Monocyclic *Psaronius* from the lower Pennsylvanian of the Illinois Basin

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A new species of *Psaronius* is described from permineralized monocyclic stems with distichous leaf scars. Diameters for the steles are 3.5–4.4 cm, up to 6.5 cm for the stem, and 8 cm for the trunk which includes inner and outer roots; the longest of 11 specimens is 32 cm. These specimens from the lower Pennsylvanian of western Illinois are the oldest known histologically preserved stems and roots for the genus. ***Psaronius simplicicaulis*** sp.nov., with its distichous leaf arrangement, is very similar to Mississippian – early Pennsylvanian *Megaphyton* specimens, indicating that the earliest known marattialean tree ferns were smaller in diameter than their late Pennsylvanian relatives and probably monocyclic with distichous fronds. The middle Pennsylvanian increase in the distribution and abundance of *Psaronius* generally coincides with increased size, polycyclic stelar anatomy, and polystichy.

Tree ferns of the Marattiales in Euramerican floras exhibit a marked increase in stem diameter from the time of their relatively sparse occurrences in the Mississippian – early Pennsylvanian to their dominance in many coal swamps during the late Pennsylvanian and Permian. Since this order has the longest known geologic range among ferns and was such an important component of the Pennsylvanian and Permian vegetation, its origin and earlier evolution are of considerable interest. The number of *Psaronius* stems (permineralized) or *Megaphyton* specimens (compression cast with leaf scars) recovered from the Mississippian – early Pennsylvanian number less than a dozen. Practically all of them conform to a smaller stem type with distichously arranged leaf scars. The oldest known polycyclic stems of *Psaronius* occur in roof nodules in the lower Westphalian A of England and this represents a time for the coexistence of monocyclic and polycyclic forms, both of which were quite rare. Older specimens reported thus far with evidence of their stelar configuration have a simple siphonostele. The most primitive form of the Marattiales known at present is smaller in size and exhibits monocyclic stem anatomy and distichous frond arrangement. The oldest stratigraphic occurrence of the Marattiales is *Megaphyton protuberans* in the 'Lower Chesterian' of Illinois, about equivalent to the uppermost Visean, Lower Carboniferous of Europe (Pfefferkorn 1976).

Psaronius stems described here are early Pennsylvanian (late Namurian equivalent) in age and represent the earliest known occurrence of histologically preserved *Psaronius* and from North America the first reported monocyclic psaronii. They provide the first clear anatomical evidence for relating *Megaphyton* specimens with monocyclic anatomy and distichous leaf arrangement to the Marattiales and to the early evolutionary history of *Psaronius*. As a result of studies of middle and upper Pennsylvanian psaronii of the Americas, Morgan (1959, p. 62) treated the genus as polycyclic. The only previously known psaronii from the early Pennsylvanian are from Great Britain and their phyllotaxy is unknown (Williamson 1876; Scott 1908; Bower 1930). Several *Megaphyton* stems exhibit evidence of both a large siphonostele and distichous leaf arrangement but they lacked indisputable evidence of being marattiaceous (Goodlet 1957; Pfefferkorn 1976). Such vegetative evidence can be derived from the root mantle and the anatomy of roots and stem cortex of the tree fern trunks. The evolutionary increase in stem diameter of *Psaronius* accompanied by the development of a complex polycyclic stelar system and a polystichous frond arrangement (*Caulopteris* is the compression-cast form), is coincident with the marked rise of the genus in the Pennsylvanian from rare to a dominant part of the coal swamp flora. The permineralized peats of the middle Pennsylvanian and younger deposits have provided many of the anatomical details on the polycyclic stems of *Psaronius* (Morgan 1959) including basal stem anatomy (Stidd and Phillips 1968), root system ontogeny

(Ehret and Phillips 1977), frond anatomy (Stidd 1971), and fructification-spore morphology (Millay 1975).

Materials and Methods

Eleven permineralized stems were collected from a pyritic black shale in the Allied Stone Company quarry, Vandruff Island, Milan, Rock Island Co., IL. This locality is on the western edge of the Illinois Basin and the deposits are given a tentative Morrowan age by Leary (1974*b*). Of the 11 specimens, three of the stems are well enough preserved for detailed structural and histological study. They are specimens No. 10646, 10648, and 10649. Five others are crushed, but cellular preservation is good. Over a metre of *Psaronius* stem fragments was collected; the longest piece is 32 cm.

The root mantle surface of the stem specimens is largely coalified, as in coal-ball preservation, and portions beneath the coal are pyritized. There is no evidence of leaf scars (Fig. 3). To determine the phyllotaxy, cylindrical specimens were ground down to the leaf traces and wraparound peels were made.

Stems were sectioned and cellulose acetate peels were prepared after etching in HCl, and when pyritic, in HNO_3.

All specimens and slides are in the Paleobotanical Collections (Morrill Hall), Department of Botany, University of Illinois, Urbana, IL, U.S.A.

Results and Discussion of Anatomy

Vascular Tissue

In comparison with other psaronii, the most distinctive feature of the stem is the monocyclic stele (Fig. 4). The stele diameter is 3.5–4.4 cm. Leaf traces are distichous and alternate. Leaf gaps are about 1 cm in width and gap closure, by simple union of the free margins of the stele, occurs within a length of 8–10 cm; the next leaf trace in the same orthostichy is initiated just above the level of gap closure. As illustrated in Fig. 1, the leaf gaps from opposite orthostichies may overlap up to 2 cm. The leaves are regularly alternate so that at about the level where a leaf trace enters a leaf on one side, gap closure and initiation of a new trace occur on the opposite side.

The two halves of the stele, separated in cross section by leaf gaps, are unequal; the arc of vascular tissue on one side is consistently smaller with a difference in arc length from less than 0.7

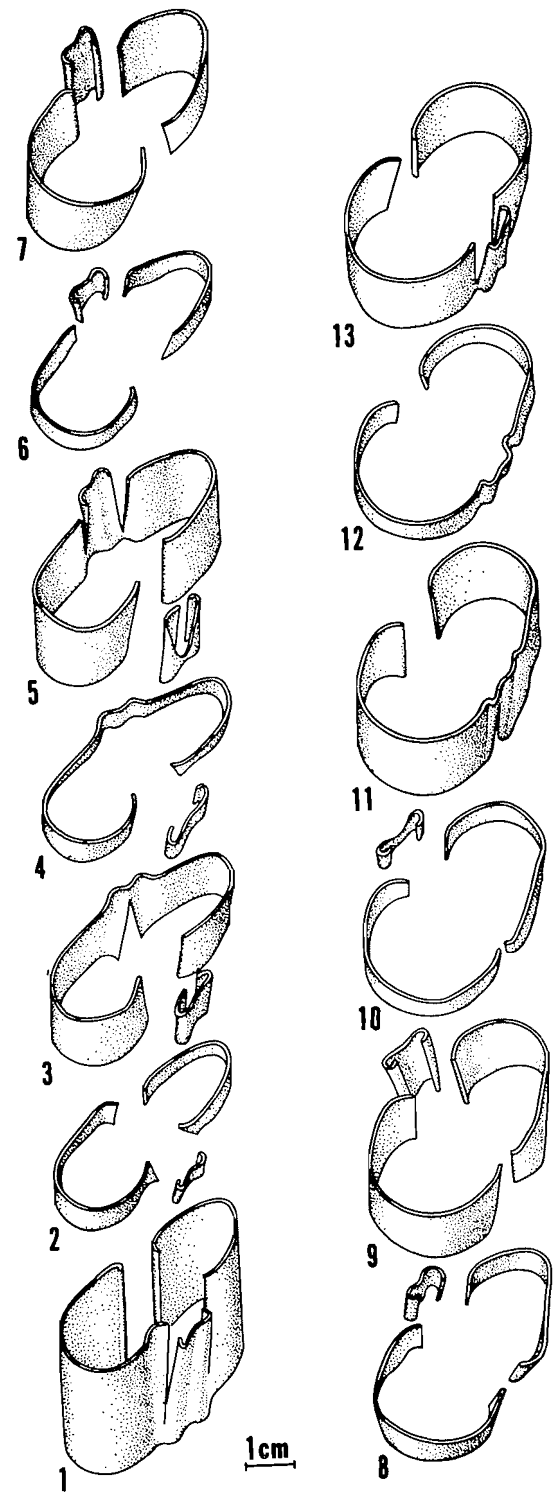

FIG. 1. *Psaronius simplicicaulis.* Partial reconstruction of the vascular system separated in segments to show the opposite rows of alternately arranged leaf traces and the slightly overlapping leaf gaps. The trace on the right side of segment 5 terminated with leaf abscission. Based on specimen 10646.

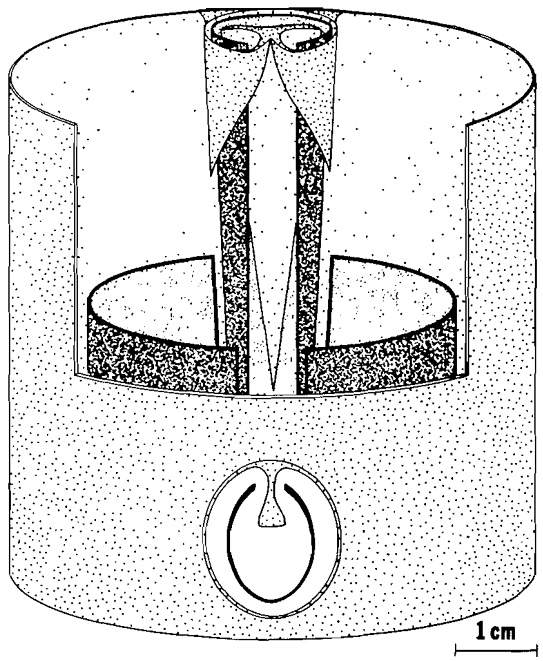

FIG. 2. *Psaronius simplicicaulis*. Partial reconstruction of the stem, bounded outside by sclerenchyma (light stippling) which also envelops the leaf trace, U shaped on stem surface and C shaped in cross section. Cutaway portion of sclerenchyma sheath shows xylem of stele and departing leaf trace (dark stippling). Based on specimen 10646.

cm up to 1.5 cm (Fig. 4). Only the xylem is preserved. Xylem maturation is endarch and protoxylem is located in irregularly spaced groups of three to eight tracheids (Fig. 6). The protoxylem tracheids are 25–60 μm in diameter. Metaxylem tracheids are 60–250 μm in diameter and form a band of xylem usually 6–8 tracheids in width, but occasionally 10 or more. Metaxylem tracheids have scalariform thickenings (Fig. 7).

A narrow zone without cellular preservation is usually present on both sides of the xylem in all stems (Figs. 5, 6). These areas probably represent unpreserved phloem and it is presumed that the siphonostele was amphiphloic.

Ground Tissue

The most distinctive feature of the ground tissue is the presence of longitudinally oriented secretory ducts, some of which are at least 6.7 cm long. The ducts, which do not have an epithelial lining (Fig. 8), are often filled with an amber-colored substance and form three fairly distinct rings in the stem; one is beneath the outer cauline sclerenchyma sheath and there is one along each side of the vascular tissue (Fig. 5, at arrows). Ducts are also randomly scattered in the ground tissue and rarely in the root mantle. The vertically oriented ducts of each ring do not form a network; there are some horizontally oriented secretory ducts without any connections to those oriented vertically. Ducts beneath the cauline sclerenchyma sheath are the smallest in diameter with an average of 550 μm (325–800 μm); those near the vascular tissue average 735 μm (500–1050 μm).

Secretory ducts are also associated with the leaf traces. They form a row on the abaxial and adaxial sides of the trace (Figs. 10, 13) and apparently enter the base of the leaf along with the vascular trace. The ducts associated with leaf traces are not connected with those of the cauline system. After the departure of a leaf trace from the stele, the ducts of the next younger trace arise *de novo*. Most such ducts appear at a level below that of the associated leaf trace's point of departure from the stele; others appear when the trace is far out in the cortex. Occasionally there

FIGS. 3–12. *Psaronius simplicicaulis*. Fig. 3. Partially coalified exterior of stem with root mantle. Specimen 10649B. × 25. Fig. 4. Transverse section of monocyclic stem with opposite overlapping leaf gaps (LG) and remains of inner root mantle. Slide 113352. × 1. Fig. 5. Partial transverse section of stem with three rings of secretory ducts (arrows); larger diameter ducts form a ring on each side of the xylem (X) and a ring of smaller diameter ducts parallels the cauline sclerenchyma sheath. Slide 113558. × 3. Fig. 6. Transverse section of a portion of an endarch stele with two protoxylem groups (PX). Slide 113533. × 25. Fig. 7. Metaxylem tracheid with sclarariform thickenings. Slide 113548. × 250. Fig. 8. Secretory duct with degraded cells along inner margin; an epithelium is not present. Slide 113546. × 20. Fig. 9. Partial transverse section of stem with coalified outer sclerenchyma sheath (SC), secretory ducts, and inner root mantle. Slide 113561. × 3. Figs. 10–12. Representative sequential transverse sections of a leaf trace illustrating the progressive development of a sclerenchyma sheath (SC) as the trace approaches the outer edge of the cortex (at the right in the photographs). Secretory ducts (M) are in bands on the abaxial and adaxial sides of the trace (X). See Fig. 13 for diagrammatic drawings. Slides 113565, 13571, 13527. × 6.


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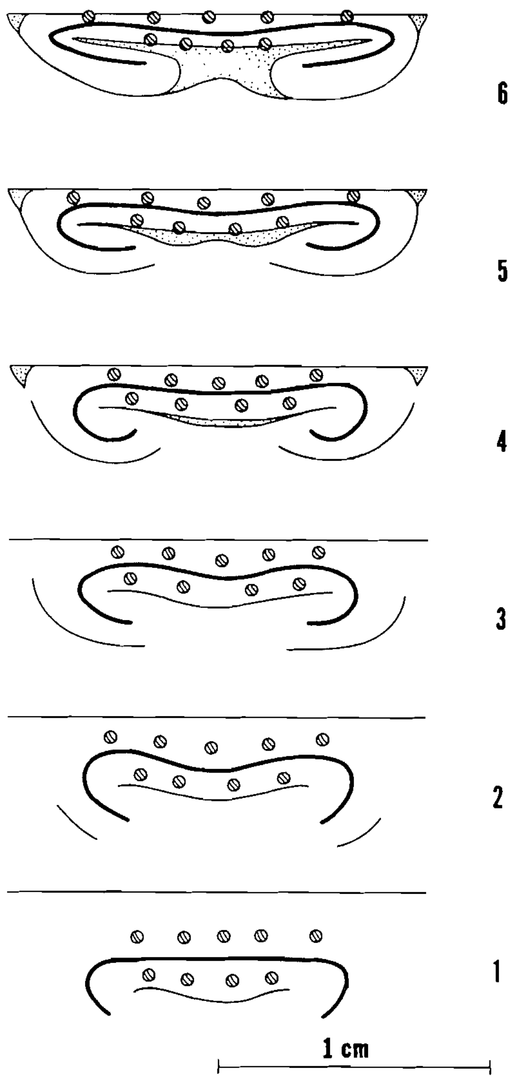


FIG. 13. *Psaronius simplicicaulis*. Schematic drawings of sequential transverse sections of a leaf trace (heavy lines). The trace is progressively ensheathed by sclerenchyma (light lines and stippling) as it nears the cauline sclerenchyma sheath at the outer edge of the cortex. Secretory ducts (circles) are present in two bands on both sides of the trace. Based on specimen 10646.

are proliferated, short, irregularly shaped ducts at the base of a leaf trace.

When seen in transverse section the stem is surrounded by a continuous sheath of sclerenchyma without any discontinuities. The sclerenchyma sheath was often partially coalified in our specimens (Fig. 9). Sclerenchyma is associated with each departing leaf trace (Figs. 10–12). A sheath is formed around the trace in a manner very similar to that in *Psaronius melanedrus* Morgan (1959). As viewed in serial transverse sections (Fig. 13), sclerenchyma appears initially on both flanks of the trace as it nears the edge of the cortex. The sclerenchyma occurs as two bands that extend laterally toward each other and are joined on the adaxial side of the trace; abaxially they are joined to the cauline sclerenchyma sheath. A band of sclerenchyma usually forms within the adaxial concavity of the trace. The laterally extending sclerenchyma may connect with the adaxial band when it is present. Figure 2 illustrates the relationship of the vascular system to the sclerenchyma.

Leaf Traces

The leaf trace is about 1 cm in width basally and its formation begins almost immediately after closure of the preceding gap in the orthostichy. A constant width is maintained up to the level of encirclement by sclerenchyma where the vascular supply expands to about 1.5 cm. In cross section the xylem strand is bracket shaped both below and immediately above its point of separation from the stele; however, the edges of the xylem progressively inroll until a C shape is formed in cross section. The C shape becomes flattened near the cauline sclerenchyma sheath. In tangential sections the trace appears U shaped (Fig. 2). Leaf traces depart at a steep angle and their protoxylem is adaxial in discrete groups.

Roots

An inner root mantle surrounds each of the stem specimens. Roots of the inner root zone (Fig. 14) are 1–3 mm in diameter. Each is surrounded by a sclerenchyma sheath, the only cortical tissue preserved. The stele is a polyarch, exarch actinostele. Interstitial tissue was present within the inner root zone but its preservation was generally poor. There is some indication of the radially elongate and undulatory cellular arrangement described from other specimens of *Psaronius* (Morgan 1959; Ehret and Phillips 1977). The tissue is composed of uniseriate rows of elongate cells that apparently arose from the outer edge of the sclerenchyma sheath surrounding the inner roots (Fig. 15).

A few outer roots were present in depressions in the inner root zone (Fig. 16), indicating that there was at least a partial outer root mantle. Outer roots are up to 0.75 cm in diameter with an aerenchymatous cortex typical of free outer

Psaronius roots. Inner roots were rare or absent next to the leaf scars and it was in these areas that the outer roots were found.

Specific Diagnosis

Psaronius simplicicaulis DiMichele and Phillips sp.nov. Stems up to 6.5 cm in diameter with endarch, amphiphloic monocyclic steles up to 4.4 cm in diameter; leaf traces alternate in two opposite orthostichies, one-half phyllotaxy or distichous; leaf traces C shaped in transverse section, U shaped in tangential section of stem, maximum of 1.5 cm wide and 2.8 cm high; ground tissue of stem characterized by three rings of secretory ducts without epithelium, one ring beneath the stem sclerenchyma sheath and one on each side of the vascular tissue; stem surrounded by a sclerenchyma sheath without cross-sectional discontinuities; secretory ducts and sclerenchyma associated with departing leaf traces; inner and outer root zones present.

HOLOTYPE: Specimen 10646 and slides I13523–13538, 13541–13556, 13563–13572.

PARATYPES: Specimen 10648 and slides I13540, 13557, and 13558. Specimen 10649 and slides I13539, 13559–13562.

LOCALITY: Allied Stone Company quarry, Vandruff Island, Milan, Rock Island Co., IL, U.S.A.

STRATIGRAPHY: Caseyville Formation, McCormick Group, Morrowan Series (early Pennsylvanian).

Species name derived from the Latin *simplex* (simple) and *caulis* (stem).

Discussion

Geology

The stems of *Psaronius simplicicaulis* were collected from shales attributed to the Caseyville Formation, McCormick Group, which is lower Pennsylvanian. The rocks probably represent the basal Pennsylvanian sediments on the western edge of the Illinois basin; however, their exact age is uncertain. At the Vandruff Island locality and at nearby sites with similar deposits, the shales fill channels which developed on the pre-Pennsylvanian surface of the Devonian Cedar Valley Limestone. Leary (1974*a*, 1974*b*, 1975) has done most of the recent work in this area and has determined that similar channel-fill shales in Brown Co., IL, are of Morrowan age (Namurian C – Westphalian A) on the basis of both palynology and compression floras associated with the shales (Leary 1974*b*). The Vandruff Island shales contain a similar but not identical flora.

Most of the channels were up to 8 m wide and 5 m deep and were filled with gray, locally sandy shale which contains a distinct nonswamp (probably upland) compression flora. The *Psaronius* stems were collected from a pyritic black shale that filled the upper 1–1.5 m of some channels. The gray shale flora differs from that of the black shale which has a much higher percentage of lycopods and sphenopsids, in addition to the presence of *Psaronius*. *Psaronius* apparently grew and was buried in a swamp environment associated with channel fill of the black shale type.

Taxonomic Treatment

Monocyclic *Psaronius* stems have not been reported previously outside of Great Britain and those vary considerably in degree of preservation and thus the extent to which their monocyclic nature can be determined with certainty. The relatively large size of the stems described herein and their consistent monocyclic nature throughout at least a 1-m length indicate that the simple siphonostele is a mature feature and not just an early ontogenetic stage as occurs in polycyclic species (Stidd and Phillips 1968; Stidd 1974). The regularity of stele diameter (3.5–4.4 cm), the consistent size of the leaf traces (approximately 1 cm wide), and the development of secretory ducts to an equal extent indicate that the stem specimens are characteristic for the species and include neither near-basal nor near-apical regions of the plants.

Near-basal levels of polycyclic *Psaronius* in middle and late Pennsylvanian specimens indicate that dicyclic and tricyclic conditions are attained at smaller stelar and stem diameters than those of *P. simplicicaulis*. The young sporophyte stages of *Psaronius* described by Stidd and Phillips (1968) showed increases in stem diameter from 1.5 mm to 5 mm along a 4.5-cm length with a 0.5-mm stelar diameter for the base of the simple siphonostele and a 2.5-mm stelar diameter at the dicyclic stage. Morgan's (1959) specimen A of *P. blicklei* exhibited a dicyclic stage at the basalmost preserved level with a stem diameter of 2.3 × 1.5 cm. Almost 1 m higher the stem approached 3 cm in diameter with the origin of the third cycle; the stelar system was 2 cm in maximum diameter.

Stems of *Psaronius*, thought to be monocyclic, have been assigned in the past to *Psaronius renaultii* (Westphalian A age) with relatively little information about other morphological aspects. Each of the specimens attributed to *P. renaultii* does contribute something to our knowledge of the early psaronii but there have been very few overlapping features from previously described specimens with which to establish a coherent species concept of *P. renaultii* or to evaluate differences in specimens reported from the early Pennsylvanian equivalent of western Europe.

Williamson (1876) described *Psaronius renaultii* from some root mantle fragments with the distinctive hair-like interstitial tissue and an associated stem fragment. The incompiete stelar portion of the stem is quite small, 1.4 cm in diameter, and it could be from one-half of a monocyclic stem or only a portion of a polycyclic stem; Williamson considered it to be polycyclic, although he acknowledged the possibility that it was monocyclic in structure. No leaf traces are preserved in his specimens, consequently the phyllotaxy and trace related characteristics are unknown. The ground tissue contains secretory ducts apparently with distinct epithelia. Another feature claimed to be characteristic of *P. renaultii* is the loosely woven, hair-like interstitial tissue (Fig. 11), but this grades into a more typical compact tissue elsewhere in the root mantle similar to other species of *Psaronius*. The locally hair-like interstitial tissue may be a preservational feature and it is the source of the interpretations of Williamson (1876), Farmer and Hill (1902), Solms-Laubach (1911), and Scott (1920) that the interstitial tissue is composed of interwoven root hairs. In summary, the specific assignment of other specimens to *P. renaultii* is doubtful because of the lack of information about them and the type material with which they must be compared.

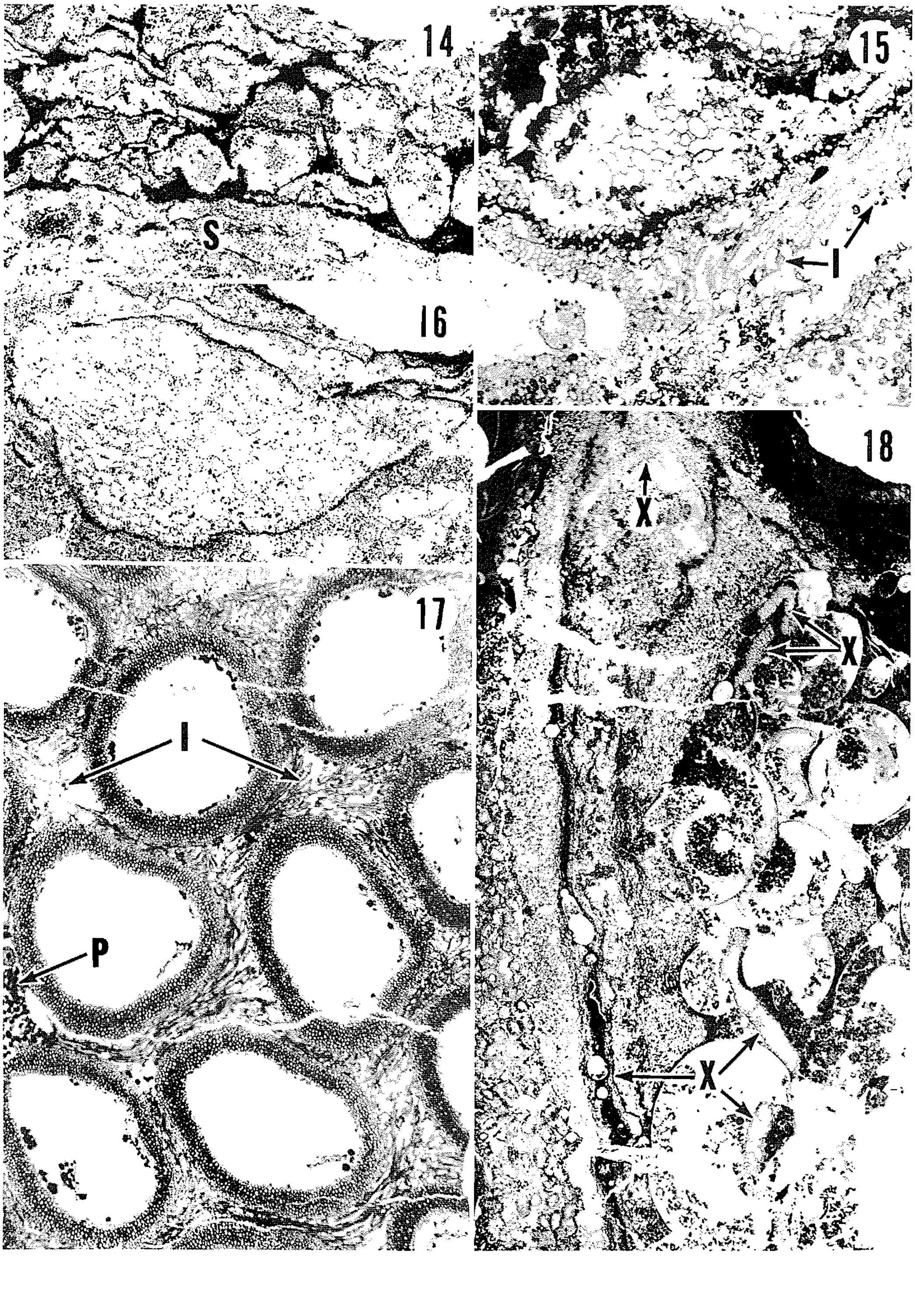
The only clearly established monocyclic *Psaronius* known from Europe was described by Bower (1930) from the Kidston collection (K986–987; Fig. 19). It was designated as *P. renaultii*, although the interstitial tissue is densely packed as in other psaronii. The stele is 3.2 cm in diameter, slightly smaller than *P. simplicicaulis*, but no ground tissue is preserved. One leaf gap is present but no leaf traces are preserved. Kidston's specimen was found in a stream bed in Ayrshire, Scotland; it was apparently from the Boulder Clay in the upper series of the Scottish Lower Coal Measures (Kidston 1892, pp. 308–309), low in the Westphalian (Currie 1954, p. 532).

There are several thin sections attributed to *Psaronius renaultii* in the Scott and Gordon collections, but in each case there is reason to doubt the identification or question the basis for the morphological interpretations. One such specimen (S2016) is an isolated mass of inner roots with interstitial tissue typical of psaronii. A root mantle fragment with hair-like interstitial tissue, as in *P. renaultii*, occurs in the Gordon Collection, King's College, London (Fig. 17). It is likely, however, that this represents another section of Williamson's specimen rather than a second specimen with the same character.

Another specimen (S2173–2180; Fig. 18), partially illustrated by Scott (1920, Fig. 125), has a highly crushed and incomplete stelar system with protoxylem in such positions as to suggest that the two bands of xylem are not part of a collapsed siphonostele but two separate parallel cycles. In this specimen there are no secretory ducts in the ground tissue, no leaf traces, and no clearly defined leaf gaps. It was Scott's treatment of this stem as monocyclic that firmly established the monocyclic concept of *Psaronius renaultii*.

None of the specimens of supposed or established monocyclic psaronii from Great Britain, designated *Psaronius renaultii*, can be demonstrated to be identical with each other or with

FIGS. 14–16. *Psaronius simplicicaulis*. FIGS. 17, 18. European psaronii attributed to *P. renaultii*. Fig. 14. Transverse section of inner root mantle with stem (S) below. Slide I13538. × 6. Fig. 15. Transverse section of a portion of the inner root mantle; interstitial tissue (I) is shown on the abaxial side of an inner root. Slide I13527. × 25. Fig. 16. Transverse section of an outer root with aerenchymatous cortex. Slide I13549. × 10. Fig. 17. Transverse section of inner root mantle with loosely packed, hair-like interstitial tissue (I) and an area of degraded interstitial tissue (P); specimen attributed to *P. renaultii*. Gordon Collection, King's College, University of London. × 10. Fig. 18. Cross section of a supposedly monocyclic *P. renaultii* from a Westphalian A roof shale nodule. Protoxylem positions suggest that the vascular tissue (X) represents two similarly oriented cycles rather than broken pieces of one. Scott illustrated the hooked part of the vascular system in the upper left (see text). Scott Collection Slide 2175, British Museum (N.H.). × 2.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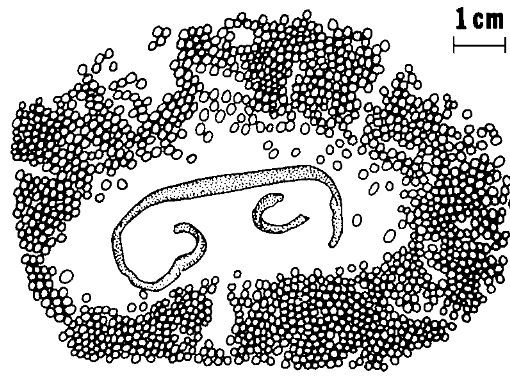

FIG. 19. *Psaronius* sp. Cross section of monocyclic stem attributed to *P. renaultii* by Kidston. Kidston Collection Slide 986, Hunterian Museum, University of Glasgow.

the American specimens. Therefore, it is recommended that the specific epithet *Psaronius renaultii* be restricted in usage to the type specimen of Williamson. Other specimens of *Psaronius* assigned to *P. renaultii* should be considered *Psaronius* sp.

Comparisons with Compressions–Impressions

Psaronius simplicicaulis corresponds closely to the form genus *Megaphyton* sensu Pfefferkorn (1976) for tree fern stem compressions–impressions with a distichous leaf arrangement and leaf trace of the stipitopterid or stewartiopterid configuration. At least two species of *Megaphyton* have been described with a stelar outline that indicates they were monocyclic.

The specimen of *Megaphyton chalmersii* Goodlet (1957) is preserved in sandstone and the internal structure is deduced from a carbonized stele with overlapping leaf gaps. The stele is 2.5 × 4.2 cm and the stem 3.8 × 5 cm; the size and leaf trace disposition are quite similar to those in *Psaronius simplicicaulis*. The specimen is from the Limestone Coal Group in Fife, Scotland, in the lowermost Upper Carboniferous (Namurian) (Currie 1954; Wittard and Simpson 1960). It is lower in the Limestone Coal Group than the two *Megaphyton* species described by Crookall (1955).

The second species of *Megaphyton* considered monocyclic is from Corda's Radnitz Basin (Bohemia), Czechoslovakia, locality. While the exact age in the Westphalian C–D (Schopf 1941; Andruslov and Prantl 1960) is uncertain, it is much younger than other known specimens. *Megaphyton cordai* O. Fstm. was originally described as *Zippea disticha* by Corda (1845). It is apparently monocyclic although there are some unidentified minor arcs of carbon internal to the stele of the sandstone specimen. The leaf traces are C shaped, distichous, and alternate. The stele is 2.4 × 5.5 cm and the stem 4 × 7 cm. The preservation is very similar to that of *M. chalmersii*.

There are three additional species of *Megaphyton* which are known from the Mississippian or early Pennsylvanian. The oldest (Chesterian), *M. protuberans* Lesquereux, has recently been redescribed by Pfefferkorn (1976). It is the largest, with a trunk diameter of 10 cm. The two species described by Crookall (1955) are *M. circulare*, which is the same diameter as *P. simplicicaulis*, 6.5 cm, and *M. obscurum*, which is 8.9 cm in diameter and too poorly preserved for further comparison. Species of *Megaphyton* are based largely on leaf scar characteristics. The leaf scars of *P. simplicicaulis* are vertically elongate as in *M. protuberans*; those of *M. circulare* are circular. The leaf scars of the *Megaphyton* species are 3.5 cm in diameter (*M. circulare*) to 5.0–5.5 cm wide and 6.5–7.5 cm high (*M. protuberans*). *Psaronius simplicicaulis* leaf scars are 1.5 cm wide and 3.5–4.3 cm high. The distances between successive scars are 5–5.5 cm in *P. simplicicaulis* and 0.5–0.9 to 1.3–1.7 cm in *M. protuberans* and *M. circulare*. The C-shaped leaf trace occupies the center of the leaf scar in *P. simplicicaulis* and is 2.5 cm high and 1 cm wide. In *M. protuberans* the C-shaped leaf trace occupies the lower third of the leaf scar and is wider than high, 2.6 cm by 2.1 cm. In *M. circulare* there are two oval depressions in the center of the scar and each oval is about half of the dimensions of the leaf trace of *P. simplicicaulis*. *Megaphyton circulare* somewhat resembles *Artisophyton*, a genus erected for *Megaphyton*-like plants with leaf trace configurations that are deeply indented abaxially or divided into two separate closed traces (Pfefferkorn 1976).

Summary

In the foregoing comparisons the *Megaphyton* specimens are either monocyclic or could have been monocyclic. There is a good possibility that many *Megaphyton* specimens of early Pennsylvanian and Mississippian age are the remains of monocyclic marattialean ferns. However, it is not implied that monocyclic anatomy can be inferred from distichous leaf arrangement.

Distichous species of polycyclic *Psaronius* from the Permian of western Europe include *P. brongniartii* Corda, *P. cottai* Corda, *P. gutbieri* Corda, *P. levyi* Zeiller, *P. musaeformis* (Sternberg) Corda, *P. spurievaginatus* Stenzel, and *P. tenuis* Stenzel (see Dijkstra 1963). Such stems could be preserved as *Megaphyton*. The only known occurrence of a polycyclic *Psaronius* stem quite low in the Pennsylvanian was reported by Scott (1920) from the lower Westphalian A of Lancashire. The lowest stratigraphic occurrence for a distichous polycyclic *Psaronius* in North America is from the Mazon Creek Flora in the lower part of the Carbondale Formation, Desmoinesian Series (middle Pennsylvanian) (Morgan 1959, specimen U).

At the present time there are three known occurrences of monocyclic marattialean stems with a distichous frond arrangement: two from the lower Pennsylvanian or Namurian equivalent, *Megaphyton chalmersii* and *Psaronius simplicicaulis*, and one from the Westphalian C–D, *Megaphyton cordai*. A fourth monocyclic occurrence is Kidston's specimen with unknown phyllotaxy and of early Westphalian age.

The larger polycyclic psaronii were probably derived from smaller tree fern ancestors. Because of the scattered and rare occurrences of *Psaronius* and *Megaphyton* in Mississippian and lower Pennsylvanian strata, it can only be speculated that the evolution of polycyclic forms occurred before the lower Westphalian A. Monocyclic forms of the Marattiales are not known to have been abundant anywhere and the importance of *Psaronius* in Pennsylvanian–Permian vegetation of the Euramerican floral province seems to be effected in large part by evolutionary changes relating to their increase in size. As the only tree forms without secondary growth in Pennsylvanian swamps, *Psaronius* species competed successfully with taller lycopods, cordaites, and calamites with the development of polycyclic stems buttressed by massive root mantles. Their large fronds were predominantly polystichous. The increase in dimensions from Namurian to Permian time is quite impressive. The stem of *Psaronius simplicicaulis* is 6.5 cm in maximum diameter compared with a *Psaronius* stem from Autun which is 13 × 30 cm. While the largest individual outer roots of polycyclic *Psaronius* stems usually do not exceed 2 cm in diameter (compared with 0.75 cm in *P. simplicicaulis*), in the Autun collections (1584 Roche) at the Museum National d'Histoire Naturelle, Paris, there is an outer root which is more than 3.5 cm in diameter. It lacks the outermost cortical layer and has nine protoxylem groups. Of the monocyclic psaronii, *P. simplicicaulis* is the largest known and its vascular tissue would be considerably less than in a polycyclic stem of comparable diameter. Its siphonostele is greater in diameter than Kidston's *Psaronius* specimen which Bower (1930) cited as the record size for a simple siphonostele.

The increase in anatomical complexity concomitant with further increase in size in *Psaronius* may not have taken place initially in coal swamps. The aerenchymatous inner cortex of outer roots of *P. simplicicaulis* indicates an aquatic adaptation early in the evolution of the genus, but the monocyclic forms were very rare in swamp habitats as are all psaronii in the coal-ball floras of the lower Westphalian A and A–B boundary in western Europe; they are unknown elsewhere in that stratigraphic interval. The time when *Psaronius* became an important element in the swamp floras is suggested by the abrupt and abundant appearance of marattialean spores in the upper part of the Abbott Formation, McCormick Group, Atokan Series in the Illinois Basin (Phillips *et al.* 1975). The anatomical records of *Psaronius* in coal swamps above this stratigraphic position have thus far been exclusively polycyclic forms. As the last major group of plants to become widely adapted and distributed in coal swamps, these marattialean tree ferns formed the dominant vegetation by Stephanian (late Pennsylvanian) time in the Euramerican floral province.

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