

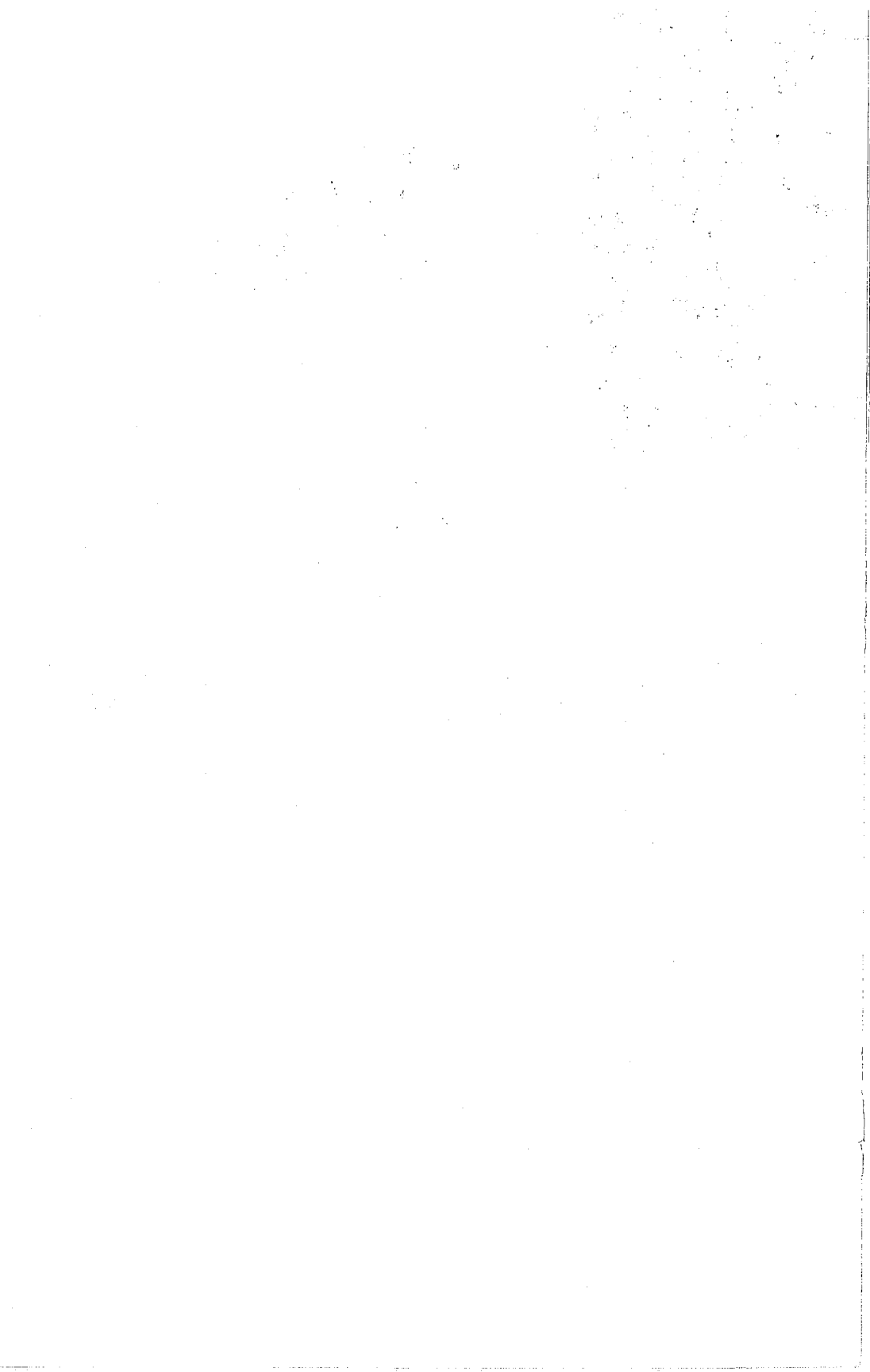
BRIGHAM
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GEOLOGY STUDIES

Volume 16 Part 3 December 1969

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A publication of the
Department of Geology
Brigham Young University
Provo, Utah 84601

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Brigham Young University Geology Studies is published semi-annually by the department. *Geology Studies* consists of graduate student and staff research in the department and occasional papers from other contributors, and is the successor to *BYU Research Studies, Geology Series*, published in separate numbers from 1954 to 1960.

Distributed June 15, 1970

Price \$4.00

Notes on the Fern Family Matoniaceae from the Western United States

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ABSTRACT.—A Cretaceous fern flora has been recently discovered near Westwater, Grand County, Utah. Among specimens collected from Westwater are many forms related to extant members of the fern family Matoniaceae.

This family was widely distributed geographically throughout most of the Mesozoic Era, and matoniaceous ferns have been collected from several fossil localities in the United States. The Matoniaceae was especially important in the United States during Lower Cretaceous times.

Five species, *Matonidium brownii* Rushforth, *Matonidium* (?) *lancipinnulum* Rushforth, *Matonidium galleyi* (Miner) Rushforth, *Matonidium americanum* Berry em. Rushforth, and *Matonidium* (?) sp., and one variety, *Matonidium brownii* var. *magnipinnulum* Rushforth, are considered in the present paper.

ACKNOWLEDGMENTS

The author wishes to express his appreciation for the assistance rendered by Dr. W. D. Tidwell and Dr. J. R. Bushman during the preparation of this manuscript. The author also wishes to thank Dr. C. A. Arnold of the University of Michigan for loaning type specimens of matoniaceous fossils.

Partial support for this study was obtained from Brigham Young University Research Grant 115-77-482 to Dr. William D. Tidwell.

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INTRODUCTION

A Cretaceous fern flora has been recently discovered in the Dakota Sandstone Formation near Westwater, Grand County, Utah. Among specimens collected from Westwater are many fossils related to the fern family Matoniaceae. This family is an interesting taxon with many unique characteristics, and is known from both fossil and living members.

The family Matoniaceae was widespread throughout most of the Mesozoic Era. Members of this family have been collected from Triassic rocks from several localities in the United States and Greenland, and in some floras of this age they are very abundant. Occurrence of matoniaceous fossils increases markedly during Jurassic and Lower Cretaceous periods. Genera included in this family are well known components of floras of these periods from many parts of the world. The family Matoniaceae is perhaps best known from Europe, although this may be due in part to lack of collections from other areas of the world.

HISTORICAL REVIEW

Historically, the family Matoniaceae was first known from the fossil record, and secondarily from modern floras. The fossil genus *Phlebopteris* was proposed in 1828 by Adolphe Brongniart for the placement of several European Jurassic ferns. Specimens placed in this genus are unique in leaf configuration in that all pinna radiate from a common point on the petiole (pedate arrangement). Sori are borne in a single row on each side of the midvein, and sporangia are not covered by an indusium.

In 1830 Robert Brown proposed the genus *Matonia* for the placement of extant fern specimens collected from the Malayan Peninsula. The ferns described by Brown are extremely beautiful, ranging up to eight feet in height and exhibiting pedate pinna disposition similar to that found in *Phlebopteris*. Brown recognized that the material he described differed in many ways from other extant ferns although he did not consider these differences great enough to warrant the proposal of a new tribe or family. The family Cyathaceae was considered by many early workers to be the probable family for the placement of *Matonia*. Other workers have subsequently proposed placing *Matonia* in the family Gleicheniaceae. Moore (1857) considered *Matonia* to exhibit characteristics unique enough to warrant the formation of a new tribe, and he proposed Matoniaceae for its placement. Christ (1897) proposed the formation of a separate family, the Matoniaceae, for *Matonia* and related forms, and this is the classification commonly followed today.

The genus *Laccopteris* was established by Presl (1838) for the placement of sterile and fertile pinna fragments from the Keuper Formation of Europe. Specimens placed in this genus again illustrate a pedate pinna arrangement similar to *Phlebopteris* and *Matonia*. Although not recognized by Presl, *Laccopteris* is extremely similar to *Phlebopteris* in both sterile and fertile morphology, and the two genera are for all purposes essentially identical.

During the following years, several authors described various genera which have subsequently been referred to the family Matoniaceae although in some instances this placement is questionable. These genera include *Andrianea*, which was described by Braun in 1843, *Carolopteris*, described by Debey and Ettinghausen in 1859, *Selenocarpus*, described by Schenk in 1867, and *Microdictyon*, described by Saporta in 1873.

Matonidium was proposed by Schenk (1871) for fossil ferns exhibiting the same characteristics as the extant *Matonia pectinata* R. Br. Thus fossils placed in this genus are morphologically very close to modern matoniaceous ferns, both vegetatively and in reproductive structure. Zeiller (1885) discussed this, and came to the conclusion that members of the fossil genus differ from extant species by having a more oval sorus, and often more sporangia per sorus. These differences are very slight however and are not constant, as species of *Matonidium* vary with respect to both of these characteristics. It should also be mentioned that the structure of the two fossil genera *Phlebopteris* and *Laccopteris* is also very similar to that of modern members of the Matoniaceae, and placement of fossils in one of these genera became more or less arbitrary. This is especially true when fertile specimens were absent.

Seward (1899) in his consideration of the family Matoniaceae recognized several taxonomic problems within this family and determined that *Phlebopteris* and *Laccopteris* are indeed synonymous. However, Seward proposed uniting these two genera as *Laccopteris*. Seward also proposed the placement of *Microdictyon*, *Guthiera*, *Marzaria*, and probably *Nathorstia* in *Laccopteris*. This proposal was made as the result of a good deal of critical study by Seward, and certainly must be regarded as basically accurate. However, Seward's proposal to unite these genera under *Laccopteris* must not be followed since *Phlebopteris* was proposed ten years prior to *Laccopteris* and is therefore taxonomically correct. This was pointed out by Hirmer and Hoerhammer (1936) and most authors since 1936 have used the preferred generic name.

The problem of differentiating between *Phlebopteris* and *Matonidium* is difficult as the two are very similar in many vegetative features. However, we note from the descriptions of these genera and as mentioned by Harris (1961), the two may be separated based upon soral morphology. The genus *Phlebopteris* is non-indusiate, whereas in *Matonidium* the placenta is expanded to form a large peltate indusium. Obviously then, firm placement of matoniaceous fossils in one of these genera is dependent upon fertile material, and the placement of sterile specimens is problematic. *Phlebopteris* commonly is present in older rocks than is *Matonidium*, and as mentioned by Harris (1961), the series *Phlebopteris*, *Matonidium*, and *Matonia* is commonly considered to be an evolutionary sequence.

The family Matoniaceae is best known from Europe, and relatively few occurrences of matoniaceous ferns have been reported from the United States. Fontaine (1883) figured but did not identify pinna fragments from Triassic rocks of North Carolina. Fontaine (1900) subsequently placed these fossils in *Laccopteris lanceolata* (Goeppert) Ward. Fontaine (1899) identified pinna fragments from the Black Hills of Crook County, Wyoming, as being matoniaceous and placed them in *Matonidium althausii* (Dunker) Ward. Ward (1905) used *Matonidium althausii* for the placement of pinna fragments collected from the Knoxville beds near Lowry, Tehama County, California. As discussed by Arnold (1956), all of the above references to the Matoniaceae from the United States are somewhat problematic.

Cockerell (1916) placed fern fossils collected from Hovenweep Canyon and Cutthroat Gulch, Montrose County, Colorado, in *Matonidium althausii*. This material was subsequently sent to E. W. Berry for further study. Upon critical examination, Berry (1919) determined these fossils to be distinct from *Matonidium althausii* and proposed *Matonidium americanum* Berry for their placement. This material is unquestionably matoniaceous based upon sterile and reproductive morphology although venation is not preserved.

Berry (1911) referred to the family Matoniaceae for the placement of the genus *Knowltonella*. This genus was proposed for the placement of sterile pinna fragments collected from the Patapsco Formation of Maryland. *Knowltonella* does exhibit characteristics that may align it with matoniaceous ferns, although firm placement of this genus in the family Matoniaceae is not possible until fertile specimens can be collected. As reported by Berry (1933), *Knowltonella* has also been collected from the Black Hills of Wyoming.

Miner (1935) described a pinnule fragment collected from a drill core of the Dakota Sandstone Formation of Kansas as *Laccopteris galleyi* Miner. Venation of this specimen was not preserved, although soral and spore morphology are undoubtedly matoniaceous. Arnold (1956) transferred this fern to the genus *Phlebopteris*.

Laccopteris smithii Daugherty was proposed by Daugherty (1941) for matoniaceous ferns collected from the Chinle Formation (Triassic) of Arizona. These ferns were placed in the family Matoniaceae based upon both sterile and fertile morphology. The sori of these ferns are non-indusiate and composed of seven to fourteen radially disposed sporangia. Arnold (1956) transferred *Laccopteris smithii* to *Phlebopteris*.

Roland Brown (1951) reported on matoniaceous ferns collected by himself and others from the Dakota Sandstone Formation near Naturita, Montrose County, Colorado. These ferns were placed with *Matonidium americanum* despite several differences between the two. Brown also noted similarity between the Naturita ferns and *Matonidium weisneri* Krasser which had been described by Krasser (1896).

In 1956, C. A. Arnold dealt with several members of the Matoniaceae from the United States. As mentioned, he transferred two ferns previously placed in the incorrect *Laccopteris* to *Phlebopteris*. In this paper, Arnold described a new species, *Phlebopteris utensis* Arnold which was collected from the Chinle Formation near Hite, Garfield County, Utah. This species is similar in many respects to *Phlebopteris smithii* Daugherty which was contemporaneous.

Hall (1965) reported isolated intact sori of a matoniaceous fern from the Magothy Formation. These sori were composed of nine to eleven radially arranged sporangia which were covered by a peltate indusium. Hall further reported that leaves representing this family have not been collected to date from this formation.

DISTRIBUTION AND EVOLUTION

Modern representatives of the Matoniaceae are highly restricted geographically, being known only from the Malayan Peninsula and the immediate surrounding area. They are restricted to humid tropical upland regions. As discussed by Seward (1899), the geologic history of the family as it is presently known does not allow the understanding of how modern matoniaceous ferns became thus restricted. Seward (1899) discussed the history of this family as follows:

Matonia may reasonably be classed among present-day survivals in the southern hemisphere of ancient Mesozoic types, and it would seem that this generic type originated in the northern hemisphere late in the Triassic or early in the Jurassic Period. The apparent absence of satisfactory fossil Matoniaceae (Matoniaceae) in the Tertiary Floras lends support to the view that this section of the Filices (Filicophyta) reached its maximum development in the Mesozoic Era, and towards the close of the Cretaceous Period its geographical range had become considerably restricted.

As information regarding the fossil Matoniaceae increases, it becomes more apparent that Seward was likely correct in his analysis of the decline of this taxa. Bower (1928) further discussed this point and arrived at a similar conclusion. However, Bower (1928) realized that determining the geographical point of origin of this family posed a more difficult problem. Indeed, as data on Mesozoic floras increases, it becomes more apparent that the family Matoniaceae was widely distributed, and the reason more matoniaceous fossils are not known from the southern hemisphere is that the fossil record as a whole is poorly known from this part of the world.

It is evident that the family Matoniaceae originated much earlier than postulated by Seward. Matoniaceous fossils of well defined characteristics have been collected from Triassic rocks older than suggested possible by Seward. Examination of recent and past collections from the Chinle Formation of Utah indicates that the family Matoniaceae had already achieved a good deal of diversification by this time. With this in mind, it is likely that matoniaceous ferns originated in earliest Mesozoic, or more likely, in late Paleozoic times.

Solms-Laubach (1891) discussed the family Matoniaceae, and came to the conclusion that this family occupied a phylogenetic position between the families Gleicheniaceae and Cyathaceae. Seward (1899) agreed with this position and added supporting evidence based upon stem anatomy and other features.

Upon examination of the characteristics of these three families, it is apparent that they share many common characteristics, and that in morphology and anatomy it does seem likely that the Matoniaceae is intermediate between the other two, with the Gleicheniaceae occupying a more primitive phylogenetic position and the Cyathaceae being somewhat more advanced. The characteristics of these families will be considered briefly in the following paragraphs.

Matoniaceous ferns are characterized by having superficial sori which are radiate with a single ring of sporangia. All sporangia mature simultaneously within the sorus (Simplices). Sporangia are large and with an incomplete oblique annulus which causes lateral sporangial dehiscence (although as discussed by Bower [1928] this lateral dehiscence is weakly defined). The number of spores produced per sporangium is relatively small, and the spores are large, trilete, and commonly rounded-tetrahedral in shape.

The family Cyathaceae is characterized by having superficial sori which are radiate with a single ring of sporangia. Sporangia are smaller than those of either the Gleicheniaceae or Matoniaceae, and they exhibit well defined lateral dehiscence. An important advance is noted in this family as the maturation of sporangia within the sorus is not simultaneous but rather is graded so that at any one time a sorus will contain sporangia in various stages of maturation (Gradatae). Spores are produced few per sporangium and are small and trilete.

Gleicheniaceae ferns are characterized by superficial sori with a single radiate ring of sporangia. Sporangia are large, and with an incomplete oblique annulus which causes longitudinal sporangial dehiscence. Sporangia mature

simultaneously within the sorus (Simplices). Spores are small, trilete, and produced in large quantity.

When we consider that the Gleicheniaceae is phylogenetically more primitive than the Matoniaceae, and is a more ancient taxon, it is likely that gleicheniaceous ferns were the progenitors of matoniaceous ferns. Evolutionary changes necessary to obtain matoniaceous ferns from gleicheniaceous ancestors are relatively slight. These changes have included (1) a change in position of sporangial dehiscence from longitudinal to lateral (although the annular position in both is oblique), (2) a decrease in the number of spores produced in each sporangium, (3) an increase in spore size, and, (4) a change in pinna disposition. Some members of the family Matoniaceae have become further adapted for soral protection through the development of a large peltate indusium.

MATERIALS AND METHODS

Preservation of the fossils from Westwater is such that carbonaceous remains are present, and transfer preparations are often possible. These transfers are prepared basically following Abbott (1950). When possible the specimen is coated with a single coat of Helen Neushaefer nail polish and allowed to dry for several hours. The entire coated specimen is then immersed in a 48 percent hydrofluoric acid solution and allowed to remain overnight. The peel is retrieved and dried after the rock has dissolved. Canada balsam is used to mount these transfers.

Peel transfers were examined using transmitted and reflected light and phase contrast microscopy. Photographs were taken with a dark red filter to improve contrast.

SYSTEMATICS

As discussed by Harris (1961), the common genera of the family Matoniaceae, *Phlebopteris*, *Matonidium*, and *Matonia* appear to intergrade, and the boundaries between these taxa are difficult to establish. For all practical purposes, the difference between *Phlebopteris* and *Matonidium* is that the former is non-indusiate and the latter is indusiate. In addition, *Phlebopteris* is commonly considered to be an older taxa than *Matonidium*, though some degree of overlap in age occurs between the two. As might be expected, the distinction between these two genera is difficult to establish when extremely well preserved material is not present. The problem is compounded when we note that in extant members of this family entire indusiate sori are easily detached and commonly lost at maturity, leaving a depression in the undersurface of the pinnule with a round placental projection in the center. This is often the condition in which fossil forms are collected, and inferences on the nature of the sorus are impossible. In addition, vegetative characteristics of *Matonidium* and *Phlebopteris* are almost identical. Regardless of these problems, for the present I have made no changes in the traditional usage of *Phlebopteris*, *Matonidium*, or *Matonia*. Indusiate forms treated in this paper are placed with *Matonidium*. Based upon the Cretaceous age of the ferns considered in this paper, those forms not represented by fertile specimens have also been placed in *Matonidium*, although this placement must remain tentative until fertile material can be collected.

Another serious problem with the taxonomy of this family is the relationship of the genus *Nathorstia* to matoniaceous ferns. *Nathorstia* was proposed by Heer (1880) for ferns collected from the Cretaceous of Greenland.

Nathorst (1908) discussed this genus and came to the conclusion that the sori of *Nathorstia* are synangia similar to those of marratiaceous ferns. This, of course, would not align nathorstian ferns closely with matoniaceous ferns. However, Seward (1927) discussed *Nathorstia* further and stated evidence to support the view that this genus is indeed matoniaceous and exhibits sori that are not synangial but are rather composed of tightly packed free sporangia. Hirmer (1927) also discussed the relationship of *Nathorstia* to the Matoniaceae and placed all of *Nathorstia* in *Laccopteris* (*Phlebopteris*). However, Hirmer and Hoerhammer (1936) reconsidered the position of Hirmer (1927) and revived *Nathorstia* for the placement of several unquestionable matoniaceous ferns.

In habit and venation *Nathorstia* and *Phlebopteris* are identical, and as stated by Seward (1927),

It is difficult to believe that fronds identical in habit, in venation, and in the form and disposition of the sori belong to ferns which are members of different families.

Harris (1961) discussed the relationship between *Nathorstia* and *Phlebopteris*, and concluded that the type specimens of nathorstian species should be re-examined to determine whether or not the sori are synangial or composed of crowded free sporangia. This should indeed be done, and it is likely that the latter will be found to be the case.

MATONIDIUM BROWNII Rushforth, sp. nov.

Pl. 1, fig. 2; Pls. 2-5; Pl. 6, fig. 2; Pl. 8, fig. 2; Pl. 11, fig. 1

1950 *Matonidium americanum* of Berry, Brown—U. S. Geol. Surv. Prof. Paper 221-D, p. 48, Pl. 10, figs. 7, 8.

Description.—The petiole of this species is stout, ranging between 5 mm and 15 mm in diameter. In many specimens the petiole is divided apically into two short arms which give rise to the pinnae. The number of pinnae per frond varies from four to ten or more. Pinnae are lanceolate and have been observed up to 15 cm in length.

The pinna rachis ranges between 0.5 mm and 2.5 mm in diameter and is smooth. Pinnule attachment may be opposite, subopposite, or alternate at various points on the rachis. Pinnules are completely basal in attachment and are free of each other except at the extreme pinna apex. The pinnule base commonly extends both up and down the rachis for a short distance, so that the attachment is very broad. Pinnules range in length between 3 mm for those near the pinna base, and 30 mm for the longest of the frond. In breadth the pinnules vary between 5 mm and 9 mm. Pinnules arise nearly perpendicular to the rachis and become oriented toward the pinna apex. Pinnule margins are entire, and apices are rounded.

Each pinnule contains a major primary vein which remains prominent to the apex. Secondary veins arise from this midvein at intervals of approximately 1.7 mm. In sterile pinnules these secondary veins divide immediately above the midvein forming veinlets which anastomose parallel to the midrib forming costal aeroles. Veinlets arise from these aeroles, and the secondary veins redivide. Veinlets formed in this manner anastomose to form well defined angular aeroles in the lamina above the costal aeroles. Anastomosis is less frequent as the laminar margin is approached.

In fertile specimens secondary veins again divide immediately above the midrib. However, the veinlets formed in this manner do not anastomose to form costal aeroles. These veinlets extend directly to the placenta of the sorus. Secondary veins redivide at a point approximately one half of the distance from the midrib to the pinnule margin, and the resulting veinlets anastomose to form an arch above the placenta. Veinlets arise from this arch and extend to the placenta. Other veinlets arising from this arch extend to the pinnule margins. Anastomosis occurs between veinlets derived in this manner, although this is somewhat infrequent.

The upper epidermis is composed of more or less isodiametric, rounded to somewhat angular cells that average $45\ \mu$ in diameter. Lower epidermal cells have not been observed. Guard cells are unknown, although many depressions are noted on the undersurface of the pinnules, and it is thought that the stomata were slightly sunken, as they are in the extant *Matonia pectinata*.

Sori are borne in a single row on each side of the midvein and range between 1.7 mm and 2.0 mm in diameter. Each sorus contains from 10 to 14 sporangia in a single radiate ring around a central placenta. Sporangia are entirely covered by a large peltate indusium, which appears to have been rather persistent. Sporangia are wedge shaped with oblique annuli and range between 0.6 mm and 0.8 mm in length. Sporangia are sessile or nearly so. Entire sori have been shed from many specimens, leaving a depression in the lamina on the undersurface of the pinnule with a central placental protrusion.

Spores are trilete, with the laesurae reaching approximately three fourths of the distance to the equator. The commissures are bordered by a rather weakly defined margo. The contour of the equator is rounded triangular, with the sides being convex. The spore wall is psilate and averages 1.1 microns in thickness. Spore diameter is typically 57 microns.

Discussion.—The author has recently examined the collections of Roland Brown from the western United States. The collections are housed in the United States National Museum, Washington, D. C. It is apparent that Brown and others collected *Matonidium brownii* from near Naturita, Montrose County, Colorado. However, these specimens were not treated by Brown (1950) as being specifically distinct, as he included them in *Matonidium americanum* Berry.

Matonidium brownii differs from *Matonidium americanum* by being much larger, with fewer pinnae per frond; by having anastomosing rather than open venation; and in soriation (Table 1). *Matonidium brownii* differs from *Matonidium wiesneri* Krasser by having anastomosing venation as opposed to free venation, and by being larger and having more numerous sori. *Matonidium althausii* (Dunker) Ward differs from *Matonidium brownii* in pinnule shape and habit, and in venation (*Matonidium althausii* has open venation). Soriation of *Matonidium althausii* also differs from that of *Matonidium brownii* in that the former exhibits sori borne to the extreme pinnule apex, decreasing in size as the apex is approached.

In venation, *Matonidium brownii* is similar to *Phlebopteris dunkeri* (Schenk) Schenk.

Occurrence.—*Matonidium brownii* is known from the Dakota Sandstone Formation near Naturita, Montrose County, Colorado, and from near Westwater, Grand County, Utah.

Figured specimens.—Holotype: BYU 1557; paratypes: BYU 1558-1565.

MATONIDIUM BROWNII var. *MAGNIPINNULUM* Rushforth, var. nov.

Pl. 6, fig. 1; Pl. 7, fig. 2; Pl. 14, fig. 1

Description.—This variety is known from frond fragments, several of which are fairly complete and illustrate pedate pinna disposition.

Pinna fragments have been observed up to 30 cm long. The pinna rachis is rather delicate, ranging from 0.5 mm to 1.5 mm in diameter. Pinnae are lanceolate.

Pinnules may be opposite, subopposite, or alternate in disposition on the rachis. Pinnules are completely basal in attachment and are often decurrent. Pinnules have distinct sinuses and are separated from each other by gaps of up to 4 mm. Pinnule length ranges between 5 mm for those nearest the base of the pinna, and 60 mm for the largest on the pinna. Pinnule width ranges between 2.5 mm and 6 mm (commonly 4 mm). Pinnule margins are entire and apices are rounded. Pinnules arise nearly perpendicular to the rachis and become more or less oriented toward the pinna apex.

A prominent midvein which remains strong to the pinnule apex is present in each pinnule. Strong secondary veins arise from this midrib at intervals of 1.2

Table 1

Vegetative and Reproductive Morphology of *Matonidium brownii* Rushforth and *Matonidium americanum* Berry em. Rushforth

	<i>M. americanum</i>	<i>M. brownii</i>
Petiole characteristics	Expanded apically into a reflexed collar; furrowed	Expanded apically into two short arms; collar absent; smooth
Number of pinnae/frond	Up to 39	Up to 15, commonly 8-10
Length of pinna	20 cm-25 cm	Up to 15 cm
Width of pinna	Up to 11 mm, commonly 8 mm	Up to 50 mm, commonly 35 mm
Pinnule attachment	Rounded sinuses	Distinct sinuses
Pinnule length	Up to 9 mm	Up to 30 mm
Pinnule width	Up to 3 mm	Up to 9 mm
Number of sori per pinnule	Up to 15, commonly fewer	Up to 15
Soral characteristics	Round; indusiate; born to pinnule apex	Round; indusiate; not born to pinnule apex
Number of sporangia per sorus	Unknown	10-14
Venation	Prominent midvein; prominent secondary veins which bifurcate; anastomosis absent	Prominent midvein; prominent secondary veins; costal aerioles present; anastomosis common
Pinnule characteristics	Margins entire; apices rounded; lamina coriaceous	Margins entire; apices rounded; lamina not coriaceous

mm to 1.7 mm. In sterile pinnules, and in the tips of fertile pinnules, these secondary veins bifurcate immediately above the midrib and anastomose laterally to form costal aeroles. These aeroles in turn give rise to other veinlets which anastomose, forming angular aeroles for approximately two thirds of the length of the pinnule in sterile pinnules. Veinlets remain free in pinnule tips.

Secondary veins remain prominent in fertile specimens to a point approximately one half of the distance from the midrib to the margin. At this point they bifurcate and anastomose laterally with veinlets of similar origin to form an arch above the placenta. Veinlets arise from this arch and extend to the soral placenta where they merge to form a mass of vascular tissue. Other veinlets arising from this arch extend to the pinnule margin, anastomosing infrequently.

Lower epidermal cells are large, with some reaching a size of 95 microns by 45 microns. The outline of these cells is highly and repeatedly lobed, although this is less prominent near the soral placenta. Stomata have not been observed, and it is thought that they are somewhat sunken as in the modern *Matonia pectinata*. Upper epidermal cells have not been observed.

Spores are unknown.

EXPLANATION OF PLATE 1

M. PECTINATA AND M. BROWNII

- FIG. 1.—*Matonia pectinata* R. Br. Portion of a frond illustrating the pedate pinna disposition.
FIG. 2.—*Matonidium brownii* Rushforth. Portion of a frond illustrating the pedate pinna disposition (XI). Holotype: BYU 1557.

EXPLANATION OF PLATE 2

M. BROWNII

- Matonidium brownii* Rushforth. Portion of a frond illustrating pinnae and pinnule disposition (XI). Holotype: BYU 1557.

EXPLANATION OF PLATE 3

M. BROWNII

- FIG. 1.—*Matonidium brownii* Rushforth. Fertile pinna fragment illustrating soriolation. (X3.2). Paratype: BYU 1564.
FIG. 2.—*Matonidium brownii* Rushforth. Near apical pinna fragment. Note the rounded sinuses near the apex which become distinct. (X5.5). Paratype: BYU 1565.

EXPLANATION OF PLATE 4

M. BROWNII

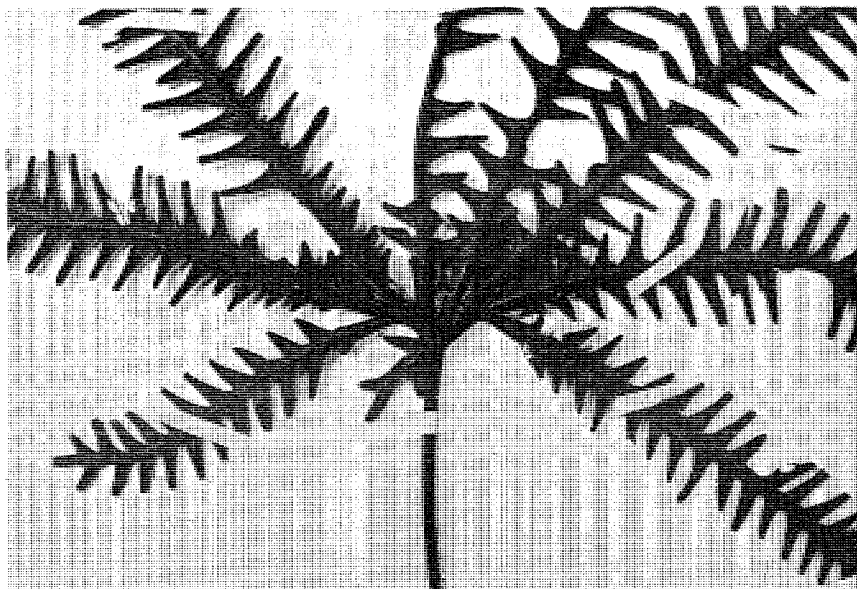
- FIG. 1.—*Matonidium brownii* Rushforth. Pinnule transfer illustrating upper epidermal cells. (X670). Paratype: BYU 1562.
FIG. 2.—*Matonidium brownii* Rushforth. Pinna transfer illustrating soriolation and venation. (X2). Paratype: BYU 1563.

EXPLANATION OF PLATE 5

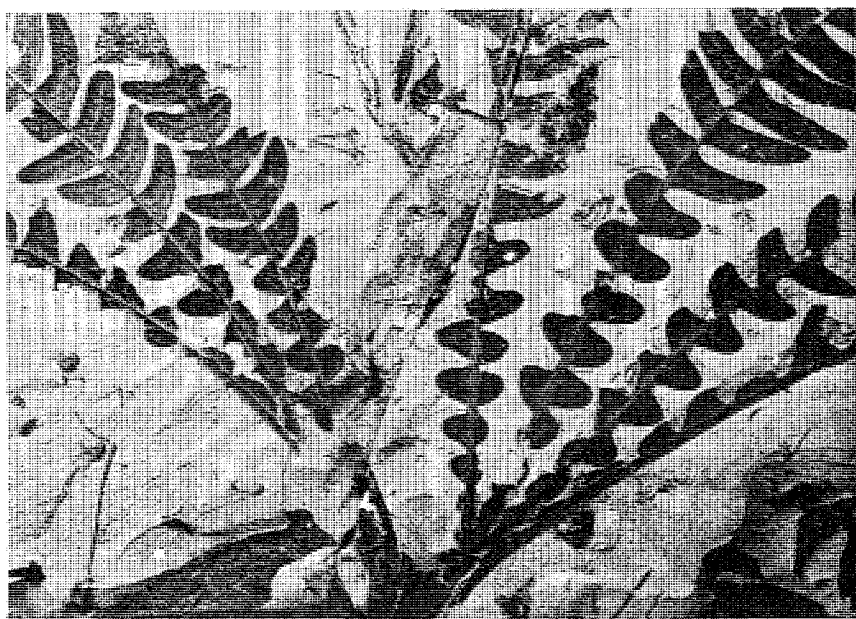
M. BROWNII

- FIG. 1.—*Matonidium brownii* Rushforth. Non-indusiate sorus illustrating sporangia. (X50). Paratype: BYU 1560.
FIG. 2.—*Matonidium brownii* Rushforth. Indusiate sorus. (X60). Paratype: BYU 1559.

PLATE 1



1



2

PLATE 2

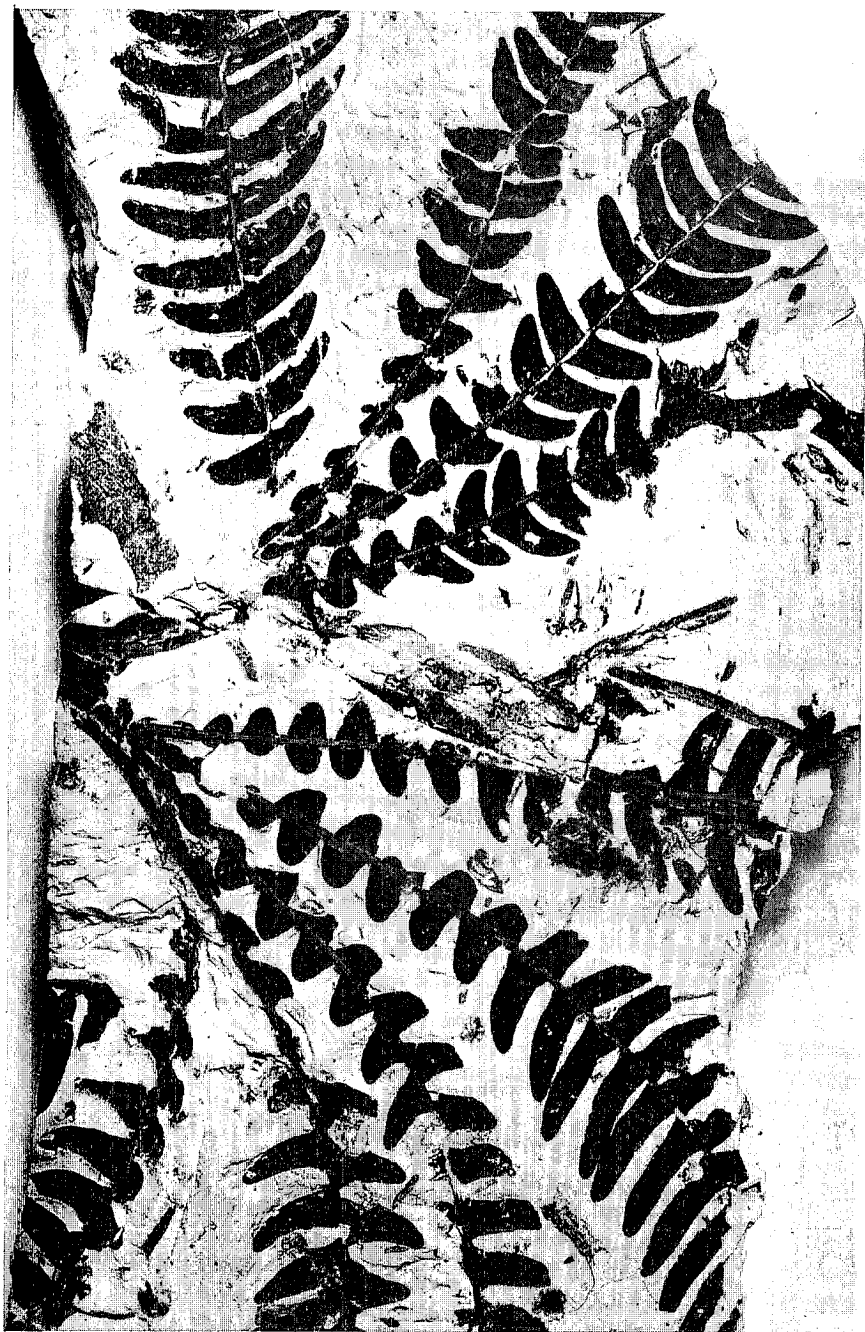
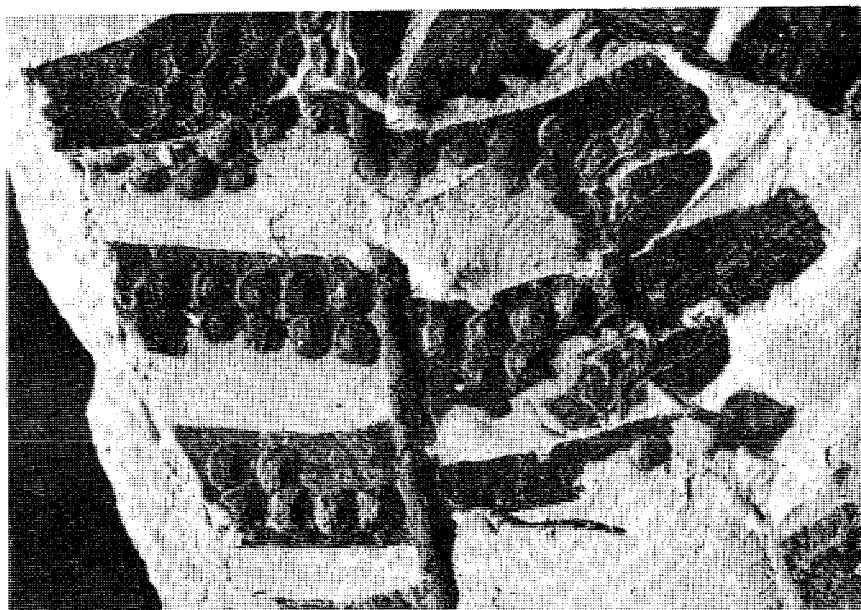


PLATE 3

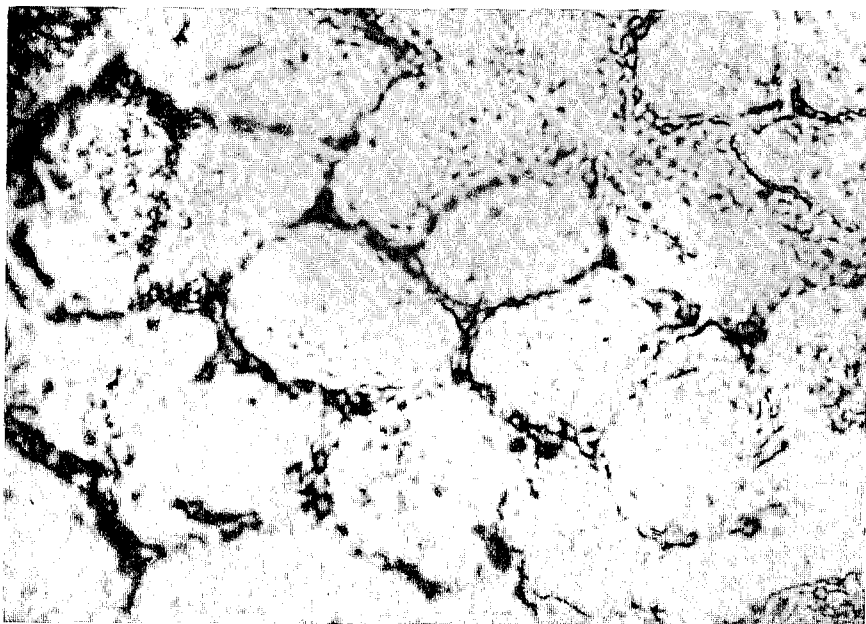


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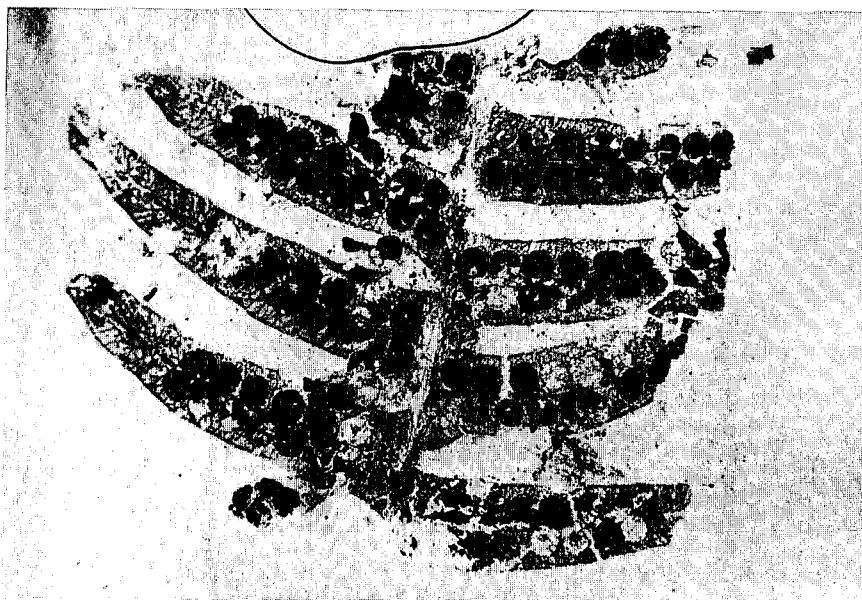


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PLATE 4

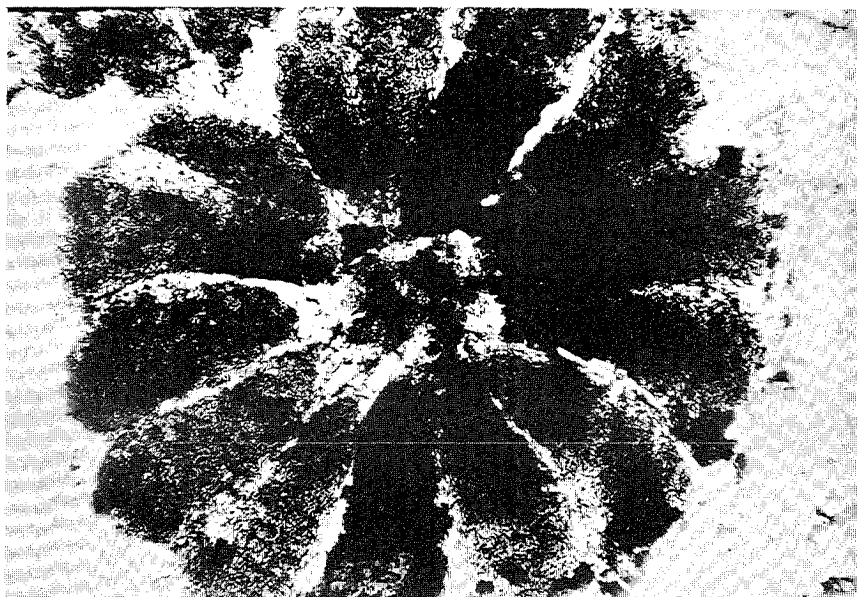


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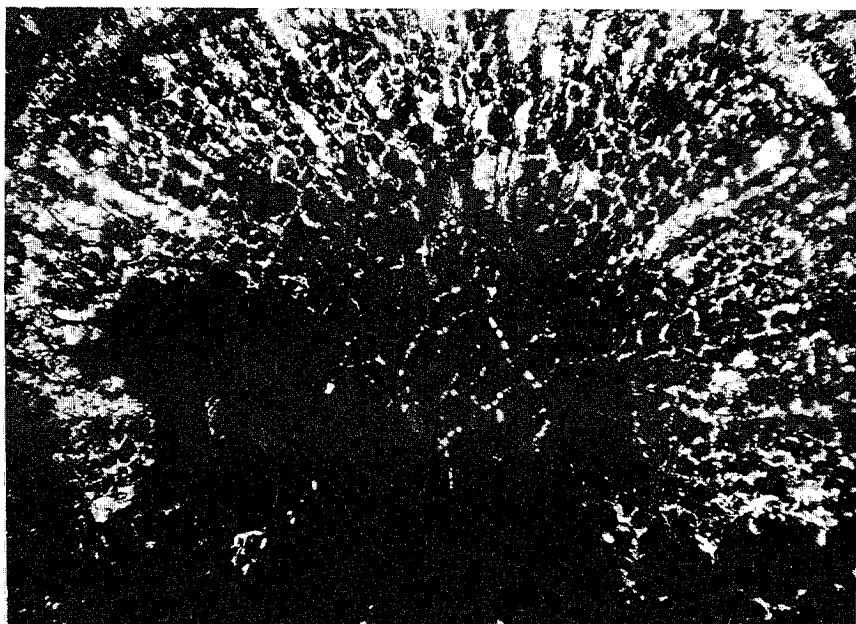


2

PLATE 5



1



2

Discussion.—*Matonidium brownii* var. *magnipinnulum* is similar in many respects to *Matonidium brownii*. This is especially the case in venation. However, the pinnule of *Matonidium brownii* var. *magnipinnulum* differs in that it is consistently much longer and narrower. Pinna size is also much greater in *Matonidium brownii* var. *magnipinnulum*.

This fern is truly magnificent and is quite rare in the Westwater flora. It is easily distinguished from other matoniaceous ferns of the area due to its extreme pinna and pinnule size. One specimen has been collected that shows incomplete pinna fragments 30 cm long, and based upon the amount of tapering, it is possible that pinna length exceeds 40 cm.

It is not without precedent in the family Matoniaceae to have forms with highly extended linear pinnules. Bell (1956) proposed *Phlebopteris* (?) *elongata* for sterile pinna fragments illustrating pinnules up to 6 cm in length collected from the Nikanassin Formation, Alberta, Canada, and the Hazelton Group, British Columbia, Canada. *Phlebopteris muensteri* is also characterized by having long nearly linear pinnules.

EXPLANATION OF PLATE 6

M. BROWNII VAR. MAGNIPINNULUM AND M. BROWNII

- FIG. 1.—*Matonidium brownii* var. *magnipinnulum* Rushforth. Base of two pinnules illustrating venation and decurrent attachment. (X10). Paratype: BYU 1567.
FIG. 2.—*Matonidium brownii* Rushforth. Pinna transfer illustrating venation. (X7). Paratype: BYU 1559.

EXPLANATION OF PLATE 7

M. LANCIPINNULUM AND M. BROWNII

- FIG. 1.—*Matonidium* (?) *lancipinnulum* Rushforth. Pinna transfer illustrating pinnule shape and disposition. (X1.25). Holotype: BYU 1569.
FIG. 2.—*Matonidium brownii* var. *magnipinnulum* Rushforth. Undersurface of pinnule illustrating epidermal cells. a) is at a major secondary vein, and b) is at the soral placenta. (X100). Paratype: BYU 1568.

EXPLANATION OF PLATE 8

M. AMERICANUM AND M. BROWNII

- FIG. 1.—*Matonidium americanum* Berry em. Rushforth. Portions of two pinnae illustrating venation. (3.2X). BYU 1572.
FIG. 2.—*Matonidium brownii* Rushforth. Pinna fragment illustrating soriation and venation. (1.2X). Paratype: BYU 1558.

EXPLANATION OF PLATE 9

M. ? LANCIPINNULUM

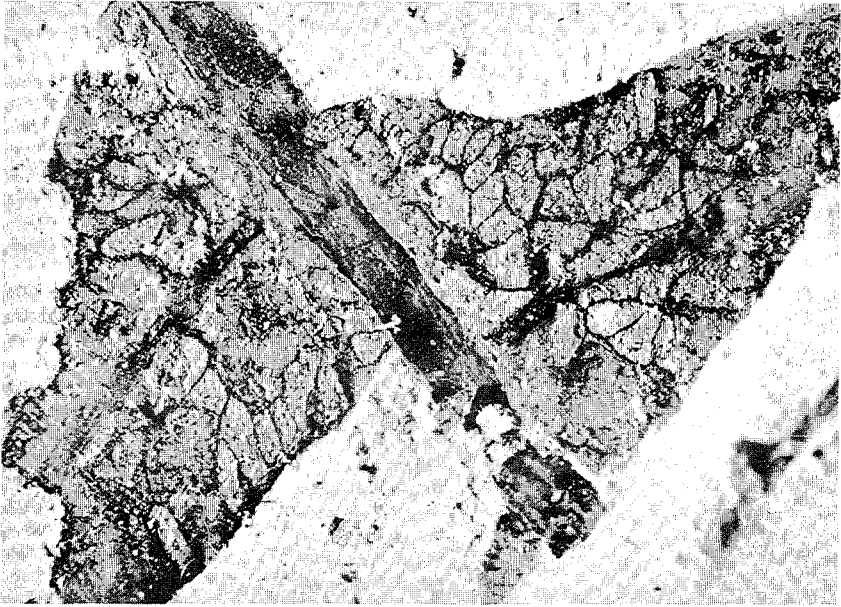
- FIG. 1.—*Matonidium* (?) *lancipinnulum* Rushforth. Pinnule transfer illustrating guard cells and stomata. (X200). Holotype: BYU 1569.
FIG. 2.—*Matonidium* (?) *lancipinnulum* Rushforth. Enlargement of two stomata with well defined guard cells. (X1000). Holotype: BYU 1569.

EXPLANATION OF PLATE 10

M. ? LANCIPINNULUM

- FIG. 1.—*Matonidium* (?) *lancipinnulum* Rushforth. Pinnule transfer illustrating tracheids with spiral and reticulate thickenings. (X750). Holotype: BYU 1569.
FIG. 2.—*Matonidium* (?) *lancipinnulum* Rushforth. Pinnule transfer illustrating tracheids with spiral and reticulate thickenings. (X750). Holotype: BYU 1569.

PLATE 6



1

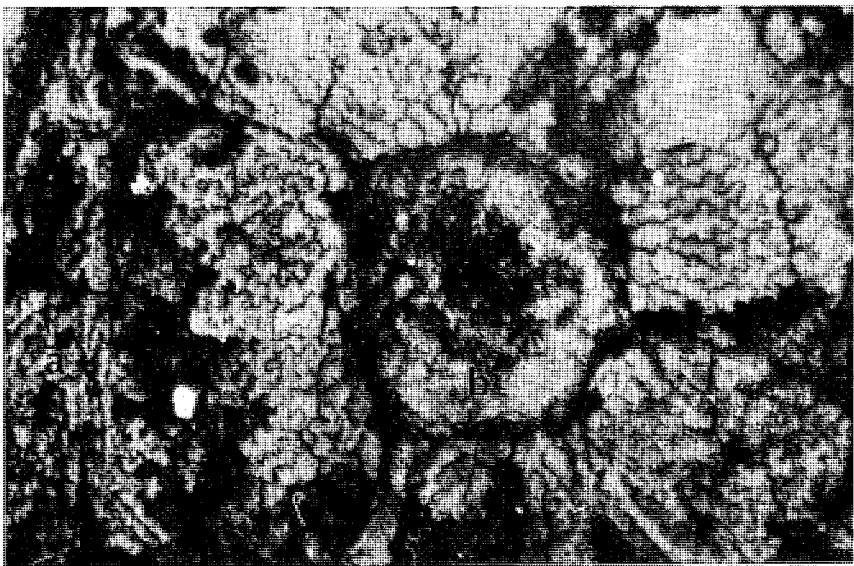


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PLATE 7

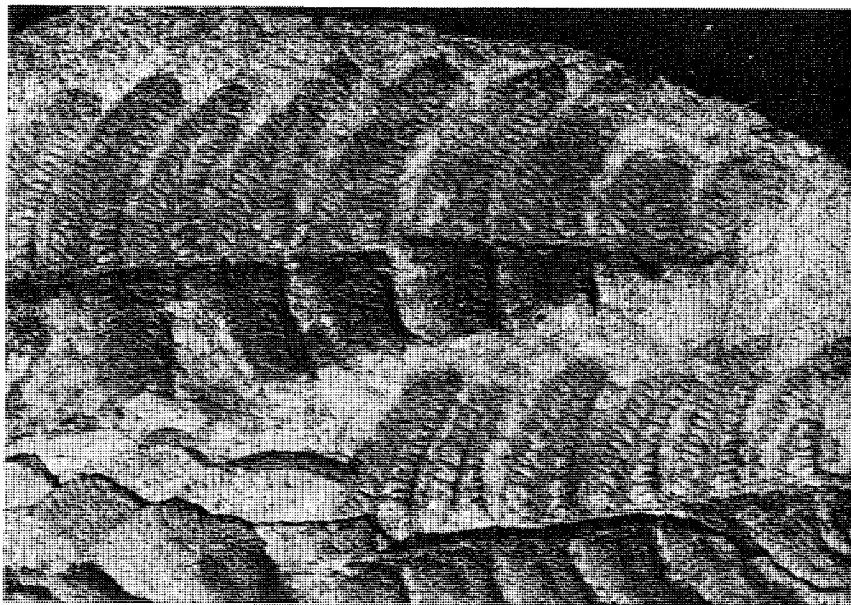


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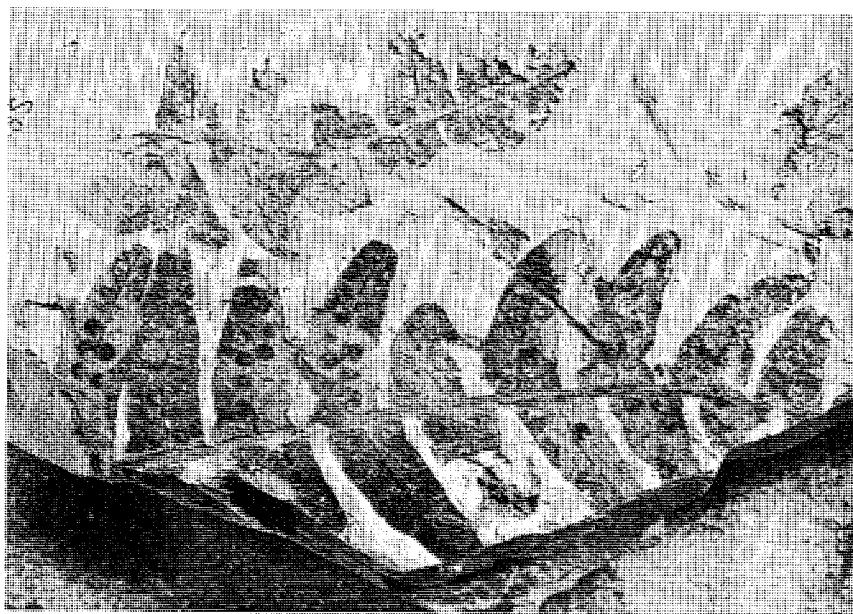


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PLATE 8

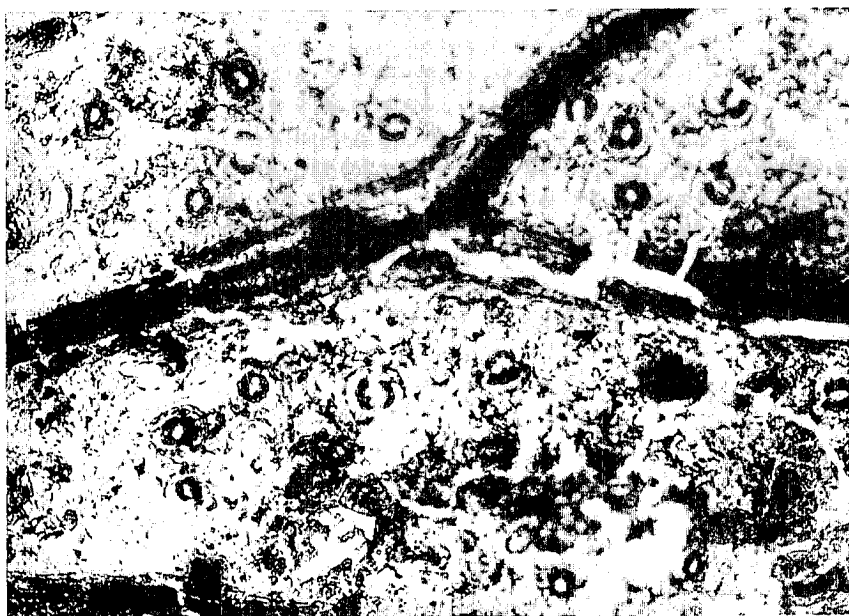


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PLATE 9

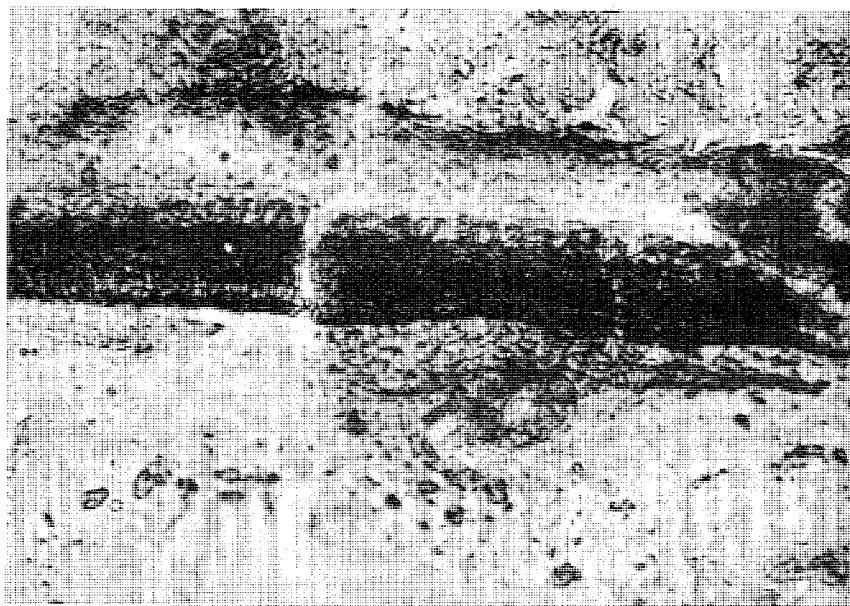


1



2

PLATE 10



1



2

Occurrence.—*Matonidium brownii* var. *magnipinnulum* is known from near Westwater, Grand County, Utah.

Figured specimens.—Holotype: BYU 1566; paratypes: BYU 1567-1568.

MATONIDIUM (?) *LANCIPINNULUM* Rushforth, sp. nov.

Pl. 7, fig. 1; Pl. 9; Pl. 10; Pl. 13, fig. 1

Description.—The leaf of this species is unknown. Pinnules are subopposite near the pinna apex, and exhibit rounded sinuses.

Pinnules are linear-lanceolate, and have been observed up to 60 mm long by 12 mm wide. Pinnules arise more or less perpendicular to the rachis and retain this orientation for approximately two thirds to three fourth of the length of the pinnule and then become slightly oriented toward the apex of the pinna.

A prominent midvein is present in each pinnule. This vein remains strong to the pinnule apex. Lateral veins arise from this midrib at intervals of approximately 1.7 mm to 2.5 mm. These laterals divide immediately above the midrib and anastomose laterally to form very prominent costal aeroles. Veinlets arise from these aeroles and anastomose to form a reticulate net of veinlets in the lamina. Anastomosis is rare near pinnule margins. Veinlets are composed of tracheids with annular, helical, and reticulate wall thickenings.

Guard cells are commonly 40 microns long by 15 microns wide. These cells are thickened on the inner walls, leaving stomata that are commonly 10 microns wide. Other cells of the epidermis have not been observed.

Fertile specimens are unknown.

Discussion.—This species is rare at the Westwater locality and is known from two specimens. Each is a near apical pinna fragment, and each illustrates pinnule disposition on only one side of the rachis. However, the venation pattern is well preserved in some pinnules, and well preserved guard cells have been observed. Other cells of the epidermis have not been observed, and it is again probable that guard cells and the remainder of the epidermis were on a slightly different level.

The venation pattern of this species is basically similar to that of several other members of this family. It differs in having secondary veins which do not remain prominent after their division to form costal aeroles. Placement of this species in the genus *Matonidium* must remain provisional until fertile specimens are collected.

Occurrence.—*Matonidium* (?) *lancipinnulum* is known from near Westwater, Grand County, Utah.

Figured specimens.—Holotype: BYU 1569; paratype: BYU 1570.

MATONIDIUM (?) sp.

Pl. 13, fig. 2

Description.—The complete leaf is unknown. Pinna are lanceolate.

Pinnules arise from a rachis that ranges between 0.3 mm and 0.8 mm in diameter. Pinnules are born at approximately a 55° to 60° angle to the rachis and recurve toward the pinna apex. This recurving is accomplished through the upper pinnule margin being essentially linear or nearly so from its point of origin to the pinnule apex, whereas the lower margin arises in a similar manner

and parallels the upper for approximately one third to one half of the length of the pinnule and then bends upward to meet the upper margin. Pinnule margins are entire to slightly crenate, and pinnule apices are obtuse. Pinnule attachment is completely basal, and pinnules are attached by a thin web of lamina along the rachis. Pinnules range in size up to 12 mm long by 4 mm wide.

A prominent midvein is present in each pinnule, which extends nearly to the pinnule apex. Strong secondary veins arise from the midrib at approximately 0.8 mm to 1.2 mm intervals. These veins bifurcate at a point approximately one third to one half of the distance from the midrib to the pinnule margin. Anastomosing veinlets have not been observed, and costal aeroles are absent.

Fertile specimens are unknown.

Discussion.—This species is known from six sterile pinna fragments which are all on a single specimen. The pedate nature of the frond, characteristic of the Matoniaceae, is inferred from the orientation of several of these fragments. Several of these fragments are apical pinna sections.

Venation of this material is poorly preserved, although it is present in some pinnules. Venation is similar to that of many other species of *Matonidium*, notably *Matonidium americanum*, *Matonidium goeppertii*, *Matonidium wiesneri*, and *Matonidium althausii*.

This species has been placed in the genus *Matonidium* based upon vegetative characteristics alone, and this placement must remain tentative until fertile specimens can be collected.

Occurrence.—This fern is known from the Wayan Formation near Wayan, Caribou County, Idaho. It was collected from a dark grey mudstone and was found associated with *Anemia* and *Tempskya*.

Figured specimen.—BYU 1571.

MATONIDIUM AMERICANUM Berry emend. Rushforth

Pl. 8, fig. 1; Pl. 13, fig. 3

1919 *Matonidium americanum* Berry—Bull. Torrey Bot. Club v. 46, p. 287, fig. 2; Pl. 12, figs. 1-12; Pl. 13, figs. 3-6.

1916 *Matonidium althausii* (Dunker) Ward, Cockerell—Jour. Washington Acad. Sci. v. 6, p. 111, fig. 2.

1916 *Cycadospodix* (?) sp. Cockerell—idem., p. 110, fig. 1.

Description.—The habit of both fertile and sterile ferns of this species was well described by Berry (1919). However, in the material described by Berry venation was not preserved.

A prominent midvein is present in each pinnule. This vein remains strong to or nearly to the pinnule apex. Prominent secondary veins arise from this midrib at intervals of approximately 0.7 mm. Secondary veins bifurcate at a point one half to two thirds of the distance from the midrib to the laminar margin. These veins extend to the pinnule margin without redividing, and no anastomosis occurs.

Venation of fertile pinnules is unknown, and spores have not been observed.

Discussion.—As mentioned by Berry (1919), the pinnules of *Matonidium americanum* are coriaceous. This is well illustrated by specimens examined by the present author and may be the reason for venation being poorly preserved. Berry (1919) described *Matonidium americanum* as having revolute margins,

and while this is possible, it is likely that this appearance is due to the coriaceous nature of the pinnules.

The material upon which the above emendation is based consists of two long pinna fragments. These specimens were placed with *Matonidium americanum* based upon the close similarity of the two in habit and size.

Occurrence.—*Matonidium americanum* is known from Cutthroat Gulch and Hovenweep Canyon west of Dolores, Montrose County, Colorado, and from Rabbit Valley, Grand County, Utah.

Figured specimen.—BYU 1572.

MATONIDIUM GALLEYI (Miner) Rushforth, comb. nov.

Pl. 11, fig. 2; Pl. 12; Pl. 14, fig. 2

1935 *Laccopteris galleyi* Miner—Contr. Mus. Paleont. Univ. Michigan v. 4(17), p. 288, Pl. 1.

1956 *Phlebopteris galleyi* (Miner) Arnold—Jour. Paleont. Soc. India, Lucknow v. 1, p. 119.

Description.—*Matonidium galleyi* was described by Miner (1935) as *Laccopteris galleyi* for a pinnule fragment 20 mm long by 7.5 mm wide. This specimen does not illustrate venation, although it is fertile, and the sori are without

EXPLANATION OF PLATE 11

M. BROWNII AND MATONIDIUM

- FIG. 1.—*Matonidium brownii* Rushforth. Trilete spore illustrating weakly defined margo bordering commissures. (X1000). Paratype: BYU 1561.
FIG. 2.—*Matonidium galleyi* (Miner) Rushforth. Spore illustrating trilete mark. (X2300). Univ. of Mich. 34564.

EXPLANATION OF PLATE 12

M. GALLEYI

- FIG. 1.—*Matonidium galleyi* (Miner) Rushforth. Pinnule transfer illustrating two sori. Note that the placental region in one is dark, apparently filled with the remains of an indusial stalk. (X33). Univ. of Mich. 34564.
FIG. 2.—*Matonidium galleyi* (Miner) Rushforth. Pinnule transfer illustrating a sorus covered with the remains of an indusium. (X55). Univ. of Mich. 34564.

EXPLANATION OF PLATE 13

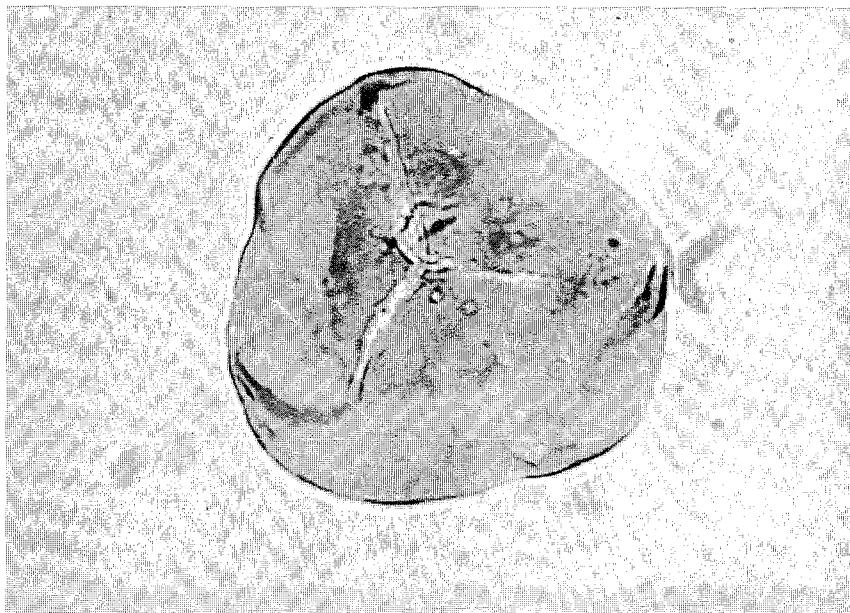
M. ? LANCIPINNULUM, M. SP. AND M. AMERICANUM

- FIG. 1.—*Matonidium* (?) *lancipinnulum* Rushforth. Pinna fragment. (X1). Paratype: BYU 1570.
FIG. 2.—*Matonidium* sp. Several near apical pinna fragments. (X1). BYU 1571.
FIG. 3.—*Matonidium americanum* Berry em. Rushforth. Two pinna fragments. (1X). BYU 1572.

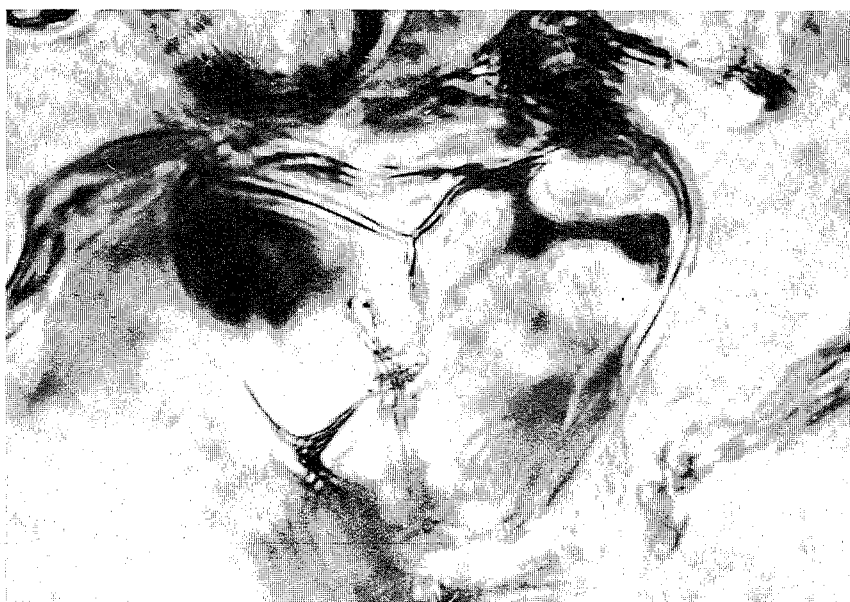
EXPLANATION OF PLATE 14

- FIG. 1.—*Matonidium brownii* var. *magnipinnulum* Rushforth. Pinna Fragment. BYU 1573.
FIG. 2.—*Matonidium galleyi* (Miner) Rushforth. Pinnule transfer illustrating three sporangia. Note the annular cells which extend for some distance between the sporangia. Univ. of Mich. 34564.

PLATE 11



1

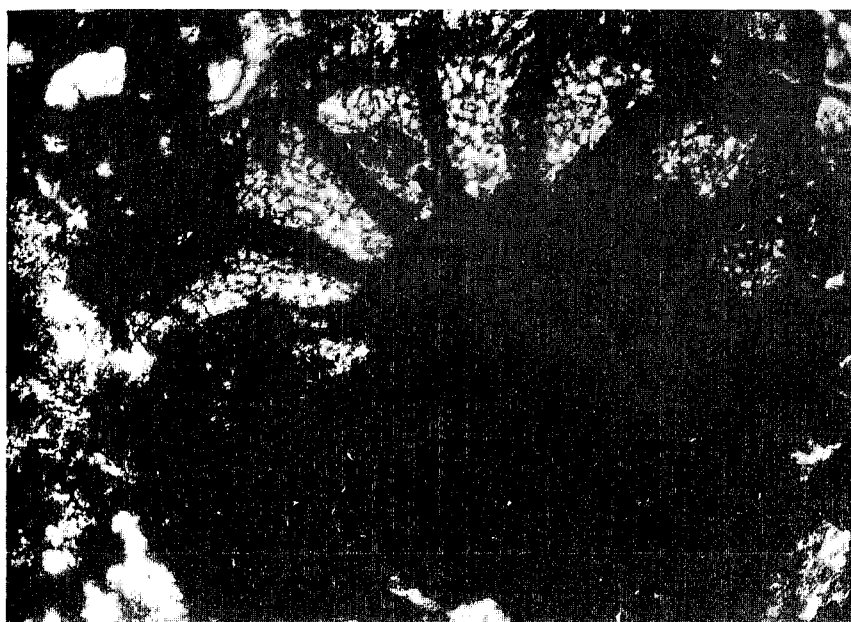


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PLATE 12



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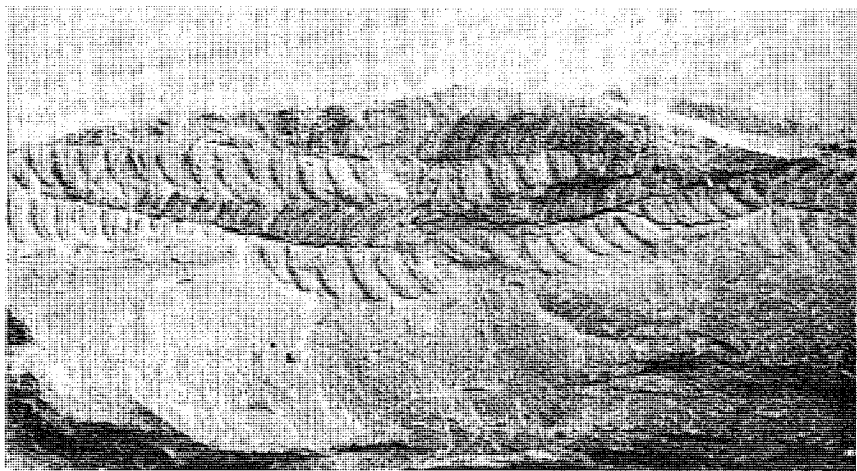
PLATE 13



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PLATE 14

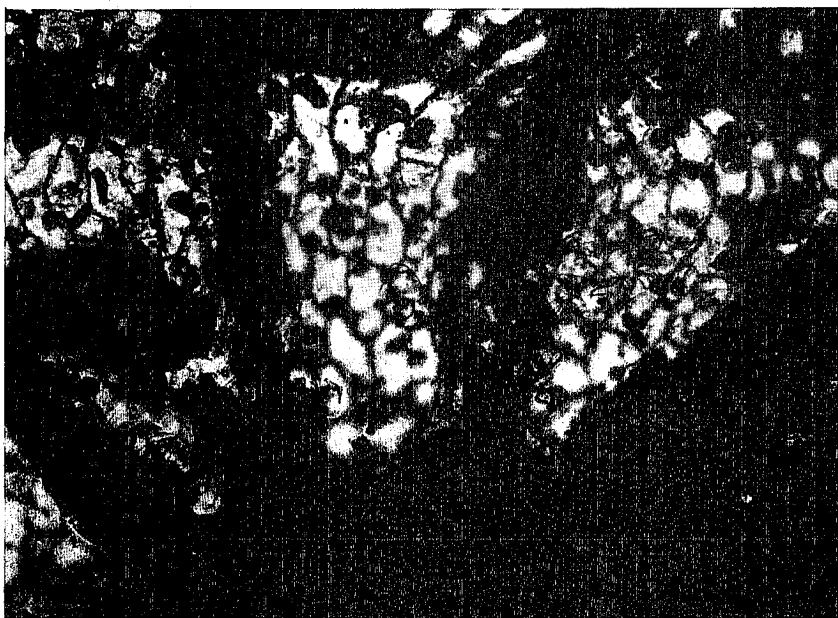
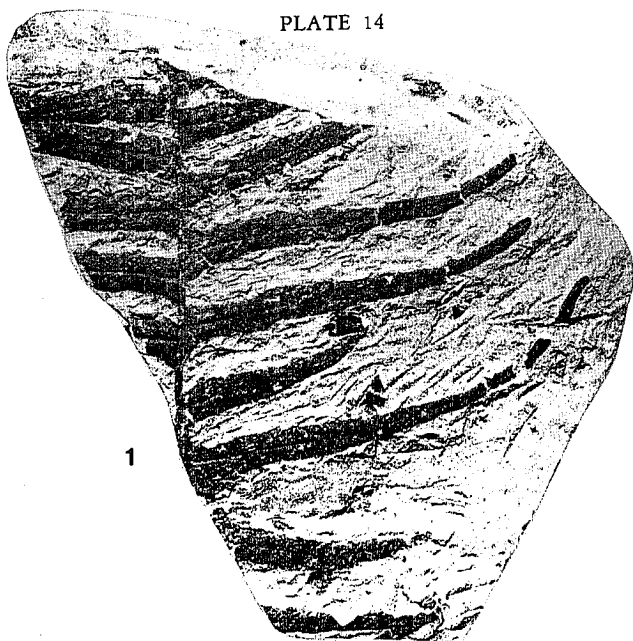


Table 2
Vegetative Morphology of Six Matoniaceous Ferns

SPECIES	COLLECTED FROM	PINNULE APEX	PINNULE SHAPE	PINNULE SIZE	VENATION
<i>Matonidium brownii</i>	Dakota Sandstone; Utah and Colorado	Rounded	Strap shaped	8mm x 30mm	Prominent secondary veins present; costal aeroles present; anastomosing veinlets common
<i>Matonidium brownii</i> var. <i>magnipinnululum</i>	Dakota Sandstone; Utah	Rounded	Linear	6mm x 60mm	Prominent secondary veins present; costal aeroles present; anastomosing veinlets common
<i>Matonidium (?) lancipinnululum</i>	Dakota Sandstone; Utah	Acute	Lanceolate	12mm x 60mm	Prominent secondary veins absent; costal aeroles present; anastomosing veinlets common
<i>Matonidium americanum</i>	Dakota Sandstone; Utah and Colorado	Rounded	Strap shaped	3mm x 9mm	Prominent secondary veins present; costal aeroles absent; anastomosing veinlets absent
<i>Matonidium galleyi</i>	Dakota Sandstone; Kansas	Unknown	Unknown	Unknown	Unknown
<i>Matonidium</i> sp.	Wayan Formation; Idaho	Obtuse to rounded	Strap shaped	4mm x 12mm	Prominent secondary veins present; costal aeroles absent; anastomosing veinlets absent

question matoniaceous. Sporangia are born radially around a central placenta and number between 11 and 16 per sorus. Sporangia are annulate, with the annulus being oblique in position and incomplete. The central placenta of these sori is interesting in that two types are in evidence. In some, the region of the placenta is unobstructed, and the lamina beneath may be observed. In others this region is filled with a dark carbonaceous material that obstructs observation of the lamina beneath. The reason for this difference is interpreted to be that in the unobstructed type an indusium has been shed with its stalk. In the type with carbonaceous material present the broad laminar portion of the indusium has been shed without its stalk. Some of the sori are covered with a black carbonaceous material that is interpreted to represent the remains of an indusium.

Spores are trilete, with the leasurae reaching approximately three fourths of the distance to the equator. Equatorial shape of these spores is triangular, with the corners being rounded, and the sides only slightly convex. Commissures are not bordered by a margo. Spore walls are psilate, commonly 1.5 microns in thickness. Spore diameter ranges between 22.0 microns and 31.8 microns, with an average diameter being 28.2 microns.

Discussion.—When Arnold (1956) transferred *Laccopteris galleyi* to *Phlebopteris*, he noted that there was a dark substance of unexplained origin that covered portions of some of the sori. He did not interpret this material as being indusial. It is the opinion of the present author that this material does indeed represent the remains of an indusium. Further, Arnold (per. com.) has suggested that *Matonidium* is likely the proper genus for the placement of this specimen.

Arnold (1956) also mentioned that sporangial annuli appear to be confined to the outer edge of the sporangium. While this specimen does appear to illustrate this, scrutinous observation reveals that annular cells are found for some distance between sporangia (Pl. 14, fig. 2). In most instances these cells are crushed due to crowding within the sorus.

The above discussion may contribute some knowledge on the problem of the relationship between *Nathorstia* and matoniaceous ferns. Harris (1961) remarked, "Miner (1935) . . . described a typical looking *Nathorstia* as *Laccopteris*. . . ." Harris was accurate in this statement, and this illustrates the problem in taxonomy among ferns that have been variously placed in *Nathorstia*, *Phlebopteris*, and *Matonidium galleyi* that they are without doubt composed of highly crowded individual sporangia, and it is likely that upon examination of other *Nathorstia*-like ferns, a similar situation will be found to exist.

Occurrence.—*Matonidium galleyi* is known from Dakota Sandstone Formation near Mankato, Jewell County, Kansas.

Figured specimen.—Holotype: Univ. of Mich. 34564.

SUMMARY AND CONCLUSIONS

The fern family Matoniaceae is an ancient taxa which was widely distributed throughout the world during Mesozoic times. This family has been collected from many parts of the United States where it was especially important during Lower Cretaceous times. Matoniaceous ferns are presently restricted to humid tropical regions of Malasia.

Five species and one variety of *Matonidium* are treated in the present paper. The characteristics of these ferns are summarized in Table 2.

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