Rhodora

JOURNAL OF

THE NEW ENGLAND BOTANICAL CLUB

Vol. 56 March, 1954 No. 663

THE GENUS TETRACOCCUS (EUPHORBIACEAE)

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Tetracoccus is a small genus of more or less xerophytic shrubs of the southwestern United States and Mexico, whose species appear to be of considerable phytogeographic and phylogenetic interest. In the present paper an attempt is made to give a complete taxonomic treatment of the genus and to make some tentative geographical correlations.

The plants of *Tetracoccus* are decidedly local and usually discontinuous in distribution, but may, in some cases, be quite abundant over limited areas. They are dioecious plants, apparently insect pollinated, whose flowering is largely governed by rainfall. Separate flushes of flowering in response to periods of rainfall have been noted on several occasions and in different species.

Tetracoccus is allied to *Securinega* and may be distinguished by its carunculate seeds and the central disk without a pistillodium in the staminate flower. *Tetracoccus* is probably, as hypothesized by Croizat (1942), one of the more primitive genera of the *Phyllantheae*, being more primitive in floral structure than *Securinega*. [This does not imply acceptance of other aspects of the phylogeny offered by Croizat]. The same author feels that there are close resemblances between *Tetracoccus* and genera of the African and Australian desert areas; this, as well as its distribution pattern, would seem to point to the group as being relictual. The present distribution of the genus is shown by Fig. 1. The genus as a whole is disjunct and, as noted above, the species are usually discontinuous. The probable phylogeny

of the species and tentative geological correlations are shown in Fig. 2. The relationships between the species and these attempted correlations are further discussed under each species. Though there is no recognized fossil evidence of *Tetracoccus* itself in western North America, our knowledge of the Tertiary floras of the western United States is sufficient to make some correlations. The geological correlations are based on floristic coincidence with floras and vegetations whose history is partially known, Gentry's "postinsular" hypothesis and morphological divergence. It is felt that the *capensis*-like population from which *T. fasciculatus* was derived, became separated from the plants in the Cape region of Baja California when the latter became an island in the early or middle Tertiary (Miocene?). On the basis of morphological divergence it is hypothesized that "pre-*capensis*" had differentiated from "pre-*dioicus*" and that the latter had separated from the population ancestral to *ilicifolius* before the Miocene. The floristic relationships of *T. dioicus* (a chaparral plant) seem to fit this plan. Too little is known of the Death Valley area for better elucidation of the history of *T. ilicifolius*.

While the separation of the two varieties of *T. fasciculatus* is thought to be relatively recent, the differentiation of the *T. fasciculatus* type may date back at least to the mid-Pliocene time of aridity, at which time Axelrod (1948) feels that the local desert floras had their beginning. Gentry (1949, p. 83), on the other hand, feels that areas of local aridity may have existed in western North America since mid-mesozoic. While the California deserts are largely the result of mountain rain shadow, and most certainly as relatively young as believed by Axelrod, it must be remembered that areas of considerable aridity can result from other factors. The present Vizcaino Desert area of Baja California is a good example.

It is possible that *T. capensis* is not a postinsular endemic, but owes its present distribution to yet poorly known Pleistocene events. Only continued paleobotanical and floristic investigation can clarify the probabilities. In any case, the area in question offers great opportunities for the study and correlation of evolution in land form and biota, as has been so ably stressed by Gentry (1949).

The taxonomic history of *Tetracoccus*, though relatively short, is not without its complications, and, for so straightforward a group, it has accumulated more than its share of synonymy. The first species of this group to be described was *T. fasciculatus*,

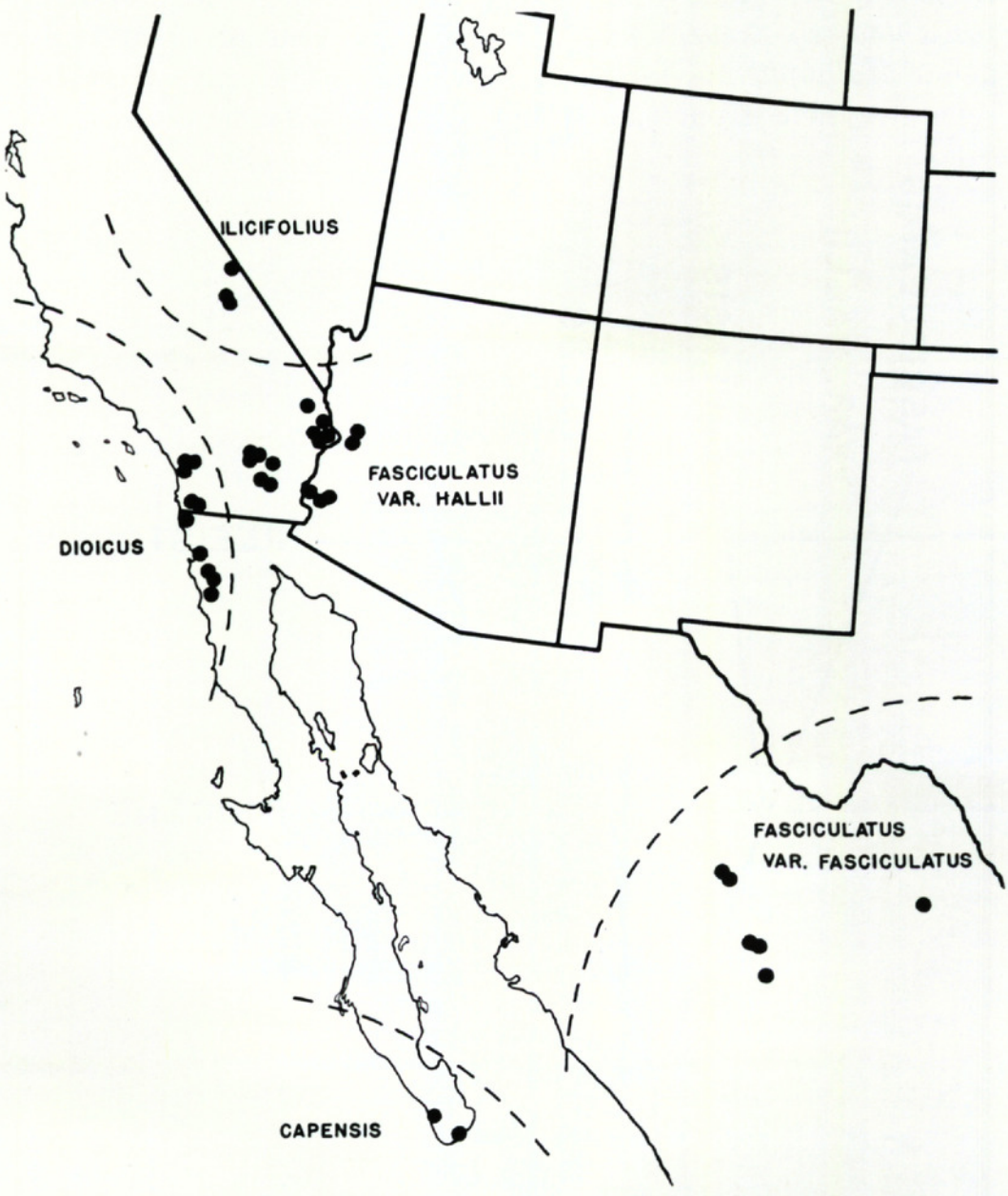

Fig. 1. Present distribution of the genus *Tetracoccus*.

which was provisionally placed in *Bernardia* by Watson (1883). The genus was described by Engelmann for *T. dioicus* and published by Parry (1885) after Dr. Engelmann's death. Brandegee, in 1906, described *T. Hallii* from the Colorado Desert of Cali-

fornia, but overlooked its close similarity to *Bernardia (?) fasciculata*, which he had correctly noted as a member of the *Phyllantheae* (1894). In 1922, Johnston described a collection (Brandegee's) from the Cape region of Baja California as *Securinega capensis* and transferred *T. Hallii* and *Bernardia (?) fasciculata* to *Securinega.* The following year he created the genus *Halliophytum* for the above species and gave a key to separate them from each other and from *Tetracoccus*, which

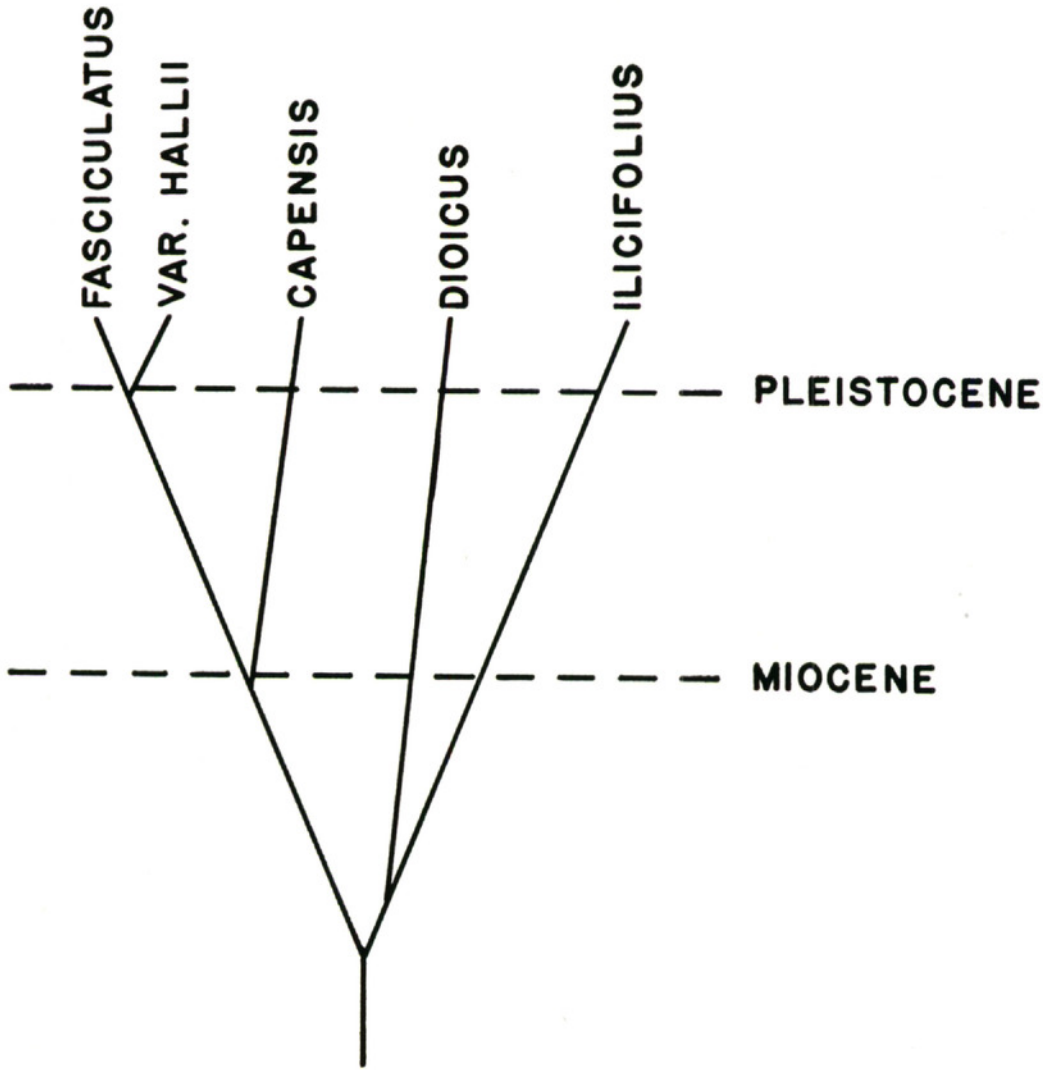

Fig 2. Diagram showing probable relationships between the species and tentative correlations with the geological time scale.

he then considered monotypic. Only in 1936 was *T. ilicifolius* described by Coville and Gilman from Death Valley. This caused Wheeler to review *Tetracoccus* and *Halliophytum* in 1939;

he concluded that they were congeneric and that he was unable to distinguish the three species of "*Halliophytum.*" Croizat then reviewed the problem in 1942, disagreeing with Wheeler as to the validity of the name *Bernardia (?) fasciculata* and publishing new combinations under *Tetracoccus* for *Halliophytum fasciculatum* and *H. capense* without comment as to their distinctness.

The author wishes to thank Dr. Louis C. Wheeler for his guidance in the present study, and the curators of various herbaria for the generous loan of specimens. The herbarium abbreviations recommended by Lanjouw and Stafleu (1952) are used in citation. These are listed here for convenience: University of Arizona, Tucson (ARIZ); Dudley Herbarium, Stanford University (DS); Chicago Natural History Museum (F); Gray Herbarium, Harvard University (GH); Iowa State College (ISC); Missouri Botanical Garden (MO); Pomona College, Claremont, Calif. (POM); University of California, Berkeley (UC); United States National Herbarium, Washington, D. C. (US).

Measurements of flower parts have been made from dried material softened and expanded by boiling, while other measurements were taken from dry herbarium specimens (these measurements were supplemented, in the case of *T. fasciculatus* var. *Hallii*, with measurements of fresh material and material from liquid preservative). The tangential dimension of the seed is that dimension tangential to the cross section of the fruit as the seed is oriented in the capsule. The radial dimension is comparable.

TETRACOCCUS Engelm.

Tetracoccus Engelmann ex Parry, West American Scientist **1:** 13. 1885. TYPE: *T. dioicus* Parry—*Tetracoccus* subgenus *Eutetracoccus* Croizat, Bull. Torr. Bot. Club **69:** 456. 1942.

Halliophytum I. M. Johnston, Contr. Gray Herb. **68:** 88. 1923. TYPE: *Bernardia (?) fasciculata* S. Wats.: the first species listed by Johnston and designated as type by Croizat.—*Tetracoccus* subgenus *Halliophytum* (Johnst.) Croiz., loc. cit.

Tetracoccus subgenus *Tetracoccaster* Croiz., loc. cit. TYPE: *T. ilicifolius* Coville & Gilman.

Shrubs; leaves alternate, opposite or ternate, often fascicled, simple, petiolate; stipules none; flowers dioecious, apetalous; staminate flowers in axillary panicles or racemes, or in fascicles from spur branches, stamens 4–10 arranged about a central, variously lobed, glandular disk; pistillate flowers solitary and axillary or fascicled on spur branches, glandular ring between sepals and ovary with lobes as many as the carpels and

alternating with them, carpels 2–5, usually 3 or 4; styles free, entire; fruit a capsule; seeds 1 or 2 per locule, carunculate, smooth and shining.

I do not use the subgenera created by Croizat (cited in synonymy) as I feel that the relationships between the species are too close to warrant it. In addition, there is little utility in a series of subgenera all of which are so nearly monotypic.

Key to the Species of Tetracoccus

A. Ovary usually 4-loculed; staminate peduncles mostly exceeding 4 mm. in length; filaments villous toward base; seeds always flattened tangentially.
  B. Leaves oblanceolate or oblong-ligulate to nearly linear, entire or remotely and minutely serrulate; staminate flowers in small racemes ..... 1. *T. dioicus.*
  B. Leaves ovate or broadly elliptic to oblong-lanceolate, manifestly serrate-dentate; staminate flowers in congested panicles .... 2. *T. ilicifolius.*
A. Ovary usually 3-loculed; staminate flowers fascicled or peduncles not exceeding 3 mm.; filaments glabrous; seeds usually flattened radially (flattened tangentially only when two develop in the same locule).
  C. Staminate inflorescence racemose, peduncles present though small; pistillate pedicels 5–7 mm. long in fruit ..... 3. *T. capensis.*
  C. Staminate flowers fascicled, inflorescence without peduncle; pistillate pedicels rarely exceeding 2 mm. in length.
    D. Caruncle usually well developed (in mature seeds), seed coat little folded ventrally, little proliferated about caruncle (plants of Mexico) ..... 4. *T. fasciculatus* var. *fasciculatus.*
    D. Caruncle rudimentary, seed coat somewhat proliferated and folded ventrally, especially about caruncle (plants of California and Arizona) ..... 5. *T. fasciculatus* var. *Hallii.*

1. **Tetracoccus dioicus** Parry, West American Scientist **1:** 13. 1885. Type: Santo Tomás Hills, Lower California, Sept. 24, 1884, *C. R. Orcutt 313* (isc 211889!, isotypes gh!, mo!, uc!, us!).—*T. Engelmannii* S. Wats., Proc. Am. Acad. Arts & Sci. **20:** 373. 1885. Type: same collection as above (gh!, isotypes isc!, mo!, uc!, us!).

Shrub 1.5–2 m. tall; young stems slender, reddish, sparsely crisp-tomentose about axils, becoming grey in age; leaves coriaceous, glabrescent, alternate, opposite or ternate, sometimes fascicled on short spur branches, oblong-ligulate to lanceolate or oblanceolate or nearly linear, sometimes falcate; petiole about 2 mm. long; margins sometimes inrolled, entire or weakly and remotely serrulate, apex obtuse to acute; staminate flowers solitary or in few-flowered (2–10 fls.) racemes to 20 mm. long; pedicels 3–10 mm. long, subtended by acuminate bracts 0.5–2 mm. long, sepals 6–10, ovate to lanceolate, 1.6–2 mm. long; stamens 5–10, filaments 2.5–4 mm. long, basally long villous, anthers about 0.5 mm. long; central glandular disk oblong to circular, ca. 1–1.5 mm. in diameter, 0.5 mm. high, flattened or blunt-carinate, sometimes papillate-lobed, margin irregularly lobed about filament bases; pistillate flowers solitary, axillary;

pedicels 6–15 mm. long, bearing 2 elliptic-oblanceolate bracteoles 1.5–2 mm. long; sepals 7–13, lanceolate or elliptic-lanceolate, acute, 2.75–5 mm. long, 1–2 mm. wide, minutely sericeous-tomentose within, margins often weakly glandular-dentate; glandular ring fleshy, lobes 4, deltoid to quadrate-lingulate, 1.5–1.75 mm. long; ovary softly crisp-tomentose; carpels 4 (rarely 5), styles 3–3.5 mm. long, spreading, flattened; young fruit reddish, sparsely crisp-tomentose; fruiting pedicels thickened; fruit depressed-globose, shallowly lobed, about 6 mm. long, 7–9 mm. wide; seed shiny, brownish red, oblong, tangentially compressed, 4.5–5 mm. long, 1.5–2.2 mm. tangentially, 2.4–2.8 mm. radially, caruncle well developed, 1.2–1.3 mm. in diameter, larger than hilum.

San Diego Co., California and northern Baja California, México. Representative specimens seen: San Diego Co., CALIFORNIA: near Temecula, just south of the Riverside Co. line, east of the road to Pala, April 12, 1900, *C. R. Orcutt* (UC); near Rainbow, March 24, 1914, *S. B. Parish 9130* (US); Lone Palm Spring on road to De Luz, Dec. 17, *Frank F. Gander 2985.2* (GH); Red Mountain near Fallbrook, alt. 1,000 ft., April 27, 1918, common shrub in Chaparral, *I. M. Johnston 1868* (ARIZ, DS, GH, POM, UC); Red Mountain Grade, local, in partly shaded chaparral on dry slope, May 14, 1932, *P. A. Munz & I. M. Johnston 12,613* (pistillate) (F, POM, UC) and *12,614* (staminate) (DS, F, POM, UC); Vista, October 28, 1933, *John S. Webb* (POM); Vista, dry slope in chaparral, April 3, 1933, *Cartwright* (POM); Jamacha, April 7, 1911, *Alice A. Murphy* (UC); along the old narrow road which runs from Lyons Valley to the Lawson Valley Road, May 18, 1929, *Helen L. Dale* (DS). Baja California, MEXICO: 8 miles this side of Table Mountain, Feb. 24, 1883, *D. Cleveland* (UC); near Table Mountain, Feb., 1883, *C. C. Parry* (GH, ISC, MO); Ensenada, *C. C. Parry* (DS); Santo Tomás hills, April 12, 1886, *C. R. Orcutt* (GH, ISC, UC, US); Guadaloupe Creek, April 27, 1873, *T. S. Brandegee* (UC); Santa Cruz road, between Santa Cruz and San Vicente, Feb. 18, 1935. *C. Epling & Wm. Robison* (GH, UC).

Both *Orcutt 313* and the *Parry* 1883 collection were available to Parry when he published the species; the former collection is here designated type since it is more complete, as stated by Parry. Wheeler (1939, p. 33) has adequately discussed the priority of *T. dioicus* Parry over *T. Engelmannii* S. Wats.

The collection by John S. Webb that is cited consists of several twigs which accompanied a letter sent to Dr. Munz. The sender stated that the plant was unusual in having apparently "perfect" flowers. One of the enclosed twigs bore a single fruiting pedicel and columella (the fruit having dehisced); this same twig still retained, at the time of examination, a single somewhat aberrant staminate flower, others apparently having broken off previously. All other twigs bore only staminate flowers. The monoecious

condition of this individual may have been correlated with an abnormal rate of growth. Mr. Webb states that the plant had attained a height of six feet and a spread of seven feet in a period of two years since being cut to the ground. The same letter contains a reference to a "delicate odor of the male blossom." This, along with the glandular tissues in flowers of both sorts, would seem to indicate insect pollination for the species. The present species, like the others of the genus, apparently flowers after every adequate rain, at least in the spring and summer. Leaf shape is quite variable, ranging from comparatively broad and flat and relatively thin in northern San Diego County to narrow, thick and inrolled, nearly needle-like leaves in interior, southern San Diego Co. The Mexican material is somewhat intermediate.

The distribution of this species, like that of the other species, is of considerable interest. It is known to occur, apparently somewhat locally, in chaparral from northern San Diego County south to about San Vicente in Baja California. It is not improbable that it is a relictual species dating to the Miocene or Pliocene when the chaparral was more generalized and (in the Pliocene) more widespread (Axelrod 1948). The present restricted distribution may be the result of temperature, rainfall or both. Among the other endemics to this general area is *Cneoridium dumosum* (Rutaceae), which, in foliage, strikingly resembles *Tetracoccus dioicus*. *T. dioicus* probably shows more primitive characters than does any of its congeners. Among these seemingly primitive characters are the larger number of carpels, the larger and indefinite numbers of sepals and stamens, and the more generalized male inflorescence. The leaves of *T. dioicus* are probably of a derived type, though they possess traces of the serrations which are so well developed in *T. ilicifolius*. This species shows resemblances both to *T. ilicifolius* and to *T. capensis* (and through the latter to the other species of the genus).

2. **Tetracoccus ilicifolius** Coville & Gilman, Journ. Wash. Acad. Sci. **26:** 531. 1936. Type: Canyon north of Titus Canyon, Grapevine Mts., Death Valley, California, May 30, 1936, *M. F. Gilman 2180* (us 1,650,292!, fragment uc!).

Open, spreading shrub to 1.5 m. in height; young twigs reddish, sparingly brownish-tomentose, becoming glabrous and grey with age; leaves op-

PLATE 1199. *Tetracoccus fasciculatus* var. *Hallii*.

Fig. 1. Area southwest of Cottonwood Springs, Riverside Co., Calif., April 6, 1952; showing *Tetracoccus* as sub-dominant on decomposed granite, with *Juniperus*, *Larrea* and *Yucca mohavensis*.

Fig. 2. Area just south of Vidal Junction, San Bernardino Co., Calif., April 19, 1952; showing *Tetracoccus* growing in shallow wash bordered by desert pavement.

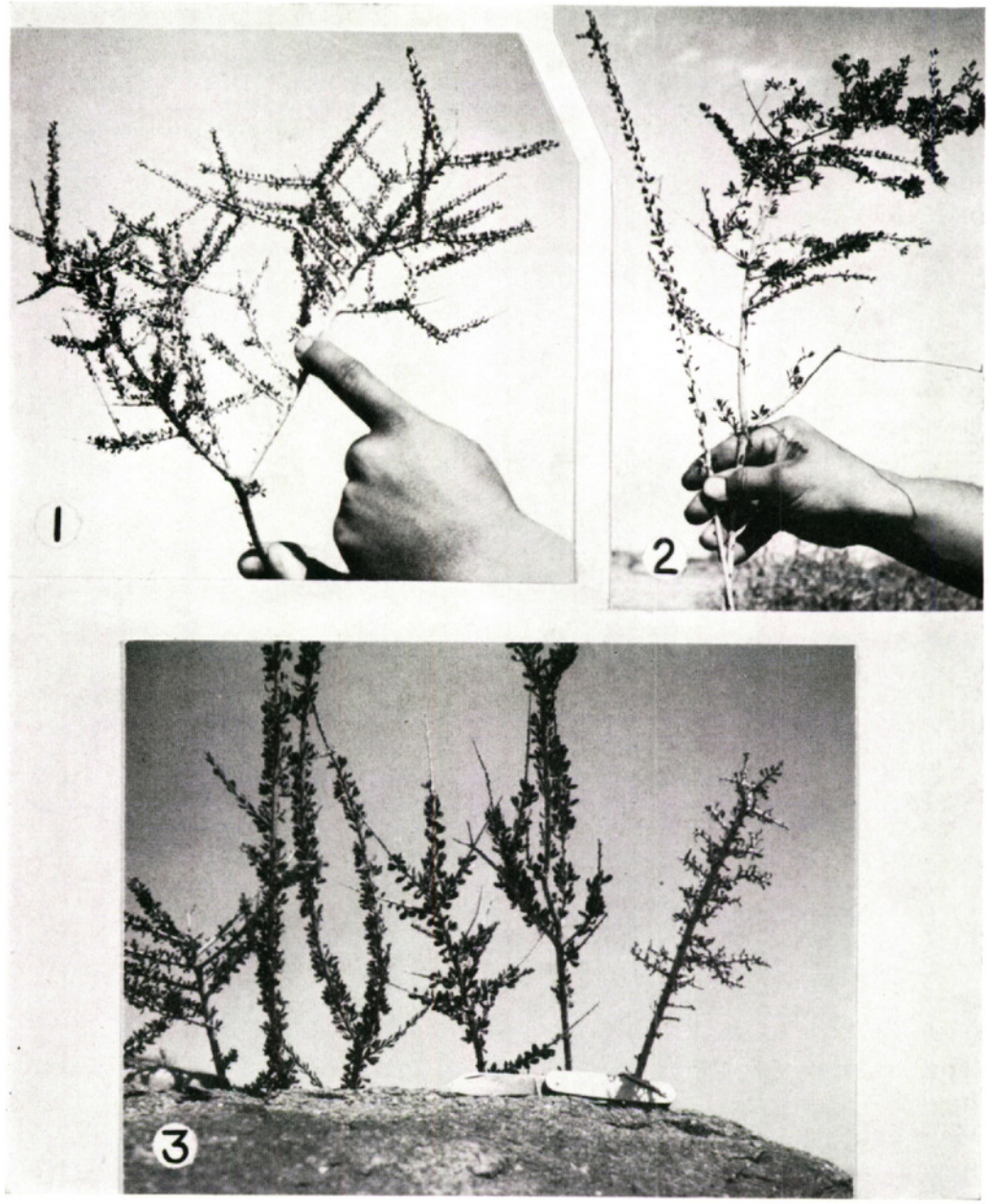

PLATE 1200. *Tetracoccus fasciculatus* var. *Hallii*.

Fig. 1. Branch of staminate plant. Vidal Junction.

Fig. 2. Young and older branches from same pistillate plant. Vidal Junction.

Fig. 3. Foliage from various plants in one locality to show variation, leaves purplish in some. Southwest of Cottonwood Springs.

posite, ovate to broadly elliptic or occasionally ovate-lanceolate, 15–30 mm. long, 7–20 mm. wide, coriaceous, sparsely tomentose when young, petiole about 2 mm. long, base obtuse, apex broadly acute or obtuse, margin distinctly serrate-dentate with 5–11 teeth on each side; staminate inflorescence an axillary, congested panicle 15–35 mm. in length, peduncles sparingly tomentose, about 10 mm. long; staminate flowers sessile or nearly so, sepals 7–9, lance-linear to lanceolate, with glandular teeth; stamens 7–9; filaments 2–3 mm. long, villous at base; anthers 0.9–1.2 mm. long, minutely papillate; disk 1–1.75 mm. in diameter, irregularly lobed; pistillate flowers solitary, axillary; pedicels 8–15 mm. long, tomentose above, bearing 2 elliptic-lanceolate, acuminate bracteoles to about 5 mm. long and 2 mm. wide (or occasionally larger and similar to the foliage leaves) with few glandular teeth; sepals in 2 series: the outer rhombic-lanceolate, acute to acuminate, 1.5–2.5 mm. wide, 3–4 mm. long, inner series slightly smaller and ovate-lanceolate, both series glandular-dentate along margins, densely tomentose within, less so without; gland lobes more or less opposite inner sepals, ligulate to deltoid and shallowly digitate-lobed, about 1–2 mm. wide and 2 mm. long; ovary 4-carpellate, densely tomentose; styles 4, spreading, about 3 mm. in length, flattened above; fruit with short brownish tomentum, oblong-globose, shallowly lobed, 8–9 mm. long, 6–8 mm. wide; seeds 1 or 2 per locule, shining, brownish red, elliptic-oblong, flattened tangentially; 4.25–5 mm. long, about 2.75 mm. radially, 1.75–2.25 mm. tangentially; caruncle yellowish, well developed, similar to that of *T. dioicus*.

Mountains on both sides of Death Valley, Inyo Co., California. Representative specimens seen (Mr. Gilman's numbers appear to refer to individual sheets rather than to collections): In large canyon north of Titus canyon [now Falls Canyon], Grapevine Mountains, 2,000 ft. Elev., August 2, 1936, *M. F. Gilman* s. n. (US); May 30, 1935 [sic], *Gilman 2182* (POM); Alt. 4,000 ft., May 30, 1936, *Gilman 2183* (POM). Tetracoccus Peak, Panamint Mountains: alt. 5,000 ft., June 4, 1938, *Gilman 3042* (POM); alt. 5,000 ft., Sept. 7, 1938, *Gilman 3357* (POM); alt. 5,500 ft., June 15, 1941, *Gilman 4376* (POM). Death Valley Canyon, Panamint Mountains: 5,500 ft., June 4, 1938, *Gilman 3036* (POM); 5,000 ft. alt., June 4, 1938, *Gilman 3045* (GH); 5,000 ft., June 4, 1938, *Gilman 3047* (DS); 5,000 ft. alt., Sept. 7, 1938, *Gilman 3350* (GH); 5,000 ft., *Gilman 3370* (DS).

This remarkable plant, a local endemic occurring in the mountains on both sides of Death Valley, is reported as very scarce and perhaps dying out at the type locality, Falls Canyon (Coville & Gilman 1936). Material from that locality shows smaller leaves and branches, which may indicate less favorable conditions there than at the other two known stations. In any case the plant is undoubtedly a relict from the relatively recent times in which Death Valley enjoyed conditions generally more

favorable to plant growth than at present. That such conditions did exist is evidenced by traces of Pleistocene lakes in the region (Miller, 1936). *T. ilicifolius* probably retreated to relatively high altitudes in response to increased aridity. This same aridity prevented its occurrence to the south and cold has probably barred its dispersal to the north, leaving the species, as it were, trapped in an unfavorable area, with poor evolutionary prospects. It is unlikely that the present population contains enough variability for rapid selection of a better adapted type.

This species is most closely related to *T. dioicus*, to which it has many similarities. In some respects it is more derived than *T. dioicus:* namely the congested male inflorescence, the double series of pistillate sepals and the more fixed numbers of flower parts. The foliage of this species, on the other hand, may be more like the ancestral type from which they were both derived than is that of *T. dioicus.*

3. **Tetracoccus capensis** (Johnston) Croizat, Bull. Torr. Bot. Club **69:** 457. 1942. Type: West side of Cape Region, Baja California, Oct. 22, 1893, *T. S. Brandegee* (UC 110393!).—*Securinega capensis* Johnston, Univ. Calif. Publ. Bot. **7:** 441. 1922.—*Halliophytum capense* Johnston, Contr. Gray Herb. **68:** 89. 1923.

Shrub; branching more or less divaricately; young stems slender, reddish, very sparsely short-strigose; spur branches short, thick, to 5 mm. in length; leaves alternate, fascicled, glabrescent, thin, oblanceolate or spatulate-oblanceolate, occasionally obovate or linear-oblanceolate, 10–15 mm. long and 2–5 mm. wide, petiole about 1 mm., apex obtuse; staminate flowers solitary or in small racemes of 2 or 3 flowers, peduncle 1.5–3 mm. long, glabrescent; pedicels 5–7 mm. long, glabrous, subtended by ovate-lanceolate bracts about 1 mm. in length; sepals 5, concave, 1–1.1 mm. long, obovate, obtuse, apically denticulate, stamens 5, filaments glabrous, about 2 mm. long, anthers about 0.75 mm. long; disk about 0.7 mm. in diameter and 0.8 mm. high, flattened or crested, somewhat notched or lobed where filaments are attached; pistillate flowers solitary or fascicled 1–3 (or more?) from a spur branch, pedicels about 1.5–2 mm. long, strigose, subtended by small bracts, lengthening in fruit; sepals 5, 1.3–2 mm. long, deltoid, glabrescent; gland lobes lingulate, 1–2 mm. long, obtuse; ovary densely strigose-tomentose, carpels 3 or occasionally 4, styles 1.75 mm. long, spreading, spatulate; young fruit strigose, reddish in color when approaching maturity; fruiting pedicels 3–5 mm. in length, thickened; capsule oblong-globose, moderately lobed, to 8 or 9 mm. in diameter, relatively woody, base not indented; mature seed not seen, apparently resembling that of *T. fasciculatus* var. *Hallii.*

Known only from the Cape Region of Baja California, Mexico. Specimens seen: Coast below Pescadero, Sept. 23, 1893, *T. S. Brandegee* (GH);

West side of Cape Region, Oct. 22, 1893, *T. S. Brandegee* (UC); San José del Cabo, Oct. 7, 1890, *T. S. Brandegee 536* (UC).

This species, endemic to the Cape Region, may well be a "postinsular endemic" (Gentry 1949, p. 86), dating back to the mid-Tertiary, when the Cape Region was insular in nature. It is probably an element of the subtropical scrub flora which occurred in the California region in the earlier Tertiary and later became extinct in this area due to increased aridity and the lack of summer rain (Axelrod 1948). The relictual *T. capensis*, with its primitive resemblances in texture, inflorescence and fruit to *T. dioicus*, would seem to represent the general type from which *T. fasciculatus*, which it more closely resembles, was derived.

4. **Tetracoccus fasciculatus** (S. Watson) Croizat, var. **fasciculatus,** Bull. Torr. Bot. Club **69:** 456. 1942. TYPE: in the mountains 24 miles north-northeast of Monclova, Coahuila, México, September 1–6, 1880, *Edward Palmer 1233* (GH!, isotypes; GH!, US!).—*Bernardia* (*?*) *fasciculata* S. Wats., Proc. Amer. Acad. Arts & Sci. **18:** 153. 1883.—*Securinega fasciculata* I. M. Johnst., Univ. Calif. Publ. Bot. **7:** 441. 1922.—*Halliophytum fasciculatum* I. M. Johnst., Contr. Gray Herb. **68:** 88. 1923.

Shrub 1–2 m. tall; branches ascending to strongly divaricate; twigs slender, shortly strigose, spur branches small, to about 2 mm. in length, usually closer together than in var. *Hallii;* leaves numerous, glabrescent, coriaceous, oblanceolate to elliptic-oblong, 1.5–7 mm. long, 0.75–2.25 mm. wide, obtuse or acute, short petiolate; staminate flowers solitary or fascicled, 1–4 (or more?) per spur branch, often subtended by a bract about 0.5 mm. long; pedicels capillary, 2–3 mm. long, sparsely strigose; sepals 5 or 6, ovate-oblong, obtuse, 0.5–1 mm. long, strigose without; stamens 4, 5 or occasionally 6, filaments about 1.5 mm. long, anthers 0.6–0.7 mm. long; disk 0.4–0.5 mm. in height, about 0.7 mm. wide, rounded or somewhat crested, more or less lobed, often 3-lobed, with filaments inserted between lobes and in small indentation at end of each lobe; pistillate flowers solitary (or fascicled?), sessile or short pedicellate, sepals 5 or 6, deltoid or deltoid-ovate, acute to acuminate, 0.7–1 mm. long, appressed strigose-tomentose without; glands deltoid or lingulate, blunt or acute, 0.5–1 mm. long, ovary densely appressed tomentose, carpels 3 or occasionally 4, styles more or less spreading, 0.8–1.75 mm. long, spatulate; capsule depressed globose to oblong-globose, 6–8 mm. long, distinctly lobed, base indented; seeds greyish to dark reddish brown, polished, deltoid-ovoid to pyriform-ovoid, 4.5–6 mm. long, about 4 mm. tangentially (about 2 mm. if 2 develop in 1 locule), 2–2.5 mm. radially, caruncle well developed, about 1 mm. in diameter.

MÉXICO, from the Mesa del Norte of the states of Chihuahua and Durango to the eastern slope of the Sierra Madre Oriental in Coahuila.

Representative specimens seen. Chihuahua: 13 mi. southeast of Saucillo, alt. 4,000 ft., with *Larrea* and *Acacia vernicosa*, July 29, 1937, *F. Shreve 8062* (ariz, us); vicinity of Santa Rosalía, alt. about 1,200 m., June 13–15, 1908, *E. Palmer 384* (gh, us); 31 miles southeast of Jiménez, divaricately branched shrub, 2 to 4 ft. high, common on *Larrea-Flourensia* covered slopes, Sept. 16, 1939, *C. H. Muller 3332* (uc); 12 mi. west of Carillo, road to Escalón, elev. 4,000 ft., shrub 1.5 m. high, July 24, 1939, *S. S. White 2040* (ds, gh). Durango: 26 miles west of Mapimí, about 5,400 ft. alt., common on rocky slope, loose dichotomous or trichotomous bush with assurgent branches, becoming 6 ft. tall, stem and leaves (*not* red) dark, Sept. 19, 1938, *I. M. Johnston* 7783 (gh, us).

The taxonomic validity of *Bernardia (?) fasciculata* S. Wats. has been the subject of some controversy (Wheeler, 1939; Croizat, 1942). The Seventh International Botanical Congress has more carefully delimited the *nomen provisorium* (Lanjouw, 1952, p. 28, Article 43), and *B. (?) fasciculata* is clearly to be considered as validly published.

This is one of those cases in which two plant populations may be designated either as species or varieties with little violence to the concepts of natural classification. Now that the nomenclatural validity of *Bernardia* (?) *fasciculata* is clarified, one feels free to use this name in a new combination. The two varieties of this species are closely related, and, while they can usually be easily distinguished and are widely disjunct, their close relationships seem best indicated by varietal status. The most easily definable differences are those in seed characters. The var. *fasciculatus* also differs from var. *Hallii* in smaller, more numerous leaves, smaller, more delicate staminate flowers with fewer parts and in having generally more slender branches. Most of these characters are probably derived from a type more similar to the present day var. *Hallii*, but the presence of a well developed caruncle in var *fasciculatus* is surely primitive.

Perry (1943) gives the chromosome number for "*Halliophytum fasciculatum* Johnst." as 2n = 24. No geographic origin was given for the material nor was there reference to herbarium specimens (cf. Just, 1951). The name used would seem to indicate that the plant was of this variety. In any case, there are not yet enough cytological data at hand concerning either *Tetracoccus* or the other genera of *Phyllantheae* to reach any conclusions.

The type collection, unlike the other collections seen, is from the eastern side of the Sierra Madre Oriental, probably the

Sierra de Hermanas. Dr. I. M. Johnston tells me there is some reason to doubt the data accompanying *Palmer 1233*, and that it may actually be from Chihuahua. This collection does, however, differ somewhat from all other collections in aspect, having larger leaves and more slender, ascending branches, as well as more oblong fruit. These may be due largely to a less xeric environment; there is not adequate material in the type series for full comparison. The region of seeming discontinuity is as yet quite imperfectly known. However the Sierra Madre Oriental in the north is neither relatively high nor altogether continuous. If var. *fasciculatus* is not now a continuous population, it may have been so in relatively recent times and under slightly different climatic conditions. For further discussion of relationships and possible geological history see under var. *Hallii*.

5. **Tetracoccus fasciculatus.** var. **Hallii** (T. S. Brandegee) comb. nov. TYPE: Chuckawalla Bench, Colorado Desert, Riverside Co., California, April 1905, *H. M. Hall 5865* (UC!, ISOTYPES DS! US!).—*Tetracoccus Hallii* T. S. Brandegee, Zoe **5:** 229. 1906.—*Securinega Hallii* Johnston, Univ. Calif. Publ. Bot. **7:** 442. 1922.—*Halliophytum Hallii* Johnston, Contr. Gray Herb. **68:** 88. 1923.—*Securinega fasciculata* var. *Hallii* Jepson, Man. Fl. Pl. Calif.: 595. 1925.—*Halliophytum fasciculata* var. *Hallii* McMinn, Ill. Man. Calif. Shrubs: 249. 1939.

Rigid shrub 1–2 m. in height; stems wandlike from base, branching divaricately above, young stems reddish, shortly gray-strigose; twigs tapering and becoming weakly spinescent by dying back from tips; spur branches 1.5–4 mm. in diameter, rarely reaching nearly 10 mm. in length, sometimes branching and becoming bi- or tri-cephalic; leaves alternate, fascicled, glabrescent, coriaceous, sometimes reddish in color, obovate, oblanceolate or spatulate-oblanceolate, 2–12 mm. long, 1–4 mm. wide, leaves of staminate plants often conspicuously smaller than those of pistillate plants from the same locality, apex obtuse, base cuneate to a very short petiole; staminate flowers fascicled, 1–20 from a spur branch; peduncle scarcely or not developed, pedicels 3–5.5 mm. long, sparsely pubescent, sometimes subtended by bract about 0.5 mm. long; sepals 4–6, 0.7–1.4 mm. long, obovate or orbicular to deltoid-ovate, acute or obtuse to truncate and denticulate, sparsely strigose-tomentose especially without, often more or less concave, often red or red-margined; stamens 4–8, filaments glabrous, 1.5–2.2 mm. long, anther 0.6–0.9 mm. long, central disk 0.5–1 mm. in diameter, about 0.8 mm. in height, rounded or crested, smooth or rugose, lobed as in var. *fasciculatus;* pistillate flowers solitary or fascicled, 1–6 from a spur branch, pedicels 0.5–1 mm. long, rarely reaching 3 mm. in length, sometimes subtended by 1 or 2 bracts about 0.5 mm. long; sepals 5, ovate to deltoid-ovate or lanceolate, obtuse

or acute, sometimes denticulate, sparsely tomentose; gland lobes more or less truncate, denticulate, 0.8–1.4 mm. long; ovary densely grey-tomentose, of 2–4 (mostly 3) carpels; styles spreading, 1.5–2 mm. long, spatulate; fruiting pedicel rarely exceeding 2 mm. in length; capsule globose to oblong-globose, shallowly lobed, especially above, 8–12 mm. long, 6–10 mm. wide, base deeply indented; seed smooth, somewhat polished, ovoid or pyriform-ovoid, radially flattened (except when 2 seeds develop in one locule, when the seed is tangentially flattened and the tangential dimension is about half that given for other seeds), 4–7 mm. long, 3–4 mm. tangentially, radially about 2.5 mm.; seed coat somewhat proliferated and wrinkled ventrally, especially about caruncle; caruncle thin, rudimentary, 0.2–0.6 mm. wide, 0.5–1.5 mm. long, sometimes nearly linear.

Local, in the Colorado Desert and the southeastern Mohave Desert in California and in western Arizona. Representative specimens seen: Arizona. Mohave Co. Northwest of Alamo, Rawhide Mts., sand and gravel, March 1940, *Lyman Benson 10082* (POM). Yuma Co. banks of small washes along Bill Williams River near Alamo, March 7, 1939, *Forrest Shreve 7841* (ARIZ, DS, F); Weaver Pass, between Quartzsite and Cibola, Dec. 18, 1939, *E. C. Jaeger* (ARIZ. POM); Kofa Mts., about 2 mi. northwest of North Star Mine, March 24, 1933, *I. L. Wiggins 6617* (DS, US); Sheep Tanks, Elev. 1850 ft., on hillsides and abundant in dry washes, March 28, 1935, *T. H. Kearney & R. H. Peebles 11005* (F, POM). California. San Bernardino Co. about 18 miles west of Needles, igneous, rocky hills with scattered vegetation of *Eriogonum*, *Larrea* and *Opuntia Bigelovii*, about 1 m. tall, frequent, April 19, 1952, *Dressler 1211* (GH); in a sandy wash near Colorado River between Parker, Arizona and Needles, California, March 22, 1931, *Kearney & Harrison 7530* (US); Carson's Wells, Turtle Mts., alt. 3,000 ft., March 27, 1940, *E. C. Jaeger* (POM); Copper Basin Mine, Copper Basin, Whipple Mts., alt. 1200 ft., coarse volcanic rock and gravel, shrub, height 3 ft., spread 3 ft., trunk diam. ½ in., April 30, 1932, *Carl B. Wolf* (DS, POM); 15 miles west of Earp, Whipple Mts., alt. 800 ft., June 2, 1942, *Robert A. Darrow* (ARIZ, POM); just south of Vidal Junction, local, silty soil of shallow washes bordered by desert pavement, *Encelia*, *Larrea*, *Krameria* and *Argythamnia lanceolata*, rounded shrub 1–1.5 m. tall, scattered, April 19, 1952, *Dressler 1205* (GH). Riverside Co. North slope of Eagle Mts., alt. 3,500 ft., quite common, May 18, 1941, *A. M. Alexander & L. Kellogg 2199* (UC); Eagle mts., the most frequently occurring shrub near the crest of the range, March 24, 1926, *E. C. Jaeger* (POM); 5 mi north of Cottonwood Spring, Eagle Mts., plateau, alt. 3,200 ft., associated with *Coleogyne* and *Polygala*, May 9, 1941, *Alexander & Kellogg 2138* (ARIZ, DS, UC); two miles from Cottonwood Springs, dense shrub 3 to 4 ft. high with cruciform branches, abundant, May 15, 1938, *R. S. Ferris & R. P. Rossbach 9540 & 9541* (F, DS, UC); above Cottonwood Spring, Eagle Mts., dry rocky slope of disintegrating granite, alt. 3,600 ft., April 13, 1949, *P. A. Munz 13050* (UC); Mansen Canyon, April 6, 1930, *M. F. Gilman 8* (POM); Lost Palms Canyon,

Eagle Mts., elev. 850 ft., sun, desert hillsides and canyons, height 4 ft., spread 6 ft., June 15, 1932, *B. D. Stark* (DS); vicinity of Corn Springs, Chuckwalla Mts., abundant on rocky slopes and in rocky gorges, alt. 2,500 ft., April 9–12, 1922, *P. A. Munz & D. Keck 4882* (POM, UC). Imperial Co. north base of Chocolate Mts., at head of Arroyo Seco, common along gullies, Feb. 15, 1939, *E. C. Jaeger* (POM); Beale's Well, 12 mi. east of Niland, April 1, 1923, *Jaeger* (DS).

According to Parish (1918) the type locality, Chuckawalla Bench, is in the vicinity of Cottonwood Springs; modern maps indicate that it may be further south, in the Chuckawalla Mts. ("midway between Cañon Springs and Chuckawalla Spring," Brandegee, 1906). The number of specimens taken from the vicinity of Cottonwood Springs, in the Eagle Mts., probably surpasses that of all other specimens taken of this species from California. This is no doubt due in part to the convenience of Cottonwood Springs with its camping facilities. However, the species is probably more abundant in this region than in any other. In this locality, the plant occupies varied slopes and soil types and is more variable in form than in most areas. In some other areas it occurs in distinct local habitats, as at Vidal Junction (see Plate 1199) and west of Needles; in these sites the morphological variation is correspondingly reduced, consisting principally of differences in age and between staminate and pistillate plants. Whatever the factor or factors which control the distribution of var. *Hallii*, the edaphic factor alone cannot explain its irregularity. This plant is apparently absent from the Iron, Granite and Coxcomb Mountains, though present in the Eagle, Chuckawalla and Chocolate ranges in the south and in the Whipple and Turtle ranges to the north, each population extending into Arizona. Such discontinuity might well be due to recent climatic changes.

The difference in size of foliage between staminate and pistillate plants is quite evident in *Dressler 1205*, from Vidal Junction, the leaves from staminate plants measuring 3–4 mm. in length while those from the pistillate plants are 6–11 mm. long. The pistillate plants of this collection show numerous flowers, many well developed young fruit and a few fruit of intermediate size, probably representing a response to two separate rains or rainy periods. The young stems from the base are long and wand-like; the upper portion, however, soon takes on by repeated,