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BASAL STEM ANATOMY OF PSARONIUS¹

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A B S T R A C T

The basal stem anatomy of three young sporophytes of *Psaronius* from the Middle Pennsylvanian of Kansas and Illinois is described. The origin of the second stelar cycle is demonstrated in the transition from a simple, amphiphloic siphonostele to a dicyclic dictyostele. Petioles with C-shaped vascular strands are attached to the stem in a one-third phyllotaxy. A root mantle is lacking. Basal stem anatomy of *Psaronius* is compared with that of living genera of the Marattiaceae.

ONTOGENETIC approaches to the study of Pennsylvanian-age plants have greatly increased our understanding of the arborescent lycopods, calamites, seed ferns, and tree ferns. Although some fossil apices have been described, the fragments usually represent more mature parts of the plant, and in many cases secondary growth has further modified the plant body. These studies have been reviewed in detail by Delevoryas (1964). For the first time small, young sporophytes of *Psaronius*, a marattiaceous tree fern, have been discovered with attached petioles in Pennsylvanian-age coal balls from Illinois and Kansas. Some of the earliest ontogenetic stages of the vascular system are described below.

MATERIALS AND METHODS—Two specimens of young *Psaronius* sporophytes were found in coal balls no. 5620; and no. 6378 from the Sahara Coal Co. no. 6 Mine, Herrin (Illinois no. 6) coal of the Kewanee Group (Kosanke et al., 1960). The collection locality is about 4 miles NW of Carrier Mills, Ill. (Sec. 30, T9S, R4E, Harrisburg Quadrangle, Williamson Co.). A third specimen, no. 1161, was collected by Dr. G. A. Leisman from the Mackie-Clemens no. 23 Mine, Bevier Coal, Cherokee Group (Abernathy, 1946). The mine is located 3 miles NE of Frontenac, Kan. (Sec. 21, T29S, R25E, Joplin Quadrangle, Crawford Co.). Both coals are Middle Pennsylvanian in age, and the Herrin coal is the younger of the two (Moore et al., 1944).

Clay models and camera lucida drawings were used as aids in the reconstruction of the xylary system. Slides 1995-2053 (no. 6378), 2054-2057 (no. 5620) and 2058-2069 (no. 1161) used in the study are deposited in the Paleobotanical col-

lections of the Botany Department (Morrill Hall), University of Illinois, Urbana.

GENERAL DESCRIPTION—The longest specimen (no. 6378) exhibits a transition from a closed, simple siphonostele to a dicyclic dictyostele through a distance of approximately 4.5 cm in which it bears five distinct leaf traces and seven roots. The diameter increases from 1.5 mm at the base to about 5 mm at the upper end (Fig. 3-15). A schematic restoration of the curved specimen with tissues intact is shown in Fig. 1a, and the straightened xylary portion is reconstructed in Fig. 2. The shortest stem (no. 5620) of *Psaronius* is 4-6 mm in length and exhibits a simple siphonostele about 1 mm in diam at the lowest preserved level. The stem bears one leaf trace and is quite similar in anatomy and method of trace formation to the longer, more informative specimen at levels shown in Fig. 5, 8. A third specimen (no. 1161), about 3 cm long, is dicyclic and bears numerous scales (Fig. 16-20). All of the stems lacked a root mantle and were not preserved at the very base.

ANATOMY—The vascular system of two stems is a radially symmetrical endarch siphonostele at the lowest preserved levels. Scalariform tracheids were observed in roots, leaf traces and in stem sections where curvature of the specimen resulted in longitudinal sections of the xylem (Fig. 6). In the stem tracheids range from 12 to 85 μ in diam. Cortical cells range from 150 μ down to 25 μ in diam in a centrifugal direction, and some cell lumens are filled with amber to black contents. Elongate cells of the outer cortex are up to 580 μ long (Fig. 10, arrow) and cells of the inner cortex and pith are nearly isodiametric. In some areas flattened cells of the epidermis are preserved (Fig. 3, 5, top).

Adventitious roots in the stem cortex are haplostelic to actinostelic and tetrarch to hexarch. The outer cortex is composed of sclerenchyma (Fig. 7, 9), and the inner cortex is not preserved.

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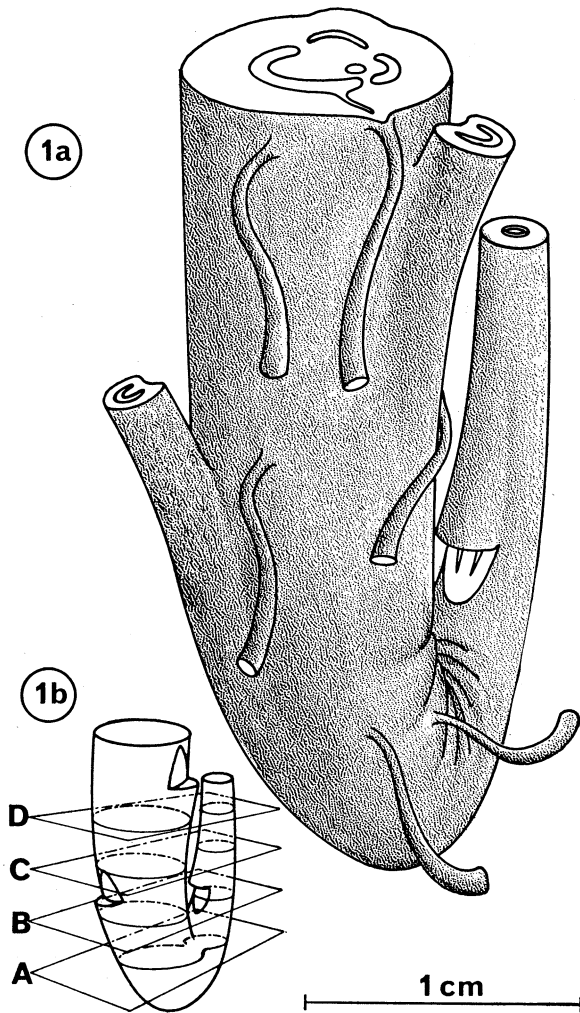


Fig. 1a-b.—a. Reconstruction of a lower portion of the stem of *Psaronius* sp.—b. Schematic drawing of 1a showing representative planes of sectioning; A-D are shown in Fig. 10-13, respectively. Reconstruction based on specimen 6378.

Representative sections of the longest stem (no. 6378) are shown at four levels in Fig. 10-13 corresponding to levels A-D in Fig. 1b. Both lower and upper parts of the stem appear in a single section as a result of the strong curvature of the specimen. The diameter of the stele is 0.5 mm at the base of the simple, closed siphonostele and 2.5 mm at the dicyclic level. Basally the xylem is two to four cells thick or about 0.1 mm in radial thickness (Fig. 3) and increases to five or more tracheids at higher levels (Fig. 12).

Leaf trace formation to the first petiole results in an elliptical outline of the xylem in transverse section (Fig. 3). The leaf trace becomes successively loop-like in its separation from the stele and finally departs with an O-shaped vascular strand which is about one-third the diameter

of the stele (Fig. 4, LT). At a higher level in the petiole the vascular strand exhibits a C-shaped configuration (Fig. 11, P) with the xylary arms directed adaxially. The diameter of the petiolar base is slightly smaller than that of the stem. The leaf gap is closed by additional tracheids which appear at the two free edges (Fig. 2c, d),

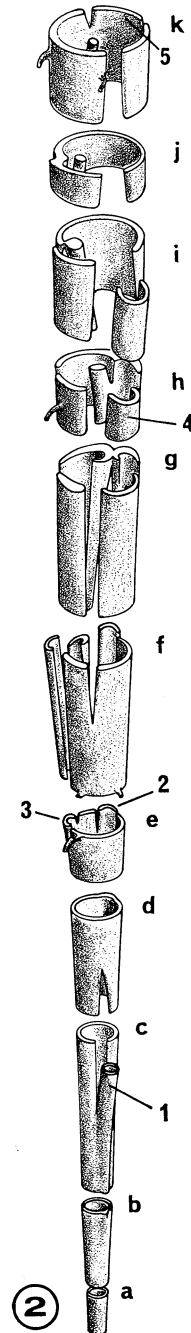
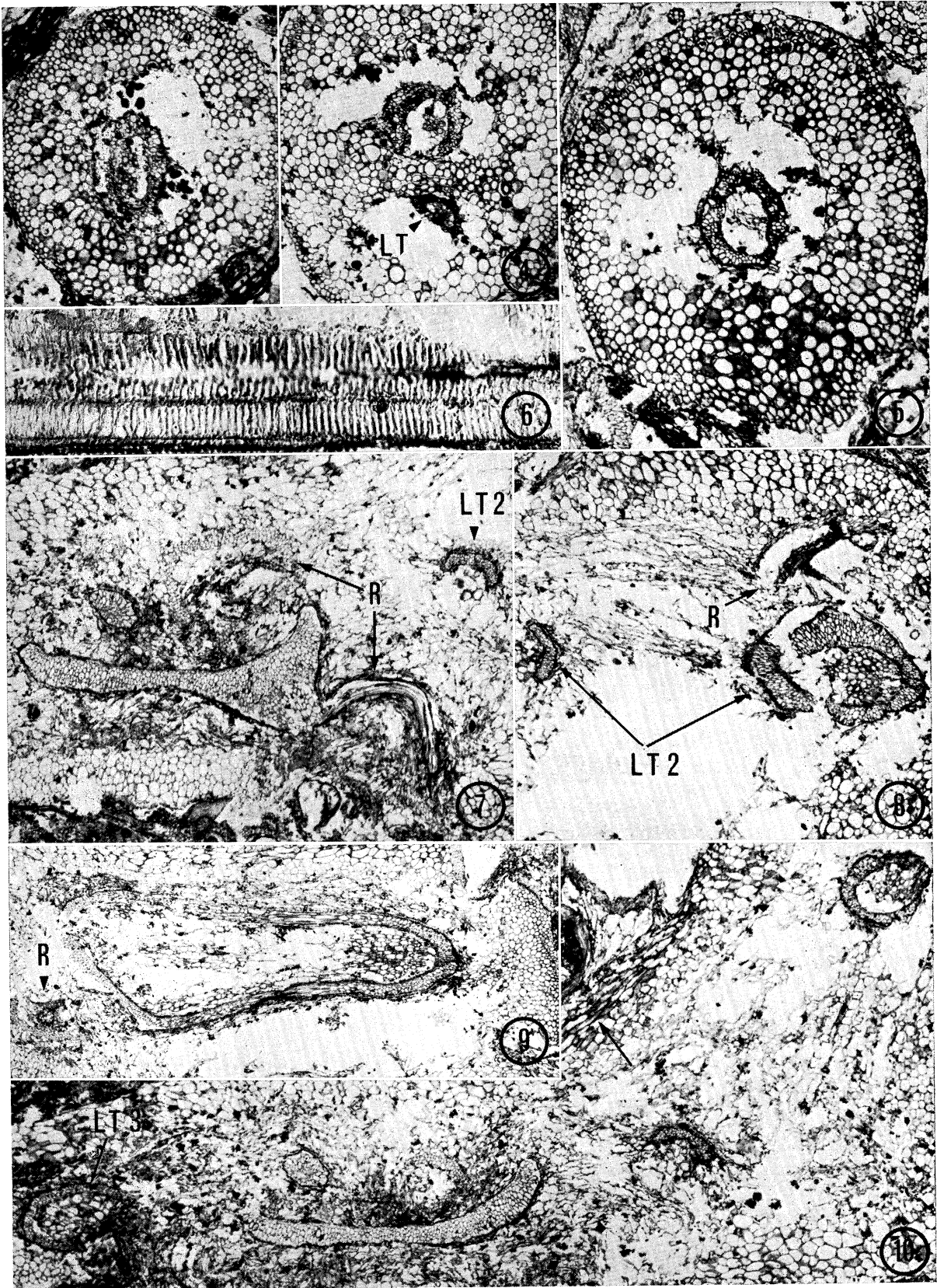


Fig. 2. *Psaronius* sp. Suggested reconstruction of straightened xylary system of stem shown in Fig. 1a separated at levels a-k, 1-5, leaf traces.



and a closed, simple siphonostelic condition is resumed. The next three petioles have C-shaped traces which are successively larger (Fig. 8 LT2, 10 LT3, 13 LT4). The leaf trace to the second petiole is sectioned in two places (Fig. 8 LT2) as a result of the sharp curvature of the specimen at this level.

Closure of the second leaf gap by the marginal addition of tracheids differs in that the convex faces of the inrolled margins join (Fig. 2g, 15), and one of the free edges of the inrolled stele separates and becomes an inner, second cycle (Fig. 12). At this level the protoxylem groups of the inner cycle are at one side corresponding to an endarch position where the strand was connected to the outer cycle.

The third leaf gap, in turn, is closed in a different manner from the preceding ones, and leaf-gap closure is coincident with leaf-trace formation which begins in the inner cycle. The inner cycle occupies a position near the third leaf gap and joins the outer cycle at one edge of the gap (Fig. 2i) and then at the other (Fig. 14). Subsequently, some of the inner portion of the xylem separates above the gap and forms the inner cycle again (Fig. 13). In a similar manner the pathway of the inner cycle can be followed to the edges of the fourth leaf gap, and following closure of the gap, the inner cycle becomes free once again. During the diagonal course from the third to the fourth leaf gap, the protoxylem of the inner cycle becomes centrarch in position as metaxylem cells appear on the face of the inner cycle toward the next leaf gap. The fourth leaf arises above the first, and the incipient trace of the fifth leaf arises directly above the second leaf in a one-third counter-clockwise phyllotaxy.

The third stem fragment has a dicyclic dictyostele and bears three leaf traces in a clockwise spiral. Two petioles are attached to the stem. The lowermost level of the stem corresponds approximately to the highest level of the previously described dicyclic stem; the maximum diameter is 2 mm. The inner cycle attains a maximum diameter of 0.6 mm and changes from a terete strand of tracheids with apparently centrarch maturation (Fig. 16, arrow) to an endarch cycle in which the ground tissue is not preserved (Fig. 18). The spatial relationships and interconnections of the inner and outer cycles are similar to those described for the

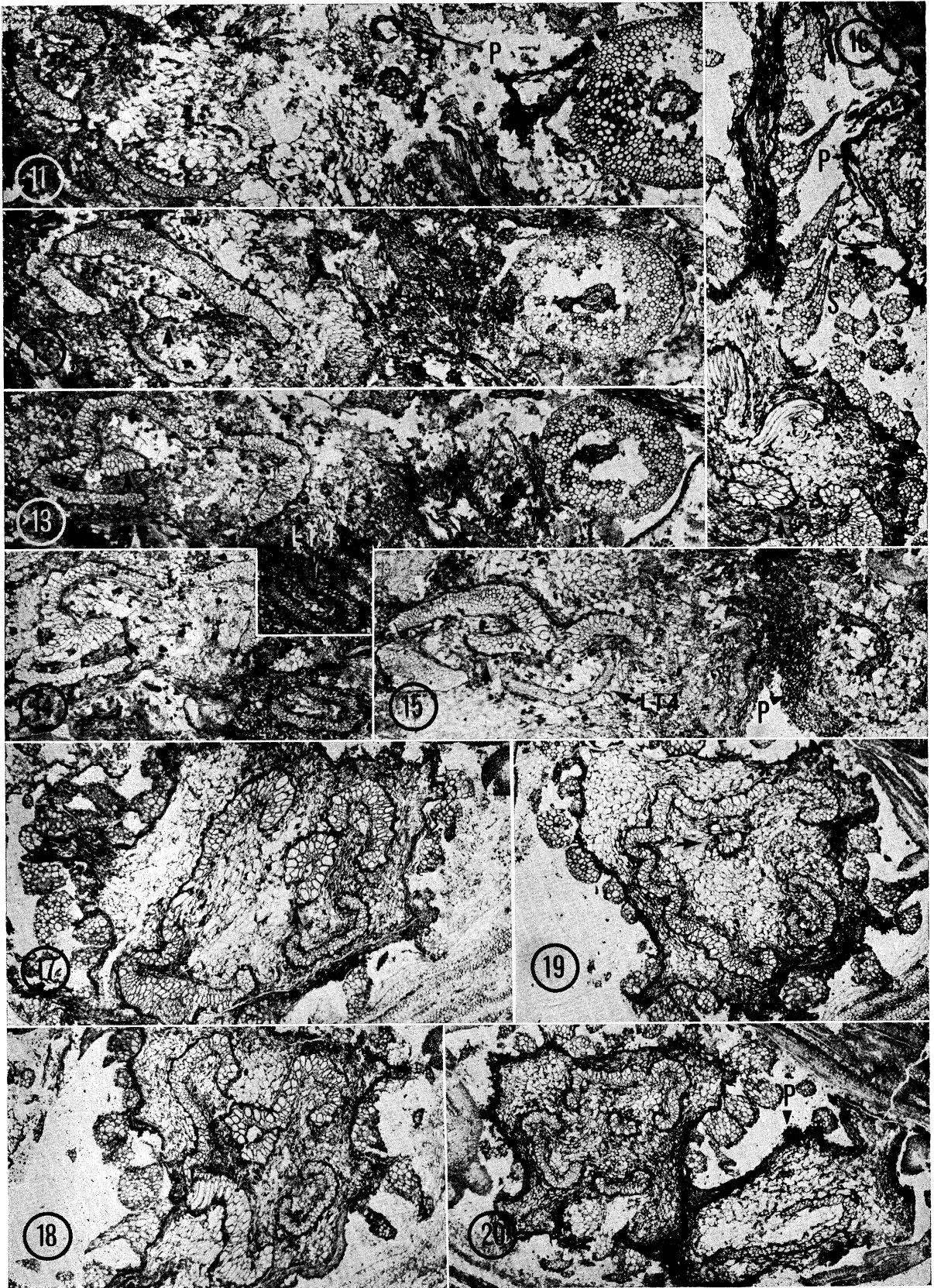
previous specimen at the dicyclic level. Prior to gap closure the two edges of the outer cycle become markedly inrolled (Fig. 17) and join the inner cycle. A portion of the inner cycle which closes a leaf gap is presumably referable to an incipient leaf trace to the next leaf directly above. The remaining part of the inner cycle (Fig. 19, arrow) separates and follows a diagonal path toward the next leaf gap (Fig. 19, lower right). The vascular supply of each petiole remains C-shaped (Fig. 16 P, 20 P), but foliar xylem could not be followed to a level of pinnae formation.

Numerous scales are present on the stem (Fig. 16 S). The scales are somewhat conical in shape, up to 1.2 mm long and up to 0.5 mm wide at the base. In transverse section scales are circular to elliptical in outline. The outermost layers of parenchymatous ground tissue of the stem and petioles are apparently crushed, resulting in a narrow dark border.

DISCUSSION—*Psaronius* stems typically exhibit polycyclic, endarch dictyosteles with scalariform tracheids. The leaf-trace scars are assigned to the *Stipitopteris* or *Stewartiopteris* type of configuration, and adventitious roots have exarch, polyarch actinosteles (Morgan, 1959). The two small dicyclic stems exhibit these characters and are identified as *Psaronius*. The $\frac{1}{3}$ phyllotaxy and dicyclic dictyosteles of two stems also coincide with the known basal stem anatomy of *Psaronius* despite tremendous differences in size. The minimal, basal stem diameter of *P. blicklei* (dicyclic stage) was 2.3×1.5 cm, and in *P. melanedrus* the smallest stem diameter reported was about the same at a tricyclic stage (Morgan, 1959). The preserved basal portions of the two stems described by Morgan are about 10 times larger in diameter than the stems in this study. Morgan's specimens were surrounded by a thick mantle of roots, up to 30 cm in radius in *P. blicklei*, indicating that they were the basal portions of quite large plants. The small sizes of the specimens described here, a relatively simple stelar anatomy, attachment of petioles, and the lack of a root mantle suggest that they are basal portions of relatively young, small, sporophytes.

The three small stems are not assigned to any species because of the lack of established taxonomic characters at the ontogenetic stages represented. The amber to black deposits in cell

Fig. 3-10. *Psaronius* sp.—Fig. 3. Transverse section of stem at lowest preserved level; siphonostele with incipient leaf trace. Slide 2038, $\times 30$.—Fig. 4. Transverse section of stem with leaf gap and LT, first leaf trace. Slide 2023, $\times 30$.—Fig. 5. Transverse section of stem following closure of first leaf gap. Slide 2013, $\times 30$.—Fig. 6. Scalariform tracheids of cauline metaxylem. Slide 2001, $\times 250$.—Fig. 7. Transverse section of stem at early dictyostelic stage; R, roots; LT 2, second leaf trace. Slide 2004, $\times 15$.—Fig. 8. Transverse section of stem with LT 2, second leaf trace; R, root. Slide 2003, $\times 15$.—Fig. 9. Oblique section of curved stem below A level in Fig. 1b; R, root. Slide 2000, $\times 11$.—Fig. 10. Obliquely transverse section of stem at level A of Fig. 1b; lower stelar portion on right, upper portion on left; LT 3, third leaf trace; arrow, elongate cortical cells. Slide 2005, $\times 15$.



lumens of the ground tissue occur in many species. On the other hand, *Psaronius* stems usually have a distinct peripheral sclerotic zone which is lacking in the small specimens described. Characters of this nature, along with lacunae in the ground tissue, have been used to delimit *P. melanedrus*, *P. blicklei* and *P. chasei*, but it is evident that in these species the degree of development and the distribution of sclerenchyma and lacunae differ ontogenetically and may be lacking in more basal portions. The specific identity of *Psaronius* from the Bevier coal and from the Herrin coal has not been established, but the two specimens from the Sahara locality probably belong to the same species as the very common *Psaronius* stems found there and associated with them in both coal balls.

The origin of additional cycles within and attached to the central cycle at point of origin has been described by Morgan (1959). In the dicyclic stage she noted the following: "... the leaf gap in the second cycle of *Psaronius* is closed simply by arching over and fusion of portions of the cycle from either side of the gap. This is different from closure of the gap in all cycles except the central one." This method of gap closure was postulated by Morgan for the basal monocyclic stage and is confirmed by our specimen 6378 (Fig. 2d, g). The origin of the second cycle differs from her hypothesis in that it arises from only one of the inwardly projecting arms rather than from two as in the third cycle. This slight difference is probably well within the range of variability to be expected in the vascular anatomy of *Psaronius*. The ontogenetic stage of a simple siphonostele further adds to the stelar changes established for *Psaronius* by Morgan.

The occurrence of scales on one stem (Fig. 16-20) is probably both a preservational and a developmental stage which has not been reported for the stem of *Psaronius*. Scales are quite abundant on immature frond parts. The secondary proliferation of parenchyma forming the ground tissue of the inner-root zone apparently results in the loss of scales from the stem surface along with some of their supporting tissues. No inner-root mantle was formed, but all roots observed exhibited the characteristic anatomy of individual roots from the inner-root zone.

This is the first reported occurrence of histologically preserved connections between stems

and leaves in *Psaronius*. The C-shaped vascular configuration of the petiole differs from *Stewartia-opteris* in that the margins of the adaxial xylary arms are not inrolled. A similar C- or U-shaped xylary configuration is present in the ultimate pinnule-bearing members of large *Psaronius* fronds. Marattiaceous stipules were not present at the petiole bases.

The anatomical similarities of *Psaronius* with the extant Marattiaceae are most striking, and the early stages of development in *Psaronius* can be compared with similar stages in some living genera of the Marattiaceae. The vascular system of extant genera is basally a protostele and becomes dictyostelic usually by passing through a more or less simple, closed siphonostelic stage. The polycyclic dictyostele (two or more cycles) is formed by successive medullary strands which arise to the inside of the original cycle or central cycle. The newly formed medullary strand (Charles, 1911) or commissural strand (Brebner, 1902; Farmer and Hill, 1902; West, 1917) duplicates very closely the development of the original vascular strand of the stem.

In *Psaronius* the internal strand (Fig. 2 g-k) is comparable to the medullary or commissural strand in the extant Marattiaceae, and the development of the internal strand may be indicative of the ontogeny of the initial, and presumably, protostelic stage of the vascular system. The centrarch inner strand becomes siphonostelic (Fig. 17), and further expansion of the outer and inner cycles would result in a vascular system comparable to the dicyclic level described for *P. blicklei* (Morgan, 1959).

The early stages of the vascular system in the extant Marattiaceae are quite similar to those demonstrated for *Psaronius*. Sclerenchyma is absent in the young sporophytes of both *Psaronius* and the extant Marattiaceae. Sclerenchyma is present at higher levels in *Psaronius* stems but is absent from the stems of the Marattiaceae (Campbell, 1911; West, 1917). Stipules are present in the living Marattiaceae, although they are usually absent from the first and sometimes additional leaves of young sporophytes (Blomquist, 1922; Bower, 1926). Petioles in the young sporophyte of *Psaronius* are exstipulate, and there is no evidence that they were present in older plants. One of the small *Psaronius* stems exhibits a counterclockwise, spiral phyllotaxy, and phyllotaxy in a second specimen is clockwise.

Fig. 11-20. *Psaronius* sp. All $\times 15$.—Fig. 11-13. Two transverse sections of stem at B, C, and D levels of Fig. 1b; lower portion of stem on right, upper portion on left; P, first petiole; LT 4, fourth leaf trace. Slides 2013, 2026, 2036.—Fig. 14. Transverse section of stelar portion with inner and outer cycles joined; fourth leaf trace at right. Slide 2035.—Fig. 15. Transverse section of stem with closure of second leaf gap; arrow, origin of inner cycle; third leaf gap at left, LT 4, fourth leaf trace; P, second petiole. Slide 2023.—Fig. 16. Obliquely transverse to longitudinal section of stem; arrow, inner cycle; P, petiole; S, scales. Slide 2067.—Fig. 17-20. Representative serial transverse sections of dicyclic, dictyostelic stem showing closure of leaf gap at top and incipient trace formation and departure to P, petiole; arrow, inner cycle. Slides 2065, 2063, 2061, 2059.

Within a single species a spiral arrangement may be clockwise in one plant and counterclockwise in another, and this has been reported in *Psaronius blicklei* (Morgan, 1959) and for *Angiopteris evecta* (Blomquist, 1922). In the young sporophytes of the extant Marattiaceae there is generally one root per leaf (Brebner, 1902; West, 1917; Blomquist, 1922), but such a precise relationship between roots and leaves was not observed in *Psaronius*.

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