

A NEW FERN FROM THE LOWER PERMIAN OF CHINA AND ITS BEARING ON THE EVOLUTION OF THE MARATTIALEANS

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ABSTRACT. A fertile marattialean fern from the Lower Shihhotse Formation, Lower Permian of Taiyuan, north China is ascribed to a new genus, *Taiyuanitheca*, as *T. tetralinea* sp. nov. The fronds are *Pecopteris*-like with two rows of synangia arranged on each side of the midvein on the adaxial surface of the pinnules. The synangia are sessile and ring-like with elliptical sporangia that are fused together along their full length. The new fern is compared with fossil and extant marattialeans and new evolutionary pathways are proposed for this group of plants.

PERMIAN strata are well developed in the Taiyuan area in north China and have been used as an index section for stratigraphical correlation in China. The Cathaysian flora proposed by Halle (1927, 1937) was based on the late Palaeozoic plants from this area. The Permo-Carboniferous plants of Taiyuan belong to the North Cathaysian flora which is characterized by lobatunnularias, tingias, emplectopterids and marattialeans (Li and Yao 1983; Zhang and He 1985). The present specimens were discovered during the course of a study on the Lower Permian plants from Taiyuan (Gao 1988). Re-evaluations of *Tingia* and *Tingiostachya*, cycadalean remains, and the enigmatic *Shuangnangostachya* have been published elsewhere (Gao and Thomas 1987, 1989a, 1989b, 1991).

Marattialean ferns are characterized by exannulate sporangia grouped into synangia. They have a long history and can be dated back to the Carboniferous. Extant genera have unbranched stems, large and fleshy adventitious roots and usually large fronds; all grow in tropical or sub-tropical areas.

During the Early Permian of North China, marattialeans played an important role in vegetation. Apart from this new fertile fern, there is also a number of associated sterile *Pecopteris* species: *P. orientalis* (Schenk) Potonié, *P. tuberculata* Halle and *P. wongii* Halle (Gu and Zhi 1974; Gao 1988).

MATERIAL AND METHODS

The specimens were collected by G.Z. in the summer of 1986 from the Lower Shihhotse Formation of Simugedong, Dongshan (East Hills), Taiyuan, north China. They are preserved in a grey shale as compressions with impression counterparts. Some *dégagement* of the specimens was achieved with the aid of tungsten needles sharpened by heating and subsequent dipping into molten sodium nitrite. Maceration of portions of the laminae and sporangia with Schultze solution unfortunately yielded neither cuticles nor spores. Sporangia were prepared for SEM observation by coating with gold, using an Emscope sputter coater, prior to examination with a Jeol T100 Scanning Electron Microscope.

The specimens (prefixed with GP) will be deposited in the Beijing Graduate School, China Institute of Mining.

SYSTEMATIC PALAEOLOGY

Order MARATTIALES G. Bitter *in* Engler and Prantl, 1902

Family MARATTIACEAE Berthold and Presl, 1802

Genus TAIYUANITHECA gen. nov.

Derivation of name. Taiyuan is the city nearest to the type locality; Greek 'theca', case or container.

Type species. *T. tetralinea* sp. nov., Lower Shihhotse Formation, Lower Permian, north China.

Diagnosis. Fertile frond at least bipinnate; pinna normally elliptical with truncated base; pinnule of *Pecopteris* type; midvein of pinnule almost to apex of pinnule. Two rows of synangia on each side of midvein; synangium sessile, ring-like. Sporangia elliptical, fused together along full length.

Taiyuanitheca tetralinea sp. nov.

Text-figs 1–2

Derivation of name. For the feature of four rows of synangia on each pinnule.

Locality. Simugedong, Dongshan (East Hills), Taiyuan, China.

Horizon. Lower Shihhotse Formation, Lower Permian.

Holotype. GP0112 (Text-fig. 2).

Diagnosis. Pinnule oblong, 12–16 mm long, 5–7 mm wide, apex rounded, attached almost perpendicularly to rachis by entire base. Margin of pinnule entire, with abaxially recurved edge about 1 mm wide. Lateral veins once dichotomized. Synangia ring-like, sessile, about 1 mm in diameter. Two rows of synangia, each with about 15 synangia, situated on each side of midvein. Sporangia elliptical, fused together along their entire length; approximately 12 sporangia in each synangium.

Description. Eight specimens (GP0032–34, 0066, 0111–0114) are compressions; some of them with their impression counterparts. The longest pinnate frond portion (GP0113) is about 220 mm long (Text-fig. 1A). The rachis is about 16 mm wide in the basal part and 6 mm in the upper part. The pinnae are about 4 mm wide, with two longitudinal ridges, and attached alternately at a 40°–60° angle to the rachis. The overall shape of the pinnae is linear-lanceolate. The longest pinna is about 120 mm long, although not complete. The pinnules alternate on the pinna rachis and are attached almost at right angles by their entire basal widths. They are 12–16 mm long and 5–7 mm wide, with parallel and entire lateral margins and rounded apices. The pinnules basipetally overlap each other very slightly. Another noticeable feature is a black coalified layer, about 1 mm wide, extending around the entire margin of the abaxial surface of the pinnule including the apex (Text-fig. 2A). This is interpreted as an abaxially incurved margin. In some pinnules the venation is seen to consist of a straight midvein almost reaching the pinnule apex and once-dichotomizing lateral veins (Text-fig. 2B). Two rows of about 15 ring-like synangia occur regularly along both sides of pinnule midveins (Text-fig. 2A) and each synangium has approximately 12 sporangia (Text-fig. 2C). The sporangia are entirely laterally fused like those of the living marattialean fern *Christensenia* Maxon.

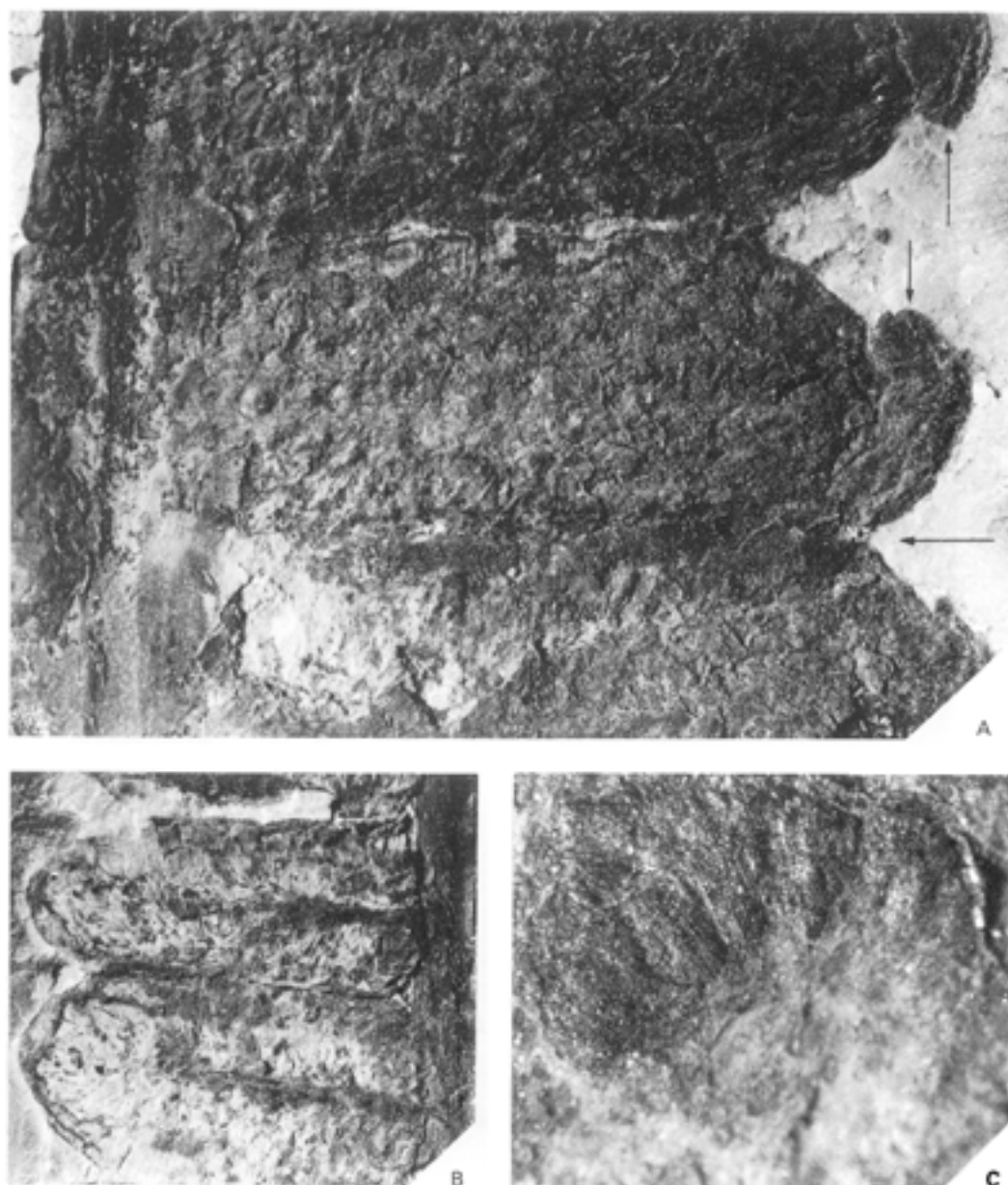
The exact attachment of the synangia to the pinnule is difficult to interpret because of the nature of the compression. Although the impression counterparts are badly preserved, it seems clear that the specimens are generally preserved with the abaxial surface of the pinna embedded into the matrix. During the splitting of the rock, the laminae of some of the pinnules have been lost so that the bases of the embedded synangia become visible. Occasionally, parts of a lamina compression, with midveins and lateral veins, have been preserved together with the synangia in the same compression. After carefully removing the midvein and lateral veins of the pinnule with a tungsten needle, the synangia can be observed beneath them. From this it seems certain that the synangia had constricted bases and were sessile on the pinnule lamina.



TEXT-FIG. 1. *Taiyuanitheca tetralinea* gen. et sp. nov. A, GP0113; bipinnate portion of frond with prominent rachis, pinna raches and the broken apex of the frond (arrowed), $\times 1$. B, GP0112; adaxial view of linear pinnules with thick pinna rachis, $\times 1$.

Comparison. The present specimens of *Taiyuanitheca tetralinea* show certain similarities to some other Permian compression marattialean ferns (*Rajahia* Konno, *Bifariusothea* Zhao, *Gemellitheca* Wagner *et al.* and *Dizeugotheca* Archangelsky and de la Sota).

Five species of *Rajahia* were described from the Late Permian of the Gunong Blumut area, Johore, Malaysia (Konno *et al.* 1970). The synangia of *Rajahia* are smaller than those of *Taiyuanitheca tetralinea*, and differ in being arranged in rows on both sides of the lateral veins running from the midvein to the pinnule margin, i.e. two rows of synangia occur between the lateral veins. Furthermore there is no visible pore on the apical part of the sporangium of *Taiyuanitheca tetralinea* unlike that in *Rajahia*.



TEXT-FIG. 2. *Taiyuanitheca tetralinea* gen. et sp. nov., GP0112. A, adaxial view of pinnules with incurved margins (arrowed) and four rows of synangia, $\times 6$. B, adaxial view of pinnules showing exposed veins, $\times 4$. C, synangium on the adaxial surface of a pinnule, $\times 4$.

Bifariusotheca was described from the Late Permian of Qinglong, Guizhou Province, south-west China (Zhao *et al.* 1980). The type species, *B. qinglongensis*, has two rows of synangia on each side of the midvein, as in *Taiyuanitheca tetralinea*, but the synangia are elliptical with their long axis at right angles to the pinnule midvein.

Gemellitheca was described from the Upper Permian of Saudi Arabia and Turkey with *G. saudica* as its type species (Wagner *et al.* 1985). Its pectopterid foliage has synangia that are exannulate, elongate in shape and situated at the distal end of the lateral veins. Each synangium is composed of two sporangial compartments (loculi), orientated at right angles to the pinnule midvein and margin that extend almost half-way across the pinnule before curving away from the lamina at their tips. The margins of the pinnules are abaxially infolded and cover a third to half of the pinnule half-width. From these characters it can be seen that the two genera have only a general overall resemblance, with their synangia and lamina margins being quite different.

Dizeugotheca was described by Archangelsky and de la Sota (1960) from Patagonia as having sori with sporangia consistently in groups of four, two of each group being largely overlapped by the other two. It differs therefore from the present specimens of *Taiyuanitheca tetralinea* in its sporangial arrangement.

There are several Euramerian marattialean ferns that bear some resemblance to *Taiyuanitheca*. *Ptychocarpus* Weiss, 1869, which was first described from the Upper Carboniferous of Breitenbach, Rhenish Prussia, is the closest. Following Weiss's original diagnosis, we understand *Ptychocarpus* to have bipartite and bilaterally symmetrical synangia, which appear to have elliptical outlines, that are arranged in one or two rows along each side of the midvein. Most distinctively the sporangia are fused along their full length such that there is a slight terminal elliptical depression at the top of the synangium. This differs considerably from the more hollow feature of the present specimens of *Taiyuanitheca tetralinea*. Furthermore, the outline of the synangia is also different, being rounded in *T. tetralinea* and elliptical in *Ptychocarpus*.

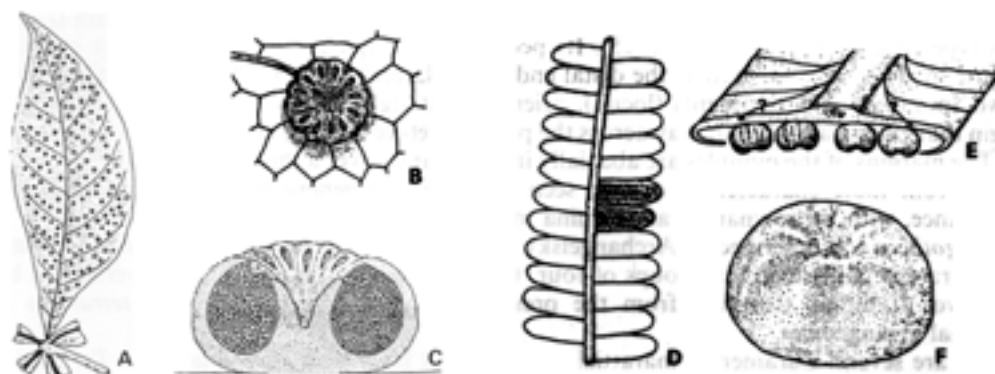
Many fertile specimens of *Pecopteris unita* Brongniart have been incorrectly named as *Ptychocarpus*. In fact, *Pecopteris unita* is a marattialean fern with both fertile and sterile pinnules. Its synangia, with a short pedicel at the base, are borne in two rows, one on each side of the pinnule midvein. Elongate sporangia are radially arranged and appear to be laterally free for a relatively short distance. The apices of the sporangia taper to an acute point. Therefore, *Taiyuanitheca tetralinea* shares certain features with *Pecopteris unita*, but differs in having its sporangia entirely fused.

Many Mesozoic marattialean ferns have been reported (e.g. Harris 1961; Van Cittert 1966; Hill 1987), but unfortunately they are usually poorly preserved compression specimens. Most of the Mesozoic marattialean ferns are difficult to distinguish from modern taxa and specimens most commonly found are similar to the extant *Marattia*, *Angiopteris* and *Danaea*.

Among the extant marattialean ferns, *Christensenia* shows the most similarity to *Taiyuanitheca tetralinea* for they both have circular and sessile synangia and almost the same number and shape of sporangia in each synangium (Text-fig. 3). The synangia of *Christensenia* are, however, irregularly distributed between the main veins on the abaxial surface whereas those of the *T. tetralinea* are regularly arranged into two rows on each side of the midvein. Furthermore *Christensenia* differs from *T. tetralinea* in having palmately compound fronds and also in having reticulate venation. Although the sporangia dehiscence mechanism of *T. tetralinea* is not perfectly understood, *Christensenia* is unusual in that each sporangium has an apical dehiscence slit for dispersing its spores rather than a longitudinal one as in some of the extant genera e.g. *Angiopteris* or a terminal pore as in *Danaea*.

DISCUSSION

Dehiscence. Dehiscence in the marattialean ferns may be by one of three methods (Bierhorst 1971). In the extant *Christensenia* Corda, dehiscence occurs by an apical slit in each sporangium. In the extant *Angiopteris*, *Macroglossum*, *Archangiopteris* and perhaps *Marattia*, dehiscence is by a longitudinal slit. In the extant *Danaea*, dehiscence is by a terminal pore. Dehiscence in the Carboniferous permineralized *Scolecopteris* can be apical (Millay 1979) or longitudinal (Mamay 1950; Millay 1977) as in *Acaulangium* (Millay 1977, 1987). In *Millaya* the sporangia probably separated distally and then dehisced through longitudinal slits on the inner-facing sporangial walls.



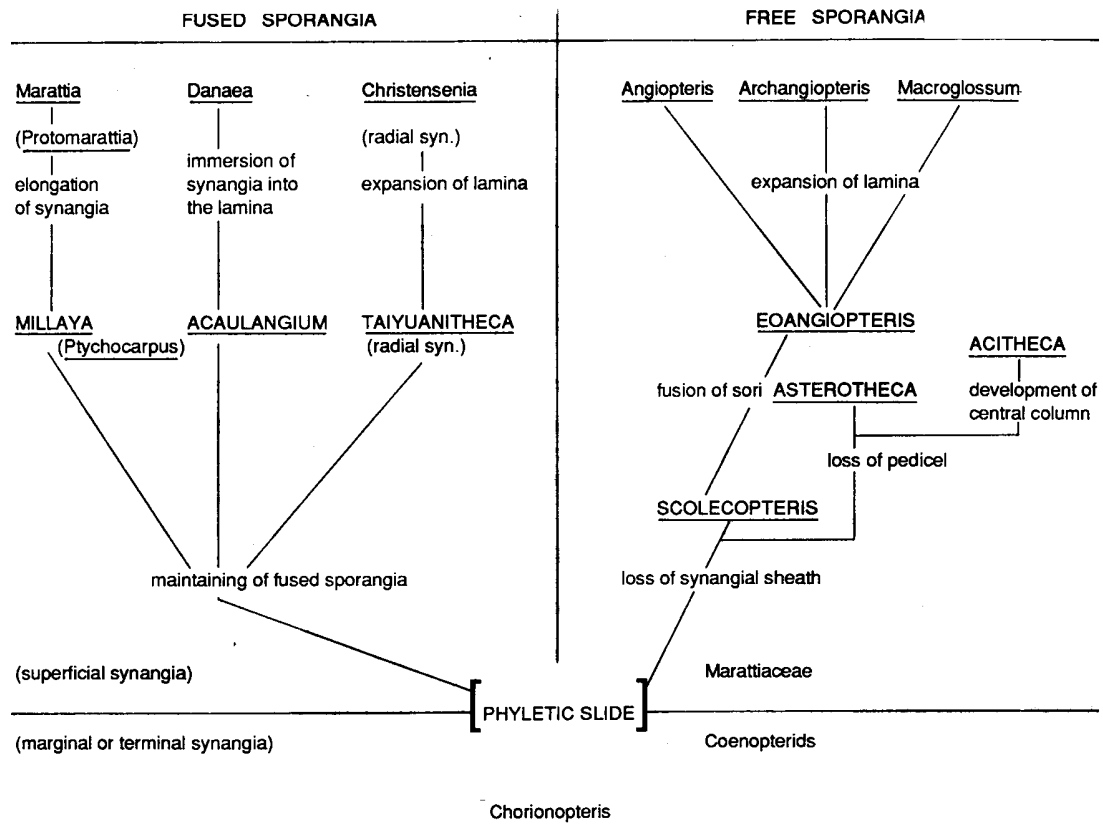
TEXT-FIG. 3. Comparison of *Taiyuanitheca* and *Christensenia*. A–C, *Christensenia* Maxon (after Bower 1926, from Engler and Prantl). A, single leaf palmately attached to a stalk with synangia distributed between the lateral veins, $\times 0.25$. B, single circular synangium viewed from its top showing sporangial composition and dehiscence split at the inside of upper part of each sporangium, $\times 5$. C, section of a synangium showing its sessile attachment to the lamina, $\times 14$. D–F, *Taiyuanitheca tetralinea* gen. et sp. nov. D, sketch drawing based on GP0112 and 113, showing the alternative arrangement of the pinnules and four rows of synangia with two on each side of midvein, $\times 0.5$. E, reconstruction of part of a pinnule, showing the synangial arrangement and incurved marginal lamina, $\times 5$. F, reconstruction of a single synangium showing the sporangial arrangement with depression in the centre, $\times 25$.

Araiangium also had its sporangia longitudinally separated for dehiscence (Millay 1982a). According to Bower (1908) dehiscence in *Ptychocarpus* was by terminal pores, although the specimens on which Bower's suggestion was based may belong to *Pecopteris unita* as discussed earlier. No special dehiscence structures can be seen in the sporangia of *Taiyuanitheca tetralinea*, although the longitudinal striations along the sporangia might indicate that the sporangia of *T. tetralinea* also dispersed their spores through a longitudinal opening in each sporangium.

Evolution. Mamay (1950) proposed two evolutionary pathways for the derivation of the *Asterotheca*-like fructifications. He considered *Chorionopteris* to be the ancestor. The *Ptychocarpus* type may have evolved from this by the retention of the pedicel and synangial sheath, along with the development of a central column. *Cyathotrachus* (*Scolecopteris* of Millay 1982b) would have been an intermediate. Then the *Asterotheca*-type may have been derived by the reduction of both the synangial sheath and the pedicel. Alternatively the *Scolecopteris* type could have been evolved by the reduction of the synangial sheath accompanied by the retention of the pedicel. With the development of a central column in a synangium of the *Asterotheca* type, an *Acitheca*-like fructification might have been produced. Although Mamay (1950) suggested that the radial sori (synangia) were more primitive than linear ones, he also stated that the radial sori (synangia) of *Christensenia* are apparently the most highly evolved form. Therefore *Christensenia* seems to occupy the highest position among those genera with fused sporangia. This seems to be supported by the fact that *Christensenia* possesses large laminae, reticulate leaf venation and creeping rhizomes (Sporne 1975; Hill and Camus 1986).

Mamay's phylogenetic hypothesis for the marattialean ferns has received little reaction although many workers have published on both fossil and extant marattialean ferns. As shown in Text-figure 3, the synangia of *Christensenia* and *Taiyuanitheca* show striking similarities. If *Christensenia* is taken, as generally accepted, to be advanced, the *Taiyuanitheca* form could then be interpreted to be an intermediate between *Ptychocarpus* and *Christensenia* in Mamay's 'phyletic slide'. Mamay's evolutionary diagram can then be modified as in Text-figure 4, taking into account the synonymy of *Cyathotrachus* and *Scolecopteris* (Millay 1982b; Stubblefield 1984).

Millay (1978, 1979), like Mamay (1950), considered *Eoangiopteris* to be the ancestor for the free-



TEXT-FIG. 4. Phylogenetic chart of marattialean ferns (based on Mamay 1950). Marattialean ferns are proposed as having been derived from the coenopterid fern *Chorionopteris* Corda. The superficial marattialean synangia and sori may have developed in one of two ways: those with fused sporangia (synangia) at the left of the vertical line, and those with free sporangia (sori) at the right. Three groups of the extant marattialean ferns with synangia (*Marattia* including *Protomarattia*, *Danaea* and *Christensenia*) may have evolved from three different groups, exemplified by *Millaya*, *Acaulanium* and *Taiyuanitheca*, as explained on left side of the chart.

sporangiate genera of marattialean ferns, because it shows many features in common with free-sporangiate extant genera like *Angiopteris* and *Macroglossum*. This idea is reproduced here in the phylogenetic chart.

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