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A PALM FROM THE UPPER CRETACEOUS OF NEW JERSEY.

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Art. XXXVIII.—*A Palm from the Upper Cretaceous of New Jersey*; by Neil E. Stevens.

The silicified palm stump which forms the basis of the present study was presented to the Peabody Museum of Yale University by Mr. R. W. Deforest in 1893. But it received no special examination for some ten years, when Dr. G. R. Wieland made several sections from the roots. These sections showed that the structure was unusually well conserved, and

Fig. 1.

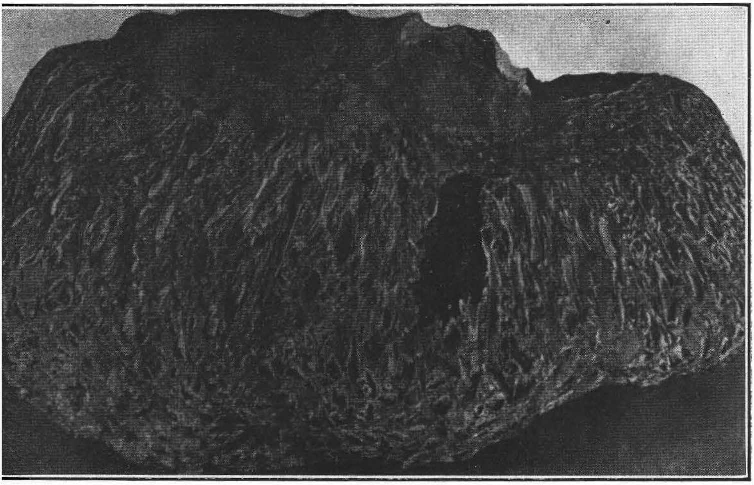


Fig. 1. *Palmoxylon anchorus.* Lateral view of entire specimen. × 2/5. Photograph by G. E. Nichols.

finally in the spring of 1911 the specimen was, at Dr. Wieland's suggestion, turned over to the writer for definite study. The various additional sections made by the writer for this study have been deposited, together with the original sections and the type, in the Paleobotanic Collections of Peabody Museum.

The fossil was found by Mr. Deforest on the beach at Seabright, not far from Sandy Hook, and comes accordingly from near the limit of the Upper Cretaceous outcrops on the Jersey Shore. Other specimens, in less perfect preservation, were seen, though the present specimen is the only one so far recovered. The matrix appears to have been a marl, or perhaps clay with little or no lime. This specimen (fig. 1) consists of the much-eroded base of the trunk of a large palm with the proximal portions of the heavy and dense clump of attach roots. Whether most of the wear preceded silicification or r must of course be largely a matter of conjecture.

Stem.

As will be seen from figs. 1 and 2, comparatively little the once large stem remains and, on the whole, the preservati of the stem parts is not nearly so good as that of the roo

FIG. 2.

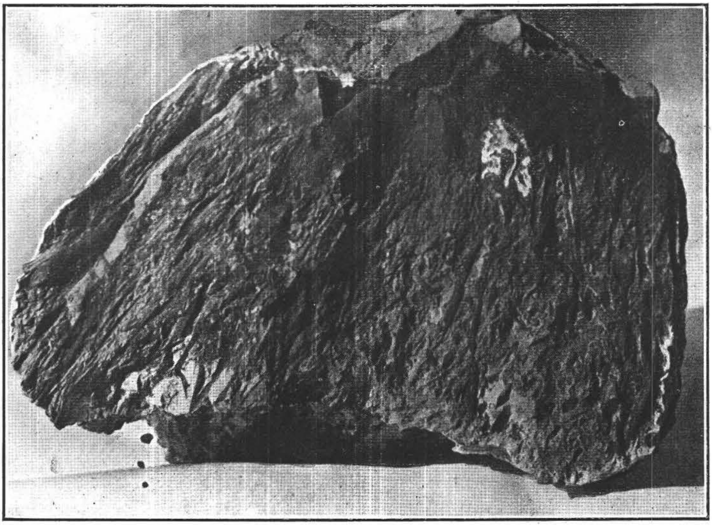


FIG. 2. Longitudinal section of specimen near the middle, showi crowded roots and small amount of wood. × 2/5. Photograph by G. Nichols.

The latter are in an almost perfect state of preservation, f exceeding that of any fossil palm roots hitherto describe This circumstance, together with the fact that fossil palm roo have so rarely been found and have not been very fully d scribed, made a rather careful study of the anatomy of th specimen seem worth while.

In the following paper no attempt is made to review tl literature either on fossil palms or on the anatomy of pal roots, as both subjects have been treated at length in rece monographs. Stenzel* describes sixty-two species of fossil pal

* Stenzel, K. G.—Fossilen Palmenohölzer. Beiträge zur Paläontologie a Geologie Österreich-Ungarns und des Orients, Band XVI, Heft IV, p. 1–18 1904.

woods and four species of fossil palm roots, while Drabble* has studied the root anatomy in a large number of living species of palm. These papers give full citations of the literature in their respective fields.

The maximum height of the specimen (cf. figs. 1 and 2) is 15^{cm}, its breadth 23^{cm}, its length 28^{cm}, and only a small portion of the base of the stem remains, most of which is less well preserved than the roots. Consequently the amount of material from which stem sections could be made was not large. More-

FIG. 3.

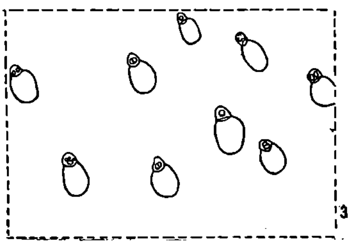


FIG. 4.

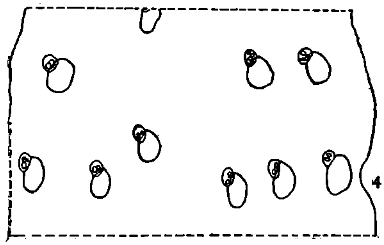


FIG. 3. Outline showing relative size and arrangement of vascular bundles in the inner portion of the stem. × 5. The bundle shown in fig. 5 was taken from this slide.

FIG. 4. Outline showing relative size and arrangement of vascular bundles in the outer portion of the stem. × 5. The bundles shown in figs. 6 and 7 were taken from this slide.

over, in this basal region of the stem the course of the bundles is considerably disturbed, so that any section cuts comparatively few bundles at right angles. However, several small sections were obtained with the parenchyma of the stem and the lignified portions of the fibrovascular bundles in a good state of preservation. The fact that none of the bundles retain their phloem elements is perchance accounted for by the presence of numerous fungus hyphæ.

The parenchyma of the stem shows no unusual features, and there are no bast strands between the vascular bnndles, so that in Unger's classification this species would belong to the second great group. Stenzel, however (p. 43), points out that this method of classification is unsatisfactory, and substitutes a system based chiefly on a comparison of the arrangement, proximity, structure, and size of the bundles in the outer and inner regions of the stem; and on the shape and size of the sclerenchyma portion of the fibrovascular bundles.

In our specimen no marked difference could be detected between the inner and outer bundles (compare figs. 3 and 4),

* Drabble, Eric—On the Anatomy of the Roots of Palms. Transactions of the Linnean Society, Second Series—Botany, vol. vi, p. 427–487, 1905.

so it apparently belongs in Stenzel's class C.,—the "Cocoa resembling stems." Again, from the shape of the sclerenchyma portion of the fibrovascular bundles it should be placed in the group "Reniformia" (p. 215), which is characterized by having the sclerenchyma portion of the fibrovascular bundle round or oval in cross section with a flat even surface or broad shallow indentation where it joins the vascular portion. This specimen does not, however, very closely resemble any one of the five species ascribed to the "Reniformia."

A typical stem bundle, that is one of the "longitudinal bundles," is characterized (fig. 5) by having in the xylem few but rather large vessels with thick walls. As shown in the figure, the sclerenchyma portion of the bundle is nearly oval in outline with a very slight indentation where it joins the vascular portion. The sclerenchyma cells near the phloem are considerably smaller than those farther away. No sclerenchyma fibers are present on the axial side of the vascular bundle. The parenchyma cells adjoining the bundles are somewhat smaller than those in the remainder of the stem, and the majority of those adjoining the vascular portion are somewhat elongated with the long axis perpendicular to the surface of the bundle.

Besides the longitudinal bundles, a few bundles were found which apparently belong to the classes designated by Stenzel as "Ubergangsbündel" or "transition bundles," and "Kreuzungsbündel" or "oblique bundles." By a "transition bundle" Stenzel (p. 139) refers to the region where a bundle that goes up through the stem, that is a longitudinal bundle, turns to go out into a leaf. In this transition region the structure resembles somewhat that of a bundle going out into a leaf. Stenzel* describes bundles of this type as follows: "The bast region is often smaller while the vascular region is larger; the peripheral vessels (that is those nearest the phloem) are more widely separated and often more numerous, while in place of median vessels we find two or more lateral ones. This type of bundle is especially distinguished by the presence of numerous smaller vessels which are found chiefly toward the axial side of the vascular region."

It will be noted that the bundle shown in fig. 6 agrees very closely with Stenzel's description of a "transition bundle," although the sclerenchyma region is not markedly smaller than in the longitudinal bundles. This bundle, which is typical of several found in the sections examined, resembles very closely the transition bundles of *Palmoxylon Aschersoni.* (See Stenzel, p. 140, fig. 234.)

By the "Kreuzungsbündel" Stenzel means those bundles which lead out toward a leaf and so are inclined at a very

* Loc. cit. 1, p. 139.

slight angle. They may also be designated as "oblique bundles." The structure of oblique bundles, according to Stenzel (p. 140), differs from that of longitudinal bundles as follows: "The bast portion of oblique bundles is similar to that of the longitudinal bundles, though very often smaller. The vascular region is much larger and prolonged inwards. Axially to the large peripheral vessels (those nearest the phloem) and separated from them by a region or zone of parenchyma, is a

FIG. 5.

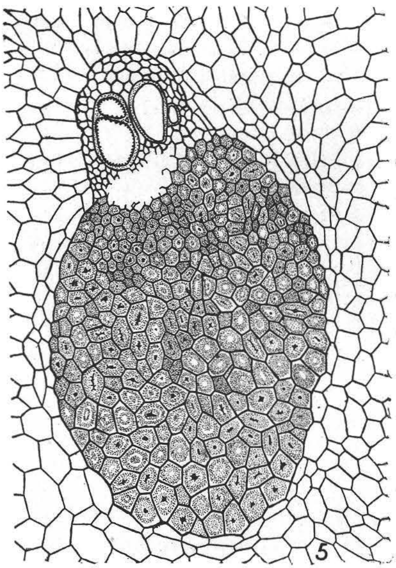


FIG. 6.

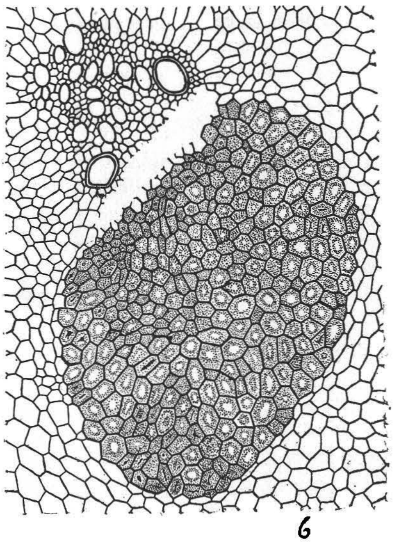


FIG. 5. A typical "longitudinal" bundle of the stem, showing the bast region and xylem containing two large vessels. × 65.

FIG. 6. A "transition" bundle showing the bast region and the xylem containing two large lateral vessels and numerous smaller ones. × 65.

group of numerous smaller vessels. The anterior (peripheral) vessels occur either in two lateral groups or are arranged in a cross row broken up by small "rays of parenchyma." Stenzel divides the oblique bundles into two classes on the basis of the arrangement of their peripheral vessels: group A having "Zwei seitliche vordere Gefässgruppen," and group B "Vordere Gefässe in einer Querreihe." The bundle shown in fig. 7 evidently belongs to the second of these classes and, among the species figured by Stenzel, most closely resembles *P. astorn* (p. 142, fig. 50). The vessels of the xylem present no notable features;

those found in longitudinal section being typical spiral vessels with the coils fairly thick and rather close together.

Tyloses.—One of the most interesting observations is that of the presence in the vessels of both stem and roots of rounded, rather thin-walled bodies which strongly resemble the tyloses of living plants. There is, of course, a bare possibility that these bodies are accretions of some sort, but they are so constant in their appearance and so characteristic in their structure that the conclusion that they are tyloses seems unavoidable. Figure 8 shows a portion of a longitudinal section of a stem vessel which contains several tyloses: fig. 9 shows the tyloses in one of the vessels of a root bundle. So far as the writer has been able to determine, tyloses have not been described in any species of fossil palm. They have, however, been observed in the wood of living palms.*

While the amount of wood available for examination was, to be sure, not large, tyloses were apparently more frequent in the vessels of the root than in those of the stem. This is more noteworthy since tyloses do not appear to have been recorded in living palm roots. They have, however, been found to occur in large numbers in the roots of some herbaceous plants (DeBary); while Chrysler† found them occurring in the heart of the root, as well as in the first growth of the axis of the ovulate strobilus in *Pinus.*

Fungi.—As noted above, no stem bundles were found in which the phloem was preserved. Moreover, only a very small amount of phloem was found in the roots. This may be due, of course, to poor preservation, but it seems more reasonable to attribute it to the action of a wood-destroying fungus, which appears to be present.

It is very difficult to represent satisfactorily on a flat surface the course of the fungus hyphæ, but figs. 10 and 11 give some idea of the number of hyphæ present in many of the vessels of the stem and roots. Hyphæ were equally abundant in the phlœm. That this is the mycelium of a parasitic or saprophytic fungus seems reasonably certain since it is confined entirely to the central cylinder, and particularly to the vascular portions; while not the slightest trace of it is found in the cortex. If it were mycorrhiza, of course exactly the reverse would be the case. Hyphæ are rather abundant in the stem, noted above as less well preserved than the roots,—a condition which perhaps suggests that the fungus first infected the trunk and

* De Bary, A.—Comparative Anatomy of Phanerogams and Ferns. English edition, Oxford, 1884 (p. 171).

† Chrysler, M. A.—Tyloses in tracheids of conifers. New Phytologist, 7:198, 1908.

later spread to the roots. In fact, as shown below, the cortical portions of the root were in an unusual state of preservation, which might indicate that infection of the roots had taken place only a comparatively short time before silicification.

That abundant hyphæ of a wood-destroying fungus should be found in tissue apparently very little injured is quite in accord with the mode of growth of these fungi. The writer has observed that *Polystictus versicolor*, growing in pure cul-

FIGS. 7-11.

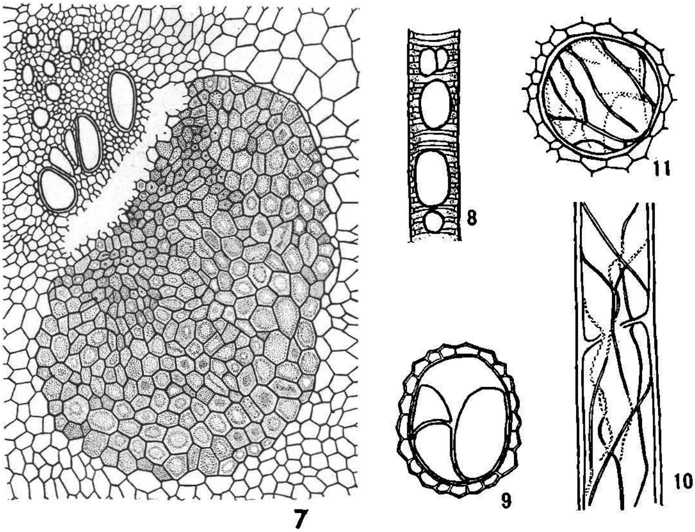


FIG. 7. An "oblique" bundle showing the bast region and the xylem containing large peripheral vessels and a group of numerous smaller vessels separated from the large ones by a zone of parenchyma. × 65.

FIG. 8. Longitudinal section of a portion of a small stem-vessel, showing tyloses. × 150.

FIG. 9. Cross section of a root vessel, showing tyloses. × 150.

FIG. 10. Longitudinal section of a portion of a stem-vessel, showing fungus hyphæ. × 150.

FIG. 11. Cross section of a root vessel showing fungus hyphæ. × 150.

ture on sapwood of *Liriodendron tulipifera*, develops a considerable mycelium extending through most of the woody tissue long before any marked effect on the lignified walls is apparent under the microscope. The fossil fungus noted here had apparently reached just this stage, having developed a considerable mycelium and destroyed much of the phloem, without affecting to any extent the more resistant tissues of the vessels and sclerenchyma.

The Root.

A cross section of the root clump shows the roots closely packed together with but little space between them for some distance below their insertion. The fully developed roots, that is the large ones, are usually somewhat oval in section and about 8 or 9^{mm} by 5 or 6^{mm} in diameter. Figure 12 shows a

FIG. 12.

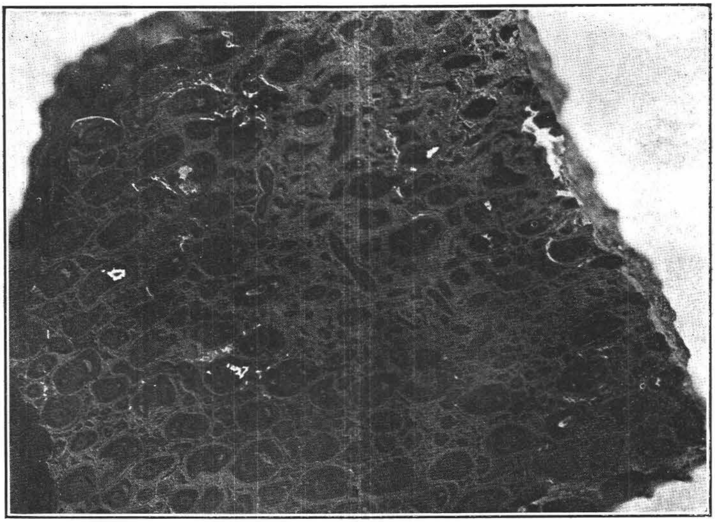


FIG. 12. Polished surface cut through root clump at right angles to the roots about one inch below the region of insertion, showing marked variation in the size of the closely packed and appressed roots. × 4/5.

number of these roots as they appear in section. The stele of the larger roots is about 2^{mm} in diameter. The numerous smaller roots vary in size down to one millimeter or less in diameter. It is, of course, impossible to determine in a section whether any particular root arises directly from the stem or is a branch of a larger root; but it is evident from the longitudinal sections that branching of the roots is frequent. So it seems probable that a large part of the smaller roots are branches of larger ones.

Cortex.—Drabble (p. 432) divides the cortex of living palm roots into four well-differentiated regions, viz.: (1) outer limiting layer, (2) outer cortex, (3) inner cortex, and (4) endodermis. These four regions are described by Drabble as follows: The *outer limiting layer* is composed of cells with cuticularized, comparatively thin, walls. It does not necessarily form a perfectly regular sheath. The *outer cortex* (p. 432) is a tegumentary system consisting of several layers of elongated, lignified, and more or less pitted cells. The *inner cortex* (p. 434) is composed of three "zones"; an outer zone usually without air spaces, a broad middle zone with large air spaces, and an internal zone of regular cells. The middle zone

FIG. 13.

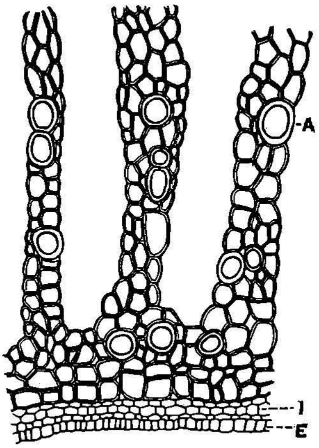


FIG. 14.

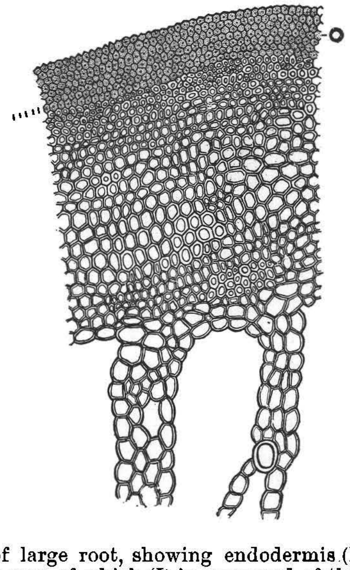


FIG. 13. Inner portion of cortex of large root, showing endodermis (E), and part of the inner cortex, the inner zone of which (I) is composed of three layers of thin-walled cells. In the middle zone of the inner cortex are shown large intercellular spaces and the heavier lignified stone cells (A). × 70.

FIG. 14. Outer portion of cortex of same root as shown in fig. 13, showing outer cortex (O shaded), outer zone of inner cortex, and a portion of the middle zone of the inner cortex. × 70.

shows considerable variation in the shape, size, and number of the air spaces as well as in the number of cell layers separating these spaces. The *endodermis* (p. 438) consists of a single layer (sometimes locally doubled) of lignified cells from three to six times as long as they are broad.

With the exception of the "limiting layer" these same regions were readily distinguishable in the present fossil specimen. Figures 13 and 14 were taken from the cortex of a fully developed root, fig. 13 being, of course, the inner and fig. 14 the outer portion. The photomicrograph, fig. 15, will give an idea of the relative size of the various zones of the inner cortex.

The outer cortex consists of from six to ten layers of elongated, lignified cells with very thick walls and small lumen. The outer zone of the inner cortex is also composed of lignified cells, but they are thinner-walled and shorter in proportion to their length. The cells of this region differ considerably in size, the outermost cells having about the same diameter as the adjacent cells of the outer cortex, while toward the center the cells become progressively larger in diameter.

The middle zone of the inner cortex contains numerous large air spaces. These air spaces (lacunæ) are radially arranged, six to ten times as long as broad, with from one to

FIG. 15.

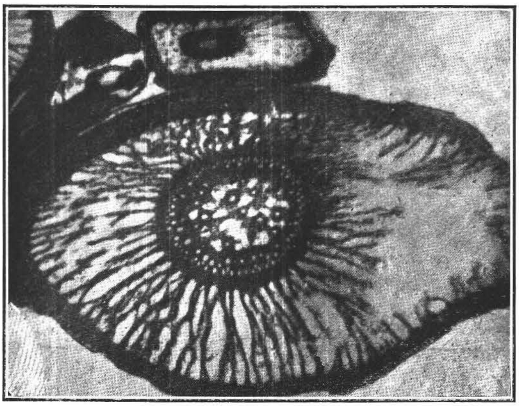


FIG. 15. Photomicrograph of cross section of palm root, showing cortex with large radial intercellular spaces in the middle zone; and stele with alternate phloem and protoxylem groups and eight internal vessels. × 8.

six layers of cells separating them. The cells of this region are only about twice as long as they are broad and much thinner-walled than those of the outer region. In addition to the large radial air spaces, triangular spaces show plainly in the longitudinal section at the intersection of cell walls (fig. 16). The cells are apparently "lignified parenchyma."

There occur also in this middle zone thick-walled cells with large cavity and large pits. These usually occur singly or scattered through the middle zone in groups of two or three, but are somewhat more numerous toward the inside. Seen in cross section, figs. 13 and 14, they usually appear rather round; and in fully developed roots the pits are not usually seen in cross sections. In smaller roots, however (fig. 22), the large pits are very evident. Figure 17 shows two of these large cells from near the origin of a root, in longitudinal section. It will be noted that these cells are from three to five times as long as they are broad and that the large pits are considerably elongated. It is difficult to place these cells in any of the recognized categories of lignified elements. They do not seem to correspond exactly to either the "Kentia" or "Raphia" types of fibers described by Drabble (p. 435), but may perhaps be designated as "stone" cells.

The internal zone of the inner cortex usually consists of three layers of rather thin-walled cells closely packed together without intercellular spaces. These cells vary considerably in size but are usually from one to three times as long as they are broad. Compare fig. 13 with fig. 16.

The endodermis is almost uniformly one cell thick, the cells two to four times as long as broad; and even in the fossil the radial walls appear markedly thicker than the tangential walls. Compare fig. 13 with fig. 16.

All the regions described for the fully developed root can be made out in the smaller root shown in fig. 22. In the smaller root, however, the various parts of the inner cortex are not so clearly differentiated and all the cells have much thinner walls.

Nuclei in cells of inner cortex.—Three longitudinal sections showed the parenchyma cells of the inner cortex in a very remarkable state of preservation. Indeed, the majority of the cells of this region contained structure so characteristic in appearance and so constant in occurrence that, if seen in fixed material from living plant tissue, they would unhesitatingly be described as the well-stained *nuclei*.

Drawings of such structures would naturally afford no certainty as to their nature; and the photomicrographs, figs. 18 and 19, are accordingly offered for what they may be worth as proof. While not fully convincing in themselves these figures are not wholly valueless. Practically every parenchyma cell in the field showed a nucleus in some focus; and in the figures nuclei appear in the cells marked N as well as in some others. It will also be noted that the triangular intercellular spaces spoken of above clearly appear in these photomicrographs; and the probability of the cells having been "fixed" when in an actively growing condition is further denoted by the occurrence of pairs of cells which have apparently just been separated by a cross wall (*y*, fig. 19). In these "daughter cells" the nuclei are still close to the dividing wall.

The Stele.—The pericycle is very readily distinguished as a single layer, or sometimes locally as two layers, of rather regular cells inside the endodermis. These cells tend to be somewhat larger than the parenchyma cells adjoining them and their radial walls are for the most part regularly perpendicular to the walls of the endodermal cells. Compare figs. 20, 21, and 23.

The vascular portions show the typical root arrangement, the phloem strands alternating with the protoxylem groups.

FIG. 16.

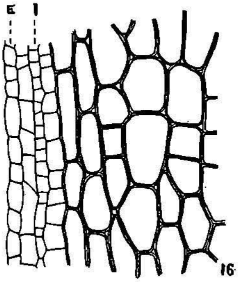


FIG. 17.

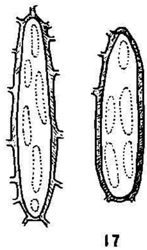


FIG. 16. Longitudinal section of inner region of cortex, showing endodermis (E), and a portion of the inner cortex with lignified parenchyma and inner zone of three layers of cells (I). × 112.

FIG. 17. Two of the large "stone" cells of the inner cortex in longitudinal section, showing large pits. × 112.

FIG. 18.

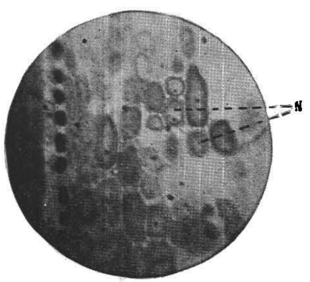
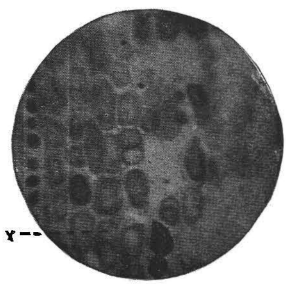


FIG. 19.



FIGS. 18 and 19. Photomicographs of parenchyma cells of the inner cortex in longitudinal section, showing nuclei (N) and cells which by their shape seem to indicate recent division (*y*). Triangular intercellular spaces may be seen in some cases. × 100 ±.

In the larger roots there are usually fifty or more protoxylem groups; in the root from which fig. 20 was taken there were fifty-five. The phloem groups and all the outer xylem elements are surrounded by a continuous zone of dense sclerenchyma fibers. These sclerenchyma fibers are considerably smaller near the vascular portions than they are toward the center of the root. This dense sclerenchyma band is usually from fifteen to twenty-five cells wide, so that in the large roots the sclerenchyma region with the vascular portions it contains occupies only about half the stele.

The central portion of the stele contains a variable number of "internal" vessels, frequently from four to six, which do not appear to be referable to any particular xylem group. Compare (Drabble, p. 441). Each of these internal vessels is surrounded by a region of dense sclerenchyma from six to ten cells in width. See fig. 20. The remainder of the central

FIG. 20.

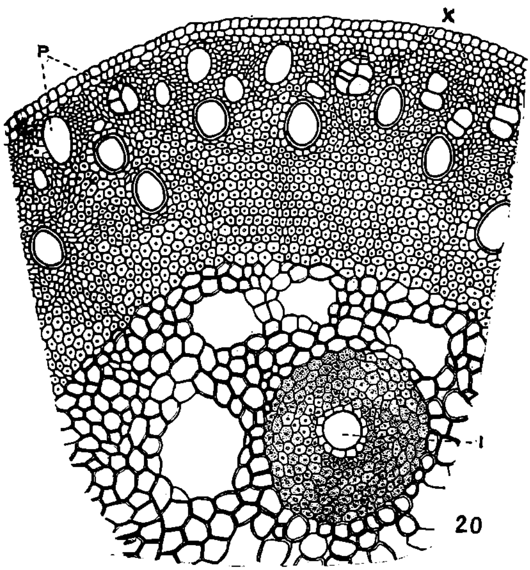


FIG. 20. Portions of stele of large root with endodermis, showing pericycle, alternate phloem (P) and protoxylem (X) groups in a zone of dense sclerenchyma. The inner region of the stele shows lignified parenchyma with large intercellular spaces, and an internal vessel (I) surrounded by a zone of sclerenchyma. × 175.

region of the stele is occupied by lignified cells with large lumen and comparatively thin walls. These cells apparently became torn apart as the root increased in size so that, in fully developed roots, this central region has large intercellular spaces.

The stele of the smaller roots shows the same structure as that of the larger ones, but the number of protoxylem groups is much smaller. The root shown in fig. 21 had thirteen protoxylem groups. In these smaller roots, of course, the central region is much smaller in proportion to the whole stele and contains no internal vessels or large intercellular spaces.

One of the most interesting sections found was that of the very small root shown in fig. 23. While no phloem elements can be distinguished in this root section, the xylem shows the arrangement of a very young tetrarch root. In this very small root, as in the larger ones, the pericycle may be readily distinguished. Unfortunately the cortical portion of this root was obscured by a deposit of some foreign substance.

Phloem.—As noted above, the phloem was preserved in comparatively few cases. Not more than five of the root sections

FIGS. 21-24.

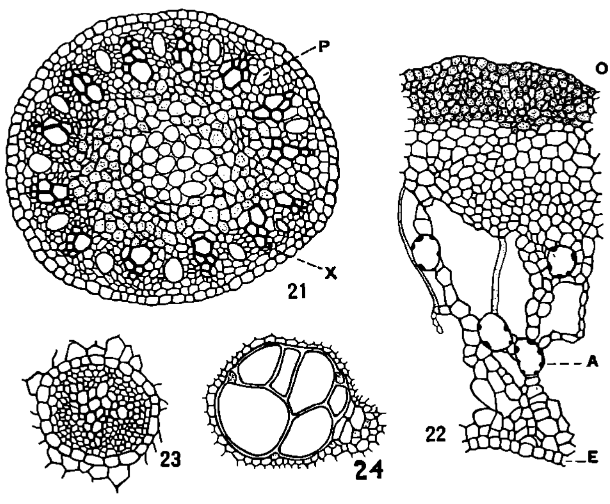


FIG. 21. Stele of a smaller root with endodermis, showing pericycle, alternate phloem and xylem groups, and a zone of sclerenchyma. × 175.
FIG. 22. Cortex of same root as that shown in fig. 21, endodermis (E), stone cells (A), outer cortex (O). × 175.
FIG. 23. Stele of very small root, the xylem of which has the typical tetrarch arrangement. × 175.
FIG. 24. Phloem group from large root. × 265.

showed well preserved phloem. Even in the root shown in fig. 20, less than half of the phloem groups remained. Fig. 24 shows, however, a group which was unusually well preserved, and this may perhaps be taken as typical. It will be noted that the protophloem consists of small cells with thin walls while the sieve-tubes of the metaphloem are very much larger and have thicker walls. No sieve-plates could be discovered in any of the sections. Neither could companion cells be definitely distinguished. It seems probable, however, that the small dark regions close to the sieve-tubes, shown in fig. 24 by the shaded areas, occupy the position of companion cells. All the preserved phloem groups were in the larger roots.

Junction of bundles of root and stem.—The transition from the solid stem to the root region of variable hardness renders the making of thin sections through the root junctions difficult, the more so because the parenchyma and other tissues in this region have taken on so dark a color that sections of moderate thickness are not very useful. These circumstances prevented satisfactory study of the junction of the root and stem bundles.

Description of species.

***Palmoxylon anchorus*, sp. nov.**

Locality.—Upper Cretaceous, Seabright, New Jersey.

Type in Peabody Museum, Yale University.

Stem.—No bast strands between the fibrovascular bundles. Sclerenchyma portions of the fibrovascular bundles usually oval in cross section and but little indented next the phloem. Little difference in the size and shape of the sclerenchyma portions of the "longitudinal," "transition," and "oblique" bundles.

Roots.—Roots considerably branched. Outer cortex composed of six to ten layers of elongated, lignified cells. Inner cortex differentiated into three zones: an outer region of thick-walled lignified cells; a middle zone of lignified parenchyma having numerous large radially arranged air spaces, six to ten times as long as broad, separated by from one to six layers of cells; and an internal zone of three layers of thin-walled closely packed cells. Endodermis usually one cell thick. Pericycle usually one or locally two layers of cells. The largest roots have over fifty protoxylem groups alternating with phloem groups. Internal vessels present in the larger roots and surrounded by a dense region of sclerenchyma six to ten cells in width.

*   *   *   *   *

It is of much interest to append the fact that petrified stems of palms are not the rare objects that their noticeable absence from collections and general lack of mention in paleontologic texts would seem to imply. It is indeed probable that they occur abundantly at times from the upper Cretaceous on, both on the coastal plain and in the formations of the continental interior.

In addition to several Tertiary forms described by Knowlton, Hatcher is known to have secured various stems from the Laramie of Converse county, Wyoming. Wieland has collected from the Pierre the splendidly conserved stems arbitrarily called by him *Palmoxylon cheyennense*.* Cannon has secured an abundance of exquisitely silicified stems from the Denver beds. And only last year Brown observed a large silicified root clump in the "Rattlesnake" beds on the "big bend" of the Rio Grande in Chisos county, Texas.

* This Journal, vol. xv, p. 216.