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NEW OCCURRENCE OF *PERIASTRON RETICULATUM* UNGER EMEND. BECK, AN ENIGMATIC MISSISSIPPIAN FOSSIL PLANT

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ABSTRACT—Two new specimens of *Periastron reticulatum* Unger emend. Beck have been collected from the Erin Slate, Talladega Slate Belt, southern Appalachians. Preserved anatomical features provide a basis for an expanded understanding of the genus and provide a biostratigraphic basis for dating the uppermost unit of the Talladega Slate Belt.

INTRODUCTION

THE GENUS *Periastron* was established nearly a century and a half ago by Unger (1856) for a single specimen from the Unterculm (Lower Carboniferous) at Saalfeld, Thuringia, Germany. Since then, the taxon has been identified in the United States from the Lower Mississippian New Albany Shale (Scott and Jeffrey, 1914; Read, 1936; Beck, 1978), and in France from the Tournaisian Lydiennes Formation in the Montaigne Noire (Bertrand et al., 1935; Böhm, 1935). Beck (1978) provided an excellent review of its histology and a revision of the genus. *Periastron* is known only from permineralized axes, all of which are interpreted to be petioles because of axial bilateral symmetry. Its anatomical features are unique in the paleobotanical record, and this taxon cannot be confused with any other mid- to late Paleozoic form. Unfortunately, its systematic affinity is a mystery. Recently, two moderately well preserved (and several very poorly preserved) silicified *Periastron* have been collected from the Erin Slate, a low-grade metamorphic phyllite of the Talladega Slate Belt, southern Appalachians (Gastaldo et al., 1993). These specimens display some features not previously recognized in the taxon and establish paleontological evidence for dating the rock sequence.

COLLECTION SITE AND METHODS

Specimens were collected from two localities within the Erin Slate, southwest of the town of Erin, Alabama (Figure 1). Specimens 121388.1 and 61091.35 were recovered from the phyllite outcrop on the north side of the railroad cut (NW¼, NE¼, Sec. 28, T19S, R7E Clairmont Springs 7.5′ quadrangle), whereas more poorly preserved specimens were recovered as float in the field west of the road running north towards Clairmont Gap (E½, SW¼, Sec. 21, T19S, R7E Clairmont Springs 7.5′ quadrangle). It is nearly impossible to discern in the field whether or not the elliptical–rounded and elongate structures are fossil plants or slightly deformed primary sedimentary structures. Therefore, it is necessary to cut and polish one surface before preliminary identification as either. It was not apparent that specimen 121388.1, when first collected, was a fossil and the specimen did not appear physically similar to those reported previously. The fossiliferous nature of the Erin Slate was controversial (Gastaldo and Cook, 1982; Tull et al., 1988). To identify the affinities of the specimen it was first slabbed transversely, then longitudinally prior to thin sectioning. This resulted in only one complete transverse section of what is now recognized as the main axis. After the longitudinal section was examined and a diverging lateral axis was recognized, this axis was serial-sectioned to a point where wafering on a Leco Vari/Cut VC50 became difficult due to blade constraints. This resulted in thin sections of only one-half of the diverging lateral axis. In order to determine the extent to which vascular tissues were preserved in the main axis, serial thin sections were made above and below the point of departure of the lateral axis. The other specimen (61091.35) was thin-sectioned in an attempt to determine if the vascular bundles dichotomized or anastomosed as reported by Beck (1978). Additional poorly preserved axes are represented in the collection generally by thin sections made to determine the quality of specimen preservation.

Coverless thin sections were prepared by Quality Thin Section, Tucson. Thin sections were photographed glass-side up on a Tru-View light box with a 50 mm macro lens/Olympic OM-1 camera, using a variety of filters to enhance contrast. Photomicrographs were taken using a Zeiss Axioskop and an accessory Dolan-Jenner Fiber Lite. Specimen descriptions will follow Beck's (1978) presentation for ease of comparison.

SPECIMEN 61091.35 (USNM 455482)

This small specimen measured about 1.5 cm in axial length and 1.5 cm in axial width. It was cut into 15 serial transverse sections (61091.35.0–61091.35.14), in which a row of only four medially aligned vascular bundles can be seen in each (Figure 2.1). There is an aerenchymatous cortex on either side of the vascular bundles that is surrounded by sclerenchymatous tissue. Secretory ducts are embedded within this outer cortex (Figure 2.2). It is difficult to observe all the histological features described by Beck (1978) because of the mode of tissue preservation and recrystallization resulting from low-grade metamorphism.

The medial row of vascular bundles is nearly straight (61091.35.1) to slightly arcuate (61091.35.11) in transverse section. Individual bundles vary in transverse configuration from subcircular to elongate, and may exhibit an indentation (longitudinal groove of Beck, 1978) on one surface. Vascular tissues do not occur in all vascular bundle sites throughout the specimen. One vascular bundle, in particular, is very poorly preserved and there is only one nearly circular bundle that is 1,360 μm in diameter. One vascular bundle, measuring a maximum of 1,480 μm in greatest transverse dimension, exhibits a single indentation. There is no evidence of secondary xylem and the conspicuous bundle sheath reported by Beck (1978) is not preserved. Protoxylem cannot be discerned, and primary xylem consists of tracheids, polygonal in transverse section, averaging 88 μm in diameter (N = 28).

The aerenchymatous cortex in transverse section appears to consist of variable-sized lacunae. These are larger on either side of the central point in the vascular bundle row, decreasing in size toward the areas opposite the ends of the vasuclar bundle row. Preserved length and width dimensions range from a maximum of 1,110 μm × 707 μm to a minimum of 353 μm × 515 μm, with the average size of all lacunae measured 644 μm × 412 μm (N = 10). Where preserved, air chambers are separated

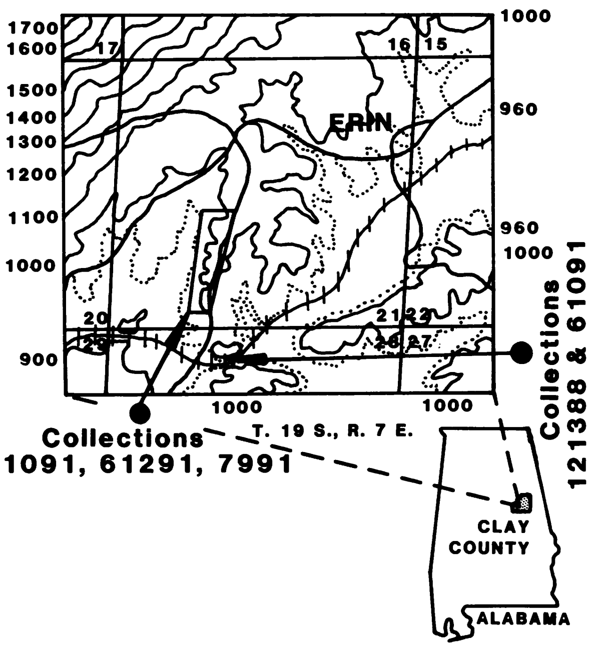

FIGURE 1—Collection sites within the Erin Slate, Clay County, Alabama. Specimens 121388.1 and 61091.35 were collected from the phyllite outcrop on the north side of the railroad cut (NW¼, NE¼, Sec. 28, T19S, R7E Clairmont Springs 7.5′ quadrangle), whereas more poorly preserved specimens were recovered as float in the field west of the road running north towards Clairmont Gap (E½, SW¼, Sec. 21, T19S, R7E Clairmont Springs 7.5′ quadrangle).

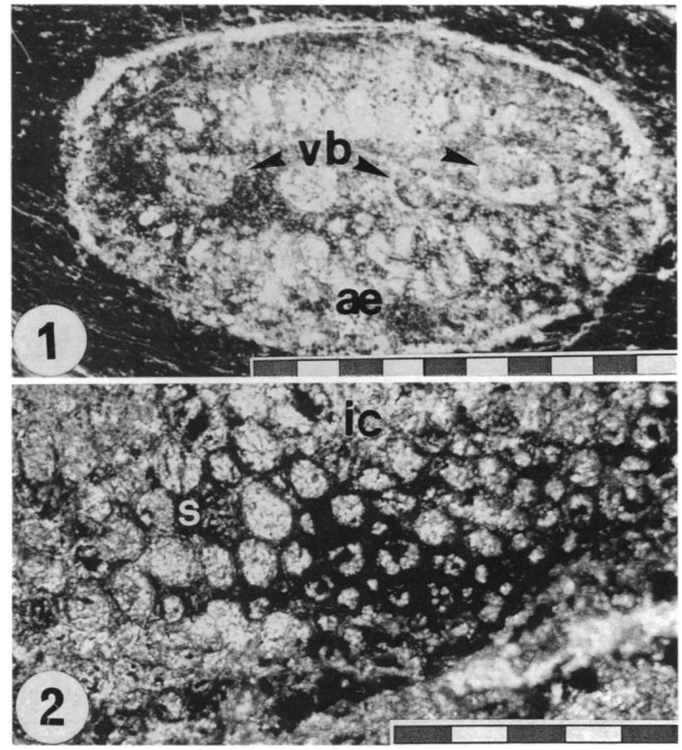

FIGURE 2—*Periastron reticulatum* Unger emend. Beck; specimen 61091.35.11 (USNM 455482). *1,* transverse section in which four medially aligned vascular bundles (vb) are surrounded by aerenchymatous tissues (æ); a sclerenchymatous cortex is preserved to the exterior of the aerenchyma; scale equals 10 mm. *2,* enlargement of cortical area in which a secretory duct (s) is surrounded by the enlarged cortical cells of the inner cortex (ic); compare with Beck's (1978) figures 32–34; scale equals 500 μm.

by sheets of thin-walled parenchyma, one to three cell layers thick.

The outermost cortical cells are polygonal in shape and range in size from 51 to 101 μm (average 72 μm; N = 35). Cortical cells outside of the lacunae have an average diameter of 144 μm (range 101 to 191 μm; N = 35). Where secretory ducts can be identified (Figure 2.2), they are located in the periphery of the sclerenchymatous zone and may be nearly circular in transverse shape. The average diameter of identifiable secretory ducts is 140 μm.

SPECIMEN 121388.1 (USNM 455483)

This specimen comprises a main axis from which a lateral axis diverges (Figures 3, 4). This lateral axis exhibits the characteristic features of *Periastron,* although there is no indication in the main axis of a medial alignment of vascular bundles. The specimen was partially decomposed prior to permineralization, and, overall, it is not extremely well preserved. Scattered pyrite occurs within voids and cellular lumens; fungal hyphae appear to be present within aerenchymatous chambers of the lateral axis (Figure 4.1). The specimen measures over 11 cm in length and 4.5 cm in width, and is vertically compressed to an elliptical shape.

Main axis.—The central portion of the main axis appears to have been degraded prior to compression (Figure 4.3–4.7). Aerenchymatous lacunae can be seen to extend only for approximately two-thirds of the circumference of the axis, after which there is no evidence for the remainder of the lacunae. Lacunae are of variable shape (probably due to distortion by compaction), but, in general, are circular to elongate (average 621 μm length × 280 μm width; N = 17). Polygonal to nearly isodiametrical cells are preserved between lacunae. There is a central linear void that extends both transversely and longitudinally through the specimen (Figures 4.5–4.7). This degraded site could have marked the position of vascular tissue. No vascular tissue has been identified without doubt in the axis, although one area of concentrated cells may have represented one xylary strand (Figure 4.4). This is equivocal because the cells that comprise this group have been crushed, and there is no evidence that the cell walls were any thicker than the polygonal to isodiametric cells within the cortex. These cells do not appear similar to the tracheary elements preserved in specimen 61091.35. Sections made above (Figure 4.6) and below (Figure 4.7) the departure of the lateral do not preserve xylary elements. The vast majority of the cortex is degraded, and there is no possibility to evaluate the position of secretory ducts in this axis.

In longitudinal section, the central axis can be seen to flare beneath the point of origination of one lateral axis (Figure 4.3), and it appears that a second lateral axis diverged at a position almost opposite, but slightly higher (confirmed in thin sections 121388.1.10A and 121388.1.11A where there is a partially preserved lateral axis adjacent to the main axis). Divergence from the main axis is nearly perpendicular. Xylary tissues are not preserved in this section, although aerenchymatous lacunae can be identified. These lacunae appear to be continuous chambers for distances less than 1 cm through the length of the axis, as deduced from their relative position and variability of lacunar thickness. The maximum width of a lacuna (representing the medial longitudinal cut of the tube) is 1,160 μm, and lacunae can be traced from the main axis into the lateral axis. Isodi-

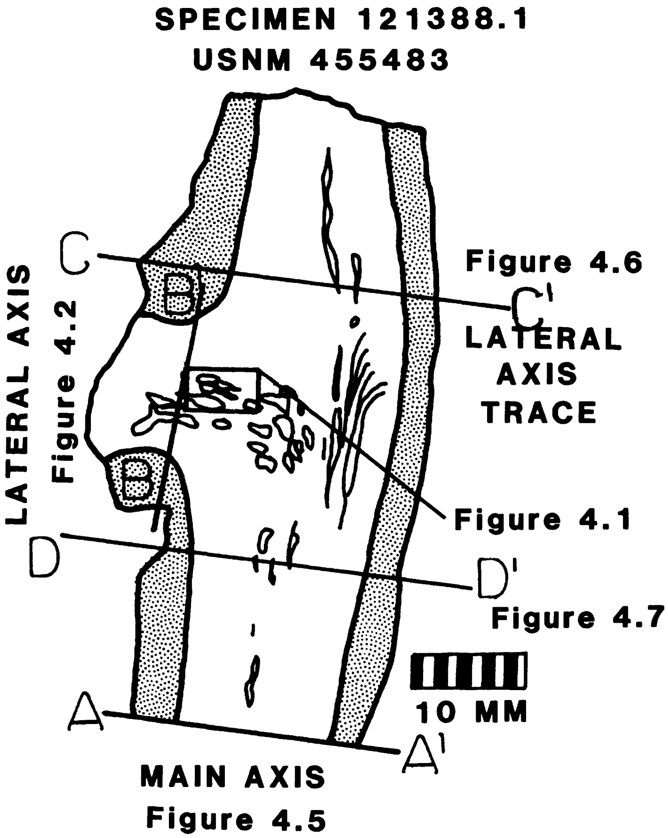

FIGURE *3*—Illustration of longitudinal section of *Periastron reticulatum* Unger emend. Beck main axis upon which are designated the positions of Figure 4.1 (within box), 4.5 (transverse main axial section A–A'), 4.2 (transverse lateral axial section B–B'), 4.6 (transverse main axis above departure of lateral C–C'), and 4.7 (transverse main axis below departure of lateral D–D'). Scale equals 10 mm.

ametrical to elongate-rectangular cells are preserved between lacunae. The variability in shape may be a function of alteration and decay prior to permineralization. Nearly isodiametric cells average 50 μm in diameter, whereas elongate-rectangular cells vary from 101 μm × 50 μm to 252 μm × 50 μm (average size 172 μm × 68 μm; N = 20). The end walls of these latter cells appear tapered, but this may be the result of the loss of structural integrity prior to silicification.

Lateral axis.—The lateral axis is represented by a partial transverse section in which two medially arranged vascular bundles are seen adjacent to two circular zones of tissue that may have been vascular bundles (Figure 4.2). This section represents more than half of the axis (probably two-thirds), which would indicate that the lateral axis possessed at least four and possibly five to six medially aligned vascular bundles. Each vascular bundle is nearly circular (average diameter 1,365 μm). The two exterior vascular bundles and possible two interior bundles are arranged in a slightly arcuate configuration. Vascular tissues are not preserved in any vascular bundle site. The conspicuous bundle sheath reported by Beck (1978) is not preserved.

The aerenchymatous cortex in transverse section appears to consist of variable-sized lacunae. These are larger on either side of the central point in the vascular bundle row, decreasing in size toward the areas opposite the end of the vascular bundle row. Preserved length and width dimensions range from a maximum of 1,111 μm × 450 μm to a minimum of 247 μm × 143 μm, with the average size of all lacunae measured 621 μm × 280 μm (N = 25). Thin-walled parenchyma is not preserved between air chambers, as in specimen 61091.35.

The outermost cortical cells are elongate in shape and may have been crushed. Polygonal to nearly isodiametric cells are preserved to the interior of these elongate cells. Polygonal cells average 98 μm × 82 μm (N = 25), whereas cortical cells outside of the lacunae are not preserved. Where secretory ducts can be identified, they are located in the periphery of the sclerenchymatous zone and may be nearly circular in transverse section. The average diameter of identifiable secretory ducts is 100 μm.

DISCUSSION

Beck (1978) summarized and emended the diagnosis for *Periastron reticulatum* Unger after examining a suite of new specimens collected from the Falling Run Member of the Sanderson Shale. He re-examined the type specimens of several species that had been erected for the genus and placed all taxa into synonymy, creating a monotypic genus. Since then, *Periastron* has been reported from the Lower Carboniferous by several additional authors from central Europe (e.g., Galtier et al., 1988). The material collected from the Erin Slate (Gastaldo et al., 1993) is similar to all other reported specimens but displays several features that amplify and emend our understanding of this enigmatic fossil plant.

The axis has been considered, generally, to represent a petiole. The discovery of specimen 121388.1 verifies that *Periastron* is a lateral axis originating from a lower axial order. Petiolar axes commonly flare at the point of departure from the main axis.

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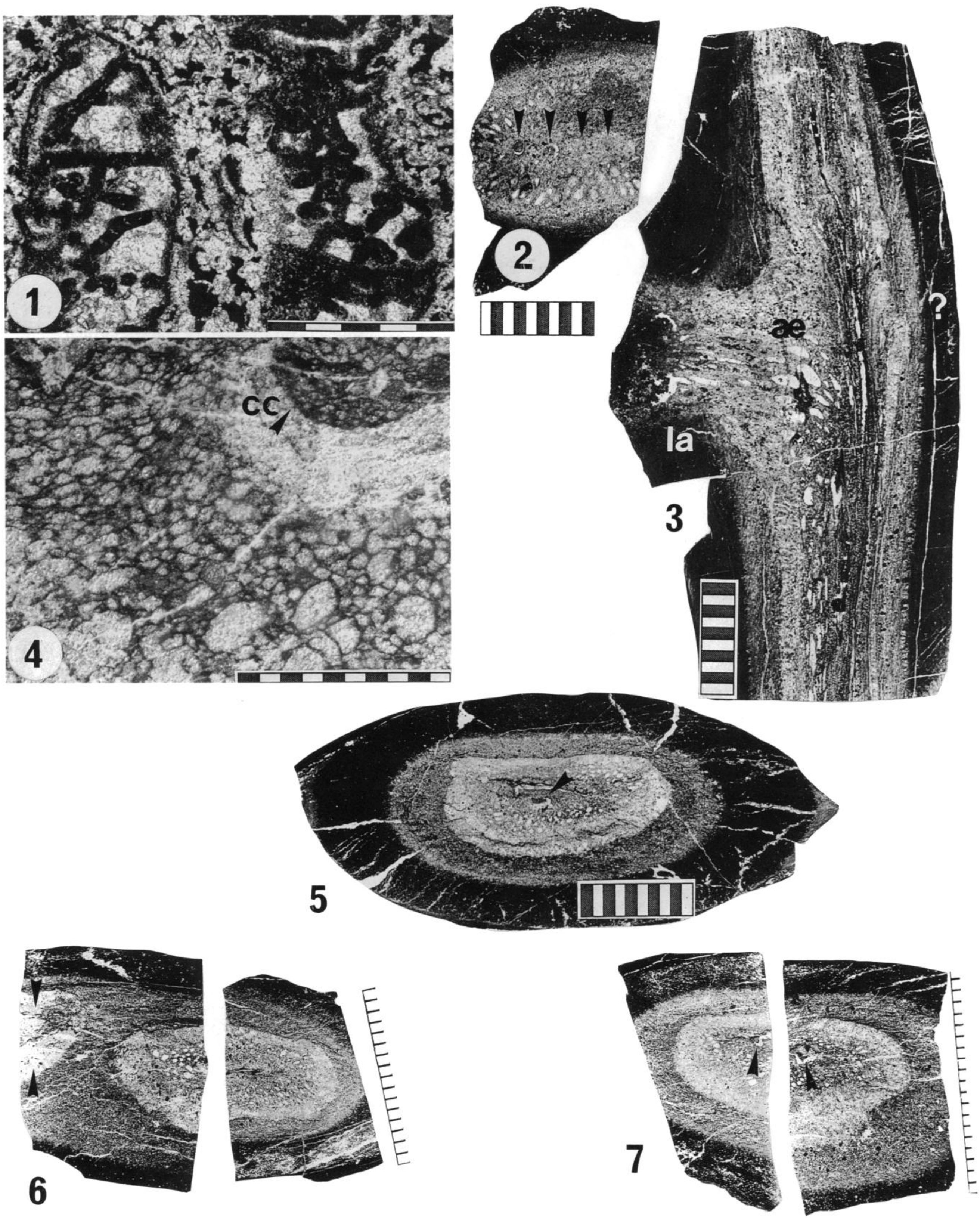
FIGURE *4*—*Periastron reticulatum* Unger emend. Beck. *1*, photomicrograph of fungal remains within air chambers positioned near the divergence of the lateral axis; scale equals 500 μm. *2*, transverse section of lateral axis; the axis is incomplete, but four medially aligned circular ?traces (at arrows) are preserved; the outermost two traces are unequivocally vascular bundles; the innermost two ?traces may mark the position of degraded or nondifferentiated bundles; aerenchymatous cortex surrounds these bundles which, in turn, is surrounded by sclerenchymatous cells; scale equal 10 mm. *3*, longitudinal section of specimen 121388.1 (USNM 455483) in which a lateral axis (la) diverges perpendicularly; longitudinal aerenchymatous ducts (æ) can be seen to diverge into the lateral; a second lateral may have developed opposite and slightly above based upon the divergence of ducts in this part of the axis (?); *5* is the transverse section across the main axis, whereas *2* is a section made through the lateral axis; scale equals 10 mm. *4*, enlargement of the central part of the main axis illustrating the concentration of cells (cc) that may mark the position of a single vascular bundle; scale equals 1 mm. *5*, transverse section of specimen 121388.1 (USNM 455483) in which air chambers can be seen to be radially arranged around the axis center; the axis center is degraded and some compression is evident; an area of concentrated cells, possibly marking the position of a single vascular bundle, can be seen to the left of center (at arrow); scale equals 10 mm. *6*, transverse composite section of the main axis of specimen 121388.1 (USNM 455483) made above the departure of the lateral axis; there are no preserved xylary elements in either half of the axis; note that there is another, poorly preserved lateral axis (at arrows), the trace to which can be seen in the main axis longitudinal section; scale equals 16 mm. *7*, transverse composite section of the main axis of specimen 121388.1 (USNM 455483) made below the departure of the lateral axis; what appear to be xylary elements in the photograph are displaced cortical cells (left arrow) and a degraded black mass (right arrow); scale equals 20 mm.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The lateral axis in specimen 121388.1 is flared at the base, lending support to the hypothesis that *Periastron* represents a petiole. The present emended diagnosis states that the number of medially arranged vascular bundles may range from five to ten. Specimen 61091.35 has only four bundles medially arranged. Beck (1978) suspected that specimens originating from the basal part of the axis might be characterized by a medial vascular bundle row with fewer than five bundles. The overall dimensions and non-flared character of specimen 61091.35 would preclude it as being an axial base (compare this with the lateral departure in specimen 121388.1). Specimen 61091.35, though, may be indicative of a smaller lateral axis (petiole?) that originated more distally in a determinate axial system.

Aerocortex kentuckiensis was established by Beck (1978) for Falling Run Member specimens that differed slightly from *Periastron.* Its histological features are very similar to *Periastron,* with the exception that a small number of vascular bundles occur in the axis and secretory ducts are scattered throughout the region between and below the vascular bundles. The vascular architecture in *Aerocortex* is known only from two specimens, and is composed of either two U-shaped or four discrete bundles (two larger bundles to the outside and two smaller to the inside of the axis). The morphology of the four bundles is not known because the single specimen upon which this observation is made is incomplete. Although the primary axis of specimen 121388.1 is poorly preserved and cannot unequivocally establish a relationship between these two taxa, the presence of an arcuate bundle of cells located towards one side of the axial midpoint (Figure 4.4, 4.5) may indicate the position of one vascular bundle. Its off-center position (similar in position to the two-bundled *Aerocortex*) may represent one of two vascular bundles in this axis. No vascular tissue is preserved opposite this trace in the other half of the main axis and there is no evidence of a larger bundle to the outside of this central area, as is in the case of the reported second specimen of *Aerocortex* (Beck, 1978). The second vascular bundle, if it were present, may have been in a position that is now marked by a degraded and compressed zone. Because preservation is poor, it is impossible to recognize if any secretory ducts were present in the axis. Therefore, it is not possible to establish whether or not *Aerocortex* is the axis from which the lateral petiole *Periastron* originates.

SUMMARY

Characters preserved in new specimens of *Periastron reticulatum* from the Erin Slate of the Talladega Slate Belt, southern Appalachians, provide an expanded understanding of this enigmatic Early Carboniferous plant. *Periastron* is a lateral axis (petiole?), originating from a main axis that exhibits similar cortical features. These include longitudinally oriented aerenchyma that is radially arranged in transverse section, and polygonal cortical cells. Degradation prior to silicification precludes the assessment of any information concerning vasculature and outer cortical features. The lateral axis that is known as *Periastron* diverges perpendicularly from the main axis. The basal region is characterized probably by four (5–6?) medially aligned vascular bundles. The characters of this axis correspond to those previously described by Beck (1978). A second axis has been found in which only four medially aligned vascular bundles occur. Beck (1978) emended the diagnosis stating that the taxon includes axes with five to ten vascular bundles. The identification of an axis with four bundles demonstrates his belief that such axes probably existed. These bundles do not anastomose or coalesce over a distance of 1.5 cm. This fragment may be representative of a lateral axis that developed more distally in a determinate axial system.

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