CYCAD ANATOMY AND FOSSIL OCCURRENCES IN TEXAS

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Cycadophyta presently consists of the living order Cycadales, which is comprised of three families worldwide. In the Mesozoic, cycads were represented by the Cycadales, plus another large order, Cycadeoidales (also referred to as Bennettitales). Cycadophyta is thought to have evolved from the Paleozoic seed ferns (pteridosperms), as did conifers, and eventually, angiosperms. However, Cycadales and Cycadeoidales likely arose from two distinct forms of pteridosperms. Their similarity is thought to be the result of convergent and/or parallel evolution (Norstag & Nicholls, 1997). Cycadeoid remains are much more prevalent in the fossil record, and thus it is thought they were a common constituent of the plant assemblage. (Conversely, Cycadales are relatively rare in the fossil record). Ultimately, Cycadeoids became extinct by the end of the Cretaceous. One theory postulates that they were dependent on specific insects to spread their pollen from plant to plant because the female ovule was completely encapsulated within the cone and that for some reason they lost their insect-pollinators (Norstag & Nicholls, 1997). However, others feel that the Cycadales had evolved a slightly more advanced megaspore and ovule structure, thus allowing them to survive into the Tertiary whereas many other organisms, including dinosaurs, failed to adjust to environmental changes at the end of the Cretaceous (Tidwell, pers. comm.).

“The two orders are very similar, particularly with respect to general growth habit and leaf organization. Trunks of both orders range from short and squat [Figure 2] to tall and columnar [Figure1] and are covered by a protective layer of leaf bases that persist after the leaves drop off…The basic difference between [the two is that] cones occur at the apex [top] of the stem [in] living cycads [Figure 1], but are embedded among the leaf bases in cycadeoids [Figures 2-5]” (Tidwell, 1998). There are other primary differences that set cycadeoids well apart botanically from the Cycadales, such as the method of origination of leaf bases within the trunk and the cellular configuration of leaf epidermis.

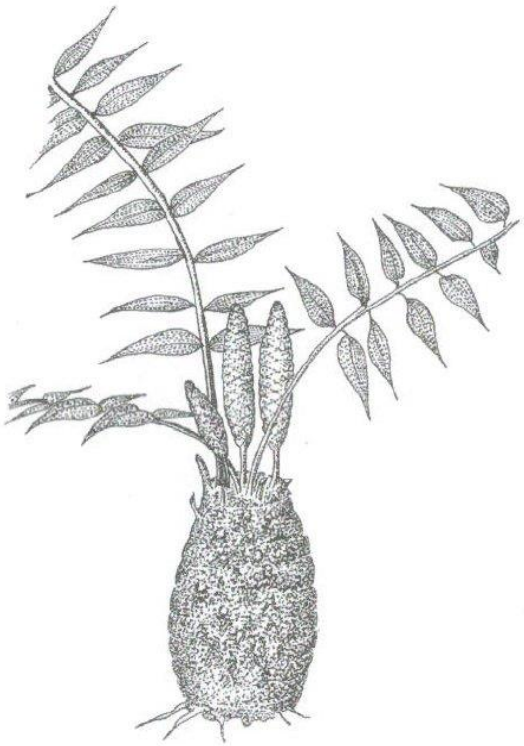

Figure 1: Cycadalean structure (from Tidwell, 1998).

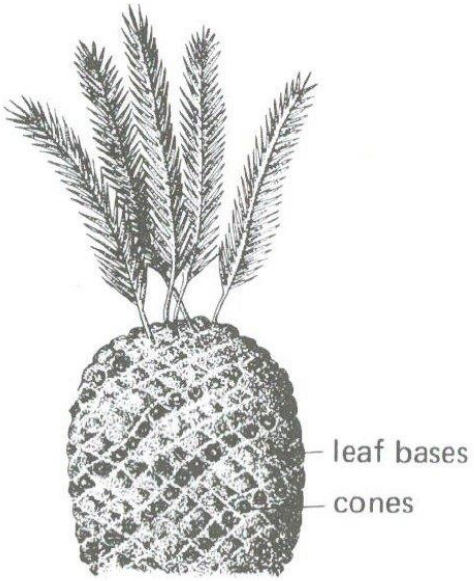

Figure 2: Cycadeoidalean structure (from Tidwell,1998)

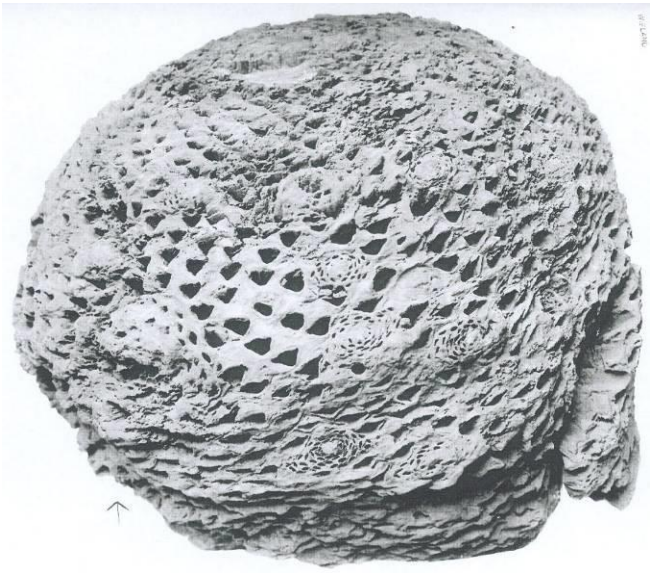

Figure 3: Cycadeoid trunk showing cones and leaf bases (from Wieland, 1916).

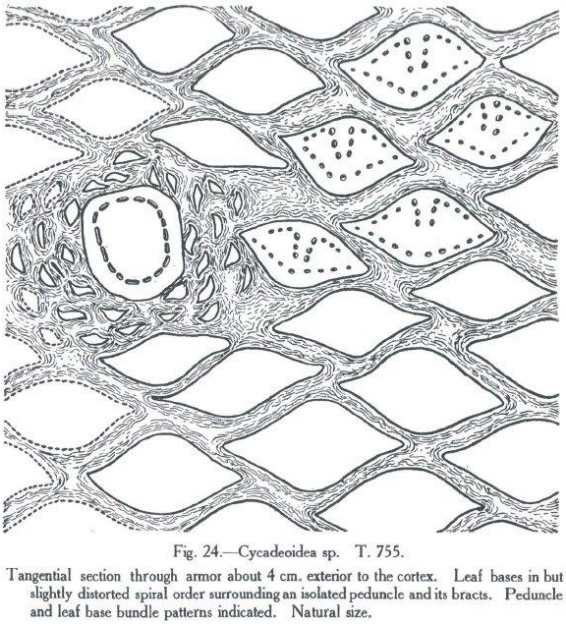

Fig. 24.—Cycadeoidea sp. T. 755.

Tangential section through armor about 4 cm. exterior to the cortex. Leaf bases in but slightly distorted spiral order surrounding an isolated peduncle and its bracts. Peduncle and leaf base bundle patterns indicated. Natural size.

Figure 4: Cycadeoid tangential section 4 cm from exterior of trunk showing leaf bases and a cone (from Wieland, 1906).

Typical Series of Piedmont-Black Hawk Cycadeoideas. ×0.09.

Figure 5: Yale University cycadeoid collection from the Black Hills of South Dakota (from Wieland, 1916).

Interestingly enough, from a distance cycads look something like small palm trees with stout stems because of the persistent leaf bases on the exterior of the trunk and the crown of spirally-arranged compound leaves. Because of this similarity, a cycad imported from the Far East and used as a potted and landscape plant in the Southern U.S. has been given the common name “Sago Palm”!

Cycad Anatomy: In transverse section, the stele (or trunk) of Cycadales and cycadeoids has a large central pith (or *medulla*) surrounded by a broad ring of vascular tissue composed of secondary xylem and secondary phloem dissected by wide rays (Figures 6 and 7). The secondary xylem is composed of a high percentage of parenchyma among the normal tracheid cells (called *manoxylic*). This is followed by a cortex and then an outer “armor” that is composed of *ramentum* (described below), leaf bases, and (in cycadeoids) cones (Figures 6 and 7). Both the pith and the cortex can contain secretory canals (Figure 7). Leaf traces in the cortex appear as a C-shaped bundle (Figure 6), similar to fern leaf traces.

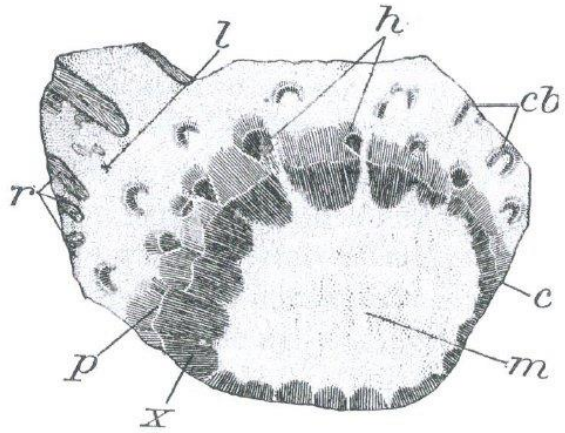

Fig. 35.—Cycadella sp.

Transverse section through the summit of a small silicified trunk from the Freezeout Hills, Carbon County, Wyoming, showing the medulla, woody cylinder, cortex, and a portion of the enveloping armor of old leaf bases. Natural size.

m, medulla; x, xylem; c, cambium; p, phloem; h, leaf (or peduncle) traces arising from the xylem or woody cylinder; cb, horseshoe-shaped cortical bundles, or leaf traces; l, insertion of leaf base in cortex; r, ramentum of leaf bases.

Figure 6: Transverse section through the upper portion of a cycadeoid trunk with anatomical features identified (from Wieland, 1906).

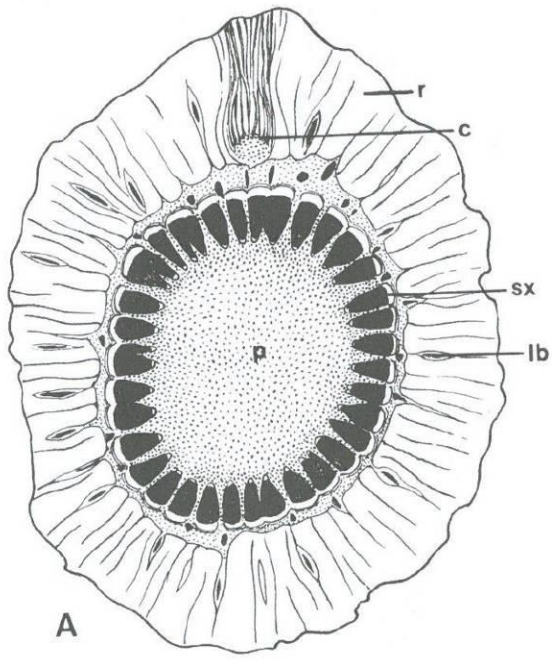

Figure 7: Transverse section through the mid-section of a cycadeoid trunk showing pith (p), secondary xylem (sx), and a thick armor consisting of ramentum (r), leaf bases (lb), and cone (c). Cortex is thin and is between secondary xylem and ramentum (from Stewart and Rothwell, 1993).

The outer armor of a cycad trunk consists of leaf bases that remain after the leaf dies and falls off. Leaf bases appear rhombohedral in cross section and give cycad trunks their distinctive look (Figures 2, 3, and 4). On the exterior of the trunk between the leaf bases is a dense packing of *ramentum*, which can either be long, scaly hairs or flat, tongue-shaped scale-like structures known as cataphylls. Their purpose is entirely one of protection. As they age, they may lose their tips and become embedded between leaves. Thus, cycad trunk armor may be half ramentum (by volume), densely packed between the leaf bases and, in cycadeoids, the cones.

Cycadeoid cones appear on the exterior of the trunk as a circular mass surrounded by small leaf traces (Figures 3 and 4). In cross-section, cones extend through the entire armor section, opening their distal end to the outside upon maturity (Figure 7). The cones themselves contain the pollen and seed producing structures (Figures 8 and 9), and are often seen in exquisite detail in fossil specimens. The presence of cones in the armor section of a fossil cycad positively identifies it as a cycadeoid rather than Cycadalean. For instance, the popular Patagonian (Argentina) cycads are Jurassic in age and show obvious cones, thus they are cycadeoids.

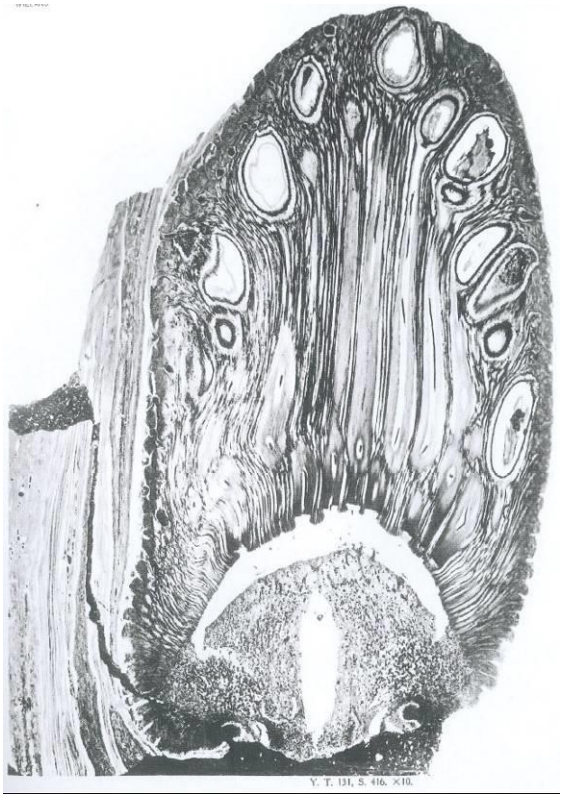

Figure 8: Longitudinal section through ovulate cone of a cycadeoid. This cone is mature and shows developed seeds (10x) (from Wieland, 1916).

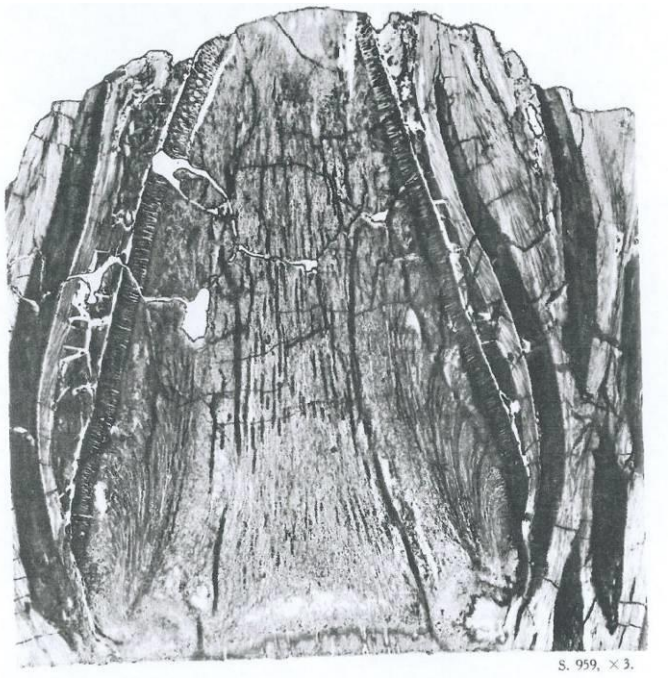

Figure 9: Longitudinal section through ovulate cone of a cycadeoid. This cone is young and is only starting to develop ovules (3x) (from Wieland, 1916).

The stem morphology of cycad trunks varies considerably depending on the species as well as on the vertical position in the trunk. A thick armor made up of leaf bases and ramentum is likely in the lower sections, thinning upward toward the apical meristem (growth tip). The secondary xylem is also likely to be thicker in lower portions which have undergone multiple years of annual growth (Figure 10). The cortex is likely to be developed in the upper portions where new growth is prominent. The pith is present through the entire stem (Figures 10 and 11), but both the cortex and the pith are less dense (more spongy) than either the secondary xylem or armor. During growth this can lead to either being squeezed or compressed, and compressive stresses during fossilization can lead to a considerable reduction in volume of both. (Note that on many of the illustrations in this text the cortex is either thin or not visible).

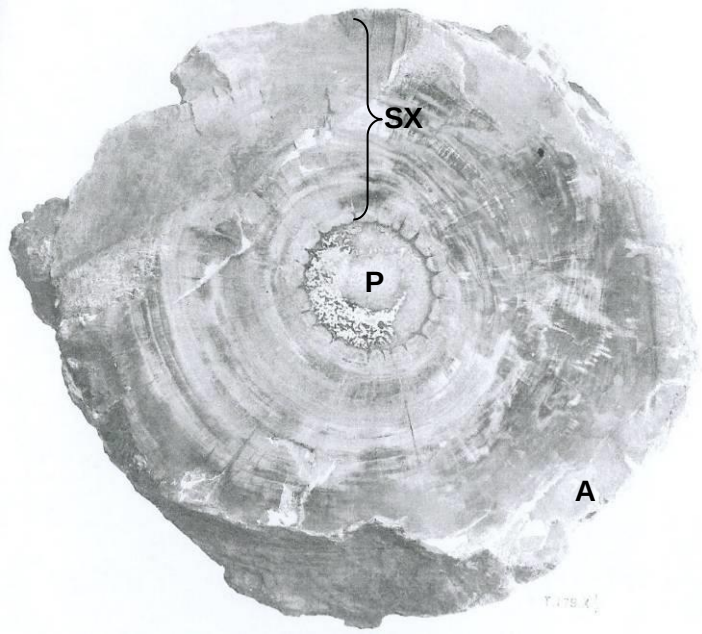

Figure 10: Transverse section through the base of a Cycadeoidea jenneyana trunk showing a small pith (P), thick secondary xylem (SX), and an armor section (A) that has been mostly eroded away (from Wieland, 1906).

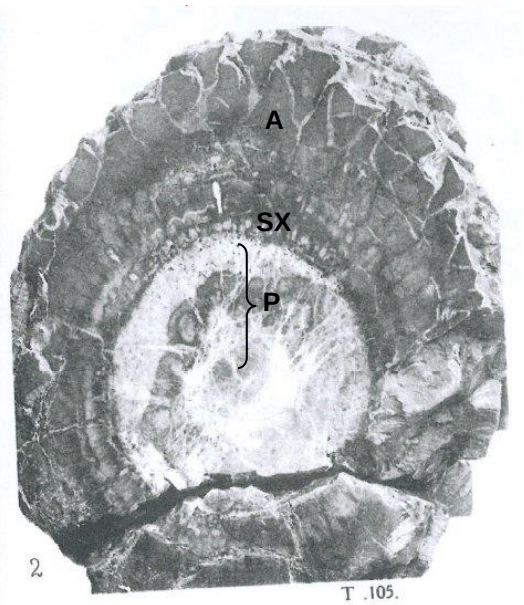

Figure 11: Transverse section through the mid region of a Cycadeoidea stillwelli trunk showing substantial pith (P), minimal secondary xylem (SX), and a thick armor (A) (from Wieland, 1916).

Occurrence in Texas: Both cycads and cycadeoids occur in Texas, although they are not common or widely reported. Fontaine (1893) described an abundance of cycad, conifer, and fern leaves from the Glen Rose Formation, Lower Cretaceous (Trinity Group), two miles up the Paluxy River from the town of Glen Rose. His specimens were from limestone that he judged was deposited some distance from shore. He did not, however, mention any cycad trunks (or any wood) being found.

Wieland (1931), the well-regarded early researcher in fossil cycads, described a visit to Stephenville where, through the courtesy of a number of devoted rockhounds, he obtained numerous cycadeoid trunks for the U.S. National Museum at Yale. Wieland identified and named five distinct species. The specimens were collected from a variety of locations, but all were from the lowest Cretaceous Trinity Group. Based on current nomenclature, the localities (and formations in parentheses) are, from north to south (Figure 12):

- Bridgeport, Wise County (Antlers Sand or Twin Mountains)
- Tolar, Hood County (Paluxy Sand)
- Stephenville, Erath County (Paluxy Sand)
- Comanche, Comanche County (Twin Mountains)
- Fredericksburg, Gillespie County (Hensell Sand)

Figure 12: Locations where cycads have been found in Texas. Five-sided stars are Early Cretaceous localities; 4-sided star is Tertiary cycad site. Map courtesy of the U.S. Census Bureau (http://quickfacts.census.gov/qfd/maps/).

Cycads occur in the Tertiary of Texas, in a region of the central Gulf Coast encompassing Karnes, Live Oak, and McMullen Counties (although the actual extent may be larger). There is some uncertainty surrounding the actual age of these cycads. They occur in the George West area (Goliad Formation, Miocene, Figure 12), and I have heard reports that they occur in the prolific Manning Formation (Upper Eocene Jackson Group). However, I have not personally verified the Manning Formation reports. Compounding this issue, the Goliad Formation in the George West area is problematic. These caliche-impregnated sediments are derived from the paleo-Nueces River and floodplain. Many (but not all) of the specimens are rounded, indicating they have undergone transport and weathering at some time in the past. Thus, they may or may not represent in-situ material, and therefore may or may not be derived from Miocene age plants. It is apparent that further research and documentation is needed on these fossil remains.

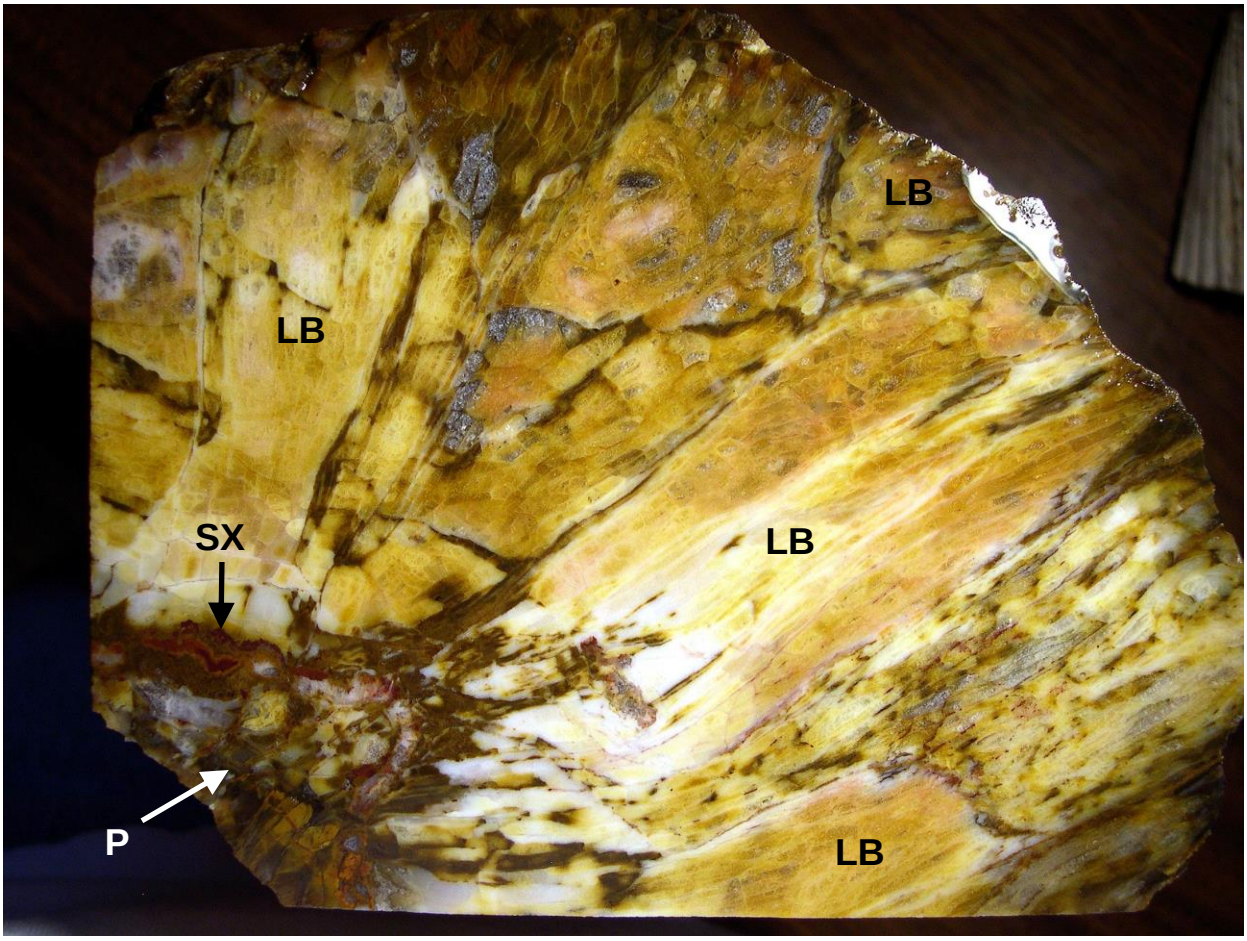

Figure 13: One quarter section of a fossil cycad from George West, Live Oak County (Goliad Formation, Miocene). Although very mineralized, several anatomical features are present [pith (P), secondary xylem (SX), leaf bases (LB)]. The outer portion of the trunk was missing due to weathering. Specimen is 5" across from left to right. (Singleton Collection)

Figure 13 shows a section of a George West fossil cycad. This specimen is from a sizable cycad trunk. Prior to slicing, it was about 6" in diameter and 10" tall, and the diameter only represented about ¼ of the trunk. The remainder had undoubtedly broken off due to natural fracturing and weathering.

Mineralization is substantial, which is typical for material from that area. Despite this, basic anatomical features of a cycad can be seen, including the pith, secondary xylem, and several leaf bases. Possibly due to the extensive mineralization, the cortex section is not apparent. However, the armor section is identifiable by the presence of several leaf bases.

Acknowledgements

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