A new species of the marattialean fern *Scolecopteris* (Zenker) Millay from the uppermost Permian of Guizhou Province, south-western China

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Several isolated marattialean synangia and sporangia are reported from coal balls collected from Coal Seam No.1 (C605) in the uppermost Permian Wangjiazhai Formation in Guizhou Province, south-western China. The synangia are radially symmetrical with diameters between 0.8 and 1.2 mm and are 1.7 mm long, consisting of 3–4 elongate sporangia that are fused basally, free distally and possess a pointed apex. The outer-facing sporangial wall is 4–5 cells thick and conspicuously differentiated. Spores are trilette, have a granular ornamentation and are nearly round equatorially with a diameter of 55–60 µm. Comparisons with other anatomically preserved Palaeozoic marattialean synangia from the Euramerican and Cathaysian floras permit their assignment to the genus of *Scolecopteris* (Zenker) Millay. In this species the thick, outer-facing sporangial walls and large trilette spores are features consistent with those of the Oliveri Group within *Scolecopteris*, a group that has previously been considered primitive within this genus. Distinctions from all other previously recognized species within the Oliveri Group lead to the creation of a new species, *S. guizhouensis* sp. nov. This species is the youngest of the reported species of *Scolecopteris* recognized from the Euramerican and Cathaysian floras, and provides important evidence on the organization of marattialean ferns from the Upper Permian strata of south China. © 2006 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2006, 151, 279–288.


INTRODUCTION

Marattialean ferns are one of the most important elements in the late Palaeozoic Cathaysian floras of China (Li et al., 1995; Shen, 1995). From these floras a large number of impression-compression taxa including vegetative and reproductive organs have been documented (‘Gu et Zhi’, 1974; Zhu, Hu & Li, 1984; Yang, 1986; Wan & Basinger, 1992; Gao & Thomas, 1993; Du & Mei, 1994; Yao & Liu, 1994; Shen, 1995; Wu, 1995; He, Liang & Shen, 1996; Yang, Wang & Sheng, 1996; He & Sun, 1998; Sun & Deng, 1999; Liu, Li & Hilton, 2000, 2001), as well as several kinds of permineralized stems conforming to the genus *Psaronius* Cotta (‘Gu et Zhi’, 1974; Tian, Li & Guo, 1992; Li & Cui, 1995; Tian et al., 1996). However, anatomically preserved marattialean fertile organs from the Cathaysian floras are less well-known, in contrast to reports of seven genera and more than 30 species documented to date from the Palaeozoic floras of Europe and North America.

In China, fertile marattialean organs have been recorded from the Lower Permian Taiyuan Formation of Northern China and from the Upper Permian Xuanwei Formation of southern China. Two species of *Scolecopteris* have been described from the Taiyuan Formation, each showing synangial, sporangial and spore morphology; *S. sinensis* Zhao L. M. (Zhao, 1991), and *S. shanxiensis* Wang S.J et al. (Wang, Li & Tian,
Those from the Xuanwei Formation are less well characterized, but show gross morphology of the synangia and sporangia allowing their determination as *Eoaangiopteris* sp. and *Scolecopteris* sp. (Hilton et al., 2004). These accounts from the Xuanwei Formation present a tantalizing glimpse of marattialean reproductive features from the Upper Permian floras of southern China, but in this example preservation and taphonomy effectively restrict the recovery of detailed botanical information on these taxa (Hilton et al., 2004).

In this paper, we describe a number of anatomically preserved marattialean synangia and sporangia that belong to a single species. Specimens occur in coal balls from the Upper Permian Wangjiazhai Formation in Guizhou Province, southern China. These coal balls contain abundant and well-preserved permineralized fossil plants, although previous studies conducted on the assemblage have not reported fertile marattialean organs (for summary see Tian & Zhang, 1980; Tian et al., 1996). This account represents the first accurately characterized, anatomically preserved fertile marattialean species from the Upper Permian Cathaysian floras of China. The specimens we detail are important as coal balls from the Wangjiazhai Formation represent the stratigraphically youngest occurrence of permineralized plants from the Permian of China, and as such provide important insights into the structure and identification of marattialean ferns from the latest Palaeozoic floras of Cathaysia.

**MATERIAL AND METHODS**

The species investigated consists of several isolated synangia and sporangia preserved in a single coal ball from Coal Seam No.1 (C605) in the uppermost part of the Wangjiazhai Formation in Shuicheng, western Guizhou Province, south-western China. The age of this Formation is late Late Permian or P2 : 2 in the Chinese lithostratigraphical system, corresponding to the Changhsingian stage of the Upper Permian strata (Tian et al., 1996). Fossil plants are abundant in coal balls from this locality, as summarized by Tian & Zhang (1980) and Tian et al. (1996). Detailed investigations of a number of individual taxa have been reported previously, including lycopsids (Guo, 1986, 1994; Tian & Guo, 1987; Wang, Tian & Chen, 2002), Osmundaceous ferns (Li, 1983, 1993), seed plants (Li, 1986a,b, 1991, 1992b) and presumed gigantopterids (Li, 1992a, 1994). However, these accounts represent a small diversity of the taxa present within Wangjiazhai coal balls (S–J. Wang, pers. observ.) suggesting that major discoveries remain to be made from this assemblage.

The coal ball was cut into two slabs with two surfaces numbered as GSW1-0001A and GSW1-0001B, respectively; each surface was prepared by the peeling method (Galtier & Phillips, 1999) and peels were mounted on slides using Eukitt. The slides were observed and photographed using a Nikon microscope under transmitted light with a Nikon Coolpix 990 digital camera. Images were adjusted using Adobe Photoshop (v.8) and plates constructed using CorelDRAW (v.12). The coal ball and peels, numbered as GSW1-0001A/1–A/5 and GSW1-0001B/1–B/4, and slides WP5-L-001 (made from peel GSW1-0001A/1) and WP5-L-002 (from peel GSW1-0001B/1) containing the specimens studied in this paper are deposited in the Coal Ball Laboratory of the Centre of Systematic and Evolutionary Botany, Institute of Botany, CAS, Beijing.

**DESCRIPTION**

Description is based on eight synangia and nine isolated sporangia revealed in cross-section (Figs 1–6) and longitudinal-section (Figs 7–10). Synangia are radially symmetrical and nearly circular in cross-section (Figs 3–5), though some of them are slightly bilaterally flattened due to partial taphonomic compaction (Figs 1, 2, 4). Synangia are ≤ 1.7 mm long and 0.8–1.2 mm in diameter. Each synangium consists of a ring of 3–4 elongate sporangia that are fused to one another basally and free from each other elsewhere in the synangium. Each sporangium has a pointed and solid apex (Figs 7, 8); the sporangia are fan-shaped in cross-section with a nearly round central cavity. Sporangia range in diameter from 250 to 300 µm (Figs 1–4).

The outer-facing sporangial wall is thick and conspicuously differentiated. The outermost epidermis consists of a single layer of small and slightly tangentially elongate cells 15–20 × 20–25 µm in size (Figs 2, 6). Two layers of sclerenchymatous cells occur beneath the epidermis that are nearly isodiametric in cross-section and elongate in longitudinal section. Of these two sclerenchymatous layers, those of the outer layer are smaller, 30–40 µm in diameter, and some of them contain dark-coloured cell contents, while those of the inner layer are larger, 50–60 µm in diameter, and lack cell contents (Figs 1, 3, 4, 5). The innermost sporangium wall is usually one cell thick and typically composed of tangentially elongated cells (Figs 7, 9). However, towards the corners between individual sporangia, the inner layer increases in thickness up to 3–4 cells thick, and the cells are nearly isodiametric in cross-section (Fig. 2).

The lateral sporangial wall consists of a single layer of columnar cells. The radial diameter of the columnar cells, coinciding with the thickness of the lateral sporangial wall, attains a maximum of 60–75 µm at the corners between the sporangia, decreasing in size out-

Figures 1–6. Synangia (Figs 1–5) and sporangia (Fig. 6) of *Scolecopteris guizhouensis* sp. nov. All scale bars = 0.2 mm. Fig. 1. Cross-section though synangium at midlevel consisting of three sporangia, showing dehiscence at the midline of the inner-facing sporangial wall (arrow). Fig. 2. Cross-section though slightly flattened synangium at midlevel consisting of four sporangia that are separated from one another and with uniseriate epidermis (arrow, ep); note the inner layer of the outer-facing sporangial wall is thickened at the corners between sporangia (arrows). Fig. 3. Cross-section though midlevel of synangium with three sporangia each of which contain spores. Fig. 4. Cross-section through synangium at midlevel with four sporangia with one containing numeral spores. Fig. 5. Cross-section near apex of synangium revealing four sporangia. Fig. 6. Two isolated sporangia in cross-section near apex showing thick and well-differentiated outer-facing sporangial walls with distinct small-celled epidermis (arrow).
Figures 7–11. Synangia (Figs 7, 10), sporangia (Figs 8, 9) and spore (Fig. 11) of *Scolecopteris guizhouensis* sp. nov.

Fig. 7. Longitudinal section through synangium showing two elongate sporangia and large, thin-walled cells of inner layer of the outer-facing sporangial wall (arrow) that increase in thickness apically. Scale bar = 0.2 mm. Fig. 8. Longitudinal section through sporangium containing spores. Scale bar = 0.2 mm. Fig. 9. Tangential section through outer-facing sporangial wall showing vertically elongate cells. Scale bar = 0.2 mm. Fig. 10. Longitudinal section through synangium with sporangia containing spores. Scale bar = 0.2 mm. Fig. 11. Spore within sporangium with prominent trilete suture. Scale bar = 20 µm.
wards and inwards (Figs 2, 3). The inner-facing sporangial wall is also uniseriate, and is dehiscent along the midline (Fig. 1).

Spores are found in many of the sporangia but in most cases are fragmentary; it has proven difficult to find intact examples. Spores are usually spherical and trilete, 55–60 μm diameter. The trilete suture is symmetrical and arms extend to about 2/3 of the radius of the spore (Fig. 11). In some spores, granular ornamentation is visible on the surface (Fig. 11). The number of spores in cross-section through individual sporangia varies, ranging from less than 20 (Fig. 3) to nearly 50 (Fig. 4). In longitudinal section 30–40 spores are typically observed (Figs 8, 10).

SYSTEMATIC PALAEOBOTANY

ORDER MARATTIALES
GENUS SCOLECOPTERIS ZENKER EMEND MILLAY (1979)
TYPE SPECIES S. ELEGANS (ZENKER) STRASBURGER, 1874
SCOLECOPTERIS GUIZHOUENSIS
HE X. Y., WANG S., HILTON J. & ZHOU Y. L. SP. NOV.

Diagnosis: Isolated synangia and sporangia; pinnules unknown. Synangia radially symmetrical in cross-section, 1.7 mm long and 0.8–1.2 mm in diameter, consisting of a ring of 3–4 sporangia. Sporangia elongate, fused together basally and free distally, and with pointed and solid tip. Outer-facing sporangial wall usually 4–5 cells thick and conspicuously differentiated: the outermost layer of uniseriate epidermis; the middle 2 cells thick, consisting of nearly isodiametric sclerenchymatous cells; the innermost layer generally 1–2 cells thick, but thicker at corners between sporangia, and consisting of tangentially elongate parenchymatous cells. Spores nearly spherical, trilete, 55–60 μm in diameter, with granular surface ornamentation.

Holotype: Specimen preserved on slides: WP, L-001, WP, L-002 from Coal ball GSW1-0001.

Type locality: Wangjiazhai Coal Mine, Shuicheng, Guizhou Province, China.

Geological horizon: Coal Seam No.1 (C605), uppermost Wangjiazhai Formation (Tian & Zhang, 1980).

Age: Changhsingian stage of the Late Permian (Tian et al., 1996).

Etymology: Specific epithet is derived from the fossil source in Guizhou Province.

Illustrations: Figs 1–11.


COMPARISON WITH ANATOMICALLY PRESERVED MARATTIALEAN SYNANGIA

In an anatomically preserved Palaeozoic marattialean fertile organs, the synangia of genera such as Araiangium Millay, Acaulangium Millay, Acitheca (Schimper) Lesnikowska and Scolecopteris Zenker emend. Millay are radially symmetrical (Millay, 1979, 1997). In synangia of Araiangium and Acitheca sporangia are fused basally to one another and also to a central columnar area that is composed of parenchyma and fibres that extends approximately a third the length of the synangium (Lesnikowska & Galtier, 1991). The present specimens lack this kind of basal columnar area and are therefore distinct from these genera. The base of the synangium in Acaulangium is somewhat enlarged by extra tissue around the sporangial bases (Millay, 1977), and this feature does not occur in the specimens we describe here (Figs 7, 8, 10). The synangium of Araiangium also has a short central columnar area at its basal part, which is different from the present specimens that lack a central columnar area (Figs 7, 10). In terms of their gross morphology, the specimens we describe here agree with the characters exhibited in synangia of the genus Scolecopteris (Millay, 1979, 1997). We therefore assign the specimens from the Wangjiazhai Formation to the genus Scolecopteris.

Scolecopteris is the most common genus of anatomically preserved Palaeozoic marattialean fertile organ noted in the fossil record (e.g. Millay, 1979, 1997): to date approximately 30 species belonging to it have been documented (Zhao, 1991; Delevoryas, Taylor & Taylor, 1992; Millay, 1997; Wang et al., 1999). Scolecopteris has a wide stratigraphical distribution that ranges from the early Pennsylvanian to the Early Permian in Euramerica, and from the Early to Late Permian in Cathaysia (Zhao, 1991; Wang et al., 1999; Hilton et al., 2004). In addition to these, another species of Scolecopteris has been recorded from the Middle Triassic in Antarctica (Delevoryas et al., 1992).

Millay (1997) divided 28 species of Scolecopteris from the Carboniferous and Permian in the Euramerican Flora into four groups based on a number of characters, but in particular on the thickness of the outer-facing sporangial wall, size of spores and the extent of modification of the fertile pinnules which bear the synangia on their abaxial surface. The four groups of Millay (1997) are:

1. Minor Group: Outer-facing sporangial walls are thin at the base but thicker at the midlevel and beyond. The lamina of the pinnules extend laterally to envelop the abaxially positioned synangia. Spores are mostly small.
2. Latifolia Group: Outer-facing sporangial walls are thin. The lamina of the pinnules laterally extends...
to completely envelop the abaxially positioned synangia. Synangia are generally composed of a small number of sporangia. Spores are mostly small.

3. Oliveri Group: Outer-facing sporangial walls are thick. Pinnules are unmodified. Spores are mostly large and trilete.

4. Alta Group: Outer-facing sporangial walls are moderately thick. Synangia possess a prominent central parenchymatous region. Synangia are generally composed of a large number of sporangia. Spores are mostly small and monolete.

The specimens we describe here are dissimilar to the Alta Group whose members possess a well-developed central columnar area (Millay, 1997), but share individual features with taxa from each of the other groups. However, since the recognition of these groups by Millay, other species of *Scolecopteris* have been recognized including species that do not readily conform to Millay’s classification (Millay, 1997). *Scolecopteris antarctica* Dele., T.N. Taylor & E.L. Taylor from the early Middle Triassic of Antarctica possesses thick, outer-facing sporangial walls (Delevoryas et al., 1992) similar to the Oliveri Group. However, other features of *S. antarctica* are atypical of the Oliveri Group, including the presence of small (23–31 µm in diameter) alete spores and modified pinnules. *Scolecopteris sinensis* L.M. Zhao and *S. shanxiensis* S.J. Wang, C.S. Li & B. Tian are both known from the Early Permian flora of northern China (Zhao, 1991; Wang et al., 1999). *Scolecopteris sinensis* possesses synangia that consist of four sporangia with thin, outer-facing walls that have a conspicuous thick and vascularized pedicel and small, monolete spores typically 18 µm in diameter. This species also appears to have pinnules that are modified; Zhao concluded from this feature that it belongs to Millay’s Minor Group (Zhao, 1991). In *S. shanxiensis*, the number of sporangia per synangium ranges from 5 to 7, and the outer-facing sporangial walls are 2–3 cells thick basally and apically, but thinner, typically 1–2 cells thick, in their middle part (Wang et al., 1999). Spores of *S. shanxiensis* are very small, 11–14 µm in diameter, and trilete, while its pinnules are moderately modified, but not as strongly as those species belonging to the Minor and Latifolia Groups. Wang et al. (1999) concluded that this species does not fit the group system established by Millay (1997), and considering its combination of characters previously noted in other taxa, established a new group within *Scolecopteris*: the Shanxiensis Group (Wang et al., 1999).

In gross morphology, and in particular considering its thick, outer-facing sporangial walls and large, trilete spores, the specimens we describe are comparable with members of Millay’s Oliveri Group. While its pinnules are unknown and thus cannot reliably be assessed in relation to other marattialean fertile organs, it must be noted that members of the Oliveri and Alta Groups with thick, outer-facing sporangial walls usually correspond with unmodified pinnules (Millay, 1997). The only species that does not comply with this generalization is *S. antarctica*, a species from the Middle Triassic of Antarctica, that possesses thick, outer-facing sporangial walls and modified pinnules which bend abaxially and nearly envelop the synangia (Delevoryas et al., 1992). Although it is possible that *S. guizhouensis* also does not fit with generalizations about the Oliveri Group, it has a thick, outer-facing sporangial wall from which we think it reasonable to deduce that the pinnules probably are unmodified.

When compared with previously recognized species within the Oliveri Group, the specimens we describe have a unique combination of characters as shown in Table 1. This distinction supports taxonomic separation from other species of *Scolecopteris*, and leads us to erect the new species *S. guizhouensis*. In particular, *S. guizhouensis* is very different from *S. sinensis* and *S. shanxiensis* previously described from the Lower Permian strata of China (Zhao, 1991; Wang et al., 1999), and also the undetermined species of *Scolecopteris* described and illustrated by Hilton et al. (2004) from the Upper Permian Xuanwei Formation of southern China. The species described and illustrated by Hilton et al. (2004) has a thin, outer-facing sporangial wall that is uniseriate, and a conspicuous central parenchymatous region, but its spores and pinnules are unknown. In gross morphology the species described by Hilton et al. (2004) is comparable to the Alta Group and is distinct from the Oliveri Group.

**Comparison with Compression/impression fertile marattialean species previously assigned to *Scolecopteris***

Yang et al. (1996) described three kinds of marattialean fertile pinnules preserved by compression from the Permian of China and assigned them into the genus *Scolecopteris*: *S. cathaysicus* G.X. Yang & H.S. Wang and *S. sinensis* G.X. Yang & A.X. Sheng, and assigned *S. unifercata* (Yang & Chen) G. X. Yang to the Early Permian of Henan Province, Northern China, and *S. unifercata* (Yang & Chen) G. X. Yang to the Early Permian of Guangdong Province, southern China. *Scolecopteris sinensis* G.X. Yang & A.X. Sheng is an invalid name because this name has been used before for anatomically preserved marattialean fertile pinnules, *S. sinensis* L.M. Zhao (Zhao, 1991). However, because the generic name
S. illinoensis Millay (1979); Data sources: (1932) and Millay (1979); S. guizhouensis S. major L
S. oliveri S. dispora S. parvifolia S. majopsis S. iowensis

<table>
<thead>
<tr>
<th>Species</th>
<th>Synangium size (mm)</th>
<th>Sporangia per synangium</th>
<th>Outer-facing sporangial wall</th>
<th>Spores</th>
<th>Age</th>
</tr>
</thead>
<tbody>
<tr>
<td>S. antarctica</td>
<td>Ø = 0.6–0.8</td>
<td>4–5</td>
<td>4–5 cells thick,</td>
<td>Alete,</td>
<td>Early Middle</td>
</tr>
<tr>
<td></td>
<td>L = 1.1</td>
<td></td>
<td>differentiated</td>
<td>23–31 µm</td>
<td>Triassic</td>
</tr>
<tr>
<td>S. charma</td>
<td>Ø = 0.8,</td>
<td>4–5</td>
<td>3–4 cells thick,</td>
<td>Trilete,</td>
<td>Late</td>
</tr>
<tr>
<td></td>
<td>L = 1.1</td>
<td></td>
<td>undifferentiated</td>
<td>49–64 µm</td>
<td>Pennsylvanian</td>
</tr>
<tr>
<td>S. conicaulis</td>
<td>Ø = 1.0,</td>
<td>4–7</td>
<td>2–5 cells thick,</td>
<td>Trilete,</td>
<td>Early</td>
</tr>
<tr>
<td></td>
<td>L = 1.2</td>
<td></td>
<td>undifferentiated</td>
<td>27–62 µm</td>
<td>Pennsylvanian</td>
</tr>
<tr>
<td>S. illinoensis</td>
<td>Ø = 0.7,</td>
<td>4–6</td>
<td>3 cells thick,</td>
<td>Trilete?,</td>
<td>Late</td>
</tr>
<tr>
<td></td>
<td>L = 0.66</td>
<td></td>
<td>differentiated</td>
<td>15 µm</td>
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<tr>
<td>S. iowensis</td>
<td>Ø = 0.9,</td>
<td>4–7</td>
<td>3–4 cells thick,</td>
<td>Trilete,</td>
<td>Middle</td>
</tr>
<tr>
<td></td>
<td>L = 1.2</td>
<td></td>
<td>undifferentiated</td>
<td>57–83 µm</td>
<td>Pennsylvanian</td>
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<tr>
<td>S. majopsis</td>
<td>Ø = 1.2,</td>
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<td>3 cells thick,</td>
<td>Trilete,</td>
<td>Middle</td>
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<tr>
<td></td>
<td>L = 1.6</td>
<td></td>
<td>differentiated,</td>
<td>45–115 µm</td>
<td>Pennsylvanian</td>
</tr>
<tr>
<td>S. parvifolia</td>
<td>Ø = 0.65,</td>
<td>3–5</td>
<td>&gt;2 cells thick,</td>
<td>Monolete,</td>
<td>Middle</td>
</tr>
<tr>
<td></td>
<td>L = 0.9</td>
<td></td>
<td>differentiated</td>
<td>11–18 µm</td>
<td>Pennsylvanian</td>
</tr>
<tr>
<td>S. dispora</td>
<td>Ø = 1.0,</td>
<td>4–5</td>
<td>2–3 cells thick,</td>
<td>Monolete,</td>
<td>Middle</td>
</tr>
<tr>
<td></td>
<td>L = 1.8</td>
<td></td>
<td></td>
<td>30–44 × 24–33 µm</td>
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</tr>
<tr>
<td>S. oliveri</td>
<td>Ø = 1.0,</td>
<td>4</td>
<td>1–2 cells thick,</td>
<td>Monolete,</td>
<td>C–P boundary</td>
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<tr>
<td></td>
<td>L = 1.6</td>
<td></td>
<td>differentiated</td>
<td>&lt;18 µm</td>
<td></td>
</tr>
<tr>
<td>S. major</td>
<td>L = 2.1–2.9</td>
<td>4</td>
<td>Undifferentiated</td>
<td>Trilete,</td>
<td>Middle</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>45–55 µm</td>
<td>Pennsylvanian</td>
</tr>
<tr>
<td>S. guizhouensis sp. nov</td>
<td>Ø = 0.8–1.2,</td>
<td>3–4</td>
<td>4–5 cells thick,</td>
<td>Trilete,</td>
<td>Late Late</td>
</tr>
<tr>
<td></td>
<td>L = 1.7</td>
<td></td>
<td>differentiated</td>
<td>55–60 µm</td>
<td>Permian</td>
</tr>
</tbody>
</table>

Data sources: S. antarctica from Delevoryas et al., 1992); S. charma from Lesnikowsk & Millay (1985); S. iowensis from Millay (1979); S. majopsis from Millay (1979); S. conicaulis from Millay (1982a); S. parvifolia from Millay (1979); S. illinoensis from Ewart (1961) and Millay (1979); S. dispora from Lesnikowsk & Willard (1997); S. oliveri from Scott (1932) and Millay (1979); S. major from Mamay (1950).

Scolecopteris is only for anatomically preserved marattialean fertile pinnules, the above three species are here transferred into the genus Asterotheca Presl. that is used for Scolecopteris-like marattialean fertile pinnules recognized in compression/impression preservation (e.g. Mamay, 1950). We therefore implement the following revision:

**Asterotheca cathaysicus** (G.X. Yang & H.S. Wang) **comb. nov.**


**A. unifercata** (G.X. Yang & Chen) **comb. nov.**


Regarding their structure and organization, synangia of A. cathaysicus consist of four sporangia and are 1.8–2.2 mm long; they are therefore a little longer than our new species, Scolecopteris guizhouensis. Spores of A. cathaysicus are smaller than those of S. guizhouensis and are 30 µm in diameter, monolete, and with a smooth surface, again differing from S. guizhouensis. Asterotheca sinensis also possesses synangia with four sporangia similar to S. guizhouensis, but its spores are very small, only about 16 µm in diameter, with rugae on their surface. In our specimens the spores are much larger and with a granulate surface, again being distinct from A. sinensis. The synangia of A. unifercata are unknown, so it is impossible to compare our specimens with it.

EVOLUTIONARY TRENDS WITHIN MARATTIALEAN FERTILE ORGANS

Millay (1979) summarized apparent evolutionary trends with *Scolecopteris*-type synangia. He concluded that differentiated outer-facing sporangial walls and small spores, less than 40 μm in diameter, represented comparatively advanced features, while thick and uniform outer-facing sporangial wall and large spores represent ancestral conditions within synangia of this kind. Our new species, *Scolecopteris guizhouensis*, possess conspicuously differentiated outer-facing sporangial walls and also has large spores ranging from 55 to 60 μm in diameter, and therefore has a combination of characters that Millay envisaged as both primitive (spore size) and advanced (sporangial wall differentiation). The same situation also exists in *S. sinensis* Zhao from Lower Permian coal balls in northern China in which synangia possess a thick and vascularized pedicle, a presumably ancestral character according to Millay (1979), and a differentiated outer-facing sporangial wall and small spores both considered as advanced characters (Zhao, 1991). Unfortunately, robust phylogenetic analyses of these taxa are not available to test the reliability of Millay’s assumptions and conclusions (Millay, 1979, 1997), but to a large extent his observations fit the stratigraphic record of species of *Scolecopteris* within Europe and North America (Table 1).

The present specimens are the second species of *Scolecopteris* discovered in the Late Permian in this district of Guizhou Province, but, unlike those described by Hilton et al. (2004), are comprehensively characterized. In age, the coal seam (C605) that yielded the coal balls from the Wangjiazhai Formation occurs at the uppermost part of the Upper Permian strata; above this horizon limestones marking the base of the Triassic Feixianguan Formation occur. This is therefore younger than the assemblage from Shanjiangshu described by Hilton et al. (2004), making the new species *S. guizhouensis* the youngest of the Palaeozoic species of *Scolecopteris* and the youngest account from the fossil floras of China (Table 1); only *S. antarctica* from the Middle Triassic Mesozoic sequences of Antarctica is younger (Table 1). These two species show the persistence of marattialean ferns within this lineage though the latest Palaeozoic into the Middle Triassic.

MARATTIALEAN FERNS IN THE UPPER PERMIAN OF CHINA

In coal balls from the Wangjiazhai Formation there are abundant plant fossils including lycopsids, sphe-
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