Transactions of the Illinois Academy of Science
(1988), Volume 81, 3 and 4, pp. 225-230

A REEXAMINATION OF THE LEAF OF ACTINOXYLON BANKSII

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ABSTRACT

Differences in interpretation of the nature of the leaf of *Actinoxylon banksii* have stimulated a reexamination of the leaf. Serial transverse sections of a leaf of the holotype show that there is a rotation of the leaf base so that the leaf is oriented in a plane tangential to the stem surface. The leaf base divides three times. The first two divisions are in the tangential plane and the third is in the radial plane, producing a three-dimensional unit.

INTRODUCTION

Actinoxylon banksii Matten (Matten, 1968) is an upper Middle Devonian (Givetian) member of the Archaeopteridales. The plant is preserved as a pyrite permineralization and all interpretations of external form are based on reconstructions from serial sections. Its protostelic stem, helical arrangement of branches, and non-planated and non-webbed leaves were considered sufficient to separate this taxon from the more completely known *Archaeopteris*. The lack of information about the reproductive morphology of *Actinoxylon* is also a reason for keeping it distinct from *Archaeopteris*.

Speculation on variability and overlap of vegetative features of *Archaeopteris*, *Actinoxylon*, *Svalbardia*, *Eddya*, and *Actinopodium* has led to the possibility that these genera within the Archaeopteridaceae represent component parts of a single variable genus, *Archaeopteris* (Beck, 1969, 1970, 1976). The original reconstruction of *Actinoxylon* (Matten, 1968) illustrated the leaf as being somewhat flexuous and branching in three-dimensions. This leaf morphology is an important distinction between *Actinoxylon* and *Archaeopteris*. Using illustrations from the original paper on *Actinoxylon*, Beck presented a reconstruction of an *Actinoxylon* leaf that appears planated and thus, more similar to the leaf of *Archaeopteris* (Beck, 1969, figure 9). Beck's figure was repeated in subsequent papers (Beck, 1970, 1976).

In 1981, *Svalbardia banksii* was described from the lower Upper Devonian (Frasnian) of New York (Matten, 1981). This species is preserved as a compression and is displaced in three dimensions within the entombing rock matrix. The reconstruction shows the leaves to be flexuous, unwebbed and forking in three-dimensions. This is the first compression member of the Archaeopteridaceae to demonstrate three dimensional branching of the leaves. The study of *Svalbardia banksii* stimulated the writer to return to the type specimen of *Actinoxylon banksii* in order to reexamine the sections of the leaves and to make a comparison of their morphology with that of the closely comparable *Svalbardia banksii*.

MATERIALS AND METHODS

The holotype of *Actinoxylon banksii* is housed in the Southern Illinois University Paleobotanical Collection in the Department of Botany and bears the number CQ 17. The type consists of 49 slides and one small, uncut piece. The slides consist of polished and etched slices of pyrite (Matten, 1968) and were examined using reflected light and a Bausch and Lomb stereomicroscope. Drawings were initially made with a Nikon Contour Projector. The drawings were then digitized with a Summagraphics drawing pad attached to a Macintosh 512E computer and arranged into figures 1 and 2. All descriptions of sections are based on transverse views of the fossil. The composite illustration of serial drawings is provided to show both the twisting nature of the leaf and the plane of division of the first three forkings of the leaf (fig. 2).

RESULTS

The most complete leaf was selected for description and drawing. This leaf extended from its decurrent ridge (CQ 17, section 4; fig. 1-4) to a point where it had divided into 8 units (CQ 17, section 25), a distance of about 5 cm.

At the lowest level (fig. 1-4) the oval trace appears below a bulge in the surface of the stem. The bulge is interpreted as a decurrent ridge. In section 6 (fig. 1-6), the base of the leaf is almost free from the stem surface and contains the trace. In section 8 (fig. 1-8), a constriction appears in the xylem strand of the trace. The dividing xylem strand is elongated in the radial plane.

In section 10 (fig. 1-10), the xylem strand of the trace is divided into two terete strands. The two terete strands are oriented slightly obliquely to the stem surface. In section 14 (fig. 1-14) the leaf base is almost detached from the stem. The two terete traces are displaced from each other and are oriented in a plane that is obliquely tangential to the surface of the stem. In section 16 (fig. 1-16) the leaf base is at the point of detachment from the stem. A constriction appears in the leaf base, separating the two xylem strands. Each of the two xylem strands is also constricted, the constriction being oriented so that each xylem strand is elongated in the tangential plane.

In section 18 (fig. 1-18), the leaf base is now divided into two segments, each tangentially displaced from the other. Each leaf segment has two tangentially displaced xylem strands. In section 20 (fig. 1-20), each of the two leaf segments is elongated in the tangential plane and possesses a median constriction.

Section 22 (fig. 1-22) shows that the leaf is now divided into four tangentially oriented segments. The uppermost segment is occupied by two terete xylem strands. The two xylem strands are oriented in the radial plane, in relation to the stem. Each of the other leaf segments is occupied by a single terete xylem strand. Section 24 (fig. 1-24) shows the four leaf segments elongated in the radial plane. The uppermost and lowermost segments are constricted and contain a terete xylem strand on each side of the constriction. Of the two middle leaf segments, the upper one shows a single radially-elongate xylem strand with a median constriction. The lower of the two middle leaf segments is radially elongate and contains two radially oriented xylem strands.

Section 25 (fig. 1-25) shows that the leaf is now divided into seven segments. The two uppermost segments and the two lowermost segments are radially displaced. Of the middle segments, the uppermost one is radially elongate and contains two radially displaced xylem strands. The other two middle segments each contain a single terete xylem strand and are tangentially displaced. These latter two segments represent the lower middle segment of section 24. A reconstruction of the leaf based on the superposition of the sections just described shows its three-dimensional organization (fig. 2)

DISCUSSION

The reexamination of the morphology of the leaf of *Actinoxylon banksii* points out two significant morphological features. First is the change in orientation from a radially produced xylem strand to a tangentially displaced unit. Second is the planes of division of the leaf segments.

The rotation of the leaf trace into a tangentially displaced unit as seen in sections 4-14 (figs. 1-4 to 1-14) demonstrates how the progymnosperm and early gymnosperm pattern of leaf trace formation (Namboodiri and Beck, 1968c) may have developed into the pattern seen in later gymnosperms (Namboodiri and Beck, 1968a,b). The rotation of the trace seen in *Actinoxylon* conforms to the model illustrated by Namboodiri and Beck (1968c). Precocious development of the tangential displacement of the xylem strand in the stele and its subsequent genetic fixation would result in the patterns we observe today.

Branching of the leaf segments occurs in both tangential and radial planes. After the initial rotation of the basal leaf segments, there are two divisions in the tangential plane resulting in four axes. The third division in at least three of these axes is in the radial plane. The fourth axis (fig. 1-24, second axis from bottom) shows a radial orientation in sections 22-24 but in section 25 is oriented in the tangential plane. This is most likely due to twisting during burial and represents an artifact. The parenchymatous nature of these leaf segments contributes to the interpretation that these segments were flexuous and were susceptible to twisting.

The leaves of *Svalbardia banksii* are very similar to those of *Actinoxylon*. The most complete leaf of *Svalbardia banksii* shows a decurrent ridge on the stem. The first two divisions of the leaf base are in the tangential plane while the third division is in the radial plane. This is one more similarity between the two taxa. However, only petrified *Svalbardia banksii* showing *Actinoxylon banksii* anatomy will justify the two being placed in synonymy.

SUMMARY

The rotation of the leaf base and the three-dimensional character of the leaf of *Actinoxylon banksii* have been demonstrated. Reconstructions of *Actinoxylon banksii* have been demonstrated. Reconstructions of *Actinoxylon* should be based on Matten (1968) and not Beck (1969). The characters of the leaf continue to separate the genus from *Archaeopteris* and serve as a basis for examining morphological change within the family.

ACKNOWLEDGMENTS

The manuscript and illustration were prepared while the author was on sabbatic leave. All work was performed at the author's residence, using the author's personal equipment. The author would like to thank the Botany Department, Southern Illinois University for support of page charges.

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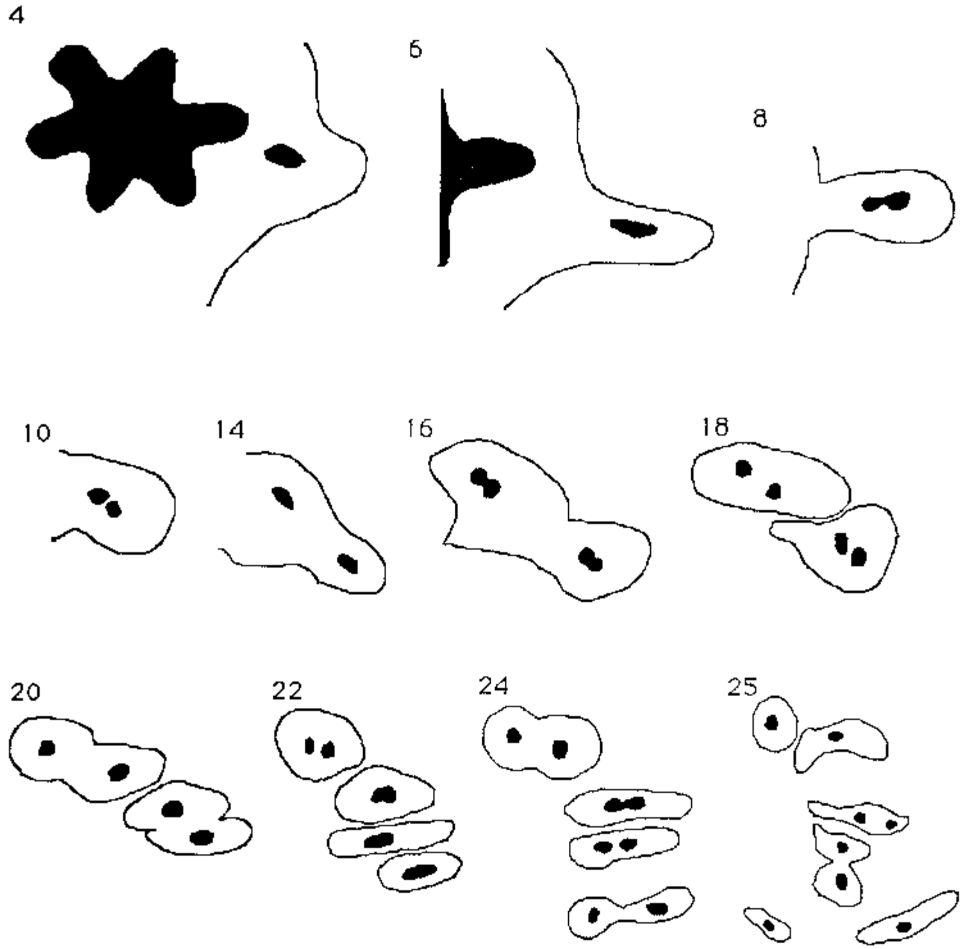

Figure 1. Serial transverse sections of leaf of *Actinoxylon banksii* holotype (Southern Illinois University Paleobotanical Collection — CQ 17). Black areas represent primary xylem. Numbers refer to the specific section of the specimen. All sections are oriented in the same manner. All sections are drawn at approximately X 9.5 normal size.

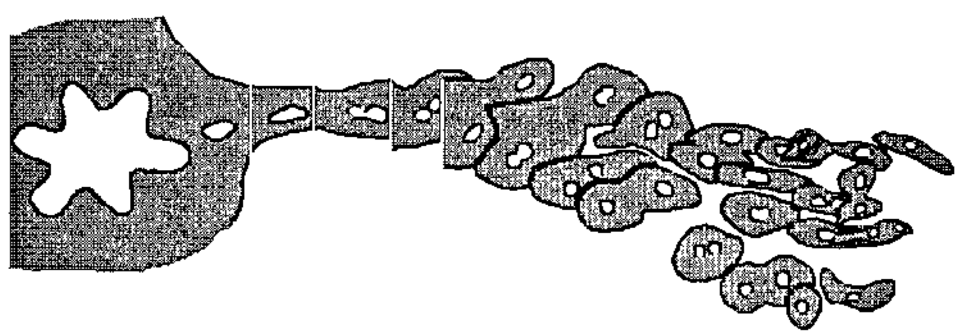

Figure 2. Reconstruction of leaf of *Actinoxylon banksii* holotype (Southern Illinois University Paleobotanical Collection — CQ 17) based on serial transverse sections shown in fig. 1. White areas represent primary xylem. All sections are oriented in the same manner.