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Review of Palaeobotany and Palynology 104 (1999) 285–298

Review of  
Palaeobotany  
& Palynology

## Two new species of *Solenostelepteris* from the Upper Jurassic Morrison Formation in Wyoming and Utah

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Received 22 April 1998; revised version received 3 August 1998; accepted 21 August 1998

### Abstract

Permineralized rhizomes of two new species of *Solenostelepteris* Kershaw, *S. leithii*, and *S. medlynii*, are described from the Upper Jurassic Morrison Formation from the Steiner and Scott's localities north of Greybull, Wyoming, and from Fremont Junction, east of Mt. Ellen, and Mussentuchit Wash sites in Utah. The species are characterized by having a heterogeneous (*S. leithii*) to homogeneous (*S. medlynii*) pith, rhizomes with branches (*S. leithii*), a sclerenchymatous (*S. leithii*) or parenchymatous (*S. medlynii*) inner cortex, and both with a parenchymatous middle cortex. The outer cortex of *S. leithii* is parenchymatous, whereas in *S. medlynii*, it is composed of round to irregularly shaped, thick-walled cells. The C-shaped leaf traces in *S. leithii* usually arise single ranked, sometimes two ranked, with short leaf gaps and short internodes. Although the rhizomes of *S. medlynii* are incomplete and lack leaf traces, they still suggest very long internodes. Because fronds and epidermal trichomes are lacking in both, the affinity of these species to modern taxa, such as members of the Loxsomaceae, remains uncertain. © 1999 Elsevier Science B.V. All rights reserved.

**Keywords:** *Solenostelepteris*; Filicales; Jurassic; Morrison Formation

### 1. Introduction

Fossil ferns previously reported in the megafossil flora of the Upper Jurassic Morrison Formation are the compression species, *Hausmannia fisherii* (Knowlton) Oishi et Yamasita, *Cladophlebis alberta* (Dawson) Bell, *C. heterophylla* Fontaine, *C. virginensis* Fontaine emend. Berry, *Adiantites montanensis* (Knowlton) Brown from Montana, and *Coniopteris hymenophylloides* (Brongniart) Seward from both Montana (Miller, 1987) and Utah (Ash and Tidwell, 1998). Permineralized material includes *Os-*

*mundacaulis lemonii* Tidwell and *Ashicaulis wadei* (Tidwell et Rushforth) Tidwell, both from localities near Moab and Castle Dale, Utah (Tidwell and Rushforth, 1970; Tidwell, 1990a,b, 1994; Tidwell and Medlyn, 1992). Matoniaceous spores have also been discovered associated with fossil fungal remains within petrified wood at the Steiner Site. The two appear to have been deposited in openings in the wood, where they were preserved. Based on the rather limited number of ferns reported from the Morrison Formation, this description of two new species of *Solenostelepteris* becomes very significant.

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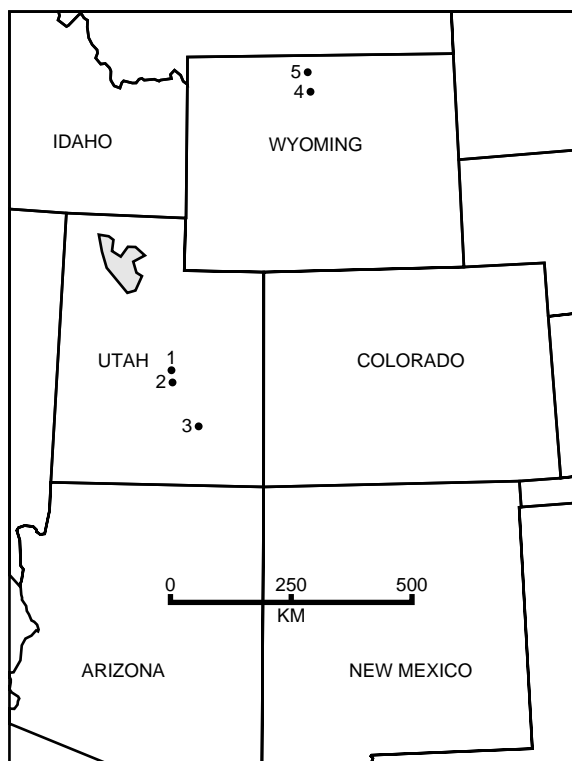


Fig. 1. Collecting sites for *Solenosteleptis leithii* Tidwell et Skog, *sp. nov.* and *S. medlynii* Tidwell et Skog, *sp. nov.* 1 = Fremont Junction, 2 = Mussentuchit Wash, 3 = Mt. Ellen site all in Utah, 4 = Scott's site and 5 = Steiner's site in Wyoming, USA.

## 2. Material and methods

Fern rhizomes having anatomical features upon which this report is based occur at two localities in the Morrison Formation north of Greybull, Wyoming (Fig. 1). These localities are the Steiner site (SW $\frac{1}{4}$ , SE $\frac{1}{4}$ , Sec. 28, T55N, R95W) and Scott's site (SW $\frac{1}{4}$ , SW $\frac{1}{4}$ , Sec. 3, T53N, R94W) and are in the upper strata of the Morrison.

The material from Utah, composed mostly of casts, was collected from the Brushy Basin Member, the upper member of the Morrison Formation (Fig. 2), at a locality east of Last Chance Road (Sec. 6, T245, R6E; Jensen, 1966) known as the Fremont Junction site, from the east flank of Mt. Ellen (NE $\frac{1}{4}$ , SW $\frac{1}{4}$ , Sec. 25, T31S, R11E) in the northern Henry Mountains, and from Mussentuchit Wash (Sec. 35, T24S, R6E) approximately 5 km southwest of the Fremont Junction site (Fig. 1).

UPPER JURASSIC	MORRISON	Brushy Basin Member
	FORMATION	Salt Wash Member 1
		Tidwell Member

Fig. 2. Chart illustrating the nomenclature of the members of the Morrison Formation at localities 1, 2, and 3 (see Fig. 1).

The specimens are weathered, but the pith and cortex are generally well preserved, whereas the vascular tissues are often not. The permineralized specimens were photographed and thin-sectioned using standard thin-sectioning techniques. They were then studied and photographed through incident and laser light microscopes.

## 3. Systematics

Order FILICALES

Family INCERTAE SEDIS

*Solenosteleptis leithii* Tidwell et Skog, *sp. nov.*  
(Plates I–III; Figs. 3 and 4)

*Holotype*: Brigham Young University 5202 (Plate I, 3, 7, 8).

*Paratypes*: Brigham Young University 5200, 5201, 5203–5211 (Plate I, 1, 2, 4–6; Plates II, III).

*Repository*: Department of Geology, Brigham Young University, USA.

*Type locality*: Holotype: Steiner site near Greybull, Wyoming. Paratypes: Scott's site, Last Chance Road, Mt. Ellen, and Mussentuchit Wash, Utah localities.

*Stratigraphic horizon*: Morrison Formation.

*Age*: Late Jurassic.

*Etymology*: The specific name honors Mr. Leith Tidwell of Provo, Utah for his diligence in collecting many of these specimens and then volunteering to thin-section them for study.

**Diagnosis:** Rhizome branching, stems dorsiventral, 10 or more mm in diameter; solenostelic, leaf traces C-shaped, mostly single ranked, sometimes two ranked; internodes short in length; leaf gaps short; pith heterogeneous, parenchymatous in middle and sclerenchymatous near inner endodermis; xylem exarch, composed only of tracheids; inner cortex homogeneous, sclerenchymatous, 0.5 mm across; middle cortex homogeneous, parenchymatous, 0.5–1 mm wide; outer cortex homogeneous, parenchymatous, 5 or more mm wide; epidermis unknown; roots arise singly from stele.

**Description:** The rhizome, which appears to be a creeping, more or less dorsiventral type, branches laterally with the subsequent branch developing laterally to upwards of a 50° angle to the main axis of the rhizome (Plate I, 1, 4; Plate II, 7; Fig. 3). Relatively large leaf traces are produced in single, or rarely two ranks, upon the surface of both the main axis and the branch (Plate I, 2; Fig. 3). The overall diameter of the fern rhizome is more than 10 mm, since the outer cortex is only partially present due to the erosion of the outermost portion of the stem (Plate I, 3). Rhizomes are broken with the longest specimen being 20 mm long, and have several leaf and root scars exposed on the cortical surfaces. Root scars on the rhizome surface are 1 mm in diameter (Fig. 3). Due to weathering, the epidermis and, thus the epidermal hairs, are absent.

**Pith:** The pith measures 3–5 mm across and consists of a parenchymatous center and sclerotic outer layers, which are similar to those in the inner cortex, occurring next to the inner endodermis (Plate II, 1). The central cells of the pith are not sclerotized. They are thin-walled and larger than the cells around the pith margins (Plate I, 8). Some of these larger cells contain rounded bodies like those Kershaw (1910) suggested as starch grains. As pointed out by Kershaw (1910), they are similar to those in living ferns such as *Microlepia*. These central cells are round, sometimes elongated radially, and fusiform to hexagonal in shape in longitudinal section (Plate I, 7). Cell diameter of the central cells varies from 50 to 70  $\mu\text{m}$  and length from 400 to 600  $\mu\text{m}$ . Around the edge of the central cells are several layers of smaller thin-walled cells that form a transition between the central cells and the outer sclerotic layers. Intercellular spaces are common between these cells.

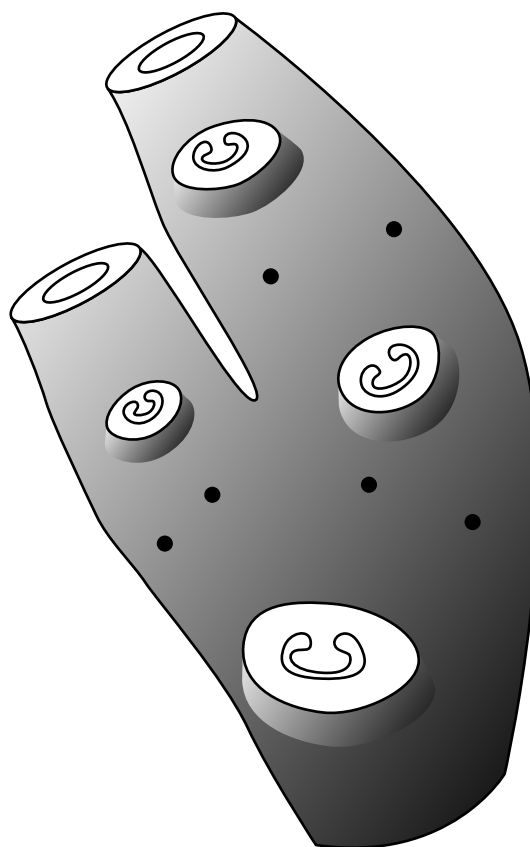


Fig. 3. Diagrammatic representation of a camera lucida drawing of branching in *Solenostelepteris leithii* Tidwell et Skog, *sp. nov.* Note the position of the leaf traces (dots = root traces).  $\times 3$ .

At the leaf gap, the cells are radially aligned. Because of their apparent fragility, these smaller cells are often not preserved. The sclerotic layer around the periphery of the pith cells is 4–6 cells in width (Plate II, 3, 4). The diameter of these cells varies from 50 to 70  $\mu\text{m}$ .

**Stele:** The stele is an amphiphloic siphonostele whose continuity is interrupted by departing leaf traces. The gaps thus produced are short and immediately close. The poorly preserved xylem is 2–4 cells in width (Plate II, 5). Both the protoxylem and metaxylem elements have scalariform thickenings (Plate II, 6). The exarch protoxylem elements are 10–20  $\mu\text{m}$  across, whereas the metaxylem tracheids measure 25–40  $\mu\text{m}$  in diameter and over 725  $\mu\text{m}$  in length (Plate III, 6, 7). Xylem parenchyma is absent.

The xylem is lined on both sides by parenchyma cells comprising the xylem sheath. The tissue is 1–3 cells wide, where preserved (Plate III, 6, 8), although it is mostly crushed. These cells are elongated, but blocky in longitudinal section and 20–25  $\mu\text{m}$  across in transverse section. Simple pits and spiral thickenings are present in the relatively thin walls (Plate III, 8a).

The phloem occurs on both sides of the xylem but is generally not preserved (Plate II, 1). Where preserved, it is 2–3 cells in width with very thin-walled cells that are 20–30  $\mu\text{m}$  in diameter (Plate III, 8b).

The pericycle and endodermis are too poorly preserved to be analyzed (Plate II, 1). They are not readily discernible, although part of the darkened zone of tissue lying outside and inside of the phloem probably represents these tissues.

*Cortex:* The inner cortex is 4 to 7 cells wide (Plate I, 5, 6; II, 2). The sclerotized cells are round to angular and of various sizes in cross section. They vary from 50–70  $\mu\text{m}$  across to 25–50  $\mu\text{m}$  long. In longitudinal section, these elongated cells taper and some contain starch-like inclusions. Several root traces can be observed in the inner cortex after leaving the stele.

#### PLATE I

*Solenostelepteris leithii* Tidwell et Skog, *sp. nov.*

- 1, 2. Specimens illustrating the branching and C-shaped trace (arrow)
  1. 5200.  $\times 1$ .
  2. 5201.  $\times 3$ .
3. Transverse section through the rhizome, note the root traces (arrows). Holotype: 5202.  $\times 3.7$ .
4. Transverse section showing the branching; 5203.  $\times 5$ .
- 5, 6. Transverse section showing the departing leaf trace and subsequent leaf gap. *a* = inner cortex of stem, *b* = inner cortex of trace, *c* = central parenchymatous pith of trace, *d* = trace vascularization, *e* = trace middle cortex, *f* = trace outer cortex; 5204.
  5.  $\times 7$ .
  6.  $\times 28$ .
7. Longitudinal section through parenchymatous central pith showing the elongated structure of the pith cells; 5202.  $\times 20$ .
8. Close-up of transverse section parenchymatous pith cells of the central pith; 5202.  $\times 75$ .

#### PLATE II (see p. 290)

*Solenostelepteris leithii* Tidwell et Skog, *sp. nov.*

1. Transverse section showing the internal structure of a rhizome. *a* = inner parenchymatous pith, *b* = inner layers of the outer portion of the pith, *c* = outer sclerenchymatous layers of the pith, *d* = inner endodermis, pericycle, and phloem, *e* = xylem, *f* = outer xylem sheath, *g* = outer endodermis, pericycle, and phloem, *h* = inner cortex, *i* = middle cortex, *j* = outer cortex; 5205.  $\times 20$ .
2. Transverse section of the stem illustrating the cortices. *a* = pith, *b* = vascularization, *c* = inner cortex, *d* = middle cortex, *e* = outer cortex; 5207.  $\times 25$ .
- 3, 4. Transverse section of close-ups of sclerenchymatous tissues of the outer pith; 5205.  $\times 160$ .
5. Close-up of a transverse section of the xylem illustrating the tracheids; 5205.  $\times 40$ .
6. Close-up of a longitudinal section of the xylem showing the scalariform thickenings of the tracheid walls (arrows); 5206.  $\times 40$ .
7. Longitudinal view of a rhizome showing a departing branch and its gap, note the root traces (arrows); 5206.  $\times 4$ .
8. Close-up of a transverse section showing a departing root trace (arrow), inner, middle, and outer cortices; 5207.  $\times 40$ .

#### PLATE III (see p. 291)

*Solenostelepteris leithii* Tidwell et Skog, *sp. nov.*

1. Longitudinal section through part of the middle section of the pith showing the elongated parenchyma cells; 5208.  $\times 50$ .
2. Close-up of a transverse of the cells of the outer cortex; 5209.  $\times 100$ .
- 3, 4. Longitudinal section through outer cortex.
  3. Close-up; 5210.  $\times 100$ .
  4.  $\times 33$ .
5. Transverse section of root in outer cortex; 5211.  $\times 25$ .
6. Enlargement of a transverse section through xylem. *a* = protoxylem, *b* = metaxylem, *c* = outer xylem sheath; 5205.  $\times 133$ .
7. Longitudinal section xylem. *a* = protoxylem, *b* = metaxylem (arrow indicates direction of outer edge of stem; 5211).  $\times 165$ .
8. Transverse section of outer xylem sheath (*a*) and outer phloem (*b*). Note spiral thickenings of sheath cells; 5205.  $\times 66$ .

PLATE I

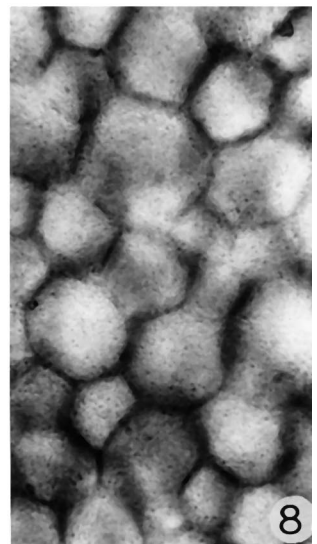
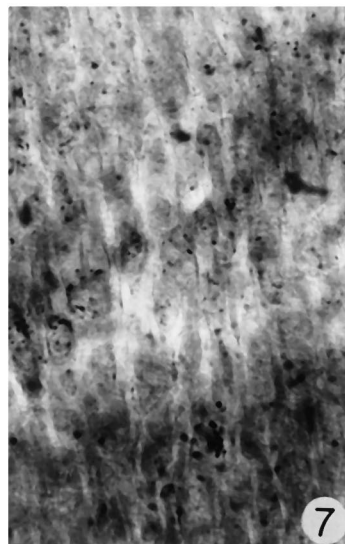
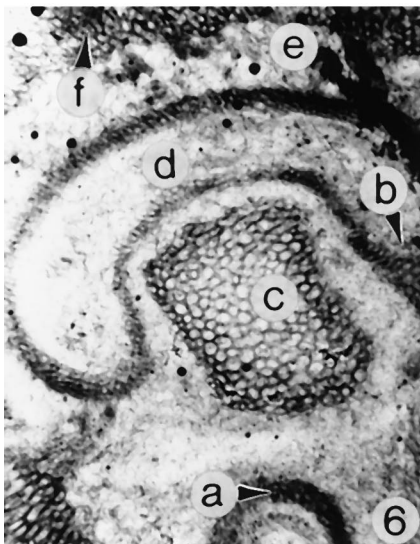
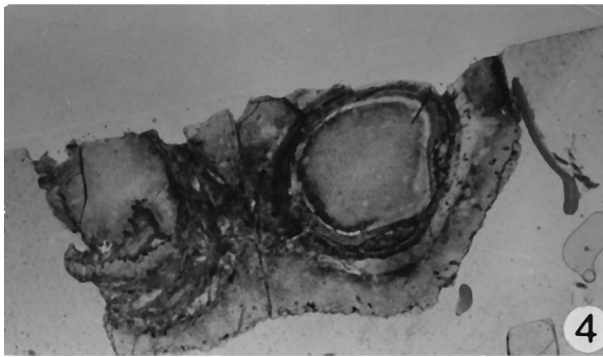
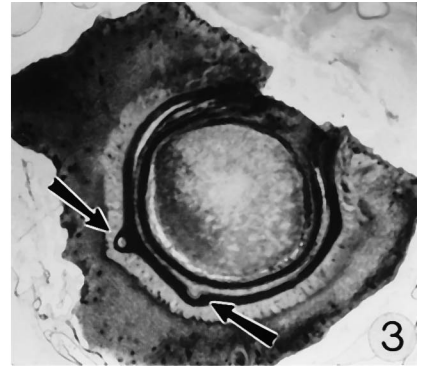
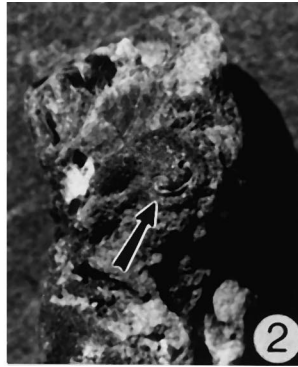
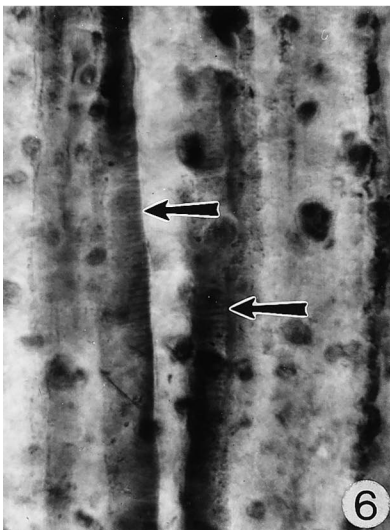
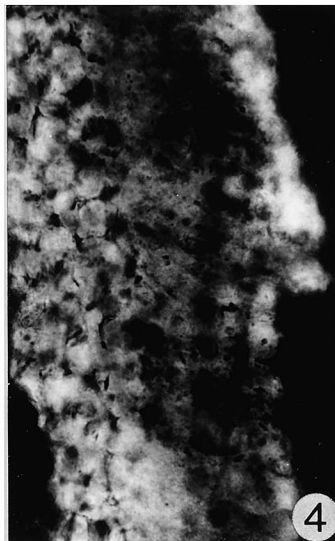
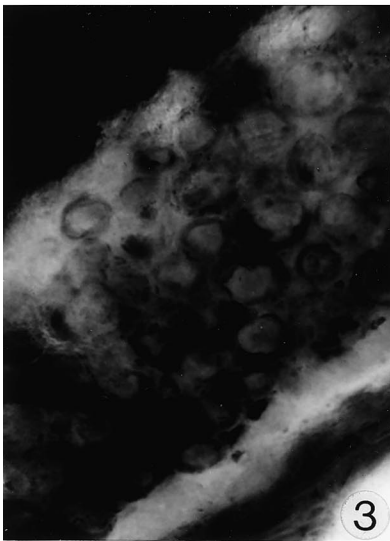
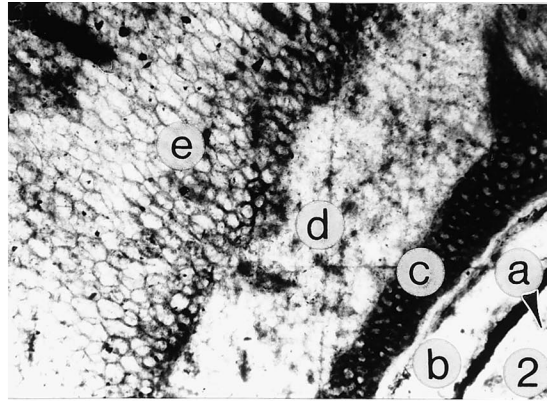
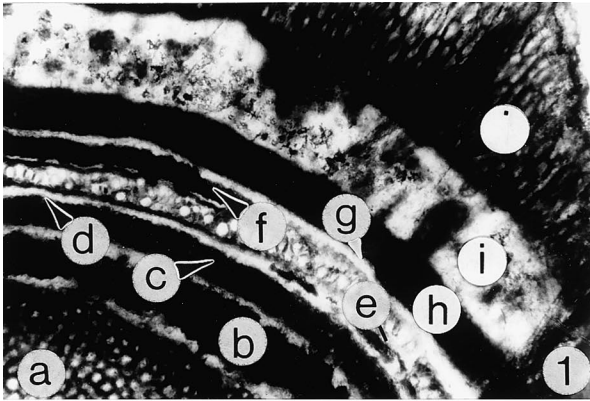
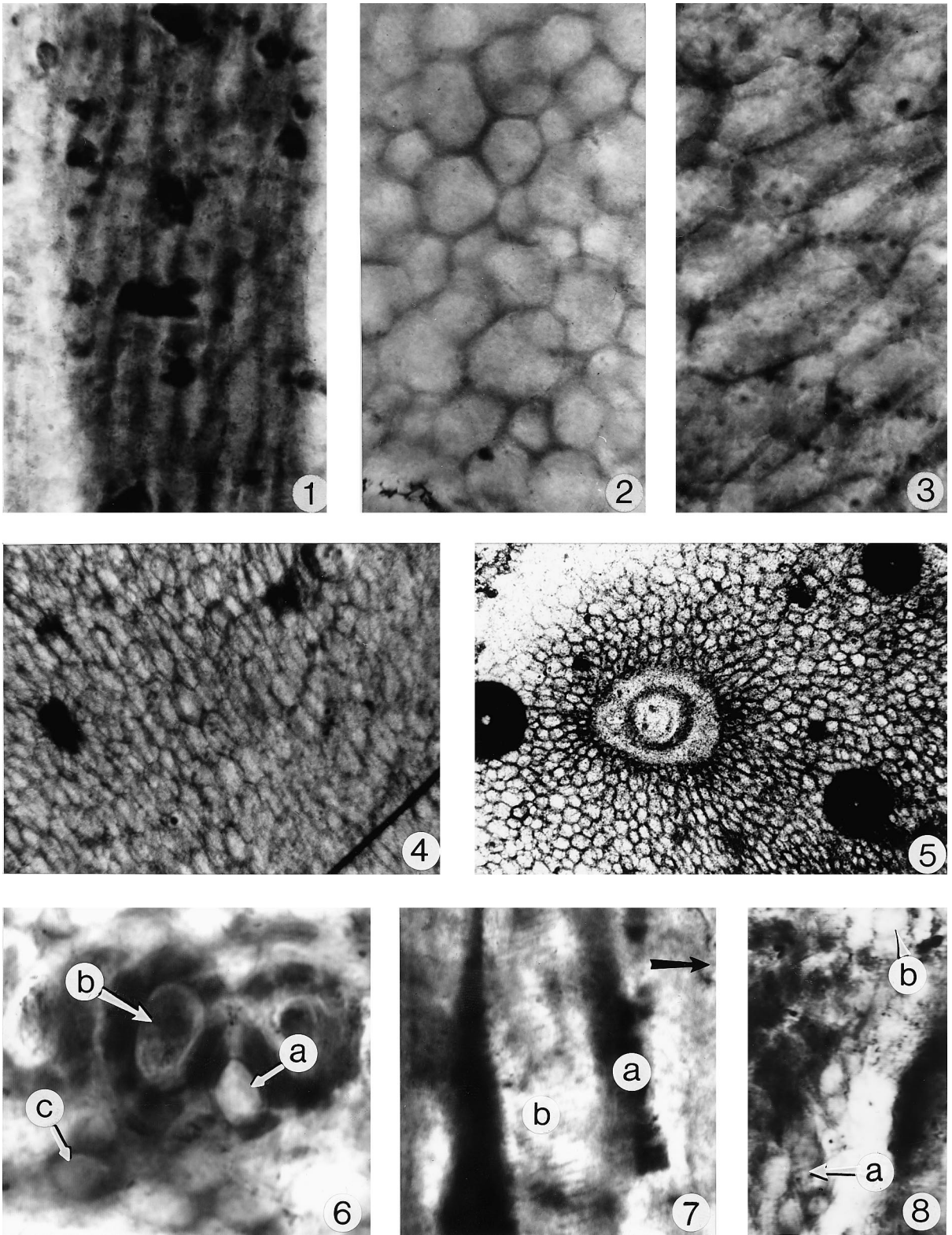


PLATE II



For description see p. 288.

PLATE III



For description see p. 288.



Small intercellular spaces occur between the generally poorly preserved thin-walled, isodiametric parenchyma cells of the middle cortex. The cells are 20–50  $\mu\text{m}$  in width. There are hints of lacunae in this tissue.

The outer cortex consists of compact cells that are round to hexagonal in shape and sometimes elongated radially (Plate II, 2; Plate III, 2–4). The cells are 70–100  $\mu\text{m}$  in diameter and, longitudinally, are both fusiform and hexagonal in shape. They are 260–350  $\mu\text{m}$  in length. Cell contents and intercellular spaces are lacking. Although thin-walled, these cortical cells have thicker walls than those of the pith. Cells of the innermost layer of the outer cortex are radially shortened where they contact the middle cortex.

**Leaf trace:** The leaf trace departs as a single continuous vascular strand so that in section it is similar in shape to a horse-shoe or an arch (Plate I, 5, 6; Figs. 3 and 4). This curved strand is so attached to the stele that its concavity generally faces towards the rhizome apex along the median dorsiventral plane of the rhizome, somewhat directly as in *Dennstaedtia punctiloba* and *Pteris incisa*. The leaf trace appears to be marked from the rest of the solenostele a little distance before it departs. The C-shaped xylem trace is thin, 1–3 tracheids wide, near its center and wider, 4–5 tracheids thick, near its tips. Although protoxylem cannot be discerned, the protoxylem elements occurring to the outside of the metaxylem in the xylem strand next to the leaf gap strongly indicate that the leaf trace can only be exarch. Phloem and the endodermides are not preserved, but they appear to have sheathed the xylem portion of the leaf trace. The gap that forms is short and closes almost immediately upon separation of the trace (Fig. 4). The leaf gap includes parenchyma cells extending from the pith and is lined with the outer sclerotic layer of the pith.

With the departure of the leaf trace, the parenchyma of the middle and outer cortex and the sclerenchyma of the inner cortex becomes continuous with the corresponding tissues of the pith through the leaf gap. The xylem, phloem, endodermides, and various cortices of the leaf trace are also continuous with these tissues in the stem. The leaf traces are encircled by the cortical tissues as they pass outward. As the trace leaves, it is surrounded

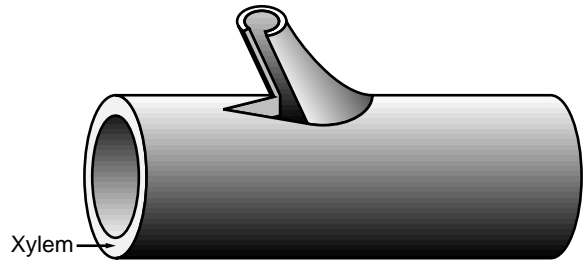


Fig. 4. Diagrammatic reconstruction of *Solenosteleptis leithii* Tidwell et Skog, *sp. nov.* illustrating the origin of the leaf trace. Only the xylem is shown (not to scale).

abaxially by the inner cortex and adaxially by the sclerotic layers of the pith which line the concavity of the vascular strand of the trace (Plate I, 5, 6). The central part of the concavity of the trace contains large parenchyma cells similar to the central cells of the pith, whereas the outer portions of the leaf base has tissues equal to those of the middle and outer cortices of the stem. No epidermis or any possible outer sclerotic layers of the petiole are preserved. Distally, the vascular strand of the petiole undergoes some changes. Further up the petiole, the C-shaped xylem strand divides into five separate strands and the sclerenchyma in the concavity of the xylem strand divides into two.

**Branching:** Before branching begins, the stele is completely round and is often, but not always, interrupted by a departing leaf trace (Fig. 3). The resultant leaf gap, if present, then closes. Within a short distance of the possible departing leaf trace and towards the stem apex, branching of the rhizome is initiated. The rhizome flattens, then begins separating by subsequent invagination of the tissues until the main stem and its branch are completely separated and both are round again (Plate I, 4; Plate II, 7). After separation is complete, leaf traces are almost immediately produced in the branch and often in the main stem as well (Fig. 3).

**Roots:** Adventitious roots depart from the stele at the point of leaf trace departure or lower (Plate II, 7, 8). Two to five root traces were observed leaving the stele at different levels immediately below the separation of the leaf trace. The root traces arise obliquely from the stele towards the stem apex at approximately 45°, they then arch strongly outward, growing horizontally through the middle and outer



cortices to the outside. The roots are poorly preserved, but in cross section appear to be protostelic with an elliptical shaped xylem that is diarch (Plate III, 5). The root cortex consists of an inner zone of thin-walled cells and relatively broad, sclerotic outer layers that connect with the inner cortex of the stem. The epidermis is not preserved on these organs.

***Solenostelepteris medlynii*** Tidwell et Skog, *sp. nov.* (Plate IV)

**Holotype:** Brigham Young University 5212 (Plate IV, 1, 6–8).

**Paratype:** Brigham Young University 5213 (Plate IV, 2–5).

**Locality:** Holotype: Steiner site near Greybull, Wyoming. Paratype: Mt. Ellen locality, Utah.

**Stratigraphic horizon:** Morrison Formation.

**Age:** Late Jurassic.

**Etymology:** This species honors Dr. David A. Medlyn of Utah State University for his significant contribution to this study and the study of fossil plants of the Morrison Formation in general.

**Repository:** Department of Geology, Brigham Young University, USA.

**Diagnosis:** Rhizomatous stems round, 8 or more mm in diameter; solenostelic; pith homogeneous, parenchymatous, large cells in middle surrounded by layers of smaller cells; xylem, only tracheids present; leaf gaps short; inner cortex parenchymatous; middle cortex parenchymatous, composed of large and small cells; outer cortex homogeneous, parenchymatous, thick walled, round to irregularly shaped cells; epidermis not preserved.

**Description:** The specimens are unbranching and incomplete due to weathering and non-preservation. They are 7–8 mm in width and composed only of stems (Plate IV, 1). The stems are round and lack the outermost tissues. No root or leaf traces are present on the specimens.

**Pith:** The pith is homogeneous and measures 4–5 mm across. It is composed of large, thin-walled parenchyma cells in its middle (Plate IV, 4) and outer layers of smaller, thin-walled cells that are crushed and very rarely preserved. The central cells are generally isodiametric with diameters between 70 and 120  $\mu\text{m}$ .

**Stele:** The stele is 0.5 mm wide and represented by a very poorly preserved amphiphloic siphonostele. The xylem, where preserved, is 3–4 cells wide. The metaxylem elements are 25  $\mu\text{m}$  in diameter with mostly scalariform, occasionally reticulate thickenings (Plate IV, 3). Protoxylem cannot be determined.

The phloem, pericycle, and endodermis were not preserved and, therefore, cannot be analyzed. In general, all that can be observed is the area where these tissues had occurred. External and internal dark layers, where the endodermis should be, has been designated this tissue although no cells with casparian strips were observed.

**Cortex:** The cortical tissue is differentiated into an inner, middle, and outer cortex (Plate IV, 2).

The inner cortex is generally not preserved. It varies in width from 0.5 to 0.75 mm and is usually 3–4 cells wide. The thin-walled, parenchymatous cells are somewhat elongated tangentially and most often crushed (Plate IV, 5).

The middle cortex is 0.75–1 mm across in transverse section and consists of large cells interspersed with smaller ones that are sometimes elongated in cross-section. This cortex, often poorly preserved, has an uneven contact surface with the inner cortex. The larger cells measure 18–20  $\mu\text{m}$  across, whereas the smaller ones are 10–13  $\mu\text{m}$  in diameter. Intercellular spaces, 5  $\mu\text{m}$  wide, also occur.

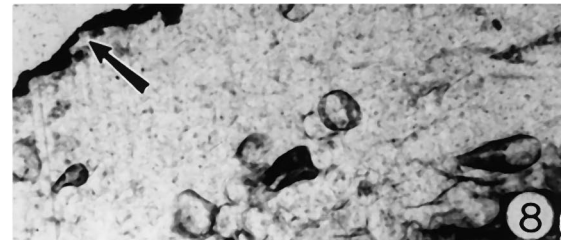
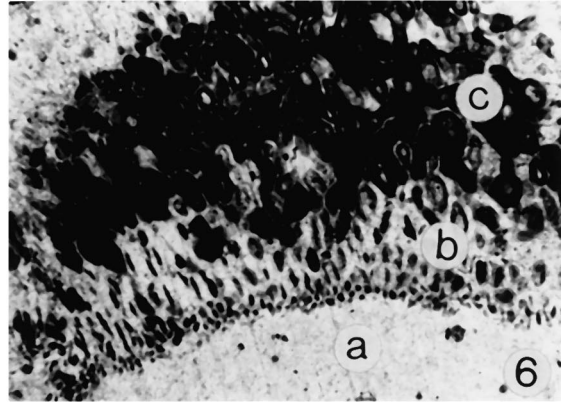
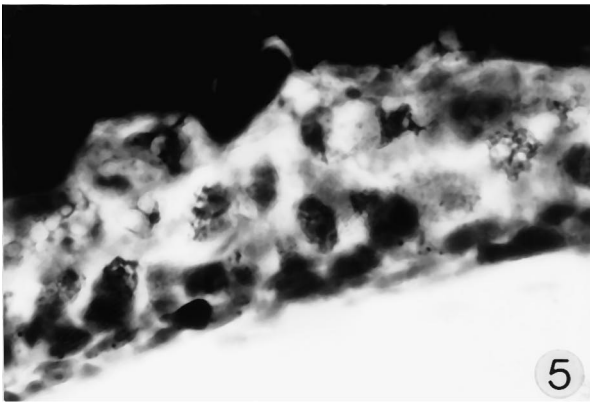
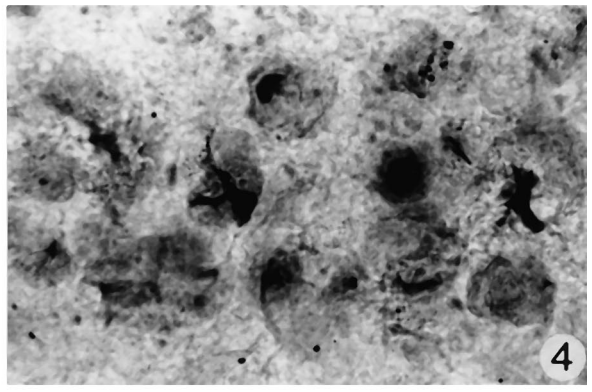
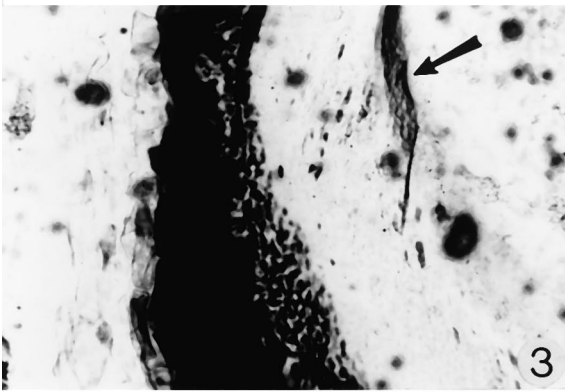
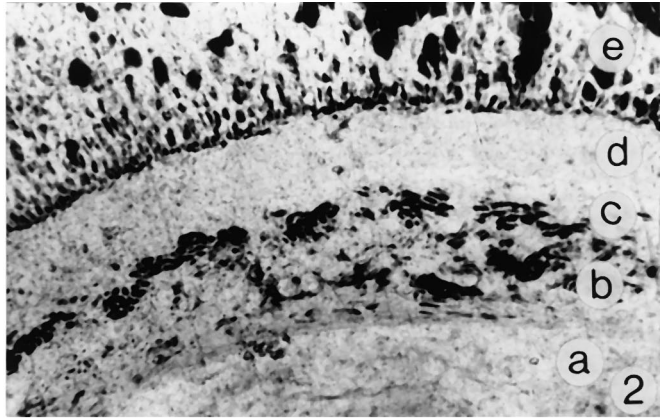
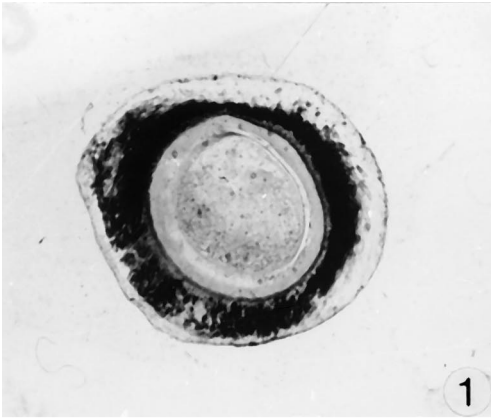
The outer cortex is incomplete due to weathering (Plate IV, 6–8). It is over 2.5 mm in width as preserved. The thick-walled cells of the outer cortex are round to irregularly shaped, although some are elongated in conjunction with the leaf gap. They measure 15  $\times$  30  $\mu\text{m}$  across with their walls being 5  $\mu\text{m}$  wide.

#### 4. Comparisons and discussion

The solenostelic (amphiphloic siphonostelic) nature of the rhizomes, the exarch placement of the protoxylem points in *S. leithii*, mostly scalariform tracheids, and the dimensions of the rhizomes, relate these specimens from the Morrison Formation to the form genus *Solenostelepteris* Kershaw, 1910.

Like most species of *Solenostelepteris*, e.g. *S. japonica* Kershaw, 1910, *S. nipanica* Mittre, 1959, and *S. sahnii* Mittre, 1959, neither *S. medlynii* nor

PLATE IV



*S. leithii* have preserved epidermal hairs (Table 1). Thus, comparison to the one species of *Solenostelopteris* with epidermal hairs, *S. sp.* Sharma et Bohra, 1976, and those of *Loxomopteris*, *L. loxsomoides* (Ogura) Nishida et Nishida, 1982, and *L. anasilla* Skog, 1976, are incomplete. However, because of their other anatomical similarities, all species are included in these comparisons.

*Solenostelopteris leithii* differs from *S. medlynii* in having a sclerotic inner cortex and sclerenchymatous outer layers of pith; both are only parenchymatous in *S. medlynii*. Scalariform and some reticulate tracheids occur in *S. medlynii*, whereas they are only scalariform in *S. leithii*. The rhizomes branch in *S. leithii*, but branching was not observed in specimens of *S. medlynii*.

A sclerified pith occurs in *S. japonica*, *S. nipanica*, and *L. anasilla*. *Loxomopteris loxsomoides*, *S. japonica*, and *S. sp.* each have a sclerified inner cortex, which is mixed in *L. anasilla*. All these features are not represented in the specimens of *S. medlynii* and, although *S. leithii* has a sclerified inner cortex, its pith is only partially sclerified. The sclerotic outer cortex of *L. anasilla* is also unlike the parenchymatous outer cortices of both *S. medlynii* and *S. leithii*. The lateral branching in *S. leithii* is not like the branching in *S. japonica* and *S. sahnii*, which occurs in the same plane as the trace. Xylem parenchyma is also present in *S. sahnii* and *S. japonica*, but lacking in the Morrison specimens. *Solenostelopteris sp.* has spiral as well as scalariform tracheids, whereas the tracheids of the other species are entirely scalariform with the exception of *S. medlynii*, which has some that are reticulate (see Table 1 for summary).

The species of *Solenostelopteris* have been compared to various living forms (Gwynne-Vaughan,

1901, 1903). A solenostele with exarch maturation of the xylem and mainly scalariform tracheids occurs in several families. Unfortunately, information concerning xylem maturation is not consistently reported, especially within large families such as Dennstaedtiaceae and Pteridaceae, and maturation patterns may change during developmental stages (Bierhorst, 1971). Kershaw (1910) considered *S. japonica* comparable to taxa of the Dennstaedtiaceae, particularly *Microlepia*. Sharma and Bohra (1976) noted their species of *Solenostelopteris* was similar to *Loxsomopsis*, *Dennstaedtia*, and *Marsilea*, but differed from them by the structure of the epidermal hairs, the manner of ground tissue, and the structure and mode of leaf trace development. On the basis of its outer cortex and characteristic hairs, *Loxsomopteris* was assigned to the Loxsomaceae (Skog, 1976). In *Pteris ludens*, *Jamesonia imbricata*, and *Loxsoma* species, the leaf traces face directly toward the apex (Bower, 1926). In the latter genus the leaves are inserted along the upper surface in a single median row similar to the fossils. Many other fern taxa have this same general character as well. Another feature, short leaf gaps similar to those in *S. leithii* is not a good character for determining familial relationships as short gaps occur in several different fern families, e.g. Dipteridaceae and Dennstaedtiaceae.

Without fronds, sporangia, and epidermal appendages, the affinities of *S. medlynii* and *S. leithii* remain uncertain. The two species are included in *Solenostelopteris* because they have, "Rhizomes of fossil ferns, vascular system a solenostele", which, as pointed out by Ogura (1930), is the diagnosis of Kershaw (1910, p. 689) for this form genus.

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#### PLATE IV

*Solenostelopteris medlynii* Tidwell et Skog, *sp. nov.* (all transverse sections).

1. Stem (Holotype: 5212).  $\times 4.5$ .
2. Close-up of a portion of a stem. *a* = inner pith, *b* = outer pith, *c* = vascularization, *d* = inner and middle cortex, *e* = outer cortex; 5213.  $\times 15$ .
3. Illustration of one tracheid with reticulate thickenings (arrow); 5213.  $\times 15$ .
4. Enlargement of cells of inner pith; 5213.  $\times 60$ .
5. Enlargement of the inner cortex; 5213.  $\times 60$ .
6. Cortices. Inner cortex (*a*), middle cortex (*b*), and outer cortex (*c*); 5212.  $\times 15$ .
7. Cortices. Inner cortex (*a*), middle cortex (*b*), and outer cortex (*c*); 5212.  $\times 45$ .
8. Outer cortex. Note the eroded edge of the specimen (arrow); 5212.  $\times 45$ .

Table 1  
Comparison of *Solenostelopteris* and *Loxosomatopteris* species

	<i>S. leithii</i> Tidwell et Skog, sp. nov.	<i>S. medynii</i> Tidwell et Skog, sp. nov.	<i>S. japonica</i> Kershaw, 1910	<i>S. niponica</i> Vishnu-Mittre, 1958	<i>S. sahani</i> Vishnu-Mittre, 1958	<i>S. sp.</i> Sharma et Bohra, 1976	<i>L. loxosomoides</i> (Ogura) Nishida et Nishida, 1982	<i>L. anasilla</i> Skog, 1976
Size (diameter; mm)	10+	8+	?; 3–3.5 cm long	1	(6–8) × (2–3) elliptical	(1.1 × 1.6)–(2.8 × 3.5)	6–11	5; 2 cm long
Branching	Lateral	?	Same plane as leaf trace	?	Same plane as leaf trace	?	?	?
Pith	Parenchymatous central cells, sclerenchymatous outermost layers, layers of small, thin-walled cells form transition between central cells and sclerotic layers	Parenchymatous, central cells large outer layers small, thin-walled cells	Sclerized, central larger, less sclerized than along edge, contain possible starch, irregular parenchyma layer in pith	Sclerized, hexagonal, radially elongated cells with air spaces, irregular parenchyma layer 1–2 cells wide between pith and xylem	?	Thin-walled parenchyma	Thick-walled cells, possible starch	Sclerotic pith
Xylem	General — 2–4 tracheids wide, no parenchyma PX — exarch, scalariform MX — scalariform	3–4 tracheids wide, no parenchyma Not preserved Scalariform, some reticulate	1–8 nm, 1–2 tracheids wide, xylem parenchyma Exarch grouped, scalariform Scalariform	1–3 tracheids wide, xylem parenchyma Exarch, scattered singly, or grouped ?	4–5 tracheids wide, xylem parenchyma Exarch (?), scattered Scalariform	1–3 tracheids wide, no parenchyma Exarch, grouped 4–6 cells, spiral, scalariform Spiral, scalariform	1–3 tracheids wide	2–3 tracheids wide
Cortex	Outer — parenchymatous, round to hexagonal, elongated vertically, no air spaces Middle — parenchymatous, thin-walled, isodiametric, intercellular spaces Inner — Sclerenchymatous, round to angular, taper longitudinally	Parenchymatous, thick-walled Parenchymatous, large and small cells, intercellular spaces Parenchymatous, thin-walled	Hexagonal cells; no intercellular spaces Several rows parenchyma with air spaces 3 cells wide, sclerenchymatous	Inner cells darker Poorly preserved Parenchymatous	5–6 cells, tangentially elongated, black substances 4 cells, thick-walled large, polygonal cells Thin-walled cells	Large, hexagonal, thin-walled cells NA Inner few layers, narrow, thick-walled cells	Thin-walled, large parenchyma, hair bases NA Thick-walled cells	Dense sclerenchyma NA Mixed sclerenchyma and parenchyma

Table 1 (continued)

	<i>S. leithii</i> Tidwell et Skog, <i>sp. nov.</i>	<i>S. medlynii</i> Tidwell et Skog, <i>sp. nov.</i>	<i>S. japonica</i> Kershaw, 1910	<i>S. nipanica</i> Vishnu-Mittre, 1958	<i>S. sahani</i> Vishnu-Mittre, 1958	<i>S. sp.</i> Sharma et Bohra, 1976	<i>L. loxomoides</i> (Ogura) Nishida et Nishida, 1982	<i>L. anastilla</i> Skog, 1976
Epidermal hairs	?	?	?	?	?	Uniseriate, multicellular, cylindrical	Conical, multicellular base, uniseriate tip	Bristle-like multicellular base, tapering, uniseriate tip
Leaf trace	C-shaped, vascular strand surrounded by sclerotic cells	?	C-shaped (?)	C-shaped, slightly incurved margins	C-shaped	Large C-shaped	?	C-shaped (?)
Leaf gaps	Short	?	?	?	Closed in internodal region	Broad gaps	?	?
Roots	Round; elliptic stele, diarch	?	Diarch	Appears diarch	Diarch, oval	Diarch	Smaller, thick-walled cortical cells, but poorly preserved	Diarch
Age	Late Jurassic	Late Jurassic	Late Cretaceous	Jurassic	Jurassic	Jurassic	Late Cretaceous	Early Cretaceous
Geogr. distr.	Wyoming and Utah, USA	Wyoming and Utah, USA	Japan	India	India	India	Japan	Maryland, USA

## Acknowledgements

The authors wish to thank Jerry Anderson, A. Daniel Simper of Holbrook, AZ, the late Homer Behunin of Redmond, UT, James Jensen of Provo, UT, Mr. and Mrs. Paul Rechten of Harvard, IL, Mr. and Mrs. Walter Scott of Powell, WY, Richard Steiner of Worland, WY, Drannan and Leith Tidwell of Provo, UT, Mr. Steve Hatch of Hanksville, UT, and Dr. David A. Medlyn of Utah State University, for donating specimens and/or assistance in collecting, and George Munzing of Provo, UT, for his assistance with thin-sectioning of the specimens.

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