

**TWO COEXISTING, PERMINERALIZED *ALETHOPTERIS*
MORPHOLOGIES FROM IOWA AND A NEW METHOD FOR
DIFFERENTIATING THEM BASED ON LEAF GEOMETRY**

A Senior Scholars Thesis

by

MATTHEW WEHNER

Submitted to the Office of Undergraduate Research
Texas A&M University
in partial fulfillment of the requirements for the designation as

UNDERGRADUATE RESEARCH SCHOLAR

April 2009

Major: Geology

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Approved by:

Research Advisor:
Associate Dean for Undergraduate Research:

Anne Raymond
Robert C. Webb

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ABSTRACT

Two Coexisting, Permineralized *Alethopteris* Morphologies from Iowa and a New Method for Differentiating Them Based on Leaf Geometry. (April 2009)

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This research focuses on a new morphology of *Alethopteris*, the frond of a Carboniferous seed-fern tree, based on a series of orthogonal cross-sections of the leaflets, which are preserved in coal balls. The coal balls, which are chunks of coal saturated in calcium carbonate, were recovered from the Williamson No. 3 Mine in Lucas County, Iowa. From close examination of already prepared and sectioned coal balls, I identified criteria that distinguish the new *Alethopteris* morphology from other *Alethopteris* morphologies in the same coal bed and even coal balls. These criteria consisted primarily of measures made on orthogonal cross-sections. Results of comparisons of two populations of *Alethopteris* from the Williamson No. 3 Mine using the student t-test suggest that the two morphologies differ significantly and hence, are different species. I compared the new Williamson No. 3 *Alethopteris* morphology to *Alethopteris* species known from other coal ball localities. The new Williamson No. 3 *Alethopteris* is different from all these species, and represents a new species.

DEDICATION

To my mother, Melissa Wehner, who, I am sure, would have been proud of my progress at Texas A&M University for obtaining an undergraduate degree and also for the honor of conducting research under the guidance of Dr. Anne Raymond in one of my several favorite research topics: paleobotany.

ACKNOWLEDGMENTS

I wish to acknowledge Dr. Anne Raymond's efforts in encouraging me to enroll and finish the Undergraduate Research Scholars Program at Texas A&M University. I cannot thank her enough for all the tireless hours she spent providing me with copies of articles, lab access, lab instruction, proofreading, and most importantly, the research study material. This thesis would not have been possible without the contribution of Ms. Elizabeth Slone, who did the initial research on the *Alethopteris* pinnules at the Williamson No. 3 mine in Iowa.

On a more personal note, I cannot overemphasize the importance that my grandmother, Nana, has in my life. She was with me every step of the way starting with convincing me to accept the challenge of being an Undergraduate Research Scholar. She has been supportive of my goals in college and in education.

NOMENCLATURE

AH	Amount of vaulting between lamina peak and margin, perpendicular to adaxial surface.
Ave	Average or mean of a sample size
D. F.	Degrees of freedom; used in statistics
EEW	Edge-to-edge width of pinnules at the edge of the lamina as viewed in plane perpendicular to their surface
ICS	International Commission on Stratigraphy
MRW	Midrib width
MLT	Midrib plus lamina thickness
No.	Number of specimens used in sample (equivalent to N)
OL	Overlap
Petiole	The stem coming from the trunk or woody branch that bears a leaf or compound leaf
Pinna	A unit of compound leaf consisting of the rachis and the pinnules attached to it
Pinnule	Leaflets that make up a compound leaf
PP	Vault-to-vault width, measured on adaxial side of pinnule at peak of each vault
Rachis (Rachides)	The branch (or axial unit) of a compound leaf that bears pinnules or other rachides
STDV	Standard deviation of a sample
Ultimate rachis	The branch in a compound leaf to which pinnules are attached

Var	Variance of a sample, defined as the square of the standard deviation
VD	Vault depth (can be thought as degree of “sunkeness”)
W	Width of pinnule at top of vault

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CHAPTER I

INTRODUCTION: *ALETHOPTERIS* AND ITS CONTEXT

While this thesis focuses primarily on the description of a new species of seed fern, which had been designated as morphotype 2 by earlier researchers, there are several contexts in the realms of paleoecology, paleogeography, and systematics that should be considered in an introduction before delving into a more focused description of the plant itself. So the first section will cover classification and systematics of *Alethopteris*, the plant of interest.

Classification of *Alethopteris*

Alethopteris, belongs to the pteridosperms, an extinct group of plants that resembles both cycads and ferns. Wagner (1968) explained that pteridosperms have foliage like that of a fern (i.e branched, compound leaves) and cycad-like stems (Fig.1). Pteridosperms are informally referred to as “seed ferns” because a few workers found seeds attached to their compound leaves (Oliver and Scott, 1905; Kidston, 1905; Arnold, 1947; Zodrow and McCandlish 1980). This is why pteridosperms, along with cycads and conifers are placed in the gymnosperms. Pteridosperms are found from the uppermost Devonian and range all the way to the Eocene epoch, however, most pteridosperms are known from the

This thesis follows the style of Journal of Paleontology.



FIGURE 1—1, A typical isolated pinnule of *Alethopteris*. Image from www.museum.gov.ns.ca, Catalogue # 987GF74.1. 2, a frond that contains many pinnules of *Alethopteris*. These fronds can be up to several meters in length. Image courtesy of Dr. Don Chestnut, University of Kentucky.

Carboniferous (Arnold, 1947; McLoughlin et al, 2008). *Alethopteris* was first officially described from Germany by Sternberg in 1825 based on fronds, which are large compound leaves. The leaflets in the fronds of seed ferns are called pinnules. Since *Alethopteris* pinnules have been linked with the stem genus *Medullosa*, it is considered a medullosan along with *Neuropteris*, *Odontopteris*, and a few other genera. These genera, named from pinnules, have also been linked with *Medullosa*, a genus assigned to a type of pteridosperm stem (Stidd 1981). The undisputed age range of medullosan pteridosperms, which includes genus *Alethopteris*, extends from Early Carboniferous (Mississippian) through into the Permian (Serbet et al, 2006). More specifically, the earliest known occurrence of medullosans, as shown by stem-genus *Medullosa*, is in the late Chesterian, which is the Serpukhovian stage of the Late Mississippian (Dunn et al, 2003).

The *Alethopteris* tree

Wnuk and Pfefferkorn (1984) reconstructed *Alethopteris* and other medullosans as free-standing trees (Fig. 2). The trunks did not branch, but sprouted huge fronds at the top, similar to modern palms and tree ferns. In life, surmised Wnuk and Pfefferkorn (1984), medullosan trunks may have had up to several dead fronds hanging down just below the crown of fronds. Based on pteridosperm trunks preserved *in situ* in Pennsylvania, Wnuk and Pfefferkorn estimated the trunk length at 3-5 meters (1984). Given that the fronds that formed the crown were easily 4-6 m in length and likely grew out from the top before curving outward or downward, the fronds would have likely added a meter or two to the overall height of the tree. These dimensions yield an estimated height of 4-7 meters high. The fronds themselves have been reported to be up to 6m, perhaps 7 ½ meters (Laveine 1986). At the base of the trunk, medullosan pteridosperms have aerial roots coming out from the stem, which shows that medullosans thrived in water-saturated areas (Pfefferkorn et al, 1984; Wnuk and Pfefferkorn 1984).

Paleoecology and paleogeography

The fossils of *Alethopteris* used in this study were recovered from a coal bed (the Williamson No. 3) in south-central Iowa. The coal beds are reported as the Late Atokan-

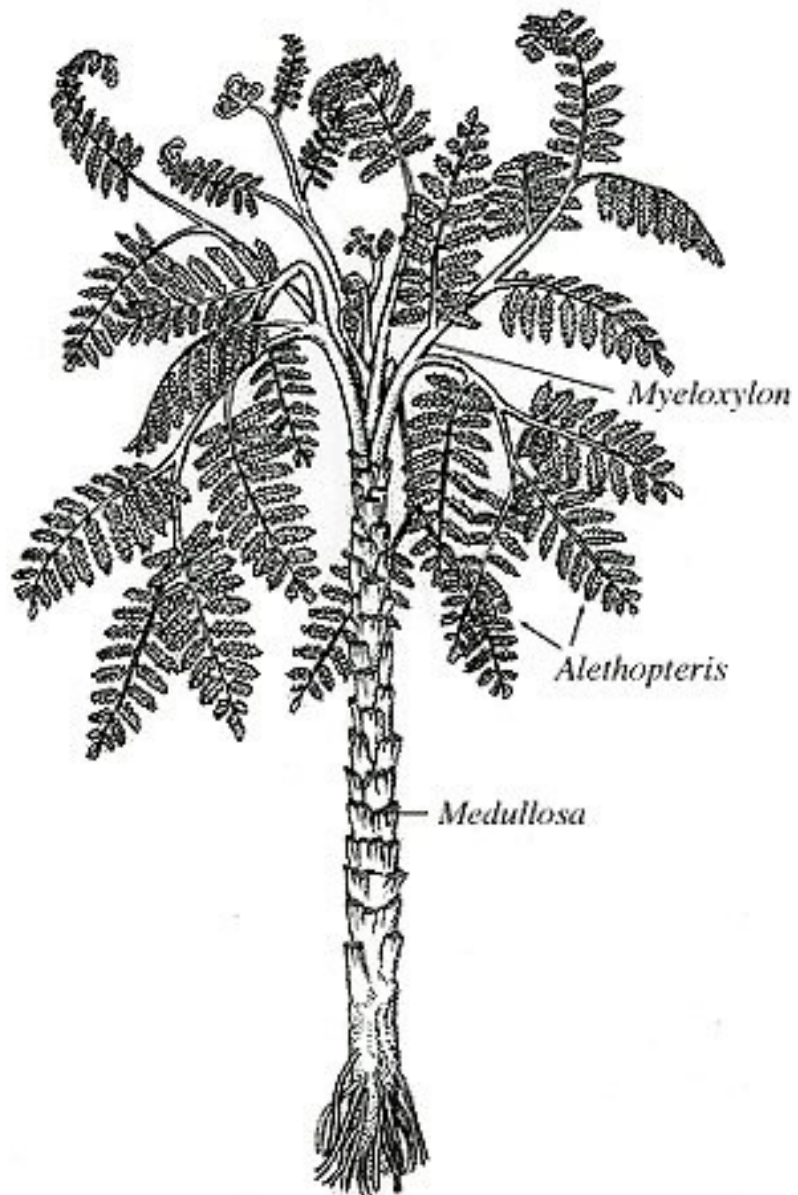
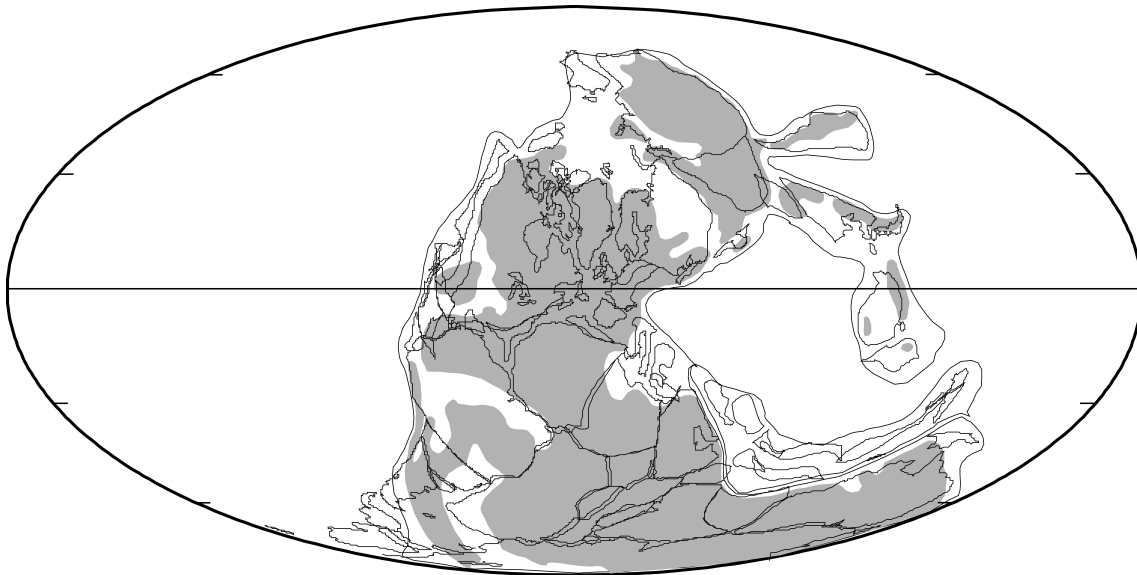


FIGURE 2—Composite *Alethopteris* tree built from the organ genera: *Medullosa* (stem), *Myeloxylon* (petioles or branches) and namesake "foliage" genus *Alethopteris*. The scale bar represents approximately 5 meters. Based on an illustration found at www.ucmp.berkeley.edu.

early Desmoinesian (Pennsylvanian) in age (Slone, personal commun., 2003). According to the latest ICS revision of the geologic time scale, this would correspond to the Moscovian stage (Gradstein et al, 2004). The coal deposits formed in a peat-accumulating, low-lying swamp in the central USA. These swamps in Iowa and surrounding areas were near the paleoequator and the plant fossils they contain indicate a tropical climate. At this point in time (during the mid to late Pennsylvania), the majority of the continents had merged to form a supercontinent referred to as Pangaea. The North American plate was tilted at an angle so that the paleoequator runs approximately through Texas, Illinois, and New York (Fig. 3). During the Pennsylvanian, the central



Carboniferous

FIGURE 3—A map showing Pangaea as it thought to look in the late Pennsylvanian. The shaded area represents areas above sea level for said period. Provided by C. R. Scotese (1999 Paleomap Project)'s collection of reconstructed maps on CD.

region of North America was dotted with several very large basins that were near the paleoequator. The three main basins were: Western Interior Basin, Eastern Interior Basin, and Appalachian Coal Region. These basins had peat-accumulating swamps that eventually became the famous coal beds of the Carboniferous Period.

The interpretation of the paleoclimate of the Pennsylvanian has been the subject of intense scrutiny in recent years. Cecil (1990) observed that major accumulation of coal deposits are primarily in the Pennsylvanian epoch and not so much in the Mississippian epoch or in the Permian. Thus climate changed on the stage and epoch scale. Cecil suggested that peat-accumulation and coal formation is possible in the tropics and paleotropics during wet times without long dry seasons. He stated that these wet tropical times were characterized by times of little siliciclastic or carbonate deposition. Cecil suggested that many factors contributed to Pennsylvanian climate change and presents a classification system based on those factors. Long-term climate change is influenced by plate movements and orogenic events. An example of a long-term pattern is the Mississippian, Pennsylvanian, and Permian cycle: the Mississippian is generally characterized as a warm, interglacial period with high sea levels, followed by an interval of major glaciation during the Pennsylvanian and Early Permian, with a return to warm climate by the Late Permian (DiMichele et al 2002). Shorter term climate factors (which may span only stages or less) include cycles based on the earth's eccentricity. This cycle and others are collectively referred to as the Milankovitch cycles. It is widely thought that these Milankovitch cycles are associated with eustasy, that is, the rise and fall of sea

level, which varied as much as 100 meters, due to expansion and retraction of glaciers (Driese and Ober 2005; Rygel et al, 2008).

Since the lowland basins of interest (i.e. Appalachian coal basin) are near the paleoequator, the tropical climate would transition to a more arid and seasonal climate as a warm period (glacial retreat) oscillated to a cool period (glacial advance) (Cecil 1990). Prior to Cecil's 1990 suggestion that tropical climates became more seasonally dry during part of the glacial portion of the cyclothem, the majority of thick peat-accumulating swamps occurring near the equator were thought to form under warm, continually-wet, tropical conditions with little seasonality (Peppers 1996). At this point it should be noted that the major coal-forming basins, while are part of the much larger midcontinental basin, are not at the same the paleoaltitude throughout the basin, that is the altitude of the swamp surface during the Pennsylvanian. Thus these basins would have experienced the rising and falling of sea levels at different times within a cyclothem (i.e. a single cycle of glacial advance, resulting in falling sea-level, and glacial melting, causing rising sea-level). An interesting implication of these differences in basin altitude for Cecil's recognition of variation seasonality during glacial cycles is that the inferred paleoclimate during the formation of coal could vary from one basin to another. For instance, the Appalachian Basin, which has high paleoaltitude, could accumulate coal during times of maximum glacial retreat (sea-level low) and advance (sea-level high), whereas the Western Interior Basin, which has lower paleoaltitude, could only accumulate during intervals of low sea-level (maximum glacial advance).

Paleoecology of swamp forests provides additional information concerning water levels within swamps, and thus the climate of coal deposition. For instance, the Appalachian and Illinois coal beds contain abundant lycopsid plants that are more associated with continually wet climates (Peppers 1996). This is in contrast to the cordaite-pteridosperm flora observed in the Williamson No. 3 coal bed which exhibits xeromorphic traits. This is why the newly reported *Alethopteris* morphologies that are described in this work and in Slone (personal commun., 2003) share many xeromorphic characters, and support the idea that the Williamson No. 3 coal in the Western Interior Basin accumulated under drier conditions than lycopsid-dominated coals of the Illinois and Appalachian Basins.

Previous work

Fossil pteridosperm leaves generally occurs as adpression fossils, i.e. fragments of compound leaves deposited in mud, silt and sand, preserved as flattened carbon films and imprints in shale, siltstones and sandstones. For example, the *Alethopteris* pinnules described by Sternberg (1825) were adpressions. In adpressions, external morphological characters, primarily the size and shape of pinnules on the surface of the rock as well as the density and form of the venation, form the basis for identifying different species.

Permineralization preserves the cellular anatomy and certain aspects of the three-dimensional morphology of pteridosperm foliage, not generally apparent in adpressions. Leisman (1960) first described a permineralized species of *Alethopteris*, which he placed in the adpression species, *A. (Callipteridium) sullivanitii*. This species, which occurs in the mid- to upper Desmoinesian of North America, ranges from 10 to 14 mm (av. 12

mm) in width, and from 17 to 26 mm (av. 22 mm) in length. The midrib is embedded in the lamina; the midline depth (the depth of the midrib plus lamina in the middle of the pinnule) is 1445 μm .

Baxter and Willhite (1969) described a narrow, enrolled species of *Alethopteris* with a similar stratigraphic range, which they placed in the adpression species, *A. lesquereuxi*. *A. lesquereuxi* has been documented from the Fleming Coal in southeast Kansas (Baxter and Wilhite (1969), and the Lovillia coal deposit in Iowa, (Reihman and Schabilion, 1976), both mid-Desmoinesian in age (Fig 4). The midline depth of *A. lesquereuxi* from Kansas varies from 720-750 μm (Baxter and Wilhite, 1969). Reihman and Schabilion (1976) report a midline depth of 888 μm for *A. lesquereuxi* from Lovilia, Iowa. A layer of extremely large hypoderm cells (100 μm x 70 μm), occurs immediately below the adaxial epidermis (Baxter and Wilhite 1969). Reihman and Schabilion (1976) noted that the parenchymatous bundle sheath extensions of the secondary veins of *A. lesquereuxi* protrude to form “ridges” on the abaxial surface of the pinnule. Uniseriate trichomes (hair a single cell wide) occur on the abaxial surface of the midrib and the bundle sheath extensions of the secondary veins, as well as the abaxial surface of the

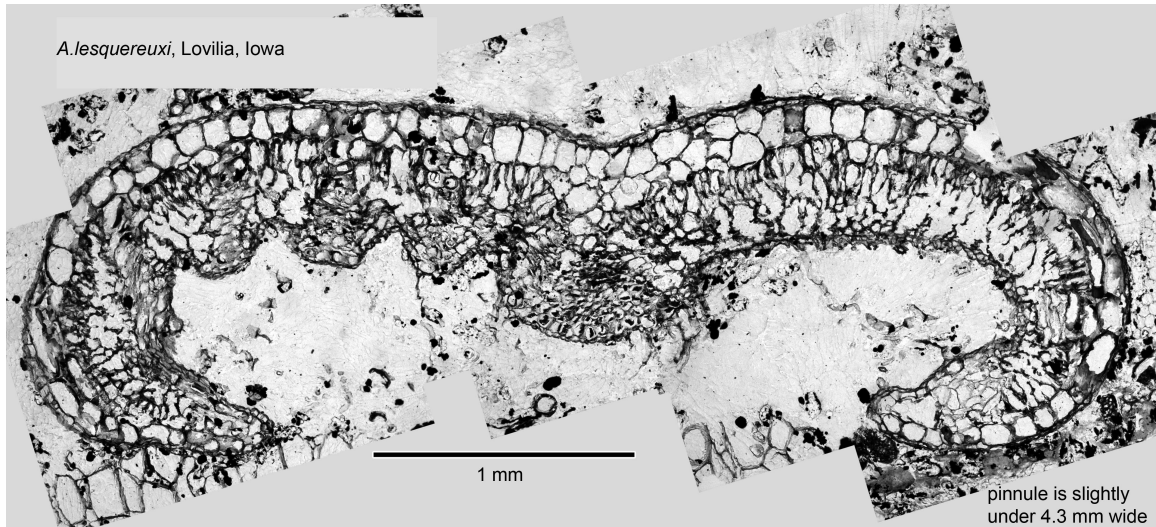


FIGURE 4—*Alethopteris lesquereuxi*: example is from Lovillia Mine, Iowa

revolute margins of the lamina (Baxter and Wilhite 1969). Parenchymatous abaxial surface ridges associated with the bundle sheath extensions of the secondary veins and large hypoderm cells distinguish this species.

Mickle and Rothwell (1982) discussed a narrow, vaulted species of *Alethopteris* in permineralized peat from the the Berryville and Stubenville localities in the Appalachian Basin, both Missourian in age . Mickle and Rothwell (1982) felt that their pinnule belonged to the adpression *A. serli*-group of Scheihing and Pfefferkorn (1980); Cleal (personal commun, 2009) suggested that the Berryville and Stubenville *Alethopteris* belong to adpression species, *A. zeilleri*. A prominent palisade mesophyll characterizes this pinnule, which ranges in width from 4 - 8 mm and in length from 7 - 17 mm.

Elizabeth Slone's work (M.S. thesis) is very important because she was the first to report the existence of two previously unrecognized leaf morphologies of *Alethopteris* in permineralized peat from the Williamson #3 mine in the Forrest Western Interior Basin of southern Iowa (personal commun., 2003). She described the first leaf pinnule morphology, designated *Alethopteris* 'morphotype 1', in her thesis (Fig. 5); and the other morphology, designated *Alethopteris* 'morphotype 2' will be covered at length in this work (Fig. 6). As described by Slone (personal commun., 2003), morphotype 1 from the Williamson No. 3 mine is a narrow, vaulted pinnule with a decurrent base and a wide, sunken midrib. Slone (personal commun., 2003) reported a width of 1.7 mm and a length of 5.6 mm for 'morphotype 1' pinnules. In peridermal section, the midrib is slightly decurrent; however, this might not be evident in an adpression of this pinnule. The midline depth of the pinnule averaged 1069 μm ; midrib width averaged 1201 μm (N = 10 pinnules). In well-preserved pinnules, the midrib is rectangular in cross-section.

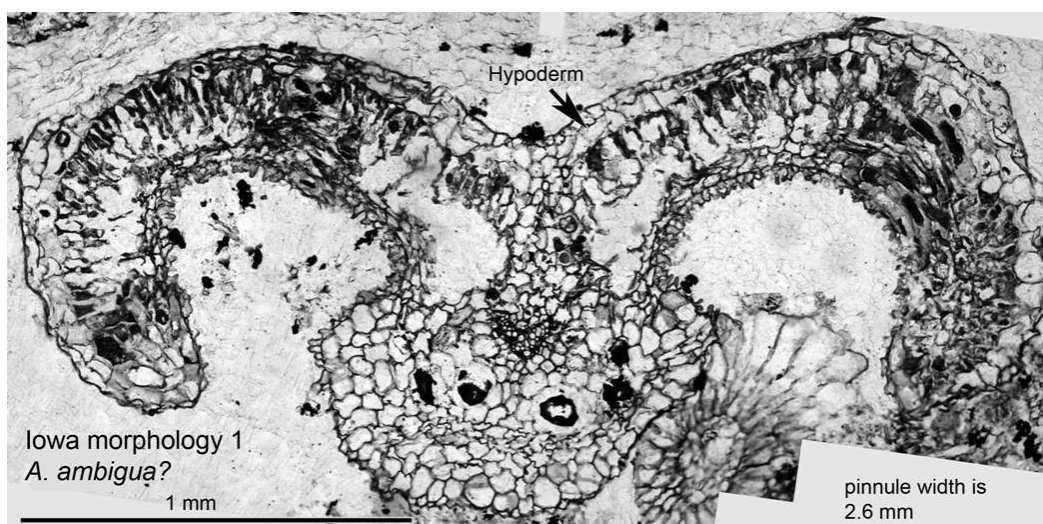


FIGURE 5—*Alethopteris* “morphotype 1”

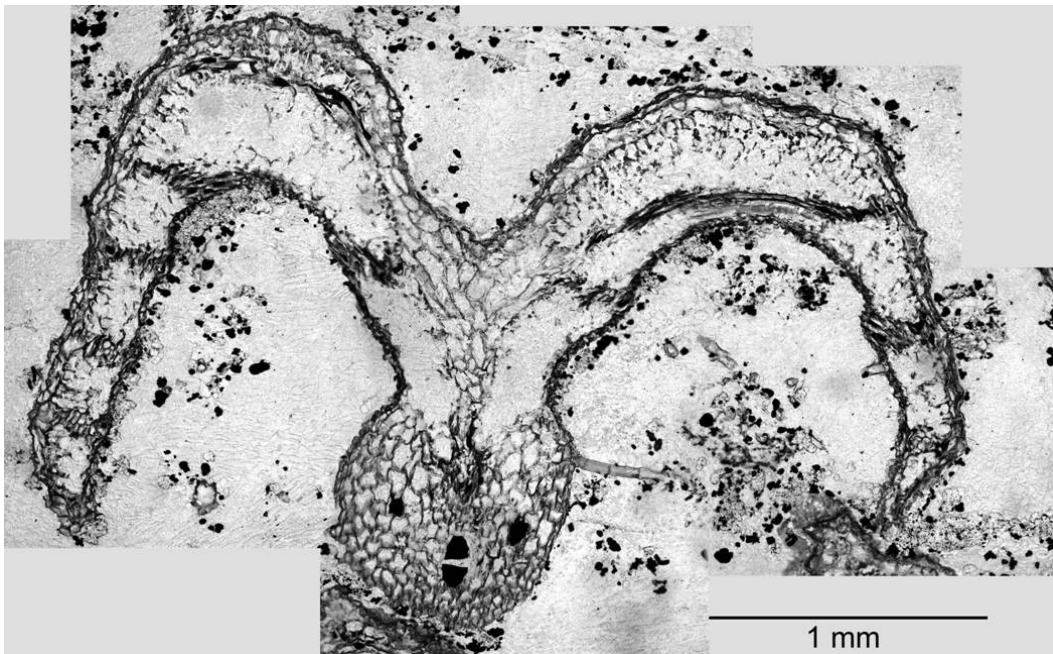


FIGURE 6—*Alethopteris* "morphotype 2"

CHAPTER II

MATERIALS AND METHODS

Background on coal-balls from Williamson No. 3 mine

The bulk of the *Alethopteris* fossil material used in this study comes from coal balls. Coal balls are hard, often rounded, “balls” of limestone, usually of calcium carbonate with traces of silica, pyrite, and often clay minerals (Scott and Rex, 1985). Coal balls contain a good percentage of organic matter, including leaves, seeds, and stems. Coal balls are known only from Carboniferous coal seams, mostly from the paleotropics which in modern times is in central USA and Eurasia, and seem to be concentrated mostly in the upper part of these coal seams (Andrews, 1951). The process of coal ball formation has not been satisfactorily determined, though there is great interest but actual studies on the subject have been few (Scott et al 1996).

The *Alethopteris* fossils used in this study were recovered from a mine called William No. 3 Mine in Lucas County, Iowa. The coal balls containing these fossils are part of the Thompson-Darrah coal-ball collection of the Harvard Botanical Museum, and are currently on loan to Texas A&M University. Frederick Thompson was a Harvard Alumni, class of 1907, and very successful in real estate (Morey, 1995). Thompson was very keen on field fossil collecting and donated a major portion of his collection to William Darrah at Harvard. Around 1938, Thompson acquired many coal balls in Iowa, including some from Williamson No. 3 Mine, and eastern Kansas (Andrews, 1951). The several coal balls used in this study appear to come from that collection.

Geologic setting

Thomposon did not record detailed stratigraphic information when he collected these coal balls. Based on the cordaites seeds found in the Williamson No. 3 deposit with the *Alethopteris* fossils, Raymond et al (2001) suggested that the deposit is one of the two Kalo Fm. coals. The Kalo Fm. is reported to have two major coals, the Blackoak Coal at the base and higher is the Cliffland Coal (Pope et al 2002). According to Pope et al (2002), the Kalo Fm. straddles the Atokan-Desmoinesian boundary of the Pennsylvanian. However, it is not possible to identify which of the two coal seams that are known to be in the Kalo Formation is the one present in the Williamson No. 3 Mine.

Methods

The methods include sectioning coal balls, preparing peels, digital photography, applying a set of taphonomic grading criteria, and making direct measurements on the peels themselves. Fortunately, some already prepared peels were available for this study.

Sectioning and peels

The principal coal ball (labeled as W3 PC2+6) used in this study had already been sectioned four times. As part of this study, it was further sectioned two more times. Before the peels can be made, the cut surfaces must be polished using progressively finer polishing grit such that the surface becomes smooth.

The process for making cellulose acetate peels is similar to the method as described by Joy et al (1956), with a few modifications. Starting with an already polished cut surface of a coal ball section, the surface is etched with dilute (5%) hydrochloric acid and washed gently with distilled water to remove the acid. The etched surface is dried by directed compressed air. The dried surface is moved to a stable and horizontal location and several drops of acetone are placed on top of etched surface with an eye dropper. A piece of cellulose acetate film is placed on the etched surface gently, while making sure there are no trapped air bubbles. Then the etched surface with the affixed peel is set aside for 20-30 minutes to dry. When dry, the cellulose acetate film is peeled off and placed in between two surfaces, such as the pages of a thick book, to help prevent wrinkling.

The hydrochloric acid removes a thin layer of calcium carbonate and exposes the organic cell walls, which do not dissolve in this acid. When the acetone is placed on the dry surface of the coal ball causes the cellulose acetate film to dissolve around the exposed cell walls on the surface. As the dry film is peeled from the coal ball, the organic cell walls are ripped from the coal ball surface because they are now embedded in the film. Cellulose acetate peels of coal balls are translucent and can be used for transmitted or refracted microscopy.

Measurements

Morphotype 2 can be distinguished from morphotype 1 by having: 1) a deep v-shaped indentation above the midrib caused by the high, vaulted pinnule; 2) a midrib that is circular in cross-section; and 3) pinnules that are widest at the margin (Fig. 7). For

purposes of comparison with previously described species, only orthogonal sections (cross sections at right angles to the midrib of the pinnule) were used. The following measurements were made on the nearly orthogonal cross-sections:

1. Lamina edge to lamina edge (EEW on Fig 7, part 1);
2. Distance between the peaks of the vault on either side of the midrib (PP on Fig. 7, part 1);
3. Depth of the trough-like space above midrib and between the arched lamina (VD on Fig. 7, part 1);
4. Abaxial height of the vault (arch on the bottom side of the pinnule) on the left and right side of the midrib (AH on Fig 7, part 1 shows this measurement on the left side of the pinnule only);
5. The thickness of the midrib plus lamina (MLW on Fig 7, part 2)
6. The width of the midrib neck (N on Fig. 7, part 2);
7. The width of the midrib at its widest point (MRW on Fig. 7, part 2);
8. The overlap that is evident from looking at the portion of the VD segment that is below W (abbreviated OL and is not directly illustrated but can be observed by comparing both Fig. 7, part 1 and 2);

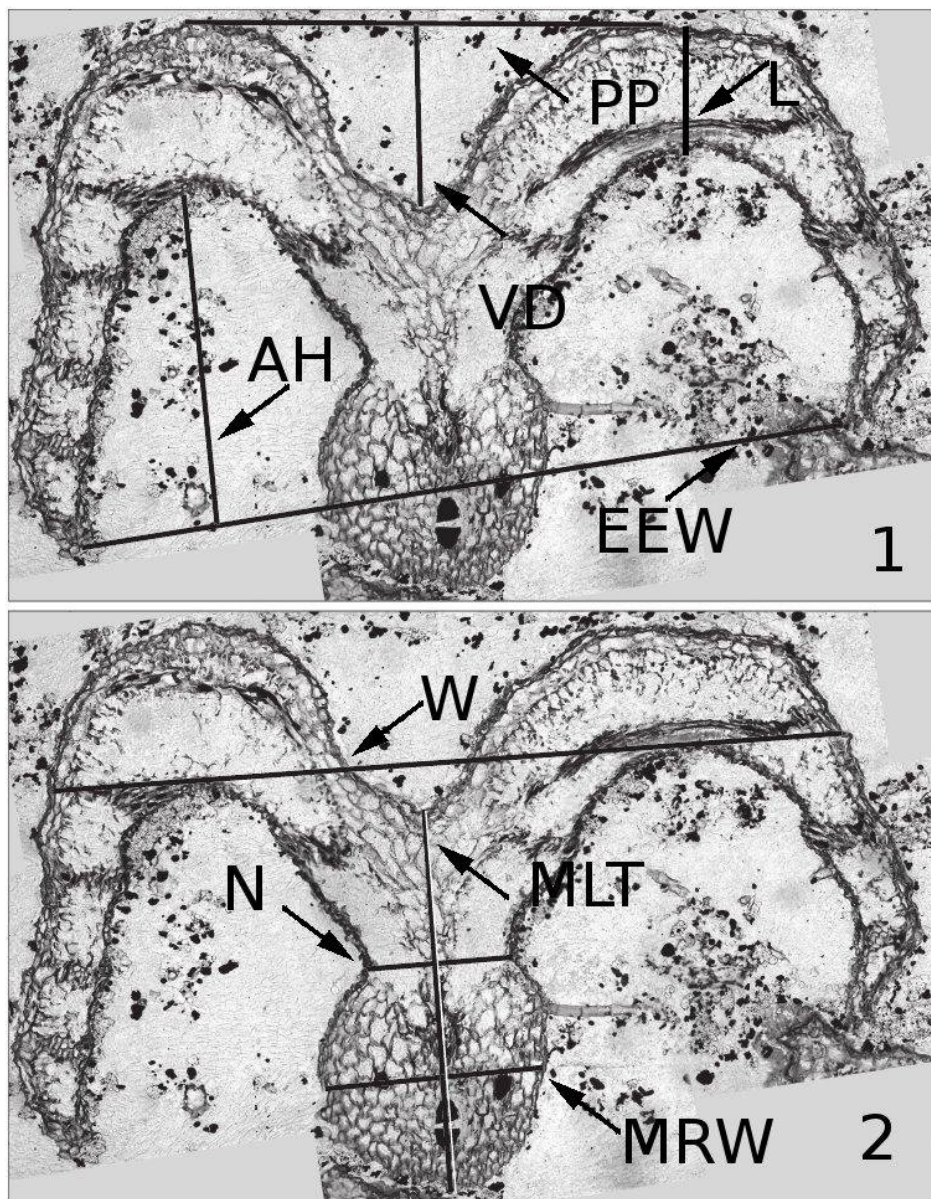


FIGURE 7—Illustration showing the types of measurements made of pinnules in cross-section. Both images are duplicates of the same pinnule to provide enough space to show the measurements; 1, the following measurements: edge-to-edge width (EEW), arch height (AH), midline depth below arched lamina (VD), peak-to-peak (PP), and lamina thickness (L); 2, neck width (N), width at top of vault (W), midrib and lamina thickness (MLT), and midrib width (MRW).

9. The thickness of the lamina, measured at each of the peaks of the vault

(L in Fig. 7, part 2).

In addition, we measured the vein density along the edge or margin for all known peridermal sections of morphotype 2, and at least 4 large fragments of peridermal sections.

Taphonomy

Decomposition and exposure at the surface may distort pinnules, causing the two populations to appear more similar. In order to evaluate the effect of exposure and decomposition on species differences in *Alethopteris*, we assigned all the pinnules included in this study to one of four taphonomic conditions. The taphonomic conditions are assigned a “grade” indicating the state of preservation. The grading criteria are described as follows:

A = Spongy mesophyll and palisade mesophyll are clearly defined. No empty areas, especially in neck area

B = Palisade and mesophyll present throughout pinnule cross-section and empty spaces exist in pinnule

C = Remnants only, palisade mesophyll and papillate lower margin not well preserved.
Neck area empty

D = Boundaries of pinnule “fuzzy”

F = “Spiky” appearance often on adaxial surface and midribs of pinnules in a low preservation state, empty cavities in the midrib.

Since statistics are a part of this study, the letter grades were also assigned a numerical values on a one to five scale as shown in Table 1, so that we could check to see if any of the traits that we measured are affected by taphonomy. However, the grade was a tool for eliminating poorly-preserved pinnules.

TABLE 1. The numerical values of assigned letter grades

Letter Grade	Numerical Value
A	5
B	4
C	3
D	2
F	1

Comparisons

I compared measurements for morphotype 2 with comparable measurements made on a population of *A.* morphotype 1 pinnules and used the t-test, which is a measure of the statistical significance of differences in mean value for two populations. We also subjected certain ratios of measurements to the same test because the ratios represent character traits and is sometimes more helpful than the dimensions themselves.

Extremely decayed pinnules are more prone to distortion than well-preserved pinnules.

Accordingly, we excluded all pinnules with the taphonomic grade of F from the study. I also excluded pinnules if the cross-section was not sufficiently orthogonal to the midrib.

CHAPTER III

RESULTS

Dataset

The main goal of the study was to determine whether *Alethopteris* morphology type 2 is distinct from other alethopterid morphologies, particularly the coexisting morphotype 1 found in the same coal bed in the Williamson No. 3 deposit. For the purpose of comparison, two datasets were collected, each containing 20 to 30 pinnules (for which measurements were made), of each morphology.

The primary morphology of this study is relatively rare compared to other morphologies, particularly morphotype 1. I found 40 pinnules of morphotype 2 on five cut surfaces of at least two coal balls. However, through a careful examination of their taphonomic condition and the geometry in the pinnules' cross-sections. I then eliminated 16, leaving a total of about 24 pinnules in the dataset for morphotype 2. This number does not include the numerous pinnule fragments, which were excluded mostly because they were not orthogonal cross-sections even if it was technically possible to get one or two of the 9 types of measurements used in this study from the fragments. The exact number of measurements retained for analysis varies slightly with type of measurement. At least eight reasonable peridermal cross-sections of morphotype 2 were identified. Intriguingly enough, at least three good "v-shaped" arrays of pinnules were found in apparent organic connection to the ultimate rachis (the branch of the compound leaf that bears the pinnules or leaflets). As a bonus, a single pinnule is exposed on the surface of a third coal ball, that

is, otherwise devoid of well-preserved material on account of the secondary pyritization of the coal ball. This lone pinnule shows that morphotype 2 is a short, relatively narrow pinnule and has highly vaulted lamina as described in the general morphology section. The pinnule's dimensions, as directly measured, are 9.75 mm long and 2.25mm wide.

For the comparison, 40 morphotype 1 pinnules were examined and 32 were included in the dataset for morphotype 1.

Statistical analysis

The first round of statistics simply involved the tabulation of data, finding means, and standard deviation. These statistics were compiled on the measurements illustrated in Fig 4. The general results of the measurements that are available for both morphologies are listed in Table 2.

TABLE 2. A tabulation of measurements available in both morphologies from orthogonal cross-sections of pinnules. The average values are in μm .

	Morphotype 2				Sauki			
	Ave	STDV	Var	No.	Ave	STDV	Var	No.
MRW	805	122	14880	24	1085	189	31916	32
MLT	1311	395	156128	22	909	174	30279	32
W	3071	341	115947	21	2707	376	141176	32
EEW	2879	453	204874	19	1743	329	108439	32
N	542	121	14677	24	764	167	27754	32
VD	796	292	85118	21	294	120	14308	32
Ahave	1242	323	104200	21	594	97	9479	23

The features, OL (the portion of VD below W) and PP, could not be measured on most of the morphotype 1 specimens, and were not used in the comparison. On the other hand, the presence of these traits, along with others, in morphotype 2 indicate that it has a unique pinnule geometry. When neck widths of morphotype 1 were plotted as a function of taphonomy, it was found that neck is unreliable trait for identification. In the coal ball containing the majority of the morphotype 2, 6 partial to nearly complete peridermal cross-sections were found. From peridermal cross-sections the number of veins per mm at the pinnule margin (reported as veins per cm) was counted where possible.

The average number of secondary veins per cm is 36 per cm with a range of 32-43 veins per cm. Sometimes biological entities are not distinguished merely by trait dimensions, but by proportions, which can be represented simplistically as ratios. The ratio statistics are recorded in Table 3. Although morphotype 1 and 2 are close in size, the ratios facilitate comparison of the shape of pinnules standardized for size.

TABLE 3: Ratio Statistics

Type of Measure	Morpho 2				Sauki			
	Ave	STDV	Var	No.	Ave	STDV	Var	No.
N/MRW	0.689	0.190	0.036	24	0.709	0.129	0.017	32
EEW/W	0.945	0.107	0.012	19	0.644	0.089	0.008	32
MRW/MLT	0.639	0.151	0.023	23	0.847	0.164	0.027	32
VD/W	0.275	0.104	0.011	21	0.110	0.049	0.002	32

Results of student t-test

The dataset contains a fairly small sample of pinnules, the student t-test was selected to determine whether morphotype 1 and morphotype 2 are statistically distinct groups by determining which of the hypothesized distinguishing traits pass the t-test. The hypothesis, essentially, is that if there are traits that statistically distinguish between morphotype 1 and morphotype 2, then they are biologically distinct entities and perhaps different species as argued in the discussion section.

Once it was known for certain that we had two unequal sample sizes and particularly, unequal variance size. It had been presumed that this would likely be the case. So in the case of unequal sample size and unequal variance, the Welch's t-test was used. The following formula for calculating t is:

$$t = \frac{\bar{X}_1 - \bar{X}_2}{s_{\bar{X}_1 - \bar{X}_2}} \text{ where } s_{\bar{X}_1 - \bar{X}_2} = \sqrt{\frac{s_1^2}{n_1} + \frac{s_2^2}{n_2}}$$

The variables are defined as follows:

\bar{X} is the average or mean of a sample

s^2 is the variance, that is, the square of standard deviation.

n is the number sampled for a given morphology

So the student t-test was applied to 7 different measurements and 4 ratios that are common to both morphotypes 1 and 2. The results of the t-tests are displayed in Table 4. The value for critical t-value was obtained from Beyer and Selby (1976). According to them, for 40 D. F., the t-value is ± 3.55 .

TABLE 4: Calculated t-values for measured traits and ratios based on the Welch's t-test. The critical t-value is ± 3.55 . The average values for MRW through MLT are in μm for both morphologies.

Type of Measureme	Morphotype 1			Morphotype 2			D. F.	T-value
	Ave	Var	No.	Ave	Var	No.		
MRW	1085	31916	32	805	14880	24	56	-6.95
MLT	909	30279	32	1311	156128	22	54	4.48
W	2707	141176	32	3071	115947	21	53	3.65
EEW	1743	108439	32	2879	204874	19	51	9.55
N	764	27754	32	542	14677	24	56	-5.76
VD	294	14308	32	796	85118	21	53	7.48
Ahave	594	9479	23	1242	104200	21	44	8.84
Lave	395	5097	32	506	7835	22	54	5.07
N/MRW	0.709	0.017	32	0.689	0.036	24	56	-0.44
EEW/W	0.644	0.008	32	0.945	0.012	19	51	10.29
MRW/MLT	0.847	0.027	32	0.639	0.023	23	55	-4.88
VD/W	0.110	0.002	32	0.275	0.011	21	53	6.74

Thus, tests that result in a t-value well outside the domain ± 3.55 indicate a low probability (< 0.9995) that the two morphotypes came from the same population. Table 4 contains the t-values for both the measurements covered in Table 2 and the ratios in Table 3.

So from Table 4 it can be seen that most of the measurements pass the t-test. The ratio N/MRW obviously does not and it was judged that W is not helpful because its t-value is so close to the critical t-value. While most of the traits and ratios pass the t-test, the following are the most diagnostic as seen from their large t-value: EEW, VD, AHave, and EEW/W. Good graphs that illustrate the distinctiveness include the MLT/MRW, the MLT/MRW ratio over VD, and the MRW/MLT ratio plotted against the EEW/W ratio (Figs. 8, 9, 10).

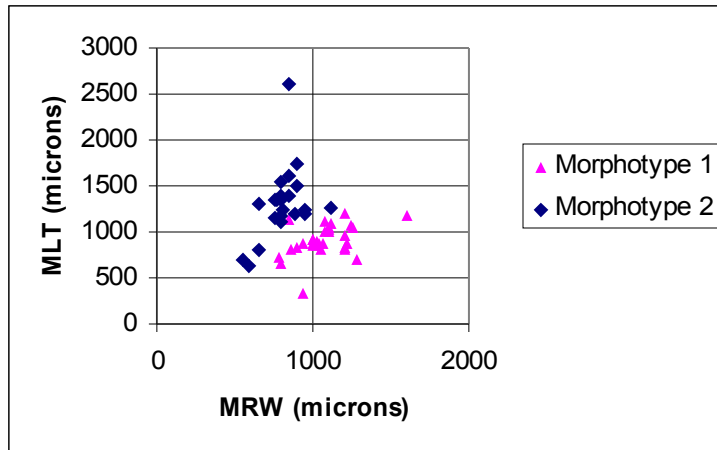


FIGURE 8—A graph that shows the tendency of morphotype 2 to be thicker in the midline depth and thinner in midrib width in comparison to *A.* morphotype 1.

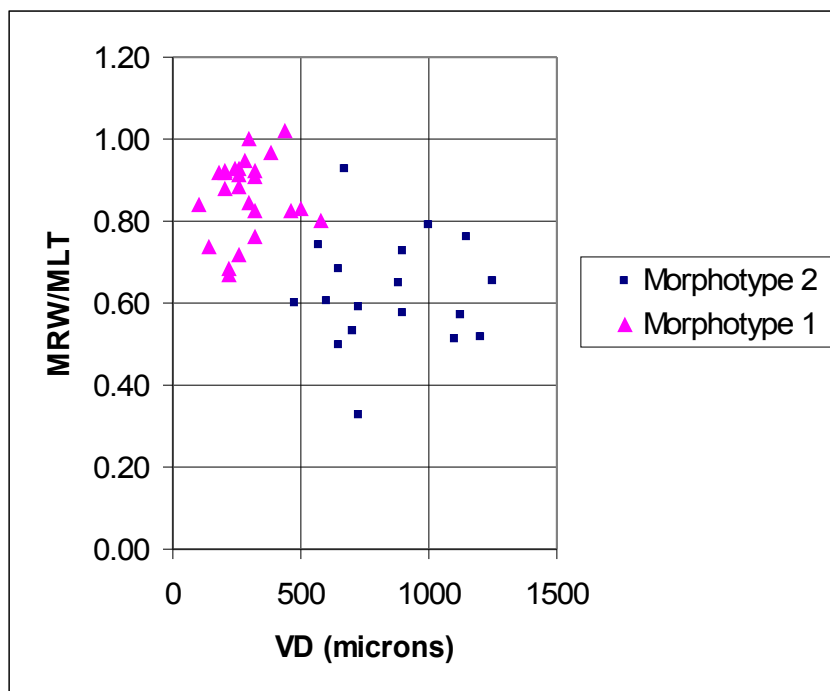


FIGURE 9—Midrib shape vs “Sunkeness.” VD is the depth of the midrib below the lamina surface. The midrib of morphotype 2 is narrower in width relative to its depth, and more sunken than the midrib of *A.* morphotype 1.

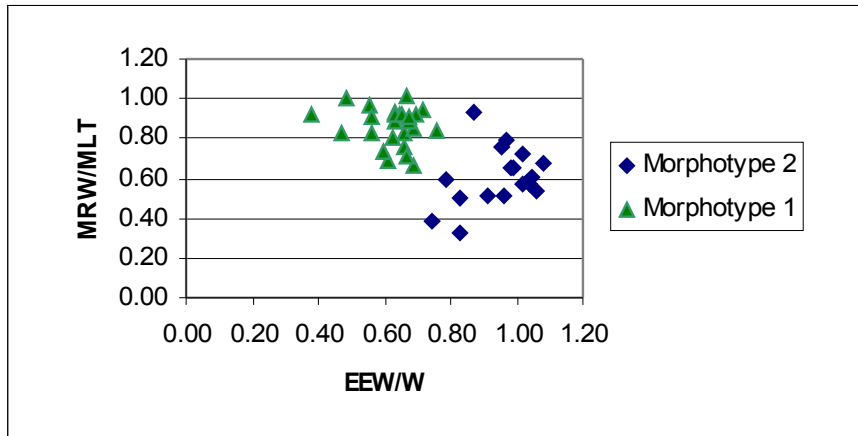


FIGURE 10—This graph effectively plots the ratio MRW/MLT, which serves as a proxy of roundedness of midrib, against EEW/W, which measures the degree of curling at pinnule margin. This graph effectively shows how combining at least two diagnostic traits further augments the differences between morphologies in a single trait or ratio.

General morphology

Alethopteris 'morphotype 2' has narrow, almost linear, vaulted pinnules with a wide, profoundly sunken midrib. The tip is extremely enrolled under the upper surface of the lamina. The pinnules range about 8mm to a little over 11mm in length. The width can be confidently stated to be 3.1 mm on average with a range of 2.3 mm to 3.6 mm. So the length over width ratio range is 2.2 to 4.8, where the average ratio is more like 3:1.

The midrib is prominent and the lamina attaches at a high angle from the midrib, giving rise to the “sunken” appearance described by Wagner (1968). Partial peridermals indicate that secondary veins depart from the midrib at a 90° angle. Most dichotomize once, near the midrib, although some do not. The pinnule margin has 32-43 (average is 36) secondary veins per centimeter. From the tip of the pinnule to the base, the midrib widens

uniformly. At the base of the pinnule, the midrib flares drastically where it inserts into the ultimate rachis (Fig. 11).

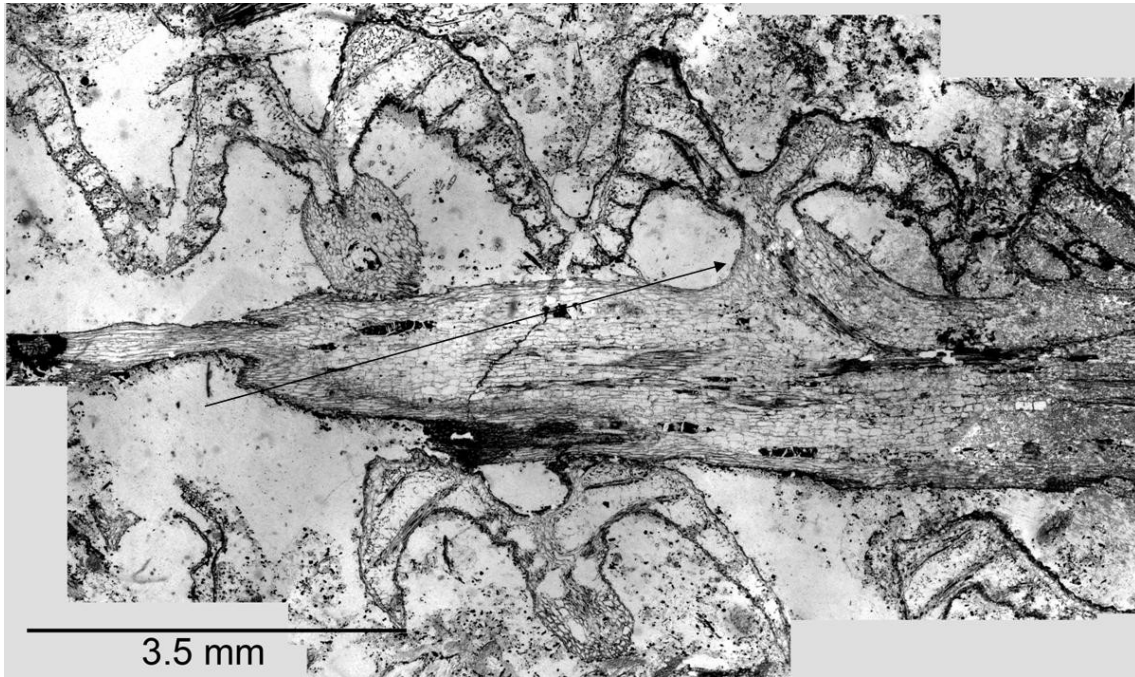


FIGURE 11—The arrow points to the “flaring” of the midrib as it attaches to rachis

The lamina is strongly arched along the entire margin and tapers in thickness toward the margin. The curling of lamina is so extreme that the lamina is arc-shaped in orthogonal cross-section to midrib. The midrib is circular in cross-section and extends virtually to the distal tip of the pinnule. On the abaxial surface there are papillate hairs, both on the lamina surface and midrib.

Internal morphology

Baxter and Wilhite (1969) and Reihman and Schabilion (1976) used the size of the hypodermal cells (the cells in the pinnule immediately below the upper epidermis) to distinguish permineralized *Alethopteris lesquereuxi* from permineralized *A. sullivanii*.

The hypodermal cells of morphotypes 1 and 2 are similar in size.

CHAPTER IV

DISCUSSION

Traits for distinguishing morphotypes 1 and 2

It is thought that, given the overall dimensions of the pinnules of both morphotypes, that as adpression fossils they would be difficult to distinguish, and both would be identified as *Alethopteris ambigua*. Wagner reports the dimension as 7-14 mm long the width as 2-4mm (1968). These dimensions are similar to Zodrow and Cleal's dimensions of 8-17 mm and 3-6 mm (1998), but narrower. Both morphologies are also similar in having a nearly perpendicular insertion angle of pinnule into rachis, more secondary veins visible on abaxial than adaxial surface, and wide midrib relative to pinnule width. One source for the differences in reported measurements is that Wagner (1968) included *A. friedeli* in *A. ambigua* in his famous monograph on *Alethopteris* and Zodrow and Cleal excluded *A. friedeli*. Zodrow and Cleal also included permineralized *A. lesquereuxi* in the same species as adpressed *A. ambigua*. *A. lesquereuxi* is a larger morphology and therefore the inclusion of *A. lesquereuxi* with *A. ambigua* would have increased the average dimensions. The general dimensions of the morphologies have been summarized in Table 5. While still on the subject of the overall dimensions of length and width, it should be noted that morphotype 2's width would likely be wider in adpression fossils than in permineralized fossils because the arched lamina would get flattened and therefore appear wider. So while the identification of morphologies 1 and 2 as *A. ambigua* may be possible, the results of this research suggest that it might be difficult to distinguish between the two morphologies in adpression without knowing the shape of the midrib.

TABLE 5: Summary of general dimension of *Alethopteris* species known from permineralized coal balls

Morphology	Length (mm)	Width (mm)
Morphotype 1	~5-9	1.8-3.4
Morphotype 2	8-11	2.3-3.5
<i>A. lesquereuxi</i>	6-20	4-5
<i>A. sullivantii</i>	12-24	7-12

There are six traits that can be used to distinguish morphotype 1 and 2 and most involve traits of permineralized pinnules:

1. The lamina of morphotype 2 is very curved, almost crescent-shaped (can be seen in AH measurements). This is in contrast with morphotype 1's lamina which form a nearly flat adaxial (little "sunkeness") surface and bend at right angles to create an almost box-like shape in orthogonal cross-section
2. The ratio of EEW to W is much closer to 1 for morphotype 2 than for morphotype 1. In other words, the margins in morphotype 2 do not enroll as they do in morphotype 1.
3. The degree of roundedness of midrib as viewed in orthogonal cross-section and the MRW/MLT ratio serves as a proxy to demonstrate the difference between morphotypes 1 and 2. The midrib of morphotype 2 is almost perfectly circular in cross-section and is more rectangular in cross-section for morphotype 1.
4. Degree of "sunkeness" as revealed by VD measurements. In morphotype 2, the midrib appears to be deeply sunken, though this has more to do the angle of

- lamina attachment than the midrib actually being embedded in the lamina. The midrib in morphotype 1 is level with adaxial surface of lamina because lamina attach to midrib horizontally.
5. The apex of morphotype 2 is enrolled to the point where the apex actually points backward towards ultimate pinna, much like an upside down jester slipper with exaggerated curly toes. Morphotype 1 is the opposite in having an apex that does enroll and has a blunt edge.
 6. Morphotype 1 appears to be shorter than morphotype 2, however pinnule lengths taken from permineralized pinnules in peridermal section are minimum lengths. If the pinnule is significantly curled or arched and passes out of the plane of section, the length on the peel is not the entire length of the pinnule.

Other, less conclusive, distinguishing traits include the observation that the lamina of morphotype 2 gradually tapers to a sharp margin and this is in contrast with morphotype 1's lamina, which does not taper and has rather blunt margins. Based on the results of this study, morphotypes 1 and 2 should be named as separate permineralized species, both of which would belong to *Alethopteris ambigua* if found as adpression fossils.

Distinguishing morphotype 2 from other permineralized species

Both morphotype 1 and 2 can be readily distinguished from *Alethopteris lesquereuxi* because *A. lesquereuxi* has three traits that set it apart from other alethopterids, including morphotypes 1 and 2. They are:

1. Up to several large sheath bundles that protrude on the abaxial surface of lamina

2. Stomatal papillae
3. Extremely large hypodermis cells

The hypodermal cells in *A. lesquereuxi* are reported as 96 x 76 μm by Reihman and Schabilion (1976) and as 140 x 100 x 70 μm by Baxter and Willhite (1969). The hypodermal cells of morphotype 1 average 64 x 66 μm ; those of morphotype 2 average 67 x 73 μm . (Table 6). Both are smaller than reported dimensions of *A. lesquereuxi*.

TABLE 6. Size of hypodermal Cells in Morphotypes 1 and 2

Morphotype (N)	Ave. anticlinal dimension	Range	Ave. periclinal dimension	Range
1 (25)	64 μm	48-82 μm	66 μm	49-100 μm
2 (36)	67 μm	35-88 μm	73 μm	44-123 μm

Distinguishing morphotype 2 from *A. sullivanii* (the other well-known foliage species already described from coal balls) is hardly difficult given the extreme differences in cross-sectional proportions. *A. sullivanii* has large pinnules in comparison to either morphotype 1 or 2. The dimensions of *A. sullivanii* are 12-24 mm long and 7-12 mm wide (Fig. 4) (Reihman and Schabilion 1976). The midrib of *A. sullivanii* is very small and rarely protrudes through the abaxial surface and represents a truly sunken midrib, that is, contained within the lamina. The lamina are very straight and wide (as already noted at over 7 mm). The secondary vein density count is much lower in *A. sullivanii* than either morphotype 1 or 2. Also Morphotype 2 is easily distinguished from *A. zeilleri* and

similar pinnules found in the Calhoun and Duquesne Coals (Mickle and Rothwell, 1982) based on midrib size, lamina thickness, narrow pinnule width and degree of “sunkeness.”

Pinnule geometry

One of the chief advantages of using cross-sections of permineralized pinnules (or any other type of plant fossil one wishes to study) is that one has more character traits to work with when describing new species. The main disadvantage is that it is more time-consuming to prepare peels as described in the methods section and to sort through many cross-sections before one has enough material to make an identification and reconstruction.

In essence, during the course of this study, I realized that it was possible to determine the orthogonality of the cross-section (i.e. is the cross-section dipping in a distal adaxial or distal abaxial direction?). It is also possible to identify highly skewed cross sections and the part of pinnule that each side of the cross-section intersects (Fig. 12). More

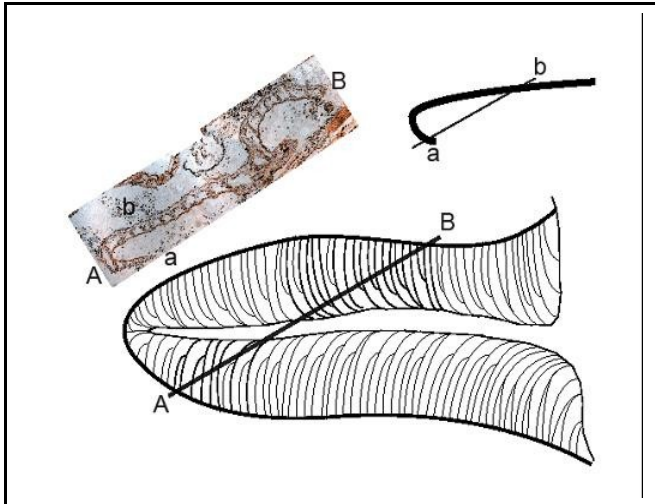


FIGURE 12—Different Views of a Pinnule Cross-section that is skewed, meaning extremely non-orthogonal

importantly, distal cross-sections are easily identifiable and eliminated from the dataset because they contain few diagnostic traits and can resemble the distal cross-sections of similar morphologies. Figs. 13 and 14 show the type of information that is possible to ascertain about the pinnule geometry, which is how some of the information used in the general morphology description were derived. One special type of cross-section is the peridermal one where the cross-section is roughly parallel to W and if complete enough, shows the general outline of the pinnule (Fig. 14).

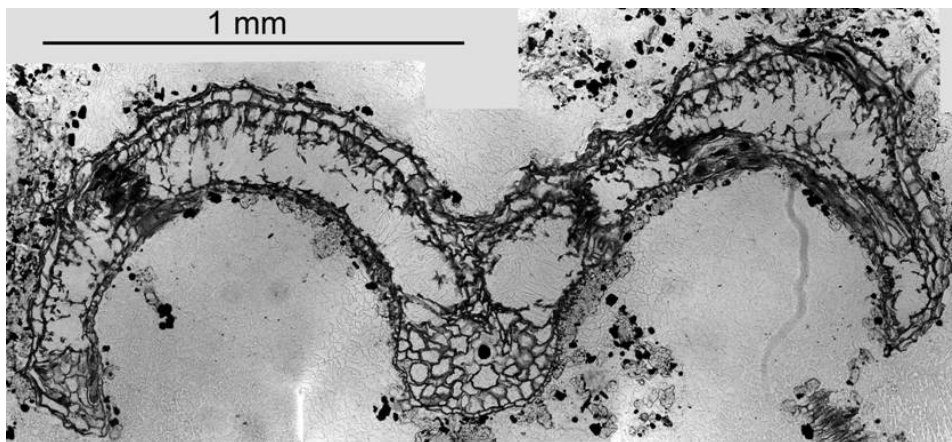


FIGURE 13—Cross-section of morphotype 2 in distal (tip) region of pinnule

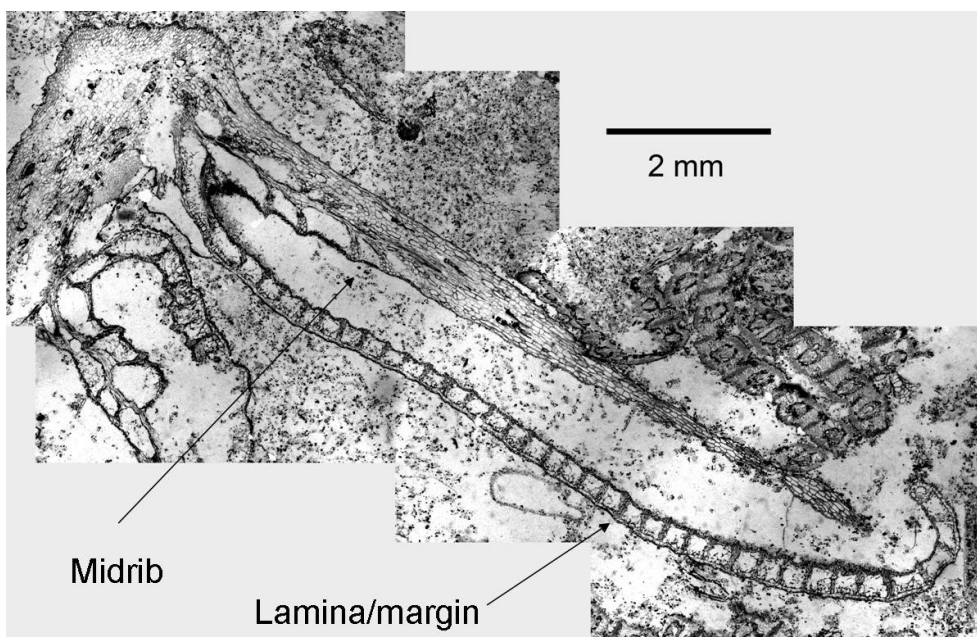


FIGURE 14—A peridermal cross-section of morphotype 2

Paleoecology and paleoclimate

As already noted, the new *Alethopteris* leaf morphologies are quite within the dimensions of *Alethopteris ambigua*, but the two new morphologies are clearly distinguishable from each other when permineralized. The stratigraphic range of *A. ambigua* is reported by Wagner (1968) to span from Westphalian C to Stephanian A, which in ICS terms translates to from middle Moscovian to middle Kasimovian. My research and Slone's 2003 M.S. thesis extends the range of *A. ambigua* into the early Moscovian. This stratigraphic range includes intervals characterized by relatively drier and relatively wetter climate (Phillips and Peppers 1984). These two leaf morphologies are characterized by several xeromorphic traits: thick lamina, enrolled lamina and margin, abundant trichomes, and possibly a low surface-to-volume ratio (Esau, 1977).

So then morphologies 1 and 2 both have xeromorphic traits and coexisted in the same environment as evidenced by their presence in the same coal balls from the Williamson No. 3 Mine. The other morphologies, *Alethopteris lesquereuxi* and *A. sullivantii*, that are known from permineralized coal balls, do not have as many of the xeromorphic traits listed by Esau (1977). Peat swamps, the ecological environment implied by the occurrence of all these pinnules in coal, are generally associated with warm, continuously wet climates (Parrish 2001), yet the traits of morphotypes 1 and 2 seem to indicate dry climates. One possibility is that when the coal bed in the Williamson No.3 Mine was a swamp, it was inundated periodically by salt water. Under this scenario, the xeromorphic features of morphotypes 1 and 2 could indicate the presence of salt water. The correlation between salt water and xeromorphy is discussed by Saenger (2002), who also listed

papillate hairs on the abaxial surface and added a thick epidermis to the list. If this hypothesis were true, it would follow that morphotypes 1 and 2 were adapted for living in salt water, much like mangroves, or were salt-tolerant taxa. The xeromorphic features of these pinnules do not necessarily indicate coal accumulation in arid climates.

CHAPTER V

SUMMARY

An examination of coal balls from the Kalo Fm., Williamson No. 3 Mine, Iowa, revealed two distinct morphologies that are probably assignable to adpression species *Alethopteris ambigua*. Permineralized specimens of the two morphologies are distinct, because permineralization preserves pinnules in three dimensions.

The morphotype 2 population consisted of 24 pinnules; the morphotype 1 population consisted of 32 pinnules. I used 7 measurements and 4 ratios to establish the size and shape of each morphotype and Welch's t-test to determine the statistical significance of the traits used to distinguish the two morphotypes. In comparison to morphotype 1, morphotype 2 has: 1. a significantly narrower midrib relative to midrib width; 2. a midrib that is significantly lower than the lamina surface; and 3. a significantly more arched pinnule. The results of this study indicate that morphotype 1 differs significantly from morphotype 2, and that the two permineralized morphotypes should be described as separate species, both of which would be identified as *Alethopteris ambigua* if found as adpressions.

The other three permineralized alethopterids (*A. lesquereuxi*, *A. sullivantii*, and *A. zeilleri* and related species) are very different from morphotype 2.

Establishing the dimensions and shape of permineralized pinnules requires orthogonal cross sections and orthogonal peridermal sections whenever possible. However the asymmetry of enrolled pinnules that taper in width distally allow identification of non-orthogonal cross sections and, determination of the angle of section (dipping in an abaxial distal direction vs an adaxial distal direction).

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