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# MATONIACEOUS FERNS (GLEICHENIALES) FROM THE MIDDLE TRIASSIC OF ANTARCTICA

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ABSTRACT—The Matoniaceae is one of the most ancient lineages of extant ferns, with a fossil record that extends from the early Mesozoic. Currently they are considered to be a systematically isolated group that occupies a basal position in the phylogeny of leptosporangiate ferns. Although the extant taxa of Matoniaceae are today restricted to the Malaysian archipelago, a diverse assemblage of matoniaceous ferns occurred on every continent, including Antarctica, during the Mesozoic. Here we describe anatomically preserved, detached fern sori and sporangia from the Fremouw Formation with a combination of characters that affiliates them with the Matoniaceae. Sori are peltate with more than 25 crowded sporangia that display simple maturation. The indusium is multiseriate and centrally attached to a massive, vascularized receptacle. Sporangia are globose to ovoid with vertical, meandering, incomplete annuli, and are helically attached to the receptacle in three to four gyres. This report places this fern as the earliest known occurrence of the Matoniaceae in the fossil record. Characters observed in the sori offer insights regarding organizational patterns of reproductive structures in the family. Additionally, the presence of a peltate indusium in the earliest known representative of the family contradicts the hypothesized evolutionary sequence in development of this structure in the family.

THE MATONIACEAE, along with Gleicheniaceae, Dipteridaceae, and Hymenophyllaceae, are among the most ancient lineages of extant leptosporangiate ferns, with an evolutionary history that extends into the early Mesozoic (Skog, 2001). *Matonia* R. Br., like the Wollemi pine and dawn redwood, is a living fossil, since Brongniart (1828) first figured matoniaceous compression fossils prior to its description as an extant genus (Brown *in* Wallich, 1829). The first definite association of fossils with the Matoniaceae, however, was not made until more than half a century later (Zeiller, 1885). *Matonia* and *Phanerosorus* Copel., with two species each, comprise the extant taxa of the monophyletic family and are today restricted to the Malaysian archipelago (Kato, 1993, 1998; Kato and Setoguchi, 1999). In contrast, during the Mesozoic, a diverse array of matoniaceous ferns occurred on every continent, including Antarctica (Skog, 2001). The first record of the family has been suggested to occur in the Middle Triassic (Millay and Taylor, 1990), and *Matonia* is known from at least the Early Jurassic (Harris, 1980). With this extensive fossil history, these ferns provide an opportunity to explore patterns of character evolution in the Matoniaceae through geologic time.

At least 23 fossil taxa, including an unnamed rhizome from the Jurassic of India (Sharma and Bohra, 1976), have been assigned to the Matoniaceae (see Tidwell and Ash, 1994 and references therein; Givulescu and Popa, 1998; Nishida et al., 1998). Most are known only as compressions, although the number of reports of anatomically preserved rhizomes has increased significantly within the last 30 years (Seward, 1910; Nishida, 1973; Sharma and Bohra, 1976; Snigerevskaya, 1977; Millay and Taylor, 1990; Tidwell and Skog, 1992; Nishida et al., 1998). Assignment of fossil taxa to the Matoniaceae is based primarily on venation patterns and branching of the frond, structure of the sorus and sporangia, and anatomical organization in the rhizome. Isolated sori attributed to the Matoniaceae have been reported from the Cretaceous of North America (Hall, 1965), but soral and sporangial characteristics are otherwise known only from compression fossils. These characters are of particular interest, since reproductive structures have historically been important features in taxonomic delimitation in pteridophytes (Kramer and Tryon, 1990).

As one of the few localities in which Triassic ferns are anatomically preserved, the flora of Fremouw Peak in the central Transantarctic Mountains of Antarctica is critical in documenting early evolutionary history in several modern fern families. Nine taxa of structurally preserved ferns, most of which are referable to extant families, including Marattiaceae (Delevoryas et al., 1992), Osmundaceae (Schopf, 1978; Rothwell et al., 2002), and Gleicheniaceae (Millay and Taylor, 1990; Phipps et al., 2000), as well as provisional Matoniaceae and Cyatheaceae/Pteridaceae (Millay and Taylor, 1990), have been identified from this locality. Here we describe structurally preserved fern sori and sporangia from Fremouw Peak with a combination of characters that clearly affiliates them with the Matoniaceae and places the early Middle Triassic of Antarctica as the earliest known occurrence of this family. The combination of characters observed in these structures is unique in the Matoniaceae and provides insights regarding organizational patterns of reproductive structures in the family. Furthermore, the presence of a peltate indusium in the earliest known representative of the family contradicts the hypothesized evolutionary sequence in development of this structure in the Matoniaceae.

## MATERIAL AND METHODS

Specimens are preserved in silicified peat collected from Fremouw Peak in the Queen Alexandra Range of the central Transantarctic Mountains (84°17′41′′S, 164°21′48′′E, 7,826 feet above sea level, Barrett and Elliott, 1973). The peat occurs in carbonaceous mudstones of the upper Fremouw Formation, which is early Middle Triassic in age based on palynology and vertebrates (Kitching et al., 1972; Kyle and Fasola, 1978; Kyle and Schopf, 1982; Farabee et al., 1990). The polished surfaces of the peat blocks in which specimens are preserved were etched in 49 percent hydrofluoric acid and prepared using the cellulose acetate peel technique (Galtier and Phillips, 1999). Peels were mounted on standard microscope slides. Slabs (11248A, 11248B), peels, and slides are housed in the Division of Paleobotany of the Natural History Museum and Biodiversity Research Center, University of Kansas, slide accession numbers 20460–20529.

## SYSTEMATIC PALEONTOLOGY

Class POLYPODIOPSIDA Cronquist, Takhtajan and Zimmerman, 1966
Order GLEICHENIALES A. B. Frank *in* Leunis, 1877
Family MATONIACEAE Presl, 1847
TOMANIOPTERIS new genus

*Type species*.—*Tomaniopteris katonii* new species.

*Diagnosis*.—Detached sori with a peltate indusium and leptosporangia with simple maturation. Sori are circular, with more than 25 sporangia helically arranged in up to four rows around the receptacle. The indusium is multiseriate and centrally attached to a massive receptacle, with margins that extend over or encircle the sporangia. Scalariform tracheids occur in the receptacle and form strands that radiate from the center to the margins of the indusium. Sporangial stalks are short and thick. Sporangia are globose to ovoid and slightly flattened in the lateral plane. Annuli are vertical and meandering, incomplete, and one cell thick.

*Etymology*.—An anagram of *Matonia* and -pteris, (Gr.), a fern.

### TOMANIOPTERIS KATONII new species
Figure 1

*Specific diagnosis*.—Sori measure up to 2 mm in diameter and 0.7 mm tall. The indusium measures up to 200 μm thick at margins. Sporangial stalks range from 45 to 60 μm wide and two to three cells long, with one row of six to eight cells around a central cell. Sporangia range in dimensions up to 300 μm long and 200 μm wide.

*Description*.—Specimens consist of detached sori with peltate indusia. Up to four rows of undehisced sporangia are attached to the receptacle (Fig. 1.1, 1.2). No sori have yet been found attached to pinnules. Sori are small, up to 2 mm in diameter and 700 μm high. The indusium, which is centrally attached to the receptacle, completely covers the sporangia (Fig. 1.3, 1.4); in one incompletely preserved specimen, the margin of the indusium appears to be rolled in around the sporangia (Fig. 1.1). In longitudinal section, the indusium is multiseriate, with up to seven rows of cells near the margin, and measures up to 200 μm thick (Fig. 1.2). The receptacle is massive and nearly conical in longitudinal section (Fig. 1.4), tapering from almost 900 μm at the base to approximately 400 μm at the junction with the indusium. Cells of the indusium and receptacle are isodiametric and range from 9 to 45 μm in diameter, with unevenly thickened walls. A crescent-shaped cavity often occurs in the center of the receptacle (Fig. 1.4). Elongate, scalariform tracheids are incompletely preserved around the periphery of the cavity (Fig. 1.5). These do not appear to be transfusion tracheids, which typically are shorter and wider. Scalariform tracheids also occur in the center and margins of the indusium; the indusium appears to have an undetermined number of vascular strands that radiate from a central point out to the margins.

Within each sorus, sporangia vary in size but appear to be at approximately the same level of development since annular cells are distinct in all sporangia. Up to 28 sporangia have been counted in a single specimen; however, the total number is likely greater since no sorus was observed with all sporangia intact. Sporangia are helically arranged in three to four crowded rows (Fig. 1.1) and predominantly oriented so that the annulus and one flattened surface of each sporangium are roughly parallel to the indusium (Fig. 2). Each sporangium is attached to the receptacle by a short, stout stalk two to three cells long and 45–60 μm in diameter (Fig. 1.2). In cross section, six to eight stalk cells are organized in a ring around a central cell (Fig. 1.6). Sporangia are globose to ovoid and slightly flattened and measure up to 300 μm long (from stalk to apex), 250 μm high (perpendicular to annulus), and at least 200 μm wide (parallel to annulus). Sporangial walls are one cell thick. Cells of the annulus are typically much larger than other sporangial wall cells (Fig. 1.2, 1.7) and measure up to 75 μm wide and 75 μm high in longitudinal section. There is no obvious thickening of cell walls in the annulus. Cells of the annulus often occur on opposite sides of the sporangium in both longitudinal and cross sections (Fig. 1.2) and their position indicates a vertical to slightly oblique orientation, although the path of the annulus around the sporangium meanders slightly (Fig. 2). There are oblique longitudinal sections for many sporangia in which annular cells can be distinguished only on one side (Fig. 1.3), which suggests that the annulus is incomplete and interrupted by the stalk.

Although numerous sporangia are preserved, no spores have been observed. Small, spherical bodies up to 40 μm in diameter occur within sporangia and cells of the sporangial wall, receptacle, and indusium (Fig. 1.2). Similar structures have previously been noted in sporangia assigned to *Gleichenipteris antarcticus* Phipps, Taylor et Taylor and are suggested as representing chytridomycetous fungi (Phipps et al., 2000). Their presence in *Tomaniopteris katonii* is likely due to the aquatic environment in which the Fremouw peat accumulated and was preserved.

*Etymology*.—The specific epithet is named in honor of the contributions of Professor Masahiro Kato to current understanding of morphology and systematic relationships of the Matoniaceae.

*Type*.—Holotype, 49 slides of specimen 11248Aα, slide Nos. 20461–20465, 20466–20510, Figure 1.2–1.6. Paratype, 18 slides of specimen 11248Bα, slide Nos. 20460, 204513–20529, Figure 1.1, 1.7.

*Occurrence*.—Upper Fremouw Formation, Fremouw Peak, Queen Alexandra Range, central Transantarctic Mountains (84°17′41′′S, 164°21′48′′E, 7,826 feet, GPS), Buckley Island Quadrangle, Barrett and Elliott, 1973. Early Middle Triassic.

## DISCUSSION

Due to the fragmentary nature of these Antarctic specimens, the number of characters that provide clues to their taxonomic affinity remains limited. Fortunately, characters of reproductive structures are among the most taxonomically informative. The combination of characters observed in the specimens provides enough information to permit comparisons with fossil and extant fern families. With respect to the ferns that are known to occur at Fremouw Peak and other extant leptosporangiate ferns, only the Matoniaceae share a majority of characters in the combination found in *Tomaniopteris katonii*. Key characters of both *T. katonii* and Matoniaceae include: circular to elliptical sori with a peltate indusium, short sporangial stalks comprised of a peripheral ring of cells surrounding a central cell, and sporangia with incomplete, meandering annuli and simple maturation. *Tomaniopteris katonii*

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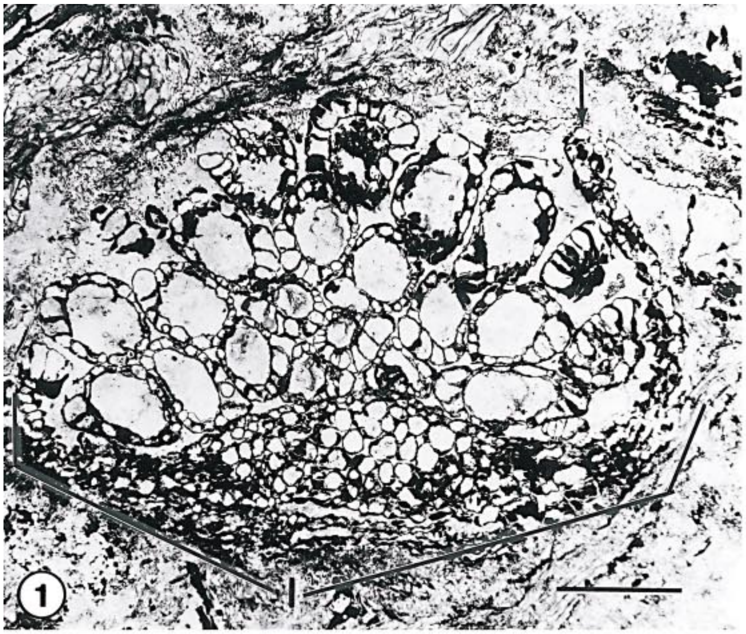
FIGURE 1—*Tomaniopteris katonii* n. gen. and sp. from the Upper Fremouw Formation, early Middle Triassic, Central Transantarctic Mountains, Antarctica. *1,* Longitudinal section through lateral margin of indusium (I) and sporangia. Note margin at right rolled in around sporangia (arrow) and sporangia helically arranged in four layers. Scale bar = 250 μm. Slide #20460, 11248B #4; *2,* longitudinal section through five sporangia, receptacle (R), and indusium (I); note stalk (S) and partial base of attached sporangium, large annular cells (A), chytrid within the empty sporangia (arrowheads), and multiseriate organization of the indusial margin at lower right. Scale bar = 100 μm. Slide #20461, 11248A #7; *3,* longitudinal section through lateral margin of indusium (arrows) and sporangia; note sporangia with annular cells on only one side. Scale bar = 250 μm. Slide #20462, 11248A #4; *4,* near median longitudinal section through receptacle (R), indusium (I), and sporangia; note crescent-shaped central cavity (C) and subtle difference in cells of the indusium and receptacle. Scale bar = 250 μm. Slide #20463, 11248A #17; *5,* scalariform tracheids at periphery of crescent-shaped cavity in the receptacle. Scale bar = 25 μm. Slide #20464, 11248A #19; *6,* cross section through two sporangial stalks (S) showing ring of cells surrounding a central cell. Scale bar = 50 μm. Slide #20465, 11248A #5; *7,* oblique cross section through a sporangium showing enlarged annular cells on one side. Scale bar = 100 μm. Slide #20460, 11248B #4.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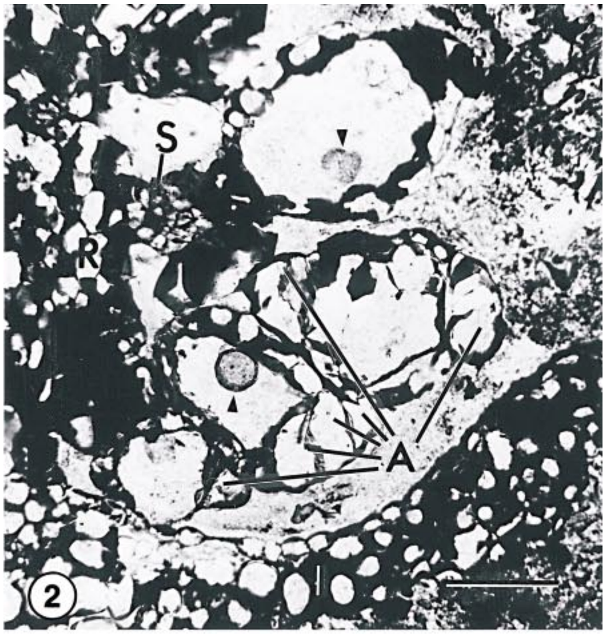
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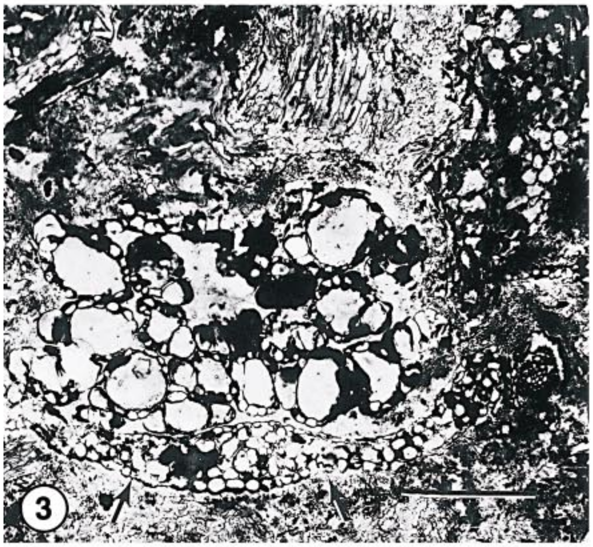
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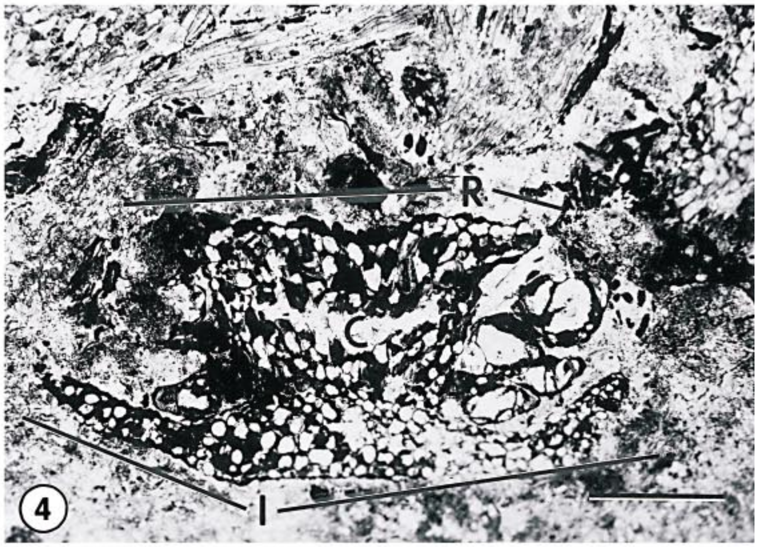
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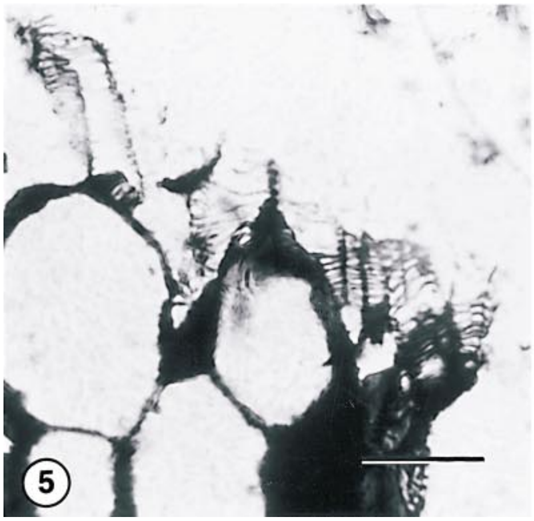
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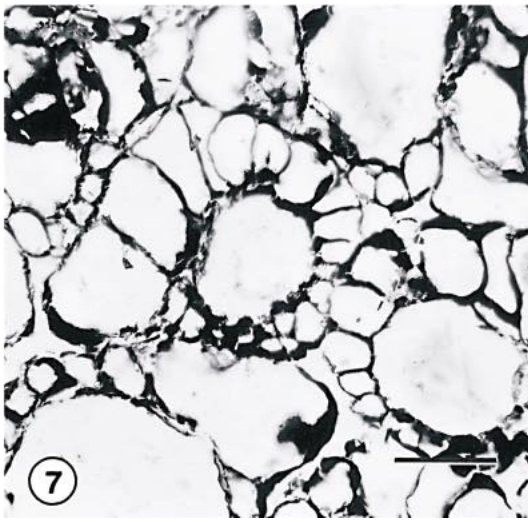
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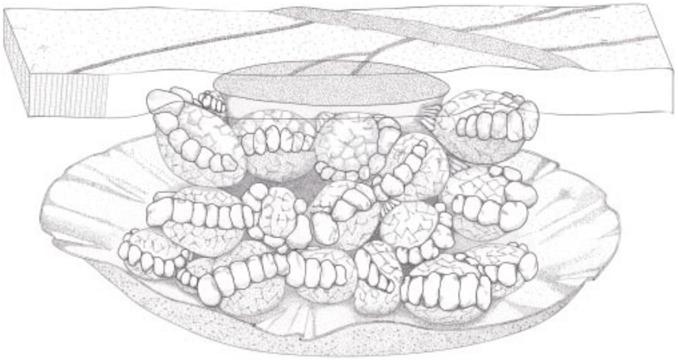

FIGURE *2*—Idealized reconstruction of *Tomaniopteris katonii* with sorus attached to abaxial surface of leaf.

differs from previously described fossil Matoniaceae, since it represents anatomically preserved, detached, isolated sori, rather than rhizomes or fronds, and also in that it clearly shows details of the organization of the sori. Although there are characters in *T. katonii* that do not occur in the extant taxa, we consider that the number of shared features supports assigning it to the Matoniaceae. In our opinion, distinct differences in *T. katonii* justify assigning it to a new genus (Table 1).

The primary anatomical differences between extant Matoniaceae and *Tomaniopteris katonii* are the cellular organization of the receptacle and indusium, which concomitantly influences sporangial attachment, and the organization of these two tissues to form the peltate structure that covers the sporangia. In the following discussion, the term receptacle refers to the region to which sporangia attach and indusium refers to the sterile structure that is attached above this. In *Matonia* and *Phanerosorus*, the receptacle and indusium are separate structures with distinctly different cellular organization. The receptacle consists of a pad of tissue comprised of isodiametric cells and is slightly elevated from the abaxial surface of the pinnule; sporangia are attached in a ring (*Matonia*) or in multiple layers (*Phanerosorus*) below the base of the indusium. The indusium is a peltate structure that consists of a stalk, comprised of thin-walled, elongate cells, which expands at the apex into a circular to elliptical disk (pelta), two cells thick at the margin, that covers the sporangia (see fig. 210 in Smith, 1955). The diameter of the stalk increases from four to six to more than 15 rows of cells before the biseriate margins of the pelta expand. Tracheids occur in the pinnule mesophyll near the receptacle, but do not appear to extend into the receptacle or indusium (Seward, 1899). In contrast, the receptacle and indusium of *T. katonii* together form a peltate structure. The receptacle is massive, comprised of thin-walled, isodiametric cells, and nearly conical, with its widest point at the base where it attached to the abaxial surface of the pinnule (Fig. 1.4). Sporangia are attached in a helix around the receptacle, which forms the central stalk of the peltate structure. Scalariform tracheids occur in the the receptacle and ultimately extend into the indusium. The indusium is multiseriate, up to seven cells thick at the margin, and comprised of thin-walled, isodiametric cells. There is a subtle difference in cellular structure between the receptacle and indusium (Fig. 1.4); a line of cells at the transition may indicate a zone of dehiscence. Thus the sorus of *T. katonii* is peltate, but the stalk is developmentally derived from a different tissue (receptacle) when compared with modern Matoniaceae (indusium). Nonetheless, the peltate structures in both fossil and extant Matoniaceae show overall similarity that supports assignment of these detached sori to the extant family.

The number of sporangia per sorus in *T. katonii* (more than 28) is greater than previously reported in most species of Matoniaceae. This character is comparable only to extant *Phanerosorus* and the North American compression fossils *Phlebopteris smithii* (Daugherty) Arnold from the Upper Triassic and *Delosorus cystopteroides* (Fontaine) Skog et Litwin from the Cretaceous (Table 1) (Ash et al., 1982; Skog and Litwin, 1995; Kato, 1998). The fossil record of matoniaceous ferns indicates that most taxa are morphologically similar to *Matonia* and bear 10 or fewer sporangia in a single layer per sorus (Tidwell and Ash, 1994). Contrary to statements in Copeland (1947) and Yoroi and Kato (1987), there are no vegetative matoniaceous fossils that we are aware of that display the characteristic morphology of *Phanerosorus* (Walker and Jermy, 1982; Collinson, 1996). *Phanerosorus* differs from *Matonia* in having elongate, linear, pinnately compound fronds. This distinctive organization has been attributed to its specialized epilithic habit and limestone habitat (Compton, 1909). *Phanerosorus* was previously interpreted as similar to *Matonia* in having approximately 10 sporangia in a single layer (e.g., Baker, 1891; Walker and Jermy, 1982), but recently has been found to have as many as 20 sporangia in up to three layers per sorus (Kato, 1998). The fossil species *P. smithii* and *D. cystopteroides* may bear up to 20 and 50 sporangia per sorus respectively (Ash et al., 1982; Skog and Litwin, 1995) (Table 1). Matoniaceous taxa with fewer than 10 sporangia per sorus, including *Matonia*, are first reported from the Early Jurassic (Harris, 1980; Givulescu and Popa, 1998). Considered with the number of sporangia documented here in *Tomaniopteris katonii*, these data suggest that there are at least two distinct patterns of sorus organization in the Matoniaceae by the middle of the Mesozoic: sori with a large number of sporangia arranged in multiple layers, as observed in extant *Phanerosorus*, and those with few sporangia in a single

TABLE *1*—Characteristics of sorus organization in selected matoniaceous taxa.

| | *Tomaniopteris katonii* | *Phlebopteris smithii*[a] | *Delosorus cystopteroides*[b] | *Matonia* sp.[c] | *Phanerosorus* sp.[c] |
|---|---|---|---|---|---|
| Indusium | Peltate, round | Exindusiate | Peltate, round | Peltate, round | Peltate, round or elliptic |
| Indusium thickness | Multiseriate | N/A | Not known | Biseriate | Biseriate |
| Sorus diameter (mm) | 1.6–2.0 | 0.8–1.2 | 0.5–1.0 | 1.0–1.1 | 1.4–1.9 |
| Receptacle vascularization | Present | Not known | Not known | Absent | Absent |
| Number of sporangia | More than 28 | Up to 20 | Up to 50 | 5–10 | Up to 20 |
| Sporangial attachment | Helical in 3–4 layers | Single layer? | Basal? in two layers | Basal in single layer | Basal in 2–3 layers |
| Sporangia | Globose-ovoid | Ovoid | Ovoid | Globose-polygonal | Globose-ovoid |
| Annulus | Vertical, incomplete | Vertical to slightly oblique, incomplete? | Oblique, complete | Oblique, incomplete | Oblique, incomplete |
| Occurrence | Middle Triassic | Late Triassic | Early Cretaceous | Jurassic-Modern | Modern |

[a] Ash, Litwin, and Traverse, 1982.
[b] Skog and Litwin, 1995.
[c] Kato, 1998.

layer, represented today by *Matonia*. Given that the total number of sporangia in extant *Phanerosorus* was misinterpreted for nearly a century, it is possible that careful examination of matoniaceous compression fossils may yet demonstrate a greater number of sporangia in some taxa than previously reported. This character is likely to be taxonomically informative at the species level and may reveal greater diversity in Mesozoic Matoniaceae than is currently recognized.

The absence of spores in *Tomaniopteris katonii* is unusual, since sporangia appear to be mature and undehisced. Palynological investigation of the silicified peat in the Fremouw Formation has identified dispersed spores assigned to *Dictyophyllidites mortonii* (de Jersey) Playford et Dettman (Kyle and Fasola, 1978; Kyle and Schopf, 1982; Farabee et al., 1990), which are closely comparable to spores of *Phlebopteris smithii* from the Upper Triassic (Ash et al., 1982; Litwin, 1985). As new material becomes available, it is possible that spores of this type will be found within the sporangia of *T. katonii*.

*Tomaniopteris katonii* is found in association with small fern rachides, however, none of the sori has yet been found attached. In their description of ferns from Fremouw Peak, Millay and Taylor (1990) provisionally assigned *Soloropteris rupex* to the Matoniaceae, citing ‘‘rings’’ of sporangia cooccurring in the matrix as support for the assignment. A reexamination of these sporangia, however, reveal that they are specimens of *Gleichenipteris antarcticus* (Gleicheniaceae) rather than *T. katonii*, which underscores the organizational similarity of reproductive structures in these basal fern families. On the other hand, the presence of the matoniaceous reproductive structures described here confirms the early Middle Triassic of Antarctica as the earliest currently known occurrence of the family and further adds support to the assignment of *S. rupex* to the Matoniaceae (Millay and Taylor, 1990).

These structures are interpreted here as isolated sori with a peltate, vascularized indusium rather than as fragments of fertile pinnules with slightly expanded receptacle apices, as it would appear if the specimen in Figure 1.1 were rotated 180 degrees. A number of characters, or lack thereof, refute the hypothesis that these are pinnule fragments. No stomata or substomatal chambers have been observed on either surface of the laminate structure. Although the vascular bundle in the center of the laminate structure is extremely reduced, not unlike those of fertile pinnules, the orientation of the vasculature in the receptacle indicates that the vascular strand expands in the direction opposite that which would be predicted if the laminate structure was a pinnule. Furthermore, the size of the laminate structure relative to the sporangia and receptacle is out of proportion for these to represent cross sections of pinnules. Finally, in preparing sections, there is no evidence of additional laminar organization of pinnules. These observations support the identification of the specimens as detached, peltate sori.

*Evolution of the indusium in the Matoniaceae*.—As noted by Bower (1923), the term ‘‘indusium’’ denotes a protective structure over the sporangia that occurs in many fern taxa, but is not necessarily derived from the same developmental processes across taxonomic groups. Indusiate leptosporangiate ferns are known from the Paleozoic (Rothwell, 1987; Galtier and Phillips, 1996), however, none of these show clear affinities with modern families. Among the basal gleichenioid ferns, the Matoniaceae are the only indusiate representatives, which has led to some speculation regarding the evolutionary history of this structure in the family. *Tomaniopteris katonii* is thus of particular interest in documenting structural modifications that may have led to the organization observed in extant representatives of the Matoniaceae.

Based on compression fossils, the peltate indusium in modern Matoniaceae has been hypothesized as evolving as a result of continued expansion of the receptacular apex (Hirmer and Hoerhammer, 1936; Harris, 1961; Semaka, 1971; Tidwell and Ash, 1994). The earliest-occurring taxa assigned to the Matoniaceae, the Late Triassic genera *Selenocarpus* Schenk and *Phlebopteris smithii*, are interpreted as lacking an indusium, with sporangia arranged in a ring around a raised receptacle (Schenk, 1867; Hirmer and Hoerhammer, 1936; Ash et al., 1982). Taxa that appear later in the fossil record, e.g., *Matonidium* Schenk from the Cretaceous (Schenk, 1871), are interpreted as showing slight extensions of the receptacle apex over the sporangia. Continued expansion of the receptacle has been suggested to ultimately result in the peltate indusium that is characteristic of the family. The presence of a fully expanded peltate indusium in *T. katonii* does not support this hypothesis, as it predates the appearance of exindusiate *Phlebopteris* in the Late Triassic. Furthermore, indusiate *Matonia* from the Jurassic predates the Cretaceous appearance of a partial indusium in *Matonidium* (Harris, 1980). The suggested evolutionary developmental sequence in which elaboration of the receptacle through time ultimately results in the development of an indusium in the Matoniaceae remains a valid hypothesis. The timing of this proposed sequence, however, is no longer supported by the fossil record. If this is indeed the developmental pathway by which the peltate indusium was derived in this family, *T. katonii* documents that the basic structural organization observed in the Matoniaceae today was achieved by the early Middle Triassic. Further efforts to confirm this developmental sequence will need to focus on ferns from the Permian and Early Triassic.

Harris’s (1980) discovery of indusiate sori in *Phlebopteris braunii* Goeppert from the Jurassic of Britain and the resulting transfer of these specimens to *Matonia braunii* (Goeppert) Harris call into question whether any currently known matoniaceous fossil taxa are truly exindusiate. In extant Matoniaceae, sori frequently detach either in part or entirely from the abaxial surface of the pinnule, and thus can appear to lack an indusium (Baker, 1891; Seward, 1899; Bower, 1926; Harris, 1980; Walker and Jermy, 1982; Ash et al., 1982; van Konijnenburg-van Cittert, 1993). Dehiscence can occur either at the point of transition between the isodiametric cells of the receptacle and the elongate cells of the indusium, which leaves a receptacular stump and its attached sporangia on the abaxial pinnule surface, or the entire sorus (receptacle, sporangia and indusium) may dehisce at the point of attachment of the receptacle to the pinnule. Some authors have recognized that this may also have occurred in fossil taxa, which could explain the apparent lack of an indusium in compression fossils (Seward, 1899; Harris, 1980; Ash et al., 1982; van Konijnenburg-van Cittert, 1993). Thus, the possibility that indusia simply may not be preserved has not been ruled out. Bias against compression specimens in which sporangia are obscured may also play a role in collecting indusiate material (Harris, 1980). The fossils described here document that the pattern of dehiscence of the entire sorus from the pinnule surface is present even in the earliest known representative of the family. Based on a subtle difference between cellular organization of the receptacle and indusium (Fig. 1.4), there is some indication that the indusium in *Tomaniopteris katonii* may be dehiscent as well, which could explain the common exindusiate appearance of many matoniaceous compressions. It remains possible that the Matoniaceae include exindusiate fossil taxa, since there are families that include both indusiate and exindusiate genera (e.g., Cyatheaceae). It seems more likely, however, that with further careful collection and detailed examination, many fossil taxa currently interpreted as exindusiate will be found to possess an indusium.

*Implications for phylogenetic reconstruction*.—The Matoniaceae have long been considered to be a systematically isolated group that, along with Gleicheniaceae and Dipteridaceae, occupies a basal position in the phylogeny of leptosporangiate ferns

(Seward, 1899; Bower, 1926). These three families and Cheiropleuriaceae are generally regarded as members of a ''gleichenioid'' grade, but relationships among the members of this informal group remain unresolved (Hasebe et al., 1994; Pryer et al., 1995; Hennipman, 1996; Stevenson and Loconte, 1996; Wolf et al., 1998; Kato and Setoguchi, 1999). The Matoniaceae are frequently interpreted as derived from the Gleicheniaceae, which are exindusiate, as are the other gleichenioid ferns, Dipteridaceae and Cheiropleuriaceae. Phylogenetic analyses using only morphological data do not support this interpretation, and the Matoniaceae group with either Cyatheales (Pryer et al., 1995; Wolf et al., 1998) or Dennstaedtiaceae (Rothwell, 1999) in the resulting cladograms. Analyses of molecular data, however, do show support for a basal gleichenioid grade. In resulting cladograms, Matoniaceae are sister to either Gleicheniaceae (Hasebe et al., 1994) or Dipteridaceae + Cheiropleuriaceae (Kato and Setoguchi, 1999). In other analyses, however, they resolve as sister to Hymenophyllaceae, another ancient leptosporangiate family with a fossil record now known to extend into the Triassic (Hasebe et al., 1994; Vangerow et al., 1999; Axsmith et al., 2001). Use of combined morphological and molecular data in phylogenetic analyses thus far fails to fully resolve these relationships. In these analyses, Matoniaceae again occur as sister to either Dipteridaceae + Cheiropleuriaceae (Pryer et al., 1995; Stevenson and Loconte, 1996; Wolfe et al., 1998) or Gleicheniaceae (Pryer et al., 2001). The basal groups in the gleichenioid grade have an extensive evolutionary history that may not be fully accessible using molecular techniques based on the few remaining representatives today. The fossil record, on the other hand, provides direct documentation of characters that can clarify these as-yet-unresolved relationships.

Initial radiation of leptosporangiate ferns is suggested to have occurred in the Early Carboniferous, with a second radiation beginning in the Permian that resulted in the appearance of taxa that can be assigned to the basal families in the extant gleichenioid group (Rothwell, 1987; Tidwell and Ash, 1994). Of these, the Gleicheniaceae may have been the first to appear. Although Collinson (1996) did not accept reports of Gleicheniaceae prior to the Cretaceous, Skog (2001) suggested that the first record of this family occurs in the Permian, with further divergence of the remaining basal gleichenioid groups in the Middle Triassic. Recent description of gleicheniaceous sporangia from Fremouw Peak (Phipps et al., 2000) and the matoniaceous sori described here confirm that the two families were well established and distinct by the early Middle Triassic. This supports the hypothesis that the split occurred earlier, perhaps during the Permian.

Our understanding of the diversity and complexity of the Middle Triassic flora of Antarctica continues to increase, based in part on the extraordinary preservation of the plants at Fremouw Peak. This flora provides unparalleled opportunities to document early organizational patterns in both extinct and extant plant groups, which can be utilized in exploring patterns of character evolution through time.

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