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The Morphology and  
Anatomy of American Species  
of the Genus *Psaronius*

JEANNE MORGAN

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ILLINOIS BIOLOGICAL MONOGRAPHS: *Number 27*

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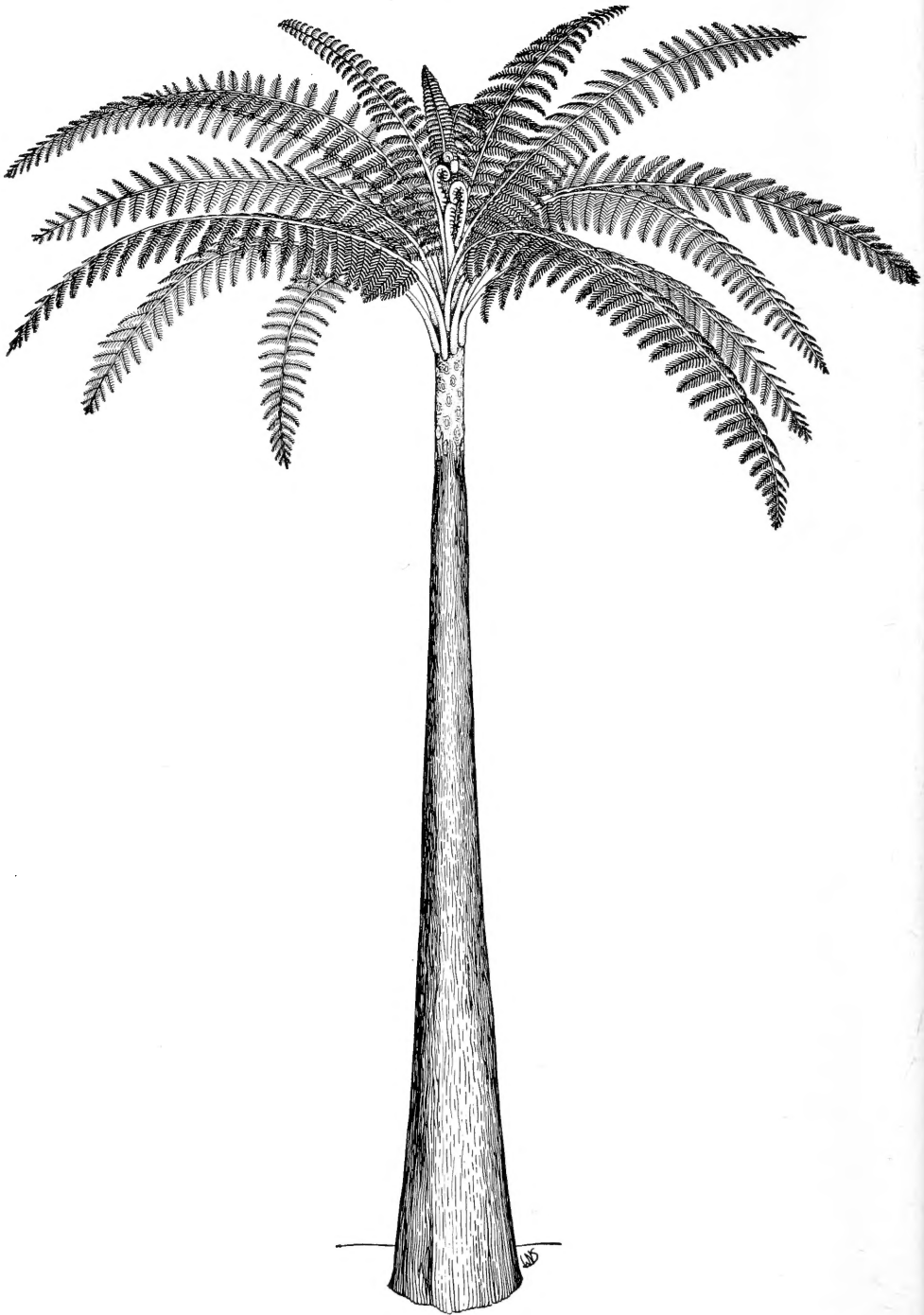
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THE MORPHOLOGY AND ANATOMY OF  
AMERICAN SPECIES OF THE GENUS PSARONIUS



Reconstruction of a psaroniacean tree fern showing *Caulopteris* features in leaf scar arrangement (spiral arrangement). This reconstruction is based on a plant approximately 20 to 25 feet tall.

The Morphology and  
Anatomy of American Species  
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## I. INTRODUCTION

*Psaronius* is an organ genus first proposed by Cotta (1832) for the fossil stems of certain tree ferns belonging to floras of the Carboniferous and Permian periods of geological time.

In gross structure (see frontispiece) *Psaronius* was an erect, unbranched stem up to 50 feet high with an apical crown of large compound leaves. The leaves were arranged in vertical rows or in a spiral. As the leaves aged they abscised, leaving large elliptical scars on the surface of the stem. Older parts of the stem toward the base were covered with a thick mantle of adventitious roots, causing the base of the stem to appear much enlarged.

The general appearance of these ancient ferns compares favorably with modern tropical tree ferns belonging to the families Cyatheaceae and Marattiaceae of the Filicineae. However, the structure of their stem, roots, and sporangia show that the affinities of these extinct ferns are with the eusporangiate Marattiales. For reasons explained later in the text, *Psaronius* is placed in the family of Psaroniaceae of the Marattiales.

Judging from the structure of its roots, *Psaronius* grew in a swamp environment along with seed ferns, lepidodendrids, coenopterid ferns, calamites, sphenophylls and other plants typical of the Carboniferous landscape. As in many existing tropical rain forests, the Paleozoic environment in which these plants existed was uniform in temperature and available water. Not until the Permian period is there any evidence of important environmental changes in the upper part of the Paleozoic era. These changes apparently brought about the extinction of the Psaroniaceae as evidenced by the absence of their stem remains in younger strata.

In Europe during the eighteenth and nineteenth centuries, specimens of *Psaronius* were prized as semiprecious stones and were called *Staarsteine*, meaning "starling stones," because the cross-section of the root mantle resembles the markings on the breast of the European starling. Stenzel (1854) suggested that this was a corruption of *Stern Steine* (star stones), referring to the stellate arrangement of the actinosteles of the roots. The descriptive term *Wurmsteine* has also been applied to specimens of *Psaronius*, referring to the rather wormlike appearance of the vascular bundles in cross-section.

Sprengel (1828) was the first to recognize that these fossil specimens were remains of fern stems for which he established the genus *Endo-*

*genites*. Cotta in 1832 removed them from that genus when he established the genus *Psaronius*. Since that time, hundreds of *Psaronius* stem fragments have been collected from the Carboniferous of central France, Bohemia, England, and the United States. Until the present, however, little has been learned about the plant as a whole.

Since the discovery of *Psaronius* the literature has been filled with conflicting ideas concerning the morphology of these stems. Some papers (Zeiller, 1890; Stenzel, 1906) reveal a knowledge of the genus advanced for the time, but many of the morphological interpretations of these authors are now known to be incorrect. In these papers, and in certain other treatments of the genus (Hirmer, 1927; Seward, 1910; Scott, 1920) the more internal parts of the vascular system were described, without critical examination, as a series of very complex anastomosing strands. Diagrams of the cycles of vascular tissue seen in longitudinal section have been prepared by Farr (1914), Hirmer (1927), and Schoute (1938), in an attempt to show its organization. Shoute's simple diagram approximates the generalized condition of a *Psaronius* vascular system but leaves much to be desired in morphological interpretation. Many stem specimens have remained undescribed because of their complex and often confusing vascular systems. With new information gained from the present study, these specimens may now be correctly interpreted and named.

One of the primary objects of this research was to obtain some idea of ontogenetic variability present in a stem of *Psaronius*. It was necessary to study a large number of stem fragments and in this way determine the spectrum of variability occurring from base to apex. After the extent of ontogenetic variability within a species had been established, it was then possible to evaluate that variation which remains constant among different stems and characterizes species. Enough stem material was available to observe the morphology and ontogeny of two species of *Psaronius* from a level near the base of the stem to a point near the apex. With this knowledge of ontogenetic variability for two species it was then possible to interpret variability in species represented by only a small number of stem fragments.

For the sake of simplicity and clarity most specimens mentioned in this article have been referred to by capital letter. Although a large number of additional stem fragments were investigated, they are not referred to specifically. A list of coal-ball and ironstone specimens is presented below. The reference letter, accession number, and source is given for each specimen. Unless otherwise indicated, the specimens are now in the paleobotanical collection, Department of Botany, University of Illinois, Urbana, Illinois. Stratigraphic position of various collecting sites are given at the end of this list.

- Specimen A Washington University Coal Ball 108 (now at the University of Illinois)—Berryville, Illinois.
- Specimen B C.B. 2841—Berryville, Illinois.
- Specimen C C.B. 189, 196, 266, 267 (this specimen was found as several isolated fragments which have since been cemented together)—Berryville, Illinois.
- Specimen D C.B. 2844—Berryville, Illinois.
- Specimen E C.B. 2778, 2779, 2789 (these three fragments are all part of a single stem)—Dix, Illinois.
- Specimen F C.B. 2842—Berryville, Illinois.
- Specimen G C.B. 2680—Berryville, Illinois.
- Specimen H C.B. 2681—Berryville, Illinois.
- Specimen I C.B. 2682—Berryville, Illinois.
- Specimen J University of Minnesota Coal Ball 35 (now at the University of Illinois)—West Mineral, Kansas.
- Specimen K Washington University Coal Ball 698 (now at the University of Illinois)—West Mineral, Kansas.
- Specimen L C.B. 1539—West Mineral, Kansas.
- Specimen M Washington University Coal Ball 649 (now at the University of Illinois)—West Mineral, Kansas.
- Specimen N Illinois State Geological Survey Coal Ball 803 (at the Illinois State Geological Survey, Urbana, Illinois)—West Mineral, Kansas.
- Specimen O Illinois State Geological Survey Coal Ball 1254 (at the Illinois State Geological Survey, Urbana, Illinois)—West Mineral, Kansas.
- Specimen P C.B. 2111—West Mineral, Kansas.
- Specimen Q C.B. 3066—West Mineral, Kansas.
- Specimen R C.B. 1221—Berryville, Illinois.
- Specimen S C.B. 1700—St. Wendel, Indiana.
- Specimen T Illinois State Geological Survey Coal Ball 51 (now at the University of Illinois)—New Delta, Illinois.
- Specimen U Ironstone concretion Specimen 2608—Wilmington, Illinois.
- Specimen V Ironstone concretion Specimen 2609—Wilmington, Illinois.
- Specimen W Ironstone concretion Specimen 728—Coal City, Illinois.

#### Stratigraphic Position of Collecting Sites

Berryville, Illinois—Upper McLeansboro group, upper Pennsylvanian System.

Coal City, Illinois—Lower Carbondale group above No. 2 coal, middle Pennsylvanian System.

Dix, Illinois—Upper McLeansboro group, upper Pennsylvanian System.  
New Delta, Illinois—Top of Carbondale group, middle Pennsylvanian System.

St. Wendel, Indiana—Parker coal, lower McLeansboro group, upper Pennsylvanian System.

West Mineral, Kansas—Cherokee shale, Des Moines series, middle Pennsylvanian System.

Wilmington, Illinois—Francis Creek Shale above No. 2 coal, middle Pennsylvanian System.

## II. OBSERVATIONS

### A. *Psaronius blicklei* sp. nov.

#### 1. Description

A well-preserved fragment of *Psaronius* (figs. 1, 2, 25, 26 specimen A) was recovered from a stream bed near Berryville, Illinois. With the possible exception of one stem of another species described later, this stem has the smallest cross-sectional dimensions in its lower portions of any known American specimen. At the lowest portion of the three-foot length of stem preserved in the coal ball, cross-sectional dimensions are  $2.3 \times 1.5$  cm. in its slightly crushed condition. At the upper extremity the diameter approaches 3 cm. The vascular bundles are arranged concentrically to produce a polycyclic condition and each bundle possesses groups of protoxylem along its internal face. The metaxylem cells, which make up the bulk of the bundle, average 75 microns in diameter and are interspersed with xylem parenchyma cells occurring singly or in groups. The tracheids themselves are long and tapering, with scalariform thickenings. Secondary thickenings on the walls of protoxylem are spiral and scalariform. The region of the phloem is not well preserved, but a band of poorly preserved cells completely encircles each vascular bundle. The phloem zone is in a better state of preservation in some of the larger stems and will be discussed under the section on histological details. No endodermis is present around the bundles. The steles are embedded in a rather compact parenchymatous ground or fundamental tissue which is limited at the periphery of the stem by a thin band of sclerenchyma. Also embedded in the ground tissue at various places, in association with the steles, are groups of sclerenchyma fibers.

Interspersed throughout the fundamental tissue are numerous cells with dark contents very closely resembling the tannin cells of some of the living Marattiaceae (West, 1915). Lysigenous lacunae in the fundamental tissue, characteristic of this species, are sparse in the more basal

portions and average 1 mm. in diameter. They resemble, at least superficially, the mucilage canals of extant marattiaceous ferns (West, 1915). These lacunae do not appear to be filled with a deposit of any kind and there is no evidence of an epithelial layer. They are believed to be lysigenous in origin because of the lack of any epithelium and the presence of remains of disintegrated cell walls which are found at the periphery of the cavity.

At the time of leaf trace separation, a "bulge" appears in the sclerenchyma sheath, and a leaf trace which has separated from the stem stele bends up and out into it. The sheath then inrolls upward and inward until it completely surrounds the trace on its inner face. The break in the leaf base and the included trace resulting from abscission of the frond is responsible for the apparent presence of two separate vascular strands in a leaf base near the periphery of the stem. The free trace is actually a curved strand which at successively higher levels has progressively larger amounts of the abaxial portion broken off (figs. 3, 27).

Immediately surrounding the limiting layer of the stem is a zone composed of adventitious roots. The vascular supply of these roots originates from the peripheral cauline bundles. Surrounding the roots is a compact mass of sinuously radiating rows of parenchyma cells which arise by proliferation of parenchyma cells of the ground tissue of the stems and roots, and also from parenchyma cells interspersed among the sclerenchyma which surrounds both stem and adventitious roots. This will be discussed later in the detailed description of the root mantle. Still farther to the outside is a zone of roots, not encased in the secondary parenchyma, called the free root zone. These roots have for the most part arisen from more distal portions of the stem, and in their downward and outward course have either grown free of the compacted mass of the inner root zone or have not yet been incorporated in it. The roots of the inner layer are, as a rule, smaller in diameter than the free roots and are surrounded by a layer of sclerenchyma intermixed with parenchyma cells. The parenchyma cells are somewhat sparse and not readily visible in cross-section, but their presence is attested by their proliferation to form the secondary parenchyma in which these inner roots are embedded. Within the sclerenchyma sheath surrounding roots of the inner root zone there is a cortex composed of relatively large compact cells. Tannin-like deposits similar to those found in the fundamental tissue of the stem are present in these roots and in the secondary parenchyma cells surrounding them. Embedded in the ground parenchyma is an actinostele bearing four to seven arms. Protoxylem is found at the tips of the arms. Scattered xylem parenchyma cells are found interspersed among the tracheids; pockets of phloem alternate with the xylem arms of the actinostele. The free roots are also surrounded by a layer com-

posed of sclerenchyma cells. Although not directly observed, parenchyma cells are probably intermixed with the sclerenchyma cells. Parenchyma cells, if present, do not proliferate while the roots are in the free condition. Proliferation most likely does take place later in development as the plant grows taller, encasing the roots in a mass of secondary parenchyma cells. Development of this kind would be necessary to allow for increased diameter of the root mantle in larger stems. The root zones of some basal specimens have a somewhat layered appearance which might correspond with periods of secondary parenchyma production. The more peripheral region of the cortex of a free root is composed of very loosely arranged parenchyma, giving it a "netted" appearance (fig. 77). An analogous condition is found in the stems of certain extant aquatic ferns, e.g., *Marsilea*. The more internal cells of the cortex are compact and surround a stele similar in structure to roots of the inner zone. Tannin-like deposits are also present in the compact inner cortical cells of free roots. *Psaronius* roots have been observed to branch (Reed, 1949), and branching is common in roots obtained from the Berryville locality (fig. 77).

At the lowest level of the stem (specimen A, figs. 1, 25) with the smallest diameter, the vascular system is characterized by a dicyclic condition. In this region, while the plant was small, there were three orthostichies of leaves. This is revealed internally by the presence of three vertical rows of leaf gaps in the outer stelar cycle. Leaf gaps are situated above the point of separation of the leaf traces, and the overlapping of these gaps produces a dictyostelic structure. Cross sections at certain levels of the stem give the appearance of a siphonostele with only a single leaf gap, but levels slightly above or below show the dictyostelic condition again (fig. 11). Leaf traces always arise from discrete parts of the outer cycle, and alternate in specimen A, with three vertical vascular strands which are cauline.

*In all of the stems to be discussed, the cycles are numbered successively from the outside toward the center.* Leaf traces have their origin in the innermost cycle, a relatively simple open cylinder at the lower stem levels. As this cylinder passes upward and across the ground tissue it fuses with two peripheral cauline bundles, filling the gaps in the outer cycle in a spiral sequence corresponding to the separation of leaf traces (fig. 10A, B). The portion of the open cylinder which fills the gap is a leaf trace originating in the central cycle. The two free arms (fig. 10C) of the inner cycle separate and turn back toward the center of the stem where they fuse (fig. 10D), closing the first gap in the inner cycle. This cylinder in its upward course then passes across the ground tissue, filling the gap of the next higher leaf trace in the phyllo-tactic sequence with a new leaf trace. It should be noted that the next

inner cylinder, like the outer cycle, is composed of leaf traces alternating with cauline bundles.

Above the point of separation of the inrolled edges (fig. 10E, F), the two central vascular bundles fuse—not at the edges, but along their convex portions—thus leaving two short edges projecting for distance toward the center of the stem (fig. 10G). These projections separate as a single curved strand, thus initiating the third cycle (fig. 10H). The second cycle continues in its upward course, filling, in sequence, the spirally arranged gaps in the outer cycle. Each time the second cycle gives off a leaf trace to the outer cycle, it passes between two peripheral bundles. Only rarely does the second cycle fuse at the same level to both edges of the gap of the outer cycle; instead, one of the two sides fuses with a peripheral bundle at a lower level than the other (fig. 10I). The third cycle, which originated from the cycle immediately to its outside, functions in the same way as the second, filling the leaf gaps in the latter in a manner identical with gap closure in the outer cycle by the second vascular cylinder. At its lowermost level the third cycle is represented by a slender strand (figs. 2, 26) which fuses to one edge of the gap in the second cycle (fig. 10I, J). The closing of the gap is completed by an inrolling of the cauline portion. Where the innermost cycle is fused to one side of a gap in the second cylinder, it is represented by a curved edge which is met by an inrolling of the cauline bundle on the opposite side of the gap. A pinching off of the two recurved ends (fig. 10J, K) reconstitutes the third cycle.

At this level, the third cycle is a very small strand (fig. 10K, L) because a part of it has been contributed to the formation of a leaf trace. At higher levels this strand increases in volume through the additional differentiation of tracheids. A similar increase in volume is also brought about in each of the investing steles. Because of this volumetric increase, accompanied by an increase in stelar number, the dimensions of the vascular system keep pace with over-all increase in stem volume.

An idealized, three-dimensional reconstruction of the stelar system of specimen A is portrayed in fig. 11 (lowest portion at bottom left; highest at top right). In the length represented by this figure, three leaf traces arise and the addition of a new cycle in the center of the stem can be followed. The diagram also shows the course of the second cycle, which contributes traces to the outer one. Beginning at the top of the sixth section from the bottom, the method of initiation of the third cycle is portrayed. Above that section is shown the manner in which both the most internal and next outer cycles contribute traces to their respective outer cycles.

Specimen A just described is probably the most nearly basal portion

of a *Psaronius* stem thus far described. That it is a basal portion is shown by the relative simplicity of the stem with only three rows of leaf traces, its rather small diameter, and the correspondingly large ensheathing growth of adventitious roots extending approximately 12 inches around the stem in all directions. Based on the evidence presented, it is obvious that as large and complex a stem as *Psaronius infarctus*, which has as many as fourteen rows of leaf traces and an extremely polycyclic vascular system, could not be a basal fragment of *Psaronius*.

Fragments of large and complex stems have been found in America during recent years. By establishing an intergrading series composed of many of these fragments, (specimens A through H; figs. 25-33), it is possible to recognize progressive stages of an ontogenetic series from the simple base to the complex distal portions of the stem. Because fragments representing this series were not found organically connected, certain anatomical characters must be relied upon for verification of the fact that these fragments belong to one species. The specimens used in the ontogenetic series to be described retain the same stelar morphology throughout. They are also similar in the presence of tannin cells, lysigenous lacunae, and the characters of the sclerenchyma. Very basal portions of these stems may lack certain of these characters; however, higher levels in the same fragment show them.

Specimen B is a stem fragment that has a four-cycled stelar condition (figs. 3, 27). The level of the stem depicted by these figures appears to have only three cycles; however, the fourth and innermost cycle is fused with the next outer cycle before contributing to the formation of a leaf trace which will be given off at a higher level. That specimen B is a portion of a stem taken at a slightly higher level is evidenced by the larger number of cycles and also by the five well-developed orthostichies of leaves present at this level. The manner in which a cycle may be added to the stelar system has been shown in specimen A, and the method by which this stem was able to add a new row of leaf traces will be discussed in connection with specimen E, which is one of the still more distal portions of *P. blicklei*. In addition to increased complexity of the vascular cylinder, the lacunae characteristic of this species become increasingly larger and more numerous. These are found in abundance scattered throughout the ground parenchyma, and several are usually found associated with the concave face of a departing leaf trace. Often two or more lacunae coalesce to form a large, irregular cylindrical cavity in the cortex.

Specimen C (figs. 4, 28) shows the structure in a *P. blicklei* stem but at a somewhat higher level than in specimen B. The fragment actually possesses five concentric cycles, only four of which are visible in this representative cross-section. There has been no increase in the number



of leaf traces in this specimen; it exhibits five rows as does specimen B. Thus, it becomes apparent that there is no exact correlation between increasing size, number of cycles, and numbers of rows of leaf traces through short distances. A generalized pattern is apparent, however, as evidenced by a correlation between a very large number of orthostichies in a stem and a correspondingly large number of stelar cycles. This generality holds true for specimens with the spiral and whorled leaf bases but not in distichous, and possibly not in the tetrastichous and hexastichous species to be discussed later.

Specimen C also shows a larger number of lacunae than were present at lower levels. In addition to the isolated patches of sclerenchyma described for specimen A there are, at this higher level, bands of sclerenchyma fibers which roughly follow the configuration of the steles. These will be discussed in greater detail in the description of specimen F.

A diagram of the stelar pattern present in a specimen having a spiral phyllotaxy with few orthostichies is shown in fig. 12, which represents an idealized cross-section of specimen C. Leaf traces and "potential" leaf traces are represented in fig. 12 by solid black, while the cauline portions of the steles are unshaded. The interpretation of the stippled areas will be explained in connection with description of fig. 14. In stem cross section (fig. 12) there are five concentric cycles although only four appear to be present. The fifth or innermost cycle is fused to the fourth cycle (fig. 13A, B) at the left side of the lower gap in the fourth cycle. When that gap is closed the two strands combining the fourth and fifth cycles do not fuse along the edges but the part of the strand composed of the fifth cycle bends toward the center of the stem (fig. 13C). The gap is closed as a result of fusion of the two flanking strands along their convex faces leaving two projections directed toward the center of the stem (fig. 13D). These inner projections, which actually represent the fifth cycle, separate as a single strand which migrates toward the other gap in the fourth cycle (fig. 13E). Similar to specimen A the fusion of the innermost cycle to the next outer one results in the transfer of a portion of the central cycle (leaf trace) to the one just outside. At the same time there is a compensation for the diminution in size of the innermost cycle by an addition of vascular elements originating from one of the incurved edges of the next outer cycle at the point of closing of the gap.

The fourth cycle in the stem diagrammed in fig. 12 behaves in the same way as the second cycle in specimen A. The convex portion in the lower left part of the fourth cycle, which consists in part of a leaf trace, fuses with the inrolled edges of the third cycle filling the gap in the third cycle immediately to outside of the fourth cycle. In this manner a trace is passed from the fourth to the third cycle and when the trace

becomes separated a gap is left in the fourth cycle. This gap is again partly filled by the fifth cycle at a higher level. The third transfers a trace to the second in a similar way, and with slight modifications the second cycle passes traces to the outermost one. All of the stelar changes just described proceed simultaneously in the stem; for example, the fourth cycle passes off a trace to the third while the gap on the opposite side of the third cycle is being filled in part by the fifth cycle. These various fusions and gap formations often make it difficult on cursory examination to distinguish the cycles and occasionally (as in fig. 11) there may appear to be fewer cycles than is actually the case. However, a section a short distance above or below the level in question readily shows the true number.

The free edges of the peripheral cauline strands are usually conspicuously inrolled (figs. 12, 14A). The fusion of a trace in the second cycle next to the outermost cycle takes place at positions along the convex portion of the peripheral bundles a short distance from the edges of those bundles (fig. 14B). When the second cycle separates from the outer one, a part of each peripheral bundle flanking the trace (the free edges) is added to either side of the gap in the second or more internal cycle (fig. 14C). Before the trace becomes free from the outermost cycle, the parts of the adjacent cauline bundles represented by stippled areas in the diagrams are contributed to the leaf trace (fig. 14C). In a diagram (fig. 12) it is difficult to specify the exact portions which function as leaf traces, cauline bundles, or portions of bundles which are contributed either to leaf traces or the next inner cycles. These have been designated only arbitrarily in the diagram and do not show that with increasing vertical distance there are pronounced changes in tangential dimensions and in configurations of the vascular bundles. For example, a peripheral cauline bundle which contributes segments to a leaf trace and the next inner cycle must necessarily become enlarged at higher levels before the next higher leaf trace of the same orthostichy fuses to it. Because of this, the exact amount of vascular tissue which the peripheral bundle contributed to a leaf trace or to the second cycle can be only an approximation in a diagram of a cross-section. Similarly, the tangential extent of the leaf traces or their exact position within a stele are only approximations.

At its point of separation a leaf trace is slightly curved with the convexity outward. At successively higher levels the convexity increases and eventually the free edges become inrolled and approach each other. Not infrequently, a trace in any of the cycles may separate in a position to one side of its point of fusion from the cycle immediately within. This "shift" in position of the trace often obscures the pathway of a trace

from the center of the stem to the periphery. Figure 12 shows a "shift" in which the position of the gap on the right side of the third cycle does not coincide with the position of the leaf trace in the second cycle.

Specimen D (figs. 5, 29) is a stem that has six cycles and six rows of leaf traces. The sixth and most internal cycle is shown in fig. 29 by a small strand now fused with the next outer (fifth) cycle.

The lowest portion of the stem of specimen E (figs. 6, 30) is characterized by seven orthostichies of leaf traces. Because of the increased number of rows of traces, the circular outline of sclerenchyma tissue common in smaller stems is replaced by a more sinuous configuration of the sclerenchyma which cuts in on the adaxial faces of leaf bases. The encircling band of sclerenchyma is also much thicker than that of specimen A. The stem at this level has reached such a degree of complexity that it is difficult to ascertain with accuracy the exact number of cycles present in the stem. As the number of rows of leaf traces increases, the number of leaf traces which must originate from the innermost cycle likewise increases. This accounts for the much dissected appearance of central portions of larger stems caused by overlapping of numerous leaf gaps. Further, because of fusions of strands of one cycle with those of the next outer cycle, the internal stelar situation becomes much more complex and impossible to follow unless many serial peels are closely observed. There is actually no necessity for such detailed observations because the morphology in such complex specimens is very likely nothing more than a compounding of the simple condition described for specimen A. Although the actual anastomoses of the individual strands vary with the stem and even within different levels in the same stem, the overall pattern of leaf trace initiation appears to be the same.

Near the bottom of specimen E the stem within the root mantle measures  $8 \times 6.5$  cm. in cross-sectional dimensions, while near the upper end of the well-preserved portion corresponding dimensions average  $10 \times 7.5$  cm. Only a small portion of the root mantle is preserved around the stem.

These observations made of fragments forming the ontogenetic series A-E show that the number of rows of leaf traces range from three in the most basal specimen A to seven for specimen E. The fact that orthostichies are added as the stem grows was recognized by Zeiller (1890) and others. In spite of these observations, confusion remained concerning the interpretation of stem structure because workers before and after Zeiller (1890) persisted in indiscriminately naming species of spiral forms based on the number of orthostichies present. Specimen E just described clearly shows a series of steps in the addition of an eighth

row of leaf traces to a previously seven-rowed condition, and provides additional evidence that the number of orthostichies is the product of ontogenetic variability.

In fig. 15A (specimen E), three of the seven peripheral cauline bundles have been labeled *a*, *b*, and *c*. There is one well-established pathway of leaf trace divergence situated between cauline bundles *a* and *b*. At 15B a "bulge" on the bundles of the next inner cycle indicates that a leaf trace will join with bundles *a* and *b* at a higher level. The leaf trace connecting peripheral bundles *b* and *c* has separated below the level of 15B, but has separated farther to the right than would be expected, considering the usual pathway of divergence. This leaves peripheral bundle *b* unusually large in tangential extent. There is a slight indentation in the bundle emphasized by a band of sclerenchyma (15B). In fig. 15C it may be observed that a large portion (left side) of the bundle formerly labeled *b* has been set free from the right side and has assumed the nature of an additional leaf trace at the periphery of a stem before its departure into a petiole base. The portion labeled *b'* (fig. 15C) is actually a small remaining segment of *b* to which the leaf trace is still attached. To the left edge of peripheral bundle *b* is attached a leaf trace which will be given off at a somewhat higher level, and which is not yet fused to bundle *a*. A slight outward projection at the point of attachment of the two is caused by a partial section through an adventitious root departing from the peripheral bundle. A slight inward projection is a part of the stelar contribution to the next inner cycle.

Thus, it is clear that a single, unusually large peripheral bundle divides to give off a leaf trace from its middle portion, leaving its two ends with inrolled edges; each of these ends forms a single peripheral cauline bundle (*b'* and *b*). As a result there has been added to the stem one new leaf trace, representing the beginning of a new orthostichy, and one new peripheral bundle (*b'*). The new peripheral bundle *b'* attains a normal size because the leaf trace between bundles *a* and *b'* is set free farther to the left than would ordinarily be expected for that channel, and also because additional tracheids were differentiated by the apical meristem to give the bundle a longer tangential extent. The separation of the leaf trace fused to peripheral bundles *b* and *c* (fig. 15A) slightly to the right of its usual place of separation forms a gap in the outer cycle which does not correspond to the path of divergence of traces of the same orthostichy evidenced in the inner cycles. There is actually no "shift" of the leaf trace, but rather one part of the trace is contributed to peripheral bundle *b* while the opposite edge of the trace consists of a portion of peripheral bundle *c*. The leaf trace supplying the next higher leaf of the same vertical row originates in the center of the stem and

bends upward and outward through the previously established pathway. When it has fused to the second cycle it "shifts" in a manner similar to that described for the leaf trace at fig. 15A. The separation of the trace from the second cycle (fig. 15C-F) forms a gap in that cycle directly opposing the gap in the first cycle. By similar "shifts" of traces in the cycles nearer the center of the stem there is eventually created a straight pathway for leaf traces supplying leaves in the orthostichy relocated by the departure of the trace (fig. 15A). Thus, the shift in position of the leaf trace starting in the outermost cycle is repeated all the way toward the center of the stem at successively higher levels by the cycles within. A strikingly analogous situation prevails in the establishment of a new (eighth) pathway for traces to leaves in the orthostichy initiated by the trace arising from peripheral bundle *b* (fig. 15B). The new leaf trace has originated entirely from a cauline strand. The trace directly above originates in an identical manner from a cauline strand in cycle two (fig. 15E-I), thus extending the pathway of leaf trace divergence one cycle toward the interior. Successively higher traces owe their origin to cauline bundles of cycles closer to the center.

In a higher portion of the stem fragment an identical method of origin of another orthostichy has been observed. As before, one of the peripheral bundles becomes larger as a result of the "shift" in position of separation of a leaf trace attached to it. The first trace of the new row (ninth) arises from the middle portion of the large peripheral cauline bundle leaving two peripheral cauline strands after it separates. Although only a small portion of the specimen is well-preserved above this region, it may be assumed that the establishment of the ninth pathway of leaf trace divergence into the center of the stem is the same as that for the new orthostichy added at a lower level. The separation of the first trace in the ninth row initiates the new pathway in the outermost cycle, but the gap formed there is opposed only by cauline material in the cycle just within. Since cauline strands gave rise to leaf traces in the eighth row, it seems likely that a similar condition prevails for the ninth orthostichy.

It is apparent that with the addition of one or more orthostichies of leaves on the stem a change in phyllotaxy results. While the lower part of the specimen showed seven rows of leaves in a  $2/7$  spiral sequence, this succession of leaves must be replaced by another series in the eight-rowed condition, and still another when nine rows are present. In the eight-rowed spiral condition the only regular phyllotaxy that can prevail is a  $1/8$  or  $3/8$  spiral. The  $1/8$  spiral probably never occurs in the plant kingdom. Because the lower levels of the stem of this species have already passed through a  $2/5$  sequence, a  $3/8$  spiral phyllotaxy might be expected for progressively higher levels on the stem. In de-

termining the phyllotaxy from a single cross-section, traces are counted beginning with those closest to the periphery of the stem and progressing inward in order. In a  $3/8$  phyllotaxy two traces would be by-passed between the lowest trace and the one next in sequence. Two more traces would be passed before the next higher trace is reached. Thus, with three turns about the circumference of the stem, eight traces are encountered before reaching the one in the same orthostichy as the first. A stem fragment described by Blickle (1940, fig. 1) represents such a spiral condition with a regular  $3/8$  phyllotaxy.

In specimen E it is not possible to by-pass two rows of traces between successive leaf traces in the eight-rowed condition, nor is there a  $1/8$  progression. Instead, the nearest phyllotactic spiral that can be determined is one which passes through a leaf trace in every other row. It would be impossible to arrive at the eighth leaf of the series (the leaf directly above the starting point) by stopping at intervals separated by arcs of equal magnitude (in this case, arcs of  $90^\circ$  or the distance on the circumference between two rows of leaves). This would result in the spiral passing through the same four rows at all times. Thus, in certain places, the phyllotactic spiral must necessarily pass through adjacent rows or through an interval of three rows. Since nine rows become established on stem fragment E at a higher level, the irregular sequence of trace departure prevalent in the eight-rowed condition does not persist for too great a distance. The new sequence which becomes established appears to be one of  $2/9$ , although it is not possible to fit every trace in this strict sequence. The explanation probably lies in the fact that the leaves at this level of the stem are approaching a whorled condition, each whorl consisting of leaves in alternate rows. In a whorled condition which is well illustrated in the three succeeding stems of this series there may be a slight vertical deviation among members of one whorl. However, in all cases the members of a single whorl arise much closer to a given level than the leaves of either the next lower or next higher whorl. It is obvious that in a nine-rowed state a whorled condition cannot exist unless leaves of two adjacent rows arise at the same level. Although the leaves in specimen E are still spirally arranged even in the nine-rowed state, the retention of the  $2/9$  phyllotaxy seems to suggest that it is approaching a whorled condition. Leaves encountered in the first turn around the stem may be considered the ones belonging to one whorl, while those passed through in the second turn indicated by the phyllotactic fraction probably constitute the other whorl. This, of course, depends upon the leaf chosen as the starting point.

Additional evidence indicating that the upper portion of specimen E is approaching a whorled condition is shown by a specimen from Berryville (specimen F, figs. 7, 31) in which eight rows of leaves had become

whorled by the time the eight-rowed condition was attained. Still another specimen (specimen I, fig. 34) from Berryville changes from a spiral to a whorled condition in what appears to be the eight-rowed stage. Thus, although all stems may not have reached the condition with whorled leaves at exactly the same stage of development, it seems likely that this condition in the Berryville stems was attained somewhere between seven to ten orthostichies of leaves. If a whorled specimen is cut obliquely it may appear to be a spiral form, but there is no phyllotactic fraction to fit such a condition and it can readily be detected as a poor cross-sectional cut.

Specimen F with eight rows of traces represents a well-established whorled condition. In such a stem the peripheral bundles have the appearance of being paired, a configuration brought about by the outline of the band of sclerenchyma around them, and by their association with the trace between them. At a slightly higher level the alternate pairs of peripheral bundles appear to be coupled. The external aspects of this condition will be discussed in a later section.

In stem specimen F there are approximately eight concentric cycles. Prominent bands composed of sclerenchyma cells are conspicuous throughout the fundamental tissue. Sclerenchyma tissue also often lines the concave faces of the peripheral bundles. In some areas of the cross-sections it develops hooklike extensions around the free edges of some of the vascular bundles (fig. 31) while in other parts, spur-like projections are formed. These projections are most frequently associated with the peripheral bundles and leaf traces, and at higher levels there is an extension of inwardly directed spurs from the sheath of sclerenchyma to form the lateral flanks of the leaf base (fig. 30). There is often the tendency of sclerenchyma between two cycles to fuse through a leaf gap (fig. 31). The abundance of sclerenchyma varies in amount in corresponding levels of different stems and with different levels in the same stem.

The next well-preserved specimen in the series (specimen G, figs. 8, 32) is one with 12 rows of leaves through most of the length preserved. This stem fragment has an average diameter of approximately  $11 \times 10$  cm. exclusive of the root mantle. The rather heavy band of sclerenchyma surrounding the stem emphasizes the paired condition of the peripheral bundles typical of the larger whorled specimens. Certain of the vascular bundles are often distorted or even partly obliterated by a proliferation of parenchyma cells of the ground tissue. In places the proliferation appears to have been rapid, with divisions in the same plane, since a seriation of cells can often be discerned. In other parts, added parenchyma cells appear to have been formed more slowly, dividing in various planes, resulting in a parenchyma tissue differing very little from the

original ground tissue; the distortion of some of the original structures suggests, however, that proliferation had taken place. As a general rule most of the proliferated parenchyma tissue is found near the periphery of the stem; however, in parts of specimen G proliferation occurred in the center of the stem where seriated parenchyma cells can be observed surrounding the steles. This phenomenon was responsible for the suggestion that secondary development took place in *Psaronius* steles (Moon, 1939). In many parts of the stem, proliferation of parenchyma has partly filled some of the lacunae, an observation which proves that these cavities are normal features of the stem and not the products of decomposition. The meristematic potentialities of parenchyma cells in the stem and in roots will be discussed later in an attempt to explain the nature of the tissue surrounding the inner roots.

Specimen H (figs. 9, 33) is a stem fragment with more rows of leaves than any other specimen in our collection. Although it is somewhat crushed, 14 rows of traces can be observed arranged in alternating whorls of seven. In the most complete section this stem measures  $13.5 \times 7.5$  cm.

An idealized cross-section of a stem with leaves in whorls is depicted in fig. 16. At the level of this section there are 12 rows of leaf traces (two whorls of six), and seven concentric stelar cycles. As in fig. 12, cauline bundles have been left unshaded while leaf traces are drawn in black. Stippled areas in the peripheral cauline bundles represent the parts of those bundles which are contributed to the outgoing leaf traces.

Because of the absence of the usual innermost cycle, and because it is almost impossible to determine the configuration of the inner cycle in a stem with seven or more rows of leaves, it is represented in the diagram (fig. 16) by a ring of unshaded bundles. In this stem, the leaf traces originating from the center proceed upward and outward, filling the gap between each successive adjacent pair of cauline bundles. As in smaller stems a portion of a cycle to which a leaf trace is attached moves upward and outward and fills the gap in the next outer cycle before actually passing off the trace. It is not unusual for part of a cycle to become attached to the next outer cycle on one side of the gap first, or for one edge of a leaf trace to become separated from the inner cycle before the other. In the diagram, a trace which was transferred from the fourth to the third cycle is attached on the right side only to a cauline bundle of the third cycle, while at its left edge it is attached to cauline bundles of both the third and fourth cycles. Apparently, then, it was set free first at its right edge from the cauline bundle of the fourth cycle.

*P. blicklei*, sp. nov. Diagnosis: Stem having three to fourteen or more orthostichies of leaves, the increase occurring at successively higher levels; leaves spirally arranged in lower portions, becoming whorled



higher in the stem; up to 10 or more concentric stelar cycles in the stem; cells of leaf traces smaller in diameter than cells of other vascular bundles; leaf traces near periphery of stem thinner than other vascular bundles; traces assuming the *Stipitopteris* configuration; stem surrounded by a definite sclerenchymatous layer; sclerenchyma cells present in small patches and surrounding leaf bases in lower portions of stem, becoming more abundant at progressively higher levels; parenchymatous ground tissue compact with no or few lysigenous cavities, the lacunae becoming more abundant and larger higher in the stem; tannin-like deposits in parenchyma cells of ground tissue of stem and roots, and in secondary parenchyma cells surrounding roots; proliferation of parenchyma cells occasional especially in upper portions of stem; dense mantle of roots below, becoming less extensively developed above; four to six protoxylem groups on the arms of the actinosteles of roots.

## 2. Discussion of *P. blicklei*

The supposition that the series of *Psaronius* stem fragments (A-H) described in the preceding section represents the ontogenetic development of a single plant is perhaps a new and slightly unusual approach in paleobotanical studies. It could be argued that the presumed ontogenetic stages represented by the different stem fragments form a series of closely intergrading species. Based on other reports (Hirmer, 1927; Gillette, 1937; Baxter, 1953), six or more species might be named from this group of fragments. A multiplicity of species could be anticipated if earlier classifications (Zeiller, 1890; Stenzel, 1906; Hirmer, 1927) were used, in which the number of orthostichies, shape of leaf traces, number of internal strands, and certain invalid characters of sclerenchyma tissue were relied upon. It is obvious that if two such stems as shown by figs. 25 and 33 were to be compared without the knowledge of the series described above, they would undoubtedly be considered distinct species. It is understandable that previous workers, because of incomplete knowledge of the subject, set up different portions of the same plant as separate species. If, with the information obtained from studying stem fragments in the sequence A to H, however, one considers any two adjacent specimens of the series, it becomes impossible to make distinctions among the members. If this group of stems is a series of closely related intergrading species, then their characters overlap to the point where it is impossible to separate them.

A thorough study of approximately 24 specimens from the Berryville and one from the Dix localities has been made with reference to possible points of species differentiation. It seems appropriate to consider each of these characters with relation to segments from the base of the apex of *P. blicklei*.

One of the more obvious features of *P. blicklei* is the great number of lacunae found in the ground tissue at higher levels of the stem. These are much more sparse at lower levels, gradually increasing in number and in size as higher levels. Even lower in the stem than the level shown in fig. 1, the ground tissue appears very homogeneous. At a slightly higher level in the same coal ball (fig. 1), lacunae definitely appear in association with the concavity of the leaf trace, as well as other places in the ground parenchyma. This is not an unusual occurrence, since these cylindrical cavities are lysigenous in origin. Thus these cavities may develop at a later stage in ontogeny, with the exact time of initiation varying in different stems. Because of this, relative numbers of lacunae should be avoided as a key character and caution should be used in assuming that a stem is completely lacking in lacunae if only a small fragment is examined. A consideration of the age of the stem and the level (basal or distal portion) is also necessary. Certain types of preservation, such as a particular type of silicification or preservation in ironstone, may obscure details of lacunae distribution. In all of the specimens assigned to *P. blicklei* (including all of the fragments used in the series shown by figs. 1-9 and 25-33) these lacunae are present in the stem.

Small cells containing black or brown tannin-like remains are also present in all fragments of these stems and in the secondary parenchyma tissue surrounding the roots. All characters of the root zones in all fragments of *P. blicklei* studied seem very similar.

Sclerenchyma tissue, forming a thin band around the stem and departing leaf traces at the lowermost level of the stem, shows a great development throughout the series of specimens comprising this sequence. At higher levels it is found in association with many of the internal cycles and in cross-sectional aspect assumes many diverse configurations. In addition to the surrounding layer of sclerenchyma, every stem shows varying numbers of sclerenchyma cells in the ground tissue, depending on the stage of development.

Extreme care must be taken when considering phyllotactic characters as a source of specific differentiation. With the aid of specimen E of the series, we see that stems of this species add new rows of leaf traces in the upper levels of the stem. They progress from a  $1/3$  spiral (specimen A) to a 14-rowed whorled condition (specimen H) in our collection, and it is conceivable that in certain stems even more than seven members per whorl might be attained. Both clockwise and counterclockwise spirals were observed in specimens of *P. blicklei*, but this difference cannot be used to differentiate two species because it is well known that even within a single plant phyllotactic patterns vary (Esau, 1953). Since spiral forms can change the phyllotactic fraction by the initiation

of additional orthostichies, and since specimens can become whorled at different levels, the characters of frond arrangement are worthless except in special instances, e.g., the distichous, tetrastichous, and certain other specimens which will be discussed in detail. Modern tree ferns such as *Cyathea* also follow the sequence from a spiral to a tightly whorled condition (Ogura, 1927).

It has also been observed in specimen A that increase in complexity and size of the vascular system may be caused by the addition of a new cycle and by the differentiation of more tracheids within the same obconical vascular cylinder. Also, more highly developed polycyclic stems are not necessarily of a different species. The tendency of certain authors (Baxter, 1953) to use numbers of "internal strands" as specific characters is likewise to be avoided, since it should be obvious that these strands are complete cycles of a highly polycyclic stem. Further, leaf traces are given off in the same manner in all fragments and the basic pattern of stelar behavior is similar in all cases.

Because of intergrading characters within a single specimen, it has been impossible to delimit more than one species in this group of stems.

*P. blicklei* could easily have attained a height of 30 feet, a figure suggested by previous workers for similar stems. The basal portion is a massive structure consisting of a root mantle which surrounds a small stem base approximately  $2.3 \times 1.5$  cm. in diameter at the lowest preserved level. Specimen A approximates the length of stem (more than 20 cm.) necessary for the addition of a well-developed cycle, a change which probably required an even greater length at higher levels where the stem becomes more complex. Specimen E required approximately 40 cm. for the addition of one orthostichy and 20 cm. for the addition of another. This indicates that even in the same stem the distance may vary as would most probably be the case in different stems of the species. The stem began as a small obconical axis, later becoming encased in a huge mass of roots. By the addition of new cycles, each one more internal than the previous one, it increased in complexity. Each stelar cycle, along with the cortex and sclerenchyma sheath, increases in volume at higher levels by addition of primary tissues derived from the apical meristem. Increased complexity may also be attributed to the addition of new orthostichies of leaf traces and to the effect their pathways of divergence have on the more internal cycles. Increase in the over-all size of the stem as well as increase in diameter of each concentric cycle is well illustrated by specimen A, which varies in diameter from  $2.3 \times 1.5$  cm. in the more basal portions to approximately 3 cm. in the upper, well-preserved limits of the coal ball. A similar increase may be observed in specimen E, which at the lower end has a stem diameter of  $8 \times 6.5$  cm., increasing to  $10 \times 7.5$  cm. through a distance

of approximately 50 cm. That many of these stems attained a whorled state has been adequately proved. However, it is not inconceivable that some, for various reasons (e.g., ecological), never survived long enough to become whorled. As higher levels of both spiral and whorled conditions are reached, the vertical distance between fronds decreases as well as the horizontal distance. The latter decrease is brought about in part by the addition of new orthostichies.

All specimens of this group show evidence of a root mantle about the periphery of the stem. Logically, stem fragments with progressively more internal complexity indicate a higher level in the plant and possess fewer and fewer roots at the periphery. It might be argued that this is a phenomenon of preservation; however, the remarkable constancy of finding fewer roots in the distal regions and great masses of them at the base would suggest that preservation is not the only factor involved. Because of this mantle of adventitious roots, the leaf scar arrangement on more basal portions of the plant is often obscured. Comparison with living members of the Cyatheaceae suggests that more distal regions of the stem lacked the conspicuous sheath of roots (see frontispiece). However, this does not rule out the probable occurrence of these roots in fewer numbers growing in sinuous courses down the stem among leaf bases and over newly formed leaf scars. It is obvious that fronds did not extend through an extensive covering of roots, a fact which supports the idea that the upper portions of the stem lacked a very extensive root mantle. That some roots were present between the fronds, while they were still attached to the stem, is supported by the fact that these roots grew down over the leaf scar very soon after the frond dropped away. If these positions of frond abscission were left exposed to the drying conditions of the atmosphere for a great length of time, it is most probable that the outer cortical cells would not have been capable of secondary proliferation which helps interlock the sheath of roots to the stem.

At higher levels of the stem where leaf scars are exposed, and at lower levels where the root mantle has been removed, the external appearance of the stem varies with the conditions of its spiral or whorled leaf arrangement and with the angle of divergence of the leaf. In some lower portions of the stem the angle of divergence is slight in comparison with that of other stems; however, a greater angle is of necessity substituted at higher levels since the closely crowded condition of the whorls does not allow for even slightly decurrent leaf bases. As the closely arranged whorled condition is attained, the positions of the peripheral cauline bundles become externally prominent and they appear as sinuous strands on the surface of the stem (fig. 71). Internally, it was observed that at the level where a leaf trace is fused to two pe-

ripheral cauline bundles the bundles are closer together than they are when an adjacent trace at the next higher node becomes fused with one of those peripheral bundles and another farther around the stem. This explains the apparent paired arrangement of the peripheral bundles in cross-section and is manifested externally by their regular sinuous columnar appearance.

No fronds have yet been found attached to these stems, so it can only be postulated that at the apex of the large whorled forms, two whorls of fully developed fronds may have been retained on the stem at the same time. To have more persisting would seemingly present a serious problem of arrangement because of the closeness of the leaf bases and an entangling of the fronds themselves. It is conceivable, however, that still another whorl of young fronds could have begun the unfolding process. On the basis of compressions of *Spiropteris* found in shale and certain well-preserved circinately coiled frond tips in coal balls from Berryville, it is suggested that these fronds could have undergone circinate vernation during their development similar to living tree ferns.

## B. *Psaronius melanedruss* sp. nov.

### 1. Description

Well-preserved specimens of *Psaronius* stems from the Fleming coal near West Mineral, Kansas, have been found, but not in as great abundance as the Berryville representatives. In most of the larger stems, only the centers were preserved or the whole stem was somewhat crushed, making a reconstruction of their vascular system difficult. The quality of preservation in some of the smaller stems, however, was remarkably good. A study of closely spaced sections from a well-preserved basal portion was made in an effort to show (1) the manner in which the small, most internal cycle fuses with the next outer one when passing off a leaf trace, and (2) the way in which this small strand reconstitutes itself before its contribution to the next higher leaf trace in the phyllo-tactic sequence in the cycle immediately outside. The results of these observations were found to be in agreement with those made on the most nearly basal portion of *P. blicklei* (fig. 10, specimen A of the Berryville series). The series of diagrammatic cross-sections (specimen J, figs. 17, 35) represent the most basal specimen of *Psaronius* described from the Fleming coal. It shows the beginning of a supposed ontogenetic series of stem fragments (J through M) from Kansas. The stem at the lowest level preserved is characterized by a three-cycled condition (fig. 17). There are three orthostichies of leaves: one represented by the leaf base completely surrounded by sclerenchyma in fig. 17A, one represented by the slight "bulge" in the large bundle on the right side, and a third

orthostichy at the position of the gap between the cauline bundles at the lower left corner of fig. 17A. The third or most internal cycle is identified at this level by the small open cylinder in the center of the stem. It is oriented in such a position that, at a higher level, it will fill the gap in the next outer cycle (cycle 2). Cycle 2, at the same level, bends toward the gap on the lower left side of the first or outermost cycle. At B of fig. 17 and in fig. 35, the gap just mentioned in the outermost cycle has been filled by the leaf trace from the second cycle. At this level in the first or outermost cycle, the usual overlapping of gaps to form a typical dictyostelic arrangement is not present.

At lower and higher levels of the stem, however, such a situation is apparent (fig. 17A, C). It appears that at these levels the outer vascular cylinder is interrupted at the position of two pathways of divergence by leaf gaps. Also, at B (fig. 17) the third cycle has fused with a cauline bundle on either side of the gap in the second cycle, toward which it was migrating at a lower level (fig. 17A). The two strands projecting inward toward the center of the stem at this level (B) are the free edges of the small open cylinder representing the third cycle, with the possible addition of a few vascular elements contributed from the inrolled edges of the next outer cycle. The sharp bend in the right edge of the second cycle in fig. 17B and in fig. 35 is mechanical and should not be confused with the free edges of the central cycle. At C (fig. 17) slightly higher in the stem, the two inwardly projecting strands of the third cycle have separated from the second cycle and fused along their opposite edges. This results once again in a small open cylinder with the convex portion of this strand directed toward the gap between two bundles of the second cycle. At the same level (diagram C) the leaf trace at the lower right side of diagram C, represented in diagrams A and B as a slight bulge between two cauline bundles, has been set free and is particularly enclosed in a sclerenchyma sheath. Also at this level the leaf trace, depicted at the top of the diagrams A and B, has completely departed from the stem. A comparison of this specimen with the early stages of development of *P. blicklei* (specimen A, fig. 10) makes it clear that the manner of both leaf trace origin and reconstitution of the most internal cycle is the same in these two species in specimens where the internal cycle is very small.

Specimen J, which is slightly crushed, has cross-sectional measurements of  $2.3 \times 1.8$  cm. At the point of leaf trace departure from between two peripheral cauline bundles the vascular strand becomes much smaller in radial thickness (fig. 35), with a corresponding decrease in diameter of tracheids; the leaf traces of leaf bases at a higher level retain this relative thinness. In specimen J the leaf base is a very large structure in relation to the size of the stem, measuring 9 mm. in tangential direction.

The ground tissue as well as the secondary parenchyma tissue surrounding the roots have tannin-like deposits in some of their cells. No lacunae, like those described for *P. blicklei*, are present in this or any of the stems of this series. The stem is surrounded by a mantle of roots which are not well preserved; however, the actinosteles of many individual roots were preserved and bore five or six arms of primary xylem. A very heavy sclerenchyma sheath separates the stem and root zone except on the outer side of a departing leaf base, where it was torn off at the time of abscission of a leaf. Specimen D (fig. 28) shows that certain cells surrounding roots of the inner root mantle are produced by proliferation of stem parenchyma cells in the region of leaf bases after leaf abscission.

Specimen K (fig. 36), considered to be a fragment of a higher level of a stem of this species measures  $5 \times 2.3$  cm. in cross-section. It is characterized by five orthostichies of leaf traces and probably five concentric cycles of vascular tissue within the stem. A mantle of roots, one to three roots wide, surrounds the stem, but it is likely that more roots were sloughed off the outside of the mantle during preservation. At various places around the stem, adventitious roots connected with the peripheral cauline bundles are seen in oblique cross-section passing through the sclerenchyma sheath of the stem. The portion of the sheath immediately outside of the peripheral cauline bundle at the top of fig. 36 is incomplete, and cortical parenchyma cells inside the stem have proliferated profusely, making a homogeneous connective tissue between the fundamental tissue of the stem and the radiating rows of secondary parenchyma cells surrounding roots of the inner root zone. In all respects, features of this stem indicate that it belongs to the same species as specimen J. Such characters as an increased number of stelar cycles and a larger number of leaf orthostichies suggest that specimen K is from a higher level of the plant than the preceding stem fragment.

Specimen L (fig. 37) is a fragment of *P. melanedruss* which, judging from complexity, has reached about the same level of development as the preceding stem (specimen K). Five orthostichies of leaves alternate with five concentric cycles of vascular tissue. This stem also possesses a very thick, well-preserved sclerenchyma sheath. The leaf traces in leaf bases of specimens of K and L (figs. 36, 37) are narrower and are composed of tracheids smaller in diameter than those of the vascular bundles of the stem proper.

Through the length of specimen L (more than 10 cm.), there is no root mantle enclosing the stem. One possible explanation is that a root mantle had once been present and had been shorn away during the processes of preservation. The specimen was examined for evidence to substantiate such a suggestion, but it could not be confirmed. At various levels two to four adventitious roots were observed passing through the

sclerenchyma sheath in their downward and outward course to the periphery of the stem. However, there remained no evidence of any of these roots outside the sheath. Further, there was no evidence of the mechanical separation between the stem and roots with their surrounding secondary parenchyma tissue.

It may be postulated that in the absence of evidence that a root mantle had been broken away from around this stem, it is a distal portion of a young stem which had not developed a thick zone of roots. The few roots passing through the sclerenchyma sheath might easily have been severed at their points of emergence from the limiting layer of the stem, so that they are not visible in external view. At a later stage of development (at the level represented by this specimen), more adventitious roots could have been formed from the peripheral cauline bundles and at their points of exit from the stem the secondary proliferation of parenchyma cells might have started, the combination of these events producing the root mantle.

Specimen M (fig. 38) which averages  $10.5 \times 3.8$  cm. in diameter and measures over 6 cm. in length, represents a still higher level of a stem of *P. melanedrus*. It is characterized by five orthostichies of leaf traces which are relatively thin in comparison to the other vascular bundles of the stem (fig. 39, specimen M). The vascular system of this stem fragment is composed of six concentric cycles. In this specimen the structure of the ground parenchyma has been preserved better than in any other stems of this species studied. It is apparent that the fundamental tissue consists solely of parenchyma cells except in portions where the limits of a leaf base have been marked off by sclerenchyma tissue. Tannin-like remains are abundant in the fundamental tissue of the stem and leaf bases, and in the secondary parenchyma cells surrounding the roots. The stem is limited by a typical thick band of sclerenchyma tissue, but no sclerenchyma bands are to be found in association with steles as in *P. blicklei*.

A conspicuous feature of these stems is the configuration of sclerenchyma tissue around leaf bases at the periphery of the stem. At the lowest level of differentiation of a leaf base, sclerenchyma tissue is first visible as two inwardly projecting strands, one on either side of the trace. Often, at this level, these two strands are not connected to the limiting layer of the stem (fig. 38, bottom). As the leaf base increases in differentiation, small patches of sclerenchyma cells become fused into a flat band on the adaxial face of the leaf base, and at higher levels this becomes continuous with the two inwardly directed projections of sclerenchyma. Still higher, the sclerenchyma tissue around the trace becomes attached to the layer surrounding the stem, and in cross-section the leaf base appears to be delimited by a thick, nearly rectangular band



of sclerenchyma. As the leaf base separates from the stem, the inner face retains its square configuration, but when the leaf base is completely separated the outline of the stem at that position is smooth once again. This unusual development of sclerenchyma tissue is characteristic of this species.

Although the fundamental tissue and outer cycles of certain of the larger stems of *P. melanedrus* were not well preserved, the vascular bundles of the central portion of specimen N (fig. 40) are fusainized with almost diagrammatic clearness. The morphology of the most internal cycle is of particular interest, since in the length of stem preserved, the most internal cycle is relatively large and well-developed in comparison with the very small central strands of specimens A and J. Although basically this larger cycle functions in the same way as the smaller strands of specimens A-J in giving off leaf traces, there are, because of the greater size of the strand and greater complexity due to the presence of more orthostichies, certain peculiarities which are difficult to interpret unless the morphology of such a type has been studied in detail. A thorough knowledge of the morphology of the stem in question must be had before attempting to distinguish species on the basis of characteristics of stelar morphology.

The diagrams A-H in fig. 18 represent the three most internal cycles of specimen N at progressively higher levels. In the coal ball a more external cycle was preserved throughout most of the length. This cycle and any others remaining after fossilization have not been diagrammed with the exception of level C, in which part of this cycle has been shown.

The outermost cycle of the three in the diagram (fig. 18), which will be arbitrarily referred to as cycle 1, is not shaded and is outlined by a solid black line. The second or next inner cycle has been stippled and is outlined with a solid line, and the third or most internal cycle is represented as a solid black band. The position of a small cauline bundle belonging to the second cycle which has not been well preserved is designated by the stippled area just inside the outermost cycle at the lower left of diagram A. This strand is not outlined. Numbers have been placed to indicate the position of orthostichies in a  $2/5$  spiral, which represents the phyllotactic sequence of this stem. In all diagrams of this series the same orthostichy is designated by the same number.

At the orthostichy labeled 1 in fig. 18A, the leaf trace in the outer cycle is the first of those in this series of cross-sections to be given off. In the next inner cycle at this same position, there is a leaf gap between the small, stippled, unoutlined strand, and the tangentially expanded portion of that cycle (cycle 2). This gap has been partially closed by the uniting of one edge of the adjacent cauline bundle with one free edge of the leaf trace which is being given off from the third or most internal

cycle. The portion of the third cycle, which at this level is closing the gap in the second cycle, is actually a leaf trace, and unlike the central cycles of many other stems investigated, fusion of the central cycle to the next outer one occurs directly on the free edge of the leaf trace. As a result, no incurved cauline bundle projects inward on that side after fusion. The other side of the trace will fuse with the cauline bundle on the opposite side of the gap at a higher level. At the position of the second orthostichy of leaves in the sequence, a leaf trace is joined at both edges to a cauline bundle in the outer cycle. Here also a leaf gap in the second or next inner cycle is partially closed by a trace being given off from the third cycle. This leaf trace has fused with the cauline bundle at the right side of the gap, and will fuse on the left side and completely close the gap at a higher level. At the position of the third orthostichy, a leaf trace from the second cycle is in the process of filling the gap in the outer cycle and has already fused with the cauline bundle at the left of the gap. The cauline bundle of the second cycle, previously attached to the leaf trace which joined the outer cycle, has been set free, and at a higher level the cauline bundle on the right side will separate from the trace as the trace joins the cauline bundle on the first cycle. At the fourth orthostichy a leaf trace in the second cycle turns upward and outward before filling the leaf gap in the outer cycle. At the position of the fifth orthostichy there is also a leaf gap in the first cycle which will be filled by a leaf trace from the second cycle soon after the gap in the first cycle at the fourth orthostichy is filled.

Level B represents a somewhat higher level in which the leaf traces shown at level A are somewhat farther out, and although most traces differ only slightly in appearance from those at level A, two striking changes have occurred in the length of the stem between levels A and B. At the position of the first orthostichy, the gap in cycle 2 has been completely closed by a leaf trace from the innermost cycle. At row 3 the trace from the second cycle has been completely fused to the outer one leaving a gap in cycle 2.

At level C the leaf trace attached to the outer cycle of orthostichy 1 is being given off to fill the gap in a cycle still more external than cycle 1. Up to this point cycle 1 has been designated as the outermost cycle throughout this series. With this exception, the still more external cycle diagrammed at this level by dashed lines does not enter into the discussion and has only been included at this level for the sake of clarity since one of the other cycles under consideration is, for a time, in close proximity to it while passing off a leaf trace. At the position of the second row of leaves, a leaf trace remains attached to the first cycle between the cauline bundles. The gap in the second cycle which was only partially closed at level B has now been completely closed, and the

third cycle has released the trace. The slight constriction at the left side of the trace indicates that the leaf trace which has just been contributed to the second cycle has not completely fused with the cauline bundle of the second cycle. At the position of the third orthostichy, a leaf trace is still attached to the outermost cycle and the leaf gap in the second cycle is closed on the left side at this level by a trace contributed from the most internal cycle. At orthostichy 4 a leaf trace passes off to the outermost cycle. This is evidenced by the slight indentation in the outer cycle and by the position of the cauline bundles on either side of the gap that has been left in the second cycle. Even at this level it is apparent that the convex arm of the most internal strand is bending outward (as well as upward) to close the gap in the second cycle.

At level D there is a gap in the outer cycle at orthostichy 1 left by the trace seen departing at level C. At orthostichy 2 there is also a gap between the cauline bundles of the outer cycle left by a departing leaf trace. At the fourth orthostichy a leaf trace is attached to the cauline bundles of the outer cycle. At orthostichy 5 a trace from cycle 2 has passed to the first cycle leaving a gap in the second one. The small cauline bundle in the second cycle left after separation of the trace appears isolated in this section because of the presence of a gap on either side of it.

At level E in the third orthostichy, leaf traces are attached to both the outer and next inner cycles so that no gap is present at this level. A gap in the second cycle of the fourth orthostichy is also partially closed by the fusion of the edge of the most internal cycle with the cauline bundle on the right of the gap. At the point of fusion of these two cycles, there is an increased amount of inrolling of the adjoining edges of the two cycles involved, resulting in an inwardly directed projection. At the position of orthostichy 5, a leaf trace is still attached to the outer cycle and the gap in the second cycle is being closed by a trace given off by the most internal cycle. The small cauline bundle of the second cycle at the lower right of diagram D is not conspicuous at E, since the gap to the left of it has been filled.

At level F it may be seen that the leaf gap in the first cycle at orthostichy 1 present at level E has now been filled, and a gap remains between the cauline bundles of the second cycle. A leaf trace has separated from the outer cycle at orthostichy 3, leaving a gap. The gap in the second cycle at orthostichy 4, which was only partly closed at level E, is now filled with a trace. The inwardly directed projection in that position referred to in the description of level E has separated, and still higher (level G) fuses with the internal strand. No particular significance is attached to this fusion, and at an even higher level (level H) the small strand has become completely "absorbed" by the internal strand.

At level H, in the position of the second orthostichy, the leaf trace from cycle 2 has been given off to the first cycle. At orthostichy 4 a leaf trace has separated from the outermost cycle and at the fifth row the gap in cycle 2 which was only partially closed at level G is now completely filled with a leaf trace.

At various places along the length of the innermost cycle a very narrow gap appears, thus explaining the apparently two-stranded structure of the central cycle as suggested by figures 18E, F, G. These gaps are in no way connected with leaf traces and are closed simply by the coming together of the vascular tissue on either side. This phenomenon should not be confused with the condition in other stems in which a gap is formed in the innermost cycle after a leaf trace is passed off to the next outer cycle.

Specimen O (figs. 19, 41) is also preserved only in the center, and probably represents a portion of a stem corresponding in level to specimen N. It also has five orthostichies, and the paths of divergence of leaf traces are discernable even in the central cycles. As in specimen N, the most internal cycle (fig. 19, diagrammed in solid black) fuses to the next outer one (stippled) first along the free edge. The leaf trace of the innermost cycle is present on the edge of that cycle, and no gap is formed when the trace is passed off to the next outer cycle.

It appears then that the configurations of the inner cycles of specimen N and O are typical for *P. melanedrus*, but only for certain levels in the stem where a relatively small number of rows of leaves (e.g., 5) is present. In the three-rowed condition the central cycle is constructed like that of similar stages of *P. blicklei*. Furthermore, in stems with more than five orthostichies the innermost cycle is not a single strand, but is dissected with two or more gaps. It seems likely that the cross-sectional configuration assumed by the central cycle in specimens N and O is a result partly of the number of orthostichies and partly of the cross-sectional length of the strand at those levels. When more orthostichies are present, leaf traces are passed off from the innermost cycle to several gaps in the next outer cycle almost simultaneously. This results in the formation of two or more gaps in the central cycle, which would therefore no longer be represented by a single strand. In this region of the stem, the innermost cycle is very probably approaching the upper limit of size for an undivided strand of the central cycle, and it is quite probable that at only a slight distance above the levels represented by specimens N and O a new cycle was added in the center.

Because of the manner in which traces are contributed from the central cycle to the next outer one in specimens N and O, it is suggested that the central cycle consists of a cauline strand with leaf trace or potential leaf trace material at either end, since in almost all cases

observed the leaf traces originate at the two edges of the central cycle. The original size of the central cycle is reconstituted after traces separate from it, by differentiation of a larger number of vascular elements.

The different configurations assumed by the innermost cycle and the different ways in which it contributes leaf traces to outer cycles in various specimens of *P. melanedrus* might be considered bases for specific distinction. It should be emphasized, however, that the structure of the central cycle depends on its position in the stem. Undoubtedly closer to the base of the plant, this cycle was considerably smaller and supplied traces for fewer orthostichies. Higher in the stem it seems likely that cycles more internal to this one were added after this once most internal cycle assumed a cylindrical configuration with alternating cauline strands and leaf traces. These changes in morphology are therefore ontogenetic and do not, in this case, account for variability among species.

Evidence that the structure of the innermost cycle in specimens N and O is only temporary can be found in another stem fragment (specimen P, fig. 42) from the West Mineral locality in which again the inner cycles are the only ones preserved. Pathways of six rows of leaf traces can be observed in these cycles. Thus, this stem fragment probably represents a relatively higher level than is suggested by specimens N and O. The innermost cycle in specimen P is divided by gaps so that at no part of its length in the specimen is it a single strand. In specimens N and O it was seen that the central cycle supplied two traces to the next outer cycle in rather close succession. Specimen P, however, has an additional orthostichy, and in this stem fragment the innermost cycle gives off three traces in a very short vertical distance, thus accounting for its dissected nature. It seems certain that specimen P with a larger number of rows and increased complexity of the central cycle is simply a portion of a stem from a higher level than that of N and O. The differences it exhibits are ontogenetic and are to be expected at upper levels of such a stem.

Still another stem fragment of *P. melanedrus* (specimen Q, fig. 43) from the West Mineral locality is a rather crushed specimen 26.8 cm. long. Although the vascular system is considerably distorted, this fragment is significant in having retained certain of the features near the periphery of the stem. Six rows of leaves were borne on this stem fragment, the largest number observed in *P. melanedrus*, although certain other large stems which are badly crushed very likely had more orthostichies. Characters of the sclerenchyma tissue at the outer limits of the stem and around leaf bases are identical with those of specimens K, L, and M, all of which possess a smaller number of rows of leaves.

*Psaronius melanedrus*, sp. nov. Diagnosis: Stem with three to many orthostichies of leaves; leaves spirally arranged in lower portions, prob-

ably becoming whorled higher in the stem; two to many concentric stelar cycles in the stem; radial thickness of xylem in stem vascular bundles ranging from .4 mm. in the basal portions to at least 1.1 mm. higher in the stem; stem surrounded by a heavy sclerenchymatous layer, ranging from .6 mm. in thickness in basal portions to 1.2 or more millimeters higher in the stem; sclerenchyma cells entirely lacking in fundamental tissue except that delimiting leaf bases which are enclosed by a heavy band of fibers and are roughly rectangular in cross-section; parenchymatous ground tissue lacking lysigenous lacunae; tannin-like deposits in parenchyma cells of ground tissue and root mantle; root mantle of varying thickness in different portions of the stem; roots arising from basal portion of stem larger in diameter than roots arising at upper levels; protoxylem at the tip of each of four to six arms of the actinostele of each root; inner roots in radial files.

## 2. Discussion of *P. melanedrus*

As a result of this study of eleven well-preserved specimens and others with a poorer quality of preservation from the Fleming coal near West Mineral, Kansas, it has become evident that there are no sound criteria for establishing more than one species based on the fragments in this collection. All stems possessed the characteristic heavy sclerenchyma sheath, the tannin-like deposits in the fundamental tissue of the stem and in the secondary parenchyma tissue surrounding the roots, similar characters with regard to the morphology of the stele, and completely lacked sclerenchyma bands among the cycles such as are present in *P. blicklei*. This species is readily differentiated from *P. blicklei* because of the complete absence of lysigenous lacunae, the absence of sclerenchyma bands associated with the cycles of the stem, and the typical heavy sclerenchyma sheath forming the almost "square" leaf bases in cross-section.

Since only a single species is represented, the series shows ontogenetic development through increased size and increased complexity by the addition of more vascular cycles and new orthostichies of leaves.

In its sequence of development *P. melanedrus* follows the general pattern found in *P. blicklei*. Near the base of a plant of *P. melanedrus* the stem has a small diameter with a small number of orthostichies (as few as three were observed), and with very few stelar cycles. Although only a small number of roots was observed, it is almost certain that a root mantle of considerable radial extent surrounded the stem in this region. As in *P. blicklei*, increasing size of the stem with increasing vertical distance would necessitate the development of a basal supporting buttress. In *P. melanedrus*, cylinders of vascular tissue are added in the center of the stem in the higher portions and there is an increase in the

number of leaf orthostichies. Six vertical rows is the largest number observed among the fairly well-preserved specimens, although a very crushed stem fragment from the West Mineral locality shows indication of having possessed at least eight rows of leaves.

A very conspicuous feature of this species is the change in the ratio of size of the leaf base with respect to that of the stem. In specimen J (fig. 35), the cross-section dimensions of the leaf base while still attached to the stem are, at the level measured,  $.9 \times .5$  cm. compared to the dimensions of the stem at the same level which are  $2.3 \times 1.8$  cm. At progressively higher levels of the stem, leaf bases enlarge considerably in diameter, but the corresponding increment of growth of the stem is much greater. For example, in specimen M (fig. 38), leaf bases average  $2.7 \times 1.2$  cm. while cross-sectional dimensions of the stem at the same level are  $10.5 \times 3.8$  cm. This phenomenon occurred also in *P. blicklei*, but is much more striking in the West Mineral species where, a leaf base at a basal portion has rather large cross-sectional dimensions in relation to the stem at the same level.

At lower levels of *P. blicklei*, the sclerenchyma sheath at the stem periphery is nearly cylindrical except where interrupted by the outward passage of a leaf trace. In *P. blicklei*, as more leaf orthostichies were added, the outline of the sclerenchyma tissue in cross-section assumed a strongly sinuous configuration. Where leaf arrangement became whorled, the sclerenchyma sheath is conspicuously lobed and exhibits a definite radial symmetry. It extends farthest out around the peripheral bundles and dips inward at the position of a leaf trace. Contrary to the condition at lower levels, where a leaf base forms a "bulge" at the periphery of the stem below the point of leaf abscission (fig. 35), in higher regions the dropping off of a leaf resulted in the tearing away of some of the limiting sclerenchyma tissue between two peripheral bundles (figs. 16-18). As a result the outline of the sclerenchyma tissue in higher regions of the stem of *P. blicklei* is never smoothly cylindrical.

In *P. blicklei* the "paired" arrangement of the peripheral bundles, emphasized by the configuration of the sclerenchyma tissue, is a result of the presence of a rather large number (eight or more) of rows of leaves. This arrangement begins to become apparent, however, even with a smaller number of rows. On the other hand, for various reasons, *P. melanedrus* retains a considerably smoother outline at the periphery of the stem with relatively shallow indentations in cross-sectional outline of the sclerenchyma sheath. As a general rule, portions of stems of *P. melanedrus* have a larger stem diameter than sections of *P. blicklei*, which have the same number of orthostichies of leaves. Similarly, a portion of a stem of *P. melanedrus* equal in diameter to a given section of *P. blicklei* usually has fewer rows of leaves and a smaller number of

stelar cycles. Consequently there is less "crowding" of leaf traces and peripheral bundles in the outermost cycle. The leaf traces, therefore, generally possess a larger ratio of tangential to radial diameter when compared to *P. blicklei*. Admittedly, leaf traces of the latter species appear flat in cross-section just above the point of release from the peripheral bundles. Higher in the stem, however, just below the region where parts of the trace are lost due to leaf abscission, there is a tangential to radial diameter ratio of 1 or even less. Thus, the leaf base delimited by sclerenchyma tissue surrounding a leaf trace of *P. blicklei* has a relatively smaller tangential diameter compared to leaf bases of *P. melanedrus*. The sclerenchyma tissue on the adaxial face and flanks of a leaf base of *P. blicklei* makes a rather sharp interruption in the cross-sectional outline of the sclerenchyma surrounding the stem. The indentations of the peripheral sclerenchyma tissue become more shallow as the leaf base of *P. blicklei* progresses upward and outward. In *P. melanedrus*, because of the relatively greater tangential dimension, the leaf base appears to have a smoother limiting layer of sclerenchyma because the indentations in the peripheral sclerenchyma caused by the departing leaf base are much shallower. Furthermore, because of the greater ratio of stem circumference to number of rows of leaves in *P. melanedrus* compared with that in *P. blicklei*, there is a relatively larger portion of the peripheral sclerenchyma tissue which is uninterrupted by leaf bases.

The arrangement of adventitious roots in *P. melanedrus* is of particular interest because of the conspicuous radial alignment of the roots embedded in parenchyma (figs. 38, 43, specimens M and Q). The places of origin of adventitious root traces may possibly have been along nearly vertical rows on the peripheral cauline bundles, or on more internal cauline bundles. This would result in radiating files of roots as those from above grew downward and outward, outside of those arising at lower levels. The radial alignment, however, would have become distorted if the roots were suspended in the air. It seems certain that the direction of proliferation of parenchyma from the surface of the stem and from the periphery of each of the roots themselves must have played a large part in confining the roots to so regular a pattern, especially if they did not originate in vertical rows on the cauline bundles. Thus the roots were embedded in the secondary parenchyma soon after their emergence from the stem if the secondary parenchyma aids in their alignment.

### C. *Psaronius chasei* sp. nov.

#### 1. Description

Specimen R (fig. 44) is a portion of a stem from the Berryville locality



which is approximately 28 cm. long. The stem is a large one with many rows of leaves. Only one half of the specimen was preserved in the coal ball, but this measures  $9 \times 5$  cm. in cross-section in its slightly crushed condition. The positions of at least six rows of leaves may be observed about the periphery of the stem, but because of the incompleteness of the specimen the exact number for the entire stem could not be determined. As demonstrated for *P. blicklei*, however, the number of rows of leaf traces cannot be used for determination of species.

The stem in specimen R is surrounded by a definite sclerenchyma sheath more similar in thickness and configuration to that of *P. blicklei* than to *P. melanedrus*. Numerous adventitious roots, connected with the peripheral cauline bundles and vascular bundles of the second cycle (fig. 45), can be seen traversing the layer of sclerenchyma tissue in a downward and outward course. From their frequency and ease of discernment in the sclerenchyma sheath, it might appear that these roots continue through the sheath in a vertical direction for some distance rather than passing through it at the same angle assumed in the fundamental tissue. Such is not the case, however, since a closer observation of well-preserved ground tissue, especially on the outside of peripheral cauline bundles, shows these roots in equal abundance. A very small quantity of sclerenchyma tissue is usually located between the cauline bundles of the second and third cycles. Tannin cells are present in abundance in the fundamental tissue of the stem, in the roots, and in secondary parenchyma tissue surrounding these roots. No lysigenous lacunae like those in *P. blicklei* are found in the fundamental tissue. The vascular tissue of the stem is composed of eight or more concentric cycles, an exact determination being impossible because of the incompleteness of the specimen. The xylem cells of the leaf traces at the periphery of the stem are relatively smaller than those of the cauline bundles, and in over-all appearance these leaf traces are thinner than the other vascular bundles.

The stem is enclosed in a mantle of adventitious roots and secondary parenchyma which surrounds the roots of the inner root zone. Although many large free roots are found adjacent to this specimen in the coal ball, at no place along its length can they be observed emerging from the inner root zone and it is not known where, or even if, they were connected to this stem. It is interesting to note that in the peripheral regions of the inner root zone, the secondary parenchyma cells seem to exceed the inner roots in radial extent and the parenchyma cells may be observed in clusters forming lobed and often slightly crushed masses of tissue (fig. 46). In this particular specimen the secondary parenchyma often extends as much as 5 mm. beyond the most externally placed root.

Another specimen (fig. 47), which is apparently the same species,

was discovered at the Calhoun collecting locality in southeastern Illinois. Calhoun is approximately the same stratigraphic level as the Berryville collecting site. This stem was a large whorled form with nine rows of leaves on only a little over one-half of the cross-section. The preserved half of the stem fragment measures  $9.5 \times 3.7$  cm. in cross-section and is approximately 16 cm. long. Tannin-like deposits are present in cells of the fundamental tissues of the stem and roots and in the secondary parenchyma surrounding the roots. The fundamental tissue of the stem lacks lysigenous lacunae. A band of sclerenchyma tissue surrounds the stem and there is apparently some of this tissue between the bundles of the second and third cycles.

*Psaronius chasei*, sp. nov. Diagnosis: Stem probably having three to many orthostichies of leaves; leaves probably spirally arranged in lower portions, becoming whorled higher in the stem; up to ten or more concentric stelar cycles in the stem; stem surrounded by a definite sclerenchymatous layer; sclerenchyma bands between second and third vascular cycles; parenchymatous ground tissue with no lacunae; tannin-like deposits in parenchyma cells of the ground tissue of stem concentrated near vascular bundles and in roots and secondary parenchyma surrounding roots.

A stem from the St. Wendel locality in southwestern Indiana shows characters very similar to *P. chasei*. One specimen showing about one-half of the stem (specimen S, fig. 48), and another fragment showing two peripheral bundles (fig. 49) were used along with a more poorly preserved specimen for this study. It has been determined that no lysigenous cavities characteristic of *P. blicklei* are present in this stem. Tannin-like deposits are quite abundant in the cells of the fundamental tissue of the stem and roots and in the secondary parenchyma surrounding the roots. In stems from this locality the tannin-like deposits appear to be found in even greater abundance in the cells of the fundamental tissue adjacent to the vascular bundles of the stem (fig. 49). The presence of tannin is emphasized more in figure 49 because a different type of preservation of that substance gives it a very black appearance. The stem is surrounded by a zone of sclerenchyma tissue at the periphery, and external to this is a mantle of adventitious roots. The structure of individual roots was not well preserved.

## 2. Discussion of *P. chasei*

Although the specimens (figs. 48, 49) from St. Wendel were not preserved in their entirety, certain features of these stems indicate affinities with *P. chasei* from the Berryville locality (specimen R, fig. 44). Lysigenous lacunae characteristic of *P. blicklei* are not present in either *P. chasei* or the St. Wendel stems. Tannin-like deposits in the

cells of the fundamental tissue are very abundant about the vascular bundles of the stem. The type of preservation merely emphasizes these deposits in the St. Wendel specimen (fig. 49), however, the same relative abundance of such cells in this position may be demonstrated for specimens of *P. chasei* from Berryville. *P. blicklei* does not exhibit a concentration of such cells containing tannin-like materials in association with the vascular tissue. The sclerenchyma sheaths of *P. chasei* and specimen S from St. Wendel are very similar in appearance with no such strikingly different features in either as might be found for example in *P. melanedrus* from West Mineral.

Although *P. chasei* and the specimens from St. Wendell both exhibit similar characters, it should be recalled that the St. Wendel stems considered were not well-preserved ones and thus it is possible that when better material is available specific differences may become apparent.

With the introduction of *P. chasei* as a new species, two separate and distinct species of *Psaronius* are known from the Berryville locality. It is further known that at least two anatomical organ genera of psaroniaceous petioles (*Stipitopteris* and *Stewartiopteris*) exist both at the Berryville and St. Wendel localities. Although not reported in any publication, specimens of *Stipitopteris* have been found at Berryville and numerous specimens of the stems of *P. blicklei* show the typical stipitopterid configuration of the leaf base on the surface of the stem.

Above its point of separation from the peripheral bundles, a leaf trace assumes a horseshoe-shaped cross-sectional configuration, the concavity and inrolled ends of which are directed toward the center of the stem. At higher levels it may retain this configuration of the petiole (*Stewartiopteris*) or by further tangential inrolling and fusion of the free ends it may develop into the stipitopterid type. Specimens of *P. blicklei* may be directly associated with the stipitopteroid type of petiole, since all but two of the series of stems in figs. 25-33 (Berryville series) show at least one stipitopterid configuration on their surface. The absence of this type of petiolar configuration in the two smallest stems can probably be explained by the variation in configuration of leaf bases at various levels in a plant. In more nearly apical portions of taller stems, a leaf base is situated in a depression flanked by portions of the stem containing peripheral bundles, while in more nearly basal portions of stems a leaf base "bulges" out before its separation. As a result, abscission of leaves at lower levels on the stem tore off a trace closer to the level of its separation from the peripheral bundles and the stipitopterid configuration was probably lost. Other specimens of *P. blicklei* not figured also show at various places along their length the stipitopterid configuration.

Thus far the stipitopterid type of leaf trace has never been observed on specimens of *P. chasei*. Further, at levels much higher than the leaf

trace seen at the upper left of fig. 44, the two remaining "j-shaped" strands have still not fused along their inrolled adaxial edges. It is possible, then, that the stipitopterid type of petiole trace, which is more commonly found, is associated with the stems of *P. blicklei*. Also, *P. blicklei* is by far the more abundant of the two *Psaronius* stem species from Berryville. The less frequently discovered *Stewartiopteris* petiole could perhaps be the petiole of the less common *P. chasei* stem.

#### D. Description of Other Previously Undescribed *Psaronii*

A stem fragment (specimen T), approximately 13 cm. long, from the New Delta, Illinois, locality, is shown in fig. 50. This stem measures approximately  $14 \times 6.5$  cm. in cross-section. The fundamental tissue of the stem contains no lysigenous cavities, but cells bearing dark tannin-like deposits are present. These deposits are not concentrated in the cells adjacent to the vascular tissue as are those of *P. chasei*. This specimen is thought to be a whorled form, but the arrangement of the leaves at the levels preserved is slightly distorted due to the addition of a new orthostichy to the specimen. The length of the specimen is not sufficient to allow for a readjustment necessitated by the addition of an orthostichy, and thus presents a regular phyllotaxy. The method of addition of this new orthostichy is identical with the addition of new rows of leaves described for *P. blicklei*. Six or seven concentric cycles of vascular tissue comprise the stem stele and the whole stem is surrounded by a thick root mantle, the roots of which are often in fairly even radiating rows. The sclerenchyma sheath which completely surrounds the stem, except at points of leaf trace departure, is, for the length of the stem preserved, very similar in character to that of the West Mineral species, *P. melanedrus*.

Since characters of the sclerenchyma tissue are in agreement with those of *P. melanedrus*, and since the cells with tannin-like deposits are not clustered about the vascular bundles as in *P. chasei*, this specimen has been tentatively assigned to *P. melanedrus* rather than to *P. chasei*. The fact that the stratigraphic level of the New Delta locality is lower than that of Berryville, St. Wendel, and Dix localities (nearer the stratigraphic level of the West Mineral locality) may be of some significance.

One of the more unusual specimens of *Psaronius* described from America is specimen U (figs. 25, 51). This stem fragment represents the only known member of the distichous *psaronii* discovered in America. It is extremely unfortunate that the stem is not of the coal-ball type of preservation. Instead of being preserved, the fundamental tissue of the stem has been replaced by a fine grained claystone. The stem, which is from a collecting locality near Wilmington, Illinois, measures approximately 15 cm. in length and averages  $7.6 \times 6.8$  cm. in diameter.

Outlines of a few roots may be observed about the periphery of the stem, but it is not clear whether these roots were in the process of traversing the cortex in their downward and outward course or whether this is actually the most internal limit of the root mantle. Because of the poorly preserved nature of the specimen, only fragments of the sclerenchyma sheath remain on the sides of departing leaf bases (figs. 20, 51). It is probable that the stem was completely enclosed by such a sclerenchyma sheath as is usually the case. In figs. 20F and 51, three cavities of possible lysigenous origin, as were common in *P. blicklei*, are located close to the vascular bundle and in the concavity of the departing leaf trace. The positions of the vascular bundles are easily discernible because of a different type of preservation in this part of the stem. Calcite and other minerals are found in these regions along with some carbonaceous remains of tracheids, so that in certain instances, poorly preserved xylem cells may be observed. When peels of the stem are made, such cells are evident in the vascular bundles; otherwise only the rough outlines of the bundles are present.

The vascular system of the stem is composed of five concentric stelar cycles, each of which is composed of two tangentially elongated cauline bundles which alternate with two pathways of leaf trace divergence. Leaf traces originate in the most internal cycle and are passed off in their upward and outward course to each successively more external cycle. At fig. 20A, the most internal cycle (cycle 5) is represented by the small vascular strand within cycle 4. At level B the most internal cycle has fused with the cauline bundle on the right side of the leaf gap in the fourth cycle, and at level C, at a still higher position in the stem, the inrolled end of the right side which had fused, has now broken free. The left side of the gap is not closed until level D is reached. At level E, the trace formed just below and on the other side of the stem from the one just discussed is being given off from the fourth to the third cycle. At level F, the fourth cycle has almost set free the trace just mentioned. Throughout the length of the stem preserved two traces, one from either side, have reached the periphery of the stem. Had the stem fragment been preserved in sufficient length it would have been possible to observe the origin of these traces from the most internal cycle.

With respect to the morphology of leaf trace formation and the manner in which the most internal vascular cycle is reconstituted after contributing to a leaf trace, this stem agrees in its ontogenetic development with spiral forms of *Psaronius blicklei*, *P. melanedrus*, and a whorled form to be discussed next.

The configurations of the free edges of the cauline bundles adjacent to the leaf gap oriented at the bottom of cycle 2 (fig. 20F) are the result of contribution of vascular tissue by the peripheral cauline bundles to the second cycle.

The discovery of this specimen is of particular interest because it represents the first distichous specimen of the genus to be described from America. Although Stenzel (1906) and others have figured distichous specimens, none could be compared in detail with this specimen because none could be obtained from Europe for examination and partially because the rather unusual type of preservation of this specimen obscures histological details. Stenzel (1906) shows a specimen of *P. gutbieri*, the leaf trace of which supposedly divides into two halves as it reaches the leaf base. Hirmer (1927) shows a photograph of *P. simplex* with the same configuration of the leaf trace. Other European specimens, e.g., *P. simplex* f. *integer* figured by Stenzel, show as many as three leaf traces on one side of the stem already broken free from the peripheral cauline bundles, but none completely set free from the stem in its own leaf base. None of these has divided into two strands. As far as general morphology of the leaf trace is concerned, the American specimen resembles the European species *P. musaeformis*.

This stem does not exhibit good histological details so often necessary in delimiting species of *Psaronius*, and it is possible that better preserved specimens will be discovered. As a result there will once again be difficulties of comparison between European and American specimens. For this reason, no new specific epithet has been designated for this distichous member.

Specimen V (figs. 21, 52) is a stem also preserved in claystone and also from the Wilmington, Illinois, locality. Specimen V measures 24 cm. long. At the lowermost levels preserved, the stem averages  $9.5 \times 8.6$  cm. in diameter and approximately  $7.5 \times 6.5$  cm. at higher levels. This decrease in circumference is probably the result of a combination of causes: (1) more crushing of the stem has occurred at higher levels; (2) some of the specimen is missing at these levels so that an accurate estimation of the actual diameter is made difficult; and (3) the stem appears to vary slightly in circumference because of the various configurations of the vascular bundles within the stem, depending on the stage of departure of the leaf traces. The maximum diameter is apparently reached as the leaf traces are set free from cauline bundles. Measurements of the higher levels were all made either above or below the points of separation of leaf traces, and at those levels the stem appears almost hexagonal in cross-section.

The vascular system of the stem is composed of five or six concentric cycles, and six orthostichies of leaves are arranged in alternating whorls of three each. No sclerenchyma sheath could be demonstrated to completely surround the stem. Since sclerenchyma tissue does cut in from the periphery of the stem to enclose leaf bases, however, there is reason to assume that a typical sheath was present. Because of the type of

preservation none of the fundamental tissue was preserved, and it is not known whether this stem possessed the lysigenous lacunae previously mentioned for *P. blicklei*. In fig. 21 the series of cross-sections of the stem from A (lowest level) through I (highest level) shows the method of leaf trace departure and the orientation of the vascular cylinders. Preservation of the outline of vascular bundles was not so distinct in this stem as in the distichous specimen, making it difficult to determine in cross-section which is a fissure in the claystone and which is actually part of a stelar cycle.

One region which might be confusing in considering the anatomy of specimen V is exemplified by level G (fig. 21). In the pathway corresponding with the orthostichy at the upper left portion of cross-section G, the fifth cycle fills the gap in the fourth cycle and two free edges project toward the center of the stem. In the pathways at either side, the fourth cycle "bulges" outward before passing off traces to cycle 3. A similar stage is not apparent in other pathways at this level but higher in the stem the same configuration is assumed.

Figure 22C is a series of diagrams representing progressive changes in the fourth (stippled) and fifth (black) cycles in an idealized situation where leaf traces in alternating pathways are always at the same stage of development. In fig. 22A the innermost cycle has not yet filled the gaps in the next outer one. The cycle corresponding to the fifth cycle of fig. 22B has filled the gaps in the fourth cycle, with the free edges of the fifth cycle projecting toward the center of the stem. In fig. 22C the free arms have separated and adjacent strands are shown migrating toward each other before fusing. A similar series of steps then takes place in the alternate set of pathways.

Peripheral cauline bundles contribute to the next inner cycle in the manner described for other specimens of *Psaronius*.

It is quite possible that this specimen represents a form of *Psaronius* which, after becoming whorled at the six-rowed condition, never added further orthostichies of leaves. This would place it artificially with such forms as the distichous and tetrastichous *psaronii*, which, as far as is known at the present time, never added more orthostichies after reaching the typical number for the respective group. The whorled condition in this specimen occurs slightly earlier in ontogeny than any form yet described from America. As was suggested for *P. blicklei*, the whorled condition occurs only after a certain number of rows is attained and when that number of orthostichies is divisible by two. Members of each whorl then include alternate leaf traces as seen in cross-section.

It is possible, however, that the stem represented by specimen V, like *P. blicklei*, continued to add orthostichies after becoming whorled. Specimen V is not of sufficient length to determine this. If it is one of

the latter group, then it merely became whorled earlier in ontogeny with two fewer orthostichies of leaves than is the usual condition for *P. blicklei*.

Another stem (specimen W, fig. 53) from the Coal City, Illinois, locality, also is preserved in claystone. The tracheids of the cycles of this stem are very clearly defined, and slightly oblique longitudinal sections of adventitious roots are visible in connection with the peripheral cauline bundles. A portion of the sclerenchyma sheath is also in evidence, cutting in about the leaf bases, but no histological details of the fundamental tissue were preserved. The stem measures 10.5 cm. in length and averages  $8.3 \times 8.2$  cm. in cross-section. The stele is composed of six concentric cycles of vascular tissue and the phyllotaxy is a  $2/7$  spiral. An examination of close cross-sections of this specimen has given evidence that the sixth or most internal cycle at the levels preserved in this specimen is a very small strand, but that morphologically it resembles the internal strand of the *P. melanedrus* as depicted in fig. 17. In fig. 53 the configuration of two of the cauline bundles at the top of cycle 2 suggests that the peripheral cauline bundles of the outermost cycle have contributed vascular tissue to this cycle.

Concerning the general morphology of leaf trace origin and reconstitution of the most internal cycle, this stem exhibits characters similar to the general patterns previously described for the genus (e.g., those of *P. blicklei* and *P. melanedrus*). It is interesting to note that specimen W from the same general locality as the hexastichous specimen just described (specimen V) has seven rows of leaves but has not, at this level, become whorled, nor could it become whorled until an even number of orthostichies is reached. This could support the supposition that the hexastichous specimen is a different type of stem which never attained more than a six-rowed condition.

A point that needs further consideration when better material is available is the striking contrast of the distances between cycles of these specimens (specimens U, V, W) with those of, for example, *P. blicklei*. The much greater distance between cycles is typical of all three specimens described from the Wilmington and Coal City area, however, not enough is known yet of stems of these groups to postulate a possible significance of this feature.

### E. *P. brasiliensis* Brongniart

#### 1. Additional observations

One section approximately 1 cm. in thickness of the specimen used by Brongniart (1872) in his description of *P. brasiliensis* was obtained from a museum at Rio de Janeiro, Brazil. This silicified specimen was col-



lected from the Chapado do Jaboti, Estado do Maranhão, and is thought to be lower Permian in age. The cross-section of the stem exclusive of the root zone measures  $9.5 \times 8.7$  cm. A study of the changes in leaf trace development through one centimeter of the stem gives some information concerning the morphology of the outermost vascular bundles.

At the periphery of the stem, four peripheral cauline bundles alternate with four pathways of leaf trace divergence. The leaves are arranged in alternating whorls of two, with one member of each whorl being given off slightly below the one directly opposite it (figs. 54, 55). The second cycle is also composed of four smaller cauline bundles alternating with the four pathways of leaf trace divergence. Within the center there are many other vascular strands which, in this specimen, appear to be organized in a manner similar to the concentric cycles common in *Psaronius*.

Leaf traces are recognizable in the pathways of divergence as far in as the third cycle. In the pathways of divergence on the left and right of the cross-section (fig. 54), leaf traces are attached on either side of the gaps to the cauline bundles of the second cycle. Immediately outside these traces, on either side of the pathway of divergence, are strands of vascular tissue which are contributions to the leaf trace from the peripheral cauline bundles. It is suggested that at a somewhat higher level, the pathway of divergence widened between these two strands, allowing the leaf trace to pass upward between them. These strands, at this level, fuse on either side of the leaf trace before it departs and is enclosed in the sclerenchyma tissue of the leaf base. At the pathway of divergence directed toward the bottom of the figure, a leaf trace at the periphery of the stem is partially enclosed in a leaf base by a sclerenchyma sheath cutting in diagonally on either side of the trace. The manner of contribution of peripheral cauline bundles to leaf trace formation is best observed in the pathway at the top of figs. 54, 55. A leaf trace was set free from the cauline bundles of cycle 2 at lower levels. The edges of the peripheral cauline bundles away from the gap in the outer cycle become much elongated. The inrolled portion of each one of these separates, and after a rotation of  $180^\circ$  the free edges formerly attached to the peripheral cauline bundles fuse with the free edges of the outgoing trace. Culine bundles of more internal cycles were observed to contribute to leaf traces in the same manner (fig. 54, cycle 3, lower orthostichy). Thus, in this stem, the leaf traces separate from the cauline bundles, receive a contribution from the next outer pair of cauline bundles, and fuse with the next outer cycle in that sequence. After separating from the second cycle, the leaf traces receive a contribution from the peripheral cauline bundles but do not fuse with them.

It appears, then, that the stem consists essentially of four series of

cauline bundles alternating with four persistent pathways of leaf trace divergence. The gaps are filled only at points where leaf traces are attached to the cycles. The number of strands composing the more internal cycle is greatly increased because each time a trace is given off to the next outer cycle, the cauline bundles of that cycle contribute a small strand of vascular tissue to each side of the leaf trace.

Large leaf bases, almost square in outline, enclose the leaf trace. The sclerenchyma sheath completely surrounding the stem is relatively thick and is broken only at points of leaf trace departure. Internal bands of sclerenchyma may be observed between the leaf trace from the second cycle and the peripheral cauline bundles.

Strands of vascular tissue are found accompanying the leaf trace on the adaxial side in the concavity. Some of these strands appear to accompany the leaf trace in its upward and outward course from the center of the stem (fig. 55, c.f. leaf traces on right and left side of the stem). A close observation of the leaf traces at the top and on the left side of fig. 54 seems to indicate the possibility that some of these vascular strands may have separated from the free edges of the horseshoe-shaped leaf trace in the leaf base, as is common in many modern fern genera (e.g., *Cibotium*).

Adventitious roots which are connected with the peripheral cauline bundles may be observed in figs. 54 and 55, passing through the cortex and sclerenchyma sheath. The stem is surrounded by a root mantle averaging approximately 5 cm. in thickness. The steles of the roots are polyarch but further details were not sufficiently preserved to allow a more thorough investigation. The roots are enclosed in a mass of secondary parenchyma. Evidences of proliferation from the leaf bases may be observed in figs. 54 and 55, and farther out in the root zone these secondary parenchyma cells are visible among the roots.

## 2. Discussion of *P. brasiliensis*

Although the stem and root mantle of *P. brasiliensis* have been previously described (Brongniart, 1872) and figured by Zeiller (1840), Pelourde (1908), Scott (1920), and Hirmer (1927), the new sections obtained from the museum at Rio de Janeiro along with a re-examination of the cross section of this stem (fig. 56), as figured in Zeiller (1890), has yielded new information concerning the morphology of *P. brasiliensis*. According to Zeiller (1890), the strands in the concavity of the leaf trace were pits formed during the process of preservation. For the specimen just described they are known to be vascular tissue, part of which comes from the stem as the leaf trace departs into the petiole and, possibly, part from strands which separate from the inrolled edges of the leaf trace. This configuration of the trace appears to resemble some-

what the dissected traces of certain modern marattiaceous ferns (e.g., *Angiopteris*), and might be considered a phylogenetic advancement within the genus.

The section (fig. 56) used by Zeiller (1890) shows in detail the exact method of contribution of vascular elements from the peripheral cauline bundles to leaf traces above their points of separation from the second cycle. The section investigated by the author is not of sufficient length to substantiate the method of contribution, although there is evidence that it was similar (note the peripheral cauline bundle in the lower right of fig. 55). When one edge of the peripheral cauline bundle elongates, it also inrolls so far that the free, incurved edge fuses with the middle of the peripheral cauline bundle (fig. 56P<sub>1</sub>). A separation is formed in the resulting loop at a point adjacent to the leaf gap (fig. 56P<sub>4</sub>), and the adaxial portion "swings" inward with the point of fusion to the peripheral cauline bundle as the "hinge" (fig. 56P<sub>3</sub>). After a rotation of almost 180°, the strand separates at the "hinge" and fuses to the edge of the leaf trace (fig. 56P<sub>3</sub>) which has been released from the second cycle.

Although the method of contribution from the peripheral cauline bundles to leaf traces is unique in this species, some specimens of *P. blicklei* show in part a similar situation in which the leaf trace and the second cycle do not directly fuse with the peripheral cauline bundles (described in section on vascular system). In other characters (e.g., persistent leaf gaps, cauline bundles, root zone) *P. brasiliensis* corresponds to the usual structure of the genus.

#### F. Histological Details

In most of the stems observed, the fundamental tissue of the stem is composed of large, thin-walled parenchyma cells (figs. 39, 57, 58). This tissue is relatively compact and the cells appear to be of uniform size. A variation of the usual condition of the ground parenchyma is found in *P. pertusus* (called *P. lacunosus* by Blickle, 1940). In this species, the cells are arranged in a very loose network with large intercellular spaces between them (fig. 82). This type of cortex is very similar in appearance to the so-called "aerenchyma" of the cortex of *Psaronius* roots in their more distal portions. In such stems the net-like arrangement of the cortical cells becomes more compact near the vascular strands and at the periphery of the stem near the surrounding sclerenchyma sheath.

Certain of these cells (figs. 39, 57, 58) contain black or dark brown deposits which may possibly be tannin-like substances collected in the cells when the plant was living rather than artifacts accumulated during preservation. These cellular contents superficially resemble tannin deposits in the cortical cells of members of the Marattiaceae (West, 1915),

and may also be found in the cortex of roots and in the secondary parenchyma surrounding roots. The tannin-filled cells are generally thin-walled and do not differ in size or shape from surrounding parenchyma cells. They are fewer in number at very low levels of specimen A, which is probably very near the bottom of the stem, but increase in number higher in the stem.

It has been suggested by West (1915) that tannin cells of the Marattiaceae hold waste products of the plant and that numbers of them increase with age at a particular level of the stem. This could also be true of such cells in *Psaronius*. However, since age determination of particular levels of fossil plants having no secondary wood is very difficult, it can only be suggested that a similar condition could have prevailed in these fossil forms.

In *P. blicklei* (figs. 57, 59, 73) large lysigenous lacunae extend vertically through varying vertical distances, depending upon the numbers that have become coalesced throughout the length of the stem. These cavities are found scattered through the ground parenchyma of the stem and petiole bases (fig. 73). They are fewer in number at lower levels of stems of this species (specimen A), but become much more abundant at higher levels and probably increase in number at a particular level as the stem becomes older. They are considered to be of lysigenous origin because there is no evidence of an epithelial layer of secretory cells lining the cavities, and because there is evidence of partially broken-down cell walls within them.

The cavities superficially resemble mucilage canals described for members of the Marattiaceae (Kuhn, 1889; West, 1915). West states that most of these canals of the Marattiaceae are protogenetic, lysigenous mucilage canals; however, in the extant ferns some protogenetic schizo-lysigenous canals are found, for example, in petioles of *Angiopteris evecta*. Whether the cavities in the cortex of *Psaronius* ever contained mucilage is not definitely known, as most of these cavities are filled only with calcite in the petrifications studied. Occasionally a light brown mucilage-like deposit is found. The cells between cavities apparently break down to allow as many as five or more such cavities to coalesce either horizontally, vertically, or in both directions. The function of such structures or their contents, if any, is not known, nor is it known for members of the Marattiaceae.

Cortical cells at the periphery of the stem grade more or less gradually into apparently thicker-walled cells with large lumens, and finally into fibrous cells of the sheath (fig. 39). A sclerenchyma sheath of very thick-walled fibers completely encircles the outside of the stems except at points of leaf trace departure (fig. 31), where it cuts in around the adaxial face of leaf bases. Isolated groups of fibers are found scattered

throughout the fundamental tissue of most stems (fig. 59), and well-defined bands of sclerenchyma tissue are found in various configurations in association with the steles of certain species (e.g., *P. blicklei*) and with all leaf bases (figs. 31, 59). Further evidence that the large cavities in the ground parenchyma of stems of *P. blicklei* were formed during the life of the plant, and are not due simply to disintegration of the plant before or during fossilization, is the internal sclerenchyma present around these cavities which appears in cross-section as finger-like projections between them. The fact that these fibers are found in such configurations would seem to indicate that they differentiated later in ontogeny from cortical parenchyma cells. Thus, at a particular level, a stem could have developed more of these sclerenchyma cells with increasing age. It has also been determined that the radial thickness of this limiting layer of sclerenchyma tissue increases at higher levels of stems. In *P. melanedrus* it ranges from .6 mm. in more nearly basal portions to 1.2 or more millimeters at higher levels. Intermixed with these fibers were parenchyma cells which proliferated to form the secondary parenchyma tissue of the root mantle. The cells of the fundamental tissue of the stem were also capable of further divisions, resulting in radiating rows of cells. In certain instances the production of these secondary cells might be a reaction to wounding (figs. 60, 61). Often very large areas are filled with such cells to the complete obliteration of vascular tissue, etc. As shown by fig. 61, a leaf trace has been pushed completely to one side by this secondary growth. At other places in the stem of *P. blicklei* these proliferating cells grow into and often completely close, at least for a certain distance, the vertically extending lacunae (fig. 62). No useful function has yet been ascribed to this type of secondary growth, and the reason that these cavities should be closed again after their formation is not accounted for. It seems that once division was initiated in these cells, it continued until mechanical compaction caused the process to cease. Although the majority of the divisions are in the same plane causing the formation of radiating rows of cells, other divisions did take place resulting in some instances in a large mass of irregularly arranged cells. Certain parenchyma cells of some stems have proliferated about the vascular bundles of some stems (fig. 60). The function of this tissue is likewise unknown. Its presence in some stems has caused some erroneous interpretations because certain authors (Pohlig, 1910; Schuster, 1911; Sterzel, 1912; and Moon, 1939) have interpreted the radial rows of cells in this position as secondary xylem. The name "Xylopsaronius" was applied by European authors to forms supposedly having secondary wood.

The vascular bundles consist of primary xylem with xylem parenchyma cells intermixed among the tracheids (figs. 57, 58, 63, 64). Protoxylem

cells are situated in groups along the internal surface of these vascular strands (fig. 64) and thickenings on the walls of metaxylem elements are scalariform (fig. 65). Tracheids of leaf traces are smaller in diameter than those of the remainder of the vascular bundles of the stem (fig. 39). A zone of thin-walled cells composing the phloem completely surrounds the xylem strands (figs. 57, 64). In cross section, certain cells of the phloem zone can be seen as a discontinuous layer, usually one cell in width. The cells are large and cylindrical and have been referred to as sieve cells (Bower, 1926) (figs. 57, 63). These appear to have definite walls although no sieve areas were preserved in the longitudinal sections observed (fig. 58). These cells appear to be in layers two or three cells in thickness at the free edges of the vascular bundles. They are prominent in this region of the phloem in all stems where preservation allowed study of the phloem zone, with the exception of lower levels of specimen A. Probably sieve cells of so small a stem did not develop as great diameters and are not so readily discernible. No layer which could be referred to as endodermis has been observed.

### III. GENERAL DISCUSSION

#### A. Vascular System

Although earlier workers have described the stelar anatomy of *Psaronius* (Zeiller, 1890; Rudolph, 1906; Stenzel, 1906; Hirmer, 1927; Schoute, 1938; and Gillette, 1937), much was left undone because their specimens were too fragmentary and not well preserved, or because a thorough study of the material had not been made. This resulted in an incomplete and often mistaken understanding of the morphology of the plant. Zeiller (1890), for example, showed that stems may increase in complexity at higher levels; nevertheless, Stenzel (1906) published a key to species of the genus using numbers of inner cauline bundles as a prominent criterion of specific differentiation. It was further recognized by Hirmer (1927) that living free ferns increased in size, and the orthostichies of leaves could increase in number as occurs in members of the Cyatheaceae (Christ, 1910). Yet, Hirmer (1927) continued to distinguish, in his classification, between *psaronii polystichi spirales* and *psaronii polystichi verticillati* and did not use the knowledge of extant forms in the interpretation of the morphology of fossil ferns.

Specimen A (*P. blicklei*, fig. 25) from Berryville, Illinois, is the most nearly basal level of *Psaronius* discovered in America. The vascular system in this specimen is composed of two concentric cycles of vascular tissue. The outer cycle at the levels depicted (fig. 10A-L) usually

exhibits two leaf gaps, and, because at higher levels more gaps are formed by the addition of more orthostichies, it is referred to as a dictyostele. The most internal cycle presents more of a problem in interpretation. At levels C, E, F, G, J, and L two leaf gaps are present in the cross-section. At levels interspersed among those of the ascending series just mentioned, the strand of the central cycle bears a closer resemblance to a simple siphonostele. In fact, at levels K and L the third cycle is so small it might be interpreted as a protostele. Variations in the definitions of stelar types and a consideration of the ontogeny of many fern steles from protostele to siphonostele to dictyostele would allow several interpretations of these vascular cylinders. In the discussion to follow, describing the ontogeny of each newly added cycle, the cycles will be referred to as going through stages of development from protostele to dictyostele.

At the lowest preserved level of specimen A (figs. 1, 25) the typical pattern of development for a dictyostele is well established. It is modified only by a greater number of orthostichies of leaves at higher levels, but even this increase does not alter the established pattern of older orthostichies.

The gaps in such a dictyostele are, at least in the outer cycles, primarily leaf gaps, and contrary to the condition in many modern ferns are closed only when the next leaf trace to be given off above fuses at a higher level with the cauline bundles on either side of the gap. The first leaf trace originating at a certain position in the innermost cycle is of considerable significance, since it determines the position of one of the gaps in that cycle. Similarly, with the addition of a new orthostichy the trace supplying the first leaf in that row determines the position of the gap in the first cycle corresponding to the added orthostichy. Gaps in the second, third, and even more internal cycles are formed in the same way. Thus, all persistent gaps in all of the cycles were formed originally by a leaf trace arising from certain positions; and once formed, these gaps are closed for only short vertical distances by other leaf traces originating from farther within. Some inrolling of the cauline material into the gap to meet an approaching leaf trace does occur. Actually then, cauline material does help fill the gap. This partial gap closure would not occur, however, had not a leaf trace been approaching the gap from below and farther in toward the center of the stem.

At levels close to the base of a stem such as those diagrammed in fig. 10, the addition of a new cycle can be clearly followed and has been described in detail for *P. blicklei*. For *P. blicklei* and for *P. melanedrus* (fig. 17) at the lowest levels described, the newest and most internal cycle is always reconstituted, after contributing to a leaf trace, by bundles of cauline origin which separate from the next outer cycle after a leaf

trace from the most internal cycle has fused with it (fig. 17A-C). At higher levels, as the stem attains a greater diameter, the internal cycle also expands by further differentiation of vascular elements and becomes a well-developed cylindrical dictyostele (fig. 17A).

A slight variation of this pattern was observed in parts of *P. melanedrus* and in specimen W (fig. 53). In *P. melanedrus* (fig. 18) the most internal cycle is not reconstituted by contributions from cauline bundles on either side of the trace to the center of the stem. Rather, the traces arise from the edges of the most internal strand, making this strand theoretically all potential leaf trace material. Theoretically this cycle would cease to exist if the apical meristem had not continued to form additional vascular elements, resulting in continual expansion of the innermost cycle. It has been suggested in the description of *P. melanedrus* that at higher levels the most internal cycle sends off so many traces at approximately the same level that its S-shaped configuration, seen in cross-section, is no longer efficient and is replaced by a cylindrical dictyostele. Further, if additional cycles were to be added to such a stelar system their addition internally would necessitate a change from the S-shaped configuration of this strand.

That the pattern set by *P. blicklei* (fig. 10) and *P. melanedrus* (fig. 17) for more basal levels may occur at higher levels and even in whorled forms is confirmed by specimen U (figs. 21, 22, 52). Where three traces are given off almost simultaneously from the most internal cycle, six cauline bundles migrate upward and inward to the center of the stem as the three traces are passed off to the next outer cycle. In reality, six cauline bundles may not be obvious at one level because leaf traces, in departing from the most internal cycle, may lag slightly one behind the other. Thus, it is apparent that in spiral forms with perhaps a 2/7 phyllotaxy or in some of the larger whorled forms where, for example, seven members per whorl are given off at approximately the same level, there is considerable dissection of the more internal cycles and the anastomoses of these strands present diverse cross-sectional configurations which are very difficult to interpret.

When the second cycle containing a leaf trace joins the outermost cycle, it fuses along the convex faces of the peripheral cauline bundles. At the level where a leaf trace is released from the second cycle, that cycle separates taking with it on either side of the resulting gap, the free edge of each of the two peripheral cauline bundles (fig. 14A-C, fig. 66A-D). In addition to fusion between adjacent cycles at the pathways of leaf trace divergence each cycle, at its point of origin, is joined to the one immediately outside of it.

Once a leaf gap is established in a cycle (except the most internal cycle) it persists in that position throughout the length of the stem. The



basic pattern of each cycle is a cylinder of isolated strands which are temporarily joined at various places by leaf traces passed on from inner cycles. Since leaf traces are not released from a cycle before they fuse to the next outer one, two cycles may be joined for a time at the position of a pathway of trace divergence (fig. 67). Unlike other ferns where leaf gaps have a limited vertical extent, the presence of gaps of indefinite length is the normal condition in *Psaronius*.

In addition to the gaps in cycles at the pathways of leaf trace departure, gaps may occur at other positions in more internal vascular bundles. These are closed at higher levels without having performed any apparent function (fig. 18E-H). Occasionally a strand of vascular tissue may become separated from the inner or outer face of a cauline bundle (fig. 68) and at a higher level fuse with either the next inner or outer cycle. This characteristic is of more common occurrence in some stems (e.g., C.B. 1221, *P. chasei*) than in others, but not in so striking a manner that it could serve as a basis for specific differentiation.

The radial thickness of vascular bundles increases at higher levels in the stem. This is true of *P. blicklei* and *P. melanedrus*, and when other species are more completely known from base to apex it is likely that they will exhibit the same characteristic.

Although the simplest steles observed for species of *Psaronius* are composed of two cycles, the method of addition of other more internal cycles suggest a possible, still more simple stelar, construction at more nearly basal levels. In specimens observed having two cycles, the inner one, when considered by itself, has a structure identical with that of solenosteles in many modern fern genera (e.g., *Adiantum* and *Dennstaedtia*), although throughout most of its preserved length it is dissected by two gaps. Like steles of the ferns mentioned above, the leaf gap in the second cycle of *Psaronius* is closed simply by the arching over and fusion of portions of the cycle from either side of the gap. This is different from the closure of the gap in all cycles except the central one. In other cycles, gaps are mainly closed by leaf traces and are reformed as the trace leaves the cycle. The method of initiation of the third cycle from the second in specimen A (fig. 10) suggests that, still lower in the stem, the second cycle had a similar origin from the first or outermost cycle. If this occurred, then the gaps in the single cycle which would be present must have been closed simply by a fusion of the edges of the stele on either side of the gap.

The configuration of the stele at a still lower level can only be postulated, although some evidence suggests that it was protostelic. The predominance of a protostelic sporeling stage in ferns would indicate a similar basal structure in *Psaronius*. The structure and "behavior" of the most internal cycle in basal portions may be interpreted as showing

changes from an essentially protostelic strand to a dictyostele with many gaps. The third cycle in specimen A (fig. 10) is only a slightly curved strand as seen in cross-section and in the process of contributing a leaf trace to the second cycle, no gap is left in it because the trace originates from the edge of the strand (see also fig. 13). It is not until higher levels are attained that this internal cycle expands and gaps are formed by the separation of traces along various parts of its cylindrical structure. Theoretically, then, if the outermost cycle were traced far enough down in the stem its solenostelic structure would be expected to grade into a protostele closely resembling the third cycle in specimen A.

Ideally each cycle in *Psaronius*, from its point of origin to higher levels, recapitulates the sequence of development of each of the outer cycles. Actually, however, the situation is complicated at higher levels by the increased number of orthostichies. For example, should a new cycle be added in a portion of the stem in which leaves are arranged in alternating whorls of four, it is necessary for the central cylinder to supply four traces to the next outer cycle almost simultaneously. For that reason the protostelic nature of the innermost cycle, at its point of origin, is modified very quickly. In addition to stems having spirally arranged leaves at very low levels (e.g., such as a portion with three rows of traces), the distichous forms of the genus show such a recapitulation throughout their entire length.

The supposed ontogenetic development of the vascular system of *Psaronius* from a protostele aids considerably in attempts to trace the ancestry of those forms. A stem segment with 14 or possibly more rows of leaves possesses an extremely complex vascular system, yet it has been shown that such a stelar system developed ontogenetically from a simple solenostele and perhaps even a protostele near the base of the plant. A similar sequence of increasing complexity from a protostele to a polycyclic dictyostele could represent the derivation of psaroniaceous forms from a presumed protostelic ancestor.

A leaf trace is first observed in the outermost cycles of lower levels of stems as a "bulge" of vascular tissue which becomes progressively more pronounced at higher levels until it is set free from the outer cycle, first on one side and then on the other. Where it is free from the cycle the edges of the leaf trace become slightly inrolled on the adaxial side. At higher levels of some stems, e.g., *P. blicklei*, where there are perhaps seven leaf traces per whorl, the crowding together of the leaf traces departing at the periphery of the stem results in a very noticeable change in configuration of the trace in early stages of departure. When a trace is being given off from the second cycle to the peripheral cauline bundles, it has the appearance of an almost flat tangentially elongated strand of vascular tissue (fig. 66A, B). At a higher level (fig. 66C),

when it has joined with the peripheral cauline bundles and become free of the second cycle, the edges of the trace may precede the remainder of the trace outward for a short distance up the stem, giving the strand a concave configuration, the concavity of which is oriented in an adaxial position. This configuration is retained after the trace is released, but at still higher levels the middle of the trace migrates outward and upward more quickly, causing the free edges of the trace to lag slightly behind when seen in cross-section. At this level, the trace then assumes the typical horseshoe-shaped cross-sectional configuration. A feature exhibited by this leaf trace which is supposedly a primitive character in fern anatomy is the undissected nature of the leaf trace in most species of the genus.

A variation of the manner of contribution of the peripheral cauline bundles to leaf traces and inner cauline bundles of the second cycle is diagrammed in fig. 23A, B. At A it can be seen that the portion of the peripheral cauline bundle (diagrammed in solid black), which will be contributed to the trace and cauline bundles of the next inner cycle, has separated before the leaf trace from the inner cycle fuses with the peripheral cauline bundle. The sclerenchyma tissue around the peripheral cauline bundles has extended between this strand (fig. 23A) and the rest of the peripheral cauline bundle. The strand diagrammed in solid black separates in the middle and the outer portion next to the pathway of leaf trace divergence fuses with the leaf trace; the other portion fuses to the next internal cycle and contributes to it. This method of contribution occurs on both sides of the pathway of leaf trace divergence as suggested by fig. 23B. The leaf trace then passes out between the peripheral cauline bundles without fusing directly with either of them. The contribution of vascular tissue by the peripheral cauline bundles to the leaf traces, and to the cauline bundles of the next more internal cycle, connects all three of these at lower levels. In a sense, then, this is a double contribution (to leaf traces and to more internal cauline bundles) by the peripheral cauline bundles, but it is slightly modified from the usual condition in *Psaronius*.

This series, showing the method of contribution of peripheral bundles, was observed in three stem specimens which in all other internal features resemble *P. blicklei*. It is suggested that this method of leaf trace departure is not a specific character to be used in delimiting new members of the genus, because it is not uniform for all leaf traces around the stem. Rather, it represents a difference in "timing" of contribution of vascular tissue to departing traces and more internal cycles.

Zeiller (1890) figures a series of seven diagrams at successively higher levels of a leaf trace departing from *P. infarctus*. According to Zeiller, two small vascular strands separate from the peripheral cauline bundles

on either side of the leaf gap and migrate upward and into the pathway of leaf trace divergence. These strands then supposedly fuse along the free edges adjacent to one another and are sent off from the stem as a typical horseshoe-shaped trace. The series of diagrams figured by Zeiller to accompany the explanation does not clearly show this kind of trace formation. As the two strands migrate away from the peripheral cauline bundles on either side of the gap toward the pathway of leaf trace divergence, they pass in close proximity to the cauline bundles of cycle 2. Although not shown by Zeiller's figure, it is possible that these small strands which become much elongated at this level fused with a trace given off from the next inner cycle before their departure into a leaf base. If this were the case, then the method of leaf trace departure described by Zeiller (1890) would be identical to that just described for *P. blicklei*.

It has been observed that leaf traces generally originate in the most internal cycle and migrate upward and outward, fusing in turn with each more external cycle on either side of the leaf gap. In specimen F, a stem having approximately eight cycles, this condition is slightly modified. Fig. 24 is a series of diagrams of the third through the sixth cycles. At level A, a leaf trace from a still more internal cycle than those mentioned (3-6) is fused at the right side of the pathway of divergence with a cauline bundle of cycle 5. The left side of the trace still attached to an inner cycle is lagging behind the right side in its upward and outward course, so that it has not yet joined cycles 6 or 5. Also, at level A it should be noted that the inrolled edge of the cauline bundle of cycle 4 on the left side of the gap is much elongated and at the next higher level (level B) it has incurved so much that it has touched and fused with the cauline bundle of cycle 5. At level C this inwardly projecting strand on the left side of the pathway of divergence separates from cycle 5, taking with it as a contribution the inrolled end of a strand belonging to cycle 5. Also, between levels B and C the inwardly projecting leaf trace attached at level B to the right side of the gap in cycle 5 has migrated up and across the leaf gap so that it now fuses on the convex edge of the vascular segment contributed by cycle 5 on the left side of the gap. This strand then separates at level D, taking with it the inrolled end contributed by cycle 5. This strand at higher levels migrates back to the center of the stem and has no further part in the development of this leaf trace. The inrolled edge of the cauline bundle on the right side of the gap in the fourth cycle has become separated, and at C the leaf trace and the cauline bundle of the fourth cycle to which it is attached on the right edge fuse to the small strand along the convex face. Vascular elements have been contributed to the left part of the leaf trace by the inrolled portions. At level D the trace has

assumed a more normal configuration, although the concavity is still toward the outside of the stem and cycle 5 has not yet released this trace on the right side of the gap. The small strand diagrammed in solid black which originated from the fourth cycle at the right side of the gap contributes some vascular elements to the leaf trace and some to the cauline bundle in the fifth cycle. These elements are added before the fifth cycle and the leaf trace fuse to the fourth cycle on the right side of the gap. Although the configuration of leaf trace and cauline bundles in specimen F is identical to the normal condition, the method of contribution of material from the cauline bundles to the leaf trace and to inner cycles differs. The end result is exactly the same as in the usual sequence of trace departure, except that addition of vascular tissue to the leaf trace and inner cycles occurs in a different manner. Leaf trace divergence of this type is present in several specimens observed, differing only in details from the type of departure described above. It occurs quite often (at least four times) in the length of specimen F preserved in the coal ball, while at other points on the circumference traces are given off simultaneously in the usual manner. For this reason, and because these stems exhibiting the modified type of trace formation resemble *P. blicklei* in all other respects, this type of trace formation should not be considered as basis for specific differentiation.

At still higher levels of the petioles the inrolled edges of the adaxial side may inroll toward one another and actually fuse along their convex edges (fig. 69). The two projecting free edges then separate from the outer cylinder of vascular tissue, resulting in a complete ring of vascular tissue with a small strand in the upper portion of the center of this ring (Lenz, 1942). This configuration, which is that assumed by petioles of the organ genus *Stipitopteris*, is visible on the outside of many stems where the root zone has been removed (fig. 70). At the most basal level of *P. blicklei*, for example, the departing leaf bases are not protected at the point of emergence from the stem by projecting cauline bundles as is the case at higher levels. This petiole base was stripped off closer to the stem than those at higher levels. Because of this, more of the petiole was removed to a position at a level lower in the petiole base than the position where the stipitopterid configuration is normally assumed. Thus, the stipitopterid configuration could not be observed on the stem surface as is possible at higher levels. Petiole traces of other species of *Psaronius* never fuse along their inrolled edges, and thus in face view of the stem they exhibit an open horseshoe-shaped bundle scar, the concavity of which is oriented upward (fig. 71).

Each leaf trace in its upward course also bends outward at various angles, depending upon the nearness of leaf traces below it and those to be given off at higher levels. Figure 72 shows the angle of leaf divergence

of a specimen of *P. blicklei* having fourteen rows of leaves. Even with this large number of orthostichies, the angle of divergence is less than that depicted by Gillette (1937) for *P. septangulatus*. It is possible that the traces of such a stem as specimen H may have had a somewhat greater angle of divergence, while smaller stems send off traces at a much smaller angle (e.g., specimen A). The most obvious conclusion and one which is supported by actual measurements is that there is a correlation between levels of the stem and angles of leaf trace divergence. This would scarcely justify indiscriminate use of the angle of leaf trace divergence as a specific criterion in naming new species of *Psaronius*.

Figures 70 and 73 give some idea of the variation in size and configuration of the leaf trace scars, and can serve to point out some of the hazards of considering shapes and measurements of these scars for use as specific characters. Figures 70 and 73 are both of *P. blicklei*, the leaf trace of fig. 70 measuring  $1.75 \times 1.2$  cm. being at a much lower level of the stem than fig. 73 measuring  $4 \times 1.4$  cm. The measurements given are for specific specimens and can vary in other stems and also with the level in the petiole at which abscission took place. Higher up on the stem, where the leaves become whorled, the surface configurations often depend upon the proximity of the whorls of leaves one above the other. Several specimens of silicified stem fragments of *Psaronius* stripped of their root mantles and showing external features of the stem have been examined with regard to leaf scar configurations. In the specimen in fig. 74 the vertical distance between leaves in the same orthostichy is greater than in the specimen in fig. 75. When a leaf abscised from the stem such as that in fig. 74, the stripping-off of the limiting layer resulted in a somewhat pointed configuration below each trace. In such a stem as is shown in fig. 75, where there is a much shorter distance between leaves one above the other in the orthostichy, the vertical dimension of the petiole is restricted and leaf abscission formed a different type of scar. The configuration of leaf scars depends not only on the actual position of leaf abscission, the level on the stem at which abscission occurs, and the effects of proliferation of parenchyma at the points of abscission, but also to a great extent on the degree of weathering of the fossil. Where there has been a considerable amount of weathering the sclerenchyma bands around the individual leaf scars becomes confluent in two vertical lines flanking the orthostichy. The prominence of the positions of peripheral cauline bundles also varies in stems of the same species, at lower levels presenting a smooth, flat surface between leaf bases and at higher levels developing externally into bulging, sinuous bands among orthostichies (fig. 71).

Many species of *Caulopteris* and *Megaphyton* have been named on

superficial leaf scar characters and on size distinctions. Since anatomically it is not possible to substantiate these numbers of species, it is suggested that naming on the questionable characters just mentioned would, in part, account for this discrepancy.

At higher levels when the leaf bases are free from the stem they are known to assume at least two configurations, *Stipitopteris* (Lenz, 1942; Morgan and Delevoryas, 1952a) or *Stewartiopteris* (Morgan and Delevoryas, 1952b). Most *Psaronius* leaf trace scars which have been reported from surface features either assumed the open horseshoe-shaped configuration or the closed cylinder with a small W- or inverted V-shaped strand in the center. Baxter (1953) has attributed the horseshoe-shaped configurations visible in the leaf bases of his specimen of *P. cooksonii* to a preservational fissure between the sclerenchyma sheath of the petiole and the more internal cortex. He states that the petiole trace at this point "consists of a straight to slightly curved strand. . . . Its upward passage into the petiole is almost vertical for approximately 1.6 cm., at which level it reaches the surface of the petiole scar just within the lip of the cup-shaped petiole base. Consequently, the true vascular bundle scar is not visible in the face view of the *Caulopteris* surface but can be seen if the protruding petiole bases are viewed from the top."

The type specimen of *P. cooksonii* was examined with Baxter's interpretation in mind and it is the conclusion of the present writer that the horseshoe-shaped configuration on the stem surface represents the vascular strand of the petiole as in all other known psaronii. The leaf trace figured by Baxter (1953, 2F11) has been broken off at a level approximately 1.5 cm. below the rest of the cross-section of the stem. In face view, the broken surface is at the bottom of the leaf scar below the point where the bottom of the horseshoe configuration would have extended. The best interpretation of this condition is that because of crushing of the stem, and since this trace has not yet reached the surface of the leaf base, it has not yet attained the broadly expanded and curved *Caulopteris* trace. Other scars on the stem exhibiting the typical U-shaped configuration on the surface also show evidences of tracheids at the surface of the bundle scar.

## B. Root Zone

Surrounding the stem except in the more apical portions is a zone of adventitious roots. Roots of the more internal regions of this zone are surrounded by radially aligned parenchyma which proliferated from various parenchyma cells of the stem and roots. This tissue in which the roots are embedded is not composed of compacted hairs as suggested by earlier workers (e.g., Farmer and Hill, 1902; Solms-Laubach, 1911),

but is a solid mass of parenchyma cells which were capable of undergoing frequent divisions. Adventitious roots arise at various points along the length of the peripheral cauline bundles. Figure 57 shows the bulbous base of a root trace departing from a peripheral cauline bundle of *P. blicklei*. The roots grew downward and outward to the periphery of the stem, where, at least for a certain length of the root, they are components of the inner root mantle. While still within the stem, root traces are surrounded by a layer of cortex and sclerenchyma. Roots near their points of origin from the stem have a relatively smaller diameter which gradually increases toward the distal extremity of each root. Roots from more nearly apical regions of a plant are also relatively smaller in diameter at their points of origin than roots arising from more nearly basal portions (figs. 25, 32). Close to the point of exit from the stem, a root consists of a sclerenchyma sheath enclosing an actinostele and a very compact cortical zone. Certain cells of the cortex usually contain tannin-like deposits, and often these cells appear to form a complete ring about the stele (fig. 76). The steles are composed entirely of primary xylem and phloem, and have been observed to possess from three to nine xylem arms (fig. 77). Small, thin-walled phloem cells are situated in the furrows between these arms. Tracheids of much smaller diameter are situated in the ends of the arms of the actinostele and are presumably protoxylem. In many roots proliferation of parenchyma cells had occurred about their steles, giving the superficial appearance of secondary xylem. Branching of roots (fig. 77) which had been previously figured by Reed (1949) appears much more common in roots of the genus than was suggested. As the roots grew longer they increased in size and parenchyma cells of the cortex assumed the netted appearance often described as characteristic of roots of the free root zone. Study of specimen A, which is surrounded by a massive mantle of well-preserved roots, shows that roots need not necessarily be free of the secondary parenchyma at levels where the netted cortex is present. At distances removed from their points of origin, roots develop this type of cortex, and at lower levels in their downward course they may or may not become encased in secondary parenchyma.

The cortex of a free root is pictured in fig. 77. Large intercellular spaces become more sparse near the stele of the root. The cortex is more compact and is composed of smaller cells in this region. Tannin-like remains may be observed widely scattered through the entire cortex (fig. 77). Near the periphery of the root, outside of the netted parenchyma, the cortex is more compact and large intercellular spaces are absent. The cells are much smaller in diameter in this region and grade into a surrounding layer of thick-walled sclerenchyma cells.

It is believed that in addition to increase in size, roots also differenti-



ated more xylem arms in the distal extremities as the stele increased in size. The larger roots have an average of one or two more xylem arms on the actinostele, and it seems reasonable that more arms could have been differentiated as the exarch protostele increased in size while the root grew in length.

None of the roots observed showed evidences of pericycle, endodermis, or phellogen as were described by Reed (1949). She suggests that the so-called "lacunar" cortex is of secondary origin, being derived in more distal regions of the root by the activity of a phellogen. She further suggests that the sclerenchyma layer at the periphery of the cortex is of a periderm-like nature, this also having been derived from the phellogen. In all specimens observed by the present author the cells of the inner cortex grade gradually into the outer sclerotic layer without evidence of a phellogen, and therefore it is assumed that, with the exception of certain parenchyma cells, all tissues of these roots were normally of primary origin. They cannot be favorably compared with stems of certain modern water plants (e.g., *Decodon verticillatus*) which have an aerenchymatous "periderm" laid down by a phellogen. Rather, the situation in these roots is analogous to that in stems of *Nelumbo* and *Marsilea* where the cortex is primary in origin.

Most cells of the compact inner cortex, more external netted cortex, and certain parenchyma cells of the limiting layer are capable of secondary divisions, but these cells, because of their arrangement, could by no means be considered to be phellogen. They underwent cell divisions and the resulting radiating parenchyma (fig. 78) served to form part of the mass of secondary parenchyma of the inner root zone. Proliferation was most abundant on the surfaces of the roots away from the center of the stem, much less along the sides, and none was observed arising from internal faces of roots.

Additional parenchyma tissue of the same type was derived secondarily from cortical cells of leaf bases (fig. 76) and from parenchyma cells intermixed with the fibers of the stem sheath (fig. 36). The nature of the tissue surrounding the more internal roots then seems fairly clear. It was formed by proliferation of various parenchyma cells (although not in the form of elongated hairs) as suggested by Farmer and Hill (1902) and Solms-Laubach (1911) rather than being part of the original stem cortex through which the roots grew (Stenzel, 1906; Sahni, 1935). It seems definite that the long-debated question as to its intracortical or extracortical nature is settled.

Cells of this region also contain the tannin-like deposits (figs. 46, 76). At higher levels, lobed masses of parenchyma project beyond the root zone (fig. 46).

Adventitious roots have also been observed to arise from the second

vascular cycle of the stem. In fig. 45 one such root is seen in connection with the second cycle, and the cross-sections of four roots may be observed in the sclerenchyma band on the adaxial side of the leaf trace. If at lower levels these roots grew downward and outward into the concavity of the leaf trace, there is no path open by which they could have reached the periphery of the stem other than by growth through the vascular tissue of the trace. Unless they followed such a course, which has not been observed, or grew around the outside of the trace, these roots have neither functions of support or absorption—since they must have ceased growth while still within the stem. The majority of functioning roots originated in the peripheral cauline bundles.

Baxter (1953) made the incorrect deduction that petioles of fronds pass outward for some distance through the root mantle. It is possible that this misconception is due to the interpretation of the relationship of leaf bases and root mantle as presented by Zeiller (1890), whom Baxter cited for the authority. Although none of Zeiller's figures show leaf bases among the roots of the inner root mantle he explains their absence by supposing that the parenchyma increased in amount behind the apical meristem and that the roots passed down through it. The external surface of the stem together with portions of the petioles, became detached leaving the cortex traversed by roots exposed. As a result of evidence presented in this paper about the derivation of the secondary parenchyma surrounding the roots, the erroneous nature of Zeiller's explanation becomes apparent. Further, leaf bases have never been found attached and extending out through the root mantle. Based on his mistaken ideas concerning the relationships of roots to leaf bases, Zeiller (1900) prepared a reconstruction of the stem and root mantle of *Psaronius*. At the surface of the root mantle some distance from the stem he figured *Caulopteris* scars which were supposedly the ends of petiole bases which traversed the mantle. At a lower level of the reconstruction the root mantle was removed (since he considered this part of the stem, its removal amounted to decortication of the stem) and the actual stem surface with its scars had been designated *Ptychopteris*. This conception of *Caulopteris* is obviously not that which Lindley and Hutton (1831-33) originally described for the form genus, nor is *Ptychopteris* to be regarded as stem surface features without excessive weathering. Zeiller (1890) did, however, show some surfaces of *Psaronius* stems which were obviously much weathered and which he correctly designated *Ptychopteris*. Little is gained by the continued use of the form genus *Ptychopteris* in anatomical descriptions of *Psaronius*, since its formation is only a matter of degree of weathering and, if necessary, this condition may be adequately expressed without benefit of a generic name.

Baxter (1953) suggests that his specimen may be referred to *Ptychop-*

*teris* except that in the case of *P. cooksonii* the roots were not supposed to have been present on the stem, since the upper three-fourths of the specimen completely lacked roots. This specimen has been incorrectly compared by Baxter to the form genus *Ptychopteris* because of Zeiller's erroneous description of that genus, and further because the author of *P. cooksonii* misinterpreted the stem fragment as an apical portion. A re-examination of the type material has shown roots projecting at numerous points from the surface of the stem just outside the peripheral cauline bundles. It is probable that a complete root mantle had been broken off the stem, since very numerous roots and grooves indicating former positions of roots cover the leaf scars. Several silicified specimens in the University of Illinois collections show an almost identical configuration of the stem surface after the root mantle was broken off in the laboratory.

As previously suggested in connection with *P. blicklei*, many roots near the apex of the stem begin their course as free roots appressed to the surface of the stem between leaf bases. At lower levels they became enclosed in the proliferating parenchyma cells as did the roots produced at lower levels. These roots continued their downward and outward course through the inner root zone while gradually increasing in diameter, until their outward rate of growth exceeded that of the secondary parenchyma tissue. From this level to the base of the stem (at least until subsequent growth of parenchyma enclosed them) they are considered to be free roots. The mantle of roots about larger stems may exceed 2½ feet in diameter. Thus, by addition of roots from higher levels the circumference of the plant increased as the roots grew out and down over those formed at lower levels.

The twofold function of the root mantle is obvious when the structure of this tree fern is considered. The stem itself is an obconical structure which reached heights of 10 meters or more, but at its base may be as small as  $2.3 \times 1.5$  cm. in diameter. This is the smallest stem cross-section observed, but there must have been still smaller portions of these stems. Although some stems at higher levels, in addition to the external sclerenchyma sheath, developed bands of fibers in association with the vascular bundles, many never developed this additional means of support. Obviously, then, the root mantle was one of the main means of support of these plants.

One very essential function of the mantle has been almost entirely overlooked by previous workers. Since at the lowest levels the amount of vascular tissue of the upright stem is very small in comparison with the enormous increase at higher levels, it becomes apparent that in more nearly basal regions this small stele was not mechanically efficient enough to transport the volume of water carried by the vascular cylinders

at higher levels, nor by the leaf traces in the huge fronds borne by such plants. The mantle of roots then performs the very necessary function of directly supplying moisture to the vascular tissue of the stem at higher levels. A fact that should be emphasized in connection with conduction is that if there were no contributions of more external cycles to inner ones, and if there were no fusion of cycles of the stem one to another at the points where traces are passed from one cycle to another, then these roots would function largely in supplying moisture to the peripheral cauline bundles—since there would be no efficient means of its reaching more internal cycles.

### C. Comparisons with Other Families of Ferns and Taxonomic Position

For many years investigators have attempted to determine the relationships of the Psaroniaceae with recent ferns. The two extant families which have received the most attention are the Marattiaceae and Cyatheaceae (including the Dicksoniaceae). The characters used have been interpreted differently in existing literature. The parenchyma tissue of the root zone, for example, was compared by Stenzel (1906) with that of Marattiaceae, but it was shown before by Farmer and Hill (1902) in their work on *Angiopteris* that roots of this extant genus were intrusions into the cortical tissue. A point of similarity is that *Marattia* roots have an actinostelic vascular strand similar to that of *Psaronius* roots. In the Marattiaceae, roots arise mainly from more internal portions of the stele, while in *Psaronius* a few originate from this region but the great majority of them are in connection with the peripheral cauline bundles. The presence of secondary parenchyma tissue around them is a feature peculiar to *Psaronius*.

With regard to the stem, it was thought to resemble, for example, that of *Angiopteris* (Mettenius, 1864). *Angiopteris*, however, does not exhibit the expanded cauline bundles which play an important part in contributing to leaf trace formation, although Mettenius (1864) figured a stem of *Angiopteris* grown under abnormal conditions in which the strands of the more external cycles had fused into tangentially expanded bundles, four to six of which form a cycle. Certain authors (e.g., Bower, 1926) suggested that the modern much dissected stele of *Angiopteris* is derived by a reduction or dissection of the less interrupted, more primitive cycles in *Psaronius*. Others (e.g., Seward, 1910) believed that the peripheral cauline bundles of *Psaronius* perform a function similar to the accessory strands in members of the Cyatheaceae. The occurrence of large sieve cells in the phloem is also a feature similar to living Marattiaceae.

The psaroniaceous leaf trace, which is generally undissected, has been

compared by Seward (1910) with those of such ferns of the Cyatheaceae (Dicksoniaceae) as *Dicksonia antarctica*. It seems to the present author that if such superficial characters as shape of trace are to be cited as evidence of affinities, the vascular traces of *Matonia* should be taken into consideration. More similarity exists between petiole traces of certain of the Marattiaceae and those of *Psaronius*, in spite of the usually dissected nature of marattiaceous forms. Jeffrey (1910) and others have described the gradual change of arrangement of the separate strands in the leaf base, from an open horseshoe to an arrangement in which the strands toward the adaxial side bend inward, fuse, and become isolated in the center of a ring of bundles. Except for the fact that the trace is dissected, the sequence follows exactly that assumed by *Stipitopteris*.

Finally, a consideration of the synangia borne on fronds assignable to *Psaronius* stems seems to indicate affinities with the Marattiaceae. Strasburger (1874) has pointed out that the marattiaceous character of *Scolecopteris* is unmistakable since *S. elegana*, in its sporangial form, resembles *Marattia* and *Christensenia* in the circular disposition of the sorus, while the outline of their distal free portions resembles *Angiopteris*; in dehiscence it compares with all three, but especially with *Marattia*. The minutiae of these sporangia (e.g., *Scolecopteris*, *Ptychocarpus*, and *Asterotheca*) cannot be fully discussed here. The only point to be considered is that these sporangia are of the eusporangiate type which would logically link them with the Marattiaceae.

Most authors seem to regard the much-dissected vascular system of the stem and leaf traces of marattiaceous ferns as reduced forms of the more primitive psaroniaceous types. It has been pointed out, however (Seward, 1910), that other families of ferns exhibit characters which are primitive in nature and could themselves be derived from a psaroniaceous ancestor. It is possible that more than one modern family of ferns (e.g., Cyatheaceae including the Dicksoniaceae and Marattiaceae) was derived through reduction from a psaroniaceous ancestor. If this were the case one could assume that the line of development leading to modern marattiaceous ferns has not in some characters (sporangia, etc.) proceeded as far phylogenetically as certain members of the Dicksoniaceae, which themselves retain other primitive features (e.g., undissected leaf traces). Unlike most members of the Cyatheaceae, which are usually typified by a dissected stelar system, *Thyrsopteris elegans* and *Saccoloma elegans* (Bower, 1926) appear to have remained relatively unchanged and are strikingly similar anatomically to *Psaronius*. In these forms, leaf traces originate in the center of the stem and in their upward and outward course fill the gaps for short vertical distances in the outer cycles. It is further suggested that such features (pronounced outer cycle and much dissected inner cycle) as are found in *Psaronius brasili-*

*ensis* and *Tietea singularis* may represent transitional types leading to modern families since they show great dissection of the internal cycles and the beginning of dissection of leaf traces.

It is believed, because of uncertain evidence and the possibility that more than one modern family of ferns may have had its origin in a psaronioid complex, that the position of *Psaronius* is best expressed by placing it in a separate family as advocated by Stenzel (1854, 1906).

#### IV. TAXONOMIC TREATMENT OF THE PSARONII OF NORTH AND SOUTH AMERICA

Some authors (e.g., Rudolph, 1906) maintain that the psaronii are closely allied to the modern Marattiaceae, and on this basis there has been a tendency to group the psaronii with this family as its fossil representatives. The present author is inclined to agree with Stenzel (1906) and Seward (1910) in assigning the genus *Psaronius* to a different family. The spelling of the family name Psaronieae should be modified to Psaroniaceae in keeping with the modern spelling of taxa of that rank.

Because of the accumulation of new evidence presented in this paper, a more inclusive generic description of *Psaronius* has been compiled as follows:

Arborescent fern stems occasionally attaining a height of 10 meters or more, fronds with petioles of the *Stipitopteris* or *Stewartiopteris* type borne at the crown; frond arrangement in some stems ranging from a spiral having three orthostichies in lower portions, to a whorled condition of 14 or more rows of leaves in alternating whorls of seven, or more orthostichies at higher levels of the stem; other stems having a distichous, tetrastichous (two leaves per whorl), or possibly a hexastichous (three leaves per whorl alternately arranged) arrangement throughout the length of the stem; stem obconical having from two to twelve or more concentric stelar cycles, the number increasing at successively higher levels; each new cycle formed within the central cycle and attached to it at its point of origin; vascular bundles endarch, amphiphloic; persistent leaf gaps between cauline bundles filled only at certain positions by leaf traces; stem usually surrounded by a definite sclerenchymatous zone; certain cells of fundamental tissue and secondary parenchyma around roots often containing tannin-like deposits in many species; sclerenchyma bands, and often groups of fibers, occasionally associated with the vascular bundles; adventitious roots arising from the peripheral cauline bundles and often from more internal cycles; root traces polyarch; cortex of roots becoming netted in more distal regions; roots near the stem compacted by a mass of secondary parenchyma tissue proliferated

from stem and root cortices, and from parenchyma cells intermixed with fibers in the sclerenchyma zones surrounding the stem and individual roots; free roots generally at the periphery of this region.

It is obvious that an artificial classification of the *psaronii* such as that followed by Hirmer (1927) should be discarded. *Psaronius blicklei*, for example, could be assigned to more than one of Hirmer's categories since the leaves are spirally arranged near the base and whorled at higher levels.

As a result of this study it is necessary to reduce certain previously named species of *Psaronius* to synonymy, to add several new members, and to suggest that certain specific names be discarded since they are based on inadequately known, poorly preserved specimens. Specimens in the latter category include *P. junceus* Herzer (1900), *P. borealis* Macbride (1904-6), and *P. illinoensis* Hoskins (1928). Nomenclatural changes in existing species and descriptions of new ones are as follows:

*Psaronius giffordii* Gillette, Bot. Gaz. 99:98-100, figs. 13, 17-20. 1937.<sup>1</sup>

1937 *Psaronius septangulatus* Gillette, Bot. Gaz. 99:82-95, figs. 1-12.

1937 *Psaronius peoriensis* Gillette, Bot. Gaz. 99:95-98, figs. 14-16.

1953 *Psaronius cooksonii* Baxter, Bot. Gaz. 115:35-40, figs. 1-4, 6.

Orthostichies of leaves of available specimens numbering 6-12, probably throughout the length of the plant, ranging from three at the lowermost levels to 12 or more higher in the stem; phyllotaxy in available specimens ranging from a 2/7 spiral to alternating whorls of six each; vascular cycles numbering from six to ten, probably ranging from one to ten or more throughout the length of the plant; definite sclerenchyma sheath surrounding the stem except at points of leaf trace divergence; ground parenchyma dense; ground parenchyma with scattered gum cavities; lacunae absent; tannin cells apparently absent.

*Localities:* Princeville Twp., Peoria Co., Illinois; Stark Co., Illinois; Hamilton, Kansas.

*Age:* Upper Pennsylvanian for Illinois specimens; Upper Pennsylvanian for Kansas specimen.

*Horizon:* Unknown for Illinois specimens; Wabaunsee group, Pennsylvanian System, for the Kansas specimen.

*Holotype:* Specimen 2613 (formerly no. 32 of the Peoria Academy of Science), now in the paleobotanical collections, Department of Botany, University of Illinois, Urbana, Illinois. Pieces of specimen 32 in the Department of Botany, University of Chicago, Chicago, Illinois.

It has been necessary to group *P. septangulatus* (fig. 79) and *P. peori-*

<sup>1</sup> The ending *ii* is used here in accordance with Recommendation C, Article 82 of the 1952 International Code of Botanical Nomenclature.

*ensis* (fig. 80) described by Gillette (1937) with *P. giffordii* of the same author (Gillette, 1937, fig. 17), since a re-examination by the present author showed no distinguishing features and according to the descriptions of the specimens they vary only in numbers of orthostichies (phyllotaxy), numbers of internal strands (stelar cycles), and characters of size and shape of the leaf scars. On the basis of evidence presented previously in this paper, the characters described for each of these species may vary greatly in one species and even throughout the length of a single stem, leaving no valid means of distinguishing them. No definite sclerenchyma sheath was described for the specimen formerly known as *P. peoriensis*, although a re-examination of the specimen then serving as the type has shown that a sheath was present. *P. giffordii*, according to Gillette (1937), possessed six orthostichies of leaves in alternating whorls of three each. One orthostichy, although missing, was postulated as being present on the stem, based on his estimation of the position of the center of the stem and the arrangement of leaves about the circumference. An examination of the original specimen has led the present author to believe that originally the stem fragment bore eight orthostichies of leaves in alternating whorls of four. Other characters ascribed to this stem place it in *P. giffordii*.

The specimen described by Baxter (1953) as *P. cooksonii* differs only superficially from *P. giffordii* in number of orthostichies, size of "secretory cells" (Baxter, 1953) or "gum canals" (Gillette, 1937), and intergrades with *P. giffordii* in numbers of internal strands (vascular cycles) and size and shape of leaf bases. None of these characters is valid for specific differentiation in the case cited.

The name *P. giffordii* has been retained over *P. septangulatus* and *P. peoriensis*, since *P. septangulatus* implies a condition not constant for the species while *P. peoriensis* suggests only a restricted locality for the species.

*Psaronius brasiliensis* Brongniart, Bull. Soc. Bot.  
France 19:3-10, 1872.

Figured by Unger De palmis fossilibus, in Martius, Historia Naturalis Palmarum, p. 70, pl. 1, fig. 4. 1850.

Stem bearing four orthostichies of leaves in a decussate arrangement; at least four concentric vascular cycles with a varying number of more internal vascular strands probably representing additional much-dissected cycles; innermost strands often appearing as closed or open cylinders; four cauline bundles alternating with four pathways of leaf trace divergence; leaf traces receiving contributions of vascular tissue from the cauline bundles below the point of fusion to them, although not fusing with peripheral cauline bundles; stem surrounded by definite



sclerenchyma sheath broken only at points of leaf trace departure; leaf traces in leaf bases becoming dissected with a number of small vascular strands accompanying the trace in its adaxial concavity; vascular strands accompanying the trace in its adaxial concavity; vascular strands accompanying the leaf trace originating in part from the center of the stem and in part from dissection of the free edges of the trace; internal bands of sclerenchyma occasional between leaf trace and cauline bundles; mantle of polyarch adventitious roots; secondary parenchyma between roots of root mantle.

*Locality:* Chapado do Jaboti, Estado do Maranhão, Brazil.

*Age:* Thought to be Lower Permian.

*Horizon:* Unknown.

*Holotype:* Specimen no. 1445 in the Paris Museum, other pieces of which are at the Rio de Janeiro Museum and the British Museum.

The history of this specimen is somewhat unusual and caused considerable difficulty in determining the author and original citation. A fragment of a stem of this species was figured by Unger in Martius' (1850) *Historia Naturalis Palmarum* 22 years before Brongniart's (1872) description of *P. brasiliensis* (Pelourde, 1912). The specimen serving as the basis for Brongniart's description is considerably better preserved and more complete than that figured by Unger, and since no description accompanied Unger's illustration Pelourde (1912) suggested that the more complete fragment described by Brongniart in 1872 should be considered the type specimen. The better preserved specimen was not figured with Brongniart's (1872) description of the specimen. However, 1872 is considered to be the valid publication date of *P. brasiliensis*, since this date precedes December 31, 1911, the date after which the description and illustration must be simultaneously published.

An unusual kind of fern stem thought to have originated from the same locality as *P. brasiliensis* was described as *Tietea singularis* by Solms-Laubach (1913). This specimen, although less complete than *P. brasiliensis*, shows evidence of a larger number of orthostichies. Internal cycles are much less conspicuous than in *P. brasiliensis* and are evident only as a large number of hollow cylindrical strands of vascular tissue, some of which are completely closed. Further, the leaf traces in *Tietea* are much more dissected than those in *P. brasiliensis*, although in the latter there is some indication of dissection of the traces. There is considerable evidence that *Tietea* has affinities with *P. brasiliensis*, but the two forms must remain separate until additional material becomes available and further investigations are undertaken.

*Psaronius pertusus* A. H. Blicke, sp. nov. (fig. 81).

In the type specimen, eight peripheral cauline bundles alternate with

eight pathways of leaf trace divergence; leaves arranged in a  $3/8$  spiral phyllotaxy (probably fewer rows at more nearly basal levels, becoming whorled with more orthostichies above); five concentric stelar cycles in the length of the holotype preserved (probably having fewer below and a greater number above); ground parenchyma cells having a net-like arrangement; tannin cells scattered in ground tissue; lysigenous lacunae and gum cavities lacking; definite sclerenchyma sheath surrounding the stem.

*Localities:* Shade and Lodi Twp., Athens Co., Ohio; Morgan Co., Ohio; Calhoun, Richland Co., Illinois.

*Age:* Upper Pennsylvanian.

*Horizons:* In Ohio: Pittsburgh coal or No. 8 seam, lower Monongahela formation; Arnoldsburg sandstone, upper Monongahela formation; Little Waynesboro coal, Monongahela formation. Upper McLeansboro group of Illinois, Pennsylvanian System.

*Holotype:* Specimen no. B-202 in the Ohio University Museum Collection, Athens, Ohio.

The excellently preserved specimen showing morphological details of the vascular tissue in fig. 81 was collected from the Monongahela formation of Lodi Twp., Athens Co., Ohio, by Dr. A. H. Blickle. The diagnosis of *P. pertusus* was written by him for this specimen. Fig. 82 of the ground tissue was photographed from a specimen obtained from the Calhoun collecting locality of Illinois.

*P. pertusus* Blickle was formerly designated as *P. lacunosus* Blickle (1940—see Arnold, 1947) although never validly published as such. The name has been changed to *P. pertusus* to avoid confusion, since the lysigenous cavities of *P. blicklei* can more readily be termed lacunae than the large intercellular spaces of the ground parenchyma of *P. pertusus*.

*Psaronius blicklei* Morgan, sp. nov. (fig. 1-12, 14, 15, 25-34).

Stem having three to fourteen or more orthostichies of leaves, the increase occurring at successively higher levels: leaves spirally arranged in lower portions, becoming whorled higher in the stem; up to 10 or more concentric stelar cycles in the stem; cells of leaf traces smaller in diameter than cells of other vascular bundles; leaf traces near periphery of stem thinner than other vascular bundles; traces assuming the *Stipitopteris* configuration; stem surrounded by a definite sclerenchymatous layer, sclerenchyma cells present in small patches and surrounding leaf bases in lower portions of stem, becoming more abundant in the form of bands associated with stele at progressively higher levels; at lower levels, parenchymatous ground tissue compact with no or few lysigenous cavities, the lacunae becoming more abundant and larger higher in the stem; tannin-like deposits in parenchyma cells of ground

tissue of stem and roots, and in secondary parenchyma cells surrounding roots; proliferation of parenchyma cells occasional especially in upper portions of stem; four to six protoxylem groups on the arms of the actinosteles of roots.

*Localities:* Berryville, Lawrence Co.; near Dix, Jefferson Co.; Calhoun, Richland Co., Illinois.

*Age:* Upper Pennsylvanian.

*Horizon:* Upper McLeansboro group. Pennsylvanian System.

*Types:* Specimens A-I in the paleobotanical collections, Department of Botany, University of Illinois, Urbana, Illinois.

This species in all probability represents the most completely known of the *psaronii*. A series of specimens from close to the base to fragments high in the stem was used in the description of the morphology of the vacular system. A wealth of histological detail is also available for this species.

The species was named for Professor A. H. Blickle, who did most of the research on Ohio *psaronii* and at whose suggestion this project was undertaken. The author is also indebted to him for much aid and assistance in obtaining representative Ohio specimens.

*Psaronius chasei* Morgan, sp. nov. (figs. 44-47).

Stem probably having three to many orthostichies of leaves; leaves probably spirally arranged in lower portions, becoming whorled higher in the stem; up to 10 or more concentric stelar cycles in the stem; stem surrounded by a definite sclerenchymatous layer; sclerenchyma bands between second and third vascular cycles; parenchymatous ground tissue with no lacunae; tannin-like deposits in parenchyma cells of the ground tissue of stem (concentrated near vascular bundles), in roots, and secondary parenchyma surrounding roots.

*Localities:* Berryville, Lawrence Co.; Calhoun, Richland Co., Illinois; St. Wendel, Posey Co., Indiana.

*Age:* Upper Pennsylvanian.

*Horizon:* Upper McLeansboro group in Illinois; Parker coal a short distance above the Lonsdale limestone in Indiana. Pennsylvanian System.

*Type:* C. B. 1221 in the paleobotanical collections, Department of Botany, University of Illinois, Urbana, Illinois.

This species is named for Dr. Virginius Chase of Peoria, Illinois, who presented, to the University of Illinois, a gift of many fine silicified *Psaronius* specimens which were of considerable aid in this study.

*Psaronius melanedrus* Morgan, sp. nov. (figs. 17, 19, 35-43).

Stem with three to many orthostichies of leaves; leaves spirally arranged in lower portions, probably becoming whorled higher in the

stem; two to many concentric stelar cycles in the stem; radial thickness of xylem in stem vascular bundles ranging from .4 mm. in the basal portions to at least 1.1 mm. higher in the stem; sclerenchyma cells entirely lacking in fundamental tissue except that delimiting leaf bases which are enclosed by a heavy band of fibers and are roughly rectangular in cross-section; parenchymatous ground tissue lacking lysigenous lacunae; tannin-like deposits in parenchyma of ground tissue and root mantle; root mantle of varying thickness in different portions of the stem; roots arising from basal portion of stem larger in diameter at points of origin than roots arising at upper levels; protoxylem at the tip of each of four to six arms of the actinostele of each root; inner roots in radial files.

*Locality:* Four miles south of West Mineral, Kansas.

*Age:* Middle Pennsylvanian.

*Horizon:* Fleming coal, Cherokee shale, Des Moines series, Pennsylvanian System.

*Types:* Specimens J-Q in the paleobotanical collections, Department of Botany, University of Illinois, Urbana, Illinois.

This species is well represented by stem fragments from near the base to levels high on the stem. It has been named *P. melanedruss* because of the heavy dark sclerenchyma sheath which completely surrounds the stem.

## V. SUMMARY

During the course of the research described in the preceding pages, several approaches to the clearer understanding of the morphological characteristics of the genus *Psaronius* were employed. It has been established, through examination of a large number of *Psaronius* specimens from various localities, that it is possible to reconstruct with accuracy the vascular system of *Psaronius blicklei* sp. nov. From a detailed examination of specimens representing basal portions of this arborescent genus, it has been determined that in early ontogeny stems of *Psaronius* were exceedingly simple, consisting of one or two cylinders of vascular tissue surrounding a central strand of the same tissue. It becomes evident, at successively higher levels in the stem, that this solid inner strand of tissue, by lateral growth, gives rise to added inner cycles of vascular tissue. This observation lends support to the argument that numbers of investing steles are not in themselves good taxonomic characters.

It has also been established that the phyllotaxy undergoes several revisions throughout the length of stems of *P. blicklei*. At the base of such stems leaves produced early in development are arranged in a

loose spiral. Higher on the stem this spiral arrangement becomes more compact, until many old stems reach a tightly whorled arrangement consisting of as many as 14 orthostichies. The exact manner in which new orthostichies of fronds were added, and the way in which new and more internal stelar cycles were added to produce complex, polycyclic dictyosteles, has been discussed in detail.

It has also been observed that there is considerable increase in stem diameter at higher levels, giving the stem an obconical configuration. The unbalanced structure thus produced is compensated for by an enveloping mantle of roots which aided tremendously in support and in absorption. The situation is somewhat analogous to that of a corn plant which depends upon innumerable adventitious prop roots for anchorage, support, and the bulk of its absorption.

A number of erroneous ideas concerning the root mantle and frond origin (i.e., Zeiller, 1890; Farmer and Hill, 1902; Stenzel, 1906; Solms-Laubach, 1911; Sahni, 1935; Reed, 1949; Baxter, 1953) have been corrected in the light of knowledge gained in this study.

Morphological evidence obtained from the examination of the vascular systems of many *Psaronius* stems makes it clear that variation within the genus must be divided into:

(1) Ontogenetic variation known to occur between base and apex of a single plant, and also at the same levels of the plant with increasing age.

(2) Variation which remains constant among different species.

With a thorough understanding of the first type of variation, it has been suggested that many of the previously named American and European species are not valid because they probably represent various ontogenetic stages of stems of the same species.

Considering variation which is known to remain unaffected by growth stages, the valid American species are:

- (1) *P. brasiliensis* Brongniart, 1872.
- (2) *P. giffordii* Gillette, 1937.
- (3) *P. pertusus* Blickle, 1940.
- (4) *P. blicklei* Morgan, sp. nov.
- (5) *P. melanedrus* Morgan, sp. nov.
- (6) *P. chasei* Morgan, sp. nov.

Suggested relationships of *Psaronius* with members of such extant families as Cyatheaceae, including the Dicksoniaceae, and with the Marattiaceae were discussed. It is proposed, however, that the genus *Psaronius* be retained in its own family instead of being placed in any presently existing taxonomic group.

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## GLOSSARY

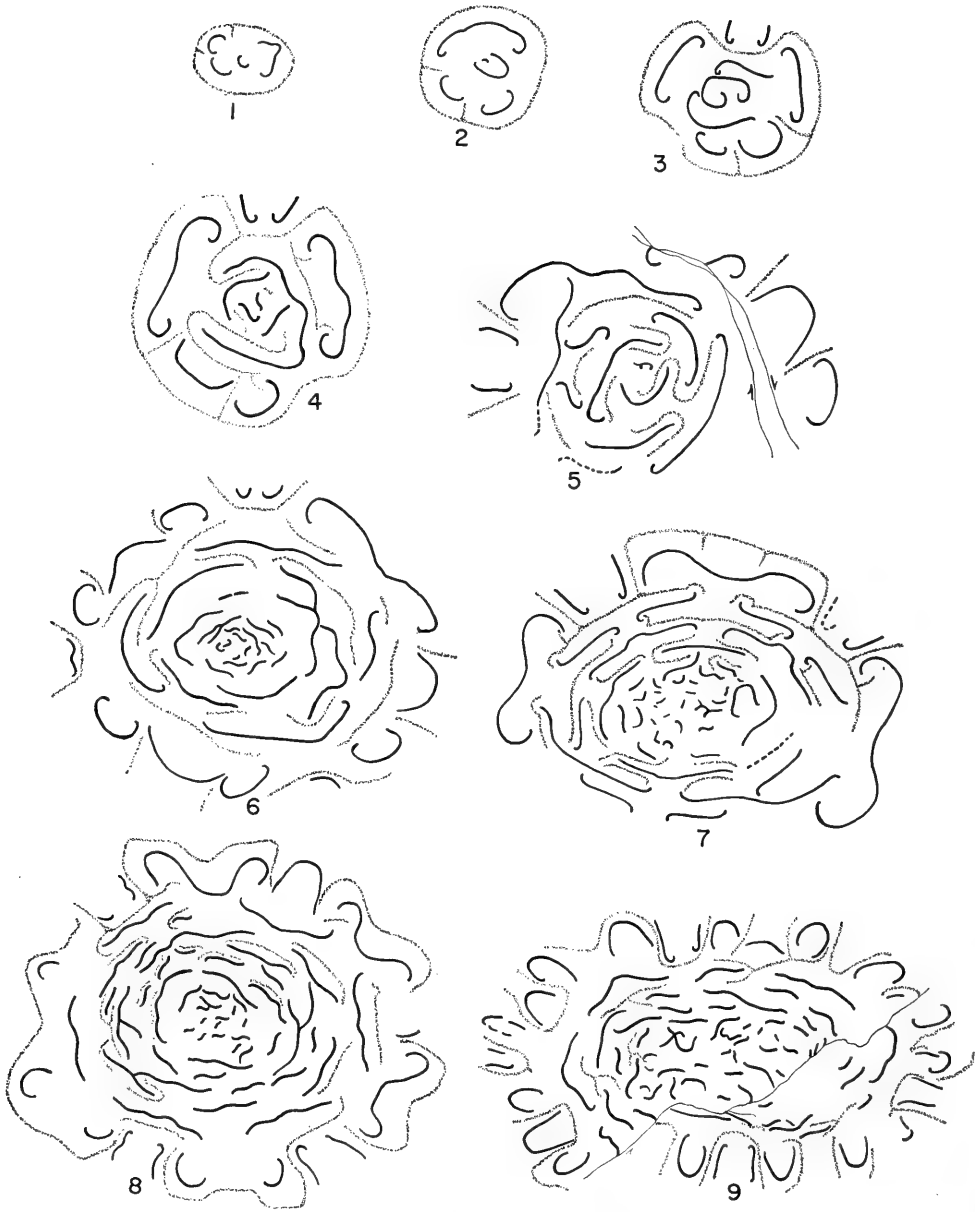
- ABAXIAL**—oriented away from the axil of a leaf.
- ACTINOSTELE**—an arrangement of vascular tissue commonly occurring in roots of plants where the primary xylem forms a core with radiating ridges. In cross section the xylem has a star-shaped configuration.
- AERENCHYMA**—parenchyma tissue forming an anastomosing network of cells separated by large intercellular spaces.
- AMPHIPHLOIC**—a condition where phloem is external and internal to the xylem.
- AXIL**—the angle between the stem and the upper face of the attached petiole of a leaf.
- CALAMITES**—Paleozoic ancestors of scouring rushes. These were arborescent plants.
- CARBONIFEROUS**—recognized in some geological classifications as a period (system) in the upper Paleozoic.
- CAULINE**—pertaining to stems.
- COAL BALL**—calcareous, dolomitic or pyritic rocks containing fossilized remains of plants. Usually found associated with upper Paleozoic coals.
- COENOPTERIDS**—an artificial assemblage of extinct herbaceous plants with fern-like sporangia and stems.
- DICTYOSTELE**—a stele with its vascular tissue dissected into smaller units by leaf and branch gaps.
- DISTICHOUS**—two-ranked, with leaves on opposite sides of a stem and in the same vertical plane.
- ENDODERMIS**—a layer of cells delimiting a stele from surrounding tissues of the cortex.
- EPITHELIUM**—a layer of cells lining a cavity.
- EUSPORANGIATE**—a condition in which spores are formed inside a thick-walled sporangium usually originating from several subepidermal initials. The eusporangium is typical of most vascular plants except for Filicales.
- FUNDAMENTAL TISSUE (ground tissue)**—extensively developed tissue composed primarily of parenchyma cells. Usually forms a matrix in which vascular bundles or steles are embedded.
- HEXASTICHOUS**—six-ranked, with leaves on six sides of the stem and in the same vertical plane.
- IRONSTONE**—a rock composed of fine clay particles and impregnated with iron compounds. In some areas ironstone forms around a nucleus of plant or animal remains.
- LEAF GAP**—an interruption in the vascular system of a stem produced by the bending out of a segment of vascular tissue (leaf trace) supplying a leaf. Leaf gaps are axillary to leaf traces.
- LEAF TRACE**—a strand of vascular tissue connecting the stem stele and the vascular system of a leaf.
- LEPIDODENDRID**—any one of a number of heterosporous, arborescent lycopsids (club mosses) common to the upper Paleozoic.



- LYSIGENOUS**—formed by the break down or dissolution of cells or tissues.
- METAXYLEM**—that primary xylem differentiated after protoxylem from tissues derived from an apical meristem.
- ORTHOSTICHY**—in phyllotaxy, an imaginary vertical line along a stem axis connecting leaf bases directly above one another.
- PALEOZOIC**—an era of geological time between the Proterozoic and Mesozoic.
- PARENCHYMA**—a tissue composed of thin walled cells. These are living cells in extant plants and usually function in food storage.
- PERMIAN**—a subdivision (period) marking the upper limits of the Paleozoic era.
- PROSTOLE**—a core of vascular tissue composed of centrally located primary xylem surrounded by a continuous layer of or patches of primary phloem.
- PROTOXYLEM**—that primary xylem first differentiated from tissues derived from an apical meristem.
- ROOT MANTLE (zone)**—a continuous layer of adventitious roots around the lower parts of the stem. This layer varies from a few roots to a mantle several inches thick.
- SCALARIFORM THICKENINGS**—horizontal, bar-like (ladder-like) thickenings on the walls of tracheids.
- SCLERENCHYMA**—a tissue derived from parenchyma cells which develop thickened walls. Usually dead at maturity and give support.
- SEED FERN**—an extinct vascular plant bearing naked seeds on large, compound, fern-like leaves.
- SIPHONOSTELE**—a stele with vascular tissue surrounding a pith and with overlapping leaf and branch gaps.
- SOLENOSTELE**—a stele with a pith but lacking overlapping branch and leaf gaps.
- SPHENOPHYLLS**—small protostelic ancestors of scouring rushes apparently becoming extinct by the end of Paleozoic era.
- STELE**—the conducting tissues of root or stem composed of xylem, phloem and usually delimited externally from other tissues by an endodermis.
- TETRASTICHOUS**—four-ranked, with leaves on four sides of the stem and in the same vertical plane.
- TRACHEIDS**—conducting and supporting cells of primary and secondary xylem. Dead cells at maturity with distinctive pits or apertures in their walls.
- VASCULAR SYSTEM**—all parts of the conducting system composed of xylem and phloem.

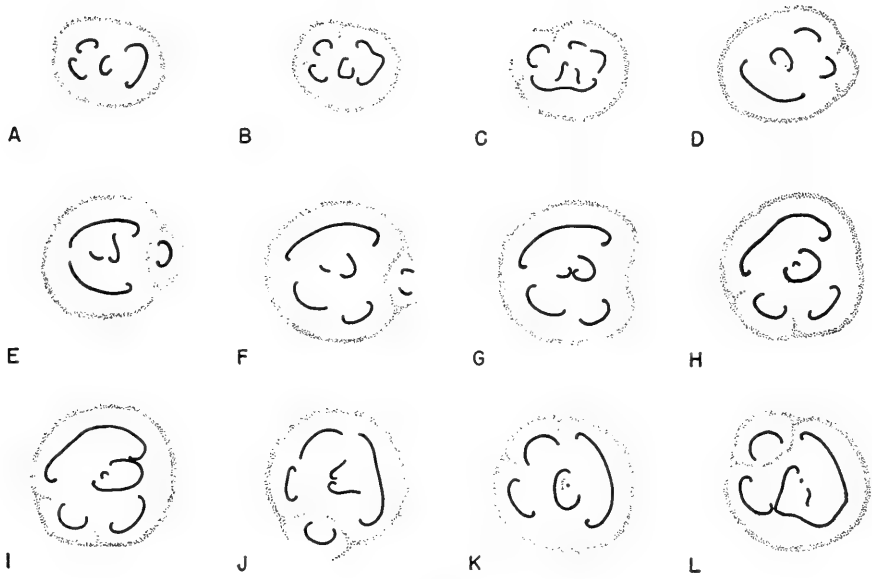


PLATES



FIGS. 1-7. *Psaronius blicklei* sp. nov. Diagrammatic cross-sections of specimens A-F. Steles are diagrammed in solid black, sclerenchyma is stippled. Fracture lines are diagrammed in fig. 15. Compare with figs. 25-31.

FIGS. 8, 9. *Psaronius blicklei* sp. nov. Diagrammatic cross-sections of specimens G, H. Steles are diagrammed in solid black, sclerenchyma is stippled. Compare with figs. 32, 33.



10.

FIG. 10. *Psaronius blicklei* sp. nov. Sections A-L represent diagrammatic cross-sections of successively higher levels, showing the origin and reconstitution of the most central cycle of specimen A. Steles are diagrammed in solid black, sclerenchyma is stippled.

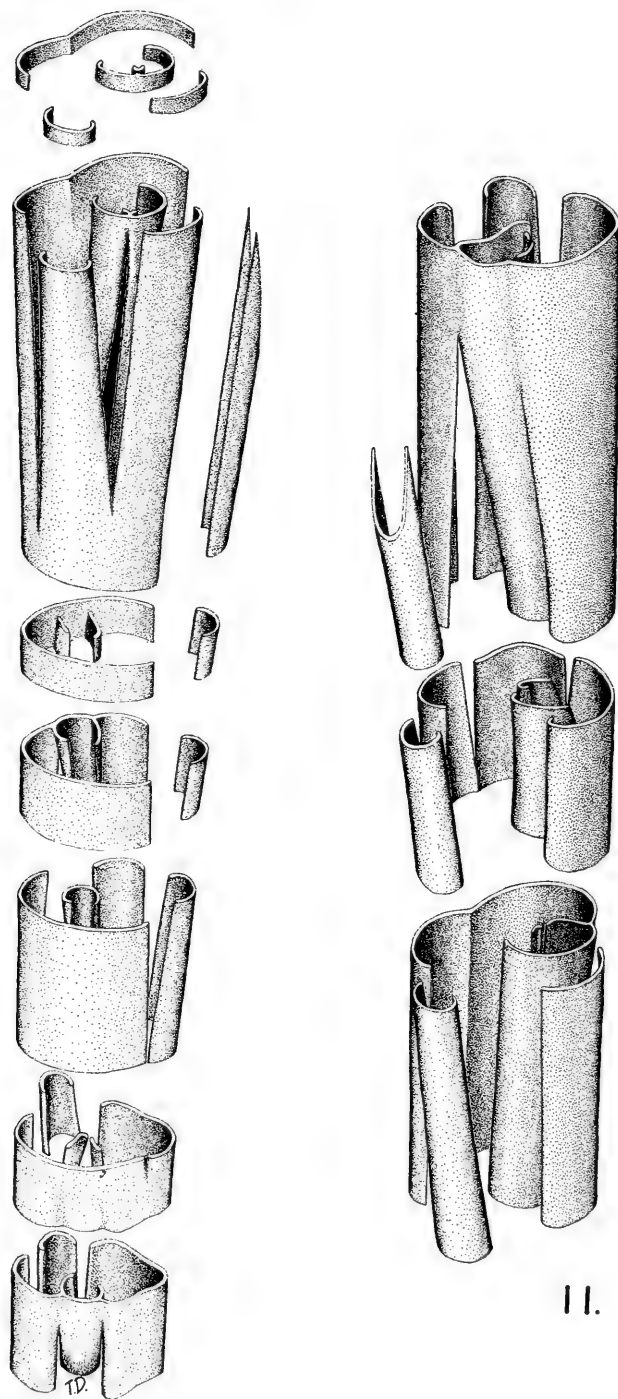


FIG. 11. *Psaronius blicklei* sp. nov. Diagrammatic reconstruction of the stele of specimen A. The section on the bottom at the left is the lowest level depicted and that on top at the upper right of the diagram is the highest.

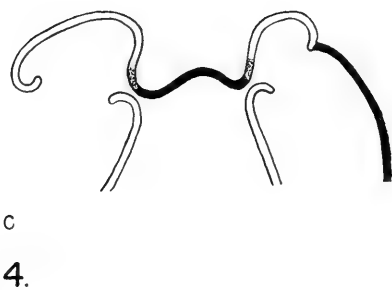
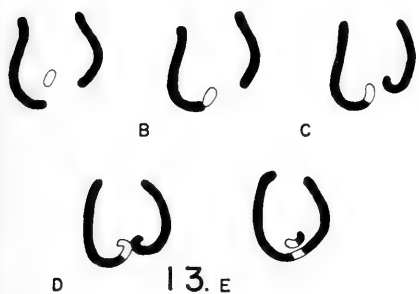
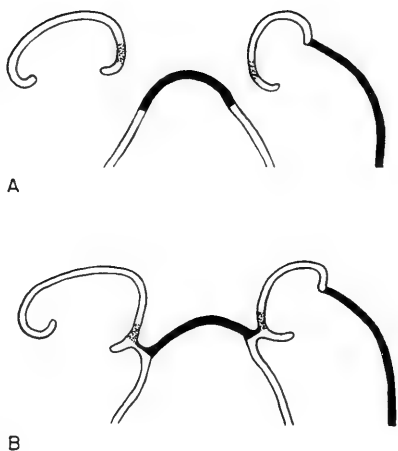
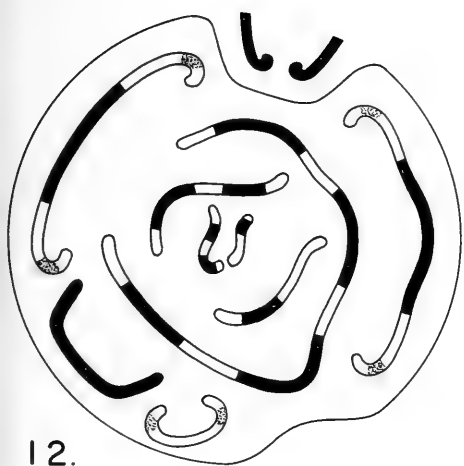


FIG. 12. *Psaronius blicklei* sp. nov. Diagrammatic cross-section of a stem portion with spiral phyllotaxy. Based on specimen C (compare fig. 28). Leaf trace and potential leaf trace material is diagrammed in heavy, solid black lines; the sclerenchyma is designated by a thin line at the periphery of the stem. Stippling represents cauline material which will at higher levels be contributed to departing leaf traces.

FIG. 13. *Psaronius blicklei*. Diagrammatic cross-sections showing successively higher levels (A-E) of the two most internal cycles of a stem at about the level exhibited by specimen C. The manner in which the innermost cycle (unshaded) fills a gap in the next outer cycle (solid black), and the sequence for its reconstruction, are shown. See text for full explanation.

FIG. 14. *Psaronius blicklei*. Diagrams A-C showing contribution of vascular tissue of peripheral cauline bundles to the next internal cycle and to the leaf trace of specimen C. Leaf traces, solid black; cauline bundles, unshaded; contribution of peripheral cauline bundles to leaf trace, stippled. See text for full explanation.

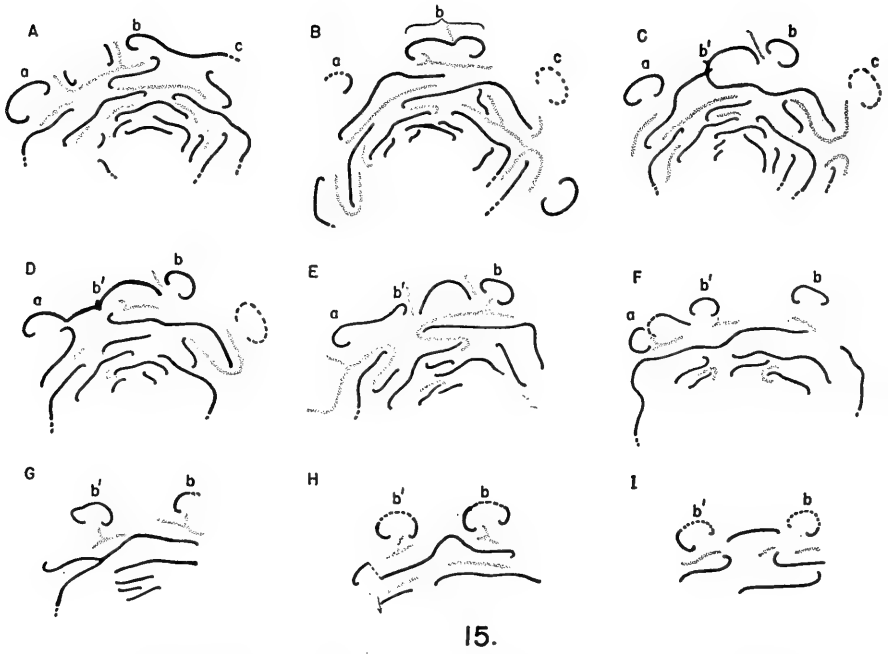


FIG. 15. *Psaronius blicklei*. Diagrams A-I showing the origin of a new orthostichy and the beginning of a new pathway of divergence for leaf traces of this orthostichy. Specimen E. See text for full explanation.



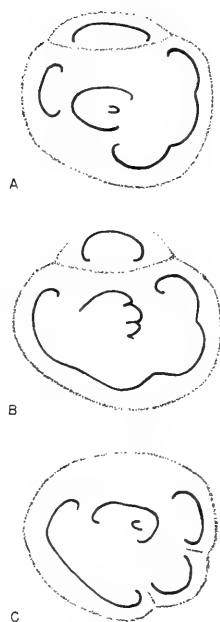
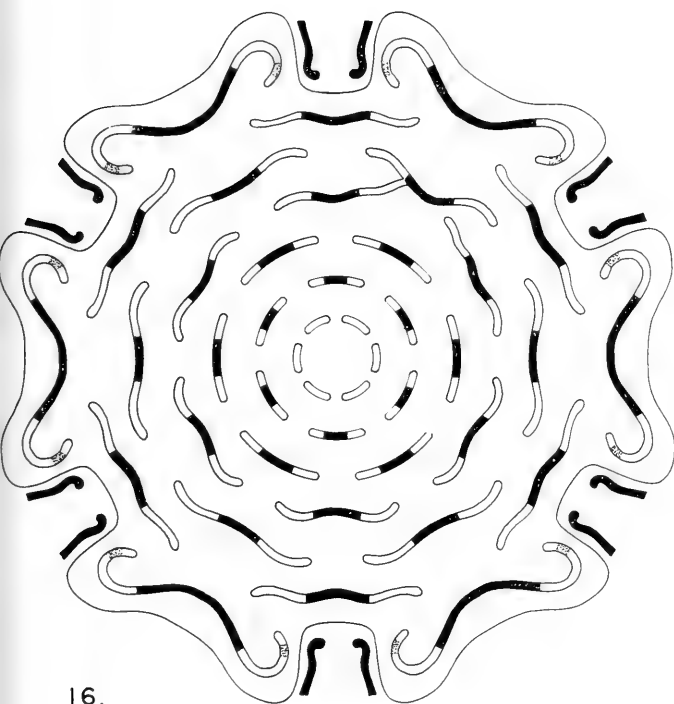


FIG. 16. Diagrammatic reconstruction of the cross-section of a large, whorled *Psaronius* stem based on specimen G. Leaf traces and potential leaf trace material are diagrammed in black, cauline bundles are unshaded, and potential contributions of the peripheral cauline bundles to the leaf traces are stippled. See text for full explanation.

FIG. 17. *Psaronius melanedrus* sp. nov. Diagrammatic cross-section (A-C) of successively higher levels, showing leaf trace contribution by and reconstruction of the most internal cycle of specimen J. Steles are diagrammed in black, sclerenchyma is stippled. See text for full explanation.

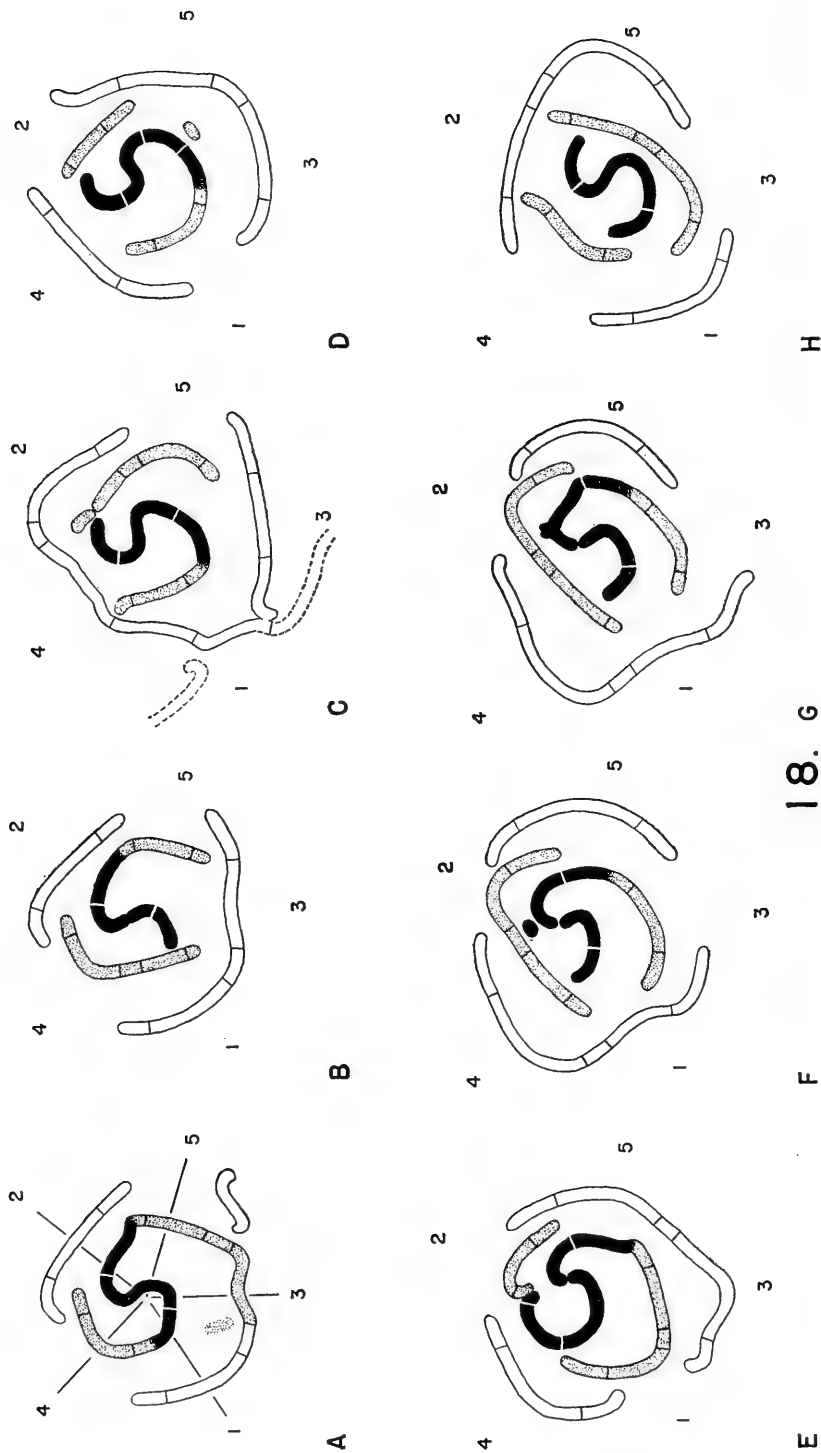
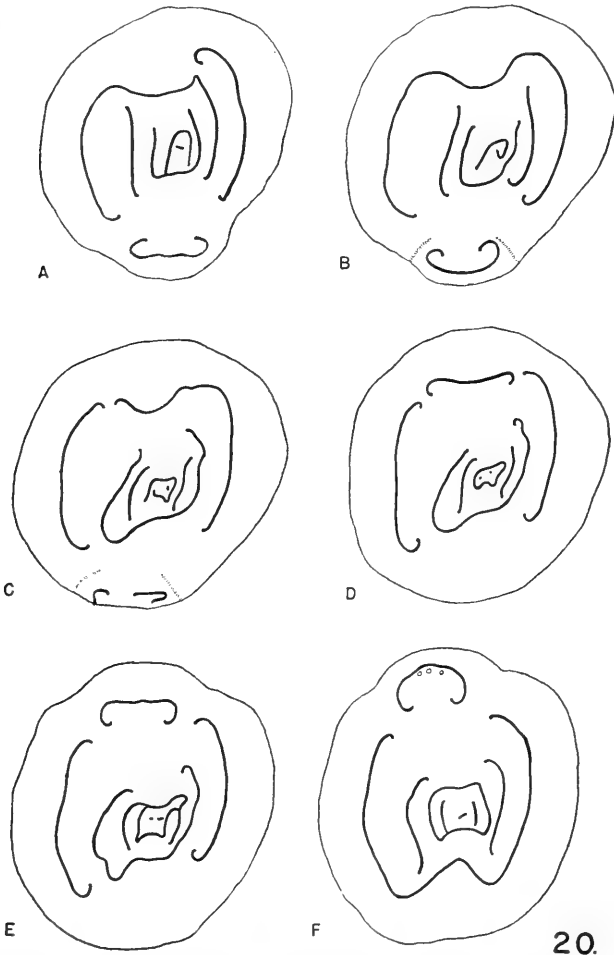


FIG. 18. *Psaronius melanodrus*. sp. nov. Diagrammatic cross-section (A-H) of specimen N at successively higher levels. The outer unshaded cycle is arbitrarily designated 1, the next inner one is designated 2 (stippled), and the most central cycle (black) is referred to as cycle 3. At C the dashed lines represent a still more external cycle than cycle 1. The small, stippled, unoutlined strand in diagram A represents a strand not preserved in that section. Vascular bundles are divided by lines to delimit cauline material from potential leaf trace material. Orthostichies are approximately numbered to show a 2/5 phyllotaxy. See text for full explanation. Illinois Geological Survey C.B. 803.



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FIG. 19. *Psaronius melanedrus* sp. nov. Diagrammatic cross-section of specimen O, C.B. 1254e bot. #1. Compare fig. 41. Outer cycle unshaded and diagrammed with dashed lines, next inner cycle unshaded and limited by solid lines, next inner one stippled, and most internal cycle is diagrammed as solid black strands.  $\times 2.62$ .



20.

FIG. 20. Specimen U. Diagrammatic cross-sections (A-F) of specimen U at successively higher levels showing method of leaf trace departure. Steles are diagrammed as heavy black lines, the edge of the stem is shown as a thin solid line, and the peripheral sclerenchyma cutting in about leaf bases is stippled. See text for full explanation. Compare F with fig. 51. Specimen 2608.

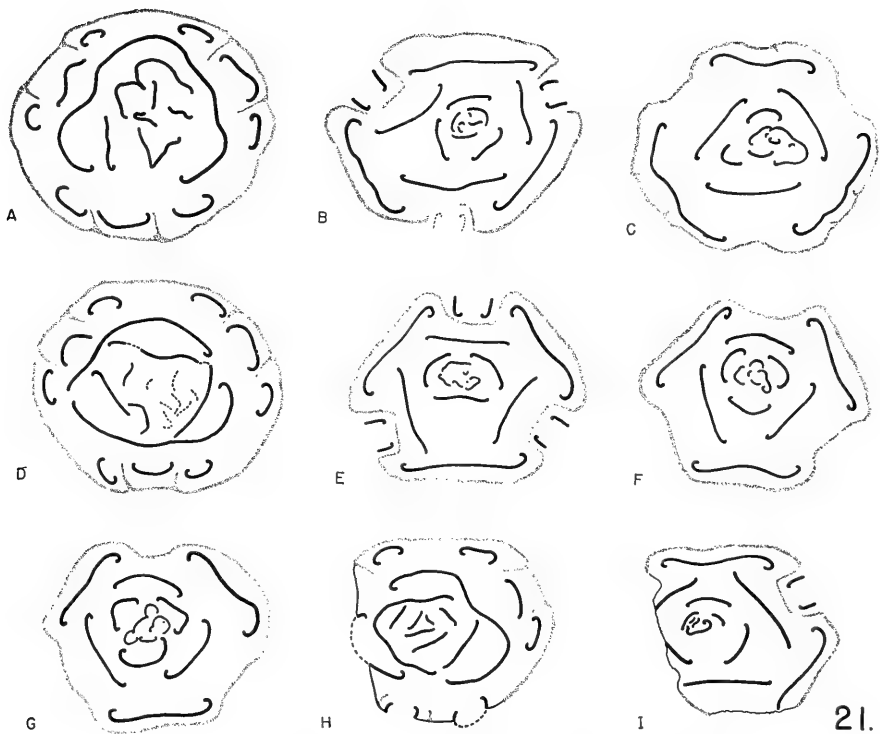


FIG. 21. Specimen V. Diagrammatic cross-section (A-I) of specimen V at successively higher levels. Compare diagram G with fig. 52. See text for full explanation. Specimen 2609.

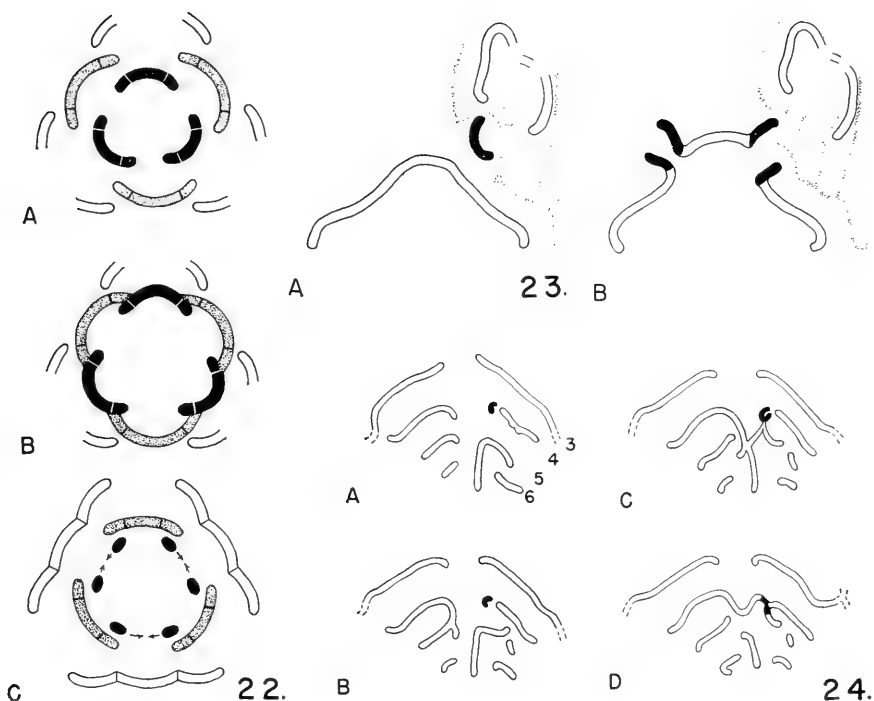
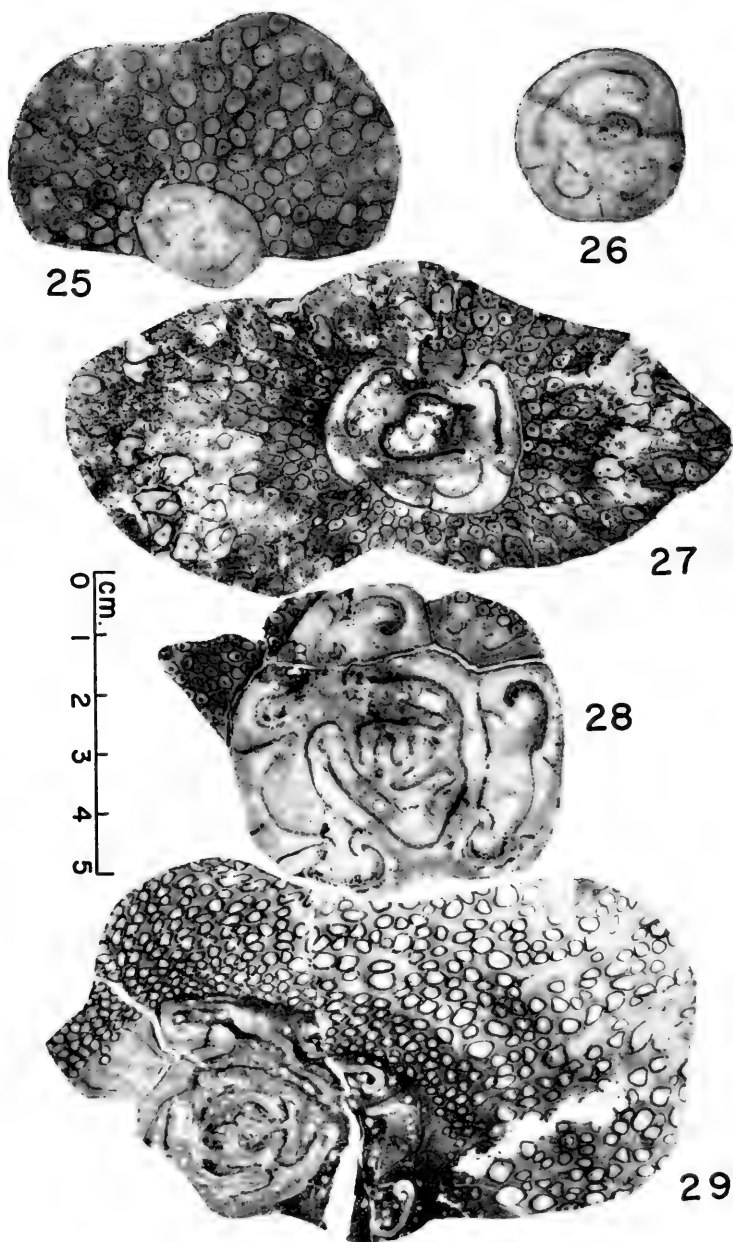


FIG. 22. Specimen V. Diagrammatic cross-section (A-C), reconstructing the manner in which leaf traces are given off from an internal cycle of specimen V. White and black lines on appropriate cycles designate cauline and potential leaf trace material. The most internal cycle is diagrammed in solid black, the next outer one is stippled, and the most external one depicted here is unshaded. Arrows indicate the directions in which strands will migrate at higher levels. See text for full explanation. Specimen 2609.

FIG. 23. *Psaronius blicklei*. Diagrammatic cross-sections (A-B) of a portion of a stem. B is at a higher level than A. See text for full explanation. Contributions from the peripheral cauline bundle to the leaf trace and cauline bundles of next inner cycle are diagrammed in solid black, all other vascular tissue is unshaded. Sclerenchyma is stippled. A—C.B. 2413b bot. #1; B—C.B. 2413c top. #1.

FIG. 24. *Psaronius blicklei*. Transverse section of a portion of a stem at successively higher levels (A-D). See text for full explanation. Contribution from cycle 4 to the next inner cycle and to a leaf trace is diagrammed in solid black. All other vascular tissue is unshaded. Cycles are consecutively numbered from the outside toward the center. C.B. 2842e bot., A—#1, B—#14, C—#16, D—#17.



FIGS. 25-29. *Psaronius blicklei* sp. nov.

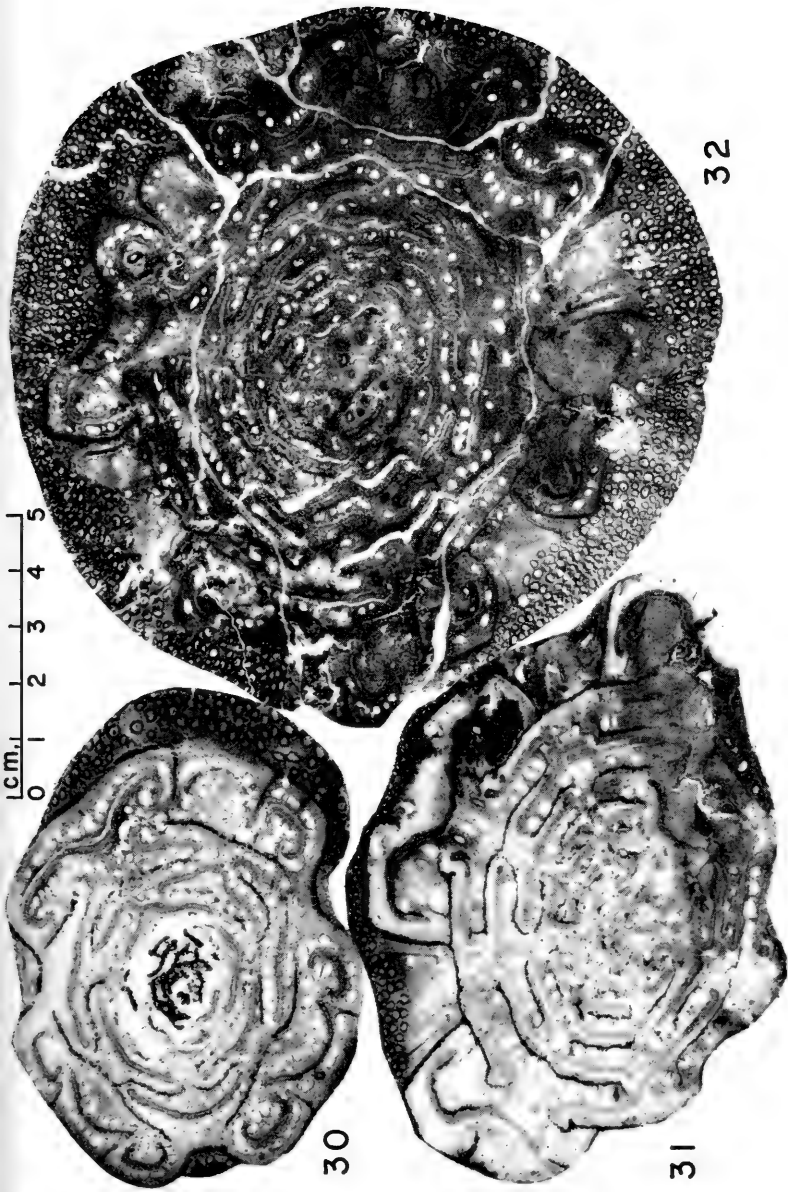
FIG. 25. Transverse section of specimen A. Washington University C.B. 108a top #6.

FIG. 26. Transverse section of specimen A at a higher level. Note most central strand representing cycle 3. Washington University C.B. 108g top #1.

FIG. 27. Transverse section of specimen B. C.B. 2841a top #4.

FIG. 28. Transverse section of specimen C. C.B. 196c top #3.

FIG. 29. Transverse section of specimen D. C.B. 2844e bot. #1.



Figs. 30-32 *Psaronius blicklet* sp. nov.

FIG. 30. Transverse section of specimen E. C.B. 2789a top #1.

FIG. 31. Transverse section of specimen F. C.B. 2842c top #1.

FIG. 32. Transverse section of specimen G. C.B. 2680d top #2.

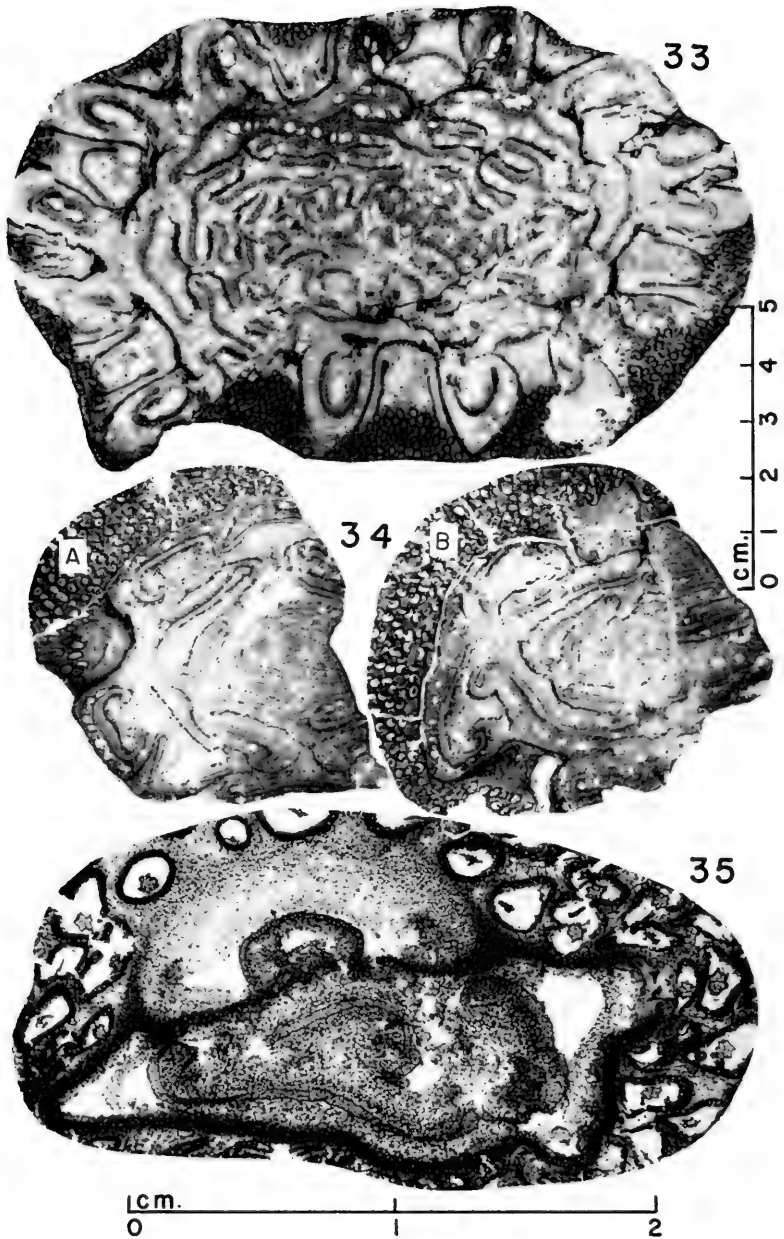
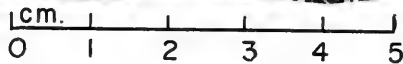


FIG. 33. *Psaronius blicklei* sp. nov. Transverse section of specimen H. C.B. 2681e bot. #1.

FIG. 34. Stem cross-sections of *Psaronius blicklei*, showing a lower level of the specimen (A—C.B. 2682b top. #1) with spiral phyllotaxy and a higher level (B—C.B. 2682g top #1) with whorled frond arrangement. Specimen I.

FIG. 35. *Psaronius melanedrus* sp. nov. Transverse section of specimen J. Note proliferation from leaf base ground parenchyma forming tissue about inner roots. University of Minnesota C.B. 35c (1) bot. #1.



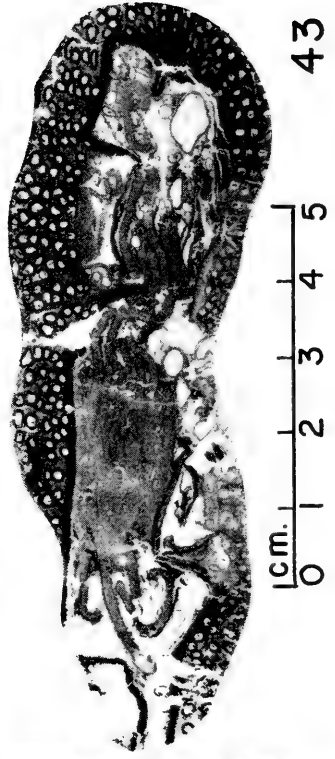
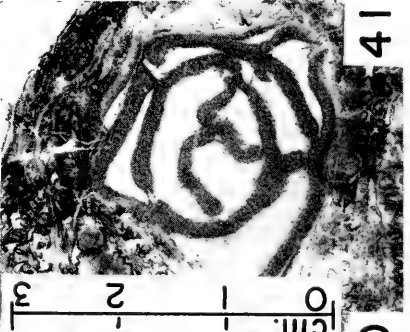
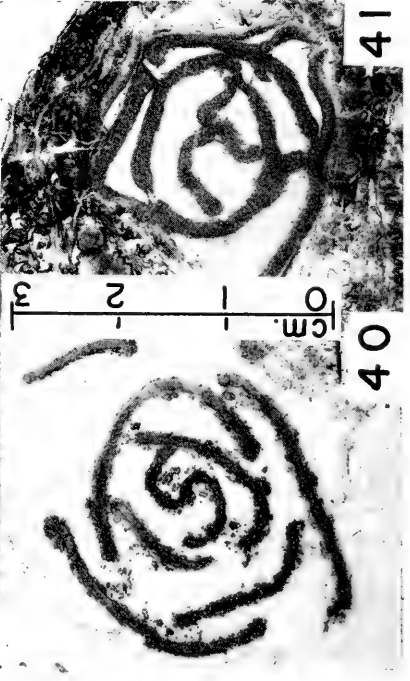
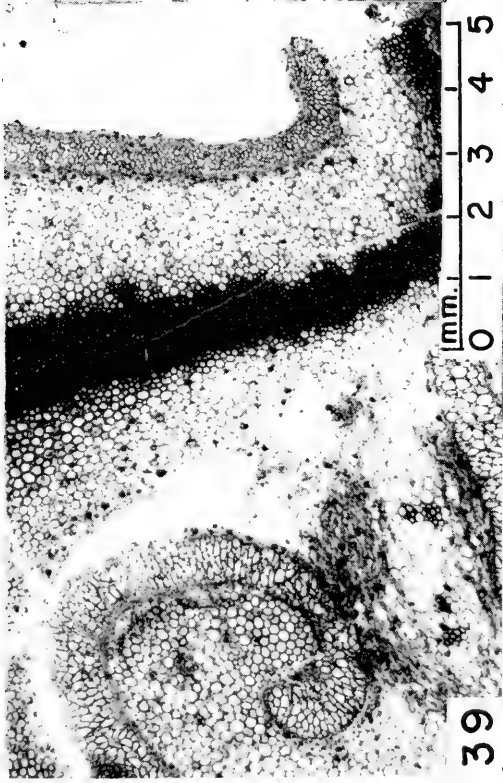


FIGS. 36-38. *Psaronius melanedrus* sp. nov.

FIG. 36. Transverse section of specimen K. Note cells of fundamental tissue of stem have proliferated through the slightly discontinuous sclerenchyma sheath shown at the top of the photograph. Washington University C.B. 698c bot. #4.

FIG. 37. Transverse section of specimen L. C.B. 1539f top #1.

FIG. 38. Transverse section of specimen M. Note configuration of leaf bases. Washington University C.B. 697c top #2.



FIGS. 39-43. *Psaronius melanedrus* sp. nov.

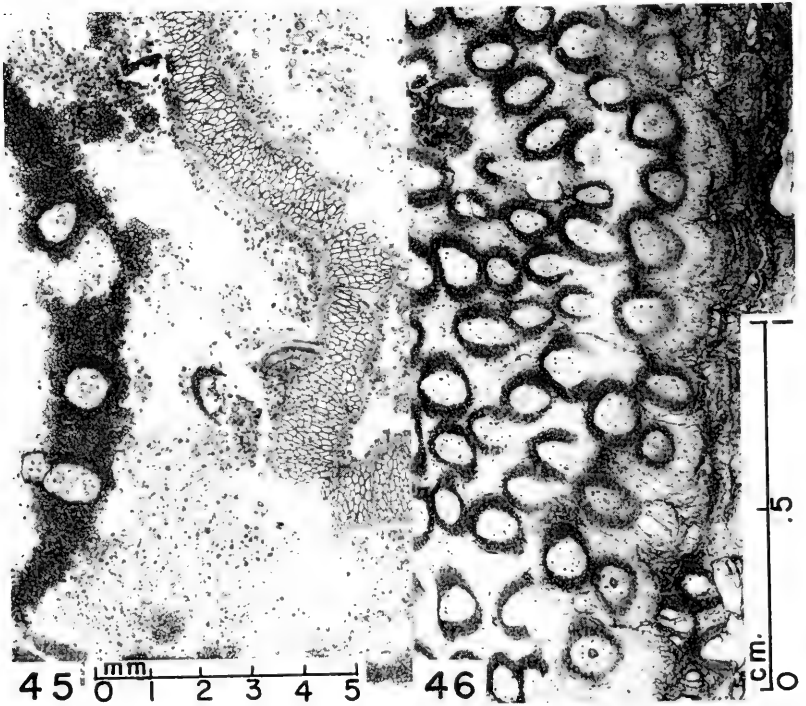
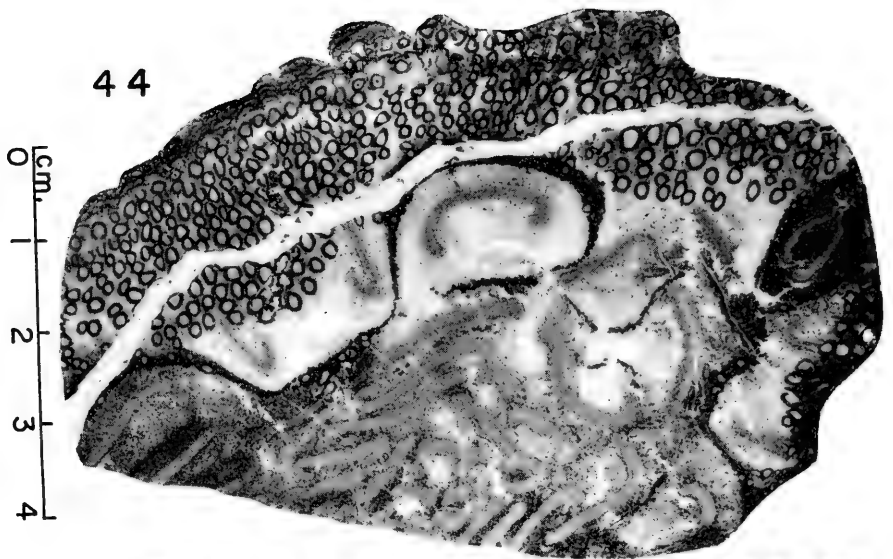
FIG. 39. Transverse section of a portion of specimen M, showing relative thicknesses and tracheid diameters of a leaf trace (right) and a peripheral cauline bundle (left). Note heavy sclerenchyma sheath and presence of tannin-like deposits in certain of the parenchyma cells. C.B. 697f top #1.

FIG. 40. Transverse section of the central portion of the stele of specimen N, Illinois Geological Survey C.B. 803a bot. #1.

FIG. 41. Transverse section of stele of specimen O. C.B. 1254e bot. #1.

FIG. 42. Transverse section of stele of specimen P. C.B. 2111a (2) top. #1.

FIG. 43. Transverse section of specimen Q. C.B. 3066d bot. #1.

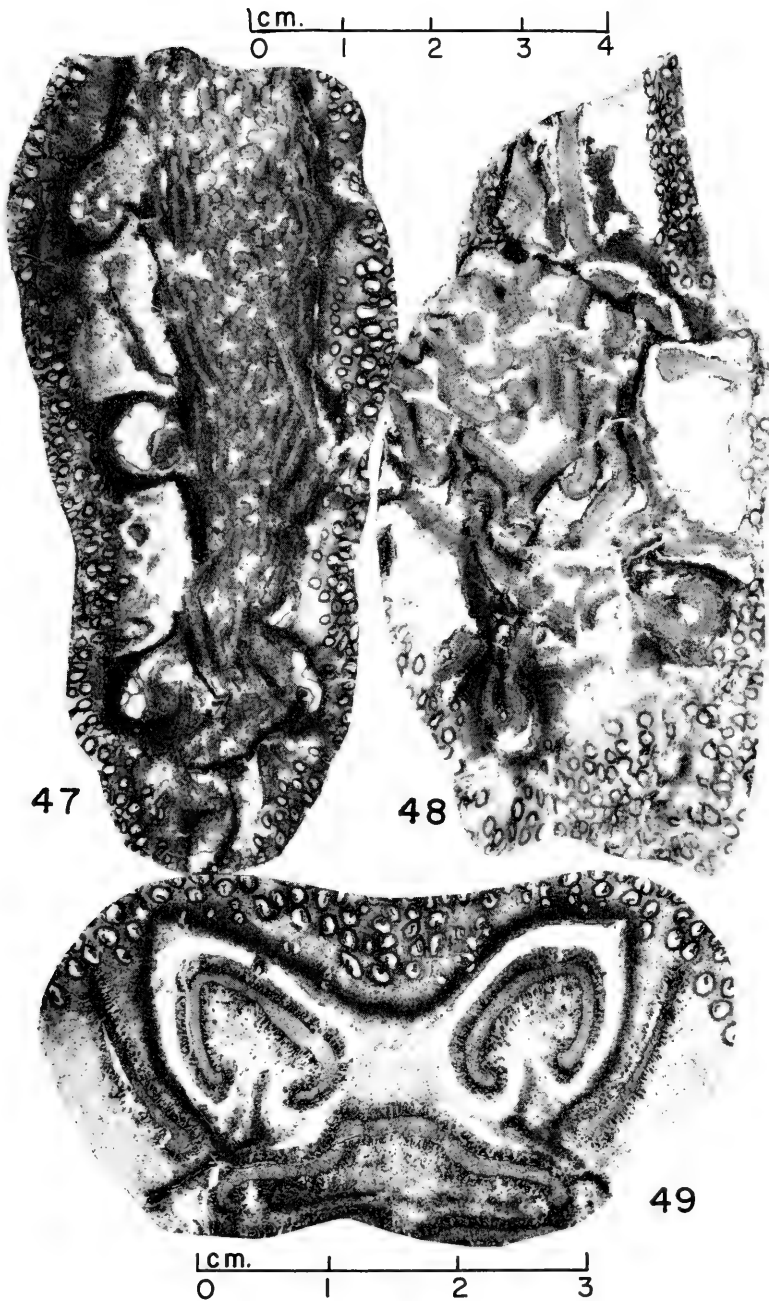


FIGS. 44-46. *Psaronius chasei* sp. nov.

FIG. 44. Transverse section of specimen R. C.B. 1221g bot. #64.

FIG. 45. Portion of a transverse section of specimen R showing an adventitious root trace in connection with the second cycle. Four other roots may also be observed in the sclerenchyma sheath on the adaxial side of the leaf base. C.B. 1221f top #33.

FIG. 46. Portion of a transverse section of specimen R, showing the secondary parenchyma exceeding in radial extent the most externally placed root. C.B. 1221g bot. #64.



FIGS. 47-49. *Psaronius Chasei* (?) sp. nov.

FIG. 47. Transverse section of specimen in Illinois Geological Survey C.B. 140a #2.

FIG. 48. Transverse section of specimen S. C.B. 1700d top #1.

FIG. 49. Transverse section of a portion of a specimen in C.B. 1607a top #1.

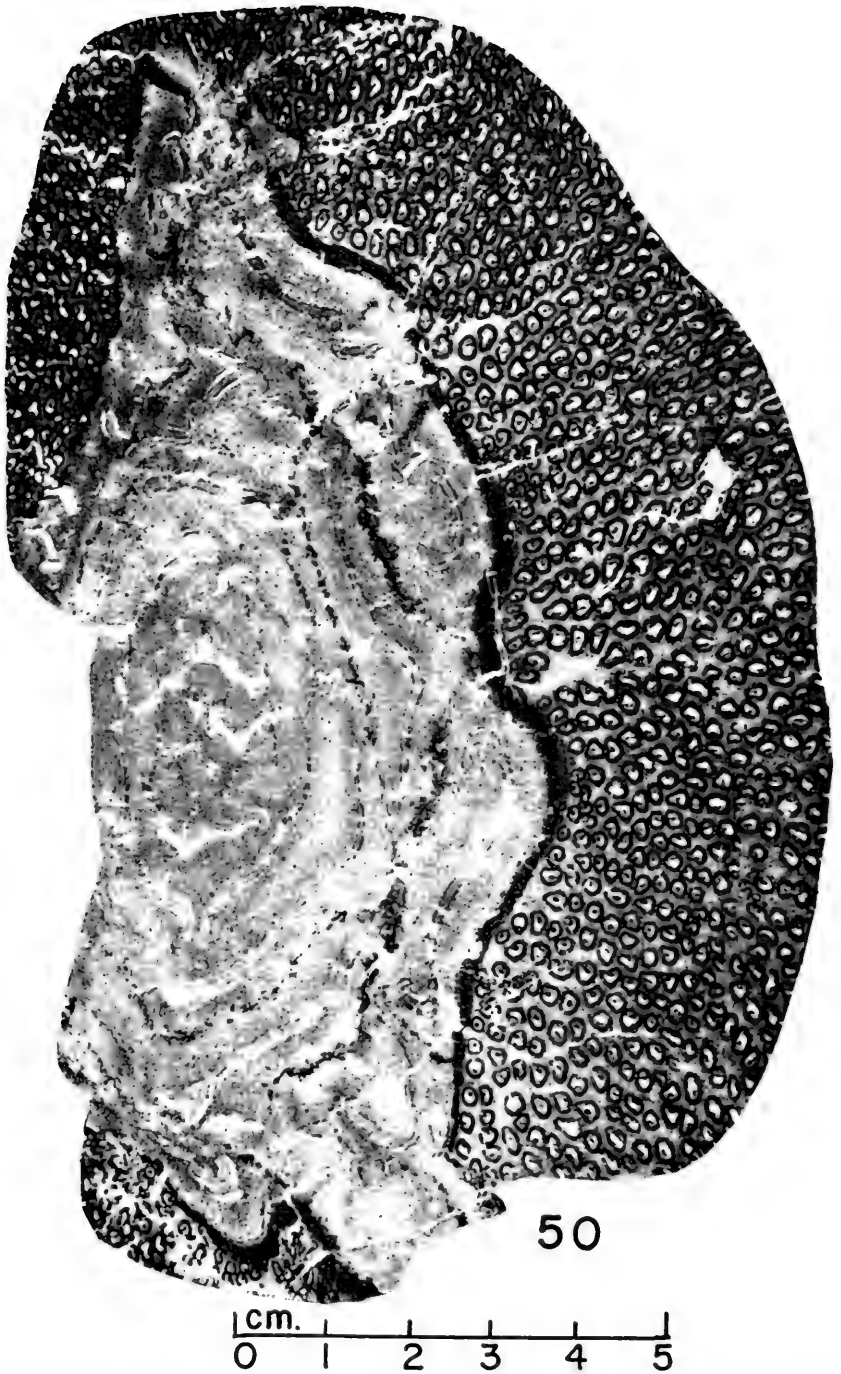
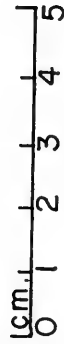


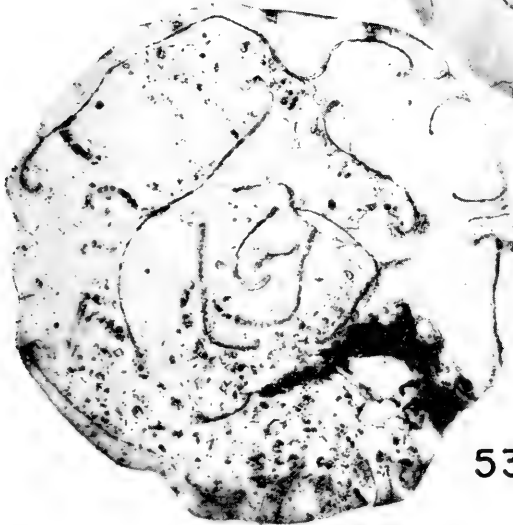
FIG. 50. Transverse section of specimen T. Illinois Geological Survey C.B. 51d bot. #1.



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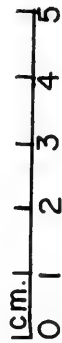


FIG. 51. Transverse section of stem of specimen U. Specimen 2608a bot. #1.

FIG. 52. Transverse section of specimen V. Specimen 2609g top #1.

FIG. 53. Transverse section of specimen W. Specimen 728a top #1.

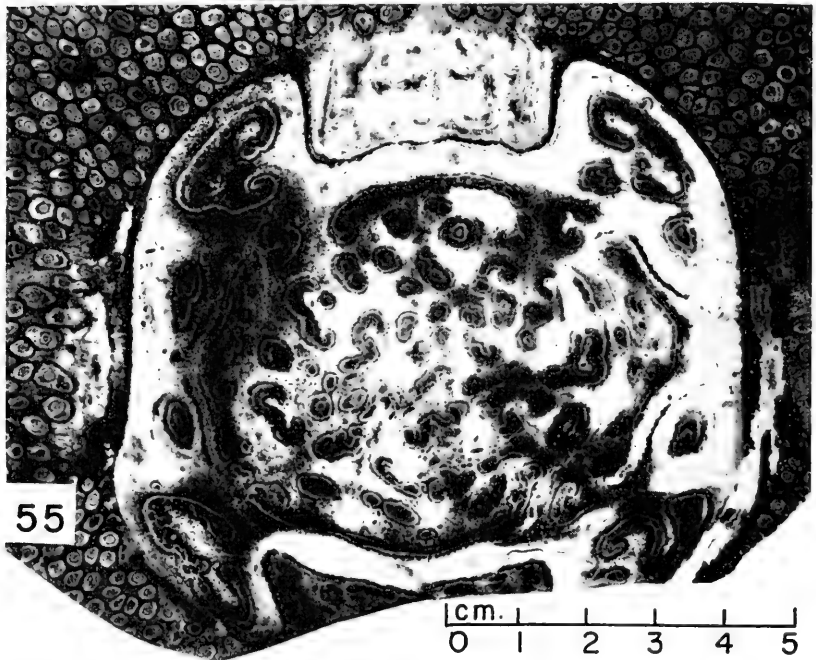


FIG. 54. Transverse section of *Psaronius brasiliensis*. Specimen at the Divisão de Geologia e Mineralogia, 404 Avenida Pasteur, Praia Vermelha, Rio de Janeiro, Brazil. Since Fig. 54 is of the lower face of the piece, the negative was reversed in printing to make the picture correspond with Fig. 55, the upper face.

FIG. 55. Transverse section of *Psaronius brasiliensis* at a higher level.



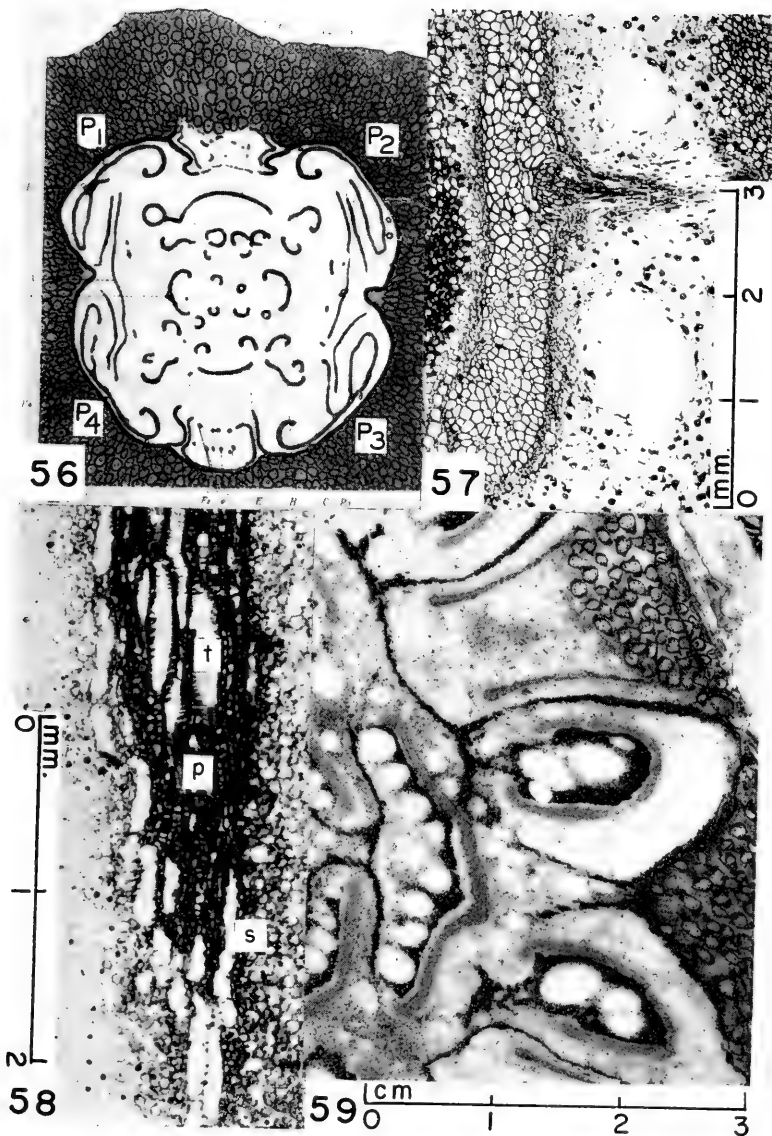


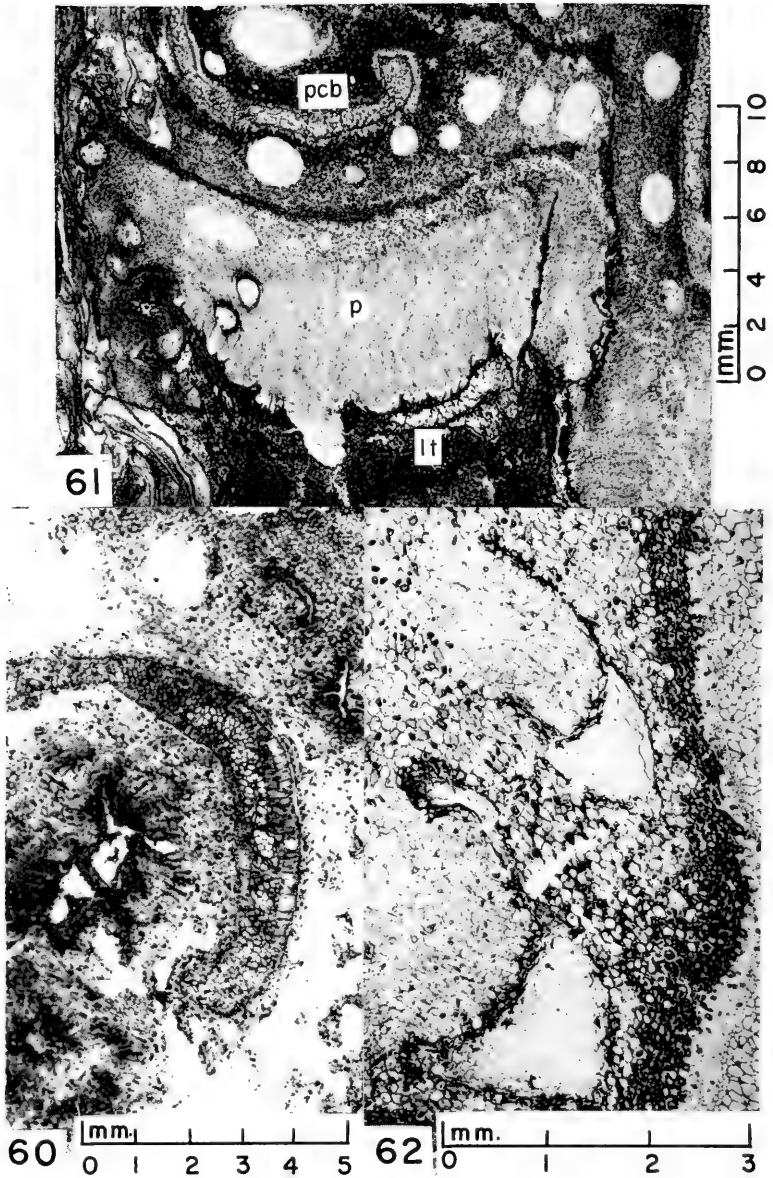
FIG. 56. Transverse section of *Psaronius brasiliensis*. After Zeiller (1890).

FIGS. 57-59 *Psaronius blicklei*

FIG. 57. Transverse section of a portion of *Psaronius blicklei*, showing an adventitious root trace in connection with a peripheral cauline bundle. Note sieve cells about xylem strand, lacunae, and tannin-like deposits in cells of fundamental tissue. C.B. 2681k bot. #1.

FIG. 58. Longitudinal section showing vascular and fundamental tissue. *s*—sieve cells; *t*—tracheids; *p*—parenchyma. C.B. 2413a edge #3.

FIG. 59. Transverse section of a portion of a stem. Note lacunae and configuration of sclerenchyma. C.B. 2681a top #2.

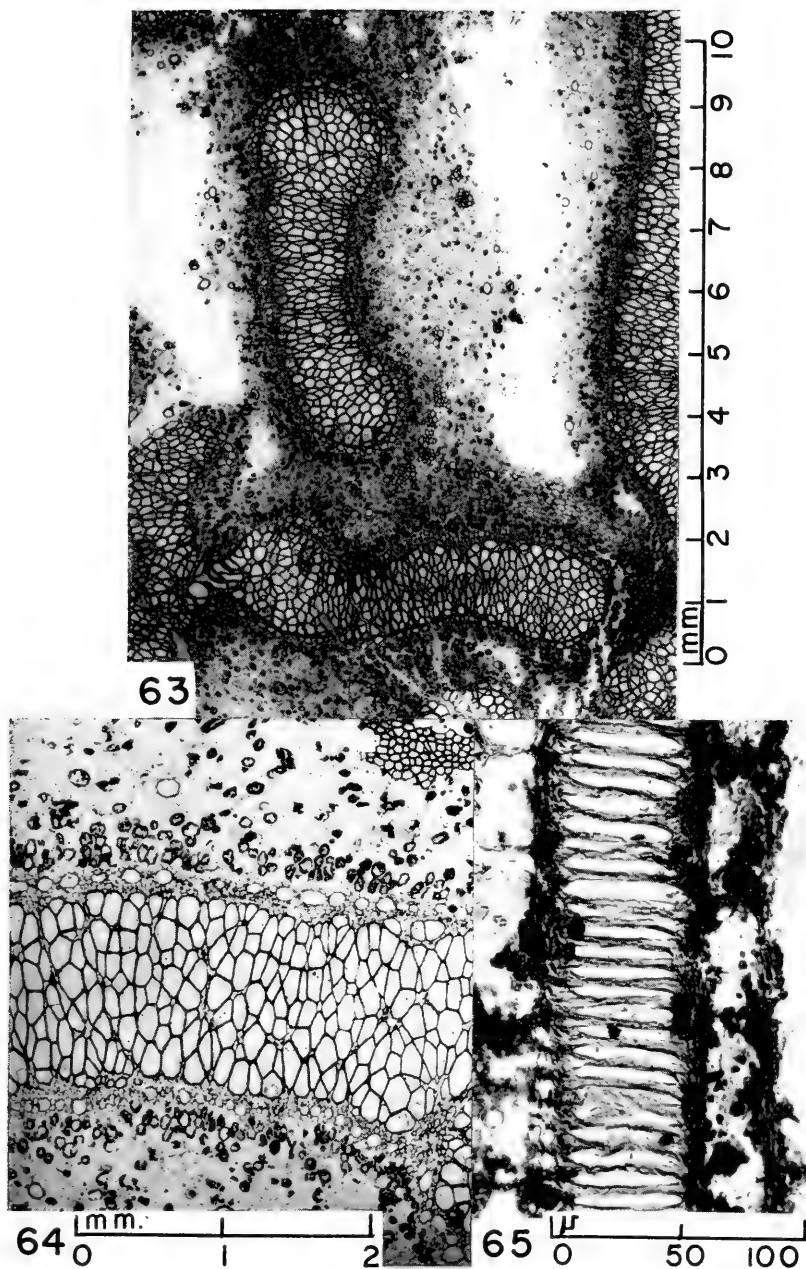


FIGS. 60-62 *Psaronius blicklei* sp. nov.

FIG. 60. Transverse section of a portion of a stem showing secondary parenchyma around a peripheral cauline bundle and in the fundamental tissue. C.B. 2680h top #2.

FIG. 61. Portion of a transverse section showing leaf trace distorted by growth of secondary parenchyma. *lt*—leaf trace; *p*—parenchyma; *pcb*—peripheral cauline bundle. C.B. 2371c bot. #2.

FIG. 62. Transverse section of a portion of *Psaronius blicklei*, showing growth of secondary parenchyma into lacunae of the stem. C.B. 2371a bot. #1.



FIGS. 63-65 *Psaronius chasei*

FIG. 63. Transverse section of a portion of *Psaronius chasei*. Note sieve cells around xylem strands. C.B. 1221f top #19.

FIG. 64. Portion of a vascular bundle greatly enlarged. C.B. 1221g bot. #22.

FIG. 65. Longitudinal section of a portion of a metaxylem tracheid, showing scalari-form secondary thickenings. C.B. 1221g edge #1.

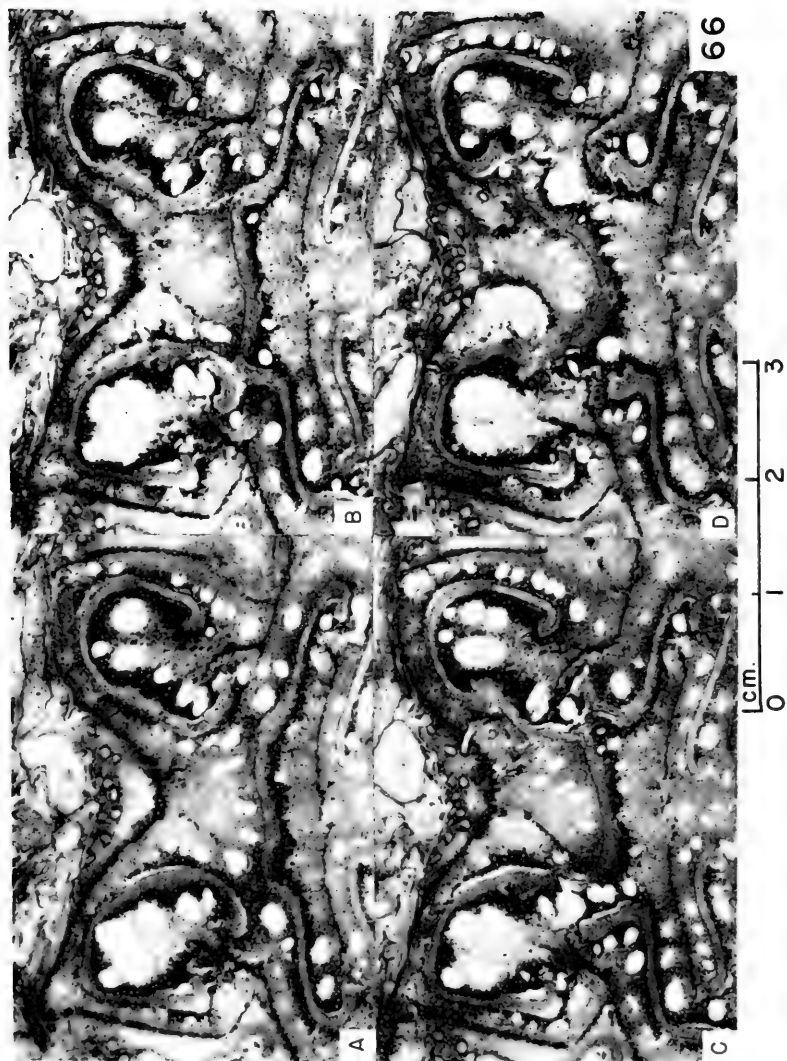
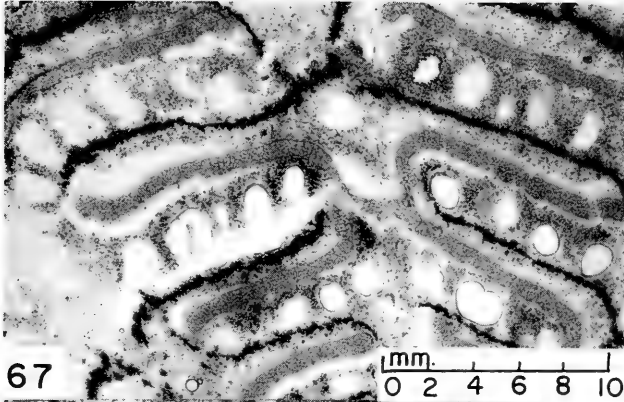
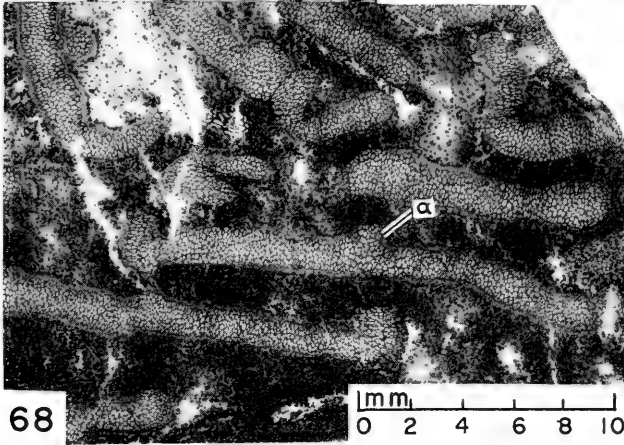


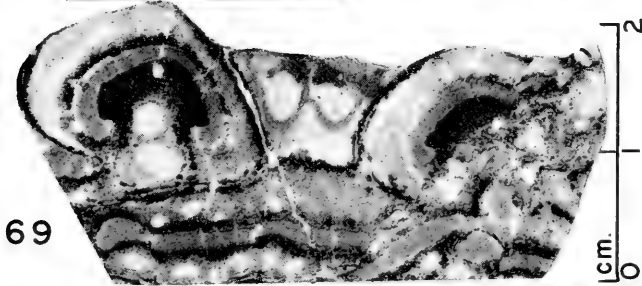
FIG. 66. Series of transverse sections at successively higher levels (A-D) of a specimen of *Psaronius blattkei*, showing contribution of peripheral cauline bundles to a leaf trace and to the next inner cycle. See text for full explanation. A—C.B. 2371d top #1; B—C.B. 2371d top #2; C—C.B. 2371d top #4; D—C.B. 2371d top #5.



67



68



69

FIG. 67. Transverse section of a portion of *Psaronius blicklei*, showing a leaf trace attached to two cycles at the same level. Note lacunae, sclerenchyma bands, and isolated sclerenchyma strands. C.B. 2842e bot. #71.

FIG. 68. Transverse section of a portion of *Psaronius chasei*. At *a* a small strand of vascular tissue is projecting from the surface of a cauline bundle. See text for full information, C.B. 1221h bot. #24.

FIG. 69. *Psaronius blicklei*. Transverse section of a portion of a stem showing leaf trace characteristics. Illinois Geological Survey C.B. 371g top #1.

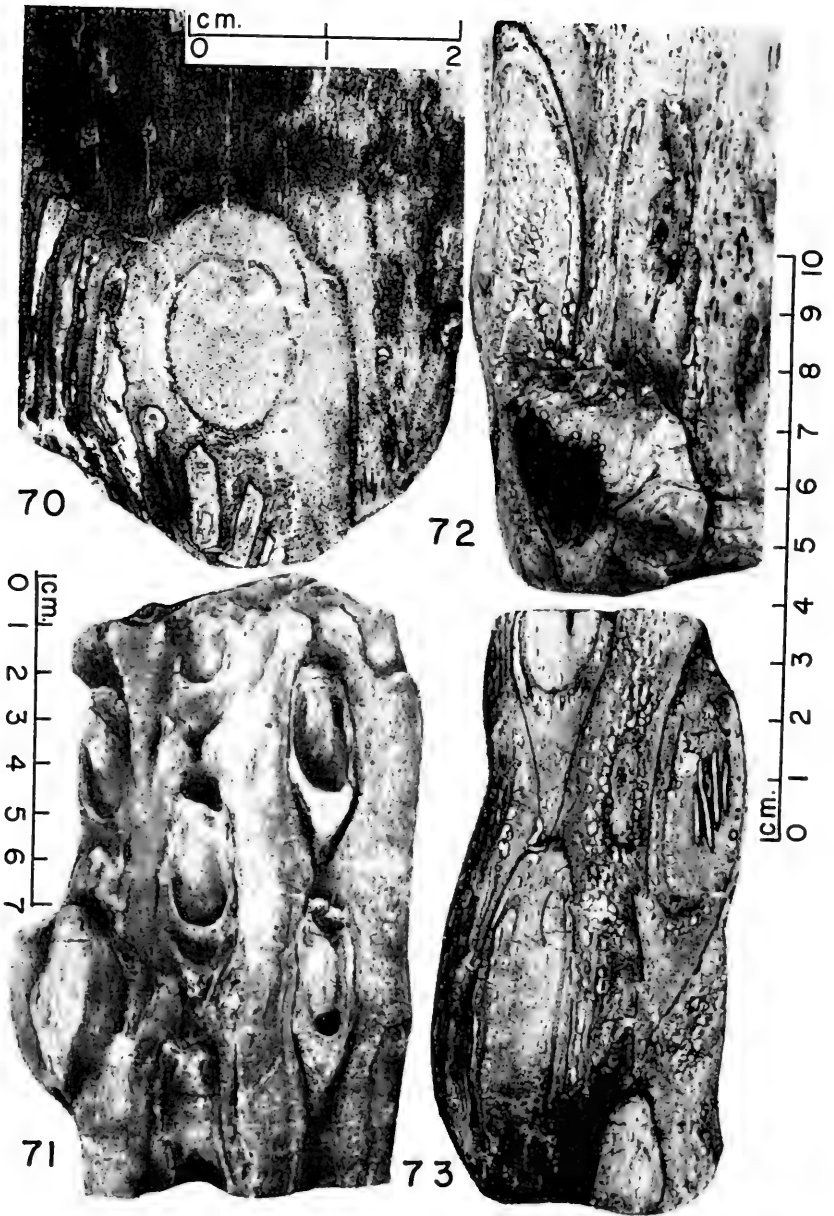
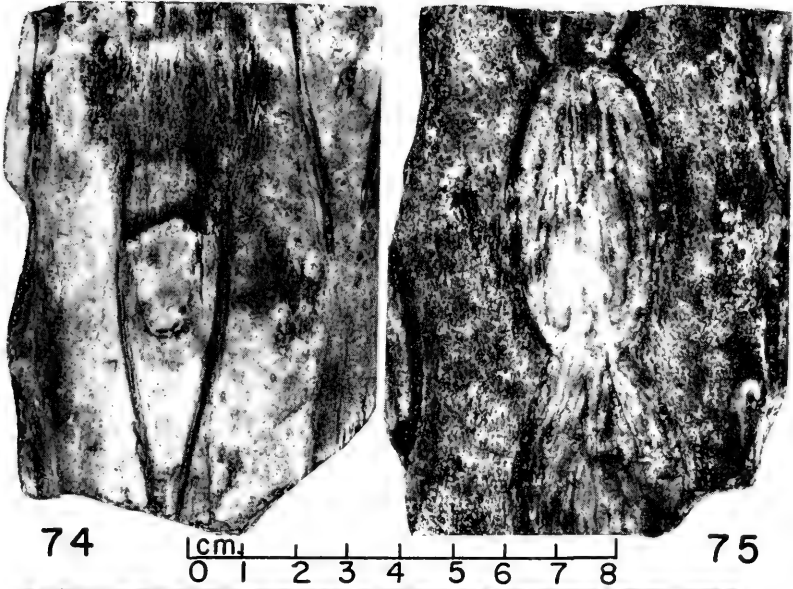


FIG. 70. *Psaronius blicklei*. Surface of a stem showing leaf trace characteristics. Note points of exit of adventitious roots from stem above leaf scar and roots over lower portion of leaf scar. C.B. 196d (3).

FIG. 71. *Psaronius* sp. Weathered surface of a stem. Specimen 2625.

FIG. 72. *Psaronius blicklei*. Surface of a stem showing leaf base characteristics from the side. Note lacunae in fundamental tissue. C.B. 2777b.

FIG. 73. *Psaronius blicklei*. Surface of a slightly weathered stem showing leaf scar characteristics and lacunae. Note roots over leaf scar at right. C.B. 2777b.

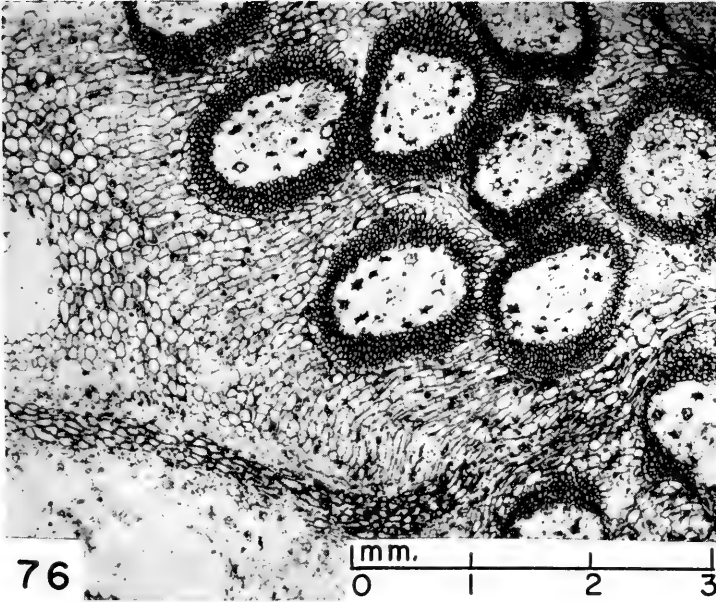


74

cm

0 1 2 3 4 5 6 7 8

75



76

mm.

0 1 2 3

FIG. 74. *Psaronius giffordii*. Surface of stem showing leaf scar characteristics. Specimen 2612.

FIG. 75. *Psaronius* sp. Surface of stem showing leaf scar characteristics. Specimen 2622.

FIG. 76. *Psaronius blicklei*. Transverse section of a portion of stem and inner root zone at the position of a leaf base. Note proliferation of fundamental cells of the leaf base and tannin-like deposits in certain of the cells of the roots. C.B. 2681k bot. #1.

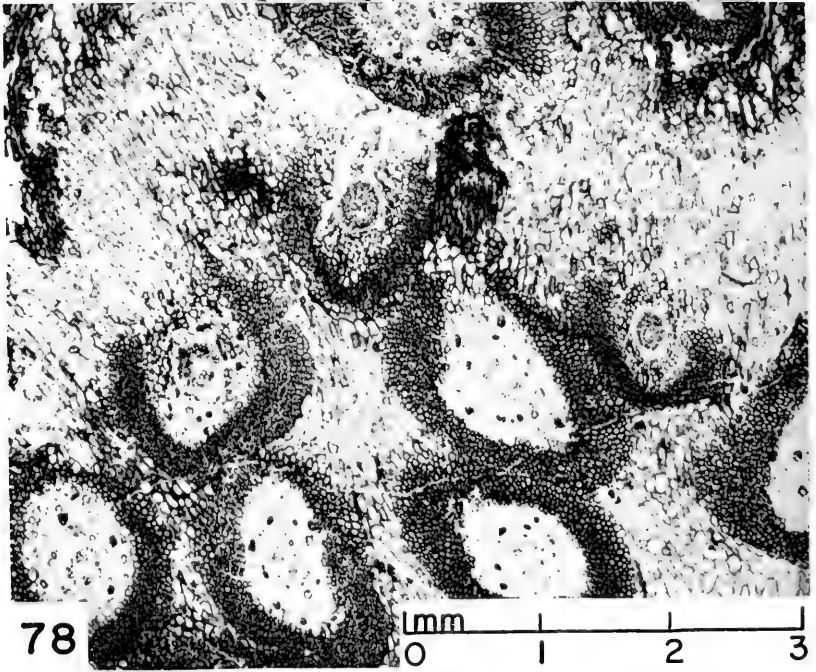
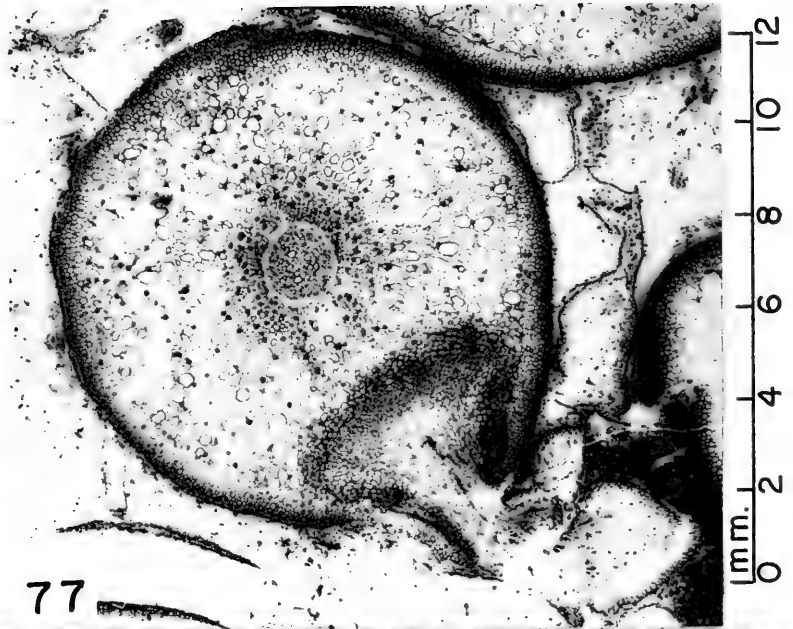


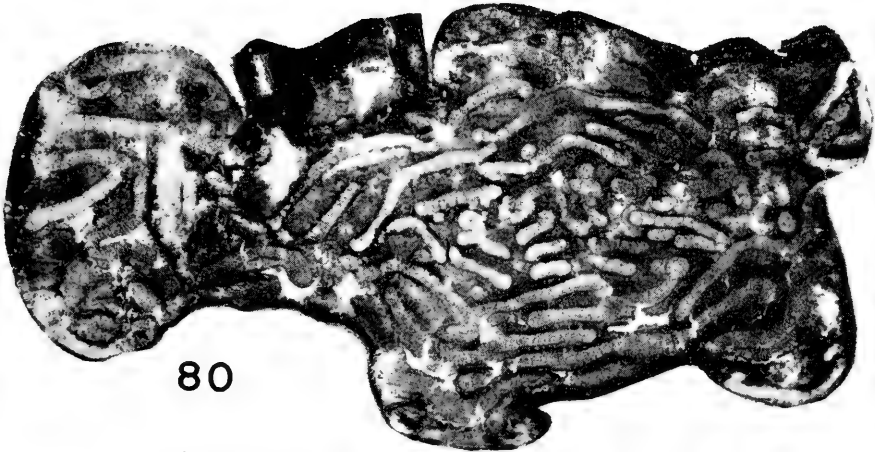
FIG. 77. *Psaronius blicklei*. Transverse section of a free root which is branching. Washington University C.B. 108c bot. #3.

FIG. 78. *Psaronius chasei*. Transverse section of the inner root zone showing proliferation of parenchyma cells. C.B. 1221 top #47.





79



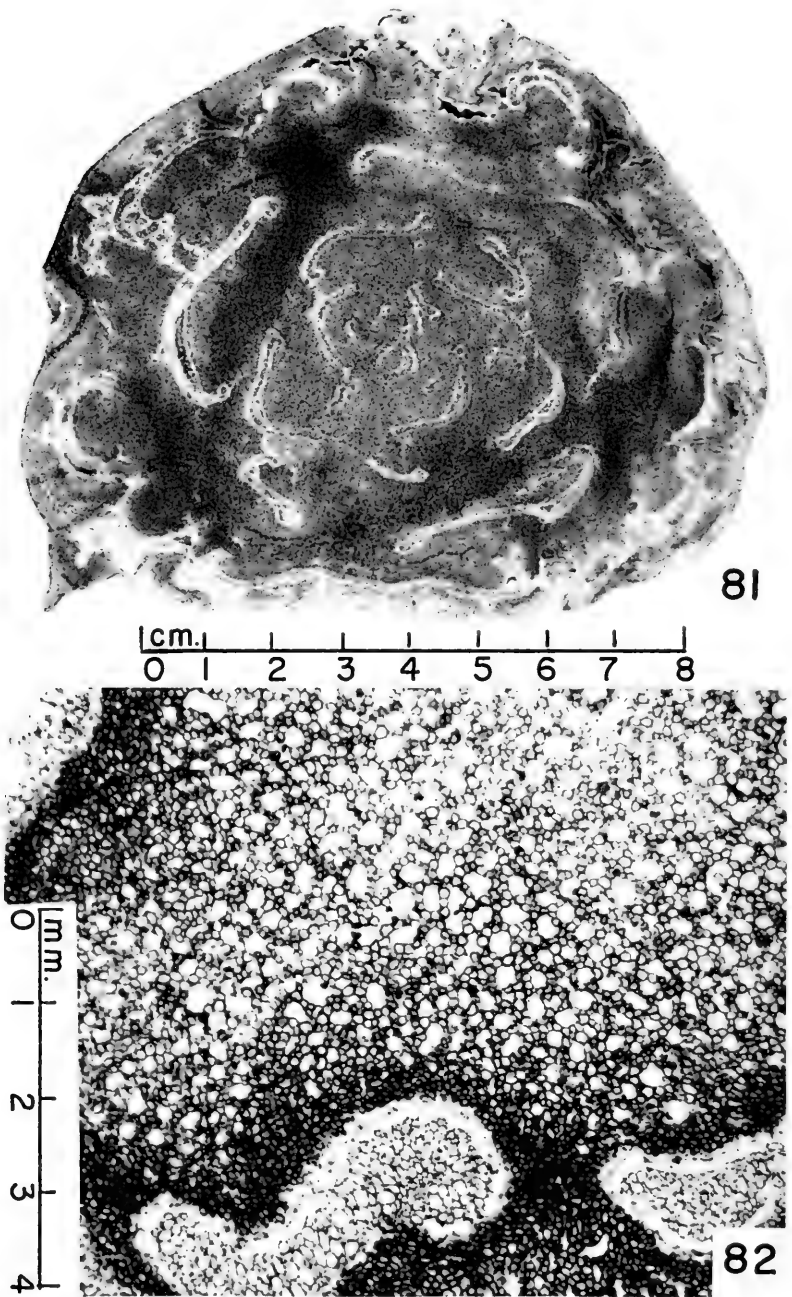
80



FIGS. 79, 80. *Psaronius giffordii*

FIG. 79. Transverse section of stem. Photograph of slide of specimen 5, University of Chicago Collection.

FIG. 80. Transverse section of stem. Photograph of slide of specimen 3, University of Chicago Collection.



FIGS. 81, 82. *Psaronius pertusus* Blicke, sp. nov.

FIG. 81. Transverse section of a stem. Specimen B—202 in the Ohio University Museum Collection.

FIG. 82. Portion of a transverse section of a stem showing fundamental tissue in detail. Illinois Geological Survey C.B. 147b top #1.

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