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Comments

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RECONSTRUCTION AND ARCHITECTURE OF MEDULLOSAN PTERIDOSPERMS (PENNSYLVANIAN)

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Abstract

A new reconstruction of the architecture of medullosan pteridosperms is proposed on the basis of three stems preserved as compression-impression fossils: one from the Southern Anthracite Coal Field of Pennsylvania (lower part of Llewellyn Formation, Pennsylvania, Westphalian D) probably belonging to *Alethopteris* foliage; a second stem from the roof shale of the Eagle coal bed (Kanawha Formation, Middle Pennsylvanian, Westphalian B) of West Virginia, associated with *Neuropteris* foliage; and a third reported from the Stephanian of Commentry, France, in connection with *Odontopteris* foliage. The diameters of the Llewellyn, Eagle, and Commentry stems are 17 cm, 13 cm, and 6.5 cm, respectively. All three stems bear remnants of petioles up to several centimeters in length. The petiolar remanants indicate that the living leaves grew upward at an angle of 30°-60° from the vertical, a growth habit that is common in present day tropical plants with similar overall architecture. Leaves drooped only when they were dying. After decay they broke off and left short petiolar remnants bent downward. The Llewellyn and Eagle stems represent plants with thick, straight stems, whereas the Commentry specimen shows a thin and slightly curved stem.

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Introduction

The medullosan pteridosperms were important elements of late Paleozoic, Euramerican tropical lowland floras. Their remains are represented by the permineralized stems *Medullosa* and *Sutcliffia*, the detached foliage *Neuropteris*, *Alethopteris*, and *Odontopteris*, seeds such as *Pachytesta*, and by numerous male fructifications such as *Dolerotheca* and *Whittleseya* (Stidd, 1981).

A number of workers have produced reconstructions of the medullosan pteridosperms based primarily on the anatomy of the permineralized stems and the morphology of compressed foliar members (Andrews, 1947; Bertrand & Corsin, 1950; Stewart & Delevoryas, 1956; Corsin *in* Buisine, 1961). Figure 1 shows these reconstructions at approximately the same scale. Recent work on reconstruction of medullosan pteridosperms has concentrated on the stelar anatomy (Basinger *et al.*, 1974) or on plant part association (Stidd, 1981).

In addition to the well-known permineralized stem and compressed foliage taxa, the stems of medullosan pteridosperms are known to occur as compressions. The presence of nonanastomosing sclerotic strands in the outer cortex of the upper portions of stems and on petioles produced a striated pattern in compressed specimens, a feature which led Grand'Eury (1877) to propose the generic name *Aulacopteris* for these axes (see Remy & Remy, 1977, for current usage of this genus). This striation is distinctly different from the one found on root mantles of tree ferns and on the decorticated trunks of other plant groups. Petioles and trunks of medullosan pteridosperms are therefore readily recognizable. Pteridosperm stems are rare in compression floras, while petioles are quite common. This fact reflects the difficulty in obtaining sufficient bedding-plane surface to see a stem, the difficulty in collecting them, and certainly, specific taphonomic conditions that negatively bias the preservation of pteridosperm stems in ancient clastic sediments. Although rare, compressed stems of medullosan pteridosperms provide excellent material with which to improve reconstructions of this group of plants. They do not preserve anatomical detail but permit determination of outer stem morphology and length, not readily obtainable with permineralized specimens. In addition, compression specimens can supply information on phyllotaxy. Therefore, compression stems can be an excellent basis for the description of growth habits of medullosan pteridosperms.

This paper provides data on the growth habits of medullosan pteridosperms derived from three compressed stems, combined with a consideration of the architecture and growth habits of modern tropical monoaxial trees. We suggest that medullosan pteridosperm leaves were borne in a fashion similar to modern tree ferns and palms and that the bases of petioles often remained attached to the stem in a downward-bent position after the death of the leaf.

Description of Material

The first stem was found in the shale below the Skidmore No. 7 coal bed of the lower part of the Llewellyn Formation (Middle Pennsylvanian, upper Westphalian D) of the Southern Anthracite Coal Field. The locality is an old strip mine about 2.7 km northeast of St. Clair on the Pottsville, Pennsylvania, quadrangle (UTM, zone 18, 4 02 500 mE, 45 09 250 mN). The specimen (PENN-001) has been placed in the paleobotanical research collections of the Department of Geology, University of Pennsylvania.

The Llewellyn stem is a fragment that is 82 cm long and on average 17 cm wide (Fig. 2). The sides are not completely parallel but show some upward flaring where petioles were attached. Three petiole bases are visible, having diameters between 4-5 cm, and are bent outward but not downward. The associated compression-impression flora is dominated by *Alethopteris* foliage but also contains *Neuropteris* pinnules and pinnae (Scheihing & Pfefferkorn, 1980).

The second stem is from the roof rocks of an abandoned adit in the Eagle coal bed (Kanawha Formation, Middle Pennsylvanian, Westphalian B). The locality is on the hillside just south of the town of Kingston, Fayette County, West Virginia, on the Pax quadrangle (UTM, zone 17, 4 73 170 mE, 42 01 000 mN). This stem was photographed and measured in the field and later collected. It has the Pennsylvanian System stratotype (Englund *et al.*, 1979) collection number PSS-79-301.

The Eagle stem is a fragment 47 cm long and on average 13 cm wide. Three petiole bases are preserved. They depart from the stem at distances of 13 and 14 cm. The petioles are 5, 6, and 7 cm wide (Fig. 3). *Neuropteris* is the only pteridosperm foliage in the associated flora.

The third stem, described by Zeiller (1888) from the Stephanian of Commentry, France, was attributed to *Odontopteris* foliage. The stem was measured and drawn in the field, but only the central portion of the stem is preserved in the Museum National d'Histoire Naturelle in Paris in the Collection Fayol under number 10719.

The Commentry stem is a complete or nearly complete stem. It is 211 cm long and 4 to 6.5 cm wide. Eighteen petioles are visible. Two to three petioles depart more or less at the same level. These levels are 10 to 30 cm apart (Fig. 4). The stem is slightly curved. A detached leaf lay next to the stem when found and the position indicated that it might have belonged to the stem. Zeiller (1888) used this association to assign the stem to the genus *Odontopteris*.

The width of stems and petioles given for compression-impression specimens is that measured

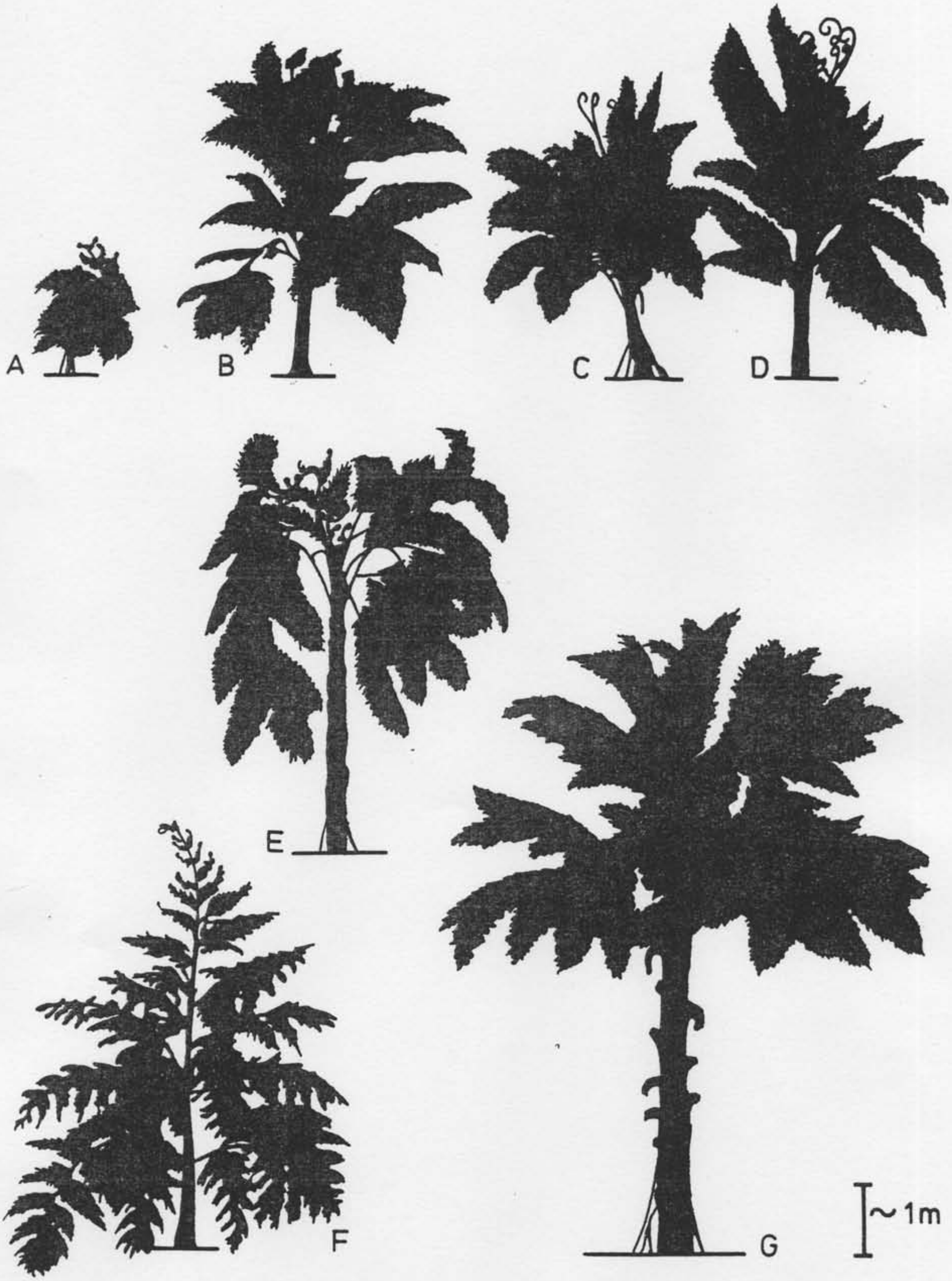

Figure 1. Comparison of previous reconstructions of medullosan pteridosperms (*A-F*) with that proposed here (*G*). All figures redrawn approximately to the same scale. *A*, Andrews (1947): *B*, *C*, *D*, Bertrand & Corsin (1950); *E*, Stewart & Delevoryas (1956); *F*, Corsin *in* Buisine (1961).

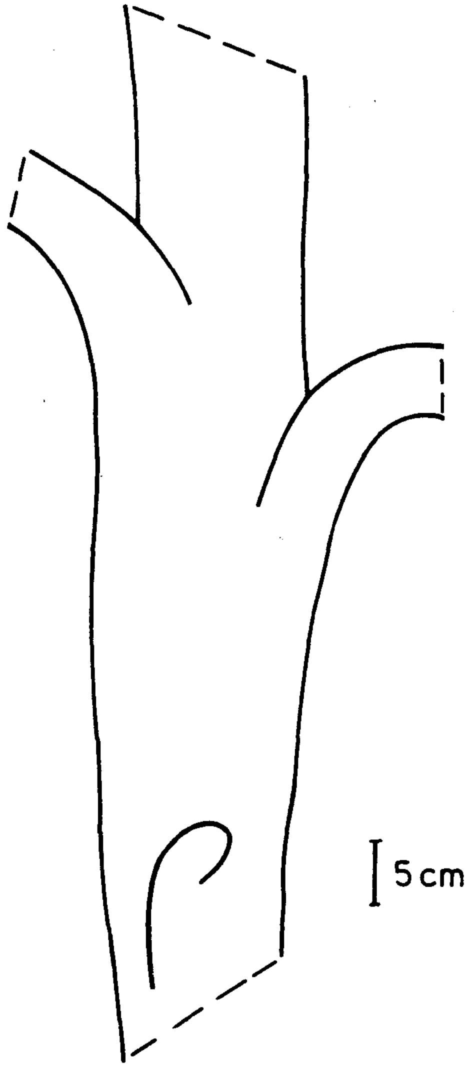

Figure 2. Outline of pteridosperm stem fragment with three petiole bases from the shale below the Skidmore No. 7 coal bed, Llewellyn Formation, upper Westphalian D, near St. Clair, Pennsylvania.

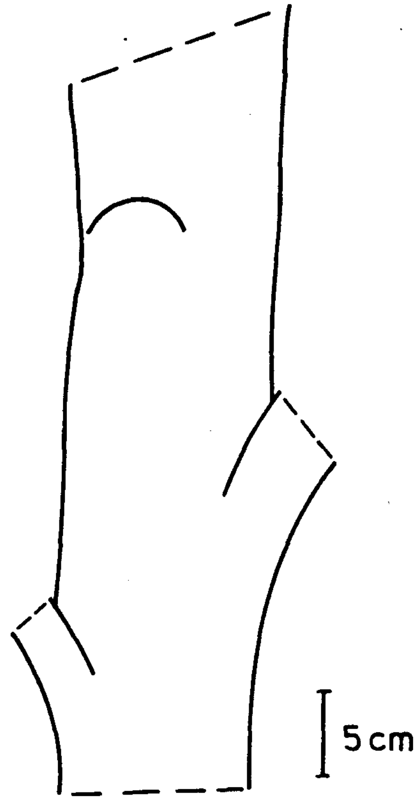

Figure 3. Outline of pteridosperm stem fragment with three petiole bases from the roof shale of the Eagle coal bed, Kanawha Formation, Westphalian B, Kingston, West Virginia.

on the rock. These measurements are used without correction because deformation during fossilization occurred mainly in the vertical dimension. This had been assumed by Walton (1936) and Schopf (1975) and was demonstrated experimentally by Rex & Chaloner (1983).

Discussion

All the previous reconstructions shown in Figure 1 were figured without scale but leaf size, stem diameter, or references in the text could be used to establish size and they are shown at approximately the same scale. Andrews (1947) (Fig. 1*A*) presented a combination of *Alethopteris* foliage with a *Medullosa* stem. The plant was about 2 m high. Only one mature leaf is shown in a hanging position. It is clear from the reconstruction that about five other leaves have been left off to show the stem. The stem is thin, curved, and shows bases of petioles that all extend for the same distance from the stem. The hanging leaves represent an unlikely growth habit and certainly one that could not be maintained by a younger plant with a shorter stem. Bertrand & Corsin (1950) gave three separate reconstructions for plants with *Neuropteris*, *Alethopteris*, and *Odontopteris* foliage (Figs. 1*B-D*). The plants are 3 to 4 m high, have straight and thick stems, and carry four to six active leaves each. The leaves are shown in natural-looking positions from nearly upright to horizontal. However, only one leaf base of a shed leaf is shown and the living leaves are attached over more than half the length of the existing stem. Stewart & Delevoryas' (1956) reconstruction (Fig. 1*E*) is the one most widely used today. The plant is 4 to 5 m high. Living leaves are attached only in the uppermost part of the stem, which is straight and thick. Remnants of leaf bases protrude very little from the stem. However, mature, living leaves are shown to droop at least in part. Buisine (1961) figured a reconstruction that Corsin had done but never published (Fig. 1*F*). The growth habit shown is that of a modern, young gymnosperm tree growing in the temperate realm and not that of a monoaxial tropical tree.

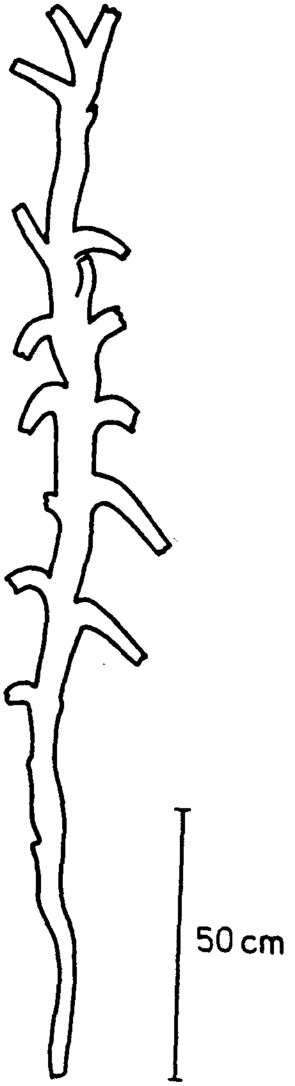

Figure 4. Outline of pteridosperm stem from Commentry figured by Zeiller (1888). The tip of the stem is straightened out.

The medullosan pteridosperms were tropical, monoaxial plants. Therefore, Hallé, Oldeman & Tomlinson (1978) assigned the medullosan pteridosperms to their Corner's Model (monoaxial trees with lateral inflorescenses and continuous growth). This is a very common growth habit in tropical plants today and occurs in many unrelated taxa. The leaves are attached near the upper end of the stem and form a tuft (our reconstruction, Fig. 1*G*). In most cases the attachment points of the living leaves are very close to the top of the stem so that the leaf bases are protecting the immature leaves and the single meristem.

Leaves in tuftlike arrangement can circumscribe planes that are either funnel-shaped, umbrella-shaped, or in the form of a horizontal disk (Hallé *et al.*, 1978, p. 295). In many monoaxial tuft trees, the young leaves will form a funnel, whereas the mature leaves form a disk-shaped crown or an umbrella. Dead or dying leaves would droop and could either hide the stem or fall off. In either case, petiole bases often would remain, protruding from the stem. The extent of protrusion might have been species specific and in some species leaves might have broken off close to the stem, as in Stewart & Delevoryas' (1956) reconstruction.

The specimens under consideration are long enough to allow an evaluation of petiole arrangement. The Commentry stem (Fig. 4) shows one, two, or three petioles at each of eight levels. Considering that petioles hidden beneath the stem or those projecting towards the observer are obscured in compression preservation, one can reasonably assume that the levels where one or two petioles are observed may have had three petioles departing at more or less the same level. This would mean that three leaves were departing from the stem at about the same level. The same situation is clearly shown in the stem fragment of an unidentified medullosan stem figured by Remy & Remy (1977, p. 116). Petioles on the Llewellyn and Eagle stems are further apart from each other but also seem to be arranged 120° apart. This angular spacing is similar to observations of *Medullosa* in coal balls where three petioles can be recognized in many cross sections in the cortical layer (see Stewart & Delevoryas, 1952, figure 2; Basinger *et al.*, 1974).

In the Llewellyn and Eagle stems, petiole bases are spaced more than 10 cm apart along the length of the stem. This is a different growth form than that of the Commentry stem. These two habits could be nearly identical anatomically and could occur in very closely or in distantly related plants. However, the outward appearance of the plants could be quite distinct. Species having closely-spaced petioles would have a more tuftlike appearance. In the other group, living leaves could be present over a greater length of the stem. In this arrangement, the leaves could appear either tuftlike (as in our reconstruction) or more like the crown of branching trees. This latter habit was reconstructed by Bertrand & Corsin (1950). The petioles of medullosan pteridosperms are relatively thick and attain the diameter of branches of smaller present-day trees; thus, the petioles of pteridosperms functionally can be equated with "throw away branches" (Givnish, 1978).

The flaring of the stems just below a petiole departure is seen in all three specimens and quite clearly shown in the preserved middle portion of the Commentry stem (Fig. 5). This feature will influence the overall appearance of the stem less in those stems where petiole departures do not occur at one level.

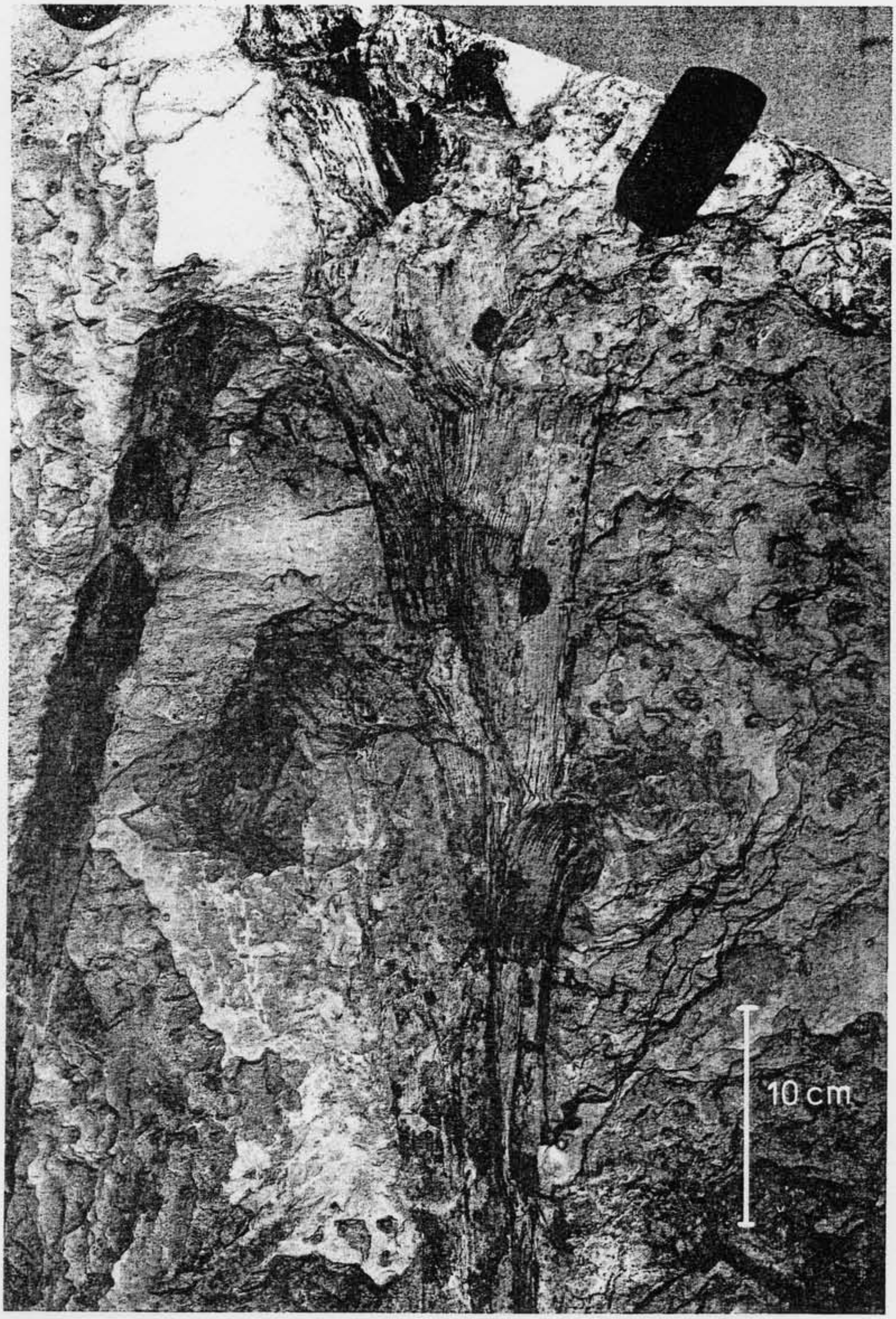

Figure 5. Partial view of Zeiller's pteridosperm stem from Commentry showing the striation produced by the sclerenchyma bundles in the cortex and the conical upward thickening of the stem below a petiole. Specimen No. 10719, Fayol Collection, photo Museum National d'Histoire Naturelle, Paris.

Figure 6. Reconstruction of *Medullosa* plant with thick, straight stems. Area of loss of petiole bases could have extended higher up the stem.

The three stems seem to represent two different growth forms present among the pteridosperms. One is represented by the stem from Commentry. The stem is thin and curved. More stems of this appearance have been found by Christopher Wnuk and have been described in detail elsewhere (Wnuk & Pfefferkorn, 1984).

The second growth form has a thicker stem that stands straight (as far as one can tell from the fragmentary specimens). The stem was apparently columnar and maintained its thickness to the top. Our reconstruction of the thick-stemmed pteridosperms is presented in Figure 6. The number of leaves remained about the same during the plant's life (after an initial, immature phase had passed). The major change in features was that the stem became taller with proportionally more area covered by petiole bases. As the stem grew taller, petiole bases were sloughed off in the lower part of the stem and adventitious roots grew out of that part of the stem.

Conclusions

1. Medullosan pteridosperms were monoaxial stems that held their living leaves in an upright to horizontal position. Only old, dying, or dead leaves would droop.

2. Petioles rotted off at irregular distances from the stem, often leaving downward-bent petiole bases on the stem.

3. In some species petioles would form a tight spiral with closely spaced petioles. In other species petioles were spaced 10 cm or more apart.

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References Cited

ANDREWS, H. N. 1947. *Ancient plants and the world they lived in.* Ithaca, N.Y.: Comstock Press, 279 pp., 166 figs.

BASINGER, J. F., G. W. ROTHWELL, & W. N. STEWART. 1974. Cauline vasculature and leaf trace production in medullosan pteridosperms. *Am. Jour. Botany*, 61:1002-1015, 19 figs.

BERTRAND, Paul, & Paul CORSIN. 1950. Reconstitution de tableaux de végétation fossile. *Annales de Paléontologie*, 36:126-144.

BUISINE, Michel. 1961. *Les Alêthoptêridées du Nord de la France.* Études Géologiques, Service Géologique Houillerès du Bassin du Nord et du Pas-de-Calais, vol. 4, 317 pp., 74 pls.

ENGLUND, K. J., *et al.* (eds.). 1979. *Proposed Pennsylvanian System stratotype, Virginia and West Virginia.* Field Trip No. 1, Ninth International Congress of Carboniferous Stratigraphy and Geology, American Geological Institute Selected Guidebook Series, No. 1, 136 pp.

GIVNISH, T. J. 1978. On the adaptive significance of compound leaves, with particular reference to tropical trees. *In:* P. B. Tomlinson & M. H. Zimmermann (eds.), *Tropical trees as living systems.* Cambridge: Cambridge University Press, pp. 351-380, 4 figs., 8 tbls.

GRAND'EURY, C. 1877. *Flore Carbonifère du Département de la Loire et du Centre de la France.* Mém. Inst. Acad. Sc. de France, vol. 24, 348 pp., 34 pls., 4 tbls.

HALLÉ, F., R. A. A. OLDEMAN, & P. B. TOMLINSON. 1978. *Tropical trees and forests. An architectural analysis.* Berlin: Springer-Verlag, 441 pp., 111 figs.

REMY, Winfried, & Renate REMY. 1977. *Die Floren des Erdaltertums. Einführung in Morphologie, Anatomie, Geobotanik und Biostratigraphie der Pflanzen des Paläophytikums.* Essen, Germany: Glückauf Verlag, 468 pp., 248 figs.

REX, G. M., & W. G. CHALONER. 1983. The experimental formation of plant compression fossils. *Palaeontology*, 26: 231-252.

SCHEIHING, M. H., & H. W. PFEFFERKORN. 1980. Morphologic variation in *Alethopteris* (pteridosperms, Carboniferous) from St. Clair, Pennsylvania, USA. *Palaeontographica*, B, 172:1-9, 3 figs., 3 tbls., 1 pl.

SCHOPF, J. M. 1975. Modes of fossil preservation. *Review of Palaeobotany and Palynology*, 20:27-53.

STEWART, W. N., & T. DELEVORYAS. 1952. Bases for determining relationship among the Medullosaceae. *Am. Jour. Botany*, 39:505-516, 27 figs.

———. 1956. The medullosan pteridosperms. *Botanical Review*, 22:45-80, 16 figs.

STIDD, B. M. 1981. The current status of medullosan seed ferns. *Review of Palaeobotany and Palynology*, 32:63-101, 9 figs.

WALTON, J. 1936. On the factors which influence the external form of fossil plants: With descriptions of the foliage of some species of the Palaeozoic Equisetalean genus *Annularia* Sternberg. *Royal Soc. Philos. Trans.*, 226:219-237.

WNUK, Christopher, & H. W. PFEFFERKORN. 1984. The life habit and paleoecology of Middle Pennsylvanian medullosan pteridosperms based on an *in situ* assemblage from the Bernice Basin (Sullivan County, Pennsylvania, USA). *Review of Palaeobotany and Palynology*, 41:329-351.

ZEILLER, R. 1888. *Etudes sur le terrain houiller de Commentry.* Vol. 2, Flore fossile. Saint-Etienne, France: Theolier et Cie., 366 pp., 43 pls.