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Wood Anatomy of Cercidium (Fabaceae), with Emphasis on Vessel Wall Sculpture

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WOOD ANATOMY OF *CERCIDIUM* (FABACEAE), WITH EMPHASIS ON VESSEL WALL SCULPTURE

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ABSTRACT

Quantitative and qualitative data are presented for wood anatomy of the seven species of *Cercidium* (including two subspecies of *C. floridum* as well as the hybrid *C. × sonorae*) currently recognized. Data on wood of *Parkinsonia* are presented for purposes of comparison. Vessel walls of *Cercidium* show unusual sculpture: coarse excrescences termed verrucae here, crateriform pits, and grooves interconnecting pit apertures. These plus crystal distribution, presence of septa in fibers, pit diameter, presence of vasicentric tracheids, and presence of diagonal vessel aggregations are probably species distinctions to various degrees. The crystal-bearing fibers of *Cercidium,* some of which have very thin walls, exemplify fiber dimorphism. Wood of *Parkinsonia aculeata* is amply distinct from that of *Cercidium.* Vessel element dimensions and density in *Cercidium* do not indicate exceptional xeromorphy for woods, perhaps because some species grow in desert washes, perhaps because other features (leaflessness, thick cuticle on stems) reduce transpiration. Vessel wall sculpture, vasicentric tracheid presence, and degree of vessel grouping are considered likely indicators of wood xeromorphy within the genus, however.

Key words: *Cercidium,* ecological wood anatomy, Fabaceae, Leguminosae, *Parkinsonia,* verrucae, vesturing, wood anatomy.

INTRODUCTION

The report by Cozzo (1953) of crateriform pits in vessels of certain species of *Cercidium* led me to make preparations of the wood in order to illustrate these structures by means of SEM in a book (Carlquist 1988). While examining sections of *Cercidium* wood under a light microscope, I discovered that protuberances could be found on vessel walls of some species. These structures provided an unusual opportunity for study by means of SEM, because adequate resolution of them could be achieved only by that means.

The diversity of wall sculpture in *Cercidium* was sufficient to make examination of all species desirable. Therefore, wood samples of all currently recognized taxa were obtained and sectioned. According to the treatments of Johnston (1924) and Carter (1974), *Cercidium* consists of seven species, one with two subspecies (see Table 1); a natural hybrid (*C. × sonorae* Rose & Johnston) is also known. The wood preparations of *Cercidium* revealed other anatomical features of interest, so a survey of wood anatomy of the genus has been undertaken here.

The highly disjunct nature of the genus prevented collection of mature wood samples for all taxa, so some woodier portions of herbarium specimens were utilized. The latter samples very likely have vessel sculpture representative for these species, but such features as vessel element length and ray dimensions represent less mature conditions than in the species for which larger wood samples were available. The presence of different degrees of maturity in wood patterns in

various samples is regarded as of interest in its own right, and for this reason, a figure for stem diameter is given for each sample studied (Table 1, column 1). Material of *C. × sonorae* was sufficient for study of vessel wall characteristics, but reliable data on other wood features could not be obtained.

The occurrence of certain types of vessel sculpture in dicotyledons may represent adaptation to dry ecological conditions (Carlquist 1982). In addition, certain other features of wood anatomy represented in *Cercidium* have been cited as indicative of xeromorphy: narrow vessel diameter (Carlquist 1975), increased degree of vessel grouping (Carlquist 1984), presence of vasicentric tracheids (Carlquist 1985), and presence of diagonal vessel aggregations (Carlquist 1987). These and other features of wood anatomy possibly related to xeromorphy are analyzed here. The species of *Cercidium* can all be said to characterize desert sites or areas of equivalent dryness. The geographical ranges of the species are as follows (data from Johnston 1924 and Carter 1974): *C. andicola* Griseb., S. Bolivia and adjacent N. Argentina (Jujuy); *C. australe* Johnston, central Argentina and adjacent Paraguay; *C. floridum* Benth. ex Gray subsp. *floridum,* desert areas of California and Arizona plus Sonora, Mexico; *C. floridum* subsp. *peninsulare* (Rose) Carter, southern half of Baja California, Mexico; *C. macrum* Johnston, Tamaulipas and Nuevo Leon, Mexico; *C. microphyllum* (Torrey) Rose & Johnston, Colorado desert areas of eastern California and southern Arizona plus areas adjacent to the Gulf of California in Baja California and Mexico, Sonora; *C. praecox* (R. & P.) Harms, southern half of Baja California, eastern and central Sonora plus southern Mexico, Dominican Republic, Leeward Islands and adjacent Venezuela, and extreme middle Western Peru; *C. × sonorae,* areas of overlap between *C. microphyllum* and *C. praecox* in Baja California and Sonora; *C. texanum* A. Gray, Rio Grande Plain northwest to Val Verde Co., southward to Starr Co., Texas, and into Mexico as far as Coahuila and Nuevo Leon.

As a generalization, one could say that *Cercidium* favors low-elevation deserts that tend to receive summer rainfall. There is, however, a considerable range of climates or at least microclimatic situations (e.g., underground water availability) within the areas occupied by *Cercidium.* Other than the pervasive theme of limited rainfall, generalizations are not useful; one notes that equatorial as well as temperate deserts are occupied by the genus. Although wood features can be analyzed with respect to ecology, one must remember that other vegetative features can play significant if not overriding roles in the water economy of desert plants. In this regard, the leafless habit during the dry season and the presence of very thick cuticle on the photosynthetic bark surfaces are noteworthy.

The diversity of vessel wall sculpture as well as the range of other wood anatomical features in *Cercidium* invites comparison to the taxonomic system at the species level. *Cercidium* has been included within *Parkinsonia* by some authors, segregated by others (see Carter 1974 for a history). A species of *Parkinsonia, P. aculeata* L., has been included in the present study in order to determine if differences between *Parkinsonia* and *Cercidium* wood support recognition of the two genera.

The presence of chambered crystals in some libriform fibers of *Cercidium* wood leads to examination of an interesting phenomenon, fiber dimorphism (Carlquist 1958, 1961), which has not hitherto been reported in Fabaceae. Wood of *Cercidium* contains interesting forms of fiber dimorphism that are analyzed here and discussed in relation to probable instances elsewhere in caesalpinoid Fabaceae.

Table 1. Wood characteristics of *Cercidium*.

Species	Collection	1	2	3	4	5	6	7	8	9	10	11	12	13	14
C. andicola	*Pereyra 43* (SI)	6	81	24	2.8	122	3.2	5	332	2.2	94	225	2.1	2.3	36
C. australe	*Romero 20 I 1947* (POM)	7	70	31	1.4	179	2.4	5	420	2.4	109	314	2.4	1.1	79
C. floridum subsp. floridum	*Wolf 2981* (RSA, RSAw)	21	39	43	1.9	318	4.0	8	725	2.0	88	434	4.1	0.7	351
C. floridum subsp. peninsulare	*Carter 4134* (RSA)	4	54	31	1.4	203	2.2	7	499	2.0	143	556	2.5	2.2	107
C. macrum	*Pringle 2537* (POM)	5	50	26	2.8	195	2.8	5	486	2.0	112	220	2.3	2.0	101
C. microphyllum	*Jones 6 May 1903* (POM)	14	45	38	3.2	223	3.3	6	223	1.5	80	218	3.2	0.6	188
C. praecox	*Wiggins 5532* (POM)	6	41	34	2.4	183	1.5	5	378	2.0	98	201	2.1	1.0	152
C. texanum	*Iltis et al. 62a* (RSAw)	20	123	28	6.2	210	4.0	7	549	2.4	93	247	3.4	1.2	48

Legend for columns: 1, diameter of wood sample, mm; 2, mean number of vessels per mm² of transection; 3, mean vessel diameter (lumen diameter at widest point), μm; 4, mean number of vessels per group (solitary vessel = 1, pair of vessels in contact = 2, etc.); 5, mean vessel element length, μm; 6, mean vessel wall thickness, μm; 7, mean diameter of pit cavity, lateral vessel walls, μm; 8, mean libriform fiber length, μm; 9, mean libriform fiber wall thickness, μm; 10, mean height of uniseriate rays, μm; 11, mean height of multiseriate rays, μm; 12, mean width of multiseriate rays, cells; 13, mean ray cell wall thickness, μm; 14, Mesomorphy index (vessel diameter times vessel element length divided by vessels per mm²).

Wood samples derived from herbarium specimens are mostly or more than twig thickness (Table 1, column 1). I am particularly grateful to Dr. Juan Hunziker for the material of *C. andicola,* without which representation of all taxa could not have been achieved. Xylarium samples are indicated in Table 1 by the abbreviation RSAw.

Localities in which the samples studied were collected are as follows: *C. andicola (Pereyra 43),* Guasamayo, Tilcara, Jujuy, Argentina; *C. australe (Romero 20 I 1947),* Charcal, Molino, Salta, Argentina; *C. floridum* subsp. *floridum (Bissing 180); C. floridum* subsp. *floridum (Wolf 2981),* Mecca, Riverside Co., California; *C. floridum* subsp. *peninsulare (Carter 4134),* Valle de los Encinos, Sierra Giganta, Baja California, Mexico; *C. macrum (Pringle 2537),* near Monterrey, Nuevo Leon, Mexico; *C. microphyllum (Jones 6 V 1903),* near Phoenix, Arizona; *C. praecox (Wiggins 5532),* between Medano and Venancio, Baja California, Mexico; *C.* × *sonorae (Carter et al. 5596),* 35 km S. of Hermosillo, Sonora, Mexico; *C. texanum (Iltis et al. 62a),* 12 miles S. of Lorado, N. Tamaulipas, Mexico.

All wood samples were available in dried form. Samples were boiled in water and stored in aqueous 50% ethyl alcohol. Despite this treatment, starch remained in some samples. Woods were sectioned on a sliding microtome. Sections were stained with a safranin-fast green combination in order to differentiate septa in libriform fibers and pits on vessel walls. Unstained sections dried between glass slides to assure flatness were used for SEM studies. SEM photomicrographs were obtained with the ISI WB-6 at the Rancho Santa Ana Botanic Garden. Macerations were prepared with Jeffrey's Fluid and stained in safranin. The quantitative data in Table 1 were based on 25 measurements each except for vessel wall thickness, vessel-vessel pit diameter, libriform fiber wall thickness, and ray cell wall thickness, in which typical conditions were measured. Vessel diameter represents lumen diameter and was measured at the widest point of a vessel as seen in transection.

ANATOMICAL RESULTS— *CERCIDIUM*

Growth Rings

All species could be said to be semi-ring porous because growth rings are present but are not well marked (Fig. 1, 9). By noting the date on which stems were collected, and noting the diameter of the most recently formed vessels on stems, one can demonstrate that earlywood of growth rings is initiated in response to water availability rather than increase in temperatures at the end of a cold season.

Quantitative Vessel Element Features

Mean vessel density ranges from 39 to 123 per mm² (Table 1, column 2). Intermediate vessel density is represented by *C. andicola* (Fig. 1) and *C. australe* (Fig. 7), whereas *C. texanum* (Fig. 27) has high vessel density.

Vessel diameter (Table 1, column 3) might be expected to be inversely related to vessel density (column 2), and in *Cercidium,* a rough inverse correlation (with several exceptions) can be seen by comparing the two columns. One should note that the range in mean vessel diameter (24 μm in *C. andicola,* Fig. 1, to 43 μm in *C. floridum* subsp. *floridum*) is not great. Age of stem may be related to mean
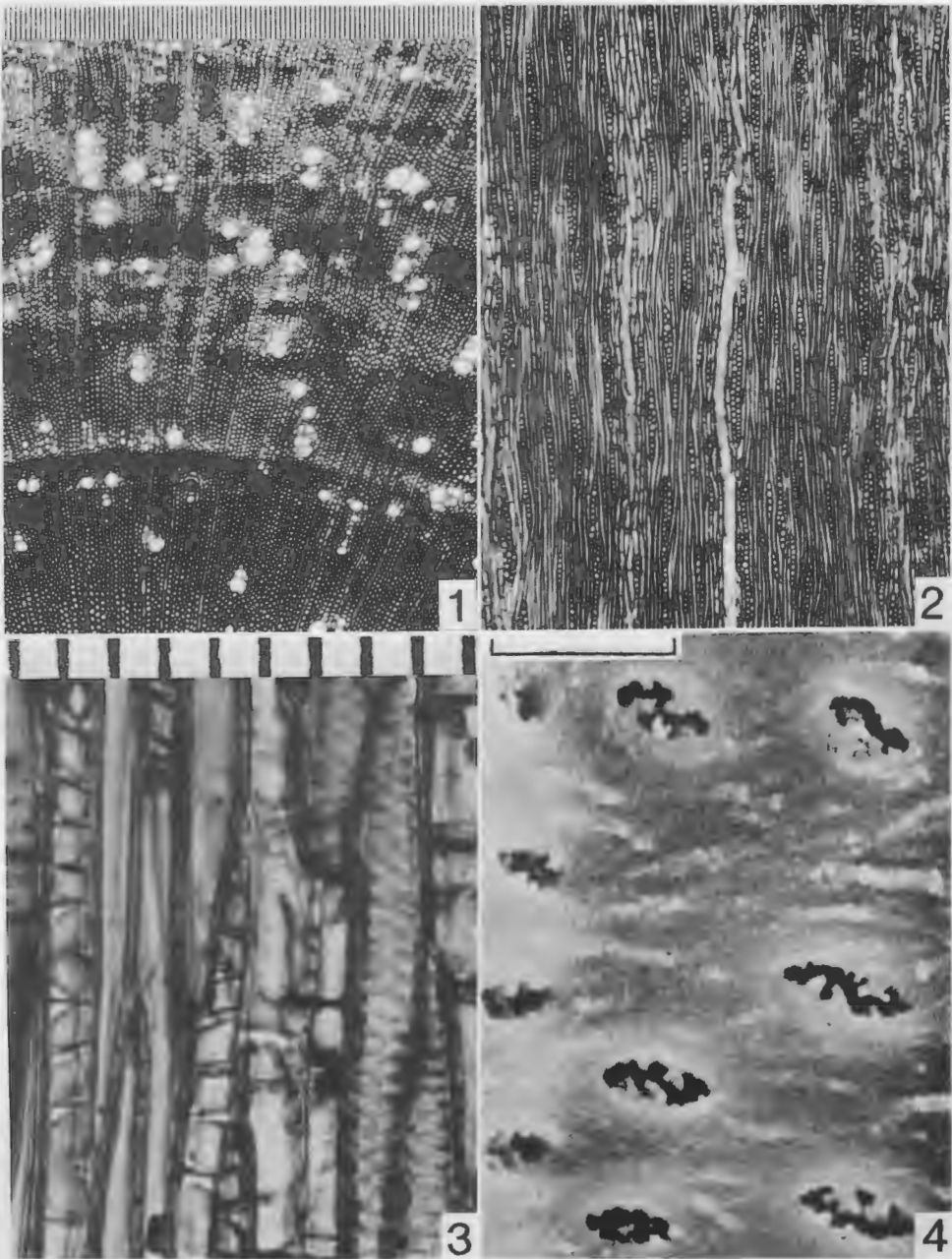
Fig. 1–4.   Wood sections of *Cercidium andicola* (*Pereyra 43*).—1. Transection; dark bands are tension wood.—2. Tangential section; multiseriate rays are relatively narrow.—3. Tangential section, showing portions of several libriform fibers containing chambered crystals.—4. Portion of vessel wall from tangential section, showing vestured pits; small verrucae, tending to intergrade with striations, are relatively sparse. (Fig. 1–2, magnification scale above Fig. 1 [divisions = 10 μm]; Fig. 3, scale above Fig. 3 [divisions = 10 μm]; Fig. 4, bracket at upper left [bracket = 10 μm].)
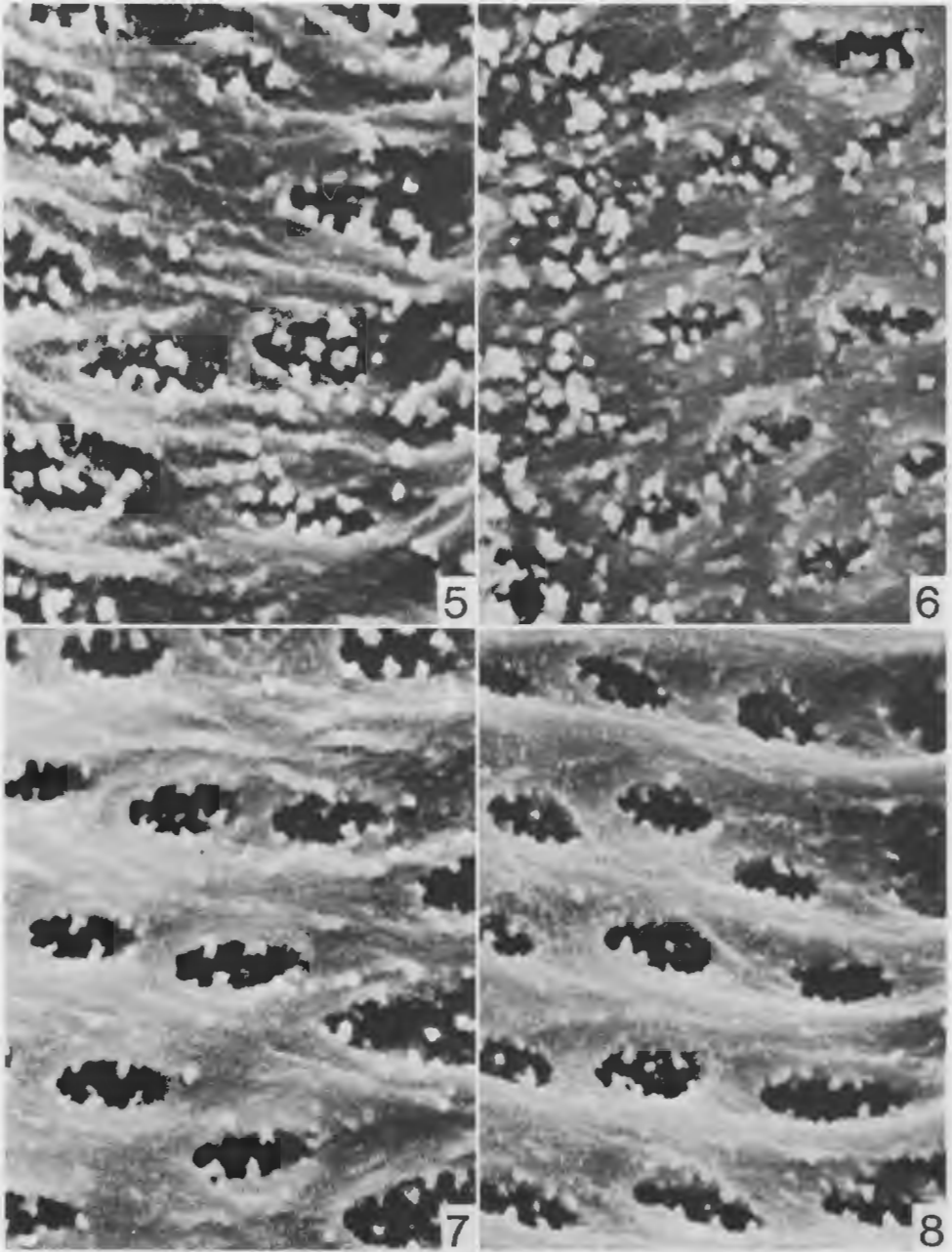
Fig. 5–8. Vessel wall portions from tangential sections of wood of *Cercidium andicola* (*Pereyra 43*).—5. Shallow grooves; bases of verrucae form striae.—6. Dense verrucae, especially at left.—7. Striae present, verrucae denser around pit apertures.—8. Long shallow grooves, verrucae around pit apertures. (Fig. 5–8, magnification bracket at top left, Fig. 4.)

vessel diameter: the two collections with the greatest vessel diameter (Table 1, column 3) have the greatest stem diameter. Had wood from larger stems been available, very likely wider vessels would have been reported.

With respect to vessel grouping, the collections of *Cercidium* mostly show moderate figures for number of vessels per group (Table 1, column 4), as in *C. andicola* (Fig. 1) and *C. australe* (Fig. 9), but *C. microphyllum* and *C. texanum* (Fig. 27) have much higher figures. The latter two species are also the only ones in which diagonal vessel aggregations (Fig. 27) and vasicentric tracheids occur. In all other species, one can say that vessel grouping tends to take the form of short radial multiples (Fig. 1, 9); solitary vessels are common in the species with a smaller degree of vessel grouping.

Vessel element length (Table 1, column 5) is notably short in *Cercidium*. The collections with the longest mean vessel element lengths are those in which sample diameter is greatest.

Vessel wall thickness (Table 1, column 6) is also greatest in the collections with the largest sample diameter.

Diameter of vessel-vessel pits (Table 1, column 7) is measured laterally rather than vertically. Pits are roundish to oval in shape, wider laterally than vertically, but have angular outlines in *C. andicola, C. australe, C. texanum,* and to a lesser extent in other species. Pit apertures are narrowly elliptical, much longer than wide (Fig. 4, 14, 15, 17, 18, 21, 22, 26). Pit apertures circular in outline may be seen in Figure 11, 12, 16, and 25. In Figure 11, 12, and 25, circular shape may be related to presence of crateriform pits. Pit diameter minimal for the genus, accordingly, tends to occur in those taxa with crateriform pits: *C. australe* (Fig. 11, 12), *C. praecox* (Fig. 22), and *C. × sonorae* (Fig. 25). The greatest mean pit diameter for the genus (7–8 μm) is found in *C. floridum* subsp. *floridum, C. floridum* subsp. *peninsulare,* and *C. texanum.*

Vessel Wall Sculpture

Characteristically some *Cercidium* species form conspicuous excrescences on the inside of vessel walls, whereas others do not. In the species in which they occur, the excrescences range from inconspicuous (Fig. 4) to densely present (Fig. 5, 6, 11, 12, 13, 24). The term "vesturing," proposed by Ohtani et al. (1984) for structures sometimes known as warts, is not regarded as applicable here because the excrescences on *Cercidium* vessel walls are so much larger; they also tend to be angular or otherwise irregular in shape (Fig. 5, 6). A number of adjectives (e.g., "budlike, coralloid") are used by other authors (Parameswaran and Gomes 1981, Castro 1988). The term "verrucae" is consequently proposed for the structures in *Cercidium*. All species of *Cercidium* have vestured pits (Fig. 11, 16, 21, 32), but verrucae do not appear to be merely vestures extending onto the inner vessel surface. Vesturing can be present without any verrucae on the vessel surface (Fig. 16).

Grooves on vessel walls are also discussed here. By "grooves" I connote the presence of shallow depressions that interconnect pit apertures laterally. Grooves vary in length and depth, as shown in Figure 8, 13, 15, and 26. The concept of helical thickenings is not applicable here, because thickenings do not account for the presence of grooves (see also illustrations of *Parkinsonia* grooves, Fig. 29, 30).
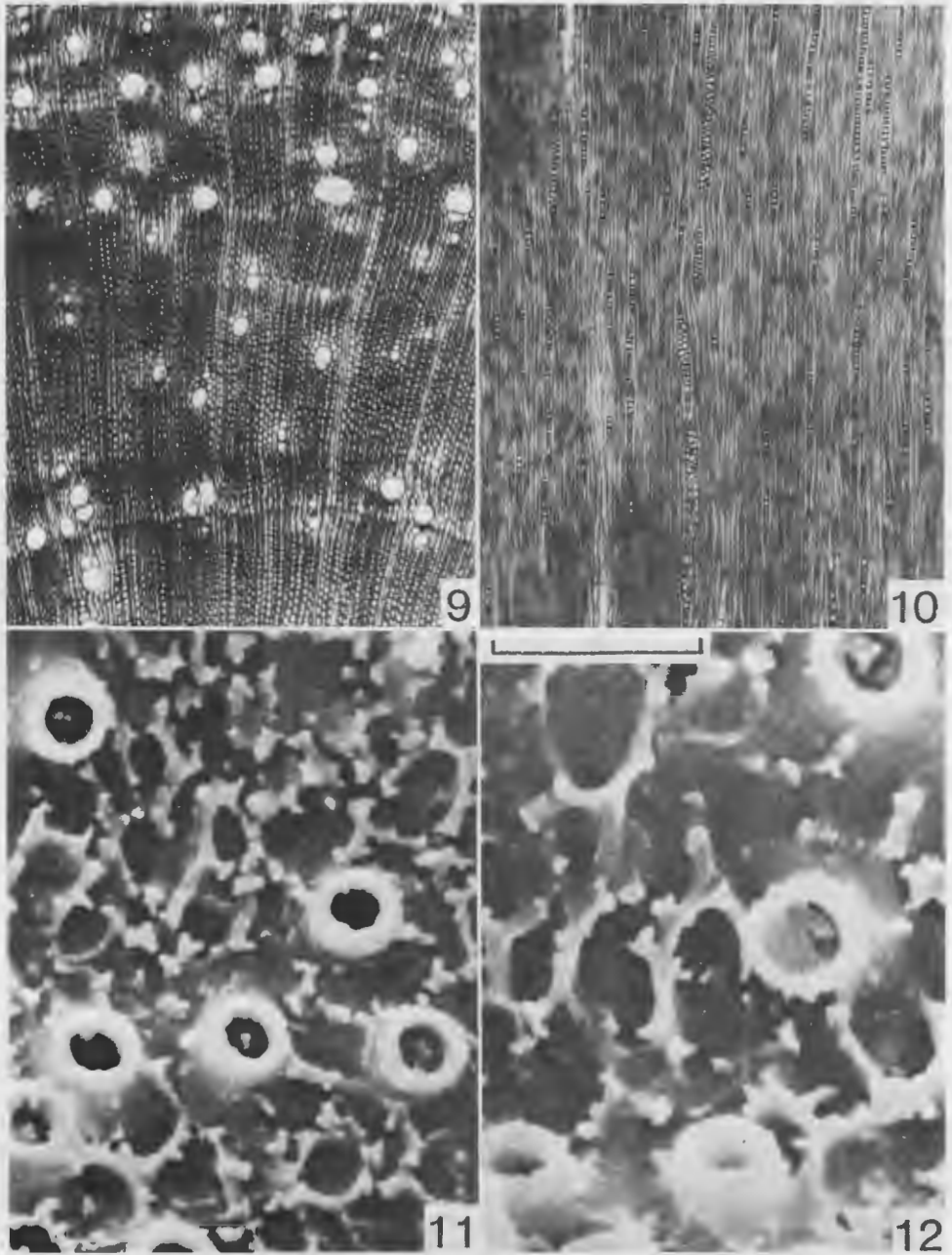
Fig. 9–12. Wood sections of *Cercidium australe* (*Romero 20 I 1947*).—9. Transection; growth ring begins near bottom of photograph.—10. Tangential section; darker areas are tension wood.—11–12. Vessel wall portion showing crateriform pits and polygonal aggregations of verrucae.—11. Appearance of crateriform pits in face view.—12. Diagonal view of crateriform pits, below. (Fig. 9, 10, magnification scale above Fig. 1; Fig. 11, magnification bracket at top of Fig. 4; Fig. 12, bracket at top left, Fig. 12 [bracket = 10 µm].)

Grooves such as those found in *Cercidium* and *Parkinsonia* account for adoption of the term "helical sculpture" as an inclusive term in dicotyledon woods, with grooves and thickenings representing distinctive respective types (Carlquist 1988). The crateriform pits reported by Cozzo (1953) in *Cercidium* are also considered a form of vessel wall sculpture.

In *C. andicola* (Fig. 4–8), a wide range of helical sculpture may be found. Verrucae appear always to be present, but are sparse and low on some vessel walls (Fig. 4, 8), crowded and larger on other areas (Fig. 5–7). There is a marked tendency for aggregation of verrucae by their bases into laterally oriented striae (Fig. 4, 5, 7). Grooves may be absent (Fig. 4, 6), very shallow (Fig. 5, 7), or relatively conspicuous (Fig. 8).

Cercidium australe is the most distinctive species of the genus with respect to vessel wall sculpture. The crateriform pits (Fig. 11, 12) have collarlike or cylindrical form and are much higher forms of relief than the relatively low crateriform pits of *C. praecox* (Fig. 22) or *C.* × *sonorae* (Fig. 25). The nature of these pit orifices is perhaps most clearly shown in Fig. 12, lower portion. In addition, the verrucae of *C. australe* are always united to various degrees into polygonal networks (Fig. 11, 12) or similar aggregations coarse enough to be seen under the light microscope. Grooves were not observed on vessel walls of *C. australe.*

In *C. floridum* subsp. *floridum* there is a wide range in sculpture of vessel walls. Verrucae are present in some vessel walls, where they range from minimal (Fig. 13, 14) to absent in others (Fig. 15). Various degrees of groove presence may be found, ranging from very deep and furrowlike (Fig. 13) to shallow (Fig. 15) to minimal (Fig. 14).

In the collection studied of *C. floridum* subsp. *peninsulare* (Fig. 16), neither verrucae nor grooves are present on vessel walls; pit apertures range from circular to oval in outline, and vestures are clearly visible within pits.

Vessel walls of *C. macrum* (Fig. 17) may be smooth or shallowly grooved; walls bear sparsely or densely what must be called vestures (or warts), less than half the diameter of the structures termed verrucae here. These vestures do not appear to be artifacts, because they seem more uniform in size and presence than droplets of resinlike materials would be.

In *C. microphyllum* (Fig. 18), vessel walls were observed to be uniformly smooth, with no appreciable degree of groove presence.

For *C. praecox,* four SEM photographs have been selected to show the range of vessel wall sculpturing (Fig. 21–24). Verrucae may be sparse, with inconspicuous striate extensions of bases (Fig. 21). Verrucae may be moderately conspicuous but separated from each other (Fig. 22). On portions of walls free from pits, verrucae may be fused into striate structures spaced closely (Fig. 23) or coralloid aggregations (Fig. 24). The laterally striate or laterally aggregated pattern is very common in *C. praecox.* Pits have orifices very slightly (Fig. 21) to more moderately (Fig. 22) raised into crateriform shape; these apertural extensions are not so conspicuous as in *C. australe,* however. Grooves interconnecting pit apertures were not observed in *C. praecox.*

Cercidium × *sonorae* has vessel walls in which verrucae cannot be said to be present, but the striate patterns like those of *C. praecox* are present inconspicuously to markedly (Fig. 25 exemplifies the latter condition). Grooves were not observed.
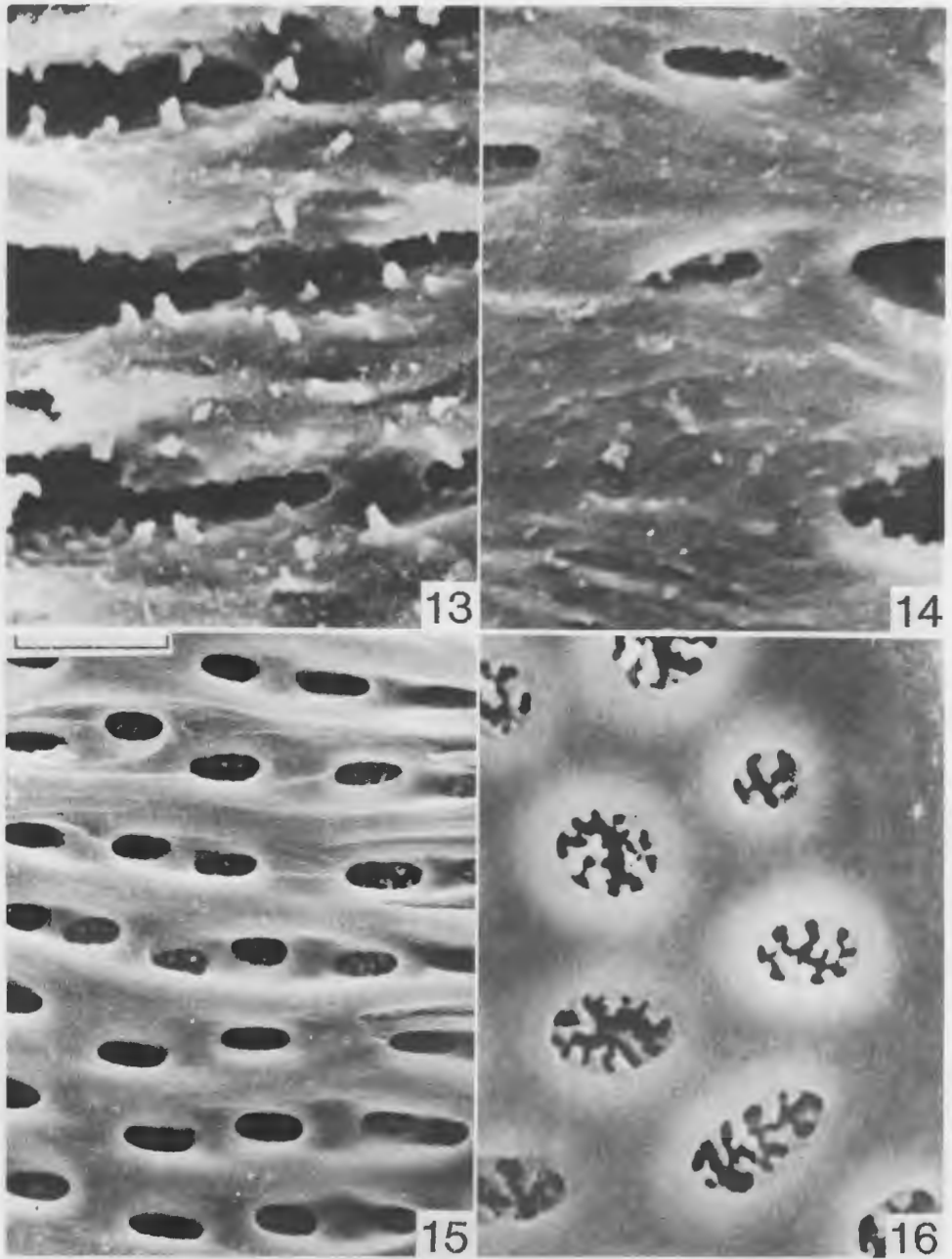
Fig. 13–16. Vessel wall portions from tangential sections of *Cercidium floridum* wood.—13–14. *C. floridum* subsp. *floridum* (*Bissing 180*).—13. Verrucae along deep grooves interconnecting pit apertures.—14. Occasional verrucae around pit apertures, striae on wall surface.—15. *C. floridum* subsp. *floridum* (*Wolf 2981*); shallow grooves interconnect pit apertures.—16. *C. floridum* subsp. *peninsulare* (*Carter 4134*); pits conspicuously vestured. (Fig. 13, 14, 16, magnification bracket at top of Fig. 4; Fig. 15, bracket at top left in Fig. 15 [bracket = 10 μm].)
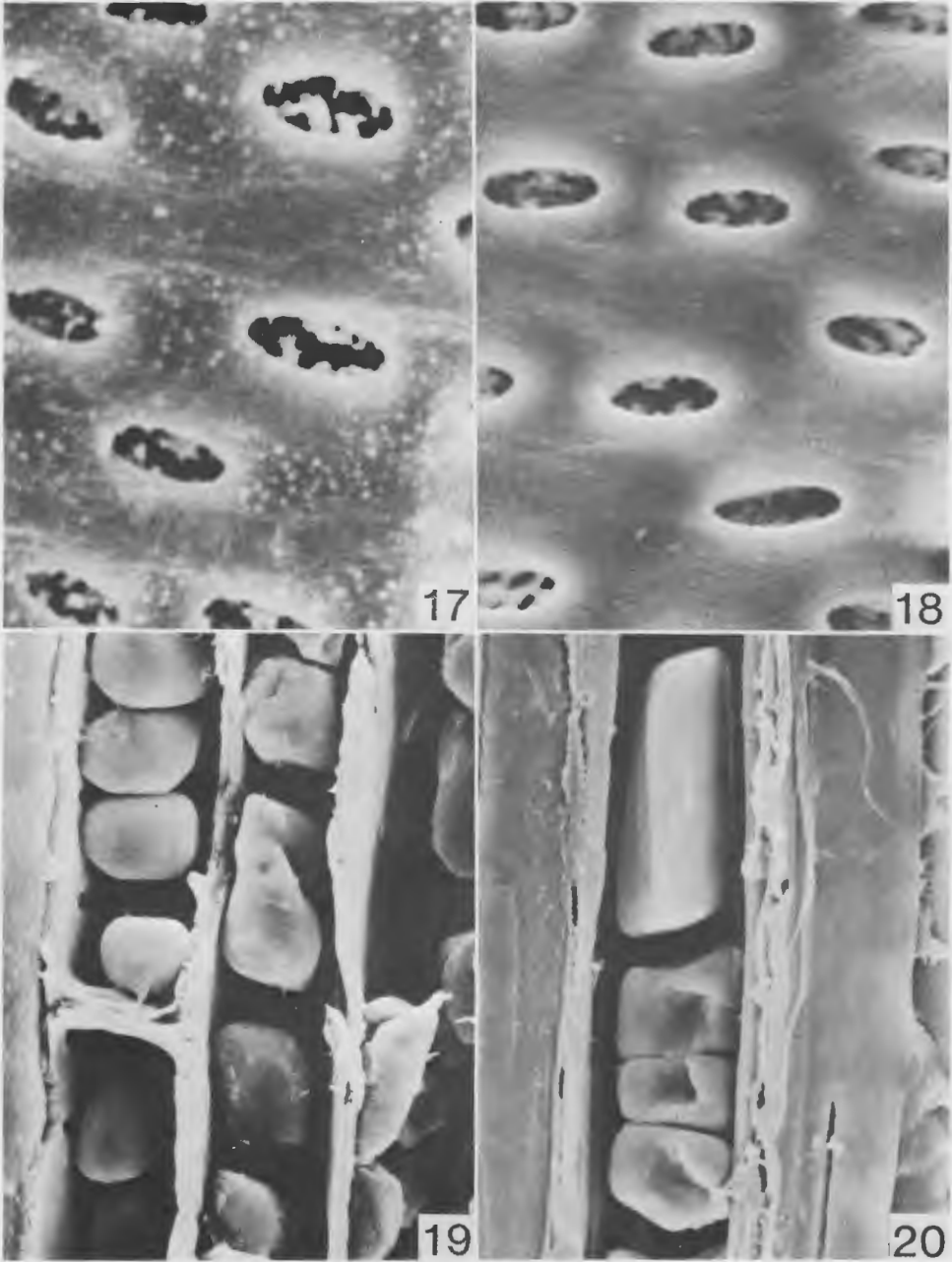
Fig. 17–20.   Vessel wall portions from tangential sections of *Cercidium.*—17. *C. macrum* (*Pringle 2537*); vessel wall smooth.—18–20. *C. microphyllum* (*Jones 17 IV 1903*).—18, Vessel wall smooth, vestures within pits evident.—19. Axial parenchyma cells filled with starch grains.—20. Starch grains in a libriform fiber. (Fig. 17–20, magnification indicated by bracket, Fig. 4.)

Crateriform pits may be seen in *C.* × *sonorae* vessels (Fig. 25), but do not have markedly upraised orifices.

In *C. texanum* (Fig. 26), vessel walls do not bear any verrucae. Grooves are marked (Fig. 26) or nearly absent, depending on which portion of a vessel wall one views.

Libriform Fibers and Dimorphic Fibers

Libriform fiber lengths (Table 1, column 8) parallel vessel element lengths, and the comments above on vessel element length apply here. Libriform fiber wall thickness is relatively uniform in the genus (Table 1, column 9); note should be taken that tension wood fibers have been excluded from these observations.

Examination of crystal-bearing fibers of *Cercidium* yields a diversity of appearances. As illustrated for *C. andicola* (Fig. 3), crystal-bearing fibers commonly are subdivided into chambered crystals, single rhomboidal crystals separated by thin primary walls. However, libriform fibers may bear crystals along only part of their length (Fig. 3, fiber one-third the distance from the left edge of photograph). Portions of such libriform fibers that are devoid of crystals are separated from the crystal-bearing portions by lignified walls similar to those in axial parenchyma strands. Sections and macerations show that a large proportion of crystal-bearing fibers have walls that are very thin, much thinner than one would expect in ordinary libriform fibers; walls of intermediate thickness may also be found on crystal-bearing fibers. The fibers that contain chambered crystals are wider and shorter than ordinary libriform fibers of *Cercidium*. If devoid of crystals, these shorter fibers may be subdivided by one (rarely two) walls like those of axial parenchyma strands or they may not be subdivided.

The shorter (and in *Cercidium,* often crystal-bearing) libriform fibers tend to occur in groups, as suggested by their abundance in the tangential section of Fig. 3, and these groupings or patches occur at various points within a growth ring.

Dimorphic fibers occur in all collections of *Cercidium* examined here, but only a fraction of the shorter fibers are crystal bearing. Crystal-bearing fibers were observed to be more abundant in *C. andicola* (Fig. 3), *C. australe, C. microphyllum,* and *C. praecox.* Crystal-bearing fibers occur mostly at the juncture between late-wood and earlywood. Crystal-bearing fibers were not observed in *C. floridum* subsp. *floridum* or *C. macrum,* and they were observed to be very scarce in *C. floridum* subsp. *peninsulare* and *C. texanum.* Several crystals per cell (chamber) were seen in some crystal-bearing fibers of *C. texanum.*

Starch was observed to be abundant in all libriform fibers of *C. floridum* subsp. *floridum, C. microphyllum* (Fig. 20), and *C. praecox.* Absence of starch in the other samples may be due to season of collection or method of drying or preparation rather than to any inability to form starch. The material of *C. floridum* subsp. *floridum* showed starch somewhat less common in the short libriform fibers than in the long ones.

Reaction wood (tension wood) libriform fibers occur commonly in *Cercidium* (Fig. 1, 10, dark patches). Stems in the present study devoid of tension wood probably are main stems or upright stems rather than diagonally leaning branches.
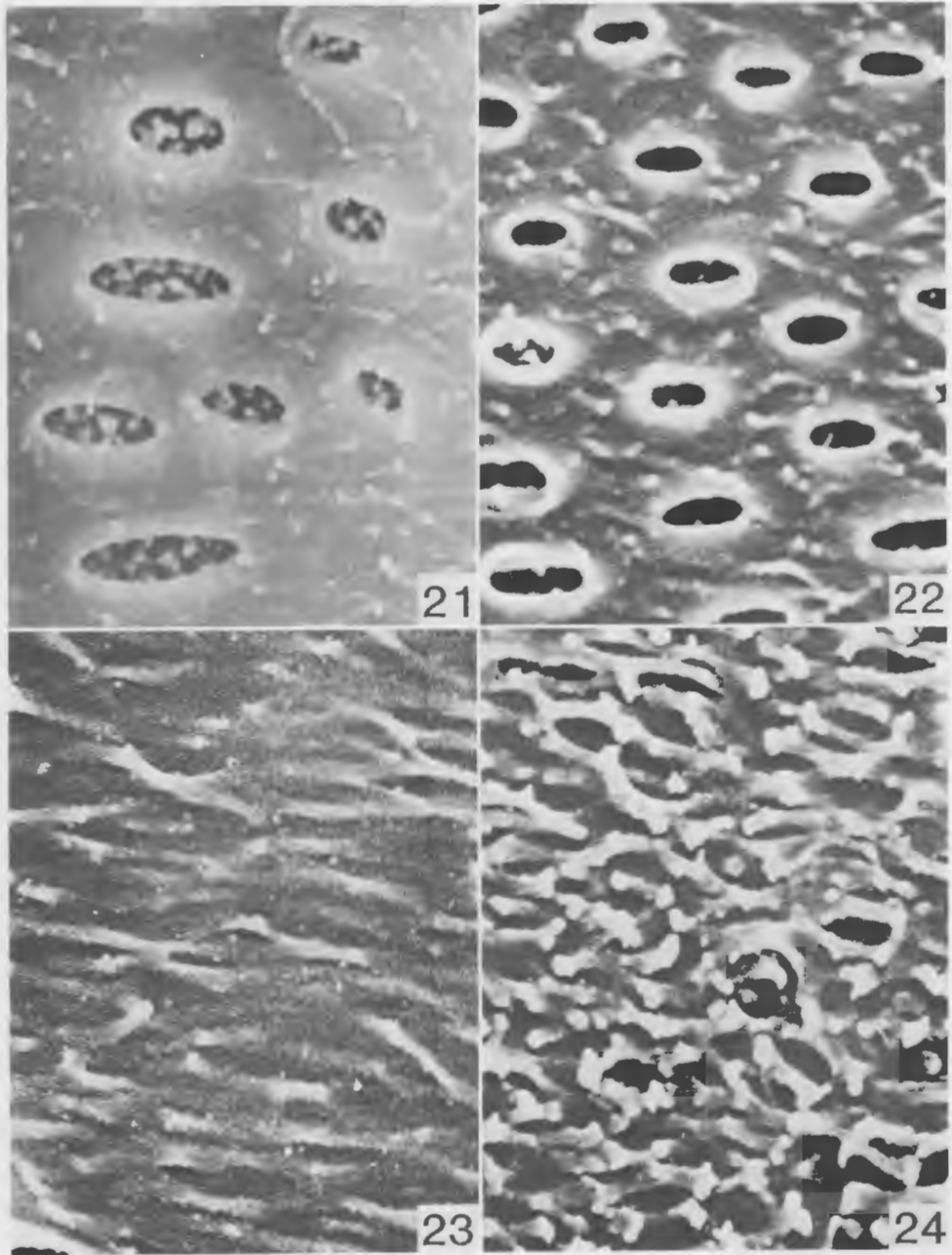
Fig. 21–24.   Vessel wall portions from tangential wood sections of *Cercidium praecox* (*Wiggins 5532*).—21. Wall with sparse low verrucae.—22. Pits crateriform, verrucae moderately sparse.—23. Verrucae essentially fused into lateral striae.—24. Verrucae prominent, fused into coralloid outgrowths from wall. (Fig. 21–24, magnification bracket at top left in Fig. 4.)

Axial Parenchyma

Axial parenchyma occurs in the form of sheaths one to three (or even four) cells in thickness in all taxa; most commonly the sheaths are two cells in thickness. Strands of axial parenchyma are composed of two to six cells, most commonly four cells. Starch was observed in axial parenchyma of *C. floridum* subsp. *floridum* and *C. microphyllum* (Fig. 19). Crystals were not observed in axial parenchyma in any of the collections.

Vasicentric Tracheids

Small numbers of vasicentric tracheids were seen in sections (presence confirmed in macerations) in *C. microphyllum* and *C. texanum*. They occur intermixed with vessels in diagonal vessel aggregations (Fig. 27).

Rays

Vascular rays in *Cercidium* are both multiseriate and uniseriate, and are composed of procumbent cells exclusively (Fig. 2, 10, 28). Thus they correspond to Krib's Homogeneous Type I (Kribs 1935), although scarcity of uniseriate rays in *C. microphyllum, C. praecox,* and *C. texanum* (Fig. 28) makes them approach Homogeneous Type II.

Uniseriate ray height (Table 1, column 10) and multiseriate ray height (column 11) are rather small compared to values found in dicotyledons at large. Mean uniseriate ray height is rather uniform throughout the genus (Table 1, column 10); the lower height in *C. floridum* subsp. *floridum* and *C. microphyllum* may relate to the fact that stems studied for these species are larger, and most taller rays that may have begun as uniseriate rays near the pith would have been converted to multiseriate rays in outer portions of the stems. Multiseriate rays are also relatively uniform in height (Table 1, column 11) except for those of *C. floridum* (both subspecies).

Ray width (Table 1, column 12) is relatively uniform (Fig. 2, 10) except for *C. floridum* subsp. *floridum, C. microphyllum,* and *C. texanum* (Fig. 27). The wood samples of these three taxa were larger, so the correlation is expected: ray width commonly increases with age (Barghoorn 1941).

Ray cell walls (Table 1, column 13) range in mean thickness from 0.7 to 2.3 μm. Some borders were observed on ray cell pits, especially on tangentially oriented walls, in both species with thick (*C. andicola*) and thin (*C. floridum* subsp. *floridum*) walls.

Crystals were observed in ray cells in all species except *C. microphyllum*. They were observed only in a primary ray in *C. macrum*. Crystals typically are not found at random in ray cells where present, but at the margins of growth rings, often in the radially shorter cells produced in latewood portions of rays. Crystals are rhomboidal and formed singly per cell where present.

Storying

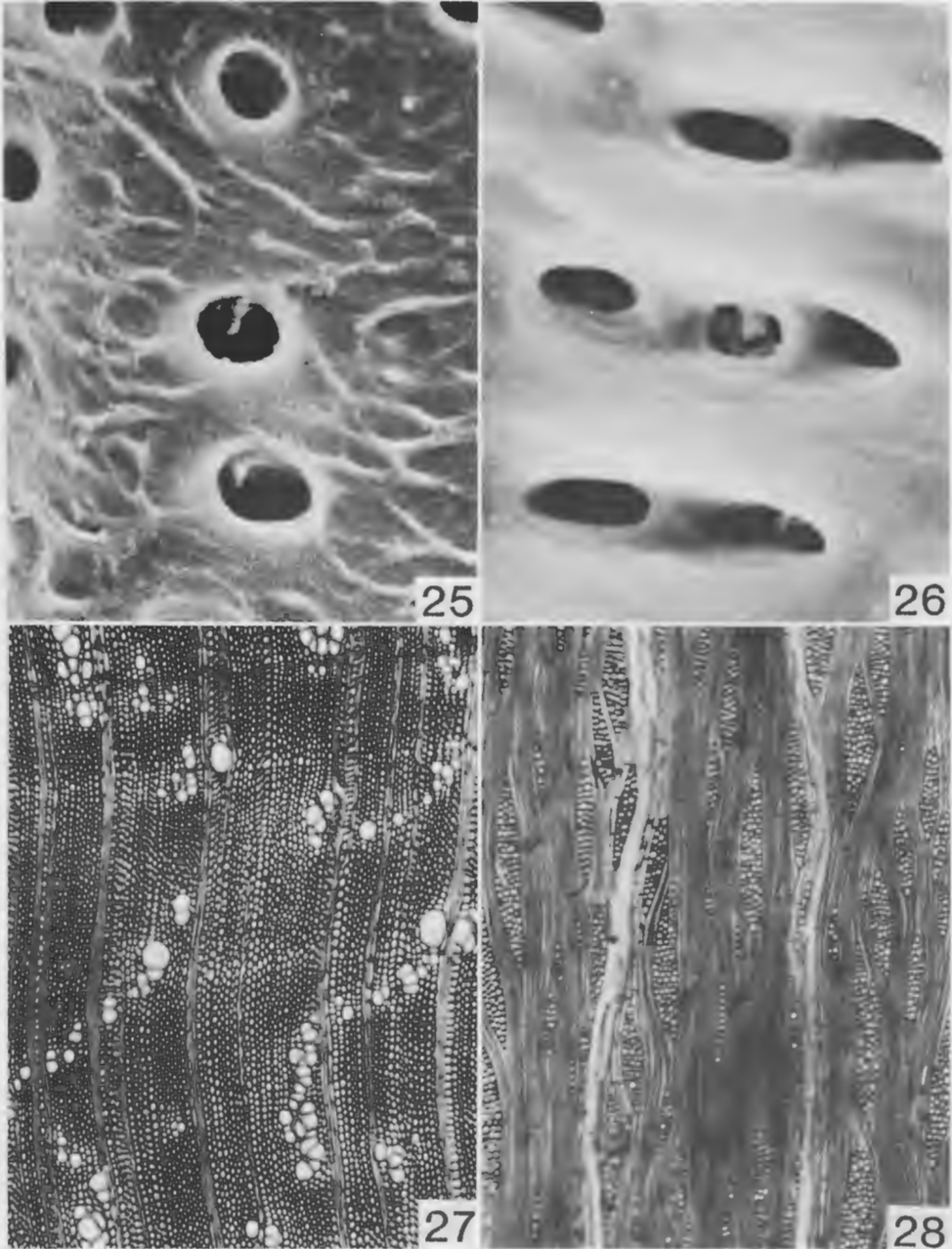No evidence of storying was observed in *Cercidium* wood.

Fig. 25–28.   Wood sections of *Cercidium*. — 25. *C.* × *sonorae* (*Carter et al. 5596*); vessel wall portion from tangential section; crateriform pits and wall thickenings oriented in various directions. — 26–28. *C. texanum* (*Iltis et al. 62a*). — 26. Vessel wall portion from tangential section; wall is smooth, grooves interconnect pit apertures. — 27. Transection; vessels aggregated into diagonal patterns. — 28. Tangential section; multiseriate rays are relatively wide and tall. (Fig. 25, 26, magnification bracket at top left of Fig. 4; Fig. 27, 28, scale above Fig. 1.)

ANATOMICAL RESULTS—*PARKINSONIA*

Only qualitative data are given here because only one species of *Parkinsonia* has been studied. In the comparison between *Cercidium* and *Parkinsonia,* qualitative data appear to be more important than quantitative data. In *P. aculeata,* vessels are solitary or in short radial multiples. Vessels have simple perforation plates. Vessel walls have narrow grooves interconnecting pit apertures (Fig. 29, 30). Vessel-vessel pits are alternate, circular to oval in shape but often with polygonal outline (Fig. 30). The pits are vestured (Fig. 31) in pit cavities. Vessel walls bear no vestures or verrucae (Fig. 29). Libriform fibers are monomorphic, nonseptate, and devoid of crystals. Axial parenchyma is both initial (narrow bands of various width present to various degrees in earlywood) and paratracheal (sheaths 2–4 cells wide around vessels or vessel groups). Rays are Homogeneous Type I, with multiseriate and uniseriate rays about equally abundant. Crystals are present in axial parenchyma cells, but not in ray cells. Wood is nonstoried.

MORPHOLOGICAL CONCLUSIONS

Vessel wall sculpture of *Cercidium* shows a remarkable range. The crateriform pits of *C. australe* have much taller orifices than do the crateriform pits of *C. praecox* or *C. × sonorae.* These crateriform pits were figured by Cozzo (1953), and the SEM studies in the present paper yield shapes similar to his drawings.

The coarse vessel wall excrescences of *Cercidium* are termed verrucae here because they are much larger than the structures termed vesturing by Ohtani et al. (1981) or the structures often termed warts in conifer tracheids. A comparable type of excrescence has been figured in *Ligustrum lucidum* Ait. (Oleaceae) by Parameswaran and Gomes (1981), who term the structures "budlike protrusions" from the vessel wall. More pertinent is the report of structures comparable to the verrucae of *Cercidium* in another genus of Fabaceae, *Prosopis* (Castro 1988). Warts on vessel walls of certain Fabaceae mentioned by Schmid and Machado (1964) are smaller in size. The diversity of verrucae in *Cercidium* is surprising, and is summarized under Taxonomic Conclusions below.

In addition, attention is called to helical sculpture in vessel walls of *Cercidium.* Helical sculpture has all too often been equated with helical thickenings in the literature on wood anatomy. *Cercidium* does have, intermittently, striate vessel wall thickenings, but these are considered here merely a form of low fused verrucae. In addition, grooves interconnecting pit apertures occur widely in *Cercidium* as well as in *Parkinsonia;* these do not involve any form of thickening in the vessel wall. Grooves in vessel walls occur in a number of dicotyledons, notably many Asteraceae. Occurence of grooves in vessel walls has been reviewed elsewhere (Carlquist 1988). The occurrences are doubtless more common than present literature, which has neglected them and stressed helical thickenings instead, would tend to indicate.

Fiber dimorphism is a phenomenon described earlier (Carlquist 1958, 1961); it has been discovered in a number of taxa (for a review, see Carlquist 1988). Fiber dimorphism can, in some dicotyledons, be regarded as a way of achieving a parenchymalike function for a portion of the libriform fibers in a wood. In *Cercidium,* libriform fibers are apparently living fibers in all species, with a prominent starch storage function in some if not all species. Therefore the dimorphism
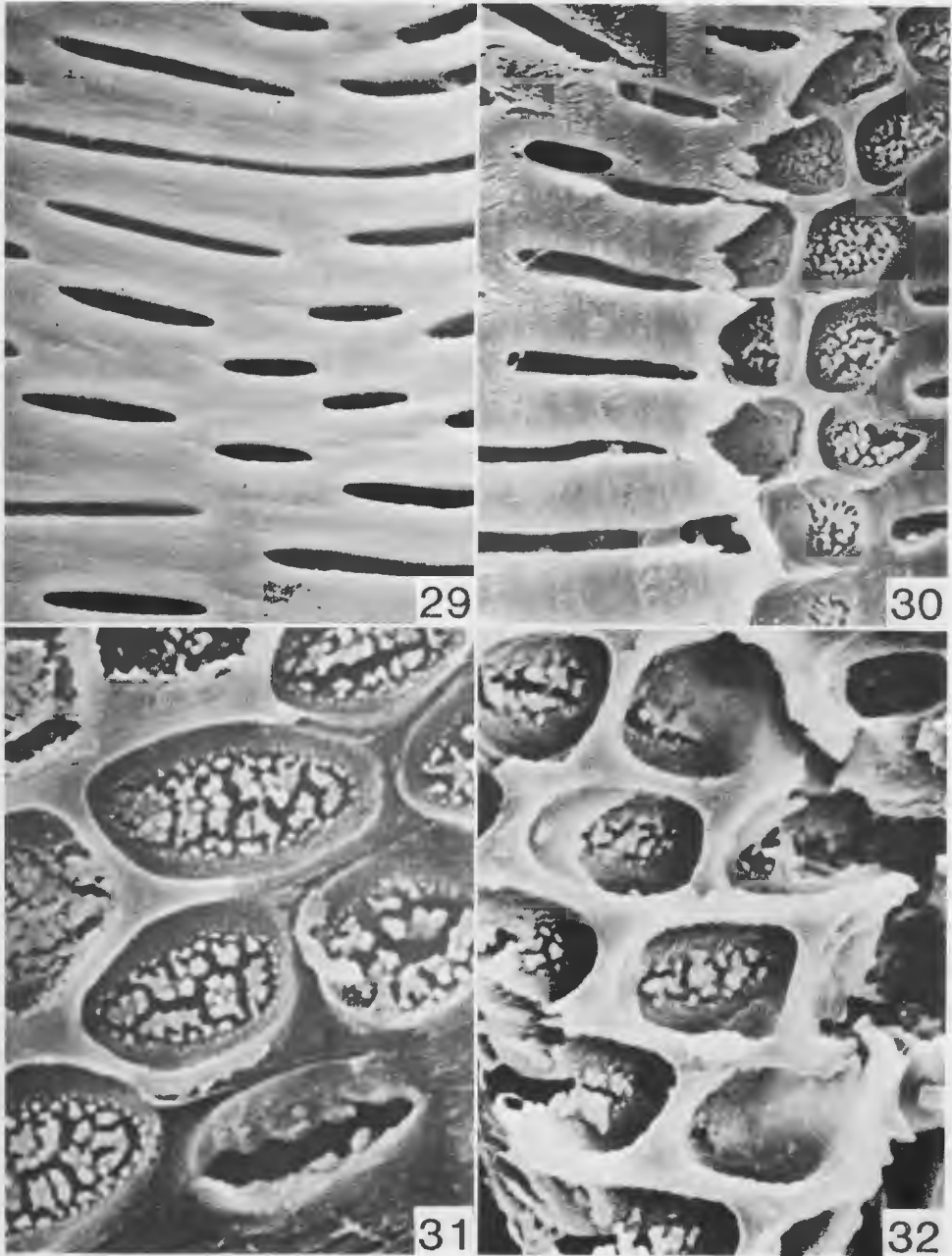
Fig. 29–32.   Vessel wall portions from tangential sections of *Parkinsonia* and *Cercidium.* — 29–31. *P. aculeata (USw-20314).* — 29. Narrow grooves (the prominent horizontal ellipses, some very long) interconnect pit apertures. — 30. Shaved away portion of vessel wall shows how grooves overlie pit cavities, which are polygonal in outline. — 31. View of pit cavities from outside of vessel, pit membrane ruptured, nature of vesturing evident. — 32. *C. praecox (Wiggins 5532),* view of pit cavities from outside of vessel; pit membranes are ruptured, nature of vesturing in the pit cavity can be seen. (Fig. 29, 30, magnification bracket at top left in Fig. 4; Fig. 31, 32, bracket at top left of Fig. 12.)

of *Cercidium* libriform fibers adds a different function: crystal accumulation. The chambered crystals of *Cercidium* libriform fibers are noteworthy not merely because they occur in fibers that are shorter and wider, but because they occur in fibers with a range of wall thickness from thick, as is normal for libriform fibers, to thin, like that of a primary wall. This range prevents one from considering the crystal-bearing fibers of *Cercidium*, even when thin walled, as a form of axial parenchyma. Axial parenchyma cells in *Cercidium* are paratracheal, as is very common in Fabaceae, whereas the crystal-bearing fibers are diffuse in distribution. Diffuse axial parenchyma is not characteristic of woods of Fabaceae. Chambered crystals like those of *Cercidium* have been reported by Metcalfe and Chalk (1950) in other caesalpinoid genera: *Bauhinia* p.p., *Bussea, Copaifera, Cryptosepalum, Englerodendron, Hardwickia, Humboldtia, Peltophorum, Saraca, Schotia, Sindora,* and *Tamarindus*. In addition, I have observed them in *Cassia armata* Wats. and *Castanospermum australe* Cunn. (new records). As noted above, they do not occur in *Parkinsonia aculeata*. The thin-walled septate fibers mentioned by Metcalfe and Chalk (1950) for *Poeppigia* may be a kind of fiber dimorphism, as may be the fusiform parenchyma cells they mention for *Dinizia, Kingiodendron, Macrolobium,* and *Pterogyne*. With more exploration of wood of caesalpinoid legumes and perhaps other legumes as well, we may expect further reports of fiber dimorphism.

Vasicentric tracheids occur in two species of *Cercidium*, and these cells are associated with the formation of diagonal aggregations of vessels as seen in transection. The association between vasicentric tracheids and diagonal vessel aggregations has been reviewed elsewhere (Carlquist 1987), and Fabaceae are among the instances in which this phenomenon occurs.

In all of the *Cercidium* species for which larger wood samples were available, multiseriate rays average more than three cells wide at their widest points. We may assume that rays of this width would be found had larger-sized wood samples of the remaining species been available. Vessel element length and libriform fiber length also tend to be appreciably longer in the species for which larger wood samples were available. This is not surprising, because in typically woody dicotyledons, fusiform cambial initial length rises with age (Bailey and Tupper 1918). In the samples studied, vessel wall thickness also appears to increase with age.

TAXONOMIC CONCLUSIONS

Although the number of collections available was limited, one may cite characteristics of the taxa of *Cercidium* tentatively.

Cercidium andicola: vessels moderately grouped; vessel-vessel pits medium sized; vessel walls often with shallow grooves; verrucae on vessel walls dense, often aggregated into striate patterns; crystals in both fibers and ray cells; septate fibers present.

Cercidium australe: vessels moderately grouped; vessel-vessel pits medium sized, crateriform, with elongate cylindrical extensions; vessel walls not grooved; verrucae in vessel walls aggregated into polygonal groupings; crystals in both fibers and rays; septa not seen in fibers.

Cercidium floridum subsp. *floridum:* vessels little grouped; vessel-vessel pits large; vessel walls with grooves or without grooves; verrucae if present not ag-

gregated, either present in grooves or walls smooth; crystals present in rays but not seen in fibers; fibers prominently septate.

Cercidium floridum subsp. *peninsulare:* vessels moderately grouped; vessel-vessel pits large; vessel walls not grooved, verrucae not present; crystals present in rays and fibers; fibers prominently septate.

Cercidium macrum: vessels moderately grouped; vessel-vessel pits medium sized; vessel walls not grooved, smooth or with small wartlike verrucae; crystals observed only in a primary ray; septa not seen in fibers.

Cercidium microphyllum: vessels in moderately large groups, diagonal vessel aggregations that include vasicentric tracheids present; vessel-vessel pits medium sized; vessel walls not grooved, smooth; crystals seen in fibers but not in rays; septa not seen in fibers.

Cercidium praecox: vessels in moderately small groups; vessel-vessel pits medium sized, crateriform; vessel walls not grooved but with verrucae dense to very dense, forming striate patterns when sparser, coralloid aggregations when denser; crystals present in some ray cells and fibers; septa not seen in fibers.

Cercidium texanum: vessels in large groups, forming diagonal aggregations in which vasicentric tracheids are present; vessel-vessel pits large; vessel walls grooved or lacking grooves, smooth; crystals present in fibers (sometimes more than one crystal per chamber) and ray cells; septa not observed in fibers.

The above tabulation illustrates a number of probable specific distinctions. Vessel wall sculpture distinguishes some species, although note must be taken that within these species, the sculpture shows a range of expressions. Clear groupings of species in the sense of subgenera are not evident on the basis of wood features alone unless one wishes to stress particular features (e.g., presence of crateriform pits). The data from wood anatomy support the decision by Carter (1974) to treat as *C. peninsulare* subsp. *peninsulare* a taxon formerly considered a species.

Although wood of *C.* × *sonorae* was not analyzed with respect to all features, vessel walls of this hybrid do show intermediacy between those of its putative parents. The crateriform pits characteristic of *C. praecox* are present in *C.* × *sonorae,* but verrucae are present in reduced form, like the striate patterns beneath lines of verrucae in *C. praecox.*

Parkinsonia has traditionally been considered to be close to *Cercidium,* so close that union of the two genera has been advocated by some. Hybrids between *Cercidium* and *Parkinsonia* are known to exist (Carter 1974; Carter and Rem 1974). Wood anatomy speaks clearly for separation of *Cercidium* and *Parkinsonia.* In *Parkinsonia,* the following features are present, with contrasting character states in parentheses: vessel walls with long narrow grooves interconnecting pit apertures (grooves where present wide, shallow, relatively short); vessel walls smooth (vessel wall sculpture where present consisting of verrucae; crateriform pits in some species); libriform fibers monomorphic (libriform fibers dimorphic, some of the wider and shorter with chambered crystals); axial parenchyma paratracheal and initial (axial parenchyma paratracheal only).

With respect to wood anatomy, resemblances between *Cercidium* and *Parkinsonia* are no closer than resemblances between *Cercidium* and some other caesal-

pinoid genera (e.g., *Cassia* has dimorphic crystal-bearing libriform fibers like those of *Cercidium*).

ECOLOGICAL CONCLUSIONS

If one computes the value "Mesomorphy" (Table 1, column 14), one finds that the values are higher than are typical for desert shrubs in southern California (Carlquist and Hoekman 1985). However Mesomorphy values that are only moderately low also characterize other desert legumes, such as *Prosopis* (Carlquist and Hoekman 1985). The tendency of the larger shrubby legumes of desert regions to grow in streamed or wash habitats and the tendency of desert legumes to have extensive roots systems were cited as reasons for their moderate Mesomorphy values (Carlquist and Hoekman 1985). In the genus *Cercidium*, *C. floridum* subsp. *floridum* occurs in washes, canyons, and similar habitats with probable protracted water availability (Carter 1974); Carter says of *C. floridum* subsp. *floridum* that "its water requirements appear to be greater than those of *C. microphyllum*." This idea is supported by the Mesomorphy values of Table 1 (column 14).

If high degree of vessel grouping is indicative of xeromorphy, as claimed earlier (Carlquist 1984), and if vasicentric tracheid presence is indicative of xeromorphy (Carlquist 1985), especially when coupled with diagonal aggregations of vessels (Carlquist 1987), the woods of *C. microphyllum* and *C. texanum* are notably xeromorphic, and this appears correlated with relatively dry habitats as cited by Carter (1974).

The habitats of some *Cercidium* populations seem to be just as dry as those of desert shrubs that have lower Mesomorphy values according to the Carlquist and Hoekman (1985) computations. A possible explanation is the modifying effect of vegetative features of *Cercidium*: short duration of leaves, with green stems forming minimally vulnerable photosynthetic surfaces. The epidermis of stems of *Cercidium* have extraordinarily thick cuticles, usually much thicker than those illustrated by Gibson (1983) for *C. floridum*. Characteristics of the photosynthetic stems may therefore be a prime tool in water management for *Cercidium*, with other features subsidiary.

One should entertain the possibility that vessel wall sculpture may be correlated with xeromorphy (Carlquist 1982). If this correlation is valid, the various forms of vessel wall sculpture in *Cercidium* (vestured pits, crateriform pits, verrucae, grooves) represent forms of adaptation to dry conditions by increasing the surface area of the vessel wall. That all species do not have degrees of vessel sculpture in exact proportion to dryness of habitat does not necessarily invalidate the possible function hypothesized: vessel grouping and presence of vascular tracheids, for example, may be highly effective features in conferring water column redundancy and safety in *C. microphyllum* and *C. texanum,* whereas the dense verrucae of *C. andicola, C. australe,* and *C. praecox* may be mechanisms for assuring water-column integrity for those respective species. These latter three species may occupy habitats dry even for *Cercidium*, judging from the data given by Johnston (1924), Shreve and Wiggins (1964), and Carter (1974).

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