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The Frond Architecture of *Sphenopteris pottsvillea* (White) Gastaldo and Boersma

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## THE FROND ARCHITECTURE OF *SPHENOPTERIS POTTSVILLEA* (WHITE) GASTALDO AND BOERSMA

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**ABSTRACT**—Recently collected specimens allow a better characterization of the frond architecture of *Sphenopteris pottsvillea* (White) Gastaldo and Boersma from the Plateau and Warrior Coalfields, Alabama. The bipartite frond consists of a naked petiole of moderate length (>0.3 m) and two pinnule-bearing sections. The angle of rachial bifurcation varies from 35° to 65°, with no one angle of divergence dominating the sample population. Basal exterior lateral rachises develop first, are oblong in outline, and do not possess spine-like prolongations. Lateral rachises develop alternately along each pinnule-bearing section. Pinnule-bearing sections of the described leaf fragment exceed 0.5 m in length, and the dimensions of an entire frond probably approached 2.0 m.

### INTRODUCTION

**D**ISARTICULATION OF Carboniferous fern-like foliage often provides little data concerning the frond architecture of the original leaf. Few large frond fragments of fern and fern-like (gymnospermous) taxa have ever been recovered. In many instances, frond architecture is reconstructed from suites of specimens representing different frond loci originating from a population of parental plants.

One of the most common floristic elements in Early Pennsylvanian coastal regimes throughout the Appalachian and War-

rior Basins was *Sphenopteris pottsvillea* (White) Gastaldo and Boersma. Its endemic character and restricted stratigraphic range (Westphalian A) have provided the basis for its use as a biostratigraphic marker in the proposed Carboniferous stratotype (Englund et al., 1979; Pfefferkorn and Gillespie, 1982). This foliage and similar appearing frond fragments were assigned by White (1900, 1943) to the genus *Mariopteris*. As demonstrated by Gastaldo and Boersma (1983a, 1983b), only a small part of White's collection is assignable to either *Mariopteris* (Zeiller) emend. Boersma or *Karinopteris* Boersma. Most species erected by White have been assigned to either *Eusphenopteris* Novik

(as proposed for nomenclatural conservation by Boersma and Gastaldo, 1983) or *Sphenopteris* Brongniart.

Gastaldo and Boersma (1983a) concluded that several of White's taxa, and parts of others, were representative of a single species, *Sphenopteris pottsvillea*. The characteristics of the fossil collections used by White to separate specimens into taxa were the result of necrological biases (fresh vs. nonfunctional state of the plant prior to burial), biostratigraphic biases, or morphological variation. Phenotypic variability is attributable to original position of the fragment within the frond, or heterogeneity of frond size as a result of growth conditions. Upon re-examination of holotypes in conjunction with specimens collected from the southern part of the Appalachian Basin, similar taxa were placed into synonymy, and a reconstruction of the frond architecture was attempted based upon a suite of fragmentary frond pieces. Although the suite of specimens used to reconstruct the frond architecture was large, only a few critical pieces were available to allow for the distinction of the "pottsvillea-complex" from both *Karinopteris* and *Mariopteris*. Subsequently, the typological and figured specimens of White were placed into perspective based on the proposed tentative reconstruction.

At the time of the development of the tentative reconstruction, several features of the frond remained unknown. These characters include: the attachment of the petiole to the stem; the length of the petiole; the presence or absence of lateral pinnae on the petiole and their number (if present); the variability in the angle of bifurcation of the petiole; the position and character of the presumed basal exterior lateral pinnae; the exterior outline of the frond section; the precise interior outline of the frond section; the exact apical portion of the leaf; the presence or absence of spine-like prolongations of the rachises; the exact frond dimensions; and the fructifications. Collections of *S. pottsvillea* recovered since the publication of the tentative reconstruction provide a basis from which to detail several features reported as unknown and to amplify others. A more accurate assessment of frond architecture of this taxon now can be proposed from these observations.

Specimens of *Sphenopteris pottsvillea* have been collected from the Plateau and Black Warrior Coalfields, Alabama. Large frond fragments preserved in a fine-grained, flaggy mudstone have been recovered from the Upper Cliff coal interval (=Rosa coal) in active and abandoned strip mines along Berry and Sand Mountains (Clarence, Blountsville, and Brooksville 7.5' USGS topographic quadrangles, Alabama). Frond fragments preserved in shales, silty shales, and homogeneous mudstones have come from strip mines excavating the Mary Lee Coal zone (after Lyons et al., 1985; Mary Lee and Blue Creek coals) in the northwestern part of the Warrior Basin (Glen Allen, Carbon Hill, and Nauvoo 7.5' USGS topographic quadrangles, Alabama). All specimens are preserved as coalified compressions or impressions. Prior to excavation, outlines of all large frond fragments were traced onto acetate in the event of damage. Inconsistencies between line illustrations (reproduced from field drawings) and photographs are due to partial loss of the specimen parts during recovery.

#### DESCRIPTION OF SPECIMENS

Two specimens, one preserving the petiole and rachial bifurcation of the bipartite frond (USNM 372376) and the second preserving the rachial bifurcation and lower portion of the frond (USNM 372377), will be used as the basis for discussion. Both specimens are preserved three-dimensionally within the mudstone matrix and, therefore, are not preserved on a single bedding surface. As a result, portions of each specimen are missing. Terminology for description of the frond parts is based on Gastaldo and Boersma (1983a, 1983b).

The petiole (R1) is assigned to *Sphenopteris pottsvillea* based on the presence of a basal interior lateral rachis (R3) upon which are preserved characteristic pinnae (Figure 1.1, 1.2). No lateral pinnae occur along the length of the petiole. The longitudinally striate petiole is greater than 29 cm in length, 2.7 cm at maximum width, and possesses a raised medial ridge that follows the petiolar bifurcation pattern distally. This ridge, occupying 15% of the petiolar width, appears to be lobed and represents the transfer of the configuration of the internal stele to the outer surface after compression (Rex and Chaloner, 1983). The lobation of the ridge may be the expression of a lobate leaf trace, and the longitudinal striae may be representative of sclerenchymatous bundles in the cortex. The petiole bifurcates into a bipartite frond at an angle of 65°, and is accompanied by an increase in width. This configuration is consistent on all frond bifurcations collected to date (N = 6), although the angle of divergence varies from this maximum 65° to a minimum angle of 35° (as reported by Gastaldo and Boersma, 1983a). The form of the bifurcation of specimens presently under consideration differs from that previously reported in that the area between the diverging R2's is more openly arcuate and tissue is developed between the rachises. Striations parallel the arcuate character of this tissue.

The proximal frond fragment (Figure 2.1) was excavated from a block, approximately 10 cm in thickness, resting on the spoils in an abandoned mine. During excavation it was noted that the petiole of this leaf was attached to a highly contorted axis cross-cutting the bedding plane. It is estimated that the axial diameter is 2 cm. Because only a small fragment of the apparent stem of the parental plant has been encountered, no further information concerning the possible habit can be described.

This proximal frond fragment, originally figured in Gastaldo (1985), has never been described. This, in conjunction with other recently collected specimens, permits clarification of several frond features (Figure 2.1–2.3). The overall length of the proximal frond fragment is greater than 0.5 m, with the width of the R2 rachises 0.7 cm throughout their preserved lengths. These rachises are striate, as is the petiole, and display a medial ridge as noted above. The medial ridge occupies approximately 40 percent of the rachial width.

Each pinnule-bearing section of the frond is an isomer of the other with regard to degree of development. The first lateral rachis (R3) to develop is that of the basal exterior lateral pinna (Figure 3), 5.0–5.5 cm distal of the petiolar bifurcation. The length of this basal exterior pinna is greater than 40 cm. It is more elaborate than the remainder of the acroscopic lateral exteriors, and is characterized by pinnules developed on R5 rachises. All exterior R3 rachises diverge from the R2 at angles varying from 135° to 140° (as measured from the basicopic angle), and the angle of departure of the exterior R3's along any R2 appears to remain consistent. The distance between subsequently developed R3's slightly decreases acroscopically, from a maximum of 9.5 cm basally to 6.0 cm apically. Inter-rachial distances between R3 rachises of other frond fragments have been noted to be as great as 13 cm. It is difficult to ascertain inter-rachial distances of R3 exteriors near the terminus of the R2 because these cannot now be differentiated from acroscopic morphologies of the exterior pinnae (P3). The lengths of exterior R3 rachises decrease acroscopically but the exterior outline of the frond section is undeterminable.

As previously described (Gastaldo and Boersma, 1983a), ultimate rachises (R4) are obliquely inserted (principally at 110° basicopic angle; Figure 2.1–2.3). Depending upon position within the frond, though, R4's may be up to 8 cm in length. Ultimate pinnae from adjacent R3 rachises overlap each other in the basalmost portions of the P3 pinnae. The first ultimate

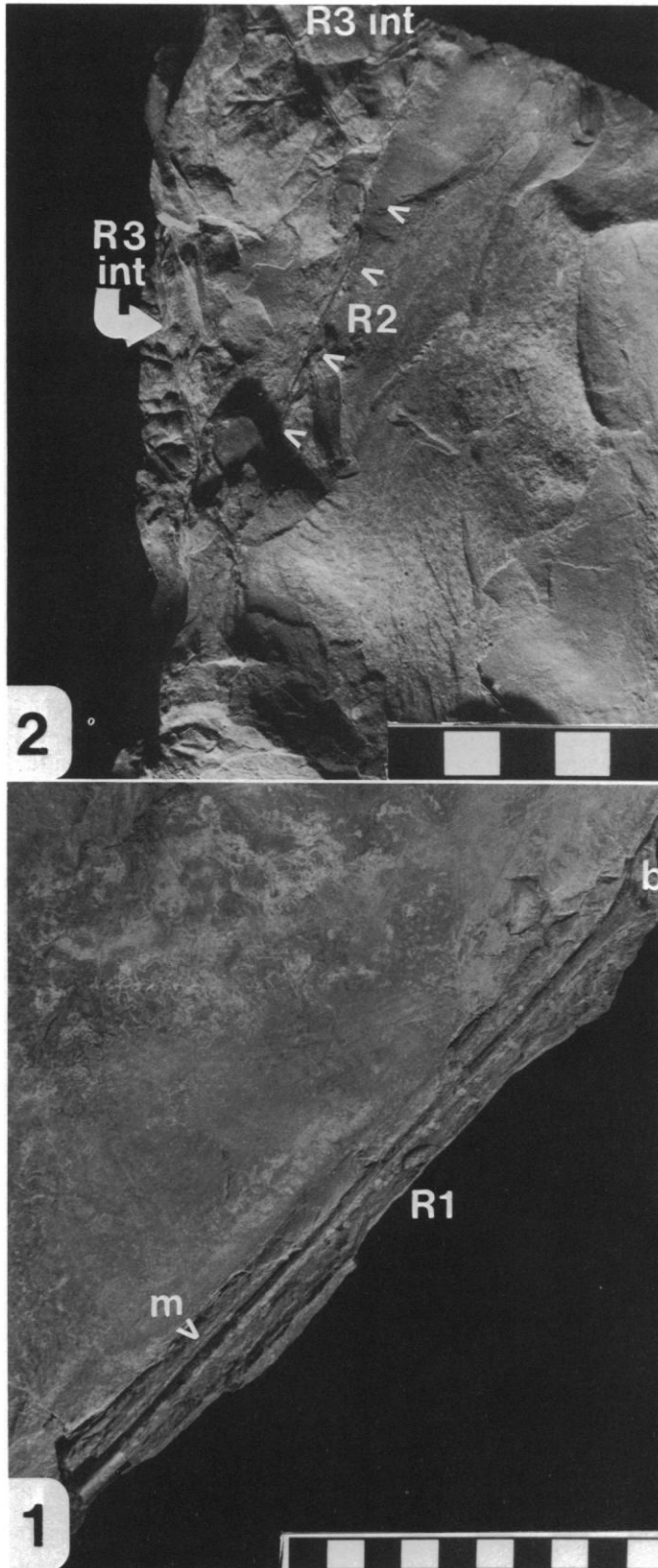


FIGURE 1-1, petiole (R1) of *Sphenopteris pottsvillea* illustrating the point of bifurcation (b) into a bipartite frond, and medial lobed ridge (m) that represents the surface expression of the internal vascularization, one of the rachises resulting from the bifurcation is preserved on the opposite side, scale in centimeters, specimen, USNM 372376A;

pinna (P4) is basiscopic and slightly larger than other ultimate pinnae on the R3. All ultimate pinnae bear alternately, obliquely inserted pinnules, the first of which is borne basiscopically. The number of basiscopic pinnules per ultimate pinna may be as many as 10. The most distal pinnules are fused to an obliquely rhomboidal terminal pinnule and there is no evidence for a spine-like prolongation of the rachis (as in *Karinopteris*, see DiMichele et al., 1984; or *Mariopteris*, see Boersma, 1972).

The basiscopic interior R3 is obliquely inserted (at a 125°–135° basiscopic angle) 10.5 cm distal from the petiolar bifurcation. The angle of insertion of more distal interior R3 rachises appears to remain consistent along each R2. The length of the basalmost R3 is slightly greater than 10 cm, the first ultimate pinna (P4) is basiscopic and is larger than the other ultimate pinnae. It appears that an unshaded, open area exists between the first interior R3 and the petiolar bifurcation. Subsequently developed interior R3's attain lengths greater than 23 cm and overlap each other in the central portion of the leaf. Angles of insertion of ultimate pinnae and characteristics of the pinnules are those as noted above.

#### DISCUSSION

Few specimens of entire fronds or large frond fragments displaying leaf architecture have been collected and illustrated (*Sphenopteris elegans*, Brongniart, 1828; *Eusphenopteris*, Zeiller, 1886; *Lyginopteris*, Scott, 1923; *Dicksonites*, *Tetratmema*, *Mariopteris*, Danzè-Corsin, 1953; *Diploptmema* pro parte, White, 1943; *Neuropteris*, *Paripteris*, *Alethopteris*, Laveine, 1967, 1986, and Zodrow and Cleal, 1988; *Fortopteris*, Boersma, 1972; *Mariopteris*, *Karinopteris*, Gastaldo and Boersma, 1983a, 1983b; *Neuropteris*, *Alethopteris*, Wnuk and Pfefferkorn, 1984). Most known leaf architectures are based on fronds that are less than 0.5 m in length and, because of their small size, are easily recovered when preserved in their entirety (i.e., *Lyginopteris*, 30 cm length; *Dicksonites*, 15–30 cm length; *Tetratmema*, 20 cm length; *Mariopteris*, 50 cm length; *Karinopteris*, 25 cm length). The recovery of a large basal frond fragment, petiolar remains, and numerous rachial fragments of *Sphenopteris pottsvillea* permits a more accurate reconstruction of the leaf architecture of a frond of moderate dimensions and a comparison with architectures of other Carboniferous taxa.

The leaf of *Sphenopteris pottsvillea* is bipartite, consisting of a naked petiole (R1) and two pinnule-bearing sections (Figure 3). The length of the petiole is now known to attain a length of at least 30 cm, although petioles attaining slightly greater lengths probably occur (the dimensions of any particular leaf in the population are dependent upon developmental, nutritional, and edaphic conditions under which the plant lived and, hence, are not valid criteria for the delimitation of taxa). The striations noted to occur along the petiole are most likely the result of the taphonomic processes of dewatering and compression, and not characteristics of the petiole during life. The petiole dichotomizes at a variable acute angle, ranging from 35° to 65°.

The two pinnule-bearing sections (R2's) usually have obliquely inserted lateral rachises (R3's) inserted at angles varying from 125° to 140° (as measured on the basiscopic side) depending upon the position of the R3 along the main rachis. The length of the R2's exceeds 0.5 m. If the spatial relationship of R4 rachises along the R3's is any indication as to the spatial ar-

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2, reverse side of specimen depicting one-half of bifurcation, an R2 rachis bears the first and second R3 interior rachises upon which are borne the pinnules of *S. pottsvillea*, scale in centimeters, specimen, USNM 372376C.

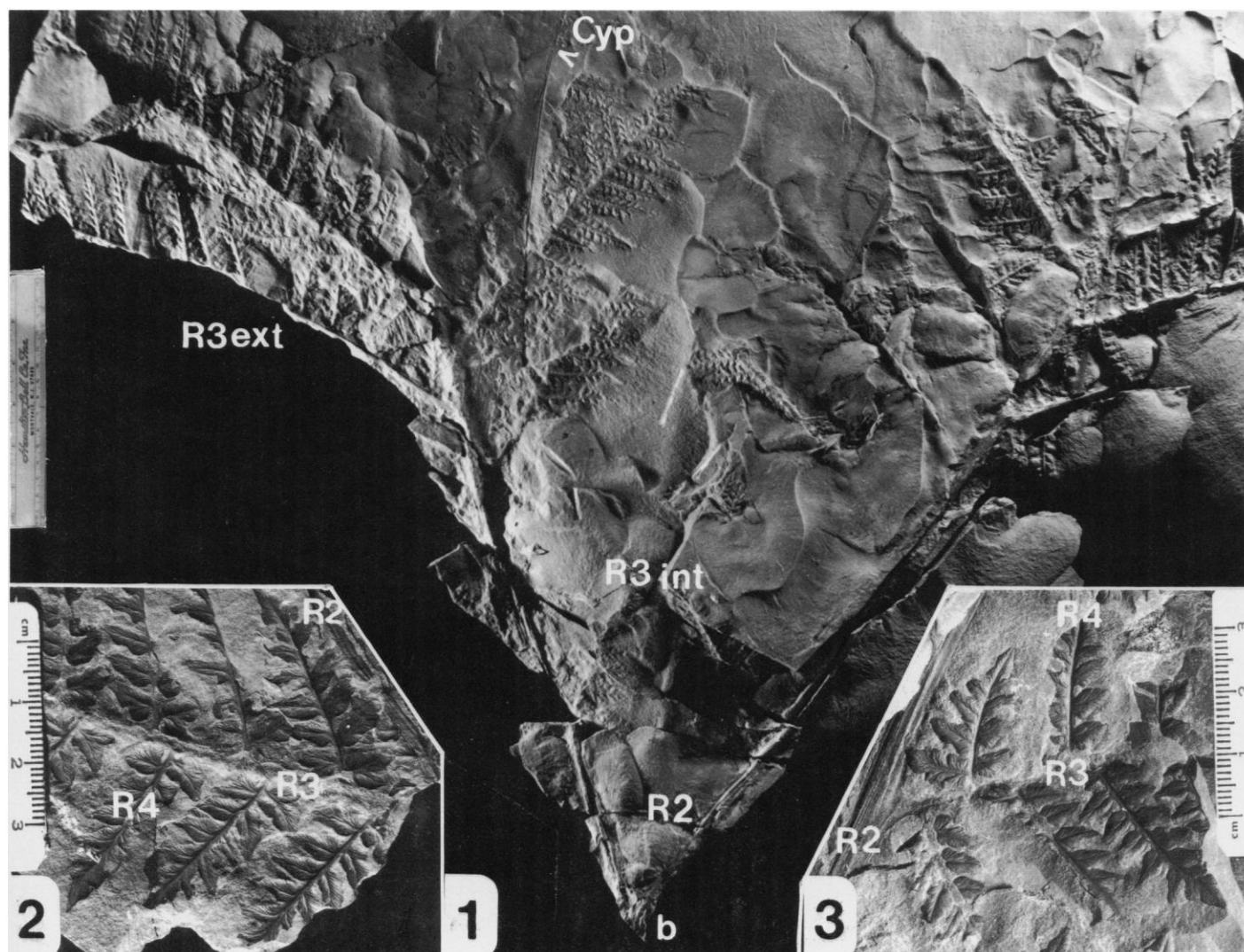


FIGURE 2—1, lower portion of bipartite frond of *S. pottsvillea* illustrating point of bifurcation (b) of rachis into two isomeric pinnule-bearing sections; third order exterior (R3 ext) and interior (R3 int) rachises develop alternately along primary rachis of pinnule-bearing section (R2); although unable to be recovered during excavation, R3 exterior rachises were preserved in the basal basicopic position and represented appropriately in Figure 3; leaves of *Cyperites* (Cyp) also preserved on specimen surface; scale represents 15 centimeters (cm), specimen, USNM 372377; 2, R2 rachis bearing exterior R3 rachis upon which originate ultimate rachises (R4), pinnules characteristic of *S. pottsvillea* occur along ultimate rachises, scale in centimeters; 3, R2 rachis bearing exterior R3 rachis upon which originate ultimate rachises (R4), note that first R4 to develop is in the basal basicopic position, pinnules characteristic of *S. pottsvillea* occur along ultimate rachises (R4's), scale in centimeters.

rangement of R3's along the R2 rachis, then a length of 1.2 m for the R2 is a conservative estimate. The total length of the frond, based upon the specimens herein described, would approach a minimum of 1.5 m.

The first R3 originates in an exterior position. Distances between subsequently developed lateral rachises decrease slightly acropically. On the basal exterior R3's originate penultimate (R4) rachises upon which are borne ultimate rachises (R5) bearing broadly attached, somewhat constricted pinnules. The exterior outline of the secondary pinnae (P2) is somewhat oblong, with the first basicopically developed pinna slightly longer than the others and, therefore, distorting its oblong character. Lateral R3 rachises borne distally have ultimate rachises (R4) upon which are borne the characteristic pinnules. The length of the R4's is such that pinnae of adjacent lateral rachises overlap

each other. The first interior lateral rachises (R3) to be borne occur distal of the first exterior laterals. These first interior laterals are short in length and probably did not overlap each other to any great extent. The basal basicopic pinna is developed more than other pinnae on the rachis. The area bounded by the petiole bifurcation, basal R2 rachises, and first interior R3's was not covered by laminar tissue. The lengths of distal interior lateral rachises increase such that the acropical portions of these R3's overlap and infill the center of the leaf.

The pinnules are lobed on the basicopic side only, and the acropical side is entire. The first borne pinnule is in the basicopic position. Pinnule lobes are ovate and the obliquely rhomboidal terminal pinnule is coalescent with adjacent pinnules. There are no spine-like prolongations of the R3 rachises. Fructifications of the plant are still unknown.

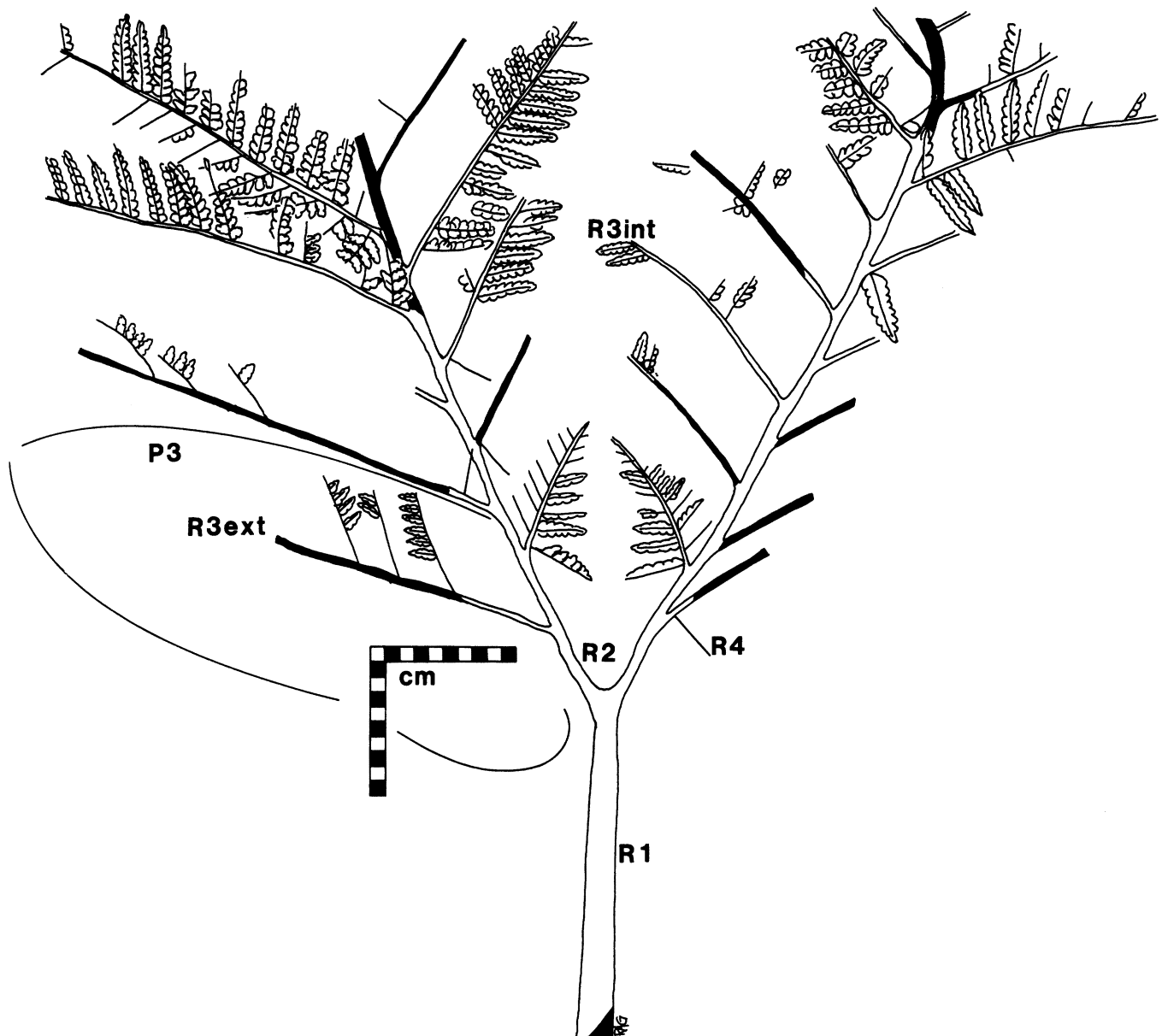


FIGURE 3—Composite line illustration of bipartite frond architecture of *Sphenopteris pottsvillea* (White) Gastaldo and Boersma; characteristics of petiole (R1) and petiolar bifurcation taken from USNM 372376 and USNM 372377; architecture of basal portion of frond copied from field drawings on acetate (originally made at  $\times 1$ ) prior to excavation of specimen; blackened parts of lateral rachises represent portions of frond that are not compressed on bedding surface of specimen figured in 2.1; see text for explanation, scale in centimeters.

#### COMPARISON OF LEAF ARCHITECTURE WITH TAXA CHARACTERIZED BY BIPARTITE FRONDS

Fern-like leaves of a bipartite character generally have been attributed to the Pteridospermales (gymnosperms; Stewart, 1983). In most instances, reproductive behavior of the plants bearing these leaves is unknown, and where fructifications have been reported, as in *Fortoperis*, the reproductive structures have been interpreted to be fern-like (Boersma, 1969, 1972). Several modifications of the bipartite leaf architecture are encountered in Carboniferous specimens. One principal permutation of the basic bipartite pattern is where there is an additional dichotomy of the R2 immediately after the R1 bifurcation. This is most pronounced in the quadripartite and four-parted fronds of the taxa *Mariopteris* (designated M-type by Boersma, 1972), *For-*

*topteris* (Boersma, 1972), *Tetratmema* (Danzé-Corsin, 1953), *Premariopteris* (pro parte; Danzé-Corsin, 1953), *Sphenopteris* (i.e., *S. elegans*, Van Amerom, 1975), and ?*Eusphenopteris* (i.e., *E. sauveurii*, Van Amerom, 1975, Pl. XLVII, fig. 6). This architecture is most dissimilar to that of *Sphenopteris pottsvillea*.

In taxa where the leaf architecture is truly bipartite (K-type according to Boersma, 1972), modifications of the leaf are primarily restricted to the presence or absence of lateral rachises and/or aplebia on the petiole, the increased development of the basal exterior basicopic R3 rachises, or differential development of external and internal R3's. Leaves that bear petiolar rachises include those assignable to *Lyginopteris* (Gastaldo, 1985), *Sphenopteris* (i.e., *S. fragilis*, Kidston, 1923, Pl. XVII, fig. 1), ?*Sphenopteridium* (i.e., *S. pachyrachis*, Kidston, 1923, Pl. LXVIII, fig. 1), *Telangium* (*T. affinis*, Kidston, 1924, Pl.



CII, fig. 1), *Neuropteris* (pro parte, i.e., *N. rarinervis*; see Laveine, 1967), and *Eusphenopteris* (Van Amerom, 1975). Although Van Amerom (1975, fig. 5) reconstructed the frond architecture of *Eusphenopteris* with lateral rachises developed on the petiole, this feature has been documented only in *E. scribanii* (Van Amerom, 1975). The consistency of this character throughout the genus remains unknown.

The extent to which petiolar rachises may be developed is variable. In some taxa, such as *Odontopteris* and some *Neuropteris* (i.e., Zodrow and Cleal, 1988), the petiolar appendages are aphylioid. In addition, the bipartite architecture in *Odontopteris* is modified such that the external R3's bear R4's upon which are borne the characteristic pinnules, whereas the interior R3's only bear pinnules (homologous to the exterior R4's; Laveine, 1967).

Genera in which lateral petiolar rachises or aphylioid appendages are not developed include *Karinopteris* (Boersma, 1972), *Urnatopteris* (i.e., *U. herbaceae*, Danzé, 1956, Pl. XXXVI, fig. 1), *Diplothmema* (White, 1943), *Spathulopteris* (Kidston, 1923, Pl. XLIV, fig. 1), *Calymatotheca* (Kidston, 1924, Pl. CV, fig. 4), and *Dicksonites* (Danzé-Corsin, 1953). From what is known at this time, the architectural modification that exists within this artificial grouping is that of the greater development, in terms of size, of the basal basicopic R4 in the proximal position of the exterior R3 rachises.

The overall leaf architecture of *Sphenopteris pottsvillea* appears most similar to that known in the form genus *Diplothmema*. White (1943, Pl. 28, fig. 1) figured a specimen of *D. cheathamii* collected from the American coal, Alabama, which bears close architectural resemblance, albeit overall size dimensions are smaller (if the scale of reproduction is  $\times 1$ ). A striated petiole (R1) of at least 11 cm bifurcates at an angle of 65° into two pinnule-bearing isomeric parts. The first developed R3 is the basal exterior rachis, and the basal basicopic R4 is developed maximally. It appears that the divergence of this basal basicopic R4 may actually be the result of a proximal dichotomy of the R3. The length of the exterior R3's exceeds 11 cm but, as in the case of *S. pottsvillea*, the exact lengths and overall configuration of the P2's are not known. The interior R3's are developed alternately along the R2 rachis. Again, the basal basicopic R4 is maximally developed and it appears that the divergence of this rachis may be the result of a proximal dichotomy of the interior R3. If the development of the basal basicopic pinnae in both the exterior and interior positions is through a dichotomy of the R3, the architectural construction of *D. cheathamii* would be reminiscent of developmental schemes noted in species of *Neuropteris* and *Odontopteris* (Laveine, 1967).

#### SUMMARY

The collection of *Sphenopteris pottsvillea* leaf fragments from the Lower Pennsylvanian of the southern Appalachian and Warrior Basins has provided the basis for refinement in the understanding of frond architecture of this taxon. Several aspects of the tentative reconstruction provided by Gastaldo and Boersma (1983a, 1983b) can now be authenticated and amplified. The pinnule-bearing sections of the frond originate from the bifurcation of a petiole of moderate length ( $>0.3$  m). No lateral appendages or rachises are borne along the length of the petiole. The angle of bifurcation within the frond is known to have a minimum divergence of 35° and a maximum divergence of 65°, with no one angle of bifurcation predominating the sample population. The first borne lateral rachis (R3) is in the basal exterior position, and the exterior outline of these pinnae is believed to be oblong. The oblong character of exterior pinnae is believed to be distorted due to the development of the basal basicopic pinnule-bearing R4 rachis. Spine-like prolongations of the distal

parts of the rachises have not been observed. Questions concerning the overall configuration of the leaf remain. These include: the attachment of the petiole to the stem and the growth habit of the parent plant; the outlines of the exterior and interior frond sections; the exact apical portion of the leaf; and the method of reproduction. The reproductive biology of the plant and, hence, its true systematic position may ultimately be known only by continued collecting. At the present, the recovery of the large proximal frond fragment, petioles, and lateral pinnae must serve as the basis for our understanding of the leaf architecture of *Sphenopteris pottsvillea*.

#### ACKNOWLEDGMENTS

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 SOCIETY RECORDS AND ACTIVITIES
 

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 REPORT OF THE TREASURER
 

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 For the year 1987  
 (excluding *Paleobiology*)

Balance brought forward from December 31, 1986			
1987 Dues for publication of <i>JP</i>			
Checking account	\$ 43,255.12		
Savings account	0.00		
Cash management account	0.00	\$ 43,255.12	
1987 Dues for other expenses			
Checking account	\$ 12,381.91		
Savings account	0.00		
Cash management account	0.00	\$ 12,381.91	
1987 Nonmbr. subscribers for <i>JP</i>			
Checking account	\$ 2,400.87		
Savings account	0.00		
Cash management account	59,297.23	\$ 61,698.10	
1987 Nonmbr. subscribers for other			
Checking account	\$ 9,509.93		
Savings account	0.00		
Cash management account	0.00	\$ 9,509.93	
1986 Page & plate (use in 1987)			
Checking account	\$ 1,500.00		
Savings account	20,573.31		
Cash management account	5,901.00	\$ 27,974.31	
1987 Page & plate (use in 1988)			
Checking account	\$ 0.00		
Savings account	5,576.54		
Cash management account	0.00	\$ 5,576.54	
PS general fund			
Checking account	\$ 8,834.90		
Savings account	8,485.51		
Cash management account	62,769.50	\$ 80,089.91	
Revolving publication fund			
Checking account	\$ 0.00		
Savings account	4,687.11		
Cash management account	7,650.20	\$ 12,337.31	