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## **Abstract**

*Marattia aganzhenensis* sp. nov. from the Lower Jurassic Daxigou Formation of Lanzhou, Gansu, China, is the second species of *Marattia* known in fertile structure from China, in addition to *Marattia asiatica*. The new species demonstrates the variability of the genus through its distinct character states. This new species is distinguished by the absence of venuli recurrentes, the shorter synangia, exclusively monolete spores without surface ornamentation, and the low number of spores produced per sporangium.

## **Keywords**

China, Gansu, Lower Jurassic, *Marattia aganzhenensis* sp. nov., Marattiales

## **Comments**

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## MARATTIA AGANZHENENSIS SP. NOV. FROM THE LOWER JURASSIC DAXIGOU FORMATION OF LANZHOU, GANSU, CHINA

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*Marattia aganzhenensis* sp. nov. from the Lower Jurassic Daxigou Formation of Lanzhou, Gansu, China, is the second species of *Marattia* known in fertile structure from China, in addition to *Marattia asiatica*. The new species demonstrates the variability of the genus through its distinct character states. This new species is distinguished by the absence of venuli recurrentes, the shorter synangia, exclusively monoete spores without surface ornamentation, and the low number of spores produced per sporangium.

**Keywords:** China, Gansu, Lower Jurassic, *Marattia aganzhenensis* sp. nov., Marattiales.

### Introduction

As one of the six extant genera of Marattiales, *Marattia* Swartz [al. *Marattiopsis* Schimper] is distributed in the pantropical region (Gifford and Foster 1989). In the fossil record, *Marattia* has been described from the Mesozoic of Europe, Greenland, and Asia (Schenk 1867; Schimper 1869; Zeiller 1903; Kawasaki 1925, 1926, 1939; Harris 1931, 1961; Lundblad 1950; Kilpper 1964; Van Konijnenburg-van Cittert 1975; Schweitzer et al. 1997). In China, *Marattia* has been recorded from Upper Triassic and Lower Jurassic strata more than 10 times. Four species, *M. horensis* (Schimper), *M. munsteri* (Goepfert) Schimper, *M. orientalis* (Chow et Yeh), and *M. asiatica* (Kawasaki) Harris, have been recorded from the Upper Triassic and Lower Jurassic of South China, North China, and northwestern China (Sze et al. 1963; Zhang et al. 1980; Sun and Zhao 1992; Wang 1999). Of these, only *M. asiatica* has been known in terms of both sterile and fertile leaves (Wang 1999). Here we describe a new species of the genus on the basis of both the gross leaf morphology and the structure of fertile organs, from the Early Jurassic of northwestern China (fig. 1A).

### Geological Setting

The specimens under study were collected from the Lower Jurassic Daxigou Formation of Aganzhen coalfield, which is ca. 30 km south-southeast of Lanzhou, Gansu Province, China (fig. 1A, 1B; 35°55'13.7"N, 103°50'15.1"E). The Daxigou Formation in the Aganzhen coalfield crops out southwest of the town of Aganzhen (fig. 1C). The formation consists of grayish-green breccia, conglomerate, grayish-green sandstone, silt-

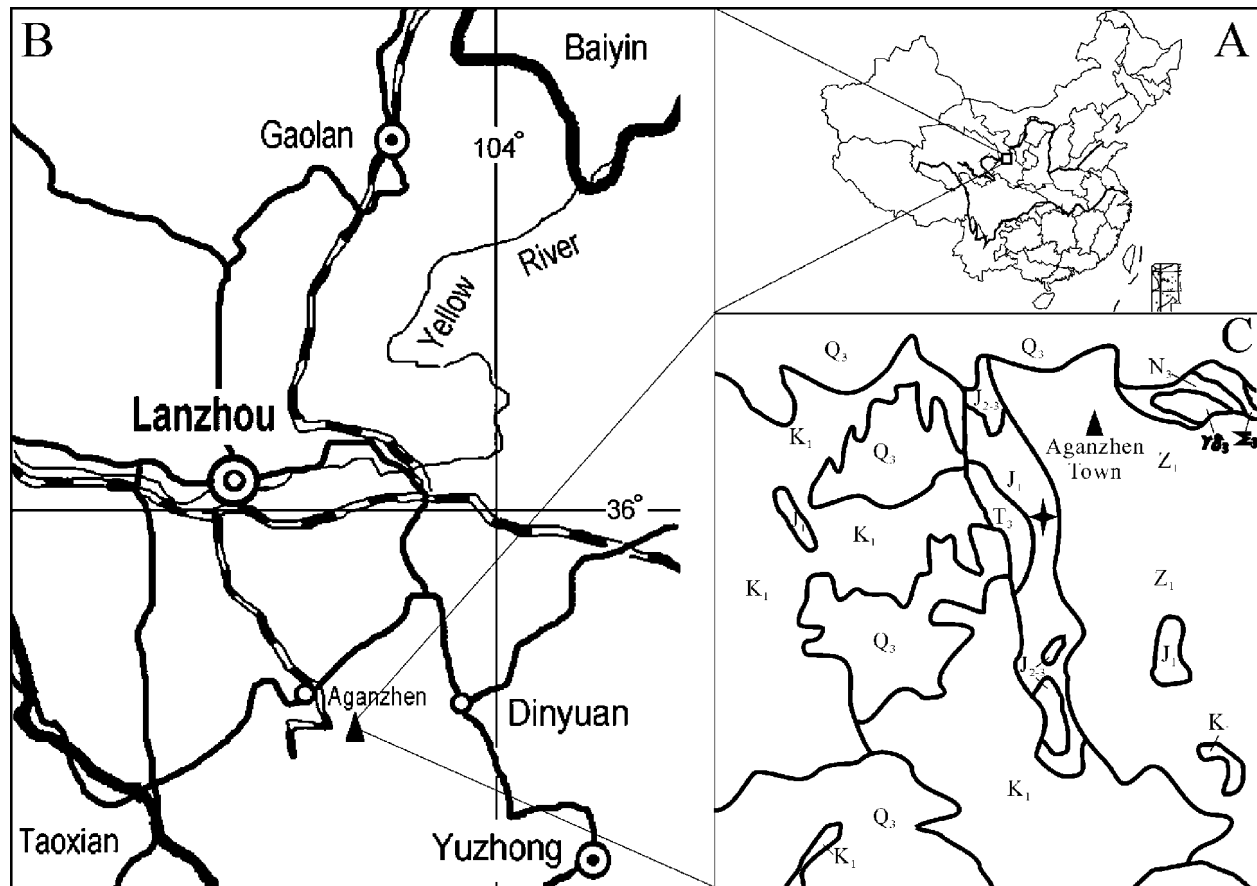
stone, and coal seams. On average, the formation is 224 m thick, discordantly overlying the Sinian Xinglongshan Group (fig. 2) and conformably underlying the Middle Jurassic Teyangou Group. Lithologically, the Daxigou Formation includes three members (fig. 2). The lower member consists of grayish-green breccia, reddish-purple conglomeratic siltstone, and gray fine sandstone. The middle member consists of gray and black fine sandstone, gray coarse sandstone, and sandy conglomerate and contains two minable coal seams. The upper member is composed of grayish-green breccia, grayish-green and gray fine sandstone and mudstone, gray conglomerate, and conglomeratic sandstone. The specimens under study were collected from the upper member.

The age assignment of the Daxigou Formation is based on the plant fossil assemblage, which includes 46 species of 23 genera (Yang and Shen 1988) and is closely comparable to the Early Liassic flora from the Issyk-kul region of the former USSR. Apart from *Marattia aganzhenensis* sp. nov., described in this article, the genera of this assemblage include *Equisetites* Sternberg, *Neocalamites* Halle, ?*Coniopteris* Brongniart, *Osmundopsis* T.M. Harris, *Hausmannia* Dunker, *Dictyophyllum* Lindley & Hutton, *Clathropteris* Brongniart, *Cladophlebis* Brongniart, *Pterophyllum* Brongniart, *Anomozamites* Schimper, *Ctenis* Lindley & Hutton, *Ginkgoites* Seward emend. Florin, *Czekanowskia* Heer, *Sphenobaiera* Florin, *Stephenophyllum* Florin, *Sagenopteris* Presl, *Storgaardia* T.M. Harris, *Elatocladus* Halle, *Podozamites* C.F.W. Braun cf. Münster, *Pityophyllum* Nathorst, *Swedenborgia* Nathorst, *Carpolithus* Wallerius, and *Radicites* Potonie.

### Material and Methods

More than 100 specimens of the new species were collected. The specimens occur in the middle-upper part of the third member of the Daxigou Formation. The fossils were mostly preserved as compressions in a bed of gray and black mudstone

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**Fig. 1** Map of the fossil locality of *Marattia aganzhenensis* sp. nov. near Lanzhou, Gansu Province. A, Position of area in China. B, Area near fossil locality. C, Detailed geologic map of area around fossil locality (from Bureau of Geology and Mineral Resources of Gansu Province, National Bureau of Geology 1965). Z<sub>1</sub> = Precambrian and other basement; T<sub>3</sub> = Late Triassic Yanchang Group; J<sub>1</sub> = Lower Jurassic Daxigou Formation; J<sub>2-3</sub> = Middle and Upper Jurassic Tiesyangou Group; K<sub>1</sub> = Lower Cretaceous Hekou Group; Q<sub>3</sub> = Pleistocene alluvial layer.

20 cm thick. Macrofossils were prepared by *dégagement*. The selected holotype for the current new species was originally ca. 50 cm long and 20 cm wide when it was found and collected in the field, but it was unfortunately broken during transportation. Subsequently, the major part available was figured and housed as holotype (fig. 3A). The other fragments were used for maceration to obtain synangia, sporangia, and spores. The synangia were detached mechanically from the fertile pinnae and (1) treated with hydrochloric acid (10%) for ca. 2–3 h and then cleaned with distilled water; (2) treated with hydrofluoric acid (37%) for 8–24 h and then cleaned with distilled water; and (3) macerated using conventional Schulze's solution for ca. 4–5 h and then washed with distilled water and treated with ammonia (5%) for ca. 10 min. Then the macerated samples were cleaned with distilled water and moved onto slides for light observation with a Leica DC300 stereomicroscope or etched with ethanol and coated with gold for observation under a JEOL JSM6300 scanning electron microscope (SEM). All specimens and samples for light and SEM observation are housed in the paleobotanical collection of the College of Resource and Environmental Science, Lanzhou University, Lanzhou, and have the numbers NWGP-90001–90005.

## Systematics

Order—*Marattiales*

Family—*Marattiaceae*

Genus—*Marattia* Swartz 1788

Species—*Marattia alata* Swartz 1788

*Marattia aganzhenensis* Yang, Wang, and  
*Pfefferkorn* sp. nov.

*Holotype*. Fig. 3A; specimen number NWGP-90001.

*Paratypes*. Fig. 3B–3E; specimen numbers NWGP-90002–90005.

*Repository*. College of Earth and Environment Sciences, Lanzhou University, Lanzhou 730000, China.

*Type locality*. Aganzhen, Lanzhou, Gansu, China (35°55'13.7"N, 103°50'15.1"E).

*Stratigraphic position*. Daxigou Formation.

*Age*. Early Jurassic.

*Derivation of name*. The species is named after the town of Aganzhen near Lanzhou, Gansu Province, China, where the specimens were found.

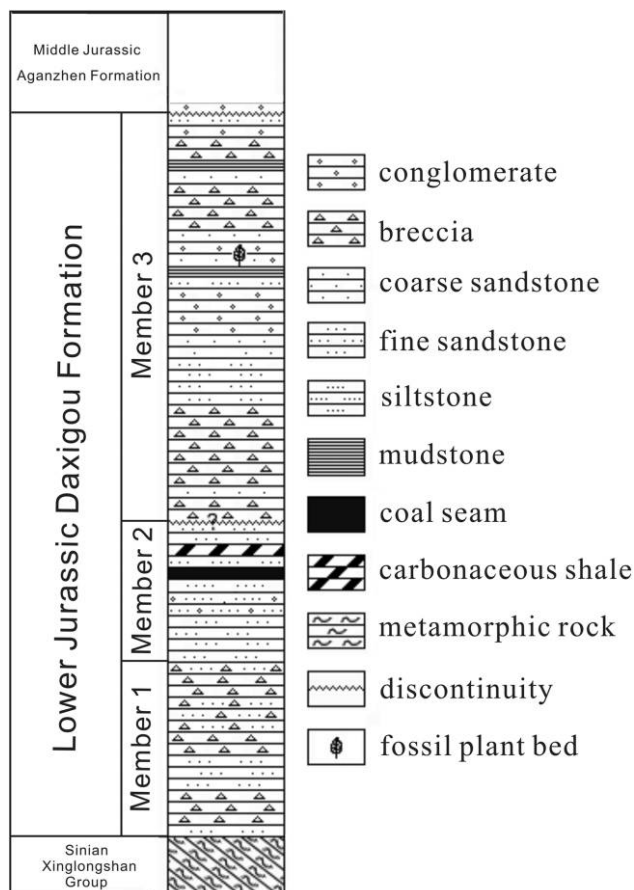


Fig. 2 Stratigraphic column at the fossil locality.

**Diagnosis.** Frond at least once pinnate. Pinnae basically rounded and apically pointed, with entire margins. Lateral veins generally arising from the midvein by an acute angle curving until nearly perpendicular to the midvein. Veins usually fork once near the midvein and sometimes once more near the margin. Venuli recurrentes absent. Fertile pinnae identical in shape and size to sterile ones. Length of synangia occupies about one-eighth (in the middle) to one-sixteenth (in apical region) of the pinna width. In situ spores monolet.

### Description

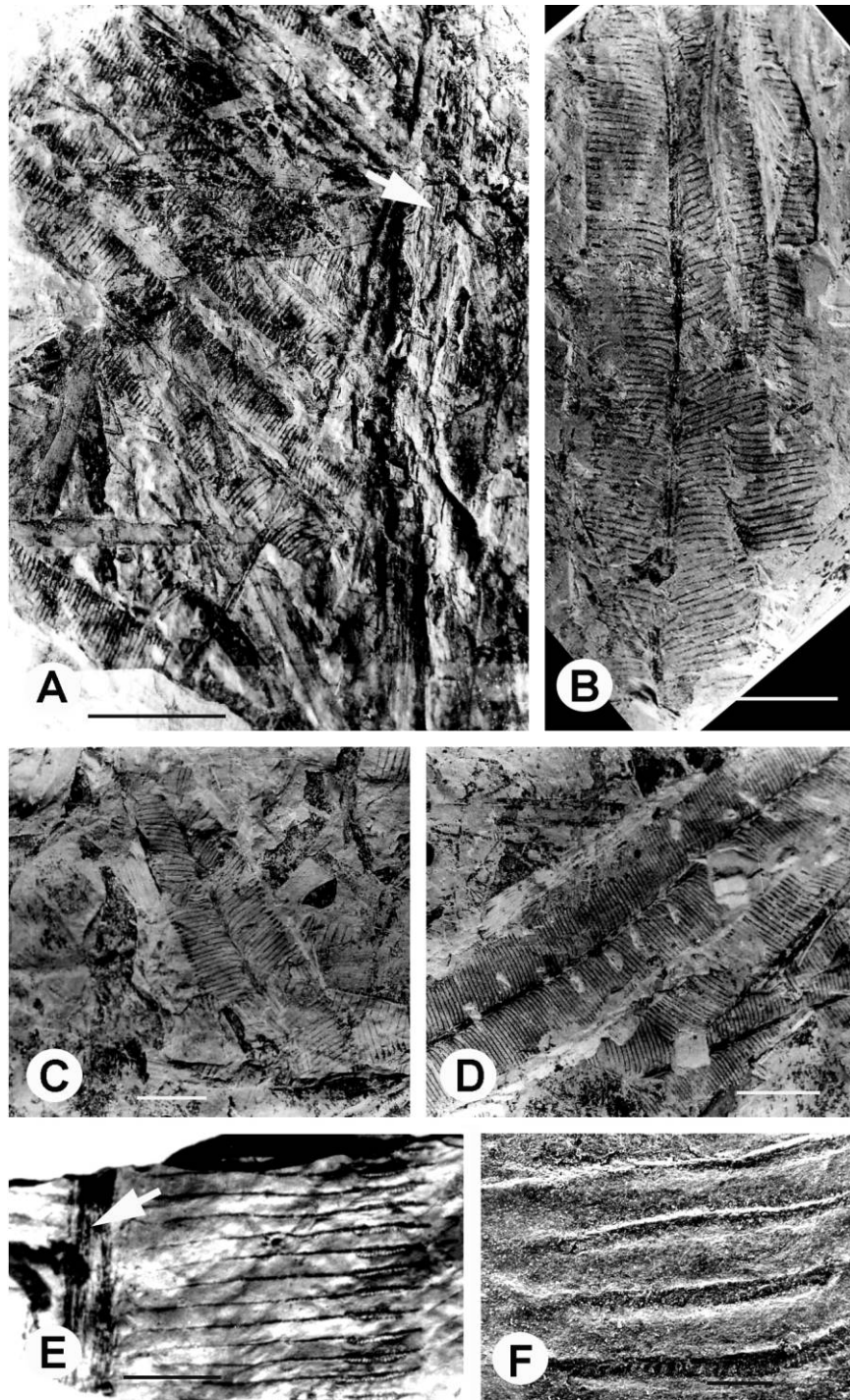
More than 100 specimens of *Marattia aganzhenensis* sp. nov. were found as individual pinnae that show the morphological features of the basal, middle, and apical regions of the pinnae. Most of them are fertile. The upper part usually carries synangia, and the lower part is sterile. The sterile and fertile pinnae resemble one another in size and shape. The holotype (fig. 3A) demonstrates the pinnate structure of the leaf. The rachis is ca. 9 mm wide and marked by irregular longitudinal striations (fig. 3A, arrowhead). On the left side, four pinnae, especially the middle two, are well preserved and arise from the rachis by an angle of ca. 50°. Their apexes are not completely preserved, and the bases are so poorly preserved that the basal margin is not recognizable. The lateral margins are parallel to each other. Most specimens represent detached individual pin-

nae (fig. 3B–3D). The pinnae are apically tapering (fig. 3C). The pinna margin is entire and broadly undulating and sometimes appears slightly wavy in larger magnification (fig. 3E). The observed pinnae are 2.2–3.0 cm wide in the lower region and near the pinna base. The greatest observed length of the pinnae is 20 cm.

The midvein is ca. 2 mm wide near the base of the pinna and gradually decreases to less than 0.5 mm near the apical region. It is marked with irregular longitudinal striation (fig. 3E, arrowhead). Lateral veins arise from the midvein at an angle of 40°, rapidly fork once, and curve to be nearly perpendicular to the midvein. Sometimes, the veins fork once more closer to the margin. Lateral veins near the pinna base are recurved toward the base, whereas those near the apex turn and meet the margin obliquely. Vein density on the margin is ca. 10 per centimeter in the middle region of the pinnae and ca. 16 per centimeter near the apical region. Occasionally, a few specimens have a vein density of 20 veins per centimeter. Venuli recurrentes are absent.

The synangia are linear and attached to the secondary veins near the lateral margin, keeping a gap of 0.5–1 mm to the margin (fig. 3E, 3F; fig. 4A). The synangium has a length of 5 mm and occupies about one-eighth of the pinna width in the middle and lower region, whereas in the apical region, it is ca. 0.5 mm long or even less and occupies about one-sixteenth of the pinna width. There are ca. 20 pairs of sporangia in a synangium (fig. 3E, 3F; fig. 4A) but fewer toward the apex. Each sporangium is 100–150  $\mu\text{m}$  wide and located below the secondary vein (fig. 3E, 3F; fig. 4B). The synangia and sporangia can be observed under visible light after maceration (fig. 5A, 5B) or in an SEM (fig. 4B–4D). In SEM observation, it is clearly shown that the synangia are bivalved and that each synangium is composed of two long strips of laterally joined sporangia (fig. 4B–4D). In transverse view (fig. 4D, 4E), the compacted synangia have a triangular outline; the two lateral sides are equal in length, each corresponding to one side of a sporangium. The bottom side is much longer because it consists of the bottoms of two joined sporangia. In light microscopic examination, that the two strips of sporangia are laterally joined can also be clearly recognized (fig. 5A, 5B). The sporangia appear rectangular in outline, with rounded corners. The sides that touch the secondary vein of the pinna and the outer side are convex, whereas the other two sides are straight and represent the septa between the sporangial compartments.

The spores are still in situ (fig. 4F, 4G; fig. 5I), but after maceration they can be mechanically separated (fig. 5D–5F). They are monolet and bean shaped. The laesura is narrow, simple, and extends from half (fig. 5J) to the whole length (fig. 5K, 5L) of the spore. The width of the spores is 10–15  $\mu\text{m}$ , and the length is 15–20  $\mu\text{m}$ . In light microscopy, the spore exine seems to be very thin (less than 1  $\mu\text{m}$  thick) with finely microgranulate sculpture (fig. 5D, 5E), but the outer surface of the spore wall observed in SEM is smooth (fig. 5L). Occasionally, the outer surface of a spore exine appears to have a finely microgranulate sculpture (fig. 5H). The inner surface of the spore wall is readily visible when a spore mass is mechanically broken, and it is smooth (fig. 5J, 5K). Although it is hard to precisely count the spores from a sporangium, the well-preserved synangia, sporangia, and spores facilitated a test of the quantity of spores in a sporangium. Two sporangia were

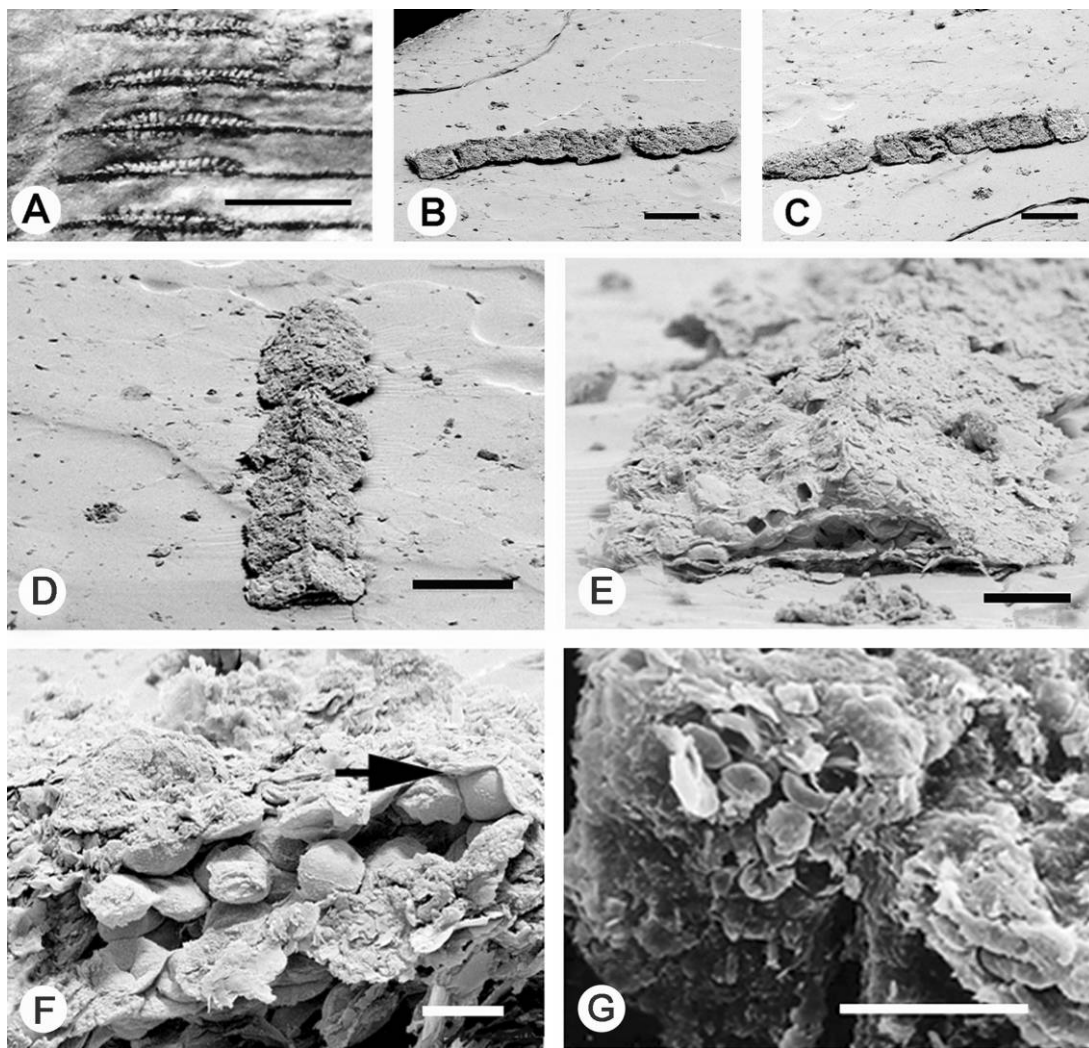


**Fig. 3** *Marattia aganzhenensis* sp. nov. pinnae and synangia. *A*, Pinnate frond with four pinnae visible; the middle two are especially well preserved. Arrowhead indicates longitudinal striations on the rachis. Scale bar = 2 cm. Holotype, specimen NWGP-90001. *B–D*, Pinna with venation pattern and attachment of synangia. Scale bars = 1 cm. Paratype, specimen numbers NWGP-90002–90004. *E*, Piece of pinna showing the venation and the attachment of synangia. Scale bar = 4 mm. Paratype, specimen NWGP-90005. *F*, Scanning electron micrograph of a piece of fragmentary fertile pinna showing the synangia. Scale bar = 1 mm.

mechanically detached from a synangium (fig. 5*B*) and then placed on a slide. Pressing the sporangium dispersed the in situ spores and made them countable. As a result, it was indicated that there are ca. 340 spores in a sporangium.

### Comparison

In gross morphology, the new species has proportionally much shorter synangia than *M. asiatica* (Kawasaki). According

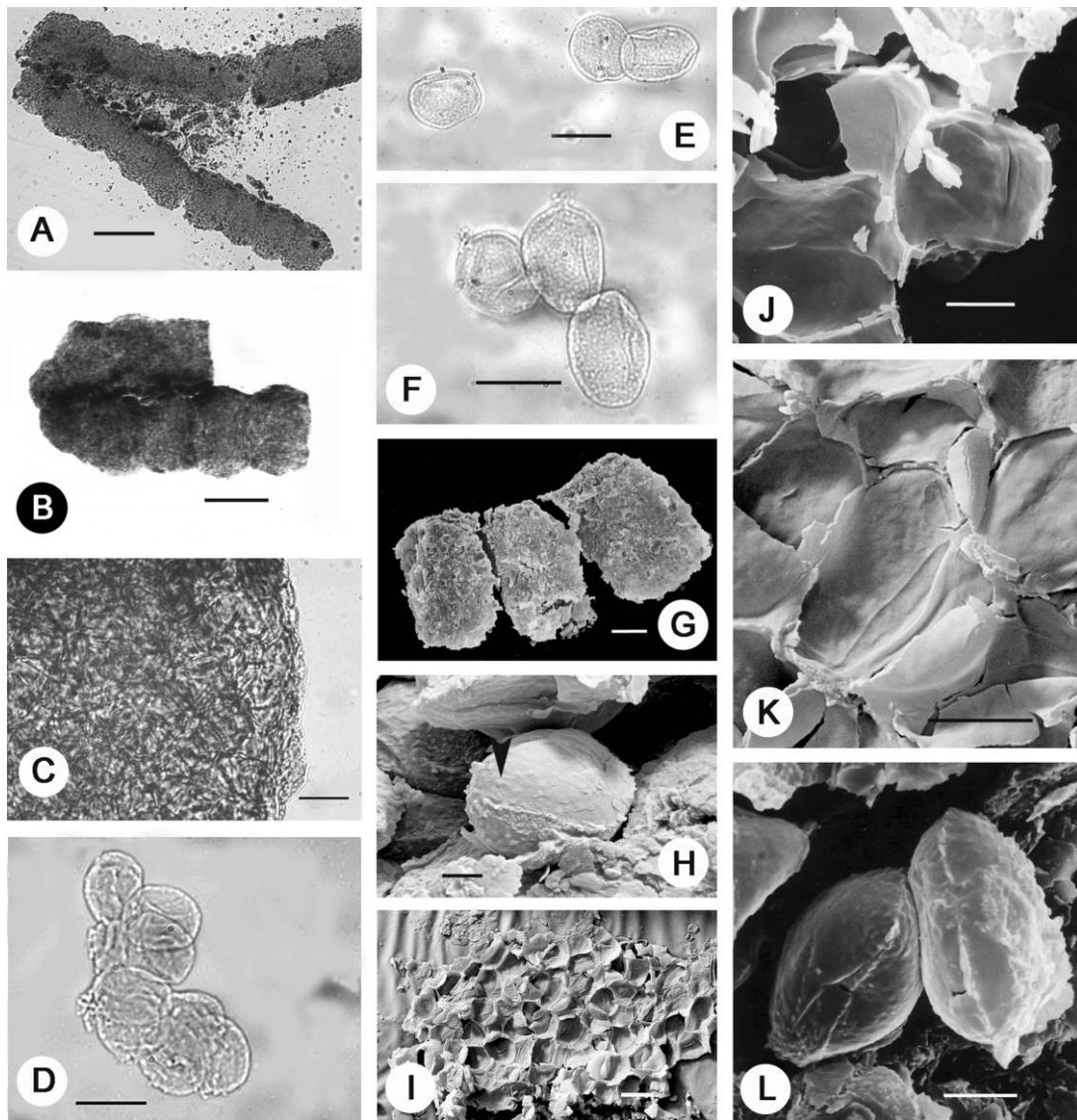


**Fig. 4** *Marattia aganzhenensis* sp. nov. synangia and sporangia. **A**, Magnification of fig. 3E showing the synangia. The synangia are located slightly distant from the margin. Scale bar = 2 mm. **B–D**, Linear bivalved synangium, showing the two lateral sides (**B**, **C**) and the transverse section (**D**), demonstrating the two opposite valves of sporangia. Scale bar = 200  $\mu\text{m}$ . **E**, Close view of the transverse section of the synangium in **D**, showing the laterally jointed sporangia. Measurements indicate that the lateral sides are ca. 113  $\mu\text{m}$  wide, the bottom side is ca. 230  $\mu\text{m}$  wide, and the height is ca. 50  $\mu\text{m}$ . Therefore, the three sides of a single sporangium are, respectively, 113, 115, and 50  $\mu\text{m}$ , which means that the side where the sporangia are joined together and contact the lateral vein is much shorter; the other two sides of a sporangium are nearly equal (as shown in fig. 6C as a reconstruction). Scale bar = 40  $\mu\text{m}$ . **F**, Magnification of the transverse section of a synangium with spores just under the synangial wall (arrowhead). Scale bar = 20  $\mu\text{m}$ . **G**, Close view of a synangium at the position where the two valves of sporangia are in contact. Scale bar = 50  $\mu\text{m}$ .

to Wang (1999, plates 1, 2, figs. 3–5), the length of the synangia of *M. asiatica* varies from 2 to 8 mm and occupies ca. 20%–30% of the pinna width. Synangia mostly contains 25–40 pairs of sporangia (fig. 6E). In *M. aganzhenensis* sp. nov. (fig. 3), the length of the synangia ranges from 0.5 to 5 mm, and they occupy ca. 6.25%–12.5% of the pinna width, with a synangium usually containing fewer than 20 pairs of sporangia (fig. 6B). Moreover, *M. asiatica* definitely has remarkable venuli recurrentes, which are always absent in the new species (fig. 6A, 6D). In addition, the synangia of *M. asiatica* are attached on the secondary veins and to the very margin (terminal

of the secondary veins) of the pinna (plate 2, figs. 1–8; fig. 3; fig. 5A, 5B in Wang 1999; fig. 6E in this article), whereas in the new species, the synangia are located ca. 0.5–1 mm from the ends of the lateral veins (fig. 3E, 3F; figs. 4A, 6B).

The synangia of both *M. asiatica* and *M. aganzhenensis* sp. nov. are composed of two long strips of laterally jointed sporangia. However, their sporangia are quite different three-dimensionally. In transverse view, the synangia of *M. asiatica* (fig. 6F; Wang 1999, plate 3, figs. 5–7) are triangular and higher than wide, so that the side where the sporangia are joined laterally is nearly the same length as the lateral sides of



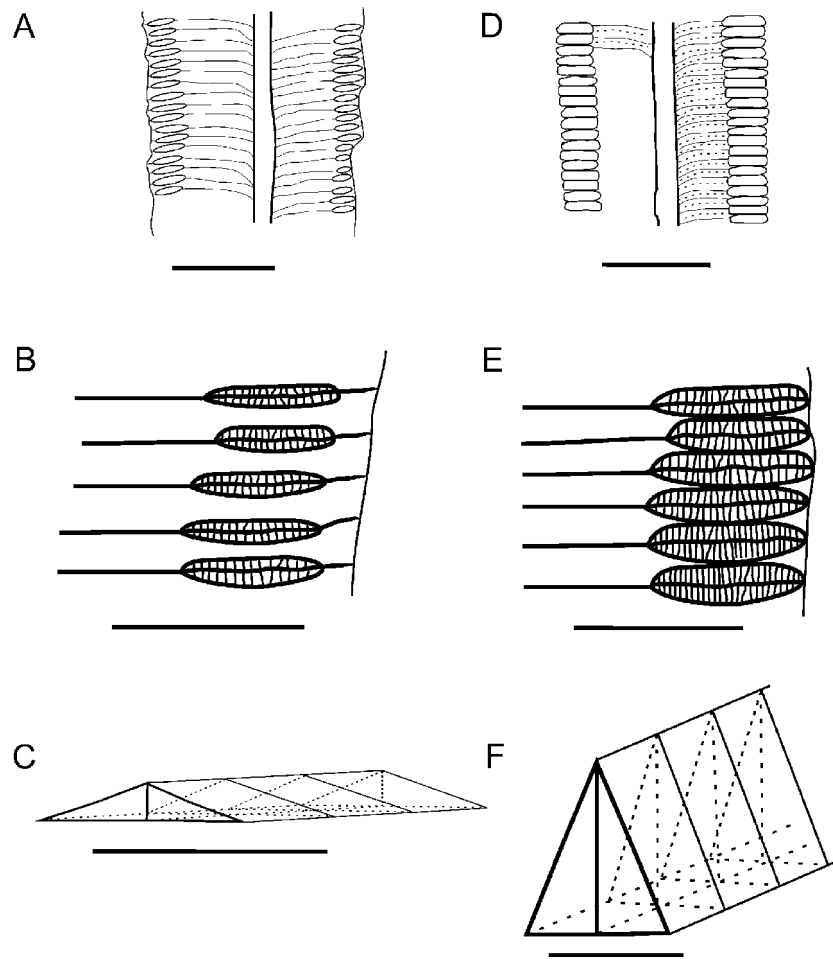
**Fig. 5** *Marattia aganzhenensis* sp. nov. synangia, sporangia, and in situ spores. A, Light micrograph of a synangium. Two rows of sporangia are shown that have started to separate during maceration but are still attached to each other at the end of the synangium. Scale bar = 250  $\mu\text{m}$ . B, Light micrograph of another synangium. Scale bar = 100  $\mu\text{m}$ . C, Further magnification of the two lower-right synangia of B. Scale bar = 20  $\mu\text{m}$ . D–F, Light micrographs showing the morphology of the spores. Scale bars = 20  $\mu\text{m}$ . G, Three sporangia isolated from the same valve of a synangium, showing that they are rectangular with rounded corners in an obverse view. Scale bar = 50  $\mu\text{m}$ . H, Magnified spore from fig. 4E, showing morphology. Arrowhead indicates an area where the spore exine is finely microgranulate. Scale bar = 4  $\mu\text{m}$ . I, Cluster of spores from a sporangium. Scale bar = 20  $\mu\text{m}$ . J, K, Magnification of I, showing the morphology of the spores. Scale bar = 10  $\mu\text{m}$ . L, Morphology of the spores. Scale bar = 5  $\mu\text{m}$ .

the synangium. In *M. aganzhenensis* (fig. 4D, 4E; fig. 6C), the synangia are also triangular in cross section but are much wider than high, so that the bottom side of sporangium is nearly the same in length as the lateral side, whereas the wall where the sporangia are joint is much shorter. In dorsal view of the synangia (figs. 4B–4E, 6C), the sporangia of *M. aganzhenensis* appear rectangular, with the two sides where the sporangia of the same strip contact each other nearly as long as or only slightly longer than the other two sides of the sporangia, whereas in *M. asiatica* (fig. 6F), the two adjoining sides of the sporangia within the same strip are much longer than the other two sides.

Moreover, the synangia and sporangia of the new species are considerably smaller than those of *M. asiatica*.

The spores of the new species differ clearly from those of *M. asiatica* (Kawasaki). (1) The spores of the new species are all monolete, while 5% spores of *M. asiatica* are trilete. (2) The spores of the new species are 10–15  $\mu\text{m} \times 15$ –20  $\mu\text{m}$  in size, much smaller than those of *M. asiatica*, which are 20–28  $\mu\text{m} \times 25$   $\mu\text{m}$  on average. (3) The spores of the new species have a smooth exine (fig. 5J–5L) that can be occasionally finely microgranulate (fig. 5H), whereas the spores of *M. asiatica* have an exine with marked granular sculptures (Wang 1999, plate 4,





**Fig. 6** Diagram illustrating characteristics of *Marattia aganzhenensis* and *Marattia asiatica* as a comparison. A–C represent *M. aganzhenensis*, and D–F represent *M. asiatica*. A, D, Part of fertile pinna. The synangium length of *M. aganzhenensis* is proportionally much less than that of *M. asiatica*. Venuli recurrentes are always absent in *M. aganzhenensis* but are present in *M. asiatica*. Scale bars = 1 cm. B, E, Further magnification of fertile pinna. The synangia are slightly distant from each other in *M. aganzhenensis* but are so crowded in *M. asiatica* that each one is always touching its neighbors. The synangia are slightly distant from the pinna margin in *M. aganzhenensis* but are extended to the very margin in *M. asiatica*. Scale bars = 5 cm. C, F, Outline of synangia and sporangia. The synangia and sporangia of *M. aganzhenensis* are markedly smaller than those of *M. asiatica*. The synangia of *M. aganzhenensis* are proportionally much lower and wider than those of *M. asiatica*. Scale bar = 250  $\mu\text{m}$  in C and 500  $\mu\text{m}$  in F.

figs. 3–6). (4) The spore output of *M. asiatica* is more than 1000 spores per sporangium, compared with ca. 340 per sporangium in *M. aganzhenensis* sp. nov.

*Marattia barnardii* (Schweitzer et al. 1997) appears comparable with the new species in terms of the pinna size, density of venation, position of synangia distant from the pinna margin, and the absence of venuli recurrentes. However, the synangia of *M. barnardii* are bean shaped and 1–3 mm in length, occupying 20%–30% of the pinna width and proportionally longer than in the new species. There are 8–16 pairs of sporangia per synangium in *M. barnardii*, fewer than in the new species. The pinna margin of *M. barnardii* is sometimes finely serrate, but that of *M. aganzhenensis* sp. nov. is entire. All these differences indicate that we are dealing with two different species. In addition, the structure of the synangia and the morphology of the spores of *M. barnardii* are still unknown, so that these features cannot even be compared.

*Marattia muensteri* (Schenk 1867; Schimper 1869) has vein densities similar to those of the new species, but it is distinguishable from the new species in its proportionally longer synangia (10%–20% pinna width) and larger spores (normally 20–21  $\mu\text{m}$  in diameter; Delle 1967). Ca. 1% of the spores are trilete, and the spores have granulate exine. Moreover, venuli recurrentes are present.

Differing from *M. hoerensis* (Schimper), *M. aganzhenensis* sp. nov. has proportionally much shorter synangia and much smaller spores. The spores of *M. hoerensis* are 28  $\mu\text{m}$  in diameter. Fewer than 1% of the spores are trilete in *M. hoerensis*, but all spores of the new species are monoete. Moreover, the venuli recurrentes in *M. hoerensis* are very strong and sometimes even more obvious than the lateral veins but definitely absent in the new species.

*Marattia anglica* (Thomas) Harris from the Middle Jurassic of Yorkshire is distinguishable from the new species because

of its larger spores (29  $\mu\text{m}$  in diameter, according to Van Konijnenburg-van Cittert 1975) and a higher percentage (30%) of trilete spores. *Marattia crenulata* (Lundblad 1950) from the Upper Triassic of Sweden is different from the new species because of its crenulate pinna margins and the proportionally very short (5%–6%) synangia, as well as the occurrence of ca. 10% trilete spores (Van Konijnenburg-van Cittert 1975).

The above-mentioned four species, *M. muensteri*, *M. hoerensis*, *M. anglica*, and *M. crenulata*, were considered by Kilpper (1964) to be synonyms of *M. intermedia* (Muenster), which was described on the basis of material from the Liassic of northern Iran. However, Schweitzer et al. (1997) thought it reasonable to keep *M. anglica* apart from *M. intermedia* because of the differing form of pinna base and spore size. Some of Kilpper's (1964) specimens of *M. intermedia* were referred to *M. barnardii* because of their smaller pinnae (1.8–2.2 cm wide), sparser venation (10–12 per cm), and shorter synangia (1–3 mm long) and the smaller number (8–18 pairs) of sporangia per synangium. The spores of *M. intermedia* were originally described as 25–35  $\mu\text{m}$  (Kilpper 1964) but later as 24  $\mu\text{m}$  in diameter by Schweitzer et al. (1997), and 10% of spores are trilete. *Marattia aganzhenensis* sp. nov. can be distinguished from *M. intermedia* by its smaller and purely monolet spores and smaller number of sporangia per synangium (table 1). According to Wang (1999), the characters of *M. intermedia* mostly vary within the same limits as those of *M. asiatica*, so the former might be a synonym of the latter.

Some other Chinese species of *Marattia* are described based solely on impression specimens showing the gross morphology of the pinnae, including *M. paucicostata* Li et Tsao (Li et al. 1976) from the Upper Triassic Yipinglang Formation of Yunnan; *M. orientalis* (Chow et Yeh, in Sze et al. 1963) for specimens from the Upper Triassic and Lower Jurassic of Yunnan, China, and Vietnam, Korea, and Japan; and *M. litanensis* Yang (Yang 1978) from the Upper Triassic of western Sichuan, China. These species can be distinguished from the new species by pinna sizes, density of venation, and the presence of venuli recurrentes. Meanwhile, the structure of the synangia of these species is unknown.

In brief, *M. aganzhenensis* sp. nov. is distinguished from other species of *Marattia* by the combination of such characters as absence of venuli recurrentes, synangia situated slightly distant from the margin, absence of trilete spores, monolet spores without marked ornamentation on the exine, and lower spore output. A comparison between the new species and other major Jurassic species of *Marattia* is presented in table 1.

## Discussion

The debate about the use of the generic name *Marattiopsis* versus *Marattia* has been long-standing. It was once considered that the major difference was the presence of venuli recurrentes in most fossil species but not in recent *Marattia*. However, similar venuli recurrentes have also been found in some species of the extant marattialean genus *Angiopteris* Hoffm. Consequently, venuli recurrentes could not be treated as a significant difference between the two genera (Harris 1961). Therefore, more and more authors use *Marattia* in preference to *Marattiopsis* because the fossils agree with the

living genus in all aspects (Kilpper 1964; Van Konijnenburg-van Cittert 1975; Li et al. 1976; Hsü et al. 1979; Li and Wu 1982; Hill et al. 1985; Schweitzer et al. 1997; Wang 1999). *Marattia aganzhenensis* sp. nov. shows the existence of a fossil marattialean species without venuli recurrentes. Meanwhile, the synangia of the new species are located 0.5–1 mm from the end of the secondary veins. This agrees well with the modern marattialean plants (e.g., *Angiopteris crassipes* Wall) and emphasizes the close affinity of the fossil and recent marattialean plants. Therefore, we also use *Marattia* in preference to *Marattiopsis*.

The distinction between fossil *Marattia* [al. *Marattiopsis*] species has been debated by many authors. Schweitzer et al. (1997) proposed that *M. intermedia* (Muenster), *M. anglica* (Thomas), *M. angustifolia* Prinada, and *M. barnardii* Schweitzer et al. did incorporate the more widely known specimens of *Marattia* in the Upper Triassic to Middle Jurassic. Harris (1961) stated that only six species were distinct (the first six in table 1). Kilpper (1964) stated that *M. hoerensis*, *M. muensteri*, and *M. anglica* should be attributed to *M. intermedia* (Munster) because the difference of the density of lateral veins of the three species might result from the different stages of ontogeny, whereas the variation of the length of the synangia might be due to the different stages of maturity and the position in a pinna. According to the investigation on the current specimens that may represent various ontogenetic stages, the density of secondary veins and the length of synangia can be very different because of the differing ontogenetic stages and the position on the pinna, but the ratio of the length of synangia to the width of the pinna varies very little at a particular position, appearing as a stable feature. Such a measurement on some pinnae with the same size from different species may be crucial. Consequently, the ratio of the length of synangia to the width of the pinna maybe used to distinguish *Marattia* species.

## Ontogenetic Development

Through light microscopy, it can be demonstrated that the spore walls of the current spores are granulate, scabrate, and morphologically well comparable to the dispersed genus *Marattisporites* Couper (1958). This is in accordance with the spore morphology of other known species of *Marattia* (Van Konijnenburg-van Cittert 1975; Wang 1999). Under SEM observation, however, there is no ornamentation noticeable on the outer (fig. 5L) and inner (fig. 5K) spore walls. Figure 5H demonstrates a spore that is finely microgranulate, possibly suggesting that the spore is still underdeveloped and ontogenetically juvenile. It is very likely that the granules visible under light microscopy represent the early phase of the granules before full maturity. At the current ontogenetic stage, they are developed only within the spore wall (exine) and may form the distinct granules during further development. The spores of *M. aganzhenensis* sp. nov. definitely suggest immaturity.

## Dehiscence

No specific dehiscence structure is visible, as is normal in other eusporangiate ferns and in living *Marattia* (Tryon and Tryon 1982; Gifford and Foster 1989, p. 234). Therefore, it

**Table 1**  
**Comparison between *Marattia aganzhenensis* sp. nov. and Other Jurassic Species of *Marattia***

	Pinna apex, base, margin	No. veins (cm <sup>-1</sup> )	Venuli recurrentes	Synangia/spores	Synangium length/ pinna width (%)
<i>M. hoerensis</i> Schimper	Apex pointed; base asymmetrically auriculate; margin entire or fine dentate	8–14, usually 10	Sometimes more obvious than lateral veins	2.5–7 mm long	20
<i>M. muensteri</i> (Goepfert)	Apex pointed; base circular; margin entire	10	Present	2 mm long?	10–20
<i>M. anglica</i> (Thomas)	Base contracted and rounded without an auricle; margin entire	10–12	Not obvious	4–7 mm long, 30 pairs of septa; spores 29 $\mu$ m, monolete, 30% trilete; spinule or verrucula	33
<i>M. angustifolia</i> (Prinada)	Apex very narrow and long; margin entire or with some blunt teeth, but the margin of pinnae with synangia are without teeth	13	Present		25
<i>M. asiatica</i> (Kawasaki)	Apex bluntly pointed; base rounded; margin entire or with blunt teeth	13–16	Present	2–8 mm long, 10–40 pairs of septa (all Chinese specimens have 25–40 septa); spores granular, 5% trilete	17
<i>M. crenulata</i> Lundblad	Margin with rounded teeth	9	Present	2–2.5 mm long, 10 pairs of septa; spores bean shaped, slightly granular, monolete, 10% trilete	5–6
<i>M. intermedia</i> (Muenster)		12–16		5–8 mm long, 21–30 pairs of septa; spores 24 $\mu$ m, 10% trilete	
<i>M. curvinervis</i> Lorch		26–34	Present	2–4 mm long	20–33
<i>M. barnardii</i> Schweitzer et al.	Apex obtuse; base cordate and slightly auriculate; margin sometimes serrate	8–14, usually 10–12	Absent	Bean shaped, 1–3 mm long, 8–16 pairs of septa; spores unknown	20–30
<i>M. aganzhenensis</i> sp. nov.	Apex pointed; base rounded; margin entire	10–16	Absent	2–5 mm long, 20 pairs of septa; spores bean shaped, all monolete, 14 $\mu$ m	12.5

Note. Based mainly on Harris (1961), Van Konijnenburg-van Cittert (1975), Schweitzer et al. (1997), and Wang (1999).

can be assumed that the synangia and the sporangia opened in a way similar to that in living *Marattia*. During preparation, when the macerated sporangia were pressed, the spores were found spreading out from three sides of the sporangia, except the side where the sporangia were attached to the secondary vein. Such a fact may suggest that the sporangia might spread its spores from the above-mentioned three sides without any special dehiscence structure. However, under SEM observation, the spores are also found exposed from the side where the sporangia are attached to the secondary vein (fig. 4G), apart from the lateral sides of the sporangia (fig. 4F).

In consideration of the immaturity of the synangia and sporangia, the exposure and spreading of the spores during preparation may be only the result of mechanical pressure, rather than any indication of a natural dehiscence of the sporangia. In brief, the dehiscence mechanism of the sporangia is uncertain. It lacks the longitudinal dehiscence structure that occurs in the extant marattialean plants (Tryon and Tryon 1982).

#### Spore Output

Examination of two sporangia and counting indicated that there are ca. 340 spores in a sporangium of the new species. Although such a result is not reliable enough to be treated as the spore output of the new species, it is thought that the sporangium of the new species certainly produces much fewer spores than other fossil species of *Marattia* of which the spore output is known (e.g., somewhat more than 1000 in *M. asiatica*, according to Wang 1999) and most extant species, which usually yield 1400–7500 spores per sporangium (Bower 1926; Rashid 1976; Hill and Camus 1986; Camus 1990).

#### Evolutionary Significance

It is thought that the extant *Marattia* can be derived via reduction from Mesozoic members, which also demonstrate a trend of reduction compared with the Paleozoic *Marattia*-like fern *Qasimia* (Hill et al. 1985; Wang 1999). From the Paleozoic

*Qasimia* to the Mesozoic and extant species of *Marattia*, the venation density and the synangium length decreased gradually. The crowded venation is regarded as good for bearing longer synangia. Meanwhile, the presence or absence of venuli recurrentes in Marattiales run parallel to this evolutionary trend. Venuli recurrentes may serve to strengthen the lamina and support the weight of the large synangia (Hill et al. 1985). They were present in most fossil species of Marattiaceae that bore longer synangia and disappeared in most extant members that bear shorter synangia. *Marattia aganzhenensis* sp. nov. demonstrates characters that are close to extant species, including the proportionally shorter synangia and the absence of venuli recurrentes. Besides, the synangia of *M. aganzhenensis* sp. nov. are slightly distant from the end of lateral veins and the margin of the pinnae. These character states also occur in the Rhaetian to Middle Jurassic species *M. barnardii* and in extant species of *Marattia*. Mamay (1950) considered

the migration of the sorus from a marginal to a more central position on the lamina as an evolved feature in several fern groups, and this may also be the case in the evolution of the synangia of *Marattia*.

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