

A NEW SPECIES OF *MILLEROCAULIS* (OSMUNDACEAE) FROM THE LOWER CRETACEOUS OF CALIFORNIA

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A small permineralized osmundaceous stem has been collected from marine sediments of the Early Cretaceous (Aptian), Upper Chickabally Member of the Budden Canyon Formation near Ono, California. The specimen, 8.5 cm long and 5.4 cm wide, represents a stem surrounded by a mantle of stipular leaf bases and adventitious roots. A large number of sections were studied through the use of the cellulose acetate peel technique. The stem was erect, 11 × 13 mm in diameter, with a parenchymatous pith and two-layered cortex. The stele is an ectophloic siphonostele with 65–79 leaf traces in the stem per cross section. Leaf gaps are only produced in 13% of the departing traces. Most leaf traces have “delayed” gaps or completely lack leaf gaps. Leaf traces are C-shaped, endarch, with one protoxylem strand, and have sclerenchyma lining the adaxial concavity. Leaf bases have stipular wings with large patches of heterogeneous sclerenchyma and a few scattered strands outside of the heterogeneous sclerotic ring. Patches of sclerenchyma occur inside the ring and outside of the vascular tissues. Numerous diarch roots arise singly or doubly from the leaf traces as they depart the axis stele. Although the stem compares fairly closely to both *Ashicaulis* Tidwell and *Millerocaulis* Erasmus ex Tidwell emend. Tidwell, it is most similar to *Millerocaulis*. However, the combination of characters observed in our specimen differs from that of the seven known species of *Millerocaulis*. This stem is described as *Millerocaulis embreei* sp. nov. and is the youngest known species of the genus and the first to be found in the Northern Hemisphere.

Keywords: *Ashicaulis*, Cretaceous, ferns, *Millerocaulis*, Osmundaceae, paleobotany.

Introduction

The fern family Osmundaceae, with 18 species included in three extant genera, *Osmunda* L., *Todea* Willdenow in Bernhardt, and *Leptopteris* C. Presl (Kramer 1990), is currently regarded as the most primitive of the filicaleans (Bower 1926; Wagner 1969; Bierhorst 1971; Holtum 1973; Serbet and Rothwell 1999). In results of recent phylogenetic analyses, Osmundaceae occur at or near the base of the leptosporangiate fern clade (Stein et al. 1992; Hasebe et al. 1995; Pryer et al. 1995; Stevenson and Loconte 1996; Rothwell 1999).

The osmundaceous ferns were much more widespread and diverse in the past, with a fossil record that extends back to at least the Permian (Miller 1971; Tidwell and Ash 1994). There are over 150 extinct osmundaceous species worldwide (Taylor and Taylor 1993; Tidwell and Ash 1994; Serbet and Rothwell 1999). Most species are based on compressed foliage, but ca. 50 taxa have been described from silicified stems with attached leaf bases and roots (Tidwell and Ash 1994; Serbet and Rothwell 1999). Today there are ca. 12 recognized fossil genera classified in two subfamilies, the Thamnopteroideae and Osmundoideae (Tidwell and Ash 1994). Although a number of characters have been used in the taxonomy of Osmundaceae, the arrangement of the sclerenchyma in the leaf base appears to be the most reliable anatomical feature for characterizing genera and species among the fossil and living taxa (Hewitson 1962).

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In this study we examined a single stem of a well-preserved, permineralized osmundaceous fern with attached roots and leaf bases from northern California. This specimen was compared to living and fossil ferns in the family Osmundaceae and is described as a new species in the Osmundoideae.

Material and Methods

The specimen was collected from the southwest corner of Section 12, T30N, R7W of the Ono quadrangle, near the town of Ono in northern California. This specimen comes from near the base of the Upper Chickabally Member of the Early Cretaceous, Budden Canyon Formation (fig. 1), and was found associated with ammonites that date the stem as Aptian age, upper Bedoulian Stage (Murphy et al. 1969). At this locality the formation consists mostly of dark mudstone interbedded with a few sandstone and limestone lenses. Irregular, light gray concretions are common and fossil wood is abundant in the formation in this area (P. Embree, personal communication, 1997). The fern presumably washed into this depositional environment by river transport.

The specimen was cut transversely into two sections. The calcium carbonate matrix allowed us to make very closely spaced cellulose acetate peels using the cellulose acetate peel technique of Joy et al. (1956). Extensive peels were made of the specimen in order to determine the stelar architecture and the nature of leaf gaps. Peels were mounted on slides using Eukitt (O. Kindler GmbH & Co., Freiberg, Germany) xylene-soluble mounting medium.

| Lower Cretaceous | Budden Canyon Formation | Member | Age (Stage) | | Guide Fossils |
|------------------|--------------------------|--------------------------|-------------|---|--|
| | | Upper Chickabally Member | Albian | | <i>Brewericeras hulenense</i> <i>Leconteites leonti</i> |
| Huling Member | Lower Chickabally Member | Aptian | Clansayes | <i>Ammoceratites reesidi</i> <i>Ammoceratites gardneri</i> | |
| | | | Bedoufian | <i>Eotetragonites wintamius</i> | |
| | | Barremian | | <i>Shastrioceras sp.</i> | |

Fig. 1 Stratigraphic occurrence of *Millerocaulis embreei* sp. nov. (asterisk) and associated ammonites (modified from Murphy et al. 1969).

The specimen (CS1044) is housed at the California Academy of Science, San Francisco.

Results

Systematic Description

Order—Filicales

Family—Osmundaceae

Subfamily—Osmundoideae

Genus—*Millerocaulis* Erasmus ex Tidwell emend. Tidwell

Species—*M. embreei* Stockey et Smith sp. nov.

Diagnosis. Stem erect, 11 × 13 mm in diameter, surrounded by mantle of stipular leaf bases and adventitious roots. Stele ectophloic, siphonostelic; pith 2.6 × 3.3 mm in diameter, parenchymatous; xylem cylinder 0.60–0.95 mm (nine to 13 tracheids) thick; incomplete gaps, extending 1/10 to 9/10 distance through xylem cylinder associated with leaf trace departure, delayed gaps, or rarely true gaps present; gaps narrow, one to two cells wide, of variable length, 50 μm to at least 1500 μm. Inner cortex 1.2 mm wide, parenchymatous; outer cortex 2.3–4.5 mm thick, sclerenchymatous. Number of leaf traces in transverse section of cortex, 65–79. Protoxylem in leaf trace, one strand, endarch. Sclerenchyma present in concavity of petiolar vascular strand and petiolar cortex; sclerotic ring heterogeneous; stipular wings with one large heterogenous sclerenchyma mass midwing and scattered smaller sclerenchyma patches throughout stipular wing. Adventitious roots diarch, arising singly or doubly, from leaf traces near departure from axis stele.

Holotype. CS1044 California Academy of Science, San Francisco.

Stratigraphy. Upper Chickabally Member, Budden Canyon Formation.

Age. Early Cretaceous; Aptian age; Bedoufian stage.

Etymology. We name the species in honor of Patrick Embree, University of California, Davis, who made this and other plant specimens available to us for study.

Description

The well-preserved specimen, 8.5 cm long and 5.4 cm wide, consists of a small stem and attached leaf bases and adventi-

tious roots that completely encircle the stem (figs. 2.2, 2.3). Leaf bases are visible externally (fig. 2.2).

The stem measures 11 × 13 mm in diameter (fig. 2.3) and contains an ectophloic siphonostele (figs 2.4, 2.6). The pith is parenchymatous, 2.6 × 3.3 mm in diameter, and the central portion is broken down and replaced with mineral matrix (figs. 2.3, 2.4). The xylem cylinder is 0.60–0.95 mm (nine to 13 tracheids) wide. Metaxylem tracheids exhibit scalariform secondary wall thickenings (fig. 2.5). Cells that resemble sieve cells of typical living osmundaceous ferns are well preserved in some areas of the phloem zone (fig. 2.6). The cortex is differentiated into two distinct layers (figs. 2.3, 2.4). The parenchymatous inner cortex is 1.2 mm thick (fig. 2.4) and the sclerenchymatous outer cortex is 2.3–4.5 mm thick (fig. 2.3).

In transverse section there appear to be no leaf gaps, or an occasional gap or a crack in the specimen. At the levels of trace departure there are incomplete gaps that extend from 1/10 to 9/10 of the way into the xylem cylinder (figs. 2.4, 2.6; fig. 3.7). In a few places the stele appears to be dissected; however, a leaf trace is not obviously associated with the gap.

As in most Osmundaceae, the protoxylem is produced in the stem just below the level of leaf trace divergence, and only in association with the leaf trace. By using 240 sections, we successfully traced the departure of 75 leaf traces. About 13% of the traces produced true leaf gaps, i.e., a gap associated with the departure of the leaf trace and at the level of leaf trace divergence. Of the 120 sections taken from the apical half of the specimen there was only one leaf gap, while gaps were more frequent in the basal half of the specimen. Lengths and appearance of the gaps were noted, and it was determined that their characters are highly variable. Gap length was ca. 50 μm to at least 1500 μm and they were usually only one cell wide (rarely two). About half of the leaf traces were associated with a “delayed gap” (Kidston and Gwynne-Vaughan 1910) only one cell in thickness that arose 0.38–0.83 mm above the level of leaf trace departure. The remainder of the leaf traces lack any sort of associated gap, immediate or delayed. In these, an incomplete gap or notch extended into the metaxylem to various depths, ranging from three tracheids into the stele to within one tracheid of the pith itself. Even though there appear to be a few very narrow gaps in the xylem cylinder, there are no visible gaps in the phloem, a feature noted by Serbet and Rothwell (1999) in extant and fossil *Osmunda cinnamomea* L.

Leaf traces departed in a helical arrangement and the phyllotaxy seemed to fluctuate. At some levels three traces arose in rapid succession departing in a clockwise direction at almost the same level. At other levels, five traces departed in rapid succession around the same helix. These zones were interspersed with zones that ranged from 0.25 to 0.50 mm in length where no leaf traces departed. Thus, leaf trace departure appears to have been cyclic and somewhat irregular.

There are 65–79 leaf traces in the cortex in any one cross section (fig. 2.3). Endarch leaf traces depart from the xylem cylinder with one protoxylem strand (fig. 2.6; figs. 3.7, 3.11). Leaf traces are circular close to the xylem cylinder and become strongly curved and C-shaped as they diverge from the stele (figs. 2.4, 2.6; figs. 3.7, 3.8, 3.11). Each trace is surrounded by a ring of sclerenchyma as it leaves the outer cortex (fig. 2.3; figs. 3.8, 3.10, 3.12). This ring of cells is heterogeneous;

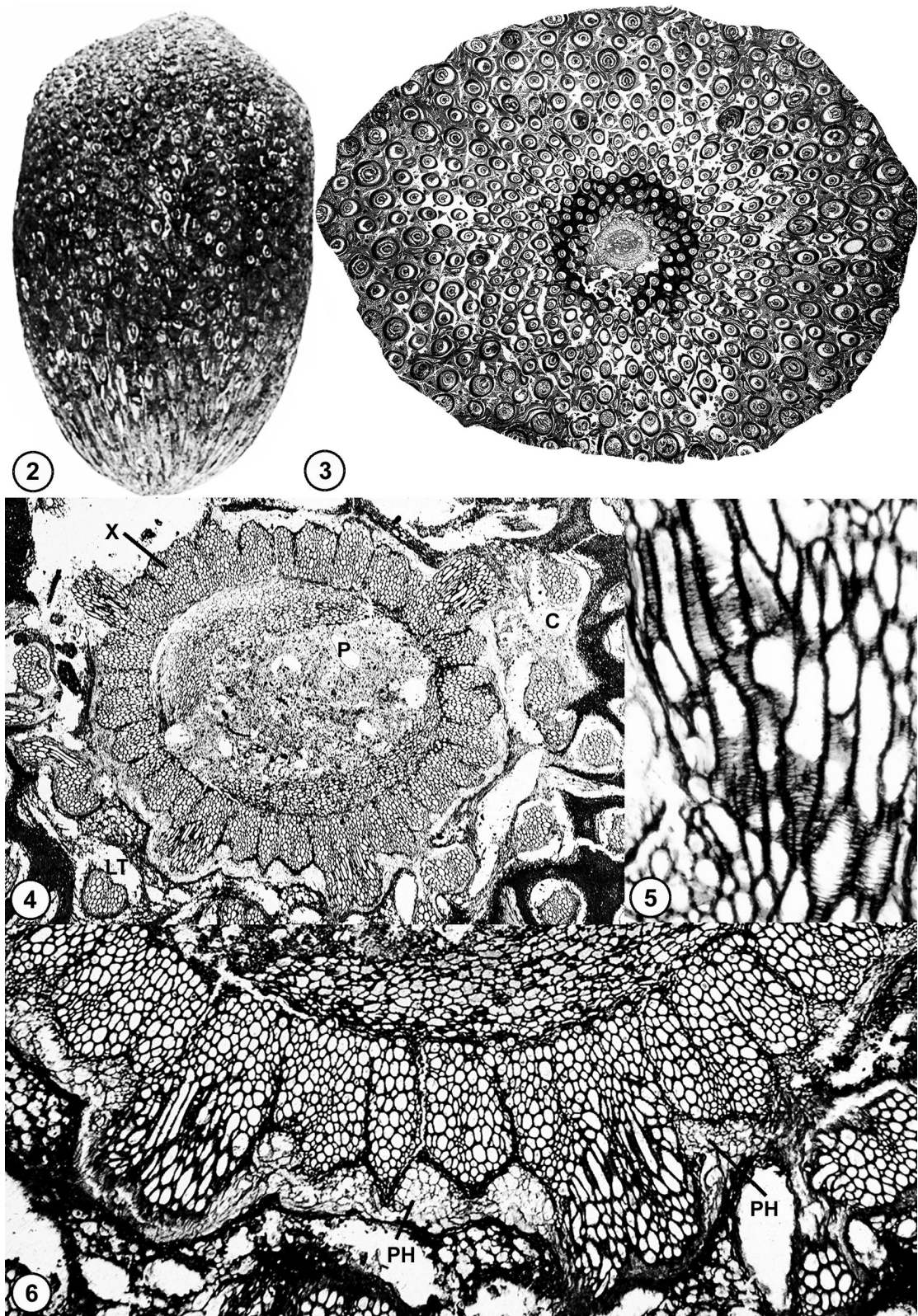


Fig. 2 *Milleroaulis embreei* sp. nov. Holotype CS1044. Fig. 2.2, External view of specimen. $\times 1$. Fig. 2.3, Cross section of stem with attached roots and leaf bases. A #3 $\times 2$. Fig. 2.4, Transverse section of stele with diverging leaf traces and partially preserved pith. A #2 $\times 15$. Fig. 2.5, Longitudinal section of metaxylem tracheids showing scalariform secondary wall thickenings. B #7 $\times 150$. Fig. 2.6, Cross section of stelar region showing well-preserved phloem, leaf trace departure, and lack of leaf gaps in the stele. Note crack in center of xylem cylinder in photo. A #2 $\times 40$.



Fig. 3 *Millerocalis embreei* sp. nov. Holotype CS1044. Fig. 3.7, Transverse section of stem showing poorly preserved inner cortex and departing leaf traces, each of which shows a departing root trace. A #8 × 27. Fig. 3.8, Cross section of stipular leaf bases showing lateral wings with sclerenchyma, sclerotic rings, and adventitious roots. A #2 × 10. Fig. 3.9, Cross section of diarch root. A #7 × 41. Fig. 3.10, Cross section of stipular leaf base showing two large bands of sclerenchyma and small patches in wings, heterogeneous sclerotic ring, and sclerenchyma in the adaxial concavity of the leaf trace. B #4 × 36.5. Fig. 3.11, Cross section of departing leaf trace giving rise to two root traces. B #64 × 30. Fig. 3.12, Cross section of leaf trace near margin of specimen showing heterogeneous sclerenchyma in wings and sclerotic ring, patches of sclerenchyma in petiolar cortex inside ring and lining the abaxial concavity. B #1 × 25.

the outer part of the ring contains thick-walled cells with small lumens while the inner cells have thinner walls and larger cell lumens (figs. 3.10, 3.12). The sclerotic ring is fairly uniform in thickness but is slightly thicker at the top and bottom of the trace (figs. 3.8, 3.10, 3.12). In transverse section the ring is oval to circular in outline (figs. 3.8, 3.10, 3.12). As the petiole separates from the stem it develops two stipular wings (figs. 3.8, 3.10). Many wings are not well preserved and probably deteriorated before fossilization as a result of the thin-walled nature of the cells, the activity of fungi, or taphonomic processes, since the specimen was probably transported some distance before burial. Each stipular wing contains a large elliptical heterogeneous sclerenchyma mass and smaller scattered patches of sclerenchyma (figs. 3.8, 3.10, 3.12). There are also scattered sclerenchyma nests in the petiolar cortex inside the sclerotic ring (fig. 3.12). In addition, one patch of sclerenchyma occurs in the concavity of the leaf trace (figs. 3.8, 3.10, 3.12). This patch occasionally splits in the outermost leaf bases into two or more strands (fig. 3.12).

Root traces diverge from leaf traces as the leaf traces separate from the xylem cylinder (fig. 2.6; figs. 3.7, 3.11). Most leaves have one associated root trace, but 14 of the 75 traces studied in detail produced two roots per leaf trace. Roots are extensively interwoven with the leaf bases (fig. 3.8) to form the outer covering of the stem. Roots have typical diarch protosteles, and the sclerotic cortex of roots is well preserved while the phloem is usually absent (figs. 3.9, 3.11).

Discussion

This small stem surrounded by persistent leaf bases and numerous roots was probably erect to slightly leaning in life. The ectophloic siphonostele and distinctly C-shaped leaf traces compare with two families of ferns that are common in the fossil record: the Guaiereaceae and Osmundaceae (Tidwell and Ash 1994). The Guaiereaceae differ from our specimen in that they do not have a cortex that is differentiated into two zones and their petiole bases lack stipular wings and sclerotic rings (Tidwell and Ash 1994). Osmundaceous ferns have C-shaped traces, a two-layered cortex, petiolar traces with sclerotic rings and stipular wings on petiole bases (Bower 1926; Miller 1971; Tidwell and Ash 1994) like those seen in *Millerocaulis embreei*.

Within the Osmundaceae, the two subfamilies Thamnopteroideae and Osmundoideae are distinguished by characters of the stele and primary xylem maturation of the leaf trace (Miller 1971). Miller (1971) characterized the Osmundoideae as having a xylem cylinder interrupted by leaf traces, a pith of parenchyma or sclerenchyma, and leaf traces that are endarch or rarely subendarch at their origin from the stele. The Thamnopteroideae were described as having protosteles or "xylem cylinder of stem not interrupted opposite leaf-traces," and leaf traces that are mesarch or subendarch at their origin (Miller 1971, p. 126). Since 1971, a large number of new fossil taxa have been described that are somewhat intermediate between these two subfamilies as defined by Miller (1971).

Tidwell and Ash (1994) include the extant genera, *Osmunda*, *Leptopteris*, and *Todea*, in the subfamily Osmundoideae along with five fossil taxa: *Palaeosmunda* Gould, *Osmundacaulis* Miller emend. Tidwell, *Aurealcaulis* Tidwell and Parker emend. Tidwell and Medlyn, *Ashicaulis* Tidwell, and

Millerocaulis Erasmus ex Tidwell emend. Tidwell (Tidwell 1986, 1994). *Osmundacaulis* has small to large stems up to 45 cm or larger in diameter with 25 or more tracheids in the xylem transverse section (Tidwell 1986), while in *M. embreei* stems are much smaller with only nine to 13 tracheids in transverse section. In *Osmundacaulis*, the inner parenchymatous cortex is as wide as or wider than the sclerenchymatous outer cortex, but in *M. embreei* the inner cortex is very narrow. Leaf traces are C-shaped in both *Osmundacaulis* and *M. embreei*; however, they flatten distally in *Osmundacaulis* species. The petiole of *Osmundacaulis* has lobed sclerenchyma in the concavity, with two to four (rarely one) protoxylem strands in the leaf trace (Tidwell and Pigg 1993; Tidwell 1994). In *M. embreei* there is a single patch of sclerenchyma in the concavity that may divide at higher levels, and one protoxylem strand in the leaf trace. The vascular system is a highly dissected siphonostele in *Osmundacaulis* while *M. embreei* lacks numerous distinct and extensive leaf gaps.

Palaeosmunda stems, like those of *Osmundacaulis*, have ectophloic siphonosteles or dictyosteles and sclerotic rings in the petiole that are rhomboidal in transverse section that become laterally extended distally (Gould 1970). Our California specimen has a round sclerotic ring unlike that seen in the Permian *Palaeosmunda*.

The living taxa of osmundaceous ferns also show dictyosteles, unlike our fossil material (Miller 1967, 1971). *Aurealcaulis* does not have leaf gaps but has a stele that is reminiscent of seed plants with leaf traces formed by the fusion of segments from adjacent xylem strands and exarch primary xylem maturation (Tidwell and Parker 1987; Tidwell and Medlyn 1991). Thus, our fossil stem does not show close similarities to any of these taxa.

The genera with the closest similarities to our fossil are *Ashicaulis* and *Millerocaulis*, which are distinguished on the basis of the trace departure from the stele. The genus *Millerocaulis* was established (Erasmus 1978; Tidwell 1986, 1994) on the basis of Miller's *Osmundacaulis herbstii* group for small stems that produced leaves with one protoxylem strand and a sclerotic outer cortex and that lack leaf gaps or "have occasional leaf gaps" (Tidwell 1986, 1994). The genus *Ashicaulis* is very similar, but typical leaf gaps are present and numerous (Tidwell 1994). The vasculature of our stem mostly closely resembles that described for species of *Millerocaulis*.

At the present time there are seven species in the genus *Millerocaulis* from the Triassic and Jurassic of the Southern Hemisphere: *M. indentata* (Hill, Forsyth et Green 1989) Tidwell (1994), *M. donponii* Tidwell et Clifford (1995), *M. juandahensis* Tidwell et Clifford (1995), *M. limewoodensis* Tidwell et Clifford (1995), *M. dunlopii* (Kidston et Gwynne-Vaughan 1907) Tidwell (1986), *M. indica* (Sharma 1973) Tidwell (1986), and *M. chubutensis* (Herbst 1977) Tidwell (1994). We compared our specimen to these species on the basis of 15 morphological characters (table 1). The California specimen shows a unique combination of characters. As Hewitson (1962) pointed out, the most significant characters used to distinguish osmundaceous stems are incorporated in the anatomy of the petiole bases and the configuration of the sclerenchyma. All species of *Millerocaulis* have small stems (table 1). *Millerocaulis embreei* is in the midrange for stem size including stele thickness, pith diameter, and thickness of the inner cortex

Table 1

Comparison of *Millerocalis* Species

| | <i>M. embreei</i> (Cretaceous) | <i>M. donponii</i> (Jurassic) | <i>M. juandahensis</i> (Jurassic) | <i>M. limewoodensis</i> (Jurassic) | <i>M. dunlopii</i> (Jurassic) | <i>M. indica</i> (Jurassic) | <i>M. chubutensis</i> (Jurassic) | <i>M. indentata</i> (Triassic) |
|---|------------------------------------|---|--------------------------------------|---|---|---|---|---|
| Stem diameter (mm) | 13 × 11 | 14 × 15 | 18 | 6.25–9.75 | 15–19 | 17–20 | 25 | 14 |
| Stele diameter (mm) | 4–5 | 9–10 | 10 | 3.5 × 5 | 4–7 | 0.9–1 | 10 × 8 | 3.5 |
| Xylem cylinder thickness (mm) | 0.6–0.95 | 0.5–1 | 1 | 1 | 0.5 | 0.25–0.28 | 1–1.2 | 0.5 |
| Xylem cylinder thickness (tracheids) | 9–13 | 5–17 | 16–17 | 9–11 | 6–7 | 8–11 | 10–13 | 18 |
| Pith diameter (mm) | 3.3 × 2.6 | 5 × 7 | 4 × 5 | 2.75 × 3.9 | 2–6 | 0.4–0.45 | 5 × 7 | 2.2 |
| Pith cell composition | p | p | p | ? | p | ? | p | p |
| IC thickness (mm) | 1.2 | 1–2 | 1–3 | Ca. 1.75 | 0.5–2 | 0.12–0.14 | 3 | 2.5 |
| OC thickness (mm) | 2.3–4.5 | 2–3 | 3.5–5 | Ca. 1.75–3 | 6 | 0.6–0.8 | 4 | 3.75 |
| Incipient leaf gap depth | 1/10–9/10 with rare gap | 1/2 with rare gap? | 3/4 with rare gap? | 1/2 with rare gap? | 3/4 with rare gap? | 1/4 | 1/2 with rare gap? | 3/4 |
| Trace no. in cortex | 65–79 | 95–102 | 69 | Ca. 30–46 | 70–79 | 7–9 | 75–77 | 40 |
| Scl in concavity | Lining | None | 2 distant from strand | 2 near strand | 2 near strand | None? | Lining | 2 near strand |
| Scl in petiolar cortex | Scattered | None | None | Scattered | Scattered | None? | Scattered | None |
| Sclerotic ring | Heterogeneous | Homogeneous | Heterogeneous | Homogeneous | Homogeneous | Homogeneous | Homogeneous | Heterogeneous |
| Scl in wing | One mass + scattered strands | One mass + scat- tered strands | One mass | Several masses aligned, some scattered strands | One mass + scat- tered strands | One mass + scattered strands | One mass + scat- tered strands | One mass + scattered strands |
| Protoxylem divides | Petiole | Petiole base | OC | Petiole | OC | ? | Petiole | Outer edge OC |

Note. Modified from Tidwell and Clifford 1995. Abbreviations are as follows: p = parenchyma, scl = sclerenchyma, IC = inner cortex, OC = outer cortex. Boldface type indicates characters similar to those of *M. embreei*.

(Tidwell and Clifford 1995). The outer cortex in our specimen is thicker than most (table 1). The number of leaf traces in the cortex in a stem cross section is in the midrange. The sclerenchyma lining the concavity of the leaf trace occurs only in *M. chubutensis* from the Jurassic of Argentina (Herbst 1977; Tidwell and Clifford 1995). In our specimen, however, this sclerenchyma strand divides into several strands distally. Scattered sclerenchyma in the wings occurs in most species, while scattered sclerenchyma inside the sclerotic ring only occurs in about half of the species (table 1). The two large masses of sclerenchyma in the wings occur in all except *M. limewoodensis* (Tidwell and Clifford 1995). However, our wing sclerenchyma is also heterogeneous, unlike any of the previously described species (W. D. Tidwell, personal communication, 1998).

The stellar architecture of *M. embreei* is unlike that described for other *Millerocaulis* species. Other taxa described are silicified permineralizations, making thin sections or polished sections, rather than peels, essential to obtain anatomical details; therefore, these species are described from only a small number of sections or surfaces while a large number of closely spaced sections were possible in *M. embreei* because of the calcium carbonate matrix. From one or a few sections, it would not have been possible for us to ascertain the mode of trace departure and the presence or absence of gaps or delayed gaps in our specimen. It may be that there is a lot more variability in steles of species of *Millerocaulis* than is suspected from previous work, but only closely spaced sections will allow this to be investigated.

Recent work has shown that the genus *Ashicaulis* is variable in stellar architecture (Cantrill 1997). *Ashicaulis livingstonensis* Cantrill from the Upper Cretaceous of Antarctica has a stele that usually produces leaf gaps; however, as Cantrill (1997, p. 317) points out, "in some places the leaf gap never completely forms." Leaf gap width in *A. livingstonensis* is only one to two cells wide, as in *M. embreei*. Fortunately, this species of *Ashicaulis*, although infiltrated by silica, was also calcareous in part, and Cantrill (1997) was able to obtain peels with a combination of acids. Therefore, the stellar architecture is fairly

well known. It is clear to us that *Millerocaulis* and *Ashicaulis* are very closely related taxa that may actually intergrade. A reexamination of all taxa, however, due to the variability in preservation, might not provide much more detail than has been published in the current comparison tables (Tidwell and Clifford 1995; Cantrill 1997). Only with better-preserved material will we be able to understand the relationships between these two genera.

The combination of characters in the California specimen and unique heterogeneous sclerenchyma strands in the wings allow us to treat this fossil in a new species when compared to known species of *Millerocaulis* or *Ashicaulis*. Since the genus *Millerocaulis* is described as lacking or having occasional leaf gaps (Tidwell 1986, 1994), our specimen has been referred to this genus. All of the previously described species of *Millerocaulis* come from the Southern Hemisphere, which seems to be the center of diversity for the family as a whole (Tidwell and Ash 1994). Ours is not only the first *Millerocaulis* reported from the Northern Hemisphere but the youngest species known to date, extending the geologic range of the genus to the Lower Cretaceous.

Acknowledgments

We thank Patrick Embree and James A. Doyle, University of California, Davis, for making the specimen available for study; Peter U. Rodda, California Academy of Science, for geologic data; Trevor Lantz, University of Alberta, for technical help; Charles N. Miller, Jr., University of Montana, and William D. Tidwell for helpful discussion; and Gar W. Rothwell, Ohio University, for technical help, useful discussion, and use of laboratory facilities. This work was supported in part by Natural Sciences and Engineering Research Council of Canada grant A-6908 to R. A. Stockey. A part of this study was submitted as an extended essay for the International Baccalaureate Diploma program at Ross Sheppard High School by S. Y. Smith, who thanks Jane Dyke for encouragement and advice.

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