are eglandular, thin and pinnatifid, or sometimes

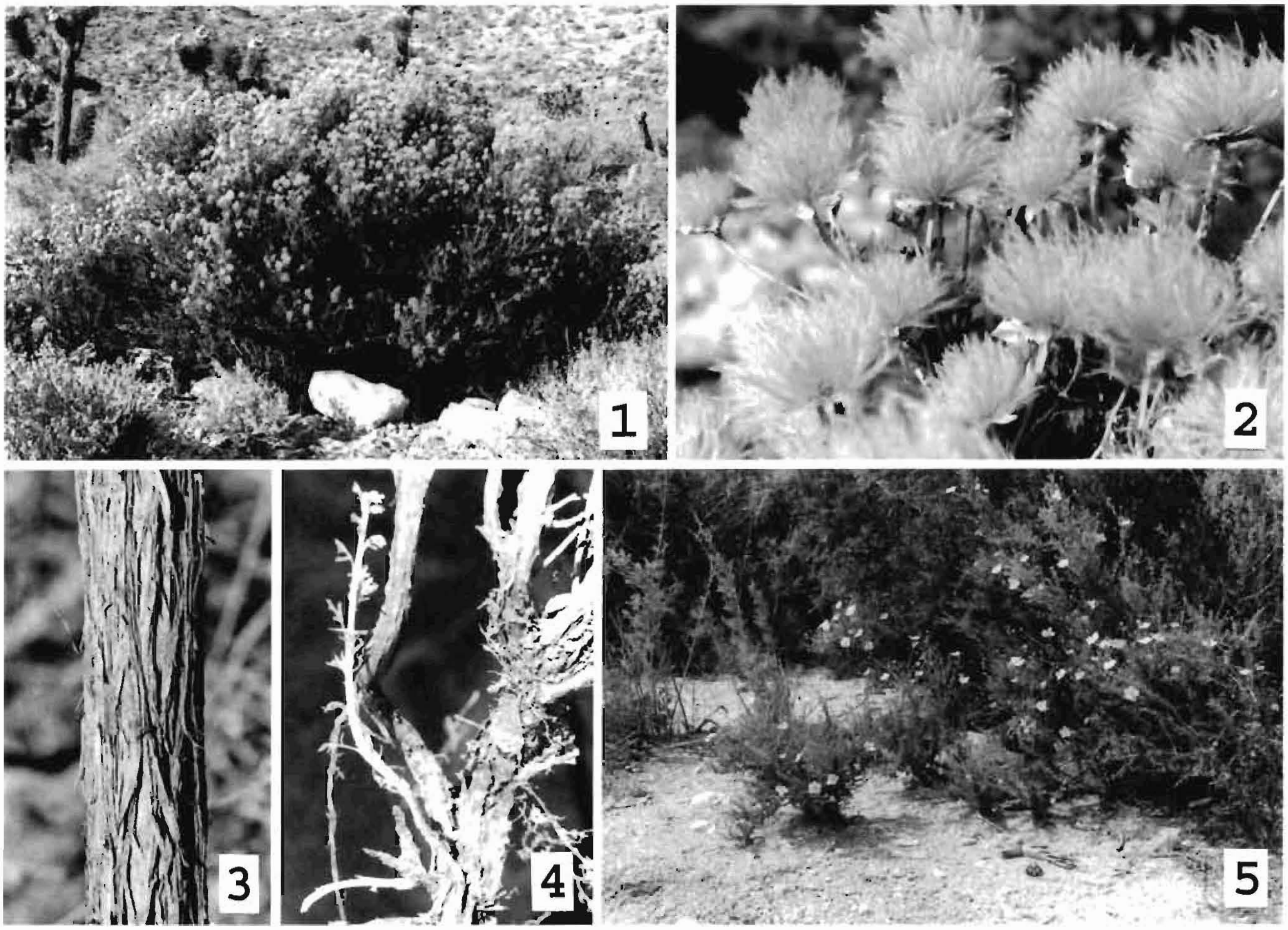

Fig. 1–5. *Fallugia paradoxa* growth habit.—1. Pistillate fruiting plant ca. 1.2 m tall from E San Bernardino Co., California (Clark Mountains).—2. Close-up of fruiting pistillate flowers showing distinctive "Apache" plumes.—3. Young stem ca. 1.2 cm in diameter showing fibrous bark.—4. Underground stems showing development of lateral sucker shoot.—5. Flowering plant showing isolated separate plants that have developed from sucker shoots of parent plant. Magnifications indicated in text.

bipinnatifid (Fig. 27, 28). The flowers are produced at the tips of elongated stems, either solitary or in irregular corymbs (Fig. 6, 17). The rim of the hemispherical hypanthium has conspicuous leaf-like bracts that alternate with the sepals to form an epicalyx (Fig. 29, 30). The hypanthia are densely hirsute within. The sepals have one or more linear, leaf-like terminal or subterminal appendages (Fig. 29, 30). The petals are white; the ovaries number 50–120, borne in a spiral pattern on a raised conical receptacle each on a distinct, hirsute stalk, and each ovary has 2 superposed amphitropous basal ovules, one borne above the other (Fig. 15). The fruit walls are 2-veined, with thin lateral walls, and the stigmatic surface extends about 0.2–0.3 mm down the style (Fig. 16). Furthermore, *Fallugia* is polygamo-dioecious, with some plants producing pistillate flowers (with reduced, sterile stamens; Fig. 32, 34) and other plants have larger staminate flowers with fertile stamens with larger anthers on longer filaments (Fig. 31, 33), and pistils that do not develop, except that in some plants the terminal flowers of a stem may be perfect and produce fruit.

In contrast, *Purshia* (*Cowania*) has been shown to have a deep root system, grows in rocky habitats, and is not rhizomatous (Henrickson in prep.). It has multiseriate stipitate glands on stems and hypanthia and sessile glands imbedded in the leaf surfaces. The flowers are borne on the lateral short-shoots all along the upper stems. The rim of the obconic hypanthia lacks an epicalyx; the petals are cream-yellow in color, the ovaries are far fewer (4–10) and whorled at the base of the hypanthium, and the stigmatic surfaces extend 2–3 mm down one side of the styles. The ovules are solitary, but, as in *Fallugia*, amphitropous with a basal micropyle. The mature fruit walls are thick and strongly 10–12-veined and all flowers are perfect and complete. Furthermore, species of *Purshia* (*Cowania*), like *Cercocarpus*, form a symbiotic relationship with the Actinomycete *Frankia*, which results in nodulation and nitrogen fixation in the host roots (Nelson 1983, see Schwintzer and Tjepkema 1990). Such nodulation and association has not been reported in *Fallugia*.

Many of the shared characters appear associated with adaptation to desert habitats, i.e., the woody growth habit, the dissected leaves with revolute margins, the long- and short-shoot development. Probably the most conspicuous difference lies in the epicalyx of leaf-like bracts alternating with the sepals on the rim of the hypanthium in *Fallugia* (Fig. 29, 30). This feature occurs elsewhere in the subfamily Rosoideae, in tribe Potentilleae (i.e., *Potentilla, Fragaria, Ivesia, Horkelia, Sibbaldia,* etc.), but in that tribe, the styles are lateral on the ovary and are deciduous at maturity. An epicalyx also occurs in largely herbaceous *Geum* and allies (*Geum, Waldsteinia, Colura* etc.), in which the styles are, as in *Fallugia,* terminal (not lateral) (Fig. 16).

Geum s.l. is highly diverse, consisting of up to 12 subgenera (Gajewski 1957, 1959); several of these are treated as separate genera by Rydberg 1913, Yuzepchuk 1941, and others. Some of these subgroups have plumose styles as in *Fallugia* and are wind dispersed (i.e., in subgenera, sections or genera *Sieversia, Neosieversia, Oreogeum,* and *Erythrocoma*) and others (subgenus or section *Geum*) the style is articulated with the terminal portion deciduous and the tip of the basal portion hooked (for animal dispersal). In *Waldsteinia* and *Colura,* in contrast, the styles are deciduous at the base and the achenes are papillate-hirtellous. Gajewski (1957, 1959) considers their fruits to be ant dispersed. Those taxa with long plumose styles also have short stigmatic areas as in *Fallugia.* Basic observations show that *Fallugia* and *Geum s.l.* have identical fruit-wall structure with thick dorsal and ventral traces with thin, inconspicuously vascularized lateral walls, whereas *Purshia* (including *Cowania*) and *Cercocarpus* have thicker fruit walls with many (10–12) thickened veins. However, *Fallugia* has two ovules, while all the *Geum s.l.* observed had but one ovule as does *Cowania* and its cohorts.

Fallugia with its epicalyx of bracts on the hypanthial rim, 2-veined achenes, small stigmatic surfaces, and high number of spirally arranged ovules on an expanded cylindrical, hirsute receptacle, shares many more characteristics with the largely herbaceous-suffruticose *Geum s.l.* than with *Purshia* (*Cowania*) and cohorts. Also, many of the *Geum* group have creeping rootstocks and become colonial (Yuzepchuk 1941) as does *Fallugia.* Gajewski (1959) considered that the most primitive members of the *Geum* group had long plumose styles adapted to wind dispersal and that these plants migrated southward from high latitudes into the high mountains of Europe and North America. He considers that it is perhaps from this stock that *Fallugia* arose and adapted to the arid habitats of western North America, perhaps entering what is often called the Madro-Tertiary Geoflora (Axelrod 1958). Nevertheless, a number of characteristics appear to be confined to *Fallugia*: the distinctive orange-rust lepidote-stellate vestiture, two ovules per ovary, and its polygamo-dioecious mode of reproduction.

Studies of Rosaceae pollen also favor relationships of *Fallugia* with *Geum* and *Waldsteinia.* Hebda and Chinnappa (1994) note that there is distinct sculpturing variation in the Rosoideae and that the above noted three genera (along with *Coluria* and *Orthurus*—segregates of *Geum s.l.*) share a distinct striate microperforate sculpturing pattern.

The decision as whether to relate *Fallugia* (n = 14) with *Geum* (x = 7) or *Purshia* (*Cowania*) (n = 9), is strongly influenced by cytological data. *Cowania, Purshia, Cercocarpus* and *Dryas* are all n = 9, as are most Spiraeoideae and their achene-bearing derivatives, e.g., the follicle-bearing *Sorbaria* and *Chamaebatiaria* giving rise to the achene-bearing *Chamaebatia* and *Adenostoma.* In contrast *Geum s.l.* is based on x = 7 with diploids ($2n$ = 14) occurring in *Waldsteinia, Coluria,* and *Sieversia,* tetraploids ($2n$ = 28) in *Novosieversia,* and *Acomastylis,* and hexaploids ($2n$ = 42) in *Erythrocoma,* while *Geum s.s.* and *Acomastylis* have still higher levels of polyploidy ($2n$ = 56, 70, 112). *Fallugia* with $2n$ = 28 would be considered a tetraploid among these x = 7 plants.

Interestingly, hybrids have been reported between *Purshia stansburiana* (n = 9) and *Fallugia* (n = 14) (Blauer et al. 1975). Baker et al. (1984) have shown that one such hybrid was just an aberrant individual of *Purshia* (as *Cowania*) *stansburiana* ($2n$ = 18) with stamens developing into pistils and petals developing into sepal-like structures. In my studies of *Purshia,* I have found other collections of *Purshia* (*Cowania*) *stansburiana* with similar aberrant conditions. No hybridization between *Purshia* (*Cowania*) and *Fallugia* has ever been documented.

Based on the characteristics shared by *Fallugia* and *Geum s.l.,* one might be tempted to place *Fallugia* within *Geum s.l.* However, while molecular data obtained from the chloroplast *rbcL* gene by Morgan et al. (1994) placed *Fallugia* closest to *Waldsteinia* and *Geum s.l.,* both taxa of *Waldsteinia* and *Geum* sampled shared a duplication of 19 base pairs near the 3′ end that distinguished them from *Fallugia.* This implies that *Fallugia* is a sister group to both *Geum* and *Waldsteinia* and was not derived from either (Morgan et al. 1994). Eriksson et al. (1998) found a similar pattern in their ITS sequence data separating *Geum* and *Waldsteinia* from *Fallugia* and indicate that the *Fallugia-Geum-Waldsteinia* clade, with the inclusion of *Rubus,* is the sister group to all the rest of the genera of Rosoideae.

The initial *rbcL* molecular data on the Rosaceae by Morgan et al. (1994) indicate that the traditional Ro-

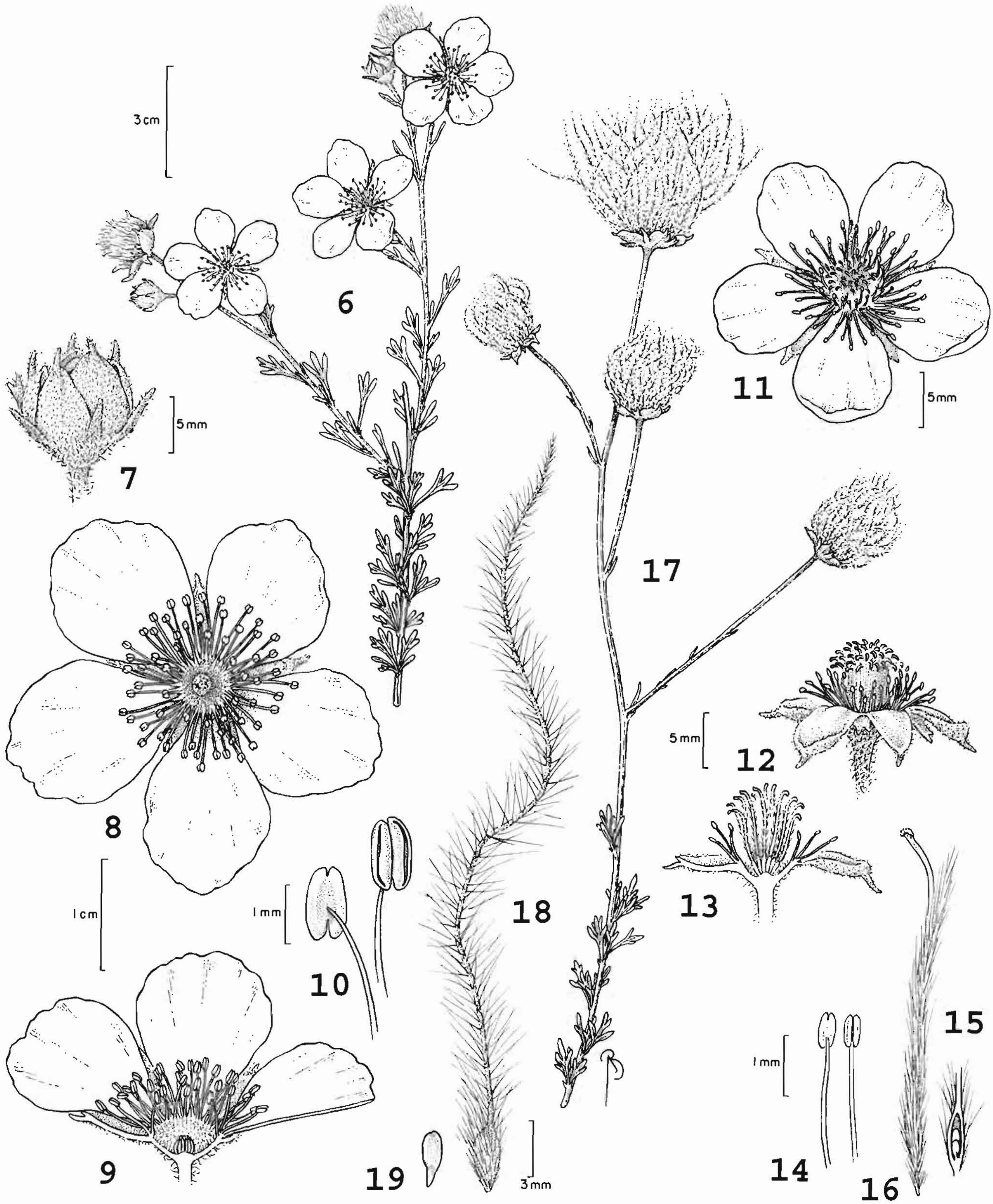

Fig. 6–19. Drawings of *Fallugia paradoxa*.—6. Flowering branch of staminate plant, showing buds, open flowers and development of pistils from terminal flowers (*Harris 31*, ASU).—7. Bud showing apiculate sepals alternating with basal bracts.—8. Staminate flower, face view, showing petals and orientation of stamens.—9. Staminate flower, side view, showing reduced central ovaries, hypanthium and location of stamens.—10. Staminate flower anthers in abaxial and adaxial views.—11. Pistillate flower, oblique view showing sepals, petals, stamens and central larger ovaries, note small anthers.—12. Pistillate flower, post-anthesis, showing sepals-bracts, stamens, and elongating central ovaries.—13. Pistillate flower side view showing sepals, stamens, hypanthium and central ovaries.—14. Pistillate flower anthers in abaxial,

soideae, long recognized on the basis of achene-type fruit and $x = 7$, 8 or 9, is not a monophyletic group. In their phylogenetic analysis, they found that members of three tribes of the traditional Rosoideae, the Kerriae (*Neviusia, Rhodotypos*), Adenostomateae (*Adenostoma*) and part of the traditional Dryadeae (*Cercocarpus, Purshia*), all $n = 9(-8)$, were allied elsewhere in the family, the latter two groups with follicular-fruited groups. Within the Dryadeae, *Cercocarpus, Purshia,* [and *Dryas,* (D. Morgan, pers. comm.)] are allied with the follicle-fruited *Lyonothamnus* ($n = 27$), while *Fallugia, Waldsteinia* and *Geum* ($n = 7$) were retained as a sister group to the remainder of the Rosoideae along with the $x = 7(-8)$ *Alchemilla, Potentilla, Fragaria, Rosa, Agrimonia, Rubus,* and *Filipendula.*

Morgan et al. (1994) also note that their rearrangement is supported by the distribution of various chemicals (sorbitol, cyanogenic glycosides, ellagic acid, flavones) as well as the distribution of rusts and nitrogen-fixing root nodules. Clearly achene-type fruits have been derived independently from follicles more than once.

Of interest, D. Don (1825) originally described our taxon as a *Sieversia,* with which it agrees in almost all characteristics except that *Fallugia* is a larger shrub with imbricate (not valvate) sepals, paired ovules, and pinnately divided (not truly pinnate) leaves.

Taxonomic History

The species we now know as *Fallugia paradoxa,* was named as new to science twice in 1825. It was initially published by David Don, who was the librarian-curator of the Lambert Herbarium in England from 1820 to 1836. Lambert had acquired sets of the Sessé and Mociño Mexican collections through Pavón beginning in 1817 and it was from these collections that D. Don observed and published *Sieversia paradoxa* D. Don. in 1825 (Miller 1970). In the same year, Seringe (1825) also published the taxon within *Geum* in his Rosaceae treatment for the senior de Candolle's *Prodromus.* His description was based on Sessé and Mociño drawings of their Mexican collections and the name attributed to de Candolle.

The story of the Sessé and Mociño expeditions, their collections and drawings of the collections has been detailed in a series of publications by McVaugh (1977, 1980, 1982, 1987, 1990, 1998, 2000) and a recent CD-Rom containing images of original illustrations. Sessé and Mociño, together or separately, collected throughout central, southern and western Mexico, coastal Alta California, southern Alaska, with additional expeditions into Central America and the West Indies, from 1787 to 1803. Their goal was the preparation and publication of a great *Flora Mexicana.* To provide illustrations to the same, a series of about 1800 paintings were prepared by artists who accompanied the expeditions. Sessé and Mociño returned to Spain in 1803, and for various political reasons the flora was never published. The specimens arrived in Spain in 1804 and duplicates were later distributed by Pavón. Sessé died in 1808, and during the French occupation of Spain, Mociño was exiled in 1812; he took about 1300 of the illustrations to A. P. de Candolle in Montpellier, France. When conditions improved in Spain, Mociño requested the return of the illustrations from de Candolle, who at this time was in Geneva, and de Candolle employed more than 100 artists in 1817 to make copies of about 1000 of the illustrations in a period of ten days. Not all drawings were copied; some of Mociño's illustrations were duplicates and these were given to de Candolle, while others were considered, by de Candolle, too common to copy. Mociño returned to Spain with the original illustrations, eventually became ill and died in 1820. The original illustrations fell into unknown private hands and were not seen again by botanists until 1979—they now reside at Hunt Center for Botanical Documentation (McVaugh 1982) where they form the "Torner Collection." According to McVaugh (1980, p. 102) about 279 names were published in de Candolle's *Systema* and the *Prodromus* from these copies of the original illustrations, including a *Geum* that is referable to *Fallugia* (Seringe 1825). Sessé and Mociño's floras, *Flora Mexicana* (Sessé and Mociño 1894) and *Plantae Novae Hispaniae* (Sessé and Mociño 1887 to 1891) were eventually published in Mexico in installments from 1887–1897 in the journal *La Naturaleza,* but by that time most of the species had been described and published elsewhere; their floras included a few species of *Geum,* but none relate to what is now known as *Fallugia.* The Lambert herbarium, from which D. Don described his *Sieversia paradoxa,* was sold in auction in 1842 after Lambert's death (Miller 1970). The type specimen now resides in the British Museum.

David Don's *Sieversia paradoxa* was published 11 May 1825 (Raphael 1970; Gage and Stearn 1988). Seringe's treatment of Rosaceae was published in the

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adaxial view.—15. Post-anthesis ovary with 2 basally attached ovaries.—16. Immature sericeous-styled ovary showing the short terminal stigma.—17. Fruiting branch showing fruits with distinctive stylar plumes (*Keil et al. 10050,* ASU).—18. Mature basal achene with long plumose awn (*Henrickson 22208,* CSLA).—19. Embryo from an achene. Fig. 7–9 and 11–16 are from liquid-preserved collections from the New York Mountains, San Bernardino Co., California (*Henrickson 22208,* TEX). Magnifications as indicated.

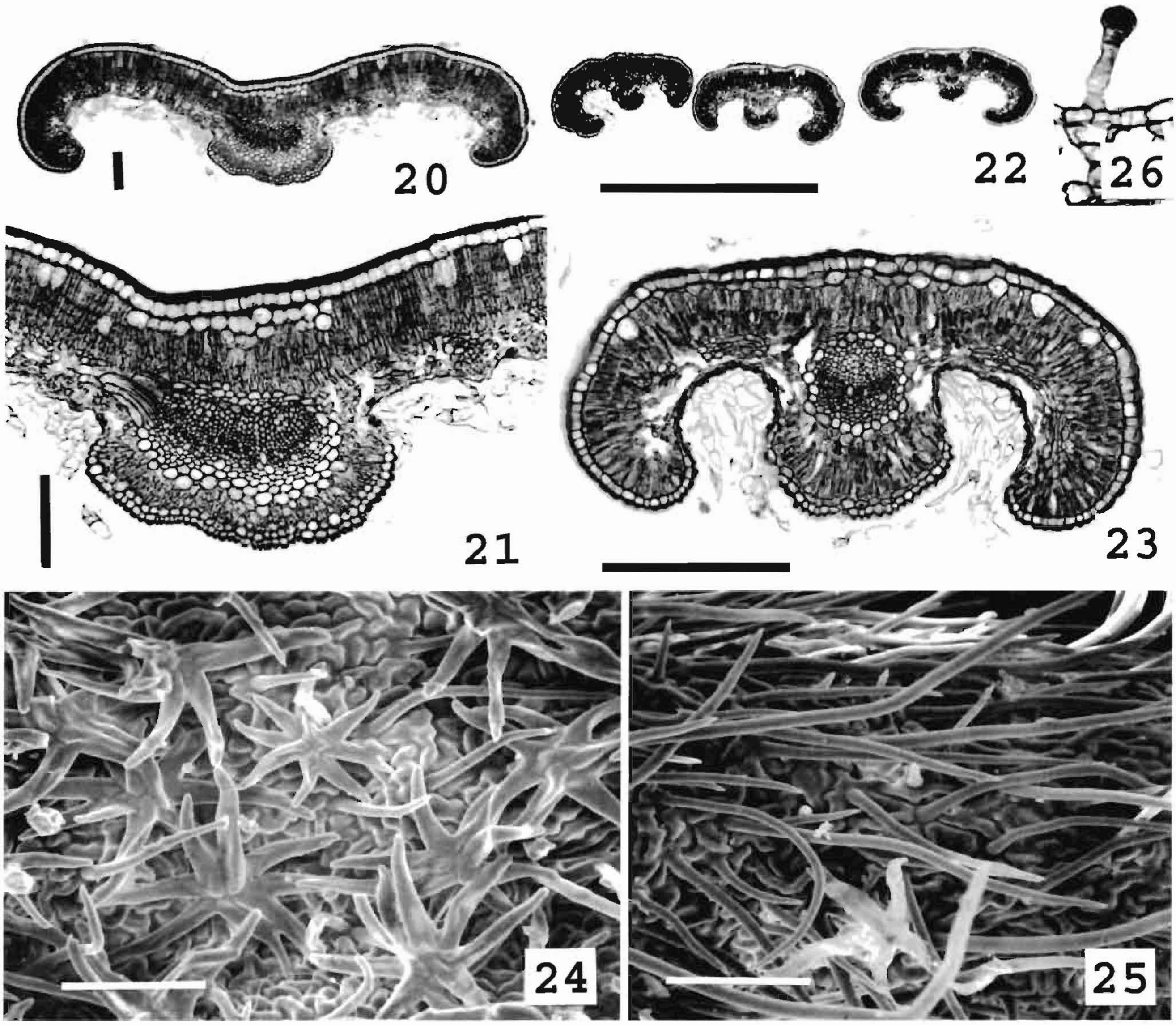

Fig. 20–26. Leaf structure and vestiture of *Fallugia paradoxa*.—20–24. Cross sections of leaves.—20. Section through base of leaf before midvein separates (section is 1.38 mm wide).—21. Expansion of midvein portion of leaf shown in Fig. 20. Note: thick cuticle, multiple epidermis, uneven lower cuticle, evidence of vascular cambium in midvein (both from *Mortenson s.n.*).—22. Section of three terminal lobes of leaf showing revolute margins (from *Coleman 124* CSLA).—23. Section of terminal leaf lobe, 1.56 mm wide, showing deposition of palisade and spongy mesophyll, vascular bundle etc. (from *Mortenson 1503*, RSA).—24–25. SEM of leaf vestiture.—24. Vestiture of lower leaf surface showing characteristic stellate trichomes mixed with simple hairs (from *Forbes* 1239, ASU).—25. Vestiture of upper leaf surface showing mostly simple hairs (From *Heward s.n.*, ASU).—26. Seedlings have uniseriate, gland-tipped hairs, this hair, from *Mortenson 1503*, is 77 μm in total length. Bars in Fig. 20–21 = 0.1 mm, in Fig. 22 = 1 mm, in Fig. 23 = 0.5 mm, in Fig. 24–25 = 100 μm.

Prodromus in mid-November of the same year (Stafleu and Cowan 1976), and the treatment included, as *Geum*? *cercocarpoïdes*, a new species based on Sessé and Mociño illustrations. The taxon was attributed to de Candolle ("*DC adnot. in icon. fl. mex.*"). It is however, not known if the description of the species came from de Candolle's study of Monciño's original illustration or from de Candolle's or Seringe's study of the copy of the original illustration. Both the copy and the original illustration have *Geum*? *pediculatum*, a *nom. nud.* enscribed on the plates. Seringe came to work for de Candolle in 1820, after the original plates were returned to Mociño in 1817, and thus did not see the original plate (McVaugh pers. comm.). I am here presuming that the name *Geum*? *cercocarpoïdes* was provided by de Candolle as indicated by Seringe. McVaugh (pers. comm.) notes that de Candolle often changed the name from that originally written on the specimens. McVaugh (pers. comm.) further notes that de Candolle's original notes are often preserved with

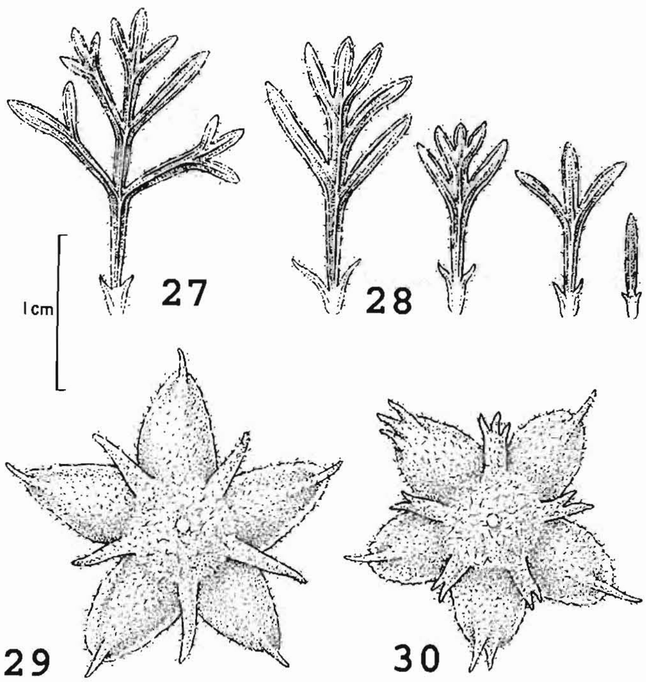

Fig. 27–30. Variation in leaves, sepals and epicalyces of *Fallugia paradoxa*.—27–28. Variation in leaf structure.—27. Bipinnately divided leaf (*Brown 408*, ASU).—28. Variation in leaves on one plant showing range from pinnately divided to unlobed (*Henrickson 10327*, TEX).—29–30. Variation in calyces and epicalyx bracts.—29. Calyx with a subterminal apiculation and simple bracts (*Trusel and Baker 4372*, ASU).—30. Calyx with 1–3-toothed sepals, and 2–3-lobed bracts (*Henrickson 22208*, TEX). Magnifications as indicated.

the copied plate at Geneva and that de Candolle was very involved with the ultimate manuscript generated for the *Prodromus*. The copies of the original illustrations, that would have been available to Seringe, are still at Geneva (McVaugh 1980, p. 106) and some, including that of *Geum*? *cercocarpoïdes*, were published with Sessé and Mociño's Flora Mexicana (1894). Some 50 years later the younger Alphonse de Candolle (1874) published ten sets of tracings of the copies of 279 taxa that were described as new taxa in the de Candolle's *Prodromus* or *Systema* as *Calques des Dessins* [tracings of the copies]. Tracing No. 297 is of *Geum*? *cercocarpoïdes*, which I have seen on microfiche.

Few specimens from the northern deserts regions are included in the Sessé and Mociño collections, as their expeditions did not extend into the area (McVaugh 1977). As location data did not accompany the collections or illustrations, the source of the two type specimens has not been determined, although one can presume they came from what was then Mexico as the species occurs only in what was then Mexico. McVaugh (1977, p. 181) notes that a one Ignacio León wrote Sessé several letters in 1792–93 from Valle de Santa Rosa or Praedio de Santa Rosa, now known as Múzquiz, Coahuila, where *Fallugia* is frequent. McVaugh notes that León also sent seeds and specimens of plants from that region to Sessé; *Fallugia* may have been among them. *Fallugia* also grows north of the city of Durango, Mexico, where Mociño met with Sessé after separate trips south from Alamos, Sonora, in late 1791 (McVaugh 1977, p. 133). Or a *Fallugia* specimen may have come from cultivated material grown in Mexico City or Puebla (McVaugh pers. comm.), so the type locality can not be established with certainty.

The two new names for the taxon had been described within *Sieversia* (now often merged with *Geum*) and *Geum*. In 1840, Endlicher elevated the taxon to the genus *Fallugia*, citing D. Don's *Sieversia paradoxa* and description. He, however, failed to make the species combination, which was done by Torrey in Emory's Notes of a Military Reconnaissance (1848).

SYSTEMATIC TREATMENT

FALLUGIA Endl. Gen. pl. 1246. (No. 6385). 1840.
With one species.

FALLUGIA PARADOXA (D. Don) Endl. ex Torr. in Emory Not. milit. reconn. 139, t. 2, 1848. *Sieversia paradoxa* D. Don. *Trans. Linn. Soc., London* 14(3): 576, t. 22, fig. 7–10, (31 May) 1825. *Geum paradoxum* (D. Don) Steud. Nomencl. bot. ed. 2. 1: 682. 1840. TYPE: MEXICO: *sin loc.* Sessé & Mociño in herb. Lambert. Holotype BM (xerograph seen—TEX!). The Sessé and Mociño specimen at BM compares well with the illustration accompanying D. Don's original description.

Geum plumosum Sessé & Moc. ex D. Don. *Trans. Linn. Soc. London* 14: 576, 1825, *nom. nud.* The name was apparently attached to the Sessé & Mociño collections. McVaugh (pers. comm.) notes that the name was attached to the specimen remaining at MA. The name was cited by D. Don.

Geum cercocarpoïdes DC. in Seringe in DC. Prod. 2: 554. (mid Nov.) 1825. TYPE: Mexico, *sin loc.* Sessé et Mociño *s.n.* (lectotype: designated by McVaugh (2000): the original Torner illustration at Hunt Center for Botanical Documentation (no. 0538), at Pittsburgh, Pennsylvania; image on CD-Rom). As noted in the text, Seringe attributed the name to de Candolle, who had seen both the original Torner illustration and the copy of the illustration (at G), McVaugh (2000) presumes that the protologue was also provided by de Candolle for de Candolle often provided protologues for his new species. As de Candolle had seen both illustrations, McVaugh designated the Torner illustration as lectotype.

Fallugia mexicana Walp. *Repert. Bot. Syst.* 2: 46. 1843. *pro syn.* Apparently a substitute name for the epithet *paradoxa*.

Fallugia paradoxa var. *acuminata* Wooton. *Bull. Torrey Bot. Club.* 25: 306. 1898; *F. acuminata* (Wooton). Cockerell. *Proc. Acad. Nat. Sci. Philadelphia* 1903. p. 590. 1903. *Fallugia acuminata* (Wooton) Rydb. *Bull. Torrey Bot. Club.* 33: 143, 1906. TYPE: U.S.A., New Mexico: Doña Ana Co., Mesa near Las Cruces, 4100 ft, 1 Jul 1897, *E. O. Wooton 65* (Lectotype: here designated NMC!, Isolectotypes: GH!, MO!, NY!, POM!, UC!, US!). The lectotype at NMC and isolectotypes at GH and NY have both male-sterile (pistillate) stems and male fertile stems; all other isolectotypes observed consist of male-sterile (i.e., pistillate) specimens, indicating that they came from different plants, but were part of the original gathering.

Fallugia micrantha Cockerell. *Entom. News* 12: 41, 1901. *F. acuminata* var. *micrantha* (Ckrl.) Cockerell. *Proc. Acad. Nat. Sci. Philadelphia* 1904. p. 109. 1904. TYPE: U.S.A. New Mexico,

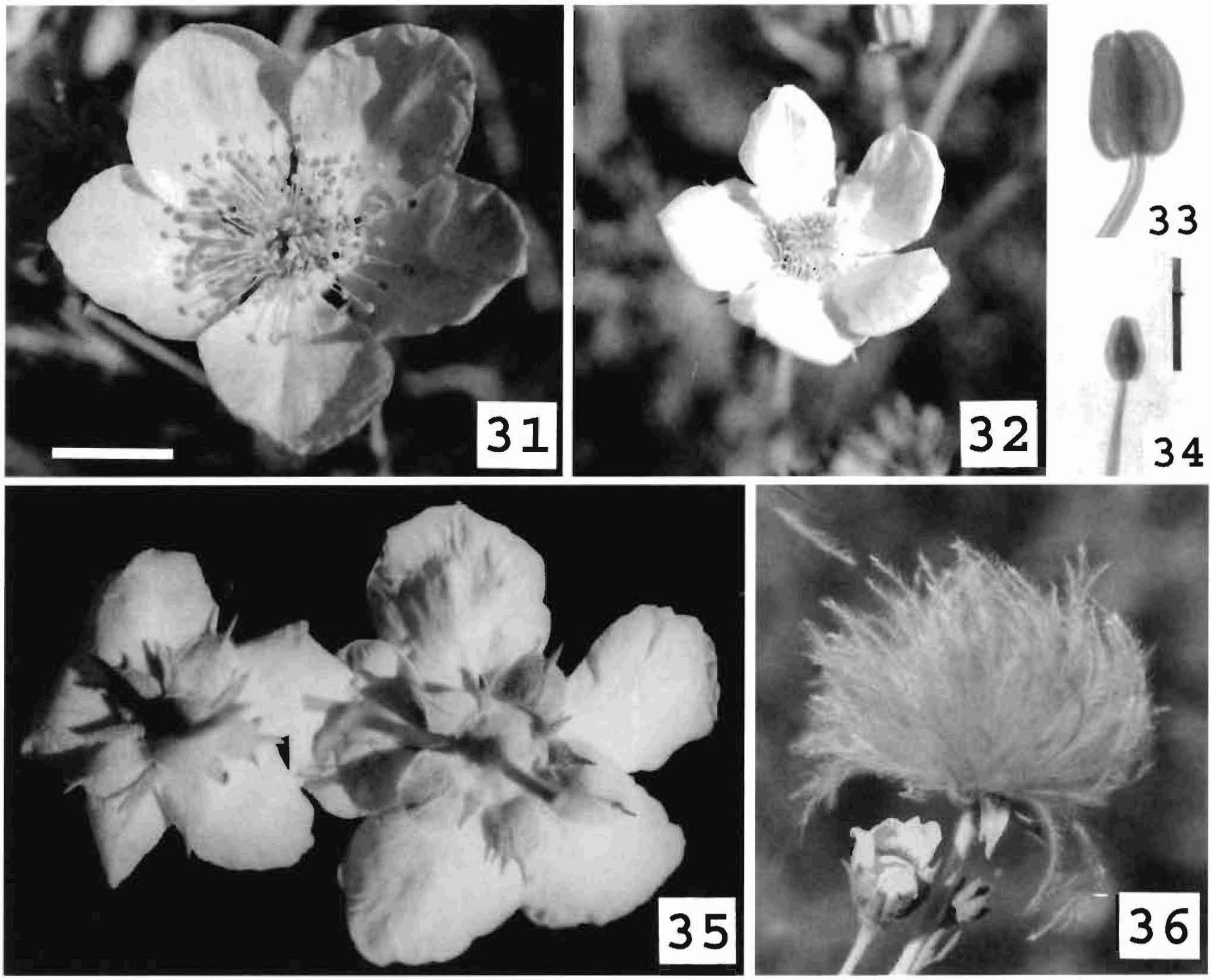

Fig. 31–36. Flowers and fruits of *Fallugia paradoxa*.—31. Staminate flower, showing large stamens.—32. Pistillate flower to same scale is smaller, and has shorter stamens (Fig. 31–32. from Clark Mts., California, *Henrickson s.n.*).—33. Anther of staminate flower.—34. Anther of pistillate flower.—35. Undersurface of pistillate (left) and staminate (right) flowers showing comparable flower size and calyx-bract structures.—36. Mature fruit from a single flower (Fig. 33–36 are from E of Ocampo, Coahuila, *Henrickson 22207*, TEX). Magnifications bar in Fig. 31 = 10 mm and holds for Fig. 31–32, 35–36; bar in Fig. 34 = 1 mm, holds for Fig. 33–34.

Doña Ana Co. Mesa west of the Organ Mountains, 4000 ft. May 1981, *E. O. Wooton s.n.* (Lectotype, here designated, NMC!—the two short stems with sterile anthers on the left side of the specimen). In recognizing *Fallugia micrantha*, Cockerell defined *Fallugia paradoxa* var. *acuminata* (Wooton) Cockerell as consisting of plants with large corollas (petals), with large stamens, large (fertile) anthers, small carpels, and bracts and sepals divided—basically having male-fertile (staminate) flowers. In contrast, Cockerell circumscribed his *F. micrantha* as having smaller flowers, small stamens, small (sterile) anthers, the carpels protruding above the anthers, bracts not divided or toothed and the outer sepals with 1(–2) appendages—basically as having male sterile (*i.e.*, pistillate) flowers. No Cockerell specimens were observed in any herbarium that could serve as a type of this taxon. Cockerell did note that he observed specimens in Wooton's herbarium and it is from these collections that the lectotype is here designated. Cockerell's characterization of *F. p.* var. *acuminata* as male fertile (staminate) is not in agreement with all syntypes as only the lectotype at NMC and isolectotypes at GH and NY actually have staminate-flowered stems present [in each case mixed with male-sterile (pistillate) stems]—therefore Cockerell's characterization of Wooton's var. *acuminata* as male-fertile is not accepted.

Evergreen, much-branched, bushy, sometimes rhizomatous and then colonial, polygamo-dioecious shrubs 1–2(–3.5) m tall; young stems erect-ascending, foliaceous below, elongating and terminating in 1-few flowers above; the young-stem surface whitish-cream in color, lightly to strongly sericeous-villous to pilose, hirtellous or pubescent with slender, straight to curved hairs 0.1–0.8(–1.5) mm long, sometimes also lepidote with scattered, orange-rust-colored, sessile stellate hairs; the initial phellogen forming in the basal cortex and the thickish, whitish cortex-epidermis vertically splitting in slightly older stems exposing the subtending maroonish periderm; older stems with a grayish, thin-layered, vertically anastomosing periderm; nodes alternate, in 2/5 phyllotaxy; cauline internodes 2.5–10(–15) mm long, heteroblastic, developing crowded fascicles of leaves on short axillary spurs 1–3.5(–7) mm long, the upper internodes subtending the flowers longer, (0.8–)1.5–3(–5) cm long. Leaves simple, obovate, oblanceolate to linear in outline, (4–)7–18(–30) mm long, (0.8–)3–12(–23) mm wide, mostly pinnately 3–7 divided in the distal half or third into linear, linear-oblanceolate, strongly revolute, spreading to ascending, opposite to subopposite divisions 1–7(–13) mm long, 0.5–1.4(–2.2) mm wide, when larger these sometimes further divided and the blades then bipinnatifid, when smaller with 3 terminal lobes or the blades simple and linear to linear-oblanceolate; the blade-divisions rounded to acute at the tips, the midveins impressed above, prominently raised, 1.2–2 mm wide beneath, the upper surface, revolute margins and sometimes the midrib of the lower surface sparsely hirtellous-pubescent with hairs 0.05–0.2 mm long or moderately to strongly sericeous-villous to pilose with spreading, straight to curved hairs 0.1–0.8 mm long, sometimes also lepidote with scattered orange-rust-colored, sessile, stellate hairs, glabrate with age, the lower surface between the midvein and margins (and sometimes also the midvein) densely lepidote with low, sessile, orange-rust-colored, stellate hairs; the blades tapered at the base, dehiscent above broad, clasping, persistent, 1–2(–2.5) mm long leaf bases, the stipules adnate to the leaf-base margins, the free stipule tips whitish, subulate 0.2–0.8 mm long or, in the primary leaves, green, long-tapering and outwardly curved, prominently veined, and 1–4.5 mm long. Flowers perigynous, solitary or more commonly 2–5 in irregular racemes or corymbose racemes terminating the long-shoot stems of the season, the upper internodes usually elongated, the nodal leaves often reduced, pinnatifid or simple, long and with well developed stipules or the leaves small and bract-like; plants diclinous with some plants producing only pistillate flowers with small sterile anthers 0.3–0.4 mm long, and other plants producing only staminate flowers with anthers 0.7–1.2 mm long and the pistils not developing, except occasionally in the terminal flower of a branch. Hypanthia ± funnelform, (4–)5–6(–7) mm in diameter, [extending (2–)3–4 mm above the pedicel] bearing 5 separate, ascending sepals alternating with 5 or more, ascending bracts on its rim that form an epicalyx; sepals imbricate, (3.2–)4–8(–10.5) mm long, 2.2–5(–6.5) mm wide, the outermost sepals broadly ovate to narrowly deltate and acuminate, hairy throughout outside, the inner ones more broadly oblong-ovate, hairy medially, with thin white, nearly glabrous margins, each with 1 (sometimes 3 in the outermost) linear, terminal, slender, leafy appendages 1–2.5(–3.5) mm long, produced either at the distal margin or abaxially and somewhat (0.1–1.2 mm) below the distal sepal margin; bracts linear, linear-lanceolate, leaflike, (1–)2–5(–8) mm long, 0.5–1.5 mm wide, simple, entire-revolute margined, rounded to acute at the tip, or variously lobed or divided at the tip, sometimes divided more deeply or to the base into 2 separate leafy, equal or unequal bracts, the bracts, hypanthia, and outer sepals externally densely lepidote with sessile, rust-colored, stellate hairs and variously pubescent to villous-pilose, the inner sepal surfaces mostly glabrous or sparsely and inconspicuously villous-sericeous; the hypanthium with a distinct thickened nectary within, this densely setaceous-villous with appressed-ascending hairs to 1 mm long; petals 5, broadly oblong-obovate, creamy-white to white, sometimes pinkish in populations in central New Mexico, (6–)10–18(–21) mm long, (6–)7–14 (–17) mm wide, the petals usually larger in male flowers; [the mature flowers 21–35(–42) mm in diameter] entire or nearly so, rounded to broadly obtuse distally, ± rounded above a short, broad claw at the base, glabrous; stamens ± (50–)100–125(–145), borne at the inner rim of the hypanthium in 2–4 irregular series; filaments slender, abruptly expanded and sometimes joined at the very base, 2.2–4.3 mm long in fertile stamens, 1.5–2.5(–4.5) mm long in sterile stamens of pistillate flowers, glabrous; fertile anthers 4 loculed, introrse, dehiscing between the anther sacs, light yellow, glabrous, 0.7–1.2 mm long; the sterile anthers 0.3–0.4 mm long and without pollen; ovaries and fruit (24–)50–95(–120), free, borne on a ovoid-cylindrical receptacle that expands to 1.6–2.5 mm long in fruit, each fruit abscising above a short, hirsute stipe 0.5–0.7 mm long that persists on the receptacle; ovules 2 per ovary, superposed, one borne above the other, amphitropous, only one maturing, the pistils initially densely crowded, erect, strongly hairy, the styles terminal, continuous, plumose, the distal styles glabrous for 0.7–1.1 mm, with a truncated conduplicate stigmatic collar ± 0.1 mm wide extending down the style for 0.2–0.3 mm. Mature fruit of fusiform, somewhat compressed, rather thin-walled, 2-veined, sericeous, whitish-tan achenes 3–4 mm long terminated by the greatly elongated, cream-white to purplish, gradually curved, plumose awns 2.5–5 cm long, with lateral hairs spreading-ascending, straight, slender, 1–2.5 mm long; embryo 1 per fruit, narrowly oblanceoloid, 2.2–3 mm long, with a thin, attached, reddish brown testa; the hypocotyl basal; endosperm absent; n = 14 (McArthur et al. 1983; Baker et al. 1984; Schaack 1987) (Fig. 1–36).

The species is widely distributed from the Eastern Mojave Desert in California to southern Nevada, southern Utah, southern Colorado, through central and eastern Arizona, through most of New Mexico, southern Oklahoma, Trans-Pecos and central Texas and south in Mexico to central Coahuila, northern Durango, Zacatecas, Chihuahua and northern Baja California

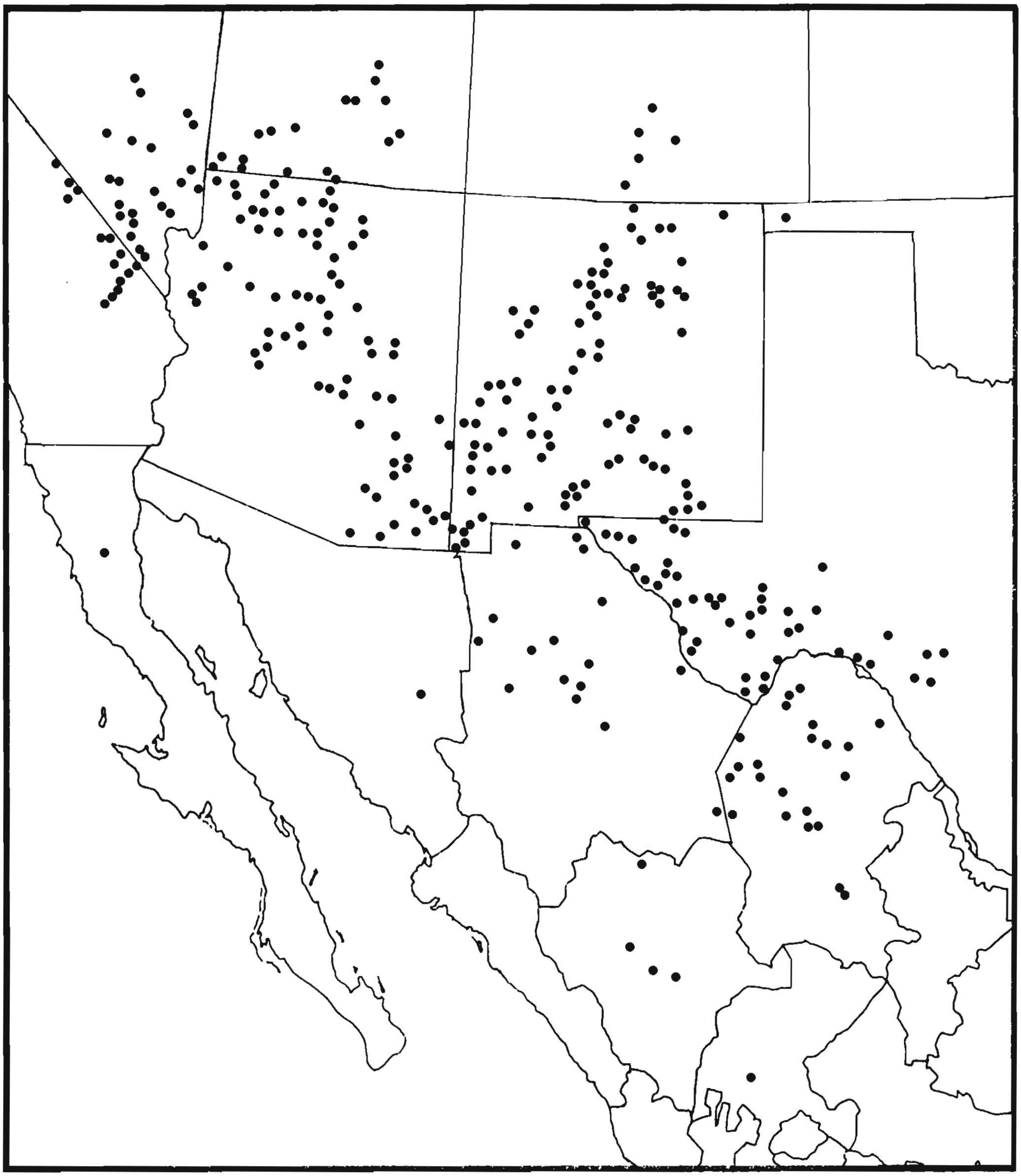

Fig. 37. Distribution of *Fallugia paradoxa* in southwestern U.S.A. and Mexico.

del Norte at (1500–)2500 to 7000(–9500) ft elevation (Fig. 37). The species extends from the Mojave Desert region with its winter rains, through the uplands of Arizona and New Mexico with its winter and summer rains and into the Chihuahuan Desert region with summer rains.

Throughout much of its range the species typically occurs in sandy to rocky drainages, but in highlands of Arizona, New Mexico and Texas it also occurs on higher rocky areas often in juniper, oak, pinyon or pine grasslands. Common associates in the Mojave Desert, where it occurs from 4000–6500 ft elevation, include:

Prunus fasciculata (Torr.) A.Gray, *Chrysothamnus paniculata* (A.Gray) H.M.Hall, *C. nauseosus* (Pallas) Britt., *Ambrosia eriocentra* (A.Gray) Payne, *Eriogonum fasciculatum* Benth., *Acacia greggii* A.Gray, and *Rhus trilobata* Torr. & A.Gray. In central Arizona and New Mexico it is often associated with chaparral (Axelrod 1958), pinyon, oak, juniper or Ponderosa pine woodlands, or Mesquite or Great Basin sage grasslands in both uplands and arroyos from 2500–7000 ft elevation. In the Chihuahuan Desert it occurs mostly in uplands and in drainages associated with *Acacia neovernicosa* Isley, *A. berlandieri* Benth., *A. greggii* A.Gray, *Chilopsis linearis* (Cav.) Sweet, *Prosopis glandulosa* Torr., *Juglans microcarpa* Berland., *Celtis pallida* Torr., *Baccharis salicifolia* (Ruiz & Pav.) Pers., and *Anisacanthus linearis* (Hagen) Henrickson & Lott from (1800–)2800–4500(–7050) ft elevation. The highest elevation recorded for the species is in northern Baja California del Norte at 9500 ft (3095 m): a collection by the indefatigable Reid Moran (25598—ARIZ). Flowering occurs from May through August in California, and May through October in the Chihuahuan Desert. The common name in English is Apache plume; in Mexico "Yerba del Pasmo" (*Stewart 626,* LL) and "Barba de Chivo" (*Stewart 1834,* LL).

DISCUSSION

Fallugia paradoxa exhibits considerable variation, much of it attributable to water resources. Well watered plants typically produce well developed, slender, long-shoot stems 30–50 cm long with well spaced nodes and long lateral branches, each terminating in one or more flowers. In contrast, plants growing in drier conditions are more strongly branched with much shorter long-shoot stems, shorter internodes, a tighter branching pattern and a gnarled appearance. Overall there is considerable variation in the thickness of young stems, and the amount of lateral branching in both stems and inflorescences.

The plants vary in their ability to form sucker shoots that results in the formation of distinct colonial clusters of plants. In California, most plants form distinct colonies when growing in sandy arroyos, with new plants clearly forming from woody rhizomes (Fig. 4–5). In the Chihuahuan Desert, *Fallugia* often occurs on upland sites where it is not colonial, as well as sandy drainages where it may or may not be colonial. In Arizona and New Mexico, I found there to be considerable variation in the development of offshoots from a plant, but colonial plants were more common in sandy drainages. Due to the variation in this feature, it can not be recognized taxonomically.

Leaf size and lobing also are highly variable and again appear to reflect moisture available to the plant. In most specimens long-shoot leaves are larger than short-shoot leaves. The long-shoot leaves typically are 10–25 mm long, divided into 5–7, slender to broad, sometimes secondarily lobed divisions (Fig. 27). These leaves appear to be produced during periods of strong terminal growth when adequate water is available and associated hormone production is high. Leaves of the short-shoot spurs, in contrast, are often smaller, 5–8 mm long, mostly divided into 3, sometimes 5 divisions, with some leaves being undivided (Fig. 28). Long-shoot leaves were also observed to be 3-lobed or undivided in some specimens. As conditions dry, the larger long-shoot leaves often abscise as do the older short-shoot leaves allowing the plant to be in balance with its water resources. This pattern is found throughout the range of the species, showing no geographical consistency.

Plants also vary considerably in their total vestiture. In some plants leaves are sparsely hirtellous with only short erect hairs or with a few scattered longer appressed hairs; other plants are more villous-sericeous with a moderate to dense covering of both short and long, straight and curved slender hairs (Fig. 25). This longer vestiture is usually also present on stems and flowers. The vestiture is variably glabrescent and falls from overwintering leaves. Vestiture is variable throughout the range of the species and exhibits no geographical patterns.

Variation also occurs in the bracts and sepals that border the hypanthium both as to size of the structures, the density of their vestiture, and the amount of lobing in the bracts and sepals (Fig. 29–30). The bracts, that alternate with the sepals on the margin of the hypanthium, are leaf-like in structure. They may be short or long, unlobed or variously lobed in the distal half or even sometimes divided to the base so that two individual bracts appear to occur between adjacent sepals. The sepals are imbricate, strongly vestitured on the exposed outer surface, with the innermost sepals having broad, thin lateral unvestitured margins. The sepals typically are broadly ovate in shape and are rounded below a slender terminal or usually subterminal green, leafy tip. When subterminal, the tips may be separated to 1.1 mm from the actual margins of the innermost sepals. The outermost sepals sometimes have three, separate, slender tips (Fig. 30). On occasional plants the outermost, or all sepals, are not distinctly rounded below the tip, rather the sepals are distinctly acuminate with convex margins below the acuminate tips. This was one of the characteristics used by Wooton (1898) to distinguish his variety *acuminata.* Therefore, analysis was undertaken to determine if there were any sepal or bract characteristics that could be used to distinguished geographical subunits within the species. Wooton (1898), in describing his var. *acuminata,* noted that plants from southern New Mexico tended to have

Table 1. Representation of the three flower types in different populations of *Fallugia paradoxa*.

	Pistillate plants	True staminate plants	Staminate-hermaphroditic plants	Total plants
San Bernardino Co., California Clark Mts.; June 1985	76 (53.3%)	41 (28.9%)	25 (17.6%)	142
Doña Ana Co., New Mexico* Organ Mts., July 1996	58 (43.6%)	20 (15.0%)	55 (41.3%)	133
E of Tesuque, New Mexico arroyo; July 1998	59 (47.2%)	29 (23.2%)	37 (29.6%)	125
SW of Las Vegas, New Mexico roadside; July 1998	45 (41.3%)	15 (13.8%)	49 (44.9%)	109
Buenavista, Coahuila, Mexico roadside; Aug 1998	8 (42.5%)	0 (0.0%)	14 (63.6%)	22
E of Ocampo, Coahuila, Mexico arroyo; Sep 1998	16 (43.4%)	6 (16.2%)	15 (40.5%)	37

* Data collected by Bob Denham and Norene Fobes.

acuminate outer sepals that contrasted with the three-toothed sepals from Texas and Mexico. While specimens from Texas and adjacent Mexico do tend to have three teeth on the outer sepals, the characteristic is not consistent on all flowers of a particular plant and similar three-toothed sepals are found in plants throughout the range of the species. A brief analysis of the frequency of multi-toothed sepals using available dried herbarium specimens for each state revealed the following percentages of specimens with at least some 3-toothed sepals (n = number of collections diagnosed): Mexico: (Chihuahua and Coahuila) 91.7% (n = 26); Texas: 95.1% (n = 62); New Mexico 23.6% (n = 72); Arizona 42.3% (n = 52); and California 40.6% (n = 32). Likewise there was no consistency in the epicalyx bract lobing, with both simple and terminal lobed and often completely divided bracts occurring on the same plant and often even on the same calyx of a flower. A separate analysis of the frequency of specimens with lobed versus unlobed or divided bracts was also conducted from available dried herbarium specimens. The percentages of specimens (n) that showed at least some lobed or divided bracts were: Mexico (Chihuahua and Coahuila) 86.4% (n = 22); Texas 51.8% (n = 56); New Mexico 35.9% (n = 64); Arizona 50% (n = 56); and California 38.7% (n = 31). While these data show a west-east trend, it was considered that the sepal and bract characteristics cannot be used to recognize geographical subunits within the species.

The plants also show considerable variation in flower size throughout the season and male flowers typically have larger petals than pistillate flowers (Fig. 31, 32, 35). Flowers produced during the active growing season are often large, with petals 10–21 mm long and 8–17 mm wide. Nevertheless, the same plants may continue to produce occasional flowers during the dry season that have smaller petals only 6–9 mm long and 6–8 mm wide. In any population petals of male-fertile flowers typically are larger than those of pistillate plants. In one brief study in the Clark Mountains in California petals on male-fertile plants averaged 16.2 × 12.4 mm in size, whereas those of the pistillate flowers were 10.8 × 8.4 mm in size. Similar differences were noted throughout the range of the species.

Throughout its range the species is polygamo-dioecious with some plants bearing male-sterile, pistillate flowers that bear abundant fruit and have sterile anthers 0.3–0.4 mm long on reduced filaments. Other plants in the same populations are male fertile or staminate, producing anthers 0.7–1.2 mm long on longer filaments. Some of these plants produce no fruit and can be considered true staminate plants, while other pollen-producing plants have scattered fruit-producing flowers, with some plants producing few such flowers and others many fruit-producing flowers. Usually these hermaphroditic flowers are terminal on a stem and inflorescence. In all pollen-producing flowers, anthers mature well before the pistils and the pistils develop in a broad central column within the flower. Richards (1986, 1997) considers this as a type of dicliny, specifically polygamo-dioecious dicliny, where there are potentially five types of plants: plants with only pistillate flowers; plants with staminate flowers; plants with all hermaphroditic flowers; plants with both hermaphroditic and staminate flowers; and plants with both hermaphroditic and pistillate flowers. Not all of these five types of flowers will occur in a species. *Fallugia* has plants with three of these flower types: pistillate, staminate and both staminate and hermaphroditic.

A series of field tallies of pistillate plants versus strictly staminate plants (i.e., with no fruit developing) versus staminate-hermaphroditic plants (staminate, but some flowers developing fruit) was conducted throughout the range of the species (Table 1).

As can be seen from the data, the relative frequencies of staminate plants and staminate-hermaphroditic plants is not consistent across the range of the species. Plants sampled in California have many more true staminate plants than the other populations sampled and those from Mexico showed the fewest true staminate plants.

In pistillate plants, all ovaries mature and develop their plume-like elongate styles. The styles apparently will elongate with or without pollination. At Rancho Santa Ana Botanic Garden in Claremont, California, the display gardens have only pistillate plants; the staminate plants have been removed as they do not show characteristic "Apache plumes." In these isolated pistillate plants that presumably are not pollinated, all ovaries still form elongated plumose styles. However, the plumose awns do not greatly elongate and the fruit are empty—they lack mature seeds. Miller and Venable (2000) discuss the origin of dioecy associated with polyploidy, which may pertain to this genus.

Representative Specimens.—UNITED STATES.—CALIFORNIA. San Bernardino Co., Granite Mts, below Dripping Spring Pond, 4100 ft, 5 Jun 1978, *Stein 113* (RSA); Providence Mountains, 1580 m, 6 May 1939, *Templeton 4584* (ARIZ, GH, LL, MO, NY, POM, TEX, UC, US); New York Mountains, near mouth of Keystone Canyon, 5450 ft, 29 Oct 1976, *Thorne et al. 47943* (ASU, RSA); Clark Mt Range, Big Pachalka Canyon, 5 mi NW of Mountain Pass, 5600 ft, 9 Jun 1974, *Prigge 1529* (RSA); Kingston Range, 2.2 mi NE of Silver Rule Mine, 4000 ft, 9 Jun 1980, *Castagnoli et al. 242* (RSA); Inyo Co., Funeral Mts, Echo Canyon, 4800 ft, 1 Jun 1938, *Gilman 2995* (JEPS, POM, UC).—NEVADA. Clark Co., Mouth of Deadman's Canyon, Hidden Forest, Sheep Mts, 5600 ft, 30 May 1940, *Alexander & Kellogg 1605* (GH, UC); Charleston Mts, Kyle Canyon, Juniper belt, 1670 m, 21 Jun 1938, *Clokey 7975* (A-2, ARIZ-2, GH-2, MO-2, NY-3, RSA-2, TEX-2, UC, US); McCullough Mts, below Pine Spring, T25S, R61E, S½, SW¼, Sec 23, 5000 ft, 18 May 1969, *Bostick 4440* (UNLV); Nye Co., Grant Range, 1 mi above Troy Mine, 22 Jun 1941, *McVaugh 6096* (UC); Lincoln Co., Below SE Sheep Range, 4900 ft, 2 Jun 1973, *Ackermann 7747* (UNLV).—ARIZONA. Mohave Co., Beaver Dam Mts, 18 May 1938, *Nelson & Nelson s.n.* (GH, UC); Grand Canyon rim at Tuweep, 4000 ft, 12 Jun 1941, *Cottam 8609* (RSA); Coconino Co., 10 km W Jacob Lake, 1050 m, 4 Jun 1982, *Trushel & Baker 4372* (ASU); Grand Canyon, Bright Angel, 20 Jun 1916, *Eastwood 5895* (A); 17 mi NE Tuba City along road to Kayenta, 6 Jun 1951, *Mason & Phillips 1910* (ARIZ); Vicinity of Flagstaff, 7000 ft, 4 Jul 1898, *MacDougal 222*, (ARIZ, GH, NY, UC, US); Navajo Co., 9 mi E Heber, rte 277, 4 Jul 1965, *Pinkava 2272* (ASU); Yavapai Co., 10 mi E Jerome Jct. 2 May 1908, *Tidestrom 927* (US); 14 mi S Prescott, 4000 ft, 3 Oct 1931, *Gillespe 8515* (GH-2); Maricopa Co., off Beeline hwy on Sunflower turnoff, 6 May 1967, *Keil 1693* (ASU); Gila Co., Mesa near Rock and Rye Creeks, 990–1050 m, *Collom 79* (ARIZ, GH, MO, NY); Graham Co., Pinaleno Mts, 10 mi E Bonita-Stockton Pass, 28 May 1977, *Minckley et al. s.n.* (ASU); Pima Co., Catalina Mts, Bear Canyon below Horse Cabin, 17 May 1914, *Shreve s.n.* (ARIZ); Greenlee Co., 20 mi E. Clifton, 19 May 1935, *Wiegand & Wiegand 953* (GH); Santa Cruz Co., E base of Santa Rita Mts, 25 Jun 1882, *Pringle 1882* (A-2, MO, US); Cochise Co., Pine Canyon, Chiricahua Mts, 6500 ft, 4 Oct 1906, *Blumer 1296* (ARIZ, GH, MO, NY-2, US); Mouth of Cave Creek Canyon, Chiricahua Mts, 4500 ft, 17 Apr 1940, *Benson 10303* (ARIZ).—UTAH: Emery Co.; San Rafael Swell, Little Wildhorse Canyon, T25S, R10E, Sec 34, 5000 ft, 28 May 1978, *Harris 31* (ASU); Wayne Co., Near Capitol Reef Natl. Mon., 3 mi W Fruita, 1500–1650 m, 4 Jul 1953, *McVaugh 14433* (NY, TEX); Garfield Co., Near Hite, near Colorado River, 3500 ft, 9 Jun 1958, *Flowers & Lindsay 2343* (UC); Iron Co., Cedar Creek, 5 mi E Cedar City, 11 Sep 1963, *Welsh & Christensen 2626* (NY); Washington Co., Mesa E of Hurricane, 3750 ft, 3 May 1932, *Maquire & Blood 1409* (POM); Beaverdam Mts, Castle Cliffs, 15 May 1966, *Higgins 594* (NY); Kane Co., 0.3 mi N Utah-Ariz. state line along W side of Cockscome, S of hwy 89, 12 Apr 1972, *Atwood 3627* (US); San Juan Co., Lake Powell, up Ticaboo Canyon, T35½S, R13E, Sec 6, 3750 ft, *Welsh et al. 22038* (NY).—OKLAHOMA. Cimarron Co., Along hwy 64, W of Boise City, 10 Jun 1948, *Rogers 5931* (US).—TEXAS. El Paso Co., N end Franklin Mts, 30 Oct 1962, *Correll 26561* (GH); Hueco Mts, near hwy. 62, 16 Aug 1942, *Waterfall 3920* (ARIZ, GH); Hudspeth Co., Eagle Mts, head of canyon above fluorite mine, 6000 ft, 8 Jul 1945, *McVaugh 7342* (RSA, TEX); Culberson Co., Guadalupe Mts, E of Guadalupe Peak, 1600 m, 14 Jul 1945, *McVaugh 7390* (GH, RSA, TEX); Jeff Davis Co., Davis Mts near McDonald Observatory, 19 May 1973, *Higgins 6831* (NY); Presidio Co., 17 mi N Shafter, 1 Jun 1938, *Cutler 1937* (ARIZ, GH, MO); Brewster Co., Glass Mts, Old Blue Canyon, 18 Jun 1941, *Innes & Moon 1225* (GH, TEX); Chisos Mts, lower end Juniper Canyon, 3800 ft, 15–18 Jul 1921, *Ferris & Duncan 2988* (NY); Pecos Co., NE side of Sierra Madera, about 25 mi S Ft. Stockton, 26 May 1949, *McVaugh 10638* (GH, LL, NY, TEX, US); Terrell Co., 5 mi NW Sanderson, 2 Jul 1945, *McVaugh 7318* (RSA); 18 mi S of Sheffield, 9 Jun 1949, *Webster 179* (TEX); Edwards Co., Cedar Creek near Barksdale, 12 Oct 1916, *Palmer 11008* (MO); ValVerde Co., Comstock, 9 Oct 1917, *Palmer 12956* (A, MO, US, UC-2); Kinney Co., N side of RM 334, 0.1 rd mi E of crossing with W Nueces River, 19 Jul 1991, *Carr 11295* (TEX); Upton Co., 4 mi E of Rankin, 11 Jul 1941, *Tharp s.n.* (TEX); Real Co., Leakey, 9 Jun 1916, *Palmer 10147* (A, MO); Uvalde Co., Llano Cañon, Jun 1885, *Reverchon s.n.* (GH); Zavala Co., Pulliam, 19 Jul 1917, *Palmer 12312* (A, MO, TEX, UC).—COLORADO. Fremont Co., Webster Park (near Canyon City), July 1873, *Brandegee 666* (UC); Alamosa Co., Base of Blanca Peak, 6 mi S of Great Sand Dunes Natl. Mon., 8400 ft, 21 Jul 1966, *Porter & Porter 10235* (GH, TEX, UC); Conejos Co., Punche Arroyo, above confluence with Rio Grande, T32N, R11E, SW¼ Sec 10, 2274 m, 10 Jul 1987, *O'Kane & Anderson 3228* (MO).—NEW MEXICO. Rio Arriba Co., ± 8 mi S. El Rito, 6500 ft, 15 Sep 1935, *Klinger 207* (UNM); Taos Co., 2 mi E Questa, 20 Jul 1938, *Hitchcock et al. 4148* (POM); Colfax Co., near Cimarron, 30 Jun 1929, *Mathias 549* (A, GH, MO, POM); Union Co., 37 mi E of Raton, Colo., 7 mi S of Colo. State Line, 7000 ft, 5 Jul 1952, *Morrow s.n.* (UNM); Sandoval Co., 2 mi W of Placitas, along hwy 44, 6000 ft, 31 Jul 1964, *Tatschl s.n.* (UNM); Los Alamos Co., Mesa N of Frijoles Canyon, Bandelier Natl. Mon., 2 Jun 1941, *Clark 9578* (UNM); Santa Fe Co., Lamy, 8 Oct 1934, *Byrne & Magner 3422* (MO); Mora Co., Basalt Mesa, 8 mi NW of Wagon Mound, on rd to Ocate, 7000 ft, 26 Jul 1924, *Bacigalupi 668* (GH, UC); San Miguel Co., Montezuma, 7000 ft, 26 May 1965, *Broeke RO-8* (UNM-2); Taos Co., Capulin Campground, canyon above Taos, 3 Jul 1957, *Fosberg 38765* (POM); Lava flow, 10 mi E of Grant, hwy 66, 9 Sep 1940, *Heller 15801* (NY, UC); Valencia Co., 4 mi S Belen & 1 mi W of hwy 85, 4800 ft, 20 Sep 1964, *Baca 7* (UNM); Bernalillo Co., Mesa NE of University of New Mexico, Albuquerque, 5000 ft, 11 Jul 1940, *Clausen & Trapido 4620* (GH, NY, UC); Torrance Co., Manzano Mts, Nuevo Canyon, 7800 ft, 23 Jun 1963, *Bedker 1071* (UNM); Guadalupe Co., Sandstone ridge overhanging Pecos River, 4750 ft, 25 Jul 1979, *Tschaikowsky 339* (ARIZ); Catron Co., 14 mi SW Horse Springs, SE edge Plains of San Augustin, 18 Jun 1948, *Smith 13* (ARIZ, A, GH); Socorro Co., 8.5 mi W Socorro, hwy 60, 23 May 1959, *Martin 3098* (UNM); Lincoln Co., Lincoln Natl. Forest, 2 mi N Alto, 29 May 1965, *Crutchfield 50* (LL, NY); Chaves Co., 6.8 km W of intersection of NM rte 24 on US rte 82, 14 Jul 1973, *Boufford 10829* (A); Hidalgo Co., Animas Mts, 7 air mi SE Animas, R19W, T28S, SE¼, Sec 12, 5000 ft, 28 Aug, 1986, *Worthington 14846* (NY); Grant Co., Gila River bottom near Cliff, 4500 ft, 13 May 1903, *Metcalf 62*, (A, ARIZ, GH, MO, NY-2, POM, UC-2); Sierra Co., Road Hot Springs-Hillsboro, 15 Aug 1934, *Goodding s.n.* (ARIZ); Luna Co., E side Florida Mts, 5 May 1985, *Worthington 13098* (NY); Doña Ana Co., Mesa W of Organ Mts, 25 Oct 1904, *Wooton s.n.* (POM, UC); Otero Co., Indian Wells, Sacramento Mts., near Alamogordo, 29 Aug 1952, *Castetter s.n.* (UNM); Eddy Co., Valley of Black River, 22 mi SW Carlsbad, 14 Aug 1942, *Waterfall 3748a* (ARIZ, GH, NY).—MEXICO.—BAJA CALIFORNIA DEL NORTE. Sierra San Pedro Mártir, W slope near Summit of El Picacho del Diablo, 30°59.5′N, 115°22.5′W, 3075 m, 5 May 1978, *Moran 25598* (ARIZ).—SONORA. Rio Yaqui, Jun 1930, *Viereck 420* (US).—CHIHUAHUA. Carretas, border of Chihuahua and Sonora, Mpio. de Janos, 4800 ft, 26–28 Aug 1939, *White 2594* (ARIZ, GH); Colonia Garcia in the Sierra

Madres, 7300 ft, 25 Jul 1899, *Townsend & Barber 161* (GH, MO, NY, POM); Lumholtz Expedition, St. Diego, 18 Apr 1891, *Hartman 616* (GH); Between Babicora & Yepomera, 7600 ft, 4 Aug 1977, *Wieder et al. 43* (NY); 29 mi S of Gallego, 5300 ft, 22 Jun 1937, *Shreve 7936* (ARIZ); 29 mi E Villa Ahumada, 30°45′N, 106°06′W, 4400 ft, 21 Aug 1971, *Henrickson 5864* (TEX); Majalca Canyon, 18–20 1935, *LeSueur 36* (GH-2, MO, TEX, UC); Hwy 45, several miles S of Encinillas village, 10 May 1959, *Correll & Johnston 21752* (ASU, LL, NY); 35 rd. mi NE of Cuchillo Parado, old rd to Ojinaga, 4400 ft, 17 Sep 1971, *Henrickson 6814* (TEX); Cañón del Rayo, N end of Sierra del Diablo, 25–29 Jul 1941, *Stewart 900* (GH, LL).—COAHUILA. Del Carmen Mts, 15 Aug 1936, *Marsh 637* (GH, TEX-2); Vicinity of Aguachile Mt, 29°18′N, 102°20′W, 28 Aug 1966, *Flyr 1137A* (MO); Rancho Carrizalejo, W of Piedras Negras, & 15 km W of Rancho Sierra Hermosa, 1300 m, 23 Jun 1952, *Gould 6452* (UC); Sierra de Santa Rosa, S of Múzquiz, 13 Jul 1938, *Marsh 1343* (GH, TEX); Cañón de Tinaja Blanca, E slope of Sierra de las Cruces, W of Santa Elena Mines, 26 Jun 1941, *Stewart 626* (GH, LL, UC); Sierra Hechiceras, Cañón del Indio Felipe, 27–29 Sep 1940, *Stewart 184* (GH); Sierra del Pino, vicinity of La Noria, 20–26 Aug 1940; *Johnston & Muller 472* (GH, LL); W base of Picacho del Fuste, NE from Tanque Vionetta, 23–25 Aug 1941, *Johnston 8408* (GH); Sierra de la Madera, Cañón del Pajarito, 6 Sep 1939, *Muller 3152* (GH, LL, UC-2); Sierra de la Paila, Oct 1910, *Purpus 4970* (GH, UC, US).—DURANGO. Santiago Papasquiaro & vicinity, Apr–Aug 1896, *Palmer 406* (A, GH, MO, NY, UC, US); S of Torreon de las Cañas, 6000–6500 ft, 22 Oct 1943, *Gentry 6960* (ARIZ, GH, NY); Tejamén, 21–27 Aug 1906, *Palmer 467* (GH, MO, NY, UC).—ZACATECAS. San José de Llanitos, 30 km al NE of Valparaiso, 24 Jun 1957, *Rzedowski 9114* (TEX-2).

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