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Flora of the Lower Cretaceous Cedar Mountain Formation of Utah and Colorado, Part I. *Paraphyllanthoxylon utahense*

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FLORA OF THE LOWER CRETACEOUS CEDAR MOUNTAIN FORMATION OF UTAH AND COLORADO, PART I. *PARAPHYLLANTHOXYLON UTAHENSE*

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ABSTRACT.— *Paraphyllanthoxylon utahense*, sp. nov., is described from the Cedar Mountain Formation and compared with similar fossil and modern woods. Fossil angiosperm woods from the Early Cretaceous are of great interest because very few have been reported from strata of this age. This species demonstrates that the angiosperms had developed many of their modern characteristics by Early Cretaceous time.

The Lower Cretaceous Cedar Mountain Formation is fossiliferous at several localities. Fossils reported from this formation include the wood of conifers, *Tempskya*, and cycadeoids, charophytes, pelecypods, gastropods, ostracods, and fish scales (Stokes 1952, Young 1960, Thayn et al. 1973, Tidwell et al. 1976), as well as dinosaur bones (Bodily 1969).

A species of dicotyledonous wood assigned to the genus *Paraphyllanthoxylon* Bailey 1924, is described in this report from the Cedar Mountain Formation. This is the first report of petrified dicotyledonous wood from the diverse flora in this formation. These angiosperm woods are of great interest in that very few Early Cretaceous angiosperm woods have been previously reported. Since the Cretaceous Period is the assumed time for the origin of the angiosperms, a taxonomic study of Early Cretaceous angiosperm wood is significant in that it expands our knowledge of the early members of this division. The petrified wood described in this study was collected from two localities. Locality 1 is 6 road miles (3.7 km) east of Castle Dale, Utah, and Locality 2 is 9 road miles (5.6 km) east of Ferron, Utah (Figs. 1, 5, 6, 7).

The Cedar Mountain Formation at Locality 1 is composed of brown to grey shales. It contains at least one horizon of nearly coalified material from which *Tempskya* has been collected in growth position (Tidwell and Hebbert 1976). The dicotyledonous woods studied here were collected from a horizon between 10 (3.1 m) and 30 (9.2 m) feet below the overlying Dakota Sandstone, which is represented by 10 (3.1 m) to 20 (6.2 m) feet of coarse brown sandstone that forms a cap rock in the area.

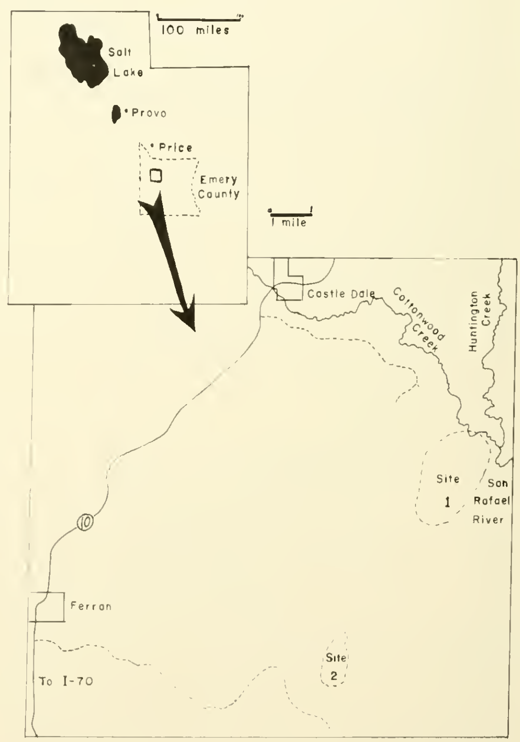

Fig. 1. Index map of collection sites.

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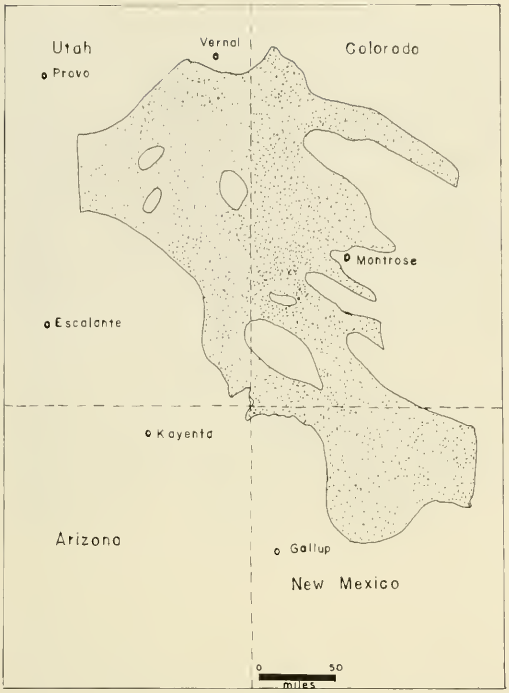

Fig. 2. Geographic extent of the Cedar Mountain Formation (after Young 1960).

Specimens were collected from seven different logs at Locality 2, where the Cedar Mountain Formation consists of a bed of coarse white sandstone underlaid by channel fills of yellow conglomeritic sandstones alternating with grey-green shales. These are, in turn, underlaid by a dark green nodular weathering shale (Figs. 5–7). The Dakota Sandstone is missing at this particular site, but reappears in the section about 3 miles (1.9 km) to the southeast. Dicotyledonous woods were found associated with *Tempskya* and fossil conifer wood at this locality.

Stratigraphy of the Cedar Mountain Formation

Stokes (1944) defined the Cedar Mountain Formation as those sediments lying between the Brushy Basin Member of the Upper Jurassic Morrison Formation and the Lower Cretaceous Dakota Formation. These strata were formerly considered part of the Morrison Formation. Cedar Mountain deposits are present over much of eastern Utah, western Colorado, and northwestern New Mexico (Fig. 2). Stokes (1952) defined two members of the formation, the Buckhorn Conglomerate at the base and the Cedar Mountain Shale at the top. At the type locality near Castle Dale, Utah, the Buckhorn Conglomerate is thick and massive, but it generally thins to the east and is absent on the eastern side of the San Rafael Swell. East of the Colorado River a mudstone and conglomeritic sandstone unit occupies the same

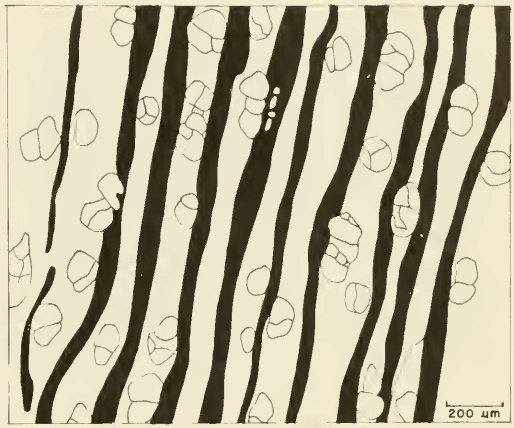

Fig. 3. *Paraphyllanthoxylon utahense*—Illustration of the transverse section showing the relative abundance of ray tissue (dark areas) and the size, shape, and arrangement of the vessel elements (open circles). Note the radial pore multiples.

Fig. 4. *Paraphyllanthoxylon utahense*—Illustration of the tangential section showing the size, shape, and arrangement of the rays (dark lines) and a vessel element (center).

Fig. 5. Ferron collecting site, showing the lithology. A is white sandstone cap, B is the surface of the yellow conglomeritic channel fill from which the specimens were recovered, and C is the underlying grey-green shale.

relative position as the Cedar Mountain Formation on the west side of the river. These rocks were termed the "Post-McElmo" beds (Coffin 1921), but were later renamed the Burro Canyon Formation (Stokes and Phoenix 1948). Young (1960) proposed that the Burro Canyon Formation and the Cedar Mountain Formation are a physically continuous unit and should both be referred to as Cedar Mountain Formation.

Based on the presence of the pelecypods *Protoelliptio douglassi*, *Unio farri*, and the conifer *Frenelopsis varians*, as well as the stratigraphic position of the Cedar Mountain Formation, Young (1960) as well as Stokes (1952), suggested that it is Lower Cretaceous in age. Another indication of its age is the presence of *Tempskya*, which Read and Ash (1961) considered to be an index fossil to the Lower Cretaceous (Albian). Fisher et al.

Fig. 6. Overview of the Ferron collecting site. Snow-capped mountains in the background are in the Wasatch Plateau. Dicotyledonous logs along with *Tempskya* were collected from the uppermost layer of sediment shown in the foreground.

Fig. 7. Petrified dicotyledonous wood shown as it is found weathered upon the surface of the Ferron site.

(1960) listed the formation as Aptian, but it may be only Albian or, most probably, may include rocks of both ages.

Paraphyllanthoxylon utahense sp. nov.
Figs. 3–4, 8–18

DESCRIPTION.— This species is described from several pieces of black petrified secondary wood. The preservation is excellent, and fine structural detail can be observed.

Growth rings: Lacking.

Vessels: Diffuse porous, approximately 12/mm², solitary or more commonly in radial rows (pore multiples) of 2–3 up to 5 cells long; individual vessels range from 204 μm radial by 165 μm tangential diameter to 58 μm radial by 48 μm tangential, average 105 μm radial by 93 μm tangential diameter; perforations exclusively simple, located on oblique end walls; thin-walled tyloses abundant, obscuring the vessel length; vessel walls 3 μm–5 μm thick; tangential pitting with numerous, often appressed, 6 μm–10 μm diameter; alternate bordered pits with slitlike apertures and occasionally up to 12 μm long, slightly bordered pits with large elliptic apertures probably representing the vessel to parenchyma pitting; radial intervascular pitting similar to tangential; vessel to ray intervascular pitting similar to tangential; vessel to ray pitting consisting of small circular or large, up to 24 μm, scalariform, elliptic to angular slightly bordered pits; 3–6, occasionally more, pits per crossover field.

Axial Parenchyma: Rare, apotracheal diffuse or scanty paratracheal.

Rays: 12/mm², heterogeneous with both uniseriate and multiseriate present; uniseriate

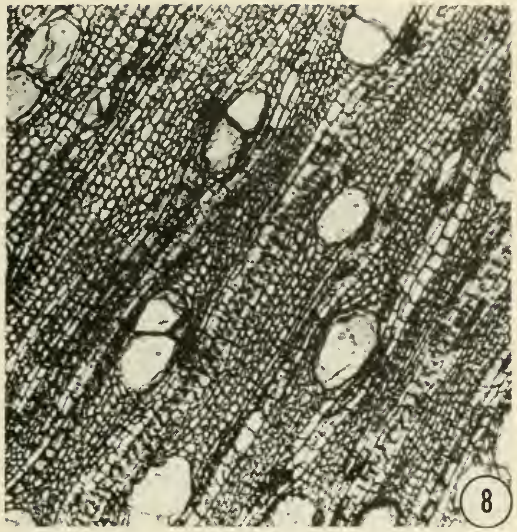

Fig. 8. Transverse section illustrating solitary vessels and vessel chains with tyloses. Note that the axial parenchyma is scarce (65X).

rays rare, many partially biseriate, with both procumbent and upright cells, uniseriate rays range from 2 cells (80 μm) to 6 cells (300 μm) high (average 5 cells, 200 μm–220 μm); multiseriate rays range from 9 cells (380 μm) to 33 cells (1360 μm) high and 2 cells (30 μm) to 5 cells (100 μm), wide with 106 rows (commonly 2) of upright border cells; procumbent cells range from 25 μm–40 μm vertical, 50 μm–80 μm radial, and 25 μm–45 μm tangential diameter; some cubodial cells present, approximately 40 μm in diameter; upright cells approximately same size as procumbent but radial and vertical dimensions reversed; ray cells' walls 2.5 μm thick, pitted and appearing beaded in radial section.

Fibretracheids: Septate, libriform, round to square in cross section, approximately 36 μm in diameter, with approximately 2.4 μm thick walls.

Repository: Brigham Young University, 2190 (Holotype)

Horizon: Cedar Mountain Formation

Age: Early Cretaceous

Discussion

Twelve species of *Paraphyllanthoxylon* have been described in the past. The features generally constant in all of these reported species are as follows:

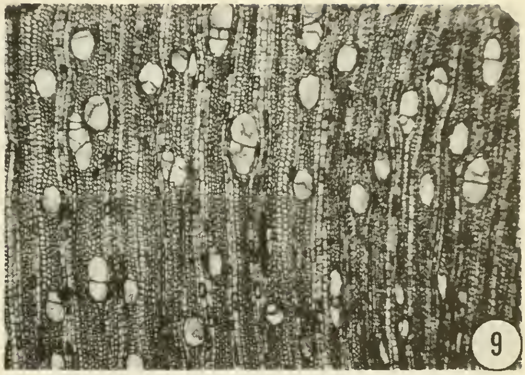

Fig. 9. Transverse section illustrating distribution of vessels and multiseriate rays (30X).

Diffuse porous wood; vessels in radial rows (pore multiples); exclusively simple perforations; alternate intervascular pitting; elongate vessel to ray pitting; rays of two sizes, 1–7 seriate, heterocellular with 107 rows of upright border cells, rays commonly over 1 mm high, axial parenchyma lacking or scanty apotracheal diffuse, scanty paratracheal, or combination of both; septate fibretracheids; vessels commonly with tyloses.

Paraphyllanthoxylon utahense fits well within the boundaries of this genus.

Comparison with Described North American Species

Three species of *Paraphyllanthoxylon* have been described from Cretaceous strata in North America.

Paraphyllanthoxylon arizonense Bailey 1924.—*Paraphyllanthoxylon utahense* differs from the upper Cretaceous *P. arizonense* in several ways. The most obvious variations are the size of the vessels and rays. Although Bailey (1924) gave no measurements and merely stated that the vessels of *P. arizonense* are large, it can be seen that the vessels shown in his figures at 35X are almost as large as those of *P. utahense* at 65X. Also, the rays shown at 35X in his figures are approx imately twice as high and wide and more parallel in outline than those of *P. utahense* at a comparable magnification. Another difference is that *P. arizonense* has slitlike pits on the fiber walls that *P. utahense* lacks. On the basis of these differences, the Utah specimens have been determined to be distinct from *P. arizonense.*

Paraphyllanthoxylon idahoense Spackman 1948.— *Paraphyllanthoxylon utahense* is closer to *P. idahoense,* which was reported

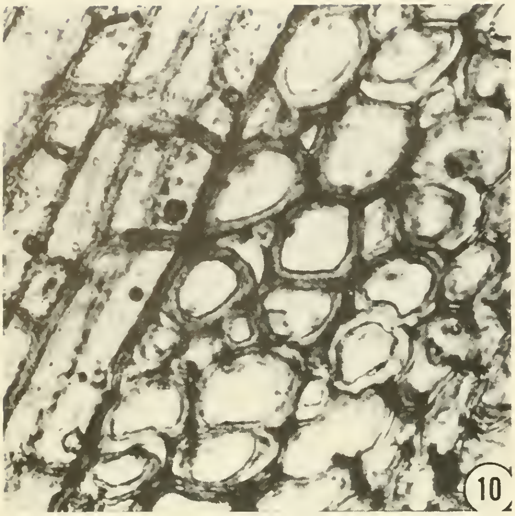

Fig. 10. Transverse section illustrating a closeup view of fibretracheids and a heterocellular multiseriate ray (495X).

Fig. 12. Radial section illustrating the relative size and distribution of the vessels and cells of the heterocellular rays (33X).

from the Lower Cretaceous Wayan Formation of Idaho, than to other *Paraphyllanthoxylon* species. The diameter of the vessels in *P. idahoense* is 60 μm–160 μm.

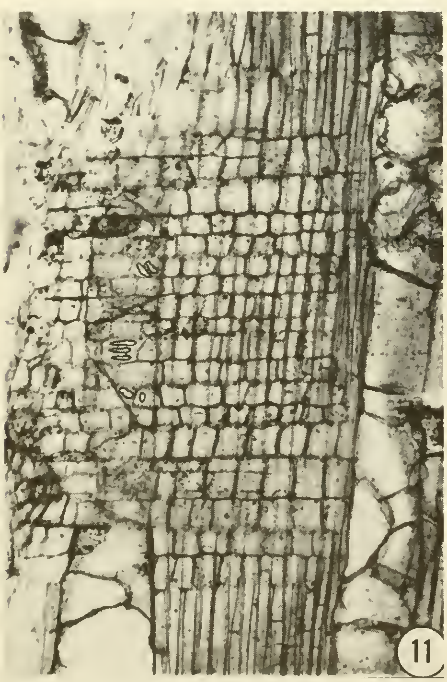

Fig. 11. Radial section with irregularly shaped vessel to ray cell crossover pits inked in. The beaded nature of the ray cell walls can also be seen (100X).

However, in comparing the holotype slides of this species with those of *P. utahense*, it can be seen that the vessels of the former are distinctly larger than those of the latter, which are 48 μm–165 μm in tangential diameter. The pitting is similar in both species, and the intervascular pits are also alternate, circular elliptical, and sometimes compacted and angular. The bordered pits of *P. idahoense* are 10 μm–12 μm in diameter, whereas, those in *P. utahense* vary from 6 μm to 10 μm in diameter. The major differences between these two species are the compaction of the vessels and the size of the rays. The number of vessels per square millimeter was not given for *P. idahoense*, but its vessels are more tightly compacted than those in *P. utahense.* The rays in *P. idahoense* are made up of smaller cells and are narrower than those of *P. utahense*, although both have multiseriate rays from two to five cells wide. Since *P. utahense* has smaller vessels that are fewer in number per square millimeter, and larger rays than *P. idahoense*, these two species are considered distinct from one another.

Paraphyllanthoxylon alabamense Cahoon 1972.– As described by Cahoon (1972) from the Upper Cretaceous Tuscaloosa Formation, this species has a wide range of variation, which can be seen by comparing Figures 5, 11, and 14 of her paper. These photos are all

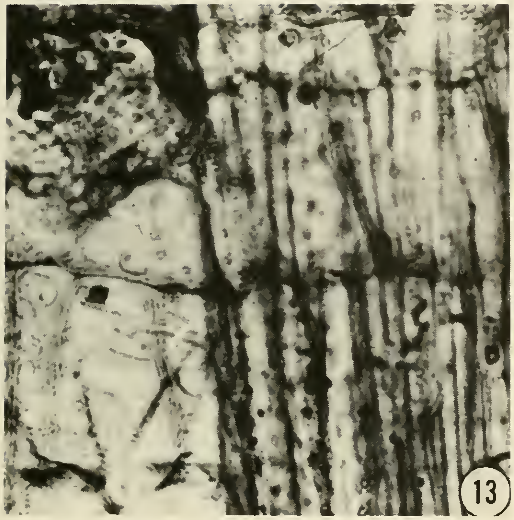

Fig. 13. Radial section illustrating the irregularly shaped, narrowly bordered vessel to parenchyma pits (495X).

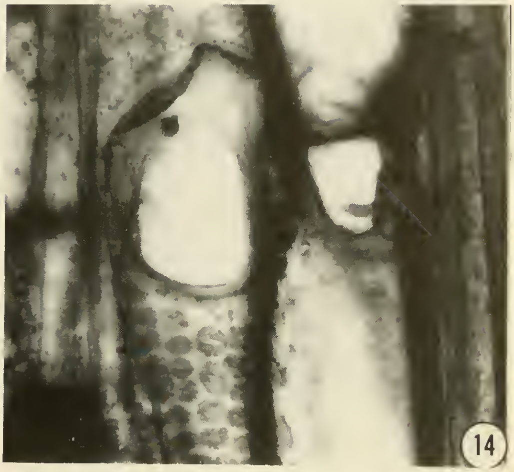

Fig. 14. Radial section illustrating oblique simple perforation plates and oppositely arranged bordered intervascular pits with slitlike apertures on the radial vessel wall (495X).

listed as being magnified 55X, but the rays in Figure 5 are approximately five times wider than those in Figure 14. She stated that this species was described from 11 different type specimens that are all similar but show some variation. The most obvious variation is in the size of the rays. Barghoorn (1941) has shown that such variation could conceivably be found within a species or even within the trunk of an individual tree, but, since paleobotanists are often restricted to working with fragments, they have traditionally described such fragments as form genera and hence form species. Spackman (1948) distinguished *P. idahoense* from *P. arizonense* because *P. idahoense* has smaller vessels, less abundant pitting, and smaller rays and ray cells. He stated that:

> The magnitude and nature of these variations are well within the range of variability found in individuals of many living species, and thus the differences in the two fossils might be accounted for on the basis of the part of the tree from which the specimen was derived, differences in growth rate, etc. In spite of this, however, it seems appropriate, because of these differences to describe this new wood as a new species with the hope that the true relationship of these two fossils will be demonstrated in the future. (Spackman, 1948, p. 108).

We agree with Spackman's reasoning, and therefore believe that *P. alabamense* as it now stands includes at least two or three form species. Therefore, *P. utahense* cannot be accurately compared to it at this time. The holotype specimen shown by Cahoon (1972) appears to differ from *P. utahense* by having larger rays. The other specimens reported by her appear similar to *P. utahense*, although one has larger rays and the other has smaller. Before any conclusions can be drawn as to the species boundaries and relationship between *P. utahense* and the Alabama specimens, more detailed measurements and comparisons need to be made.

Paraphyllanthoxylon pfefferi Platen 1908.— This species was collected from the Tertiary of California. It was originally described as *Carpinoxylon pfefferi* (Platen 1908), but was combined with *Paraphyllanthoxylon* by Madel (1962). *Paraphyllanthoxylon utahense* has larger vessels (up to 204 μm radial diameter as opposed to 137 μm radial diameter), which are fewer per square millimeter (12 compared to 44), and broader rays (100 μm compared to 50 μm) than *P. pfefferi*.

Comparison With Other Paraphyllanthoxylon Species.— Paraphyllanthoxylon utahense differs from species of *Paraphyllanthoxylon* described from geographical areas beyond the boundaries of North America (Table 1) in such features as the size and density of the vessels and dimensions of the

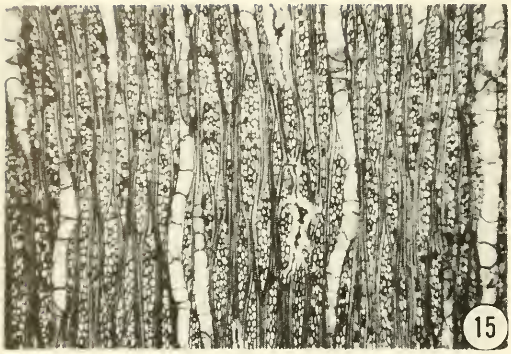

Fig. 15. Tangential section illustrating the relative size and distribution of multiseriate rays, fibretracheids, and vessels with tyloses (30X).

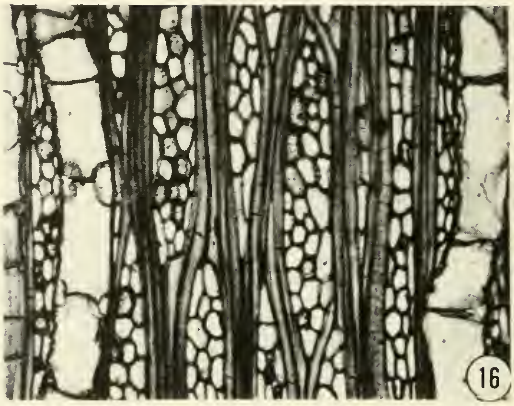

Fig. 16. Tangential section illustrating the heterocellular rays and septa in the fibretracheids (100X).

rays. *Paraphyllanthoxylon utahense* is most similar to *P. capense* but differs in having fewer vessels per square millimeter, and vessels that are larger and fewer per pore multiple.

Affinities of Paraphyllanthoxylon.— The original species, *Paraphyllanthoxylon arizonense*, was described by Bailey (1924) from silicified wood fragments of the Colorado Group in Arizona. He proposed the name to indicate a relationship to *Bridelia* and *Phyllanthus* in the section Phyllanthoidea of the Euphorbiaceae. Madel (1962) combined woods which had been described as *Phyllanthinium* and *Glochidioxylon* into the genus *Paraphyllanthoxylon* and reserved the genus for woods with general structure of the Glochidion wood group of the Euphorbiaceae. Other authors have compared their species to a number of genera in several other families.

Although *Paraphyllanthoxylon alabamense* may be an aggregation of species, further information concerning the affinities of the genus may be inferred by the leaf compressions that occur along with it in the Tuscaloosa sediments. Cahoon (1972) reported that of the families with wood similar to *Paraphyllanthoxylon* only the Sapindaceae, Euphorbiaceae, and Lauraceae are represented by fossil leaves from the Tuscaloosa.

Phylogenetic Considerations.— The processes of convergent and divergent evolution have obscured the genealogy of even modern genera and species. Pax and Hoffman (1931) considered the Euphorbiaceae to be polyphyletic in origin, making it unlikely that the Lower Cretaceous *Paraphyllanthoxylon* species are ancestral to the various groups within the family. The possibility does exist that they are ancestral to at least some members of the Glochidion group. Considering the large number of genera that are similar to the genus, *Paraphyllanthoxylon* could be related to the taxon from which several genera in many families originated.

By comparing the features of *Paraphyllanthoxylon* with Tippo's (1946) list of primitive and advanced wood characteristics (Table 2), it can be seen that the anatomy of the Lower Cretaceous members of the genus supports evidence from fossil leaf com-

Table 1. *Paraphyllanthoxylon* species from outside of North America.

Species	Author	Occurrence
pseudohobashiraishi	Ogura, 1932	Tertiary of Japan
sahnii	Prakash, 1958	Tertiary of India
tertiarum	Ramanujam, 1956	Tertiary of India
bangalamodense	Navale, 1960	Tertiary of India
keriense	Dayal, 1968	Tertiary of India
capense	Madel, 1962	Upper Cretaceous of S. Africa
yvardi	Koeniguer, 1967	Neogene of France
teldense	Prive, 1975	Oligocene of France

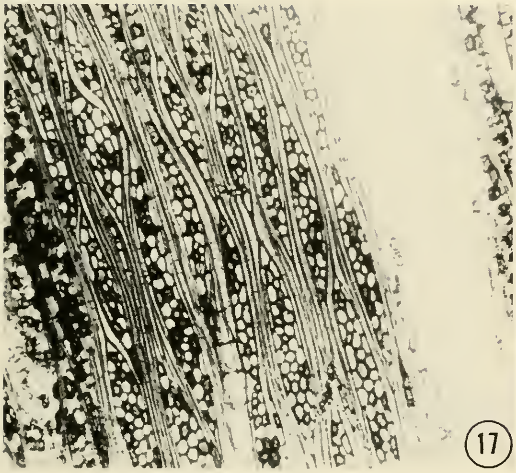

Fig. 17. Tangential section illustrating various sizes and shapes of rays and dark cell contents in many of the ray cells (50X).

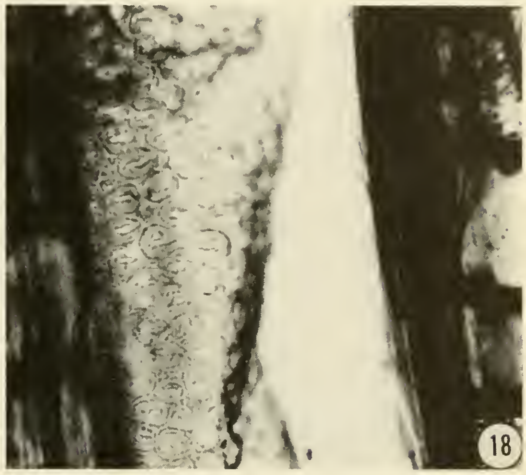

Fig. 18. Tangential section showing appressed, oppositely arranged, bordered pits with slitlike apertures on the tangential vessel wall (495X).

pressions that the angiosperms had developed many of their modern characteristics by Early Cretaceous times.

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TABLE 2. Comparison with primitive and advanced features.

	Primitive							Advanced						
	Scalariform plates	Oblique end walls	Solitary pores	Diffuse wood parenchyma	Scalariform-transitional pitting	High heterogeneous rays	Nonstratified wood	Simple perforations	Transverse end walls	Pore aggregates	Aggregate wood parenchyma	Alternate pitting	Low heterogeneous or homogeneous rays	Stratified wood
Paraphyllanthoxylon		X[a]		X			X	X		X		X	X[b]	

[a](X) indicates that species of *Paraphyllanthoxylon* possesses that feature.
[b](X) has low heterogeneous rays.

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