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THE GENUS CERCIDIUM (LEGUMINOSAE: CAESALPINIOIDEAE) IN THE SONORAN DESERT OF MEXICO AND THE UNITED STATES

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Cercidium comprises nine taxa, five of which occur in the Sonoran Desert of Mexico and southwestern United States (figs. 1, 2). Of these five, only one, *C. praecox* (Ruiz and Pavón) Harms, has a widespread distribution, occurring from western and southern Mexico south to Peru. Of the remaining taxa, two occur in Texas and northern Mexico and two in Argentina. Thus, it can be seen that the greatest concentration of species occurs in the Sonoran Desert (Shreve, 1951, 1964).

Cercidiums, with their green branches which at a distance appear leafless much of the year, and are laden from March into June with a profusion of yellow, caesalpinoid flowers, are among the most conspicuous and characteristic trees of the Sonoran Desert. The newcomer to this region tends to refer to all these green-barked trees as *palo verde*, but if he goes into the field with a *paisano*, he soon learns that there is not only *palo verde*, but there are also *dipua* (*dipuga*), *palo brea*, and *palo estribo* (fig. 3). One other green-branched tree, closely related to *Cercidium*, also occurs in the Sonoran Desert. It is *Parkinsonia aculeata* Linnaeus, known locally in Baja California as *junco*. Continued experience with *palos verdes* in the field, especially in the Sierra de la Giganta of Baja California Sur, made it evident that they merited special attention in order to understand the relationships within the group. As with so many Sonoran Desert plants, most species of *Cercidium* present an entirely different aspect in the dry season than they do following the rains. Speaking generally, in the southern part of the Sonoran Desert, the heaviest rains fall in brief, hard-hitting storms during the hot months of July through September, sometimes extending into October (Hastings and Humphrey, 1969). With this moisture most plants come into full leaf, but with the end of the rains, many are soon leafless again. In 'good' years, gentle winter rains also come to the southern part of the Sonoran Desert and many species repeat the leaf cycle. Farther north, in south-central Arizona, where the total rainfall is about equally divided between summer and winter, *Cercidium* usually has two leafy seasons. All of the cercidiums flower at the height of the dry season, March through June, when for the most part, the trees are leafless or nearly so. Sometimes there is minor 'off-season' fall flowering. Keys to the taxa are included herein for both the vegetative and the flowering and fruiting stages.

Although no attempt is made here to resolve the long-standing controversy as to whether Cercidium should be regarded as distinct from Parkinsonia, some points brought out in this paper may add fuel to the fire. Watson (1876) argued for union of these two genera; Sargent (1889), principally on the basis of the legume, maintained them as distinct; Johnston (1924a), on other grounds and after some realignment of the taxa within the two genera, also argued for their maintenance as distinct genera; Britton and Rose in 1930 erected the genus Cercidiopsis for Cercidium microphyllum; Brenan (1963), on consideration of additional African taxa which he placed in Parkinsonia, felt that it is not possible to maintain Cercidium as distinct from Parkinsonia, but he refrained from making any nomenclatural changes in the American material. In accordance with Johnston's delimitation, Cercidium in America is easily distinguished from Parkinsonia and is kept separate in recent floras. The question of generic relationships cannot be resolved without first making extensive comparative studies of these trees (their biology, morphology, cytology, genetics, etc.) from seedling stage to maturity. Lack of evidence for resolution of problems at the generic level, however, does not preclude our attaining a better understanding of relationships at the subgeneric level. For the purposes of this paper, I am following Johnston's generic delimitation.

The following key summarizes the differences between the species of *Cercidium* and *Parkinsonia aculeata* Linnaeus.

Armature comprised of the *first* leaf developing at a node having a long-persistent, indurate petiole and rachis which terminates in a sharp, stout spine; leaves with pinnae¹ 8 to 30 (-60) cm. long, the rachis 1 to 3.6 mm. wide, flattened, phyllodial, persistent; leaflets falling with drought, alternate and/or opposite, 10 to 40 on one

¹ As used herein, the term "pinnae" refers to the secondary rachises plus leaflets of a bipinnate leaf. In many representatives of Caesalpinioideae the pinnae are reduced to a single pair.





FIGURE 1. Distribution of *Cercidium microphyllum*, C. praetox and $C. \times$ sonorae in the Sonoran Desert of northwestern Mexico and southwestern United States.

side of a given rachis; axillary leaf-bearing shoots usually 2 to 12 (-23) mm. long; inflorescences developing with the leaves, the racemes much shorter than the pinnae; pedicels 10 to 21 mm. long (mean 14.4 mm.) *Parkinsonia aculeata* Armature of one or two *axillary* thorns, or lacking; leaves with pinnae 0.3 to 6.5 cm.



FIGURE 2. Distribution of *Cercidium floridum* subsp. *floridum* and *C. floridum* subsp. *peninsulare* in the Sonoran Desert of northwestern Mexico and southwestern United States.

long, the rachis less than 1 mm. wide, terete or sub-terete, not phyllodial, often falling with drought; leaflets opposite, 2 to 9 (-17) pairs; axillary leaf-bearing shoots so reduced that the leaves appear to arise in the primary leaf axil; inflorescences developing before the leaves or if with them, the racemes subequal to or exceeding the pinnae; pedicels 2.5 to 14 mm. long (mean 7.5 mm.) _______ species of *Cercidium*

Herbarium material of Cercidium belonging to the following institutions has been studied: British Museum (Natural History), London (BM); California Academy of Sciences, San Francisco, California (CAS); Dudley Herbarium, Stanford University, California (DS); Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional, México, D. F. (ENCB); Field Museum of Natural History, Chicago, Illinois (F); Gray Herbarium of Harvard University, Cambridge, Massachusetts (GH); Herbario Nacional del Instituto de Biología, Universidad Nacional Autónoma de México, México, D. F. (MEXU); Instituto de Botánica, "Antonio José Cavanilles," Madrid (MA); Missouri Botanical Garden, St. Louis (MO); New York Botanical Garden (NY); Rancho Santa Ana Botanic Garden, Claremont, California (RSA); The Herbarium and Library, Royal Botanic Gardens, Kew (K); San Diego Museum of Natural History, California (SD); United States National Museum, Washington, D.C. (US); University of Arizona, Tucson (ARIZ); University of California, Berkeley (UC). Abbreviations for these institutions are those given by Lanjouw and Stafleu (1964). Collections made by the author will be widely distributed. Specimens cited include, in addition to those indicating limits of distribution, representative flowering and fruiting specimens as well as all specimens cited in illustrative material. I wish to express my appreciation to the directors and curators of the herbaria at these institutions for enabling me to study their collections.

In citing collections from the peninsula of Baja California, political subdivisions are indicated as follows: *Baja California Sur* for the area from 28°N. southward to the tip of the peninsula, a territory of Mexico; *Baja California* [*Norte*] for the area from 28°N. northward to the Mexico-United States border, a state of Mexico.

Cercidium Tulasne

Cercidium TULASNE, 1844, Arch. Mus. Paris, vol. 4, p. 133.

Trees or large shrubs with smooth greenish bark, the branches usually armed with axillary thorns, or having short, spine-tipped branches. Stipules slender, foliaceous, caducous. Clusters of dry axillary bud scales usually present. Leaves usually not long persistent, sessile or petiolate, bipinnate with one to three pairs of pinnae, the leaflets small, opposite; leaf rachis terete or sub-terete, 1 mm. or less in diameter and terminating in a slender foliaceous or semi-indurate bract. Flowers borne in condensed to open axillary racemes. Pedicels jointed, the joint being in the distal half. Calyx tube green, broadly campanulate, 1.5–2 mm. long, 3–4 mm. wide, the lobes 5, narrowly ovate, valvate or subvalvate, 4–7 mm. long, 2 mm. wide, yellow or greenish yellow. Petals 5, yellow or creamy white, pubescent at base, the upper (posterior) with a conspicuous claw which usually elevates the limb of this petal above the others, the base of the limb auriculate, the auricles often curved over the apex of the claw to form a channel; other four



FIGURE 3. Comparison of leaves, legumes, and seeds of *Cercidium*: A, C. microphyllum, the upper figure is a single pinna of a bipinnate, sessile leaf; B, C. \times sonorae, the leaves show variation in petiole length from subsessile to short-petiolate (one pinna has fallen from a leaf in 4945); C, C. praecox; D, C. floridum subsp. peninsulare. Numbers refer to Carter, and/or Carter *et al.* collections; data for these are given under "Representative collections cited" for the respective taxa.

petals with shorter claws. Stamens 10, distinct; filaments pilose near the base; anthers versatile. Pods oblong to linear-oblong, or linear and torulose, coriaceous or papery. Seeds 1 to 4, flattened or subglobose.

Based on *Cercidium spinosum* Tulasne, 1844, p. 136: "Regionem Amazonum (Bonplandi herb. propr. *nunc* in herb. Mus. Paris), Colombiam prope Maracaibo (Plée, herb. No. 73), nec non prov. *Oaxaca* Novae Hispaniae propter Tehuacán (in Cordillera alt. 1700 metr. — Galeotti herb. No. 3212) habitat."

Key to *Cercidium* in the Sonoran Desert (Based on vegetative characters)

Branches spinescent at tip; bark yellow-green, horizontally striate on older branches; axillary thorns lacking; leaves sessile, the pinnae of the primary² leaves borne on a scale-like, semi-indurate rachis which is tardily deciduous, the leaflets minute, 0.5-5 mm. long ______1. C. microphyllum

² The term "primary" leaf refers herein to the first leaf developing at a node in contrast to those developing subsequently from a succession of buds produced on a reduced shoot in the axil of the primary leaf or primary leaf scar.

- Branches not spinescent at tip; axillary thorns usually present; leaves petiolate (sometimes subsessile in $C. \times sonorae$), the leaflets larger, usually 3-12 mm. long.
 - Pinnae usually bearing 4-12 (-17) pairs of leaflets.
 - Nodes bearing one or two stout axillary thorns 2-18 (-25) mm. long and having conspicuous clusters of dry, dark bud scales in the axils; bark waxy-coated on older branches and having a fine, quadrate-pustulate pattern; petioles 4-11 mm. long. 2. C. praecox
 - Nodes bearing a single slender axillary thorn 2-11 (-20 mm.) long (or sometimes none); dry bud scales present at nodes but usually not conspicuous; bark on older branches smooth or inconspicuously horizontally-striate, the waxy coat inconspicuous or lacking; petioles 0-3 (-12) mm. long 3. $C. \times sonorae$
 - Pinnae usually bearing 2-4 pairs of leaflets; nodes without conspicuous clusters of dark axillary bud scales; bark of older branches horizontally striate 4. C. floridum
 - Branchlets of mature trees glabrous to glabrate; leaflets 4–8 mm. long, mostly 3 pairs per pinna (Sonoran Desert except Baja California).

4a. C. floridum subsp. floridum Branchlets villous or pilose, leaflets 6-15 mm. long, mostly 2 pairs per pinna; clusters of reddish brown glandular hairs in axil of primary leaves (confined to southern Baja California). 4b. C. floridum subsp. peninsulare

KEY TO *CERCIDIUM* IN THE SONORAN DESERT (Based on flowering and fruiting characters)

Ovary glabrous at anthesis; legumes not strongly long-tapered at ends.

- Inflorescences borne in clusters along older branches; petals deep yellow, the upper often orange-dotted near base of limb; mature legumes papery, flat, conspicuously net-veined; seeds flattened, gray-brown with brown mottling. 2. C. praecox
 Inflorescences on terminal or subterminal branches; legumes when immature bearing conspicuous white dots (stomata) but these obscure in mature legumes, coriaceous, the veins inconspicuous; seeds oblong to ovate, flattened, brown with marginal area lighter and sometimes faintly mottled. 4. C. floridum
 Inflorescences open, the racemes with rachis 1.0-4.5 (-7.0) cm. long, pedicels 6-12 (-20) mm. long; petals bright yellow, the upper sometimes orange-dotted (Sonoran Desert except Baja California). 4a. C. floridum subsp. floridum
 - Inflorescences somewhat congested, the racemes with rachis mostly 0.3-1.0 (-2.0) cm. long; pedicels 4-9 (-12) mm. long; petals deep or bright yellow, the upper not orange-dotted (confined to southern Baja California).

4b. C. floridum subsp. peninsulare Ovary lightly pubescent to strigose at anthesis; legumes strongly tapered at both ends. Legumes torulose, lightly striate-veined; petals light yellow³ except for the upper

- one which is white or creamy-yellow but never orange-dotted; seeds sub-globose, brown. 1. C. microphyllum
 - Legumes sinuate, conspicuously striate-veined; petals light yellow³ except for the upper one which is variable (whitish or pale yellow and sometimes orange-dotted); seeds oblong to ovate, flattened, dark mottled brown. 3. $C. \times$ sonorae

³ Petal color is useful only with fresh material; use vegetative key to distinguish these two species if only dry material is available.

1. Cercidium microphyllum (Torrey) Rose and Johnston.

Cercidium microphyllum (Torrey) Rose and Johnston in I. M. Johnston, 1924, Contr. Gray Herb., vol. 70, p. 66.

Parkinsonia microphylla TORREY, 1857, Pac. R. R. Rep., vol. 4, p. 82; 1859, Bot. Mex. Bound, p. 59.

Cercidiopsis microphylla BRITTON AND ROSE, 1930, N. Amer. Fl., vol. 23, p. 306.

Shrub or tree 3-4 m. tall and nearly as broad, occasionally up to 8 m., the branches usually ascending and often presenting a broom-like appearance; bark yellow-green with fine horizontal striations; branches pubescent (strongly strigose in Baja California), puberulent or pilose to glabrate, the branchlets rigidly divaricate, spinose-tipped; axillary thorns lacking, the nodes bearing few to many bud scales; leaves 1-2 per node, sessile [i.e. no petiole evident on the common rachis except in seedlings (fig. 7b)], the single pair of pinnae (3-65 mm. long) of the primary leaves borne on a scale-like, indurate rachis which is sometimes tardily deciduous after the pinnae fall; leaflets 1-7 (-13) pairs, broadly elliptical, obtuse to emarginate at apex, 0.5-5 mm. long, 0.75-1.5 (-2) mm. broad, puberulent when young; rachis of the raceme 0.2-4.5 cm. long, puberulent, bearing 1-6 (-10) flowers on pedicels 4-8 (-15) mm. long; calyx pubescent to glabrate; petals yellow except for the upper (posterior) whose limb is usually white but occasionally creamy or pale yellow; upper petal 7-10 mm. long, the limb 4–5 mm. long, 3.5–6.0 mm. wide, rhomboidal or broadly ovate, the claw 3–4 mm. long, subequal to the limb in length, the other four petals slightly shorter than the upper, the limb rhomboidal or lanceolate, the margins not overlapping one another at anthesis, the claw short, 1-2 mm. long; ovary at anthesis strigose to puberulent; legumes 3.5-11.0 cm. long, 7-9 mm. wide, strongly tapered basally and apically, torulose, circular in cross-section where the seeds are borne, longitudinally striate, not coriaceous, dehiscence irregular, the valves often breaking as well as the sutures opening; seeds 1–4, brown, sub-globose, 8 (–10) mm. long, 5-7 mm. wide.

TYPE. Mexican Boundary Survey: Diluvial banks of the Colorado, Ft. Yuma, 13 January 1854. A. F. Schott (NY, holotype; F!, date of 1855 is in error) [flowering specimen]; Williams' River [Arizona], 12–22 February [1854], J. M. Bigelow (N.Y.) [in fruit].

REPRESENTATIVE SPECIMENS. MEXICO. GULF OF CALIFORNIA ISLANDS, BAJA CALIFORNIA SUR: S. end of Amortajada Bay, San José Island, 11 April 1952, *R. Moran 3772* (DS, UC); Puerto Balandra, Isla Carmen, 23 March 1971, *J. R. Hastings 71-131* (ARIZ, SD); Danzante Island, 7 April 1962, *Moran* 9228 (CAS, SD); Arroyo de los Chivos, NE. side of San Marcos Island, 29 March 1962, *Moran 8981* (CAS, RSA, SD). BAJA CALIFORNIA [Norte]: main arroyo, San Esteban Island, 26 April 1966, *Moran 13054* (DS); ca. ¹/₂ mi. S. of Refugio Bay, Isla Angel de la Guarda, 26 March 1963, *Moran 10427* (DS, UC). SONORA: Tiburón Island, 5 May 1952, *Moran 4064* (DS, SD, UC, US), 23 April 1966, *Moran 12992* (ARIZ, CAS, RSA, SD).

PENINSULA, BAJA CALIFORNIA SUR: Rancho El Salto, Arroyo Coyote (ca. 24°47'N., 110°50'W.), altitude 525 m., 5 November 1971, Moran 19020 (14 mi. [22.4 km.] (by road) W. of San Luis Gonzaga, 21 October 1964, Turner & Hastings 64-380 (ARIZ); Agua Verde, 1 April 1911, J. N. Rose 16578 (US); Portus Escondido, 2 February 1842, Wosnessensky (GH); 55 km. E. of Villa Insurgentes on highway to Loreto, 3 May 1972, Carter 5670; 1 km. W. of Las Parras summit, road from Loreto to San Javier, 6 May 1972, Carter 5672; Rancho La Venta, ca. 16 km. westerly from Loreto on road to San Javier, 21 April 1962, Carter 4415; Rancho Aguajito, Arroyo Gua between Loreto and Rancho Sauce, 24 April 1955, Carter & Ferris 3446; Arroyo Gua, N. of Loreto, 7 November 1960, Carter 4110; Rancho Naucajoa (26°16'N., 111°36.5'W.), W. of Llanos de San Juan, Carter & Reese 4531; Coyote Bay [Cove], Concepción Bay, 18 June 1921, Johnston 4172 (CAS, F, K, MO, UC, US); wash 25 mi. [40 km.] S. of San Ignacio, 19 April 1931, Wiggins 5434 (CAS, DS, GH, RSA); eastern bajada of Sierra Calvario, Systema de Sierra Viscaíno, 10-15 March 1947, H. S. Gentry 7501 (DS). BAJA CALIFORNIA [Norte]: ca. 5 mi. [8 km.] N. of Misión de San Borja along road to Bahía de Los Angeles, 17 May 1959, I. L. & D. B. Wiggins 14857 (CAS, DS); Cajón de Santa María, 12 May 1889, T. S. Brandegee s.n. (DS, UC); San Luis Gonzales [Gonzaga] Bay, 29 April 1921, Johnston 3348 (CAS, US); San Felipe Desert between El Cajón and Algodones, along eastern foot of Sierra San Pedro Mártir, altitude 2500 ft., [800 m.], 10 May 1941, Wiggins 9845 (DS, UC, US). SONORA: island in harbor, Guaymas, 14 April 1921, Johnston 3084 (CAS, US); hills NW. of shrimp cannery, Guaymas, 6 April 1962, Carter 4363; 26 km. S. of Hermosillo on Guaymas road, 21 March 1934, Ferris 8759A (DS); between Hermosillo and Kino Bay, 21 December 1968, V. Rudd 3038, with P. Bauer & A. C. Fox (ARIZ, SD, US); Sonora Alta, 1830, Coulter 490 (K, 2 sheets, one lacking collection number); N. of bay, within 5 mi. [8 km.] of coast, vicinity of Libertad, 2 May 1928, E. H. Graham 3822 (DS); 7 mi. [11 km.] S. of Altar, 4 May 1928, Graham 3906 (DS); Pasa de San Luis [Poso de Luis on US sheet], 4 June 1894, E. A. Mearns 2697 [Int. Bound. Commission] (DS, US).

UNITED STATES. ARIZONA: Tumamoc Hill, Tucson Mts., Pima Co., 8 June 1938, H. S. Gentry 3777 (CAS); 5 mi. [8 km.] S. of Florence, Pinal Co., 26 July 1927, H. W. Graham s.n. (DS); Tempe Butte, altitude ca. 1300 ft. [415 m.], Maricopa Co., 4 May 1952, E. P. Killip 42150 (US); Government Springs, 3.5 mi. [5.6 km.] N. of Bumblebee, State Highway 69, Yavapai Co., 3 July 1940, Ferris 9902 (CAS, DS, GH, RSA, UC); 14 mi. [22 km.] NE. of Topock, Mohave Co., 10 June 1967, *Carter 5243*. CALIFORNIA: 1 mi. [1.6 km.] S. of Copper Basin Lake, Whipple Mts., San Bernardino Co., 22 April 1940, *A. M. Alexander & L. Kellogg 1200* (DS, GH, RSA, US); base of Whipple Mts. adjacent to Colorado River 11 mi. [18 km.] above Earp on road to Parker Dam, San Bernardino Co., 15 March 1940, *Wolf 9721* (RSA).

Coarse soil of plains and hillslopes, mostly below 600 m., but also between 700 and 800 m. in north central Sonora and southeastern Arizona. The trees leaf out following the rainy seasons, but the leaves are ephemeral. Flowering is mostly from March through May, the height of the Sonoran Desert dry season. Leaves, if present during flowering, are confined to non-floriferous branches. This is the most widespread of the taxa in Baja California where it is known as *dipua* and extends from a little south of Latitude 25° N. northward to the United States border. It is also abundant in west central Sonora and southwestern Arizona where it extends to Latitude 35° N.

Even when leafless, the branches are an important source of food for stock. Trees with their upper branches lopped off by machetes indicate that a traveller rested nearby and provided food for his mule, burro, or horse. In times of drought, the branches are also cut to feed cattle. The seeds are edible.

As an historical aside, it is interesting to note that Thomas Coulter collected both *Cercidium microphyllum* and *C. floridum* in "Sonora Alta" [vicinity of Hermosillo, Sonora] in 1830. According to the correspondence between Harvey and Bentham [Kew archives], some years after the packages of Coulter's collections were received at Trinity College, Dublin, Harvey separated the legumes and sent them to Bentham at Kew for identification. Specimens of both taxa are annotated in Bentham's hand as new species. At about that time, Asa Gray visited Kew, presumably saw all of the Coulter material, and subsequently published *Cercidium floridum* Benth. ex Gray. Five years later, John Torrey, in describing material collected on the Mexican Boundary Survey, named *Parkinsonia microphylla*, chose a Schott specimen as type, and made no mention of the much earlier Coulter collection to which Bentham had applied the same specific epithet.

The following collections are putative hybrids between *Cercidium micro-phyllum* and *C. floridum* subsp. *floridum*: *P. Kamb 2014*. Bottom of NE. caldera of Molina Crater, altitude ca. 950 ft. [310 m.], crater region NW. of Sierra Pinacate, Sonora, Mexico, 29 April 1951 (DS, UC). The leaves are petiolate. The leaflets are larger than typical for *C. microphyllum* and there are too many leaflets for it to be *C. floridum*. It has the stem pubescence and the strigose ovary of *C. microphyllum* and thorns similar to those of *C. floridum*. On both of the above cited sheets of this collection, the flowering branch is the putative hybrid and the separate fruiting branch—presumably from a different tree—is typical *C. floridum* subsp. *floridum*. Both of the putative parents are

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known to occur in this area (Hastings, Turner and Warren, 1972). A sheet at University of Arizona bears only a fruiting branch and this is typical *C. floridum* subsp. *floridum*.

C. B. Wolf 9722. Base of Whipple Mts., adjacent to Colorado River, 11 mi. [18 km.] above Earp on road to Parker Dam, altitude ca. 400 ft. [130 m.], San Bernardino Co., California, 15 July 1940 (DS, RSA). Collector's note: "This lone tree looks like a typical C. microphyllum in olive-green color and shape, but the pods are rich brown, somewhat flattened, and not constricted between the seeds, which are larger and flattened. Leaflets somewhat larger than typical C. microphyllum and C. floridum. Both species grow here in abundance." The valves of the pods are coriaceous, striate, and white-dotted. The stems are sparsely appressed-pubescent and bear short spines.

Papers treating these and other putative hybrids in *Cercidium* are published elsewhere (Carter, 1974; Carter and Rem, 1974).

2. Cercidium praecox (Ruiz and Pavón) Harms. (Figure 4.)

Cercidium praecox (Ruiz and Pavón) HARMS, 1908, Bot. Jahrb., vol. 42, p. 91.

Caesalpinia [Sappania] praecox RUIZ AND PAVÓN, 1802, Fl. Peruv., vol. 4, pl. 376, plate only [Entire volume published by Consejo Superior de Investigaciones Científicas, Madrid, 1957].

Caesalpinia praecox RUIZ AND PAVÓN, 1833, in HOOKER AND ARNOTT, Bot. Misc., vol. 3, p. 208. Cercidium spinosum TULASNE, 1844, Arch. Mus. Paris, vol. 4, p. 134.

Rhetinophloem viride KARSTEN, 1862, Fl. Columb., vol. 2, p. 25, pl. 113.

Cercidium viride KARSTEN, 1887, Bot. Jahrb., vol. 8, p. 346.

Cercidium plurifoliolatum M. MICHELI, 1903, Mém. Soc. Phys. et Hist. Nat. Genève, vol. 34, p. 269, pl. 18.

Cercidium unijuga Rose, 1905, Contrib. U. S. Nat. Herb., vol. 8, p. 301, 1905.

Cercidium Goldmanii Rose, 1905, Contrib. U.S. Nat. Herb., vol. 8, p. 301. [Goldman 735, type (US!): leaves glabrous; waxy coating of stems only slightly visible.]

Shrub or tree usually 2–4 m. tall, but up to 9 m. in forested areas of northeastern Sonora, the crown usually rounded, or flat-topped and spreading in exposed habitats, erect and less branched in sheltered habitats; branches and trunk bright green to the base, the bark with a minute quadrate-pustulate pattern and bearing a heavy coating of wax, the branchlets glabrate to pubescent, the hairs usually appressed; axillary bud scales prominent; thorns axillary, stout, usually one but sometimes two per node, 2–18 (–25) mm. long (mean 8.6 mm.), often dark brown; leaves 1–3 (–6) per node, pubescent, the petiole (1–) 4–11 (–21) mm. long, bearing 1 (occasionally 2–3) pair of pinnae 0.4–4.5 cm. (–5.0, *Wiggins 6473*) cm. long; leaflets (3–) 5–9 (–17, *Wiggins 6473*) pairs, oblong, rounded at apex, 3–10 mm. long, 1.4–3.8 mm. wide; inflorescences borne in



FIGURE 4. Cercidium praecox, palo brea, showing typical growth form in open habitat (Carter, Hastings & Turner 5577, northeastern Sonora between Moctezuma and La Noria).

clusters along mature branches, usually compact, 1-3 (4) per node, the rachis (1.5–) 2–11 (–15) mm. long, sparingly pilose, bearing 1–6 (–9) flowers on pedicels 7–10 mm. long; petals deep yellow, the upper often orange-dotted near base of limb; upper petal 9–11 mm. long, the limb 6–7 mm. long, 6–8 mm. wide, broadly ovate, the claw 3–5 mm. long, shorter than the limb, the other four petals slightly shorter than the upper, the limb broadly ovate and sometimes auriculate at base, the claw 1–2 mm. long; ovary glabrous at anthesis; legumes 3–6 (–8) cm. long, 0.6–1.0 cm. wide, flat and papery, not narrowed between the seeds, the veins conspicuous, forming an elongate-reticulate pattern; seeds 1–2 per pod, oblong, flattened, gray-brown with dark brown mottling, up to 1 cm. long, 3–4 mm. wide.

TYPE. Middle western Peru. Ruiz and Pavón plate. [cf. Johnston, 1924, p. 67.] (Ruiz and Pavón collections, MA!).

REPRESENTATIVE SPECIMENS. MEXICO. GULF OF CALIFORNIA ISLANDS, BAJA CALIFORNIA SUR: summit, Ildefonso Island (26°37'N., 111°27'W.), 17 May 1921, Johnston 3753 (CAS), 2 April 1962, Moran 9066 (RSA, SD, US); Tortuga Island (27°26'N., 111°54'W.), 24 April 1952, Moran 4007 (DS), 30 March 1962, Moran 9016 (SD), 11 May 1921, Johnston 3592 (CAS, GH, K, UC, US). PENINSULA, BAJA CALIFORNIA SUR: San José del Cabo, 26 March 1911, J. N. Rose 14466 (US); La Paz, 10 August 1944, Maximino Martínez s.n.

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(US); along dry washes between Médano and Venancio, 29 April 1931, Wiggins 5532 (DS, RSA, UC, US); between Rancho Segundo Paso and San Javier, altitude 300 m., 21 April 1962, Carter 4412; between Cañón de Las Calaveras and La Tinaja, western side of Mesa de San Alejo, altitude 690 m. (ca. 25°51'N., 111°36'W.), 11 November 1961, Carter 4306; along old mission trail SE. of Comondú, altitude 420 m., 20 April 1955, Carter & Ferris 3424 (ARIZ, DS, GH, SD, UC, US); Cuesta de Los Encinos, SE. of Cerro Giganta, altitude 500 m., 29 March 1960, Carter & Ferris 4046 (UC), same tree, 9 November 1960, Carter 4146 (UC); 4 mi. [6 km.] (by road) E. of San Lina (suburb of San Ignacio), 29 October 1963, Turner & Hastings 63-294 (ARIZ, DS, SD). SINALOA: La Constancia, Munic. El Fuerte, December 1924 [sic! on original label at DS; US copied label is 1926], Jesus Gonzales Ortega 6200 (DS, GH, MEXU, US). SONORA: Alamos study area, 7.5 mi. [12 km.] W. of Alamos, 28 April 1967, R. D. Krizman 16 (ARIZ); Agua Caliente N. of Alamos, 2 November 1939, Gentry 4839 (ARIZ, MO, distributed as C. torreyanum and so cited by Gentry, 1942, p. 131); San Bernardo, Río Mayo, 1 March 1935, Gentry 1377 (ARIZ, GH, MEXU, UC, distributed as C. torreyanum and so cited by Gentry, 1942, p. 131); Cerro de Bayajori, 12 mi. [19 km.] W. of Navajoa, 11 April 1948, Gentry 7947 (UC, US, distributed as C. floridum); island in Bay, Guaymas, 14 April 1921, Johnston 3078 (CAS, US); low hills and flats near tannery E. of Guaymas, 28 February 1933, Wiggins 6348 (DS, RSA, US); small valley 20 mi. [32 km.] N. of Guaymas, 8 March 1933, Wiggins 6473 [spines up to 30 mm. long, pinnae 45-50 mm. long, leaflets up to 15 pairs] (DS); 20 km. S. of Carbó junction, 3 May 1971, Carter, Hastings & Turner 5597; Horcasitas, 17 April 1932, Abrams 13360 (DS); 2 mi. [3 km.] S. of Los Hoyos, altitude 810 m., 23 April 1971, Carter, Hastings & Turner 5576; 4.2 km. S. of Los Hoyos, 4 July 1971, Hastings 71-199 (SD); Colonia Oaxaca, 24 July 1938, Stephen S. White 663 (ARIZ, GH).

Ranging from coastal plains up to bajadas, mesas, hills, and mountains at elevations up to 825 m. in Baja California and 1115 m. in the mountains of northeastern Sonora. Flowering is from March through May with the peak in April, before the leaves develop.

In Baja California, *C. praecox* extends from near the tip of the peninsula $(23^{\circ}N.)$ northward to the vicinity of San Ignacio $(27^{\circ} 25' N.)$. On the mainland, it occurs in southern Mexico and is abundant in Sonora from a little south of Guaymas $(27^{\circ} 56' N.)$ almost to the United States border $(30^{\circ} 54' N.)$. Occasional collections have been made as far south as $26^{\circ}N.$ in Sinaloa. This is the only one of our Sonoran Desert species of *Cercidium* having a disjunct distribution. According to Johnston (1924a), in South America it occurs from extreme middle-western Peru to northern Venezuela.

During the months when the trees are leafless, *C. praecox* may be recognized readily by the bright green bark extending down to ground level, and the conspicuous accumulation of dark bud scales at the nodes. Development of new branch growth appears to be limited, and most seasonal growth (production of leaves and flowers) is axillary year after year on the old branches. In addition, the stout, often dark brown spines, which may reach a length of 2.6 cm., set it apart from the other taxa. It is the only one of our *Cercidium* species with bark having a quadrate-pustulate pattern. When in flower, the species may be recognized easily by the usually deep yellow flowers borne in close clusters along the length of the old branches.

The common name, *palo brea*, is derived from the fact that the waxy substance coating the bark, after being scraped from the branches and melted by heat, is used as a 'gum' for gluing together leather objects and furniture; thus it is used just like *la verdadera brea*.

The following Mexican collections are putative hybrids between *Cercidium* praecox and Parkinsonia aculeata: edge of town, Coyuca, Mina, Guerrero, 11 May 1934, G. B. Hinton 6040 (BM, NY), 25 March 1937, Hinton 9968; (ARIZ, BM, K, MEXU, NY, RSA, TEX); near Los Hoyos, northeastern Sonora, 23 April 1971, Carter, Hastings & Turner 5575 (to be distributed). This material is discussed in a separate paper (Carter and Rem, 1974).

3. Cercidium × sonorae Rose and Johnston.

(Figure 5.)

Cercidium × sonorae ROSE AND JOHNSTON, 1924 (pro sp.) stat. nov., in I. M. Johnston, Contr. Gray Herb., vol. 70, p. 66. (April). [C. microphyllum (Torrey) Rose and Johnston × C. praecox (Ruiz and Pavón) Harms].

Cercidium molle I. M. JOHNSTON, 1924, Proc. Calif. Acad. Sci., IV, vol. 12, p. 1038. (May).

Spreading tree 4–8 m. tall, usually with lax branches (but sometimes the branches short and stiff), the bark smooth or sometimes faintly horizontally striate, green to yellow-green, sometimes with an inconspicuous, thin, waxy coating, branches short-villous, pilose, or sometimes glabrate; axillary thorns present or lacking, slender (2-) 5–11 (–20) mm. long (mean 6.5 mm.), variable as to presence on a given tree; bud scale clusters prominent to inconspicuous; foliage bright yellow-green, the leaves 1 to 3 per node, the petioles usually 1–3 mm. long, but varying from 0 to 12 mm.; pinnae 1 to 2 pairs, 0.7–5.0 cm. long, the leaflets (3–) 6–8 (–12) pairs elliptical-oblong, (1.5–) 2–3 (–6.0) mm. long, (1.0–) 1.5 (–3.0) mm. wide; inflorescence usually open, the rachis of the racemes 0.5–4.0 cm. long, bearing 1 to 10 flowers on pedicels 6–10 (–14) mm. long; petals light yellow, except for the upper whose limb may be whitish, creamy, or creamy and yellow and often orange-dotted near the base of the limb; upper petal 10–12 mm. long, the limb 5–7 mm. long, 5–8 mm. wide, broadly ovate but with



FIGURE 5. Cercidium \times sonorae, palo estribo, showing typical habit of a mature tree (Carter & Reese 4554, Baja California, Sierra de la Giganta west of Loreto).

pointed apex, the claw 4–5 mm. long, shorter than the limb; the other four petals slightly shorter than the upper, the limb ovate, the claw short, 1.5-3 mm. long; ovary strigose at anthesis; legumes 3–8 cm. long, 7–10 mm. wide, slightly flattened and somewhat coriaceous, sinuate if more than one-seeded, long-tapering to each end, the surface with conspicuous longitudinal striations, dehiscing along the sutures or irregularly; seeds 1 to 2 (4), oblong to oblong-ovate or ovoid, dark mottled brown, flattened or thick, 9–10 (–12) mm. long, 4–5 mm. wide.

TYPE. Dry hills in the vicinity of Guaymas, Sonora, Mexico, 1910, Rose, Standley & Russell 12586 (US!).

REPRESENTATIVE SPECIMENS. MEXICO. BAJA CALIFORNIA SUR: Arroyo San Ramón just W. of Rancho San Ramón (25°14.5'N., 111°17'W.), 21 October 1964, Carter 4818; Rancho Tasajera, ca. 3.5 km. NE. of San José de Agua Verde, 3 June 1965, Carter & Sharsmith 4936; Agua Verde Bay, 26 May 1921, Johnston 3877 (CAS!, type of C. molle, DS, GH, K, MO, UC, US); Puerto Agua Verde [Bahía Agua Verde], 5 June 1965, Carter & Sharsmith 4945, 23 August 1971, Carter 5610; Misión San Javier, 36 km. SW. of Loreto, 6 May 1972, Carter 5679; Arroyo Ranchito, ca. 9 km. SE. of Llanos de San Julio on road from San Javier to Comondú (26°02'N., 111°39'W.), 5 June 1963, Carter & Reese 4554; Cuesta de Los Encinos, SE. of Cerro Giganta, altitude ca. 500 m., 29 March 1960, Carter & Ferris 4045, and from same tree 9 November 1960, Carter 4145; La Higuera, NE. base of Cerro Giganta, 18 October 1966, Carter & Sousa 5212; Arroyo Hondo, N. side of Cerro Giganta, altitude 540 m., 17 October 1966, Carter & Sousa 5199; Tortuga Island, 11 May 1921, Johnston 4409 (CAS, K, UC, US), 16 mi. [26 km.] from San Ignacio on road to Santa Rosalía, 10 March 1934, Ferris 8626 (US); 10.5 [17 km.] mi. ENE. of San Ignacio, 27.4°N., 112.8°W., altitude 170 m., 17 October 1971, Turner & Hastings 71-134 (ARIZ). SONORA: N. of Guaymas (0.6 mi. [.96 km.] N. of junction with Bahía San Carlos road), 2 May 1971, Carter, Hastings & Turner 5595; 25 mi. [40 km.] N. of Guaymas, 2 April 1935, Shreve 7310 (MO; sheets at ARIZ and F bear both C. × sonorae and C. praecox); 31 mi. [50 km.] N. of Guaymas, 2 April 1935, Shreve 7313 (ARIZ, F, MO); El Pozo, 26 km. S. of Hermosillo on road to Guaymas, 21 March 1934, Ferris 8761 (DS, US); Torres, 10 February 1903, F. V. Coville 1664 (US); Sierra Lopez Rancho [37 mi., 59 km. NW. of Hermosillo], 13 April 1932, Abrams 13327 (DS,F).

Plains and hillslopes below 600 m. Flowering March to June with the peak in April; leaves usually present when trees in flower.

In Baja California, where it is known as palo estribo, Cercidium \times sonorae occurs principally in the Sierra de la Giganta from about 25°15'N. (opposite the northern end of Isla San José) northward to the northern slopes of Cerro Giganta (26°10'N.). One outlying collection (Turner & Hastings 71-134) is from east of San Ignacio (27.4°N.). In Sonora, $C. \times$ sonorae is most abundant from near Guaymas northward to the vicinity of Carbó (i.e., from about 28° to 30° N.). On neither side of the Gulf of California is $C_{\cdot} \times$ sonorae as abundant as C_{\cdot} microphyllum and C. praecox, one or the other or both of which appear always to occur in the vicinity of trees of $C. \times$ sonorae. Throughout its range, but especially noticeable in Baja California, is the fact that $C. \times$ sonorae occurs only within the limits of the distributional overlap of C. microphyllum and C. praecox. In characters of bark surface, spininess, pubescence, flower color, and seed shape, $C. \times$ sonorae appears to be more variable than any of the other taxa in the group. In several morphological characters, $C. \times$ sonorae falls between C. praecox and C. *microphyllum*; furthermore, pollen of $C. \times$ sonorae stained with 'cotton blue' (aniline-blue-lactophenol) shows a much lower percentage of presumably viable grains than does the pollen of either of its putative parents. These facts lead to the hypothesis that $C. \times$ sonorae is of hybrid origin, the putative parents being C. microphyllum and C. praecox. Discussion of the hybrid origin of C. \times sonorae and of other hybrids involving species of Cercidium is published elsewhere (Carter, 1974; Carter & Rem, 1974).

In 1965 while on a field trip to Agua Verde Bay in search of Johnston's *Cercidium molle*, I was told that a large *palo estribo* tree comparing favorably to that described by Johnston (1924b) had been cut down some twenty years

before. On a subsequent trip I explored the "huge amphitheater-like canyon" (Johnston, 1924b, p. 1056) south of the *puerto* of Agua Verde Bay and found only a few trees of *palo estribo*. Collections from one of these (*Carter 5610*) closely approach the type specimen of *C. molle* in its lack of spines, its pubescence, flower size, and leaflet size, but differ in the pinnae being shorter, and the leaflets more closely spaced than in the type. Considering the amount of variation occurring in $C. \times$ sonorae, however, *C. molle* falls well within the limits of that taxon. Had Johnston been able to explore further in the Sierra de la Giganta (instead of being limited to short sallies from aboard ship), he undoubtedly would have encountered trees of *palo estribo* similar to that which he described from across the Gulf near Guaymas as *C. sonorae* and would have realized the close affinity of the trees as they occur on both sides of the Gulf.

In his excellent discussion of *Cercidium* species in the "Vegetation of the Sonoran Desert" Shreve (1951, p. 145; 1964, p. 153) unfortunately confused *C. sonorae* with the much more abundant *C. praecox*. The description and distribution given under the heading "Cercidium sonorae" and the common name *brea* apply to *C. praecox*.

The strong, tough wood of *Cercidium* \times *sonorae* is used to make stirrups, hence the name, *palo estribo*.

4. Cercidium floridum Bentham ex Gray.

[Synonymy and references given under subspecies.]

Trees or shrubs 2.5-8.0 (-12) m. tall, bark of main branches above main trunk green, horizontally striate; leaves 1 or 2 per node, petiolate; pinnae 1 (occasionally 2) pair, bearing 2–4 pairs of leaflets; flowers yellow, the petals clawed, the claw of the upper petal longer than those of the other four petals; ovary glabrous at anthesis (occasionally a very few hairs present); legumes linear-oblong, flat, cuneate at base and apex, coriaceous, white-dotted (stomata) when immature, obscurely so when mature, inconspicuously reticulately-veined; seeds oblong to ovate, somewhat flattened, brown, the lighter margin sometimes slightly mottled.

4a. Cercidium floridum Bentham ex Gray subsp. floridum.

Cercidium floridum BENTHAM ex GRAY, 1852, Plantae Wrightianae, vol. 1, p. 58, subsp. floridum.

Parkinsonia florida WATSON, 1876, Proc. Amer. Acad., vol. 2, p. 135.

Parkinsonia torreyana WATSON, 1876, Proc. Amer. Acad., vol. 2, p. 135.

Cercidium torreyanum SARGENT, 1889, Garden & Forest, vol. 2, p. 388.

Tree 4-8 (-12) m. tall, the crown spreading, branchlets of mature trees usually slender, flexuous or drooping, the trunk gray-green; bark with fine horizontal striations, often dark in the indentations; branches glabrous or

sparingly pubescent; thorns absent or 1.8-5.4 mm. long (mean 3.6 mm.), slender, solitary; bud scales not accumulating at the nodes to form conspicuous dark clusters; foliage blue-green; leaves with petiole (1-) 2–5 (-11) mm. long bearing one pair of pinnae (occasionally more) 0.3-1.0 (-1.6) cm. long; leaflets mostly 3 pairs per pinnae, but often 2 and occasionally 4 pairs, oblong or obovate, sometimes emarginate, 4–8 mm. long, 2–5 mm. wide, slightly pubescent or glabrate; inflorescence open, glabrous or nearly so, borne on the younger branches; rachis of the racemes 1.0-4.5 (-7.0) cm. long, bearing 1-7 (-10) flowers on pedicels 6-12 (-20) mm. long; petals bright yellow, the upper sometimes orange-dotted near base of limb, the upper petal 9–15 mm. long, the limb 5–9 mm. long, 6-13 mm. wide, broadly ovate, cordate at base, the claw 3-5 mm. long, shorter than the limb, the other four petals slightly shorter than the upper, the limb broadly ovate, the claw short, 1.5-2.0 mm. long; legumes linear to elliptic, not or only slightly narrowed between the seeds, 3-11 cm. long, 1.0-1.5 cm. wide; seeds usually 3 per legume, 9-12 mm. long, 5-7 mm. wide.

TYPE. "Sonora Alta," Mexico in 1830, *Thomas Coulter* (Trinity College, Dublin, Ireland; also 2 duplicate specimens bearing name in Bentham's hand, K!)

The nomenclatural problem concerning *Cercidium floridum* and *C. torreyanum* is ably discussed by Johnston (1924a) and Benson (1940).

REPRESENTATIVE SPECIMENS. MEXICO. SINALOA: La Constancia, Munic. El Fuerte, December 1924 [sic! on original label at DS; US copied label is 1926], Jesus Gonzalez Ortega 6199 (DS, GH, MEXU, US); vicinity of San Blas, 22 March 1910, Rose, Standley & Russell 13203 (GH, US), 28 January 1927, M. E. Jones 23086 (RSA); SONORA: vicinity of Guaymas, 23 April 1910, Rose, Standley & Russell 15038 (US); plain N. of Empalme, 6 April 1962, Carter 4359; 20 mi. [32 km.] from Guaymas on Hermosillo road, 20 March 1934, Ferris 8752 (DS, US); 3.5 mi. [5.6 km.] (by road) N. of Desemboque, 29 April 1964, Turner & Hastings 64-49 (ARIZ, DS, SD); El Alamo, near Magdalena, 25 May 1925, P. B. Kennedy 7010a (UC, US); W. side of Isla Tiburón just N. of Punta Willard, 19 March 1962, Wiggins 17150 (DS); Isla Tiburón, 19 March 1962, Moran 8723 (RSA, SD), desértico espinosa, altitude 60 m., 3 May 1971, C. L. Diaz Luna 2266 (ENCB); Molina Crater, crater region NW. of Pinacate Crater, 29 April 1951, Kamb 2014 (ARIZ). [The sheets of this collection number at UC and DS are mixed collections, the branch bearing only flowers being a putative hybrid between Cercidium microphyllum and C. floridum.] Papago Tanks, Pinacate region, 15 March 1959, R. M. Turner 59-30 & C. H. Lowe 2979 (ARIZ, CAS); Pozo de Luis, 4 January 1894, Mearns 2696 [Int. Bound. Commission] (US). UNITED STATES. ARIZONA: Sabino Canyon, Santa Catalina Mountains, Pima Co., 25 May 1917, Shreve 5202 (ARIZ); vicinity of Coolidge Dam, 13 May 1935, Bassett Maguire 11321 (UC); Black Cañón Road, 23 mi. [37 km.] N. of Phoenix, Maricopa Co., 21 October 1931,

John W. Gillespie 8657 [2 sheets, one fl., one fr.] (DS, GH, UC, US); washes W. of Castle Dome Mts., Yuma Co., 22 April 1949, J. H. Thomas 396 (DS); Topock, Mohave Co., 24 May 1919, A. Eastwood 8886, 8887 (CAS, GH), 29 May 1950, J. T. Howell 26618 (ARIZ, CAS). CALIFORNIA: Whipple's Expl. R. R. route, 35th parallel, 1853-54, Bigelow (K); 20 mi. [32 km.] NE. of Ogilby, Imperial Co., 6 April 1932, Munz & Hitchcock 12166 (F, GH, MO, RSA, UC); Box Canyon at Shafer's Well, Chocolate Mts., Riverside Co., 14 June 1918, Ferris 977 (CAS, DS); 10 mi. [16 km.] W. of Coachella, Riverside Co., April 1905, H. M. Hall 5784 (ARIZ, UC, US); Palm Springs (Agua Caliente), desert base of San Jacinto Mt., Riverside Co., 4-13 April 1896, S. B. Parish 4115 (BM, GH, K, MO, US); 4 mi. [6 km.] NW. of Desert Center on Aqueduct Road, Riverside Co., 10 April 1947, P. A. Munz 11722 (ARIZ, RSA, SD); ca. 5 mi. [8 km.] E. of Clark Lake in Borrego unit of Anza State Park, San Diego Co., 21 April 1955, Guy Fleming 45817 (DS, SD); near Needles, San Bernardino Co., 3 June 1929, H. L. Mason 5362 (DS, UC); base of Whipple Mts. adjacent to Colorado R., 2 mi. [3.2 km.] above Earp on road to Parker Dam, 15 July 1940, Wolf 9723 (RSA).

Flowering from March to June with the peak in April and with occasional off-season blooming from August to November.

The blue *palo verde*, as it is called in Arizona, occurs principally in fine soil along washes and on flood plains, for the most part at altitudes below 1100 m. Its water requirements appear to be greater than those of *C. microphyllum*. It occurs in the Colorado Desert area of southeastern California, in southern Arizona from 35° N. near the Colorado River, southeast to ca. 33° N. on the eastern border of Arizona and southward through the coastal and middle portion of Sonora to $27^{\circ}30'$ N. Outlying collections have been made in coastal Sinaloa as far southward as 26° N. *Cercidium floridum* and *C. microphyllum* are the most widely distributed members of the genus within the Sonoran Desert, but *C. floridum* subsp. *floridum* is the only one restricted to the mainland. Although current floras indicate *C. floridum* subsp. *floridum* as occurring in Baja California, and Goldman (1916, p. 335) cites it as being there, no specimens have been seen which support such a distribution.

In most areas, the peak of the blooming season of *Cercidium floridum* is about two weeks in advance of that of *C. microphyllum*.

4b. Cercidium floridum Bentham ex Gray subsp. peninsulare (Rose) stat. nov. and comb. nov.

Cercidium peninsulare Rose, 1905, Contrib. U.S. Nat. Herb., vol. 8, p. 301.

Shrub or tree 2.5–8 m. tall, openly branched, but with a dense, symmetricallyrounded crown; bark gray and scaly-fissured at base, bright green above, inconspicuously horizontally striate; branchlets not flexuous, having pilose or

sparse, appressed-villous hairs when young, glabrate to glabrous in age; a single axillary thorn usually present at a node, 2-3 (-7) mm. long (mean 3.87 mm.), slender to stout; axillary bud scales, when present, not dark and conspicuous; leaves with petiole 1-4 (-10) mm. long bearing 1 (rarely 2) pair of pinnae 0.3-1.7 (-2.1) cm. long, the leaflets mostly 2 pairs per pinna but many (25 percent) with 3 pairs, obovate and sometimes emarginate, 6-11 (-18) mm. long, 3-7 mm. broad, sparingly pilose to glabrate; inflorescences borne on old wood as well as on younger branchlets, more or less compact, the racemes with rachis sometimes almost absent, but usually 3-10 (-20) mm. long, pubescent, bearing 3-5 flowers on pubescent pedicels 4-9 (-12) mm. long; calyx sparingly pubescent to glabrous; petals deep or bright yellow, the upper 7.5-9.0 mm. long, the limb 5-7 mm. long, 5.0-6.5 mm. wide, ovate or rhombic ovate, the claw 2 mm. long, the other four petals slightly shorter to subequal to the upper, limb ovate, the claw short, 1.5-2.0 mm. long; legumes 1.5-5.5 cm. long, 8-15 mm. wide, flat, the margins slightly constricted between the seeds, seeds 1-2 (3) per legume, 9-10 mm. long, 6-7 mm. wide.

TYPE. La Paz, Lower California, Mexico, in 1890, Palmer 112 (US!).

REPRESENTATIVE SPECIMENS. MEXICO. ISLANDS, BAJA CALIFORNIA SUR: arroyo leading eastward from old Ruffo Ranch, Isla Ceralvo, 16 April 1962, Wiggins 17758 (DS, ENCB); Arroyo de Agueda, NE. side of San José Is., 11 April 1962, Moran 9402 (CAS, RSA, SD); arroyo above Ensenada Ballena, Espíritu Santo Is., 21 April 1962, Moran 9634 (SD, US); S. end of Santa Cruz Is., 18 April 1962, Moran 9577 (SD, UC); arroyo above spring, Santa Catalina Is., 14 April 1952, Moran 3866 (DS), 10 April 1962, Moran 9369 (SD); Puerto Ballandra [Balandra], Carmen Is., 21 May 1921, Johnston 3802 (CAS, DS, GH, K, UC, US); 4 June 1963, Carter & Reese 4546. PENINSULA, BAJA CALIFORNIA SUR: San José del Cabo, March-June 1897, A. W. Anthony 363 (F, GH, K, UC, US); Arroyo San Lázaro, ca. 10 mi. [16 km.] NW. of San José del Cabo, 2 May 1959, Thomas 7775 (ARIZ, CAS, DS, SD, UC, US); Arroyo del Salto, E. of La Paz, 30 March 1949, Carter 2595 (DS, UC); La Paz, 16 April 1899, E. A. Goldman 388 (GH, US! Type); Arroyo San Ramón W. of Rancho San Ramón (25°14.5'N., 111°17'W.), 25 October 1964, Carter 4866; vicinity of Puerto Agua Verde, 4 June 1965, Carter & Sharsmith 4943; arroyo S. of Bahía Agua Verde, 5 June 1965, Carter & Sharsmith 4946; Arroyo Peloteado, W. of Rancho Peloteado (25°45'N., 111°30'W.), 21 April 1962, Carter 4410; San Javier, 21 April 1962, Carter 4414; Rancho Viejo, ca. 28 km. from Loreto on road to San Javier, 6 May 1972, Carter 5680; Rancho Quiñí, on old mission trail SE. of Comondú, 20 April 1955, Carter & Ferris 3423 (DS, MEXU, SD, UC, US); alluvial arroyo margin, Las Cuevitas below Comondú, 12 April 1939, Gentry 4458 (ARIZ, GH, K, MO, UC, US); Valle de Los Encinos, S. side of Cerro Giganta, altitude 750 m., 8 November 1960, Carter 4134, 8 June 1963, Carter &



FIGURE 6. Bark patterns in *Cercidium*: a, b, *C. praecox* showing the quadrate-pustulate surface typical of this species, a, ca. $\times 1\frac{1}{2}$, b, ca. $\times 10$; c, *C. floridum* subsp. *floridum* showing the horizontally striate pattern characteristic of this species and of *C. microphyllum*.

Reese 4573; coastal strand, San Bruno (26°12.5'N., 111°23'W.), 1 June 1963, Carter & Reese 4537; Arroyo Mulegé, ca. 10 mi. [16 km.] W. of town on road to El Potrero, 11 April 1963, Wiggins 18231 (CAS, DS, K, MEXU, US); Picachos de Santa Clara, Desierto Viscaíno, 5–10 November 1947, Gentry 7754 (DS); wash 16 mi. [26 km.] from San Ignacio on Calmallí road, 10 March 1934, Ferris 9037 (DS, US).

Flowering is from March to June with the peak in April, the branches usually bearing leaves at the same time. The flowering period precedes that of its congeners in the same area.

It grows on coastal plains and along washes and canyons into mountain valleys from sea level up to 750 m. This tree, known locally as *palo verde* is the only taxon in *Cercidium* restricted to Baja California, where it is moderately common from near the tip of the peninsula northward to San Ignacio $(27^{\circ}25'N., 112^{\circ}52'W.)$. As noted by Gentry on one of his collections (4458), this tree has a denser, leafier, more symmetrical crown than any other members of the genus. Also, it retains its leaves for a greater portion of the year than any of the others. The upper petal of *C. floridum* subsp. *peninsulare* is not as conspicuously elevated above the other four petals as it is in the other taxa.

DISCUSSION

In an attempt to understand the relationships between the Sonoran Desert taxa of *Cercidium* as set forth above, the following characters were of use and merit some discussion.

BARK. Inasmuch as most cercidiums retain only a few leaves during much of the year, or have minute leaves, photosynthesis also occurs in the green bark which is relatively smooth except for the lower trunks of large trees. In C.

praecox, the bark is bright green clear to the ground, whereas in the others the main trunk becomes grayish and often fissured. The bark of C. praecox differs also in having a minute quadrate-pustulate surface pattern (fig. 6a,b), easily visible with a hand lens or even to the naked eye, and in being conspicuously coated with a waxy substance. Shreve (1951, p. 145; 1964, p. 153) mentioned these characteristics, but he attributed them to $C. \times$ sonorae which he at that time mistook for C. praecox. The bark of C. microphyllum and C. floridum, on the other hand, is finely horizontally striate (fig. 6c) and, especially in C. floridum subsp. floridum, often dark in the indentations, thus giving a 'dirty-neck' appearance. These striations are less conspicuous in C. floridum subsp. peninsulare. The bark of $C. \times$ sonorae is usually smooth, but sometimes horizontal striations are visible with a hand lens. On some specimens of $C. \times$ sonorae there is a thin, inconspicuous layer of waxy material which suggests C. praecox.

PUBESCENCE. Young branchlets of *Cercidium* show varying degrees of pubescence; older branchlets are glabrous to glabrate. In *C. floridum* subsp. *floridum*, branchlets are essentially glabrous, but sometimes with a few hairs, especially southward in its range. In *C. floridum* subsp. *peninsulare*, on the other hand, the young branchlets are conspicuously pubescent with pilose or sparsely appressed villous hairs. In *C. microphyllum* there is some correlation between geographic distribution and type of pubescence on the stems: all of the Baja California material is strongly strigose; the Sonoran collections studied are puberulent or pilose (especially in the interior); in Arizona and California some collections have glabrate branchlets. Branchlets of *C. praecox* vary from glabrate to pubescent. In *C. × sonorae* the branchlets may be strigose, short villous, or pilose, or occasionally the branchlets are glabrous.

The pubescence of the ovary at anthesis is of diagnostic value. In both subspecies of C. *floridum* and in C. *praecox* the ovary is glabrous; in C. *micro-phyllum* and $C. \times sonorae$ it is lightly pubescent to strigose at anthesis.

ARMATURE AND BRANCHING PATTERN. Most treatments of *Cercidium* refer to the thorns as "nodal" or "stipular," but Kearney and Peebles (1960, p. 407) describe them as "rudimentary branches transformed into spines." This concept (except for the use of the term "spine" instead of "thorn") is in accordance with Blaser's (1956) definition, which is followed herein, of a thorn being a reduced determinate shoot. Leaves of seedling plants and of young seasonal growth of *Cercidium* bear a pair of inconspicuous, slender, foliaceous stipules; these do not form spines, but are fugaceous. Thorns, when present, are the first shoots to develop in a primary (first to develop at a node) leaf axil. Their shoot nature is clearly shown in the early stages by the presence of a cluster of rudimentary leaves at the distal end of the developing thorn (fig. 7c). These soon disappear as the thorn increases in size and hardens (fig. 7d). Subsequent growth at a node results in either inflorescence, leaf, or shoot development from buds on an



FIGURE 7. Developmental stages in leaves and thorns of *Cercidium*. a, three week's old seedling of *C. praecox* showing simply pinnate basal leaves and bipinnate upper leaves (Turner); b, five week's old seedling of *C. microphyllum* with petiolate primary leaves $(Carter \& Reese 4531), \times 2$; c, young branch of *C. praecox* showing immature axillary thorns bearing rudimentary leaves at apex (*Carter, Hastings, & Turner 5597*); d, more mature thorn of *C. praecox* after rudimentary leaves have fallen (*Carter, Hastings, & Turner 5597*).

extremely shortened stem in the axil of the primary leaf. However, the positional relationship of the thorn primordia to the shoot, leaf, and flower primordia cannot be determined without more extensive morphological investigation.

In Cercidium microphyllum, none of the buds in a primary leaf axil develop



FIGURE 8. Branching patterns in *Cercidium*, based on number and length of branchlets in the terminal 25 cm. of a stem.

into a short leafless thorn; rather, at the majority of nodes one bud develops into the stout, determinate, leafy branch, spinescent at the tip, which is so characteristic of this species. *Cercidium praecox* is consistently the thorniest of the Sonoran Desert members of the genus inasmuch as at each node one, and occasionally two, axillary buds develop into thorns. When two thorns occur at a node, one is always larger. In *C. floridum* subsp. *floridum*, comparatively few axillary buds develop,—the resulting mature tree having long, slender branchlets, a less divaricately branched appearance, and fewer thorns (especially in the northern part of its range) than do most other species. However, Shreve (1951, p. 142; 1964, p. 150) states that young trees of *C. floridum* less than 2 m. in height have very thorny twigs. *Cercidium floridum* subsp. *peninsulare* and *C.* × *sonorae* are variable in the number of axillary buds which develop into thorns. In many instances, *C.* × *sonorae* is thornless.

Cercidium microphyllum, which, as noted above, has no axillary thorns but bears only spine-tipped, determinate branchlets, has the greatest number of branchlets (mean, 8) in the terminal 25 cm. of a branch, whereas C. praecox, the thorniest of the species, has the fewest branchlets (fig. 8). In C. microphyllum, there is usually a gradual reduction in length of the branchlets toward the distal end of the branch in contrast to the other taxa where reduction in branchlet length often shows no correlation with position on a stem segment. Cercidium \times sonorae has an intermediate number of branchlets in comparison with its putative parents and the branchlets are longer and more flexuous than those of either parent. The average number of branchlets developing in the terminal 25 cm. of the branches of the two subspecies of C. floridum is rather

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close: 5.4 branchlets in C. floridum subsp. floridum and 6.1 branchlets in C. floridum subsp. peninsulare, but the mean length of the branchlets diverges significantly. The flexuous branchlets of C. floridum subsp. floridum have a mean length of 13.3 cm. and the stouter and stiffer branches of C. floridum subsp. peninsulare have a mean length of 9.3 cm. (fig. 8). These means for number and length of branchlets help to indicate their relationship within the group, but in all cases, the range of these measurements within each species and the overlap with other species, is too great for use of the characters in keys.

LEAVES. The seedlings of all Sonoran Desert taxa of Cercidium have conspicuous cotyledons, 23 to 25 mm. long in C. floridum and 6 to 18 mm. long in the others. In the seedlings, each of the first few nodes (usually up to five) bears a pinnate leaf with several pairs of large leaflets; following these, the bipinnate leaves more typical of each of the various taxa develop (figs. 3, 7a). The inconspicuous, foliaceous stipules are caducous. The pinnae (i.e., the secondary rachises with their leaflets) are short (0.3 to 6.5 cm. long) and the leaflets are opposite. A small, foliaceous or semi-indurate bract is borne at the apex of the leaf rachis and at the apex of each of the pinnae. Because of the need to discuss them separately, the first leaf developing at a node is herein designated as a 'primary' leaf and those developing subsequently in the axil as 'axillary' leaves. Buds produced in the axil of the primary leaf may develop into a thorn (a short determinate shoot), or into foliaceous or floral shoots. The foliaceous shoots are usually so reduced that the leaves borne on them appear to arise directly in the axil of the primary leaf or leaf scar; one to eight such leaves may be present at a time. Leaves are deciduous in most taxa, usually falling before the blooming period or with periods of drought.

Leaves of *Cercidium microphyllum* differ from those of the other taxa in being non-petiolate, except in the seedling stages wherein the primary leaf may have a slightly winged petiole from 1 to 4 mm. long which merges inconspicuously with the broadened rachis area where the pair of pinnae arises. In later stages, the primary leaf pinnae are borne on an indurate, scale-like structure, the basal portion of which usually is not distinguishable from the rachis as a petiole. The indurate terminal bract is also indistinguishable from the rachis. The two pinnae fall separately from this scale-like rachis and it remains on the branch for some time before falling and exposing the primary leaf scar. (Sometimes in *C. microphyllum*, the leaflets fall before the pinnae do.) In the other species of *Cercidium* the entire leaf abscisses at the base of the petiole. (Occasionally in *C. floridum* subsp. *floridum* the pinnae fall from the apex of the petiole, or from the rachis if the leaf bears two pairs of pinnae, and the petiole, or petiole and rachis remain on the stem for a short time.) In specimens of *C. × sonorae* with subsessile leaves, the shortened petiole and the rachis become somewhat indurate,



FIGURE 9. Comparison of length of petioles and pinnae in Cercidium floridum subsp. floridum and C. floridum subsp. peninsulare.

but they fall with the rest of the leaf instead of being tardily dehiscent as in C. microphyllum. In C. praecox and C. \times sonorae, the scar of the primary leaf is conspicuous on younger branches; in C. floridum subsp. floridum it is inconspicuous. In C. floridum subsp. peninsulare, the scar of the primary leaf is often obscured by a cluster of reddish-brown glandular hairs in the axil.

In Cercidium praecox and C. floridum the bract at the apex of the rachis tends to be linear and foliaceous rather than indurate. In specimens of $C. \times$ sonorae with petiolate leaves, the elongate apex of the rachis is usually slightly indurate, while in those having subsessile leaves the rachis is an indurate, long-tipped scale similar to that of C. microphyllum.

Cercidium floridum leaves have pinnae usually less than 1 cm. long and

mostly bearing 2 to 4 pairs of leaflets, whereas the other three taxa (*C. micro-phyllum*, *C. praecox*, and *C.* \times *sonorae*) have pinnae up to 6.5 cm. long bearing 4 to 9 pairs of leaflets. At a significance level of 1 percent the means for both characters differ between members of the two groups.

As indicated by the graphs (figs. 9, 10), the two subspecies of *C. floridum* are similar in characters of petiole length, pinna length, and leaflet number. Each subspecies exhibits its greatest variability in length of pinnae. Mean length, however, is about the same for the two (7.8 mm. for *C. floridum* subsp. *floridum*, 7.9 mm. for *C. floridum* subsp. *peninsulare*) and the difference between the means is not statistically significant. At a 1 percent significance level the only leaf difference is the mean number of leaflet pairs. In the primary as well as axillary leaves, *C. floridum* subsp. *floridum* usually has 3 pairs (mode 3, mean 2.7) and *C. floridum* subsp. *peninsulare*, usually either 2 or 3 pairs (mode 2, mean 2.5). In all of these structures, the measurements show too much overlap to make them principal key characters. That these characters differ in degree rather than in kind supports the subspecific disposition of *C. floridum peninsulare*.

Among the other three taxa, petiole length is useful in recognizing entities: the leaves of *C. microphyllum* are non-petiolate, i.e., the pinnae are sessile (except in seedling stages); the leaves of *C. praecox* always have conspicuous petioles; those of *C. × sonorae* vary from no petioles up to petioles 12 mm. long (fig. 11). The mean petiole length for each taxon differs significantly (P = 0.99) from that of the other two. As with *C. floridum* the pinnae in each species exhibit great variability in length, but the means, although clustered, are not so close (table 1). At a 1 percent significance level the only difference occurs between those for *C. × sonorae* and *C. praecox*. As to the leaflet number, the members of this group overlap considerably and show no significant difference in mean number of pairs. Both in this character and in petiole length the mean for *C. × sonorae* is intermediate between that for *C. microphyllum* and *C. praecox*. In pinna length, however, the mean for *C. × sonorae* exceeds that of the other two taxa; but its value is close to the mean for *C. microphyllum*, and the two values do not differ significantly.

As suggested by the common name for *Cercidium floridum*, blue *palo verde*, leaf color has been utilized in identification, but because interpretations of color differ so markedly, no attempt has been made to include precise shades of green in the detailed descriptions. The following field observations, however, point up the foliage color differences in the taxa of *Cercidium* as they occur in Sonora (correspondence: Hastings to Carter, August 10, 1971).

"I made a trip to Sonora again week before last and the summer rains have wrought their usual alchemy there. The parched country we saw in April is green and incredibly lush. Also incredibly muggy, buggy and mudriy.

				C. Ju	ridum
Character	C. microphyllum	C. praecox	C. × sonorae	subsp. floridum	subsp. peninsulare
Petiole (length, mm.) Mean	00	$ \begin{array}{cccc} (1-) & 4-11 & (-21) \\ 7.6 \end{array} $	0–3 (–12) 2.0	$(1-) \begin{array}{c} 2-5 \\ 3.8 \end{array}$	$1-4 \ (-10)$ 3.13
Pinnae (length, mm.) Mean	3–65 19.7	4–45 16.7	7–50 20.3	3–16 7.8	3-17 (-21) 7.9
Leaflets, number of pairs Mean	1-7 (-13) 6.4	(3-) 5-9 $(-17)6.5$	(3-) 6-8 $(-12)6.4$	2-4 2.75	2-4 2.5
Leaflets (length, mm.) Mean	0.5-5.0 2.0	3-10 5.9	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	3–8 4.9	(3-) 6-11 (-18) 7.1
Inflorescence (pedicels) Total pedicel length (mm.)	4-8 (-15)	7–10	6-10 (-14)	6-12 (-20)	4-9 (-12)
Mean Length from calvx to	0.9	8.1	8.0	10	5.9
pedicel joint (mean) Ratio-total pedicel	1.5	2.3	2.0	2.9	1.9
length: length from pedicel joint to calyx	4.3:1	3.8:1	4.2:1	3.6:1	3.5:1
Thorns (length, mm.) Mean	00	2–18 (–25) 8.6	(2-) 5-11 (-20) 6.5	1.8–5.4 3.6	2–3 (–7) 3.9

TABLE 1. Comparison of selected characters in Sonoran Desert taxa of Cercidium

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FIGURE 10. Comparison of number of pairs of leaflets in *Cercidium floridum* subsp. *floridum* and *C. floridum* subsp. *peninsulare*.

"All four palo verdes were in full leaf and seeing them that way did a good bit to restore my ego. Not only is it possible easily to tell *Cercidium floridum* from *C. microphyllum*, [but also] *C. praecox* and *C.* \times sonorae can be distinguished at a glance. *Cercidium praecox* shows up as blue—even bluer than *C. floridum*. *C.* \times sonorae, on the other hand, is relatively yellow—not the nearly chlorotic yellow of *C. microphyllum*, but about the color of the stems on both *C.* \times sonorae and *C. praecox.*"

INFLORESCENCE. In all of the Sonoran Desert taxa of *Cercidium*, except *C. floridum* subsp. *peninsulare*, when both flowers and leaves are present concurrently, the inflorescences exceed the leaves in length. In *C. microphyllum*, *C. praecox*, and *C.* \times *sonorae*, the inflorescences normally develop before the leaves; if leaves are present, they are usually on separate branches. In *C. floridum* subsp. *floridum*, flowering precedes leafing on about 30 percent of the collections studied. In *C. floridum* subsp. *peninsulare*, where both flowers and leaves are usually present on a given branch, the inflorescences are equal or subequal to the leaves; occasionally, flowering precedes leafing.

The flowers are borne in compact or open racemes, which may be either single or fascicled at the nodes. For the most part, the inflorescences are borne in profusion on the terminal branchlets, but *C. praecox* departs strongly from this pattern in having its usually compact inflorescences strongly fascicled along the stems, none of which are as branched as in the other taxa. Shreve (1951, p. 145; 1964, p. 153) pointed out this striking characteristic of *C. praecox*, but here again, he mistakenly attributed it to *C.* × sonorae. In *C. floridum* subsp.



FIGURE 11. Comparison of number of pairs of leaflets and length of petiole in Cercidium microphyllum, $C. \times$ sonorae and C. praecox.

peninsulare, some racemes are borne on older branches; therefore the trees do not have the strong terminal flowering aspect of *C. floridum* subsp. *floridum*.

Inflorescence rachis length varies both within the taxa and between them. In C. floridum subsp. floridum the rachises vary from 1.0 to 4.5 cm., while in C. floridum subsp. peninsulare they are usually 0.3 to 1.0 cm., but occasionally up to 2 cm. In C. microphyllum they are 0.2 to 4.5 cm. long, while in C. praecox they are 0.2 to 1.0 cm. long. Those of $C. \times$ sonorae (0.5-4.0 cm.) fall between those of C. microphyllum and C. praecox.



FIGURE 12. Flowers of *Cercidium*: a, front view showing larger, elevated upper (posterior) petal ($C. \times$ sonorae, Carter 4411); b, back view (C. floridum subsp. peninsulare, Carter 4410); c, side view showing elevated upper petal bearing cinnamon-colored spots (C. praecox, Carter 4412). Numbers refer to Carter and/or Carter et al. collections; data for these are given under "Representative collections cited" for the respective taxa.

The pedicel is jointed, with the joint in the distal half. The distance between joint and calyx varies less than that between joint and rachis. In total length of the pedicel, as in rachis length, *C. floridum* subsp. *floridum* and *C. floridum* subsp. *peninsulare* fall at opposite ends of the spectrum for the five taxa. Their respective means, 10.0 mm. and 5.9 mm., differ significantly at P = 0.99. So do



FIGURE 13. Comparison of petal shape and size in *Cercidium*: a, *C. microphyllum* (*Carter 5683*); b, *C.* \times *sonorae* (*Carter 5679*); c, *C. praecox* (*Carter 5678*); d, *C. floridum* subsp. *floridum* (*Turner*, Arizona, pickled material); e, *C. floridum* subsp. *peninsulare* (*Carter 5680*). Numbers refer to Carter and/or Carter *et al.* collections; data for these are given under "Representative collections cited" for the respective taxa.

the means for *C. microphyllum* (6.0 mm.) and *C. praecox* (8.1 mm.). The average pedicel length for $C. \times sonorae$ (8.0 mm.) falls between those of its putative parents, but does not differ significantly from that of *C. praecox* (table 1).

As for the caesalpinoid flowers (figs. 12, 13), there is size variation within each taxon, but the flowers of *C. floridum* subsp. *floridum* are the largest in the group and those of *C. microphyllum* and *C. floridum* subsp. *peninsulare* are the smallest. Flowers of *C. microphyllum* differ also in having the limb of the longclawed upper petal white, or occasionally cream or pale yellow and the other four petals rhomboidal or lanceolate rather than broadly ovate (figs. 12, 13). The upper, long-clawed petal of *C. praecox* nearly always bears a cluster of small orange dots near the base of the limb; these are also often present in *C. floridum* subsp. *floridum*, but they are lacking in *C. floridum* subsp. *peninsulare*. The upper petal of *C. × sonorae* is extremely variable. It may be white, creamy, or light yellow, and it may or may not bear orange dots.

The tricolpate pollen grains, which vary in diameter from 18 to 34 microns, are prolate spheroidal and supra-reticulate (Carter and Rem, 1974). The lumina are reduced in diameter and depth near the margin of the furrows.

LEGUMES AND SEEDS. The venation of the valves of *Cercidium* legumes is of diagnostic value: the valves of *C. praecox* are somewhat papery with conspicuous reticulate venation; those of *C. microphyllum* and *C. \times sonorae* are striate—especially noticeable in the latter; and those of *C. floridum* are smooth with veins scarcely visible to the naked eye. The surface of the valves of immature legumes of *C. floridum* bear conspicuous white-dotted areas. These are stomatal pores; apparently the young fruits as well as the bark carry on photosynthesis at a time when the trees are nearly leafless. Stomata are present also in the legumes of the other taxa, but they are somewhat obscured by the prominent venation.

Although Brenan (1963, p. 207, table) used the upper suture of the pod as a distinguishing character, this is more variable within our Sonoran Desert taxa than he indicated. The legumes are tardily dehiscent along the sutures or indehiscent; in *Cercidium microphyllum* and $C. \times$ sonorae the thin-walled valves also sometimes break irregularly. Differences in shape and size of legumes and seeds may be compared in figure 3. In characters of legume venation and shape, $C. \times$ sonorae approaches C. microphyllum more closely than it does C. praecox.

As to surface pattern, seeds of C. praecox and $C. \times$ sonorae are gray-brown with various degrees of brown mottling on the flat surfaces; seeds of C. microphyllum and C. floridum are brown with the marginal area somewhat lighter and sometimes faintly mottled. In all of the taxa the hilum and micropyle are subterminal; in some species they are in a slightly recessed or notched area



(Seed coat // Endosperm & Cotyledons

FIGURE 14. Comparison of seeds (cross section and position of hilum and micropyle) in *Cercidium* and *Parkinsonia*: CEFL, *C. floridum* subsp. *floridum*, a, side view to indicate position of cross section (b) to entire seed (*E. E. Schellenger 6*, Chucawalla [Chuckawalla] Bench, Colorado Desert, California, 25 July-14 August, 1903, UC); CESO, *C. × sonorae*, note variation in form of cotyledons (*Carter & Sousa 5212*); CEPR, *C. praecox (Carter 4146*); CEMI, *C. microphyllum*, note thick cotyledons (*Ferris 9902*); CEPE, *C. floridum* subsp. *peninsulare (Carter 4821)*; PAAC, *Parkinsonia aculeata (Harbison & Higgins*, San Telmo, Baja California, 17 December 1953, UC); PAAF, *Parkinsonia africana (Rodin 2156*, Namib Desert near Swakop River, Southwest Africa, 31 October 1947, UC). Diagrams drawn after seeds had soaked in water overnight. Seeds, $\times 2\frac{1}{2}$, side view of apex, $\times 1\frac{1}{2}$.

(fig. 14). As seen in cross section, the thick, oblong or subglobose seeds of C. microphyllum are distinct in having large cotyledons in comparison to the amount of endosperm (fig. 14). The other taxa, with more flattened and oblong or oblong-ovate seeds, follow much the same pattern in cross-section (fig. 14) as that illustrated by Boelcke (1946) for C. australe Johnston, the Argentinian species closely related to C. praecox.

CHROMOSOME NUMBERS. Chromosome counts of 2n = 28 have been reported for *Cercidium floridum*, *C. microphyllum* and *C.* × *sonorae* (Turner and Fearing, 1960). Although contraindicated in the publication, no voucher was preserved for the $C. \times$ sonorae count (correspondence, B. L. Turner to Carter, 5 July 1972). It is probable, however, that the seeds provided for this count were those of C. *praecox* rather than of $C. \times$ sonorae (correspondence, R. M. Turner to Carter, 23 June and 18 August, 1972).

HYBRIDIZATION. Few putative hybrids between Cercidium microphyllum and C. floridum subsp. floridum have been noted, whereas $C. \times$ sonorae, which occurs in the area of overlap of C. microphyllum and C. praecox, is relatively abundant. A six-year record kept by W. G. McGinnies for trees in the foothills north of Tucson, Arizona, shows that C. floridum subsp. floridum blooms about two weeks earlier than C. microphyllum and C. praecox (the latter being a cultivated tree in that area). So, although there is some overlapping of the blooming period of C. floridum subsp. floridum and C. microphyllum in the Tucson area at least, the peak is reached at different times (correspondence, Hastings to Carter, 24 January 1972); no putative hybrids have been reported from this area. On the other hand, in the lower Colorado River basin between Arizona and Colorado, these two species do reach peak of bloom at approximately the same time and a small percentage of putative hybrids has been noted (pers. comm., Jones to Carter, September 1973). Ultraviolet light studies show that the flowers of these two species appear different to pollinating insects: C. microphyllum petals absorb UV light and all are "bee purple," while in C. floridum subsp. floridum only the upper petal absorbs UV light and the other four reflect it. The pollinators appear to be highly selective in accordance with these ultraviolet patterns (pers. comm., C. E. Jones to Carter, September 1973). In the case of $C. \times$ sonorae, on the other hand, whose putative parents, C. microphyllum and C. praecox, bloom concurrently and have the same ultraviolet absorption patterns as the above mentioned taxa (Carter, 1974), it appears that their pollinators are not selective in their visits inasmuch as there is apparently ample cross-pollination. No putative hybrids have been noted between C. floridum subsp. peninsulare and the other three taxa occurring with it in southern Baja California. Normally this species blooms before its congeners; its ultraviolet absorption pattern is the same as that of C. floridum subsp. floridum and of C. praecox, i.e., the upper petal absorbs and the other four reflect ultraviolet light.

RELATIONSHIP BETWEEN CERCIDIUM AND PARKINSONIA. As indicated in the key at the beginning of this treatment, a number of characters serve to distinguish members of the New World genus Cercidium from Parkinsonia aculeata Linnaeus, the only member of the latter genus considered to be native to the western hemisphere. Treatments of these two genera fail to clarify the structure of the primary leaf and its relationship to thorns or spines; many floras merely state "stems armed" or "stems unarmed." As detailed above, armature in Cercidium, when present, consists of thorns which develop in the axil of a primary leaf.

In Parkinsonia aculeata, on the other hand, there are no axillary thorns. The conspicuous armature consists of the short petiole and rachis of the primary leaf itself, which has become enlarged, thickened and indurate, plus the tip of the rachis which has developed into a long, stout, sharp spine. Hutchinson (1969, pp. 70–71, fig. 64E), misinterpreted this structure, calling it a stipule. Also, he failed to differentiate between primary and axillary leaves. The stipules are either early deciduous or develop into short, indurate lateral spines, which, however, may fall long before the indurate petiole and rachis. One to three pairs of long (10 to 60 cm.) pinnae are produced on the short leaf rachis. In both primary and axillary leaves the secondary rachises are conspicuously flattened (phyllodial). In her anatomical comparison of Parkinsonia aculeata and Cercidium torreyanum (C. floridum), Scott (1935) found that only in the rachises of the pinnae and in the pulvinae is there a marked difference between these two taxa. She did not include armature in her studies. The small, caducous leaflets borne along the margins of the pinna rachis may be either opposite or alternate on the same pinna. The long phyllodial pinnae usually remain until the onset of winter and lend the trees a graceful, drooping aspect. When pinnae of the primary leaves fall, the indurate, spinose-tipped petiole and rachis remain on the branch. On older branches, this structure (spine) also eventually falls, leaving a conspicuous scar at the node. Burkart (1952, fig. 36) illustrates the spinose nature of the leaf rachis. He does not point out, however, that these stout spines are restricted to the first leaf at a node of a main branch and are only slightly, if at all, developed on leaves of the usually short axillary branches which are from 2 to 12 (-23) mm. long in contrast to the completely reduced axillary shoots in Cercidium.

Until the recent work of J. P. M. Brenan (1963), only one other taxon has currently been considered as belonging to the genus Parkinsonia, the African species P. africana Sonder. The primary leaf of P. africana is similar in some respects to that of Cercidium microphyllum. In Parkinsonia africana a single pair (occasionally one of the pair aborts) of pinnae 4 to 17 cm. long arises from a small, bractlike, nearly sessile leaf rachis which has a short, slender, foliaceous tip; stipules are inconspicuous, caducous, bractlike structures; the pinnae are not flattened, but are elliptical in cross section and bear tiny opposite, caducous leaflets, as is the case in the axillary leaves. Troll (1939; p. 1611, fig. 1372; p. 1612, fig. 1373), considers these leaves to be a reduced form of the typical caesalpinoid leaf which is petiolate and bears several pairs of pinnae. Armature, when present, is a short, stout, determinate stem (thorn) in the axil of the primary leaf. Johnston (1924a, p. 63) erred by indicating in his key to Cercidium and Parkinsonia that both P. aculeata and P. africana have similar armature. Presence or absence of these axillary thorns is extremely variable in P. africana, as it is also in some taxa of Cercidium. In all of these characters except the

somewhat longer pinnae with leaflets caducous, *Parkinsonia africana* resembles *Cercidium microphyllum* more than it does *Parkinsonia aculeata*. Torrey (1859, p. 60) reached a similar conclusion.

The inconspicuous, bractlike rachis of the primary leaf in both *Cercidium* microphyllum and Parkinsonia africana might well be considered a rudimentary expression of the highly developed spine of the primary leaf of Parkinsonia aculeata. So, in this character, *Cercidium microphyllum* tends to resemble Parkinsonia more closely than it does its congeners with petiolate leaves (both primary and axillary) which fall entire. However, in the short pinnae which are not flattened and in the opposite leaflets which usually are not caducous, it falls within *Cercidium*.

It has not been possible to make careful examination of the other African trees placed in *Parkinsonia* by Brenan: *P. anacantha* Brenan and *P. scioana* (Chiovenda) Brenan [*Peltophoropsis scioana* Chiovenda]; so comparisons cannot be made regarding the structure of the primary leaves (matters which are not adequately treated in the descriptions of these two taxa).

There is a significant difference in pedicel length (P = .99) between *Parkinsonia aculeata* and *P. africana*, on the one hand, and the species of *Cercidium* studied, on the other. The mean pedicel length for the taxa of *Cercidium* ranges from 5.9 to 10.0 mm., with the ratio of total pedicel length to length from pedicel joint to calyx ranging from 3.5:1 to 4.3:1. In *Parkinsonia aculeata* the mean length is 14.5 mm.; the ratio, 6.4:1. In *P. africana* the mean pedicel length is 13.0 mm., not significantly different from that of *P. aculeata*. But the ratio is only 2.4:1, i.e., the joint occurs almost at the midpoint of the pedicel, whereas in *P. aculeata* it is relatively close to the calyx. In *Cercidium*, the joint is in the distal half of the pedicel, but never proportionately so close to the calyx as in *Parkinsonia aculeata*. Material was not available to carry the comparison to the other African taxa placed in *Parkinsonia*.

Pollen studies in relation to hybridization in *Cercidium* and *Parkinsonia* have shown that putative hybrids between taxa in *Cercidium* have a much higher percent of presumably viable pollen (as indicated by staining with aniline-blue lactophenol) than do the few known hybrids between *Parkinsonia aculeata* and species of *Cercidium* (Carter and Rem, 1974). In addition, pollen grains of putative hybrids between species of *Cercidium* are not malformed whereas those of putative hybrids between *Parkinsonia aculeata* and species of *Cercidium* are irregular in shape (Carter and Rem, 1974, fig. 1). No putative hybrids between *C. microphyllum* and *Parkinsonia aculeata* have been noted even though these two taxa sometimes occur in the same area.

As seen under the scanning electron microscope, pollen grains of the several species of *Cercidium* studied and those of *Parkinsonia aculeata* have similar





FIGURE 15. Pollen as seen under scanning electron microscope: a, Cercidium floridum subsp. peninsulare (Carter 2595); b, Parkinsonia africana (Seydel 1230, Namibrand: Karibib, Okomitundu, Southwest Africa, UC); c, Parkinsonia [Peltophoropsis] scioana (Burger 2731, Erer Rarea, 60 km. west of Dire Dawa, Ethiopia, 9°31'N., 41°25'E., 21 April 1963, K). All ca. × 1000. Photographs taken at Electronics Research Laboratory, University of California, Berkeley.

supra-reticulate sculpturing (Martin and Drew, 1969, 1970; Carter and Rem, 1974). Pollen of *Parkinsonia africana* (fig. 15), on the other hand, although being reticulately sculptured, has many shallow lumina as well as the deep lumina characteristic of *Cercidium* and *Parkinsonia aculeata*. Furthermore, in *P. africana* the lumina are much smaller and the muri thicker than in the abovementioned taxa. Pollen of *Parkinsonia* [*Peltophoropsis*] scioana (fig. 15) is triporate with three large pores; its sculpturing differs markedly in that the reticulate surface appears rugose and the lumina are small and the muri wide. Unfortunately, the material of *P. anacantha* available contained insufficient pollen for a scanning electron microscope preparation or for satisfactory light microscope examination.

The legumes of Cercidium microphyllum resemble those of Parkinsonia aculeata more than they do those of other species of Cercidium. They are thinwalled and strongly torulose, i.e., much constricted on either side of the 1 to 4 seeds; dehiscence is irregular, as well as occurring along the sutures. Legumes of $C. \times$ sonorae resemble those of C. microphyllum in dehiscence. Those of other species of Cercidium appear to be indehiscent, or only slightly dehiscent. Legumes of Parkinsonia aculeata are sinuate or somewhat torulose and 1 to 5 seeded; otherwise they are similar to those of Cercidium microphyllum. Legumes in Parkinsonia africana material at hand are sinuate, flattened, and strongly dehiscent, while those of P. scioana and P. anacantha are flattened, but not constricted; those of P. scioana, at least, are indehiscent. Also, P. scioana is unique in the group in having long-funicled seeds. Although Cercidium microphyllum strongly resembles Parkinsonia aculeata in the character of its legumes, it stands apart from that species, and from other species of Cercidium, in a seed character: the cotyledons are thick in relation to the endosperm (fig. 14). Also, in dehiscence of the pinnae from the scale-like leaf rachis, *C. microphyllum* approaches *Parkinsonia aculeata*, but in the majority of characters it is more at home in *Cercidium* than in *Parkinsonia*.

As stated in the introduction, resolution of the generic relationship of Cercidium and Parkinsonia should be based upon extensive comparative biological, morphological, cytological, and genetic studies. On the basis of present information, however, one can say that Cercidium forms a discrete, easily recognizable unit confined to the Americas, with C. microphyllum most closely related to Parkinsonia. Study of Brenan's comparative chart (1963, pp. 206, 207) shows that among the taxa included, Parkinsonia aculeata is the most discordant element. Furthermore, the American species of Cercidium included agree in more gross morphological characters than do the African taxa placed in Parkinsonia. Pollen of two African taxa, as seen under the scanning electron microscope is of two distinct types whereas in Cercidium it is all similar. Pollen studies (Carter & Rem, 1974) indicate that species of Cercidium are more closely related to each other than they are to Parkinsonia aculeata, a species thought to be native to America, but which has been introduced widely throughout the warmer parts of the world. I would like to suggest that Parkinsonia be considered a monotypic genus comprised of P. aculeata Linnaeus, and that the relationships of the three African species (P. africana, P. anacantha, and P. scioana) be considered further before accepting them as congeneric with Parkinsonia and Cercidium as proposed by Brenan.

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