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A 298-million-year-old gleicheniaceus fern from China

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Highlights

- Early Permian gleicheniaceus rachis with anatomical structure
- Whole-plant reconstruction proposed with rachis, fertile and vegetative fronds

- Earliest stratigraphical occurrence of a member of the Gleicheniaceae documented
- Gleicheniaceae diverged from other ferns by 298.34 ± 0.09 million years ago

ABSTRACT

The late Paleozoic genera *Chansitheca* Regè, *Oligocarpia* Göppert and *Szea* Z. Yao et T. N. Taylor are small ferns that represent putative early members of the Gleicheniaceae based on their morphology and the anatomy of their fertile organs. However, the rachis and cauline anatomy are unknown, rendering their systematic affinities controversial. Here we document rachides with partly preserved anatomical structure associated with compression/impression specimens of *Chansitheca wudaensis* from the Wuda Tuff Flora. The *in situ* preservation of the flora, occasional organic connection and close association, and matching size, proportions and xylem structure indicate that these rachides belonged to the same plant that produced fertile fronds of the *Chansitheca wudaensis* type and vegetative fronds of the *Sphenopteris* type co-occurring in this flora. The new details of the anatomy and morphology necessitate emendations to the diagnosis for this species. As the Wuda Tuff Flora has been dated to be 298.34 ± 0.09 million years ago (Asselian, Permian), this represents the oldest unequivocal evidence of Gleicheniaceae. Our results thus demonstrate that the Gleicheniaceae had already diverged from other ferns families, including the Osmundaceae, by this time.

Key word: Gleicheniaceae, *Chansitheca wudaensis*, rachial anatomy, Permian, Asselian

1 **1. Introduction**

2 Extant members of the Gleicheniaceae are mainly found in tropical and
3 subtropical regions in both the Old and New World, and encompass about 120–150
4 species belonging to six genera that include *Dicranopteris* Bernhardt, *Gleichenia*
5 Smith, *Sticherus* Presl, *Diplopterygium* (Diels) Nakai, *Gleichenella* Ching, and
6 *Stromatopteris* Mettenius (Bower, 1926; Kramer, 1990; Mickel and Smith, 2004;
7 Perrie et al., 2007). They are characterized by rhizomes with “vitalized” protosteles or
8 rarely solenosteles, pseudo-dichotomously forked fronds caused by a resting bud
9 (except for the monotypic genus *Stromatopteris*), exindusiate sori with simultaneous
10 maturation and large, round sporangia with a transverse-oblique annulus (Bower,
11 1926; Smith et al., 2006). Phylogenetic relationships of the Gleicheniaceae from
12 cladistic analyses of morphological and molecular data (e.g., Pryer et al., 2004; Pryer
13 et al., 2001; Pryer et al., 1995; Schneider et al., 2004; Schuettpelz et al., 2006; Smith
14 et al., 2006; Wikström and Pryer, 2005; Wolf, 1997; Wolf et al., 1998) demonstrate
15 they are monophyletic and closely related to the Dipteridaceae and Matoniaceae
16 (Smith et al., 2006).

17 In the fossil record, gleicheniaceous ferns are rare in the Paleozoic but become
18 more abundant during the Mesozoic. Fertile and vegetative fronds bearing lobed and
19 pecopteroid foliage have been ascribed to the genera *Gleichenia* and *Gleichenites*
20 Göppert. However, Nagalingum and Cantrill (2006), among others, pointed out that
21 the genus *Gleichenites* is invalid as the original specimens have been reassigned as
22 members of the seed ferns. Nevertheless, the genus name *Gleichenites* continues to be

23 widely used to refer to both fossil foliage and spores (e.g., Taylor et al., 2009).
24 Gleicheniaceus fossil plants with preserved cauline and rachis anatomical structure
25 are known from Cretaceous and younger strata, including *Gleichenia chaloneri*
26 Herendeen et Skog (Herendeen and Skog, 1998), *Boodlepteris turoniana* Gandolfo et
27 al. (Gandolfo et al., 1997) and *Gleichenia appianensis* Mindell et al. (Mindell et al.,
28 2006). However, even such materials were not readily linked to any extant lineage
29 (Perrie et al., 2007).

30 From the Paleozoic, *Oligocarpia* Göppert, *Szea* Z. Yao et T.N. Taylor,
31 *Chansitheca* Regè and *Henanotheca* Yang are all considered to be members of the
32 Gleicheniales (e.g., Abbott, 1954; He et al., 2016; Regè, 1920; Stevens and Hilton,
33 2009; Taylor et al., 2009; Wang et al., 1999b; Wang and Wu, 1999; Yang, 2006; Yao
34 and Taylor, 1988). *Oligocarpia*, a reproductive organ from the Carboniferous, has
35 been treated as the earliest member of the family (Abbott, 1954; Taylor et al., 2009),
36 while the oldest unambiguous evidence for such affiliation based on spore-wall
37 ultrastructure is from the Permian, *O. kepingensis* Y.D. Wang et X.Y. Wu (Wang and
38 Wu, 1999). However, *Oligocarpia* has also been regarded as belonging to the
39 Sermayaceae (Eggert and Delevoryas, 1967; Taylor et al., 2009), based on finds of
40 reproductive organs of *Oligocarpia* in organic attachment to an *Anachoropteris*-type
41 rachis (Eggert and Delevoryas, 1967). *Szea*, *Henanotheca* and *Chansitheca* are
42 reproductive organs that all show characters in general agreement with those of
43 gleicheniaceus ferns, but the rachides and stems of the plants that borne these
44 reproductive organs are still unknown. Although numerous species were established

45 for Paleozoic rachides and stems with anatomical preservation, none show the entire
46 suite of characters indicating affinities with the Gleicheniaceae (Taylor et al., 2009).

47 From 2007 to 2018, tens of thousands of fossil plant specimens were excavated
48 from the Wuda Tuff Flora (Wang et al., 2013), the so-called “vegetational Pompeii”
49 (Wang et al., 2012). This instantaneously preserved early Permian flora (Bashforth
50 and DiMichele, 2012; Wang et al., 2012) occurs in the 66 cm thick volcanic tuff
51 between the No. 7 and No. 6 coal seams in the Wuda Coalfield (Pfefferkorn and Wang,
52 2007; Wang et al., 2012; Wang et al., 2013). Amongst the large fossil assemblage
53 recovered, only a few dozens of specimens of *Chansitheca wudaensis* Deng et al.
54 (Deng et al., 2000) were discovered. These reproductive organs containing *in situ*
55 spores have been described in detail (Deng et al., 2000; He et al., 2016), but the
56 petiolar and cauline anatomy of the plant that produced them remained unknown. In
57 the present study, antepenultimate rachides, and rachides associated with fertile and
58 vegetative foliage of *C. wudaensis* are described from the Wuda Tuff Flora and a
59 review of *C. wudaensis* is given. We here present evidence that the associated
60 rachides belong to the *C. wudaensis* plant.

61

62 **2. Geological information**

63 The Ordos Basin contains abundant petroleum and coal resources and is a
64 secondary tectonic unit on the west of the North China Plate. During most of the
65 Permian, it formed a separate, large island in the tropics between the Tethys and
66 Panthalassic oceans (Wang et al., 1990; Ziegler et al., 1997; Guo and Liu, 2000). The

67 basin is constrained by the Yingshan and Daqing Mountains in the north, the Long
68 and Qiaoshan Mountain in the south, the Helan and Liupanshan Mountain in the west,
69 and the Lvliang-Taihang Mountain in the east (Wang, 1996). The basin itself is a
70 tectonic basin formed by the superposition and transformation of multi-stage
71 coal-accumulating basins, with coal-accumulation controlled by the conversion
72 process of Caledonian-Hercynian tectonic movements (Wang, 2011). The Wuda
73 Coalfield occurs at the northwestern margin of the Ordos Basin, northwestern of
74 Wuhai City, Inner Mongolia Autonomous Region of North China (Fig. 1).

75 The Permian lithological units exposed in and around the Wuda Coalfield from
76 the bottom to the top consist of the Taiyuan, Shanxi and Lower Shihhotse formations
77 (Wan et al., 2016; Liang et al., 2019). During the Permian, deltaic sedimentary
78 environments dominated this region (Wang et al., 2002); sedimentary microfacies
79 analysis indicates that the coal seams intercalated in the Taiyuan Formation were
80 deposited in deltaic plain sedimentary environments (Wang et al., 2016).

81 Palaeobiogeographically, the Wuda Coalfield belongs to the North China
82 phytogeographical realm (Shen, 1995; Shen et al., 1996; Wang and Shen, 1996; Wang
83 et al., 1999a). The Cisuralian (early Permian) plants of this area are generally quite
84 similar to those of central North China (Halle, 1927; Lee, 1963; He et al., 1995; Wang,
85 2010). During recent decades, fossil plant assemblages from the Taiyuan and Shanxi
86 formations have been subjected to detailed investigations. Taxonomy, anatomy,
87 sedimentology and taphonomy was combined to reveal the environment changes and
88 the forest succession, especially the assemblages from the No. 7 and No. 6 coal seams

89 of the Taiyuan Formation (e.g., Pfefferkorn and Wang, 2007; Wang et al., 2012; Zhou
90 et al., 2015; Liang et al., 2019). Four successive floras were recognized in the c. 5 m
91 thick section from the underclay of the No. 7 coal seam to the roof-shale of the No. 6
92 coal seam (Fig. 1; Pfefferkorn and Wang, 2007). Identification and quantitative
93 analyses of the Wuda Tuff Flora allowed the reconstruction of more than 1000 m² of
94 peat-forming forest (Wang et al., 2012). Seven groups of the plants compose the
95 peat-forming vegetation, including Lycopsidea, Sphenopsida, pteridophytes,
96 Noeggerathiales, pteridosperms (seed ferns), Cycadopsida and cordaitalean
97 coniferophytes.

98 The Wuda Tuff comprises predominantly kaolinite clay and quartz crystals. U-Pb
99 dating from zircon crystals in the tuff have determined a radiometric age of
100 298.34±0.09 Ma (Schmitz et al., 2020; this issue), thus placing the tuff in the Asselian
101 Stage of the Permian. The Rare Earth Element (REE) distribution of the tuff is
102 characterized by the enrichment of light rare earth elements (LREE) and negative δEu
103 values that indicates the tuff derived from a felsic volcano, and the magma derived
104 from a magmatic arc (Wang M. et al., 2020).

105

106 **3. Materials and methods**

107 Most of the specimens of *Chansitheca wudaensis* were collected from the lower
108 part of the Wuda Tuff horizon. In the collections, 68 *Chansitheca wudaensis*
109 specimens were examined and four specimens show the anatomical structure of the
110 rachides.

111 Anatomically preserved rachides were cut into pieces for making transverse and
112 longitudinal sections. All sections were prepared by the acetate peel technique (Galtier
113 and Phillips, 1999). Individual surfaces were successively ground on a glass plate
114 using #600 and #1000 carborundum grift, and etched using HF (concentration <10%)
115 for 120 seconds. Peels were mounted on glass slides using neutral balsam and a cover
116 slip.

117 Macrofossils were immersed in pure ethyl alcohol and photographed using a
118 Nikon D800 digital camera with a 60 mm macro lens (Kerp and Bomfleur, 2011).
119 Detail of the rachis and sorus were photographed using a Carl Zeiss STEMI 2000-C
120 stereomicroscope and DLC300-L digital camera using “dlc performance” software.
121 Microphotographs of slides were photographed using a Carl Zeiss Axio Scope A1
122 polar transmitted microscope with a digital camera ProgRes C5 using ProgRes
123 CapturePro 2.8 software. Multi-focus-level stacking was used and photomosaics were
124 composed by stitching together composite large photographs from smaller individual
125 images.

126

127 **4. Systematic palaeobotany**

128 *Family:* Gleicheniaceae (R. Brown 1810) C. Presl 1825

129 *Genus:* ***Chansitheca*** Regè 1920.

130 *Species:* ***Chansitheca wudaensis*** Deng, Sun et Li emended He et al. (Plates I–VI,
131 Fig. 2)

132 *Repository:* All preparations are from the same specimens, deposited in the

133 Palaeobotany collections of the Nanjing Institute of Geology and Palaeontology,
134 Chinese Academy of Sciences, with registration numbers PB 23071, PB 23278,
135 PB23279 and PB 23280.

136 *Locality:* Wuda Coalfield in Wuhai City, Inner Mongolia Autonomous Region,
137 North China.

138 *Geological horizon:* Lower part of the tuff between the Coal 7 and Coal 6, the
139 upper most part of the Taiyuan Formation.

140 *Stratigraphic age:* Asselian (early Permian), 298.34 ± 0.09 Ma.

141 *Emended diagnosis:* Frond at least bipinnate. Various order rachides and pinnule
142 midribs slightly flexuose. Penultimate rachides slender, with fine longitudinal striation.
143 Penultimate pinnae lanceolate, with contracted base, lobed in basal and middle
144 portions; in anadromous parts less strongly lobed, with 4–6 pairs of lobes. Midrib
145 slightly decurrent, forming a 60–70° angle to the ultimate rachis. Lateral veins
146 sympodial-dichotomously branched in lobes in the basal and middle portions of the
147 pinnules, and less branched in lobes in the upper part of a pinnule. Sori abaxial,
148 attached to the ends of lateral veins, without indusium, 2–4 per lobe. Sorus ovate to
149 elliptical, length/width ratio c. 1.5, with 4–10 sporangia, commonly 6–7. Sporangia
150 sessile, annulate, 200–400 µm in diameter, sub-triangular, pyriform or rectangular.
151 Annulus transversal, encircling middle to basal part, formed by 17–22 pairs of
152 elongated thick-walled cells, occasionally three cells high. Stomium composed of
153 narrow and elongate cells extending to basal part of sporangium. Spores trilete,
154 21.05–26.31 µm in diameter, exine smooth, with round to subtriangular amb;

155 interradial area straight or convex, radial areas rounded. Laesurae straight and
156 concave, extending to 2/3–3/4 of spore radius. Narrow interradial thickenings present
157 along and parallel to laesurae. Rachis with xylem adaxially recurved, C-shaped, 2–6
158 (mostly 2–4) cells thick, with or without strongly furled ends; 4–15 protoxylem poles
159 distributed along recurved face of the xylem. Metaxylem tracheids near furled ends
160 and xylem ends much smaller than in other places. Metaxylem tracheid walls
161 possessing uni- to multiseriate scalariform thickenings. Phloem adjacent to internal
162 face of xylem, absent from external face. Prickles, as small spines, and ridges
163 developed on upper side of rachis.

164 *Remarks:* The diagnosis presented above represents the characterization of the
165 whole-plant based on information recovered from a single bed in the Wuda coalfield.
166 The reconstruction is based on specimens in organic attachment and intricate
167 associations of morphologically similar specimens.

168 *Description:* Four specimens are demonstrated here to show the relationship
169 between the rachides and fertile fronds of *Chansitheca wudaensis*. Two of them show
170 the antepenultimate rachis of *C. wudaensis* (Plate I, 1–4), while the other two
171 represent rachides that are preserved intricately associated with *C. wudaensis* (Plate I,
172 5–8). The antepenultimate and associated rachides are about 7 mm thick (Plate I). The
173 transverse sections of the specimens shown in Plate I, 1, 2 and 5 were made from the
174 position marked by the dashed line. To obtain transverse sections of the rachis of the
175 specimen in Plate I, 6, the original slab was cut into five parts marked A–E, with the
176 cutting planes numbered 1 through 8 (Figure 2). A longitudinal section was made

177 from part E. After making the transverse sections, the surface of part C (Figure 2;
178 Plate I, 7, 8) was prepared and showed that the fertile fronds are not in organic
179 connection with the rachis.

180 The xylem strands in the transverse sections of antepenultimate rachides are
181 well-preserved and form an arc or an open C-shape (Plate II, 1–6; Figure 3 A). Four
182 protoxylem strands are present at the internal face of the xylem strand and the
183 metaxylem normally consists of 2–4 layers of tracheids (Plate II, 2–6). Tracheids of
184 the metaxylem are polygonal with smaller-sized tracheids (18–39 μm) at the internal
185 side and larger tracheids (45–72 μm) in the middle and at the external side of the
186 vascular bundle (Plate II, 1–6). At the end of the xylem strand, the tracheid size is
187 reduced to 7–22 $\mu\text{m} \times 10\text{--}20 \mu\text{m}$. On the epidermis, ridges are developed on the
188 adaxial side of the rachis (Plate II, 1–2, 4–6) and consist of elongated polygonal
189 parenchyma cells (Plate II, 6). The phloem and the cortex are not preserved.

190 The anatomical structure of the associated rachis of specimen PB 23280 is
191 imperfectly preserved (Plate II, 7, 8). However, the anatomical structure of the rachis
192 of specimen PB 23071 is preserved much better (Plate III). Although the associated
193 rachides are preserved differently, the xylem and phloem structures are quite similar.
194 The end of xylem strand is strongly enrolled with the protoxylem strand attached at
195 the internal face (Plate II, 7, 8). The phloem is present at the internal side of the xylem
196 strand (Plate II, 7, 8). Internal to the xylem, the phloem is differentiated into an outer
197 parenchymatous layer and an inner sclerotic, fibrous layer of thick-walled cells close
198 to the xylem (Plate II, 7).

199 The rachis structure of specimen PB 23071 is better preserved and less affected
200 by compaction. The outline of the rachis is asymmetrical and the xylem eccentric in
201 oblique and transverse sections of the rachis of specimen PB 23071 (Plate I, 6; Plate
202 III, 1, 2; Figure 2). The epidermis is represented by a structureless 10–40 µm thick
203 dark layer surrounding the rachis (Plate III, 1, 2). Epidermal hairs are present to the
204 right side (Plate III, 1). Ridges and prickles in the form of small spines are also
205 developed on the upper side of the rachis (Plate III, 2). In transverse section, the
206 rachis is c. 6 mm wide and c. 2.5 mm thick (Plate III, 2). The end of the C-shaped
207 xylem is 2–4 tracheids thick with strongly enrolled ends (Plate III, 2, 3; Figure 3 B).
208 Some parts of the xylem are separated by dark cells of the phloem (Plate III, 1; Plate
209 III, 2, 3).

210 Tracheids of the metaxylem are polygonal and with smaller tracheids (10–35 µm)
211 at the internal side and larger tracheids (50–100 µm) in the middle part and external
212 side of the vascular bundle (Plate III, 3). The xylem at the junction of the arch and
213 enrolled arms is constricted, and tracheid size is reduced to 6–26 × 14–34 µm (Plate
214 III, 1). On the transverse/tangential sections, most of the tracheids in the xylem strand
215 are isodiametric or slightly tangentially elongate (Plate III, 3 rectangle frame).
216 Individual tracheids are elongate and 54–91 µm (typically 60–80 µm) long and 35–90
217 µm wide, or isodiametric in diameter. Some very small and round tracheid clusters
218 occur at the internal side of the xylem (Plate III, 3 arrows; Plate IV, 1, 2). These small
219 tracheid clusters are interpreted as protoxylem poles of which fifteen are recognized
220 (Plate III, 3 arrows). In some protoxylem strands, individual tracheids are crushed

221 (Plate IV, 4) but where they are intact, they are generally in round in section (Plate IV,
222 2). Protoxylem tracheids are surrounded by large tracheids, showing endarch
223 maturation (Plate IV, 1, 2).

224 The phloem on the internal side of the xylem is well-preserved, whereas most of
225 the phloem on the external side is not preserved (Plate III, 1–3). Internal to the xylem,
226 the phloem is differentiated into an outer parenchymatous layer that is 20–120 μm
227 thick and comprised of cells with irregular shapes and sizes (Plate III, 3; Plate IV, 2,
228 3), and an inner sclerotic, fibrous layer of thick-walled cells close to the xylem (Plate
229 III, 1, 3; Plate IV, 1–4). Intercellular spaces are schizogenous and well-developed
230 (Plate IV, 4). The long axes of the cells in the phloem are along the tangential
231 direction (Plate IV, 3).

232 Most of the cortex is not preserved (Plate III, 1, 2), except for some parenchyma
233 cells adjacent to the epidermis (Plate IV, 5, 6). These cells are irregular in shape, c.
234 30–40 μm long and 15–25 μm wide, with sinuous cell walls. The long axis of the cells
235 is oriented along the tangential direction (Plate IV, 5, 6). Because this tissue is mostly
236 absent, we consider that it was entirely parenchymatous.

237 Surface ornamentation on the rachis includes ridges, prickles (small spines) and
238 unidentified appendages (Plate III, 1, 2). The ridges are strongly coalified to a degree
239 that structural details are indistinguishable (Plate III, 2). The prickles are triangular at
240 the base with long needle-like tips (Plate III, 2). The basal part of the unidentified
241 appendages is composed of irregular parenchyma cells (Plate V, 1). The cells in the
242 prickles and adjacent tissues are small, typically from 15 to 40 μm . Wall

243 protuberances occur at the internal cell walls (Plate V, 2).

244 Longitudinal sections through the rachis were all made from Part E. The lowest
245 section shows the ornamentation on the adaxial rachis surface (Plate V, 3–5). Two
246 clusters of cells are present on the adaxial rachis surface (Plate V, 3). The cells in the
247 smaller elliptical cluster are quadrangular and pentagonal, c. 50 μm in diameter and
248 approximately half of them are filled with dark material (Plate V, 4). The cells in the
249 larger lanceolate cluster are elongated polygons, considerably varying in size from 20
250 to 150 μm (Plate V, 5). When the longitudinal section cuts through the C-shaped
251 xylem and the strongly enrolled ends, the distribution of protoxylem (Plate V, 6 white
252 arrows), metaxylem and phloem can be easily observed (Plate V, 6; Plate VI, 3). Some
253 protoxylem tracheids with annular thickenings were destroyed (Plate VI, 1). In some
254 protoxylem tracheids, there are obvious spiral thickenings (Plate VI, 2, 5). Metaxylem
255 tracheids have scalariform thickenings. On narrow metaxylem tracheids, the
256 scalariform thickenings are uniseriate, while it is multiseriate in wider ones. Septa are
257 present in some wide metaxylem tracheids (Plate VI, 3 arrow). The phloem is dark- to
258 light-brown and the parenchyma cells are almost rectangular (Plate VI, 6). Because of
259 imperfect preservation, pits have not been observed (Plate VI, 6).

260

261 **5. Discussion**

262 5.1. Characterizing the *Chansitheca wudaensis* plant.

263 The associated rachis described here belongs to the fertile frond of *Chansitheca*
264 *wudaensis* in the Wuda Tuff Flora. The flora represents an instantaneously preserved

265 *in situ* fossil assemblage with minimal transport, and lacks post-depositional
266 disturbance such as burrowing or reworking. This indicates the close affinity of the
267 rachis to *C. wudaensis* in the source flora prior to the ash fall event. More important is
268 that the width of the associated rachides always matches that of antepenultimate
269 rachis of *C. wudaensis* fertile fronds. The rachides preserved associated with the
270 fertile fronds have the same anatomical structure. Furthermore, the xylem structure,
271 tracheids and ornamentation of the associated rachides are nearly identical to those of
272 the antepenultimate rachides of *C. wudaensis*. There are some differences between the
273 xylem of the antepenultimate and associated rachides, for instance, the strongly
274 enrolled ends of the xylem and the large number of protoxylem strands, which are not
275 observed in antepenultimate rachides. Furthermore, phloem is absent in
276 antepenultimate rachides. Such differences may be caused by different preservation
277 situation and/or different ontogenic stages for the antepenultimate and the associated
278 rachides. Such differences are to be expected in different organs of the same plant
279 species.

280 *Chansitheca wudaensis* is known from the morphology of the fertile frond
281 comprising naked sori, abaxially attached to the ends of the lateral veins, 2–4 in each
282 lobe; the sorus is ovate to elliptic, with 4–10 sessile annulate sporangia. The annulus
283 is transverse, encircling the middle to basal part of the sporangia. Spores are trilete,
284 21–26 µm in diameter, and have a smooth exine. Laesurae are straight and concave,
285 extending to $2/3 - 3/4$ of the spore radius (He et al., 2016). These features are
286 exclusively present in extant and fossil members of the Gleicheniaceae (e.g., Boodle,

287 1901; Ogura, 1972; Smith et al., 2006) from which we infer an affinity or close
288 relationship of this fossil to the Gleicheniaceae. However, its cauline anatomy is still
289 unknown. The anatomical structure and size of the associated rachides and
290 antepenultimate rachides of *C. wudaensis* are very similar and lend strong support that
291 they are from a single whole-plant species (see Bateman and Hilton, 2009), as does
292 their intricate association in the tuff. We consider that the associated rachides and
293 fertile fronds belong to the same whole-plant species. As in previous studies (He et al.,
294 2016), we conclude that the vegetative fronds of *C. wudaensis* were of the
295 *Sphenopteris*-type, which are also frequent in the Wuda tuff horizon, although there
296 not found in close association with the rachides. The frond is at least bipinnate. The
297 penultimate and ultimate pinnae are lanceolate. Lobed pinnules are lanceolate, with a
298 contracted base. Lateral veins are sympodial-dichotomously branched in the lobes.
299 We propose that these fossil plant species constituted a single whole-plant species
300 sensu Bateman and Hilton (2009) that represents the earliest stratigraphic
301 representative of the Gleicheniaceae.

302

303 5.2. Comparison and affinity on the rachis structure

304 During the late Paleozoic, several fern groups were characterized by C-shaped
305 petiolar xylem strands. Among these, the petiolar xylem of the Anachoropteridaceae,
306 Kaplanopteridaceae, Psalixochlaenaceae and Sermayaceae is abaxially curved,
307 whereas that of Psaroniaceae and Osmundales is adaxially curved (Ogura, 1972;
308 Taylor et al., 2009; Galtier and Phillips, 2014; Wang et al., 2014b). The rachis

309 described here is similar to that of marattialean fern *Psaronius* and members of the
310 Osmundales in having adaxially curved xylem and also in its position of their
311 protoxylem strands. However, the rachis in *Psaronius* can be distinguished from the
312 species described here in the features of its tracheid thickenings. Tracheids in the
313 rachis of members of the Psaroniaceae have uniseriate scalariform thickening (He et
314 al., 2013; Wang S.-J. et al., 2020, in this issue), whereas in *Chansitheca wudaensis* the
315 rachis it is uni- to multiseriate. Within the Osmundales, the rachis structure is very
316 similar to that of *C. wudaensis* and it is difficult to distinguish them based on their
317 xylem. However, in *C. wudaensis*, the rachis has xylem tracheids that are constricted
318 at the junction of the arch (Wang et al., 2014a). Vegetative and fertile fronds
319 belonging to members of the Osmundales are absent in the Wuda Tuff Flora, whereas
320 the here described rachides occur in intricate association with fertile fronds of the
321 putative gleicheniaceous fern *C. wudaensis* of which vegetative anatomy was so far
322 unknown.

323 Anatomically preserved rhizomes or petioles of Gleicheniaceae are rare in the
324 fossil record and most of these records are from the Mesozoic and the Eocene.
325 *Antarctipteris sclericaulis* Millay et Taylor 1990, a rhizome from the Triassic of
326 Antarctica, is assigned to the Gleicheniaceae on the basis of its mixed protostele,
327 simple frond trace, and scalariform tracheids. Unlike the rachis described here, the
328 petiolar xylem of the Antarctic specimens is C- to V-shaped vascular strands giving
329 off primary pinnae with V- to W-shaped vascular traces (Millay and Taylor, 1990),
330 which clearly distinguishes the taxa.

331 *Gleichenia chaloneri* Herendeen et Skog 1998, described from fusainized frond
332 segments from the Lower Cretaceous of England, is suggested as sister species to the
333 extant species *Gleichenia glauca*, based on cladistic analysis (Herendeen and Skog,
334 1998). *Gleichenia chaloneri* rachides resemble *Chansitheca wudaensis* rachides in
335 their simple C-shaped xylem; numerous protoxylem strands are present on the adaxial
336 side of the bundle and the features of its scalariform tracheid thickenings, although the
337 range of the number of protoxylem strands is larger in the latter. In the rachis of *G.*
338 *chaloneri*, tracheids are often in a single row unlike those in the *C. wudaensis*
339 rachides.

340 *Boodlepteris turoniana* Gandolfo et al. 1997, described from charcoalfied
341 remains from the Turonian (Late Cretaceous) of New Jersey, has been interpreted as a
342 sister species to the extant genus *Stromatopteris*. The petiole of *B. turoniana* is similar
343 to the rachides from Wuda in having a C-shaped vascular bundle, endarch
344 primary-xylem maturation and scalariform thickened tracheids. However, there are
345 many more protoxylem strands in the rachis from Wuda than in *B. turoniana*. The size
346 of the rachis is another difference between *B. turoniana* and the Wuda rachis, with the
347 petiole of *B. turoniana* being 0.8–1.4 mm in diameter (Gandolfo et al., 1997), while
348 the rachis from Wuda is much larger and is 6 × 2.5 mm in diameter.

349 *Gleichenia appianensis* Mindell et al. 2006 was described from a permineralized
350 rhizome and associated vegetative remains from the Eocene of British Columbia. *G.*
351 *appianensis* frond segments share several characters with the rachis of *Chansitheca*
352 *wudaensis*, including an inwardly folded and adaxially curved, C-shaped xylem,

353 numerous (five or more) protoxylem strands showing endarch maturation, scalariform
354 tracheids and regularly spaced horizontal septations. Mindell et al. (2006) mentioned
355 that the septa in the metaxylem tracheids of the frond trace is a feature unknown in the
356 extant *Gleichenia*, but such septa probably represent tyloses, which have been
357 observed in the stipes of numerous fern families (Ogura, 1972) and specifically in the
358 protoxylem of *Gleichenia* (Chrysler, 1943). In the rachis of *G. appianensis*, tracheids
359 are constricted at the lateral edges of the trace, whereas in the *C. wudaensis* rachis, the
360 tracheids are constricted at the inwardly folded arms.

361

362 5.3. Ornamentation

363 In extant gleicheniaceous ferns, ornamentation is commonly present on the
364 resting bud and on the abaxial side of the juvenile frond rachis (Boodle, 1901; Ogura,
365 1972; Lu, 2007), but the function is insufficiently known. Small prickles are
366 non-vascularized outgrowth from the surface of plant organs (Simpson, 2010). The
367 sharp-pointed tips usually provide physical defense against animals such as herbivores.
368 In some of the modern plant groups such as Rosaceae, prickles as hooked structures
369 could also produce frictional resistance for the function of scrambling (Gallenmüller
370 et al., 2015). In the late Paleozoic fossil record they sometimes were regarded as an
371 indicator of the vine- or liana-like growth habit (e.g., Li and Taylor, 1998; Krings et
372 al., 2001). However, *Chansitheca wudaensis* fronds with prickles on the rachis surface
373 are not associated with large tree trunks on which they could have climbed. During
374 field excavations, fronds of *C. wudaensis* were mainly preserved in the lower part of

375 the tuff bed and are in this context unlikely to have dropped from the treetops prior to
376 burial. On the other hand, the fronds of *C. wudaensis* were found preserved in clusters
377 and with individual specimens overlapping other (Plate I). This indicates *C.*
378 *wudaensis* may have grown in clumps or thickets and the fronds may have lent on on
379 each other providing mutual support like some Carboniferous species of *Medullosa*
380 (Krings et al., 2003). The prickles on the adaxial side forming prickly surfaces may
381 optimize such a growth habit. Furthermore, eight types of insect mediated damage
382 have been discovered on eleven host plant species from the Wuda flora (Feng et al.,
383 2020, in this issue). Although no feeding traces were detected on the *Sphenopteris*
384 fronds that represent the vegetative fronds of the *C. wudaensis* plant (He et al., 2016),
385 comparing with the trichomes on the leaves of *Anomozamites villosus* Pott et al. 2012,
386 the size and density of prickles on rachis of *C. wudaensis* was unlikely to have been
387 effective in warding off herbivorous insects. Therefore, the prickles of the rachis of *C.*
388 *wudaensis* are probably used for optimizing growth in thickets rather than for
389 scrambling or defending against herbivorous insects.

390

391 5.4. Timing the divergence of Gleicheniaceae

392 Previous molecular dating estimates conclude that the earliest divergence of the
393 Gleichenoids (Gleicheniaceae, Dipteridaceae, and Matoniaceae) occurred during the
394 Capitanian Stage of the Permian at approximately 263 Ma (Pryer et al., 2004), with
395 later divergence occurring in the mid-Triassic at approximately 227 Ma (Pryer et al.,
396 2004) coincident with the Carnian-Norian Stage boundary. However, divergences

397 within each of these families were estimated to be during the Cretaceous (Pryer et al.,
398 2004). Schuettpelz and Pryer (2009) predicted an older divergence for the
399 Gleicheniales at 276 Ma during the Kungurian stage of the Permian, but Pryer et al.
400 (2004) concluded they started to diversify before the end of the Palaeozoic during the
401 Capitanian Stage approximately 14 Ma after their origin. We interpret that the Wuda
402 species of Gleicheniaceae shows an earlier divergence for the Gleichenaceae at
403 298.34 ± 0.09 Ma, approximately 35 Ma before the earliest divergence time predicted
404 by Pryer et al. (2004) and 20 Ma before that predicted by Schuettpelz and Pryer
405 (2009). We also conclude that the range of other species assigned to the
406 Gleicheniaceae from the Permian (e.g., *Szea sinensis* Yao et Taylor, *Szea henanensis*
407 Yang, Sheng et Wang, *Oligocarpia kerpingsis*) indicates that shortly after their
408 origin, diversification was already underway within the group. The Cretaceous
409 diversification within the family indicated by Pryer et al. (2004) appears to represent a
410 second radiation event within the family.

411

412 5.5. Taphonomic consideration in plant morphologic restoration

413 Plant remains buried in sediments will experience compaction in diagenesis to
414 varying extents and will be compressed and deformed (e.g., Zodrow et al., 2005). This
415 phenomenon has been observed on the petrified sori and the vertically preserved
416 stems in the Wuda Tuff (He et al., 2016; Wang et al., 2013). Transverse sections of
417 gleicheniaceous fern rachides are almost circular, whereas the transverse section of
418 the rachis described here is an asymmetric, lenticular shape (Plate III) that has been

419 compressed. If we assume that the rachis did not expand laterally during compaction,
420 and the rachis originally is circular with its diameter matching its 6 mm width, the
421 compaction rate of the rachis can be calculated at 0.58 that is slightly larger than the
422 0.56 calculated for vertically preserved stems in the Wuda Tuff Flora (Wang et al.,
423 2013). The asymmetric rachis and eccentric xylem indicate the existence of slight
424 lateral expansion during compaction (Plate II, 1, 4; Plate III, 1–3). Therefore the
425 compaction rate from the rachis should be slightly smaller than 0.58. The xylem is
426 also affected by the compaction, and the elongated cells on both lateral corners may
427 be caused by compaction, because the directions of the tracheidal short axes consist
428 with the compression direction. The inrolled ends of the C-shaped xylem were nearly
429 crushed (Plate III, 1–2). Therefore, the shape of the xylem may originally have been
430 more circular.

431

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443

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653

654 **Figure and Plate Captions**

655 Figure 1. Locality maps and outcrop sections of the tuff bed in the Wuda Coalfield. A.
656 Outline map showing position of the Ordos Basin; B. Map of the Ordos Basin
657 showing main geological units and structural features (modified after Li, 2009); C.
658 Summary geological map of the Wuda Coalfield; D, E. Outcrop and lithological
659 column of the No. 7 and 6 Coal Seams and the tuff bed in between. The oldest flora
660 (Flora 1) was rooted in the underclay and initiated peat accumulation that led to the
661 formation of the lower coal (Coal 7), which is overlain by the volcanic tuff. In the
662 middle-lower part of the tuff bed, a second flora (Flora 2, the Wuda Tuff Flora) is

663 preserved, which grew on the peat at the time of the ash-fall. The upper part of the tuff
664 was rooted by a single lycopsid species (Flora 3), again initiating peat accumulation
665 (Coal 6). The roof-shale of Coal 6 yielded the fourth flora, representing the vegetation
666 that lived around a lake that flooded the coal swamp.

667

668 Figure 2. Location of saw cuts for preparation of specimen PB 23071, preparing five
669 parts numbered A–E, with cut surfaces numbered 1–8. Scale bar = 1 cm

670

671 Figure 3. Schematic diagram showing the structure of the antepenultimate rachis of
672 *Chansitheca wudaensis* and associated rachis. px: protoxylem; ph: phloem; r: ridge; x:
673 xylem. A. antepenultimate rachis of *Chansitheca wudaensis*; B. associated rachis.

674

675 Plate I. *Chansitheca wudaensis* fertile fronds showing antepenult rachides and
676 associated rachides; dashes indicate cutting positions.

677 1, 2. *Chansitheca wudaensis* fertile fronds showing antepenultimate rachis. Scale bar
678 = 2 cm. Specimen in 1 is PB 23278 and 2 is PB 23279.

679 3. Detail of Plate I, 2, showing the organic connection between the antepenultimate
680 and penultimate rachis. Scale bar = 2 mm.

681 4. Detail of Plate I, 2, showing an ultimate pinna and sori. Scale bar = 2 mm.

682 5. The thick rachis associated with fertile fronds of *Chansitheca wudaensis*. Specimen
683 PB 23280. Scale bar = 1 cm.

684 6. The rachis (arrow) preserved with *Chansitheca wudaensis* fertile fronds that are at

685 different depth in the matrix. Specimen PB 23071. Scale bar = 1 cm.

686 7. Part C of figure 2 with complete surface preparation of specimen PB 23071,
687 showing the relationship of *Chansitheca wudaensis* fertile frond (white arrows) and
688 associated rachis (black arrow). Scale bar = 1 cm.

689 8. Detail of Plate I, 7 showing the ultimate pinna and pinnules with sori. Scale bar =
690 1mm

691

692 Plate II. Transverse sections from antepenultimate rachides of *Chansitheca wudaensis*
693 and associated rachis. ep = epidermis; px = protoxylem; ph = phloem; r = ridge; x =
694 xylem.

695 1–3. Transverse sections (slide PB 23278 - T1) from specimen in Plate I, 1 (PB
696 23278), showing strongly compressed rachis preserved epidermis (ep), xylem and
697 ridge (r). Scale bar = 1000 μm . 2. Detail of Plate II, 1, showing the tracheids and
698 protoxylem (px), the epidermis was compressed and adjacent to the xylem strand.
699 Scale bar= 200 μm . 3. Detail of Plate II, 1, showing the curved end of the xylem
700 strand, arrow indicates protoxylem (px). Scale bar = 200 μm .

701 4–6. Transverse sections from the specimen PB 23279 (Plate I, 2) showing
702 compressed rachis of *Chansitheca wudaensis* with open C-shaped xylem (x) and 2
703 ridges (r) at the adaxial side. 4 from slide PB 23279-T1, scale bar = 500 μm . 5 from
704 slide PB 23279-T2, scale bar = 1000 μm . 6. Enlargement from 5, showing detail of
705 the xylem (x), protoxylem (px; arrows) and ridge (r). Scale bar = 200 μm . 7–8.

706 Transverse section of slide PB 23280-T1 from specimen PB 23280 from Plate I, 5.

707 7. showing C-shaped xylem (x) with furled ends and phloem (ph). Scale bar = 500

708 μm .

709 8. Detail of Plate II, 7, showing the xylem (x) and protoxylem (px) (arrow) born at the

710 adaxial side. Scale bar = 1000 μm .

711

712 Plate III. Transverse sections (slightly oblique) of the associated rachis from specimen

713 PB 23071 shown in Plate I, 6.

714 1. Section from cutting surface 1, showing C-shaped vascular bundle with strongly

715 furled ends and ornamentations attached on the epidermis. Slide number AT 1009.

716 Scale bar = 1000 μm .

717 2, 3. Section from cutting surface 6 with small cortex (c) adjacent epidermis (ep)

718 preserved; ornamentation including ridges (r) and spines (s) present on the epidermis

719 (ep); xylem (x) is C-shaped, and phloem (ph) present at the internal face of the xylem.

720 Slide DT 6010. Scale bar = 1000 μm . 2 Entire transverse section of the rachis, and 3

721 showing the xylem with multiple protoxylem (px) strands present at the internal side

722 of the C-shaped xylem (arrows).

723

724 Plate IV. Details of the xylem and cortex of the associated rachis from specimen PB

725 23071 shown in Plate I, 6 and Figure 2. Part D cutting surface 6; 1–5 from slide DT

726 6010; 6 from slide DT 6006.

727 1, 2. Detail of Plate III, 3, showing the xylem. 1. Protoxylem (px) present at the

728 internal side of the metaxylem (mx), and most cells of the protoxylem were not

729 preserved. Scale bar = 100 μm ; 2. Protoxylem and metaxylem on the end of the xylem.

730 Scale bar = 50 μm .

731 3. Detail of Plate III, 3, showing the metaxylem (mx), phloem (ph) and thick-walled

732 fibre cells between them. Scale bar = 100 μm .

733 4. Detail of Plate III, 3, showing the phloem and the well-developed intercellular

734 space (arrow). Scale bar = 20 μm .

735 5, 6. Detail of the cortex adjacent to the epidermis. Scale bar in 5 = 200 μm and in 6 =

736 50 μm .

737

738 Plate V. Details of the ornamentation and the longitudinal sections of the associated

739 rachis of specimen PB 23071 shown in Plate I, 6. 1, 2 are from Part D cutting surface

740 6, slide number DT 6010; 3–6 are from Part E, with 3–5 from slide E 001; 6 is from

741 slide E 006.

742 1, 2. Detail of Plate III, 2. 1 showing the base of a hair. Scale bar = 50 μm . 2. Details

743 of the prickles (small spines) and adjacent tissue. Scale bar = 20 μm .

744 3. Ridges and other ornamentation on the adaxial side of the rachis. Arrow indicates

745 the ridge. Scale bar = 1000 μm .

746 4. Detail of a in Plate V, 3, showing the elliptic base of ornamentation, composed of

747 isodiametric parenchyma cells filled with black material. Scale bar = 200 μm .

748 5. Detail of b in Plate V, 3, showing the lanceolate ornamentation, composed of

749 elongated parenchyma cells. Scale bar = 200 μm .

750 6. Longitudinal section of the xylem, showing the positions of protoxylem (px),

751 metaxylem (mx), phloem (ph) and the epidermis (ep), arrow indicates the protoxylem.

752 Scale bar = 1000 μm .

753

754 Plate VI. Longitudinal sections and details of associated rachis specimen PB 23071

755 shown in Plate I, 6. 1–3 are enlarged from Plate V, 6 from Part E, slide number E006;

756 4–6 are from Part E, slide number E 008.

757 1. Enlargement from frame a in Plate V, 6, showing imperfectly preserved protoxylem

758 (px) and metaxylem (mx) with multiseriate scalariform thickenings. Phloem (ph) is

759 dark. Scale bar = 25 μm .

760 2. Enlargement from frame b in Plate V, 6, showing spiral thickenings on the

761 protoxylem (px) tracheid walls and uniseriate or multiseriate scalariform thickenings

762 on metaxylem (mx) tracheid walls. The adjacent phloem is in dark-colored. Scale bar

763 = 100 μm .

764 3. Septa (arrow) in the multiseriate scalariform thickening tracheids. Scale bar = 25

765 μm .

766 4. Longitudinal section of the rachis showing the entire section. Scale bar = 1000 μm .

767 5. Enlargement from frame a in Plate VI, 4, showing dark brown phloem (ph), spiral

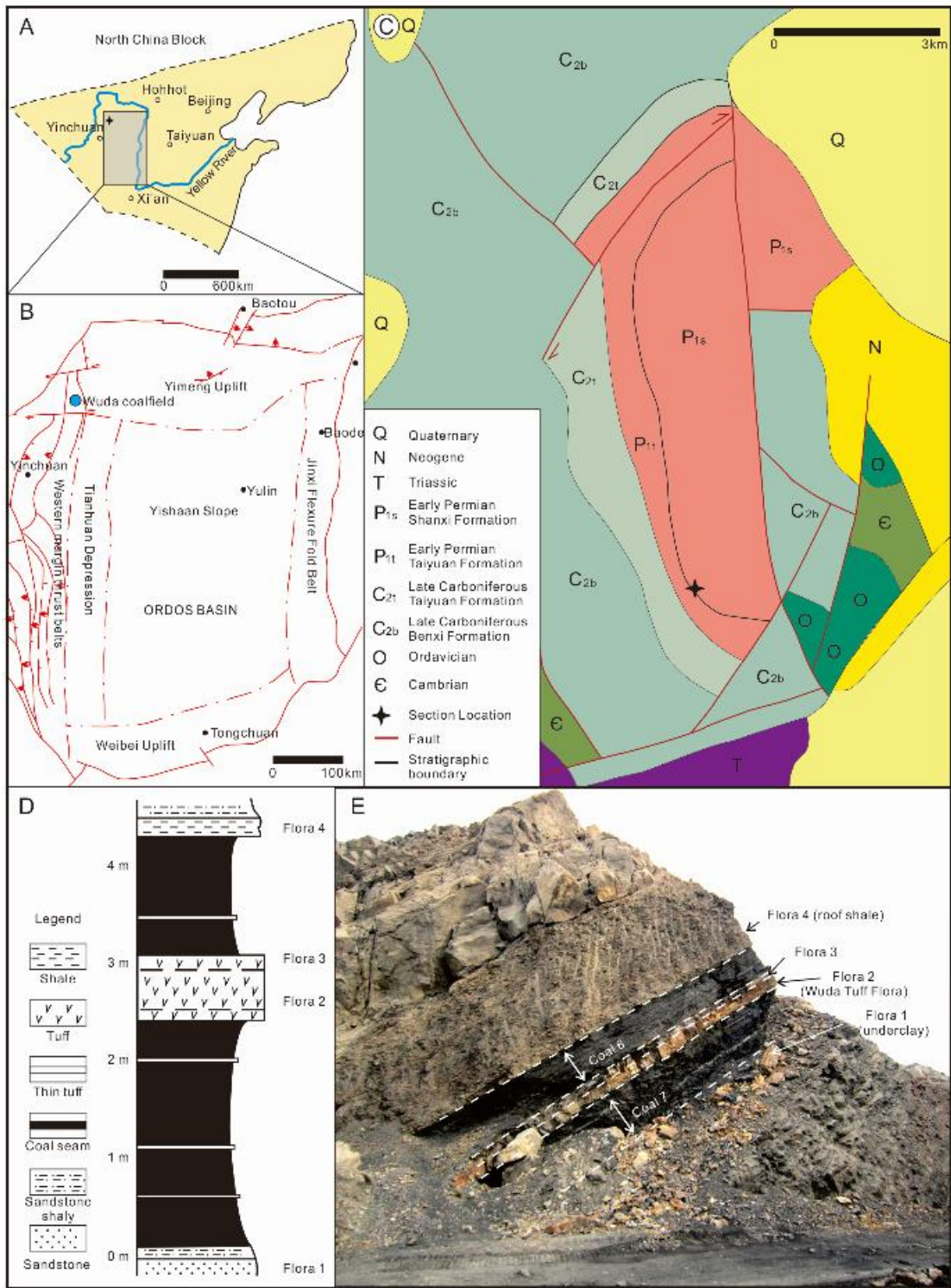
768 thickenings on protoxylem (px) tracheid walls and the scalariform thickenings on

769 metaxylem (mx) tracheid walls. Scale bar = 100 μm .

770 6. Enlargement from frame b in Plate VI, 4, showing the brown phloem (ph). Scale

771 bar = 100 μm .

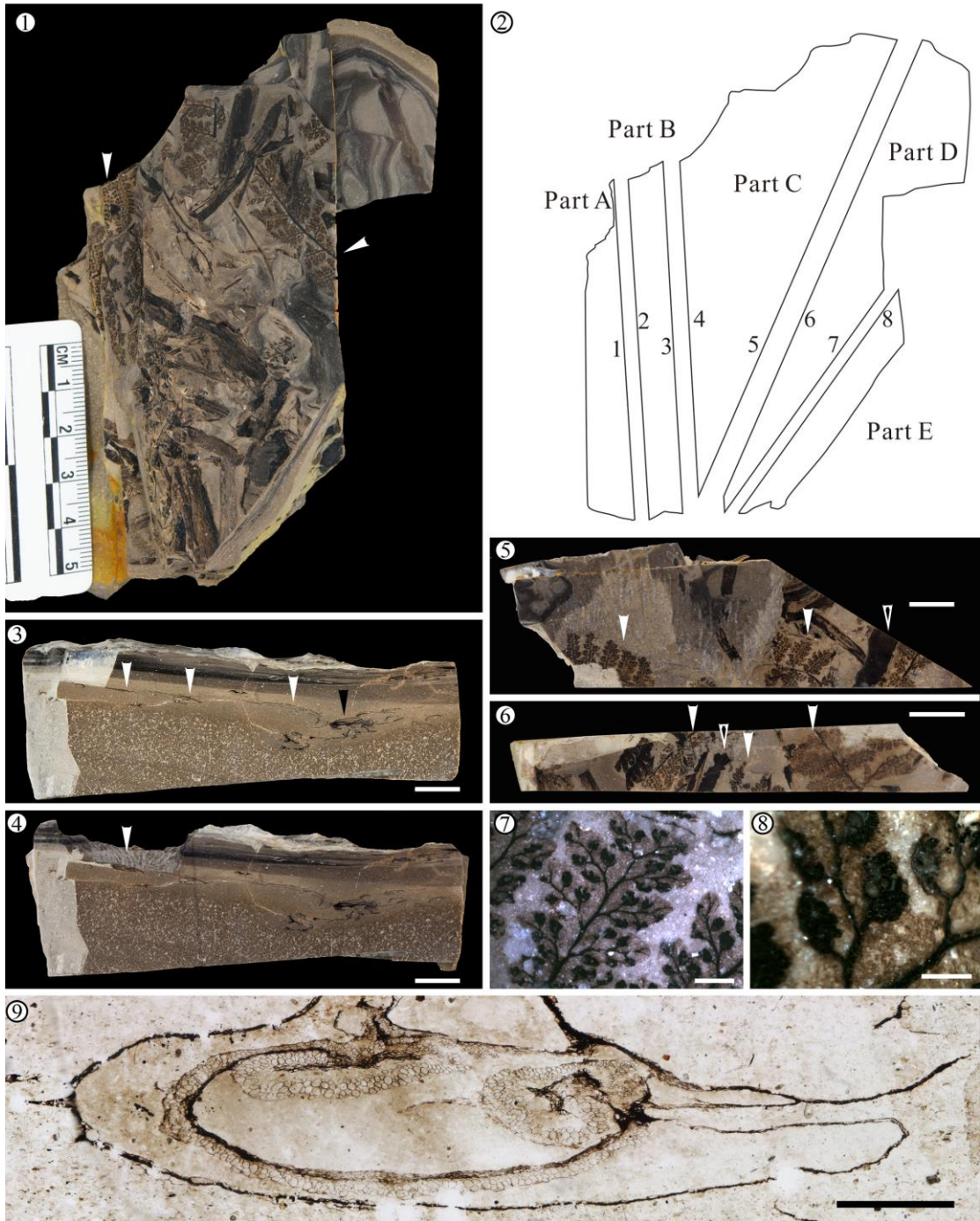
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775 Figure 1

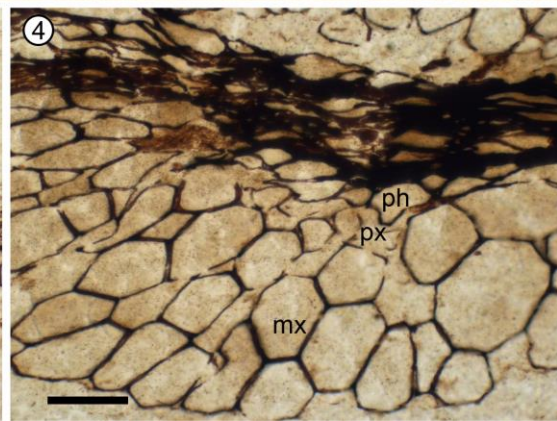
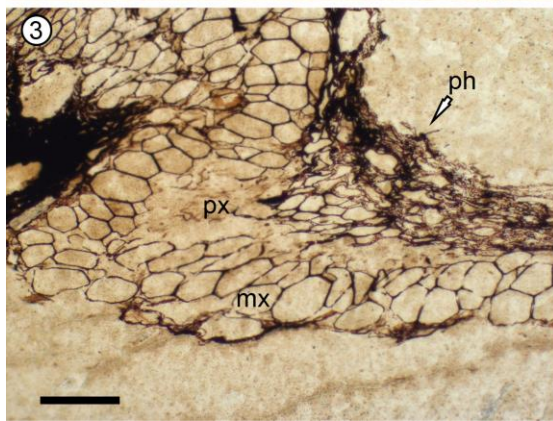
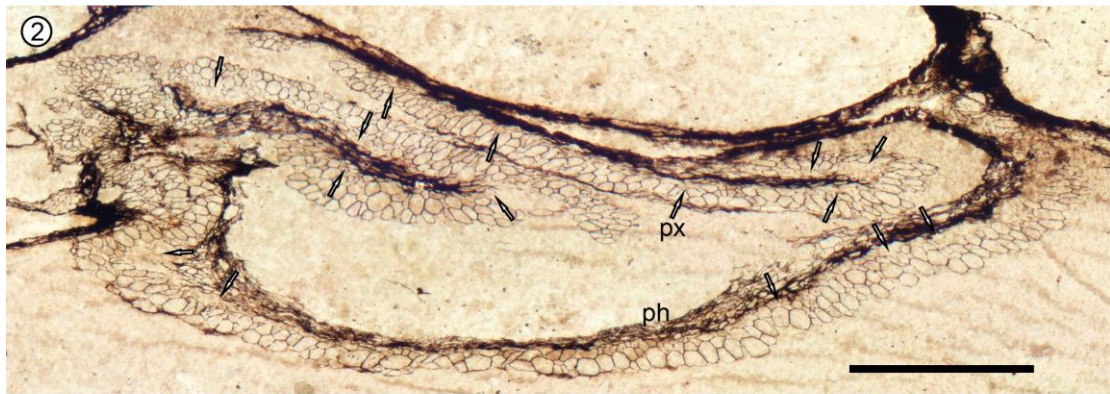
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778 Plate I

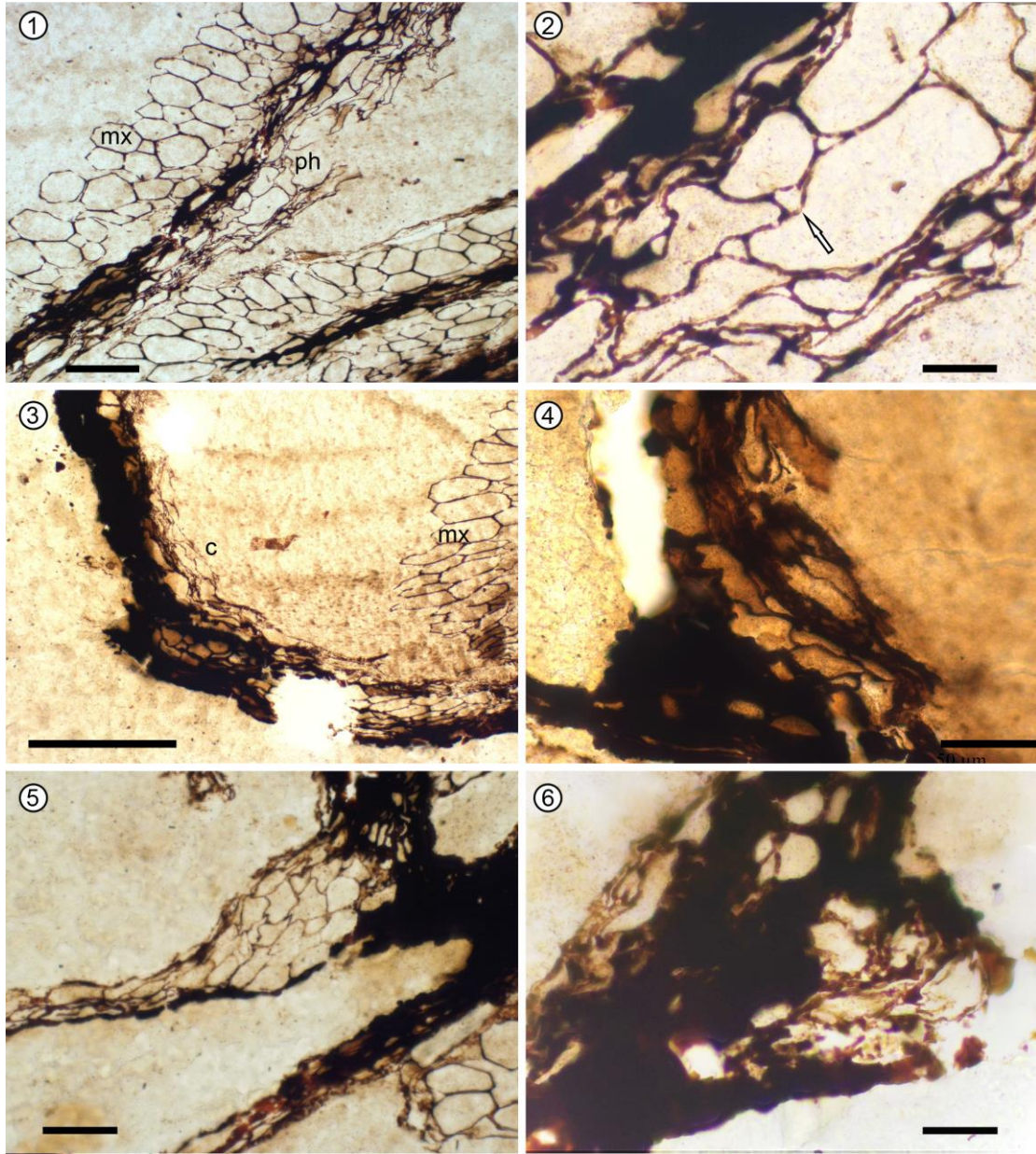
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781 Plate II

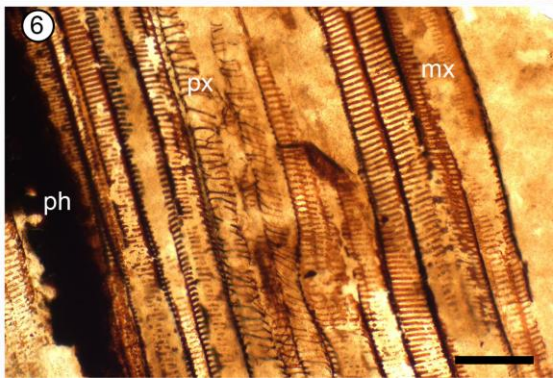
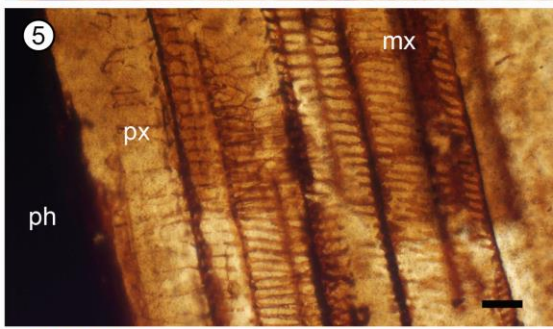
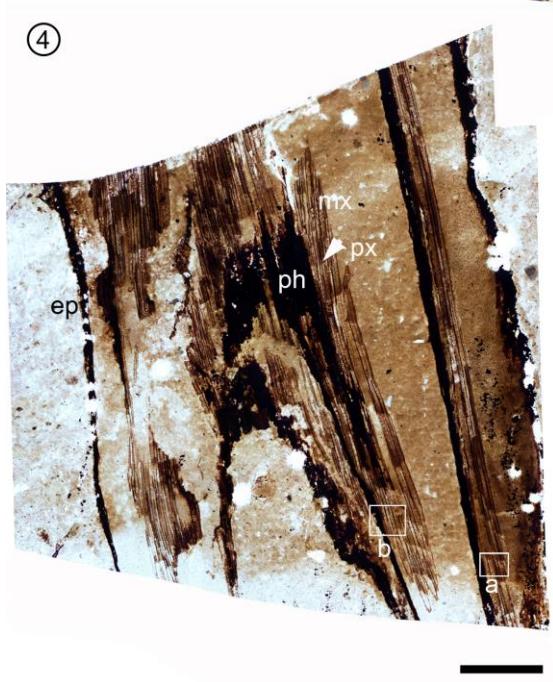
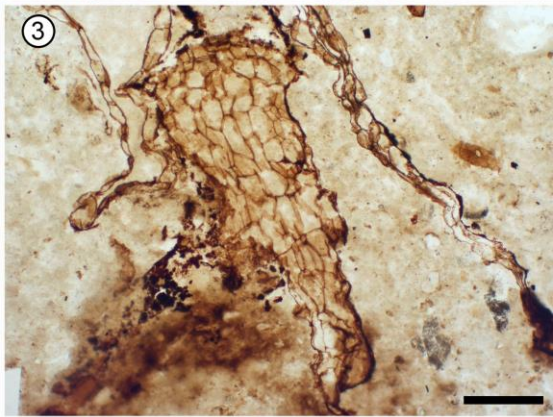
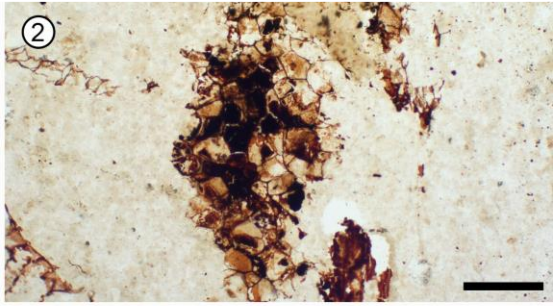
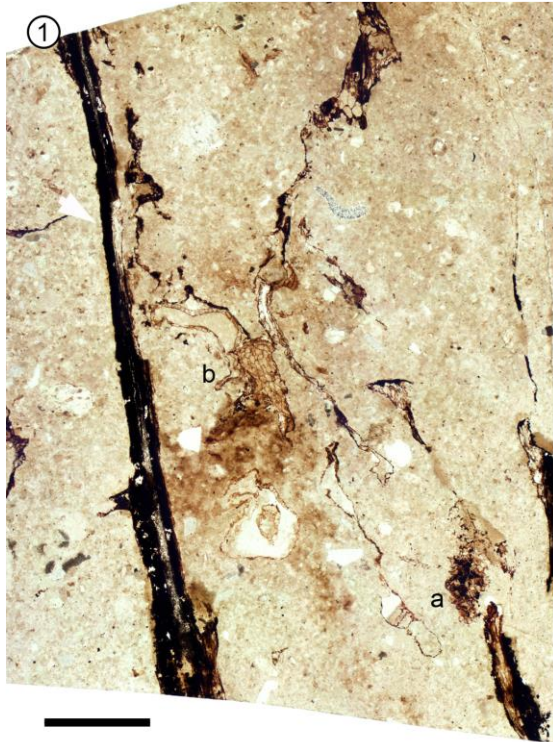
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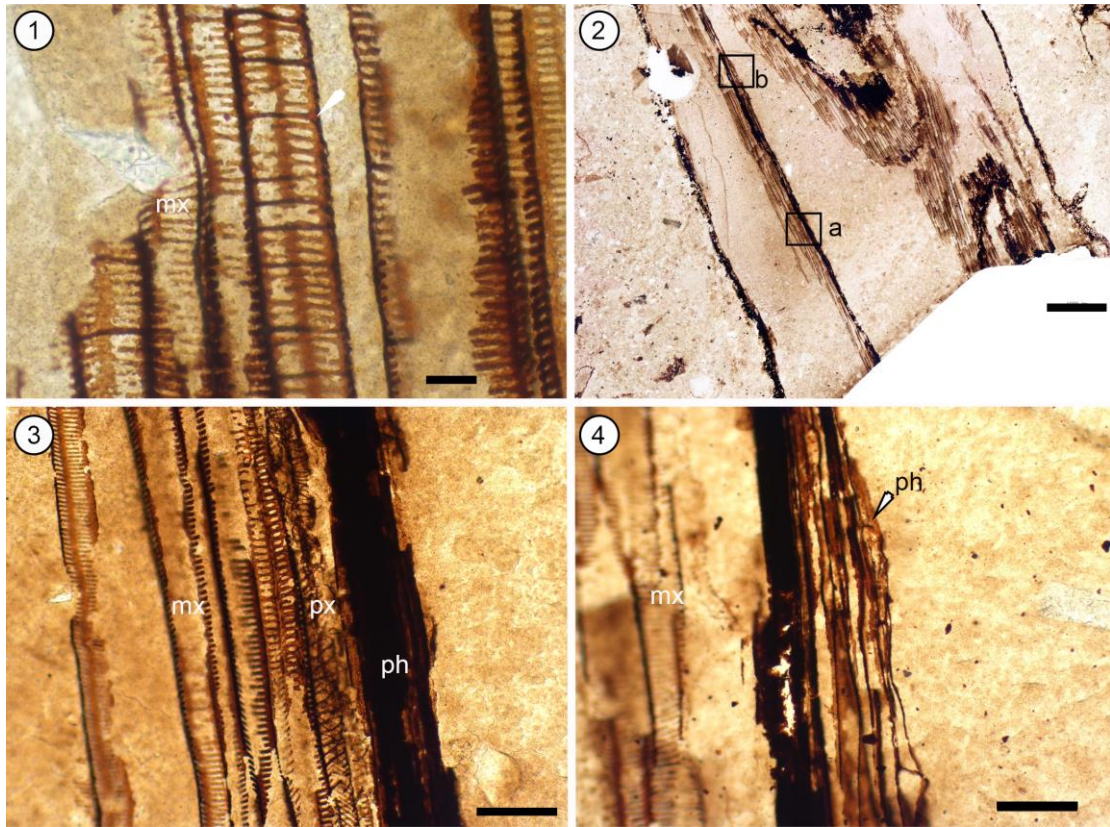
784 Plate III

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786

787 Plate IV



788

789 Plate V

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