

Yangopteris ascendens (Halle) gen. et comb. nov., a climbing alethopterid pteridosperm from the Asselian (earliest Permian) Wuda Tuff Flora

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1 ***Yangopteris ascendens* (Halle) gen. et comb. nov., a climbing**
2 **alethopterid pteridosperm from the Asselian (earliest Permian) Wuda**
3 **Tuff Flora**

4
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20

21

22 **ABSTRACT**

23 *Alethopteris ascendens* Halle is an endemic element in the Permian Cathaysian floras and is assumed
24 to be a member of the Medullosales based on its alethopterid type foliage. Previous accounts have
25 documented only its pinnae and bipinnate fronds, but other parts of the plant are unknown. Here we
26 describe new specimens from the earliest Permian (Asselian) Wuda Tuff Flora that are identified as *A.*
27 *ascendens*, but shows additional features including an integrated structure comprising an apical
28 hooked prolongation with two lateral rows of hooked spines. Investigation of previously published
29 specimens from another location confirms that they also bore the same kinds of hooked appendages.
30 Systematic comparisons demonstrate that *A. ascendens* is distinct from previously recognized
31 members of the genus but that it does not conform with the generic diagnosis, leading to the
32 establishment of *Yangopteris ascendens* gen. et comb. nov. The appendages in *Y. ascendens* are
33 interpreted as climbing devices, and are most similar to those previously described pteridosperm
34 *Karinopteris* from the Pennsylvanian of Euramerica. Similarities in the specialized climbing
35 structures in *Y. ascendens* with alethopterid foliage and *Karinopteris* with mariopterid foliage suggest
36 ecological convergence in unrelated pteridosperms within late Paleozoic peat-forming swamp
37 ecosystems of Euramerica and Cathaysia. In addition, associated naked axes that co-occur with *Y.*
38 *ascendens* are interpreted to be the main stems of the species. The growth habit of *Y. ascendens* is
39 presumed to be a semi-self-supporting plant but also with a hook-climbing habit, with this similar to
40 modern climbing palms.

41

42 **Keywords:** Medullosales, hooked prolongations, hooked spines, hook-climber, ecological

43 convergence

44

45 **1. Introduction**

46 Lianas, vines and other climbing and scrambling plants gain competitive advantage over other
47 plants by climbing upward to external supports to intercept light (Gianoli, 2015). Modes of
48 attachment to the support media were first categorized by Darwin (1867), including twining, leaf
49 bearers, tendril bearers, hooks and adventitious roots. Ancient plants with possible climbing
50 appendages can be trace back to the Middle Devonian in the lycopsid *Leclercqia* that had hooked
51 structures from North Xinjiang, China (Xu et al., 2011). In stratigraphically younger
52 Pennsylvanian-aged peat-forming swamps, numerous pteridosperms have been considered to be
53 scramblers or climbers based on a diverse range of adaptations for attachment. These include hooks
54 for grasping (Huth, 1912; Halle, 1929; Corsin, 1932; White, 1943; Boersma, 1972, 1991; DiMichele
55 et al., 1984; Kerp and Barthel, 1993; Kerp and Krings, 1998; Krings et al., 2001a, 2001b, 2003a;
56 Seyfullah et al., 2014), pads for adhering (Krings and Kerp, 1999; Zhou et al., 2019; Pšenička et al.,
57 2020), tendrils for anchoring (Krings and Kerp, 1997; Krings et al., 2003c), and also putative or real
58 examples of axis twining (Gradziński and Doktor, 1995; Cleal and Thomas, 1999; Opluštil, 2009;
59 Zhou et al., 2019). The late Paleozoic scrambling/climbing pteridosperms in ancient peat-forming
60 forests communities have been suggested to play similar roles to angiospermous lianas in modern
61 tropical and subtropical forests (Krings et al., 2003c). However, these plants differ from true lianas
62 within the angiosperms that possess water-conducting vessels that allow low resistance to water flow
63 (e.g., Rowe and Speck, 1998; Kozłowski and Pallardy 2002; Masselter et al., 2007), with all known
64 Paleozoic pteridosperms from which anatomical preservation is known lacking vessels (e.g. Hilton
65 and Bateman, 2006). Although of unknown systematic affinity and belonging to either the

66 pteridosperms or an advanced fern lineage (Glasspool et al., 2004), some late Permian gigantopterids
67 possessed vessels (Li and Taylor, 1998, 1999), megaphyllous leaves with a net venation (Glasspool
68 et al. 2004), and had hooks adapted for climbing (Seyfullah et al., 2014). These species may
69 represent Paleozoic non-angiospermous lianas. Nevertheless, based on the available data on
70 Paleozoic climbing plants, it is now clear that multiple lineages in wetland plant communities
71 explored the same ecological strategy of climbing (DiMichele et al., 2006), achieved through a
72 number of different ways (e.g., Kerp and Krings, 1998; Krings et al., 2003c).

73 The Asselian “Wuda Tuff Flora” (also known as Chinese “vegetational Pompeii”) is a fossil
74 lagerstätte preserved by a 298 Ma catastrophic ash fall (Wang et al., 2012; Schmitz et al., this issue).
75 Aerial parts of the fossil plants are autochthonously preserved and allow the fossils to be studied and
76 reconstructed in remarkable detail (e.g., Wang, 2006; Wang et al., 2009a, 2009b; Yan et al., 2013; He
77 et al., 2016; Liu et al., 2017; Li et al., 2019; Zhou et al., 2019). In particular, the fine-grained nature
78 of the tuff preserves fine structures on the plants including modified appendages such as trichomes,
79 hooks, spines/prickles, tendrils, aphanopores and aerial roots (Zhou, 2017). In this paper, we describe
80 new pteridospermous vegetative materials from the Wuda Tuff Flora that conforms to the
81 circumscription of *Alethopteris ascendens* Halle documented from other Permian locations in North
82 China (Halle, 1927; Yang, 2006). In this species we report for the first time petiole anatomy and the
83 presence of an integrated structure comprising an apical hooked prolongation with two lateral rows
84 of hooked spines on the distal part of pinna axes that demonstrate it was adapted for climbing.
85 Evaluation of previously published accounts of *A. ascendens* has identified unrecognized
86 occurrences of similar hooked appendages in specimens published by Yang (2006). This species
87 represents an alethopterid and is distinct from other species of *Alethopteris*, leading to establish

88 *Yangopteris ascendens* gen. et comb. nov. to accommodate specimens previously referred to a *A.*
89 *ascendens* Halle. We also document associated naked axes that may represent the main stem of this
90 species. Ecological implications of our findings and an evaluation of the growth habit of the plant are
91 also undertaken.

92

93 **2. Materials and Methods**

94 Specimens were collected from the uppermost part of the Taiyuan Formation in the Wuda
95 Coalfield, Inner Mongolia, China (Figs. 1A, B) [GPS of N 39°29'16", E 106°37'52"]. At this location
96 the geological succession contains four different compression/impression floras preserved in less
97 than 5 meters of vertical thickness (Fig. 1C; Pfefferkorn and Wang, 2007; Wang et al., 2012; Wang
98 and Pfefferkorn, 2013; Zhou et al., 2017). Among the floras, Flora 2 (i.e. the “vegetational Pompeii”)
99 occurs in the lower and middle part of a tuff horizon, and represents a peat-forming swamp-forest
100 community preserved *in situ* by volcanic ash (Fig. 1C, Pfefferkorn and Wang, 2007; Wang et al.,
101 2012). The specimens reported here are part of the wetland plant-community from Flora 2 for which
102 there is no post-depositional disturbance such as taphonomic reworking or bioturbation, as indicated
103 by numerous upright standing stumps and surrounding twigs and fronds (Pfefferkorn and Wang,
104 2007; Zhou et al., 2017). Radiometric dating of zircon crystals in the tuff indicate the ash layer was
105 deposited during the earliest Asselian, Permian, 298.34 ± 0.09 Ma (Schmitz et al., this issue).

106

107 [Approximate position of Fig. 1]

108

109 During fieldwork, first the sediments overlying Flora 2 were sequentially removed including the

110 roof shale containing Flora 4, the No. 6 Coal Seam, and the upper tuff layer containing Flora 3. The
111 exposed tuff containing Flora 2, comprising an area of approximately 2,000 m², was systematically
112 excavated using the quantitative quadrat method, with a minimum resolution of 1 × 1 m quadrats (the
113 white squares in Fig. 1D). Fossil plants were examined within quadrats as outlined by Opluštil et al.
114 (2014), photographed and labeled, and recorded them on a scaled plan constructed on graph paper
115 including the identity, size, position, and orientation of individual plant organs. Individual specimens
116 were then extracted, labelled, and wrapped to protect them during shipping. It is noteworthy that
117 specimens of *Yangopteris ascendens* were not found in earlier excavations (Wang et al., 2012), but
118 were encountered in three distinct patches (Sites 1, 2 and 3) during the later excavations. The general
119 composition of the forest is as outlined by Wang et al. (2012). Site 1, with an area of 6 × 7m,
120 represents a typical association of the plants that grew together with *Y. ascendens* comprising
121 *Nemejcopteris haiwangii* (Pšenička et al., this issue), *Cladophlebis* sp., *Sphenopters* spp., *Pecopteris*
122 spp., *Cordaites* sp. and *Taeniopteris* sp. (Fig. 2; Plate I, 1–6; Plate IV, 1).

123

124 [Approximate positions of Fig. 2 and Plate I]

125

126 Some specimens were directly sent to the local Wuhai Museum being built and only field
127 photographs of the specimens were available for study. The remaining scientifically significant
128 specimens were taken to Nanjing Institute of Geology and Palaeontology, Chinese Academy of
129 Sciences (NIGPAS) for detailed investigation. Specimens were examined under ethanol immersion
130 to enhance the contrast of the specimen from the matrix, and photographed by a digital Nikon D–800
131 camera with a 60 mm macro lens. Petiole with anatomy was transversely cut and polished.

132 Micrographs were taken using a Zeiss Discovery V16 microscope using an Axiocam 512 camera.
133 Terminologies applied in the description mainly follow Krings et al. (2003b), and are illustrated in a
134 bifurcate frond of *Yangopteris ascendens* (Plate II, 1). The naked axis before its bifurcation is termed
135 a “petiole (PE)”, while the main axis in the leafy portion of a bifurcate frond and the axis that bears
136 pinnules are termed “frond axis (FA)” and “pinna axis (PA)” respectively.

137

138 3. Systematic palaeontology

139 Order Medullosales Corsin, 1960

140 Family Alethopteridaceae Corsin emend. Anderson et al., 2007

141 Genus: *Yangopteris* Zhou et Wang gen. nov.

142

143 Generic diagnosis: Frond bipartite, bipinnate. Petiole longitudinally striated, hairy. Petiole anatomy
144 of the *Myeloxylon*-type, with about 15 scattered vascular bundles. Pinna linear, imparipinnate,
145 sub-oppositely arranged. Pinnules generally alethopterid, sub-oppositely to alternatively arranged.
146 Primary vein fades before reaching pinnule apex. Secondary veins straight, extend at a very narrow
147 angle, bifurcate two or three times. Pinna axis sometimes terminates in a hooked apical prolongation
148 with two rows of hooked spines.

149

150 Etymology: The new genus is named in honor of Professor Yang Guanxiu in recognition of her first
151 discovery of hooked prolongations of this plant.

152

153 Type species: *Yangopteris ascendens* (Halle 1927) Zhou et Wang comb. nov.

154

155 Basionym: *Alethopteris ascendens* Halle 1927, pp. 110–111, Plate 24, fig. 11.

156 Holotype: S138136a in Halle (1927) (re-photographed in Figs. 3A, B). Halle did not designate a type
157 specimen when he established the species *Alethopteris ascendens* as it was not required at that time.

158 However, since only one specimen was described and illustrated in his account, according to the

159 International Code of Nomenclature for Algae, Fungi and Plants (ICN) section 9.1, “A holotype of a

160 name of a species or infraspecific taxon is the one specimen or illustration either indicated by the

161 author(s) as the nomenclatural type or used by the author(s) when no type was indicated”. That

162 specimen is S138136a from the Swedish Museum of Natural History and is here designated

163 holotype.

164

165 Type locality, geological horizon and age: Taiyuan, Shanxi Province, China; bed 14, East section,

166 Lower Shihhotse Formation; Guadalupian

167

168 Repository: Department of Palaeobotany, NRM Stockholm, Sweden

169

170 Emended diagnosis: Pinnules slightly variable in size and morphology. Large pinnules almost

171 perpendicular, oblong-linear. Pinnule base decurrent. Pinnule apex slightly falcate. Lateral pinnule

172 margin parallel and entire. Margin veins 26 to 31 per centimeter. Subsidiary veins arise directly from

173 the pinna axis. Small pinnules slightly to strongly falcate. Pinnule base slightly decurrent.

174

175 Description: In specimens from the Wuda tuff, the frond is bipartite, bipinnate (Plate II, 1, 3, 4).

176 Petiole is 20.2 mm wide, with dense longitudinal striations (Plate II, 1, 3). In transverse section,
177 petiole is fairly compressed and taphonomically crushed (Plate II, 5). The cortex, when partially
178 preserved, shows a *Myeloxylon*-type hypodermis with alternating bands of parenchyma and
179 sclerenchyma (Plate II, 7). Inside of the cortex occurs parenchymatous ground tissue with about 15
180 scattered vascular bundles (Plate II, 5). Bundles have a gradient in cell size, with the larger cells
181 facing the interior of the petiole (Plate II, 6). Frond axes are 4.2 to 10.7 mm wide (Plate I, 1, 3; Plate
182 II, 1; Plate III, 1–3, 6; Plate IV, 1). Pinnae are imparipinnate (Plate III, 4), reaching more than 16 cm
183 long, and up to 33 mm wide (Plate III, 2). Pinna axes are 1.8–2.0 mm wide and sub-oppositely
184 arranged (Plate III, 1; Plate IV, 1). Large pinnules are oblong-linear, up to 21 mm long and 5 mm
185 wide, oriented approximately perpendicular to the pinna axis. Pinnule apices are slightly to strongly
186 falcate (Plate IV, 3–5; Plate V, 3). The upper pinnule margin is persistently straight, whereas the
187 lower margin curves upward when approaching the apex (Plate IV, 5). Primary veins are proximally
188 robust but gradually become thinner through their extent, tapering out before reaching the pinnule
189 apices (Plate V, 3). Pinnule bases are acroscopically constricted and basiscopically weakly decurrent
190 (Plate V, 2, 6). Secondary veins extend at a rather narrow angle, and bifurcate two or three times
191 (Plate IV, 6; Plate V, 5, 6). Several basisopic subsidiary veins arise directly from the pinna axis
192 (Plate II, 2; Plate IV, 6).

193
194 [Approximate positions of Plate II, III, IV, and V]

195
196 Some pinnules born on the common frond axis exhibit a variably smaller size (Plate IV, 3, 4).
197 They are oblong-triangular, slightly arched, 14.7–16 mm long and 6 mm wide. The apices of these

198 pinnules are falcate to slightly blunt, and the pinnule bases are acroscopically constricted and
199 basiscopically decurrent (Plate IV, 4), as in the larger pinnules. Primary veins are prominent, tapering
200 out before they reach the pinnule apices (Plate IV, 4). Secondary veins stretch out at a very narrow
201 angle, bifurcate once immediately and then slightly bend outward, bifurcate one more time at half
202 way, and finally terminate at the pinnule margin at angles of 45–60° (Plate IV, 4). The vein density at
203 the pinnule margin is 26 to 31 per centimeter in different sized pinnules (Plate IV, 6; Plate V, 3, 5).

204 In some specimens, the middle and lower parts of the pinna axes are straight and bear vegetative
205 pinnules, but the distal prolongations are strongly curved, lack vegetative pinnules and bear
206 prominent spines (Plate I, 3, 4; Plate III, 5; Plate VI, 1–7). Pinnules in the lower and middle parts of
207 pinna axes are 14 mm long and 6 mm wide, with a gross form the same as those of the small pinnules
208 described above, although the venation pattern is hard to detect due to preservational limitations. The
209 distal prolongation bearing spines in the specimen illustrated in Plate VI, 2 is 4.2 mm long, and it can
210 be even longer (Plate VI, 5). Spines are 1.3 mm wide at their base and taper quickly, oriented in a
211 downward direction. They are sub-oppositely arranged along both sides of the distal prolongations
212 (Plate I, 4; Plate VI, 6). A single spine is present at the apex of the distal prolongation (Plate VI, 3, 4
213 and 7). A field picture shows three distal prolongations each with one side of spines indicating them
214 derived from a bipinnate frond (Plate III, 5). The prolongation shown in Plate I, 3 is 5 mm long and
215 in this specimen the apex curves into a hook, with no spines detected along the pinna axis.

216
217 [Approximate position of Plate VI]

218
219 In Yang's (2006) specimens of *Alethopteris ascendens*, the pinna axes in vegetative fronds are

220 8.3 mm in diameter, long and closely spaced (Plate VII, 1). Pinnules are nearly perpendicularly
221 (Plate VII, 1) or slightly oblique to the pinna axes (Plate VII, 2, 3). Pinnule bases are acroscopically
222 constricted and basiscopically decurrent (Plate VII, 2); secondary veins stretch out from the primary
223 vein at rather narrow angles (Plate VII, 2, 3). However, although neither identified nor described as
224 spines by Yang (2006), the specimen HEP 0350 of Yang (2006) as illustrated in her plate 35, fig. 4,
225 shows the presence of hooked prolongations on the distal part of pinna axes. Re-photographing of the
226 specimen displays a bipinnate frond comprising sub-oppositely arranged pinnae with distal
227 prolongations that terminally form hooks (Plate VII, 3, 5). One pinna also shows prominent hooked
228 spines on both sides of the distal prolongation (Plate VII, 4). Spines are downward oriented, 0.8 mm
229 long and 0.4 mm wide at the base.

230
231 [Approximate position of Plate VII]

232
233 Comparison and discussion: *Alethopteris ascendens* was first described by Halle (1927) from the
234 Lower Shihhotse Formation (Guadalupian) of Shanxi Province, North China. This specimen was a
235 pinna fragment possessing alethopterid pinnules thus Halle (1927) placed it into the fossil genus
236 *Alethopteris* Sternberg emend. (Zodrow and Cleal, 1998). Halle (1927) also suggested a possible
237 assignment to *Callipteridium* Weiss, but ruled this out based on the shortage of a frond axis at that
238 time. Since then, the species has been frequently reported from the Permian of China including Inner
239 Mongolia (Li, 1963), Shanxi (Xiao and Zhang, 1985; Zhao et al., 1987; He et al., 1995), Hebei
240 (Stockmans and Mathieu, 1939), Henan (Yang, 2006), and Anhui (Wang et al., 1982) provinces, as
241 well as being recorded in North Korea (Kawasaki, 1934). All of these specimens have the same

242 unique characteristics of alethopterid pinnule organization and venation pattern, and represent a
243 distinctive element in the Permian Cathaysian floras. The discovery of bipinnate fronds of this
244 species prevent its assignment to the genus *Callipteridium* on account of the absence of intercalary
245 elements. *A. ascendens* has unique characteristics that are clearly different from those in other
246 species of *Alethopteris*, including primary veins tapering out a long distance before reaching the
247 pinnule apex, secondary veins extending at very narrow angles, and the presence of specialized
248 hooked appendages. These characters prevent it being assigned to the genus *Alethopteris* and justify
249 the creation of *Yangopteris* gen. nov. to accommodate the specimens previously assigned to
250 *Alethopteris ascendens*. Nevertheless, *Y. ascendens* should still be a member of the order
251 Medullosales on account of its alethopterid foliage and *Myeloxylon*-type petiole anatomy (Taylor et
252 al., 2009).

253 The Wuda specimens of *Yangopteris ascendens* possess alethopterid pinnules that have
254 acroscopically constricted and basiscopically decurrent bases (Plate V, 2, 6), and subsidiary veins
255 arising directly from the pinna axes (Plate II, 2; Plate IV, 6). Together with the distinctive venation
256 pattern, we are quite certain that the Wuda specimens are the same species as Halle's specimen,
257 although the Wuda specimens were yielded from stratigraphically older strata from the Asselian aged
258 upper most part of the Taiyuan Formation where they represent the stratigraphically earliest
259 occurrence of the *Yangopteris ascendens*. The Wuda specimens are also comparable to Yang's
260 specimens based on their identical pinnules and hooked appendages, but display additional features
261 not present in the type and previously figured materials that are limited in number.

262 It is noteworthy that the terminal hooked structures in *Yangopteris ascendens* are extremely
263 similar to those in *Karinopteris* from the Indiana "Paper" Coal (DiMichele et al., 1984) in the

264 Pennsylvanian of North America, although it is currently uncertain if the frond axes of *Y. ascendens*
265 could bear similar hooked prolongations as those in *Karinopteris* sp. The most likely specimen to
266 reveal this trait is the specimen HEP 0350 from Yang's collection (Yang, 2006), but this specimen is
267 unfortunately incomplete. *Y. ascendens* is readily distinguished from *Karinopteris* sp. by its
268 alethopterid pinnules, while *Karinopteris* has mariopterid pinnules (DiMichele et al., 1984).

269

270 **4. Associated naked axes**

271 Previous accounts of *Yangopteris ascendens* documented the species from either pinnae (Halle,
272 1927; Kawasaki, 1934; Li, 1963; Xiao and Zhang, 1985; Zhao et al., 1987; He et al., 1995) or
273 bipinnate fronds (Gu and Zhi, 1974; Wang et al., 1982; Yang, 2006). The bipinnate nature is also
274 seen in the Wuda specimens, and the pinnae are commonly closely positioned (Plate I, 1; Plate III, 1–
275 3; Plate IV, 1). In a further investigation, bipinnate fronds of *Y. ascendens* were not found in organic
276 attachment to any stems. However, in the tuff bed there are several isolated, naked axes closely
277 associated with and in some cases overlapping fronds of *Y. ascendens*. Some are simple axes with
278 diameters varying from 11.4 to 32.3 mm (Plate I, 4; Plate III, 6; Plate V, 4), while others have
279 two-orders of branching, with primary axes 36.5 to 47.5 mm in diameter and secondary axes 11.0 to
280 23.5 mm in diameter (Plate I, 1, 2).

281 Considering the affinity of the naked axes that are associated with specimens of *Yangopteris*
282 *ascendens*, these all come from Site 1 (Fig. 2) that is a small area of the excavation (6 × 7 m). Site 1
283 has yielded numerous bipinnate fronds of *Y. ascendens* and associated naked axes described above. It
284 also contains other plant species comprising *Nemejcopteris haiwangii*, *Cladophlebis* sp.,
285 *Sphenopteris* spp., *Cordaites* sp., *Pecopteris* spp. and *Taeniopteris* sp. The naked axes are apparently

286 not produced by *N. haiwangii*, *Cladophlebis* sp. (Plate IV, 1) and species of *Sphenopteris* (Plate I, 5)
287 and *Pecopteris* (Plate I, 6), since their fronds are demonstrated to be tripinnate in this excavation.
288 Furthermore, *Taeniopteris* sp. is a tree with a crown of simple leaves (Fig. 2) so that the naked axes
289 are also not parts of this plant. The smooth, two-ordered axes are most comparable to those of
290 *Cordaites* (Plate VIII, 1–3) for which clusters of *Cordaites* leaves co-occur with the two-ordered axes
291 and *Y. ascendens* (Plate I, 1, 2, 4). However, in the excavations at Wuda, branches of *Cordaites* sp.
292 possess spirally arranged leaf cushions resulting in a rough exterior texture of the branches surfaces
293 (Plate VIII, 5), and well-preserved *Cordaites* branches contain *Artisia*-type pith casts (Plate VIII, 4).
294 The associated naked axes have a smooth outer surface lacking indications of leaf cushions, and
295 *Artisia*-type pith casts are absent in the somewhat compressed axes (Plate I, 1, 2, 4; Plate V, 4).
296 Therefore, we consider it unlikely that species of *Cordaites* bore those naked axes, leaving only *Y.*
297 *ascendens* as the likely foliage from the plant producing these axes.

298 The monopodial stem-petiole branching system with a subsequent petiole bifurcation is common
299 in medullosans (Ramanuham et al., 1974; Wnuk and Pfefferkorn, 1984; Pryor, 1990; Laveine et al.,
300 1993; Krings and Kerp, 1999). However, the petiole could be quite long and naked before its
301 bifurcation (Laveine, 1997; Krings and Kerp, 2006). Naked, unbranched petioles attached to
302 medullosan stems and associated with alethopterid pinnules have previously been documented from
303 the Pennsylvanian of the Sydney Coalfield in Canada (Zodrow, 2002), and are comparable to the
304 studied two-ordered axes in Plate I 1 and 2. If correctly interpreted, the primary axes of the
305 associated two-ordered axes should represent the main stems of *Y. ascendens* on account of their
306 monopodial branching nature, and the secondary axes therefore represent the petiole that not yet
307 bifurcated. These narrow stems with long internodes may suggest a leaning or lianescent growth

308 habit which is similar to that of *Neuropteris attenuate* reported from the Pennsylvanian of Germany
309 (Krings and Kerp, 2006).

310
311 [Approximate position of Plate VIII]

312

313 **5. Climbing appendages and their ecological implications**

314 Pteridosperms are a paraphyletic evolutionary grade of seed plants broadly united by the
315 presence of fern-like compound fronds, woody stems and seeds (e.g. Hilton and Bateman, 2006).
316 Due in part to their phylogenetic diversity, pteridosperms display a wide array of growth forms
317 including canopy-forming and understory trees, shrubs, prostrate ground cover and
318 scrambling/climbing plants (DiMichele et al., 2006). Previous accounts of medullosan pteridosperms
319 considered them to represent small trees with upright stems that could be self-supporting or growing
320 in dense associations providing mutual support for each other (Pfefferkorn et al., 1984; Wnuk and
321 Pfefferkorn, 1984), or adapted to climbing such as *Lescuropteris genuina* (Krings and Kerp, 1997),
322 *Blanziopteris praedentata* (Krings and Kerp, 1999), *Medullosa steinii* (Dunn et al., 2003) and
323 *Neuropteris attenuate* (Krings and Kerp, 2006).

324 Hooked prolongations in fossil plants were previously regarded as a specialized form to
325 scramble (Schenk, 1892), but later were also considered to be sufficient for small to medium-sized
326 vines to climb (Menninger, 1970). Prolongations (or extensions, see Boersma, 1972) adapted for
327 climbing from the apical part of plants have been frequently reported in Paleozoic pteridosperms
328 (Krings and Kerp, 1997; Krings et al., 2003a), especially in mariopterids (e.g. Huth, 1912; Boersma,
329 1972, 1991; Remy and Remy, 1977; DiMichele et al., 1984; Schultka, 1995; Krings et al., 2001a,

330 2001b; 2003c). Regarding the nature of the prolongations, they can be extensions of veins such as
331 those in the sphenopsids *Annularia mucronata* Schenk (Schenk, 1883), *Sphenophyllum cuneifolium*
332 (Sternberg) Zeiller, *S. emarginatum* Brongniart, and *S. oblongifolium* (Germar et Kaulfuss) Unger
333 (Batenburg, 1977; Barthel, 1997), the taeniopterids *Taeniopteris mucaronata* Kawasaki (Kawasaki,
334 1934), *T. aduncata* Zhao and *T. fuchengensis* Zhao (Zhao et al., 1987), or the gigantopterid
335 *Gigantonoclea lagrelii* (Halle) Koidzumi (Seyfullah et al., 2014). They can also be the extensions of
336 pinna axes such as those in *Karinopteris* sp. (DiMichele et al., 1984), *Karinopteris acuta* (Brongniart)
337 Boersma (Krings et al., 2003a), *Pseudomariopteris busquetii* (Zeiller) Danzé-Corsin emend. Krings
338 et Kerp and *P. cordato-ovata* (Weiss) Gillespie et al. ex Krings et Kerp (Krings and Kerp, 2000).
339 Climbing prolongations occur in unrelated plant groups so clearly represent independent origins and
340 parallel evolution in unrelated lineages, but in the Paleozoic extensions of pinna axes likely only
341 occur in pteridosperms.

342 In *Yangopteris ascendens*, prolongations are seen on the distal part of pinna axes (Plate I, 3;
343 Plate III, 5; Plate VI, 1-7). Analogues in the *Karinopteris* and *Pseudomariopteris* plants suggest a
344 morphological function of climbing. Moreover, hooked spines are also present on both sides of the
345 hooked prolongations in both *Y. ascendens* and *Karinopteris* sp. (DiMichele et al., 1984).
346 Mechanically, hooked spines/prickles could produce frictional resistance in catching or hanging on
347 the supports (Krings et al., 2003a). In extant angiosperms such as in members of the leaning
348 Rosaceae, prickles on the stem surface can prevent them slipping off from supports, thus termed as
349 “hooked climbers” (Gallenmüller et al., 2015). Since the hooked prolongations and hooked spines in
350 *Y. ascendens* and *Karinopteris* sp. constitute a more specialized integrated structure, the function
351 may have increased effectiveness compared to the single structure of hooked spine or hooked

352 prolongation. The integrated structures borne on the distal part of plant bodies are biologically more
353 radical in outward expanding than the prickles developed in the central part of plant bodies (i.e.,
354 prickles on the stem surface are much more conservative as an indicator of leaning plants). The
355 integrated structure in *Y. ascendens* is therefore more convincing to be adapted for the function of
356 climbing. In modern angiosperms, the integrated structure is most comparable to the climbing palms
357 such as Arecoideae and Calamoideae, of which possess cirrus rachises with sharp, recurved hooks
358 acting as attachment devices (Isnard and Rowe, 2008). The failure of anchorage to the supports may
359 therefore result in the development of large, dense fronds. Considering the associated primary axes
360 interpreted here to be the stems of the same plant and the presence of large, dense fronds, we deduce
361 that *Y. ascendens* is probably a semi-self-supporting plant but also with a hook-climbing habit.

362 Since diverse modified appendages (hooks, tendrils, adhesive pads, and adventitious roots) have
363 been widely reported in late Paleozoic forest ecosystems (Kerp and Krings, 1998; Krings et al.,
364 2003c), it is noteworthy that such appendages could develop in different plant groups and modern
365 angiosperms (Burnham, 2009; Isnard and Silk, 2009). The rise of climbers may date back to the
366 Middle Devonian forests evidenced by hooked structures in the lycopsid *Leclercqia* (Xu et al., 2011),
367 but diversification of climbers during the Pennsylvanian appears to have been dynamically driven by
368 increases in coal-swamp habitat coupled with increasing closure of forest canopies (Krings et al.,
369 2003c). Modified appendages therefore appear to be a phenotypic reaction to the environment and
370 competition from other plant species. The integrated structure constituting of both hooked spines and
371 hooked prolongations are more specialized than those simple modified appendages. However, these
372 highly specialized structures developed in at least two different plant species (i.e. *Karinopteris* sp.
373 and *Yangopteris ascendens*) that were geographically isolated (Euramerican and Cathaysian realms

374 respectively), temporally allochronic (Middle Pennsylvanian and early Cisuralian respectively), and
375 taxonomically discrepant (probably lyginopterids and Medullosales, respectively), but living in
376 similar wetland, peat-forming environments. This implies that ecological convergence occurred in
377 late Paleozoic tropical coal-swamp ecosystems among various groups of climbing plants.

378

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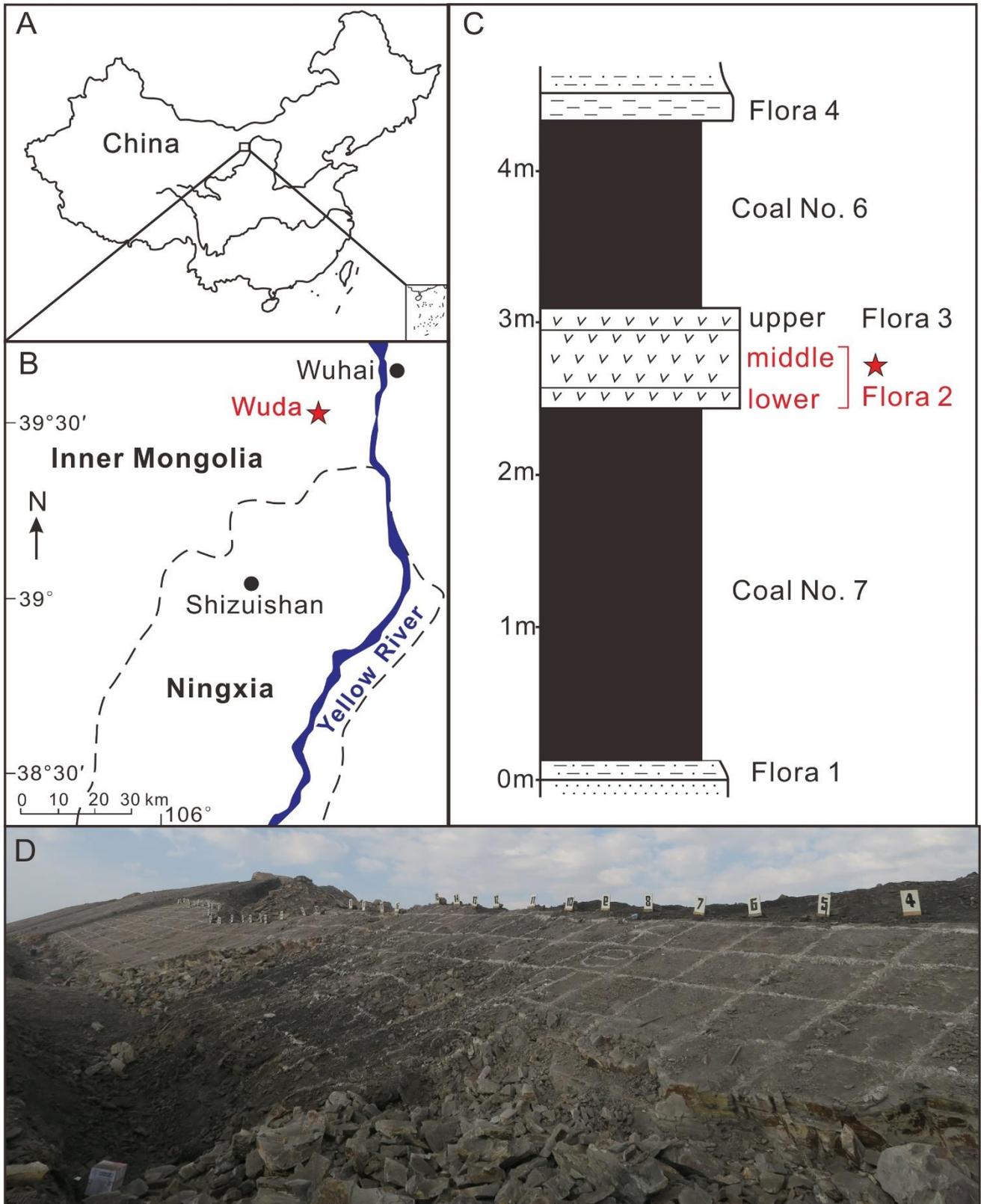
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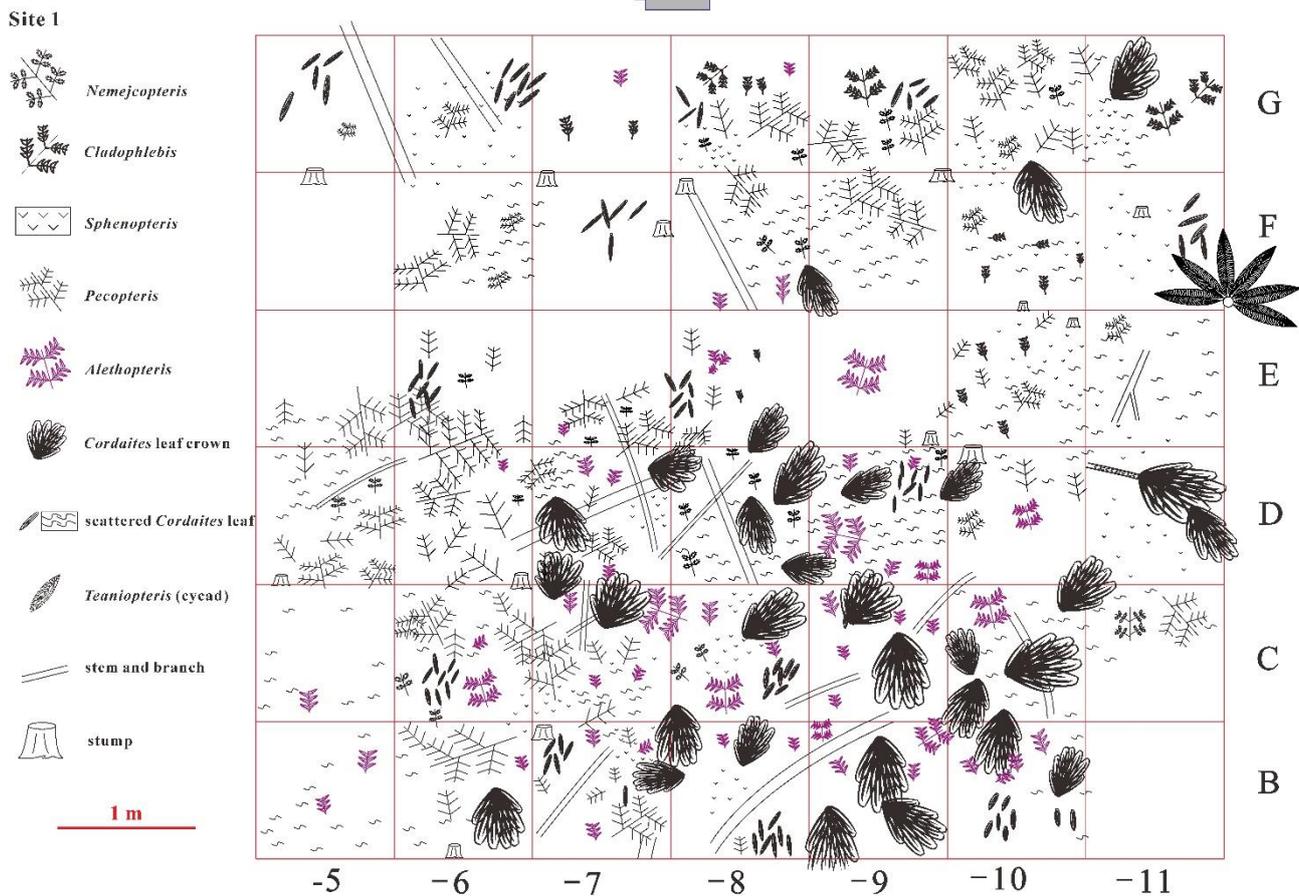
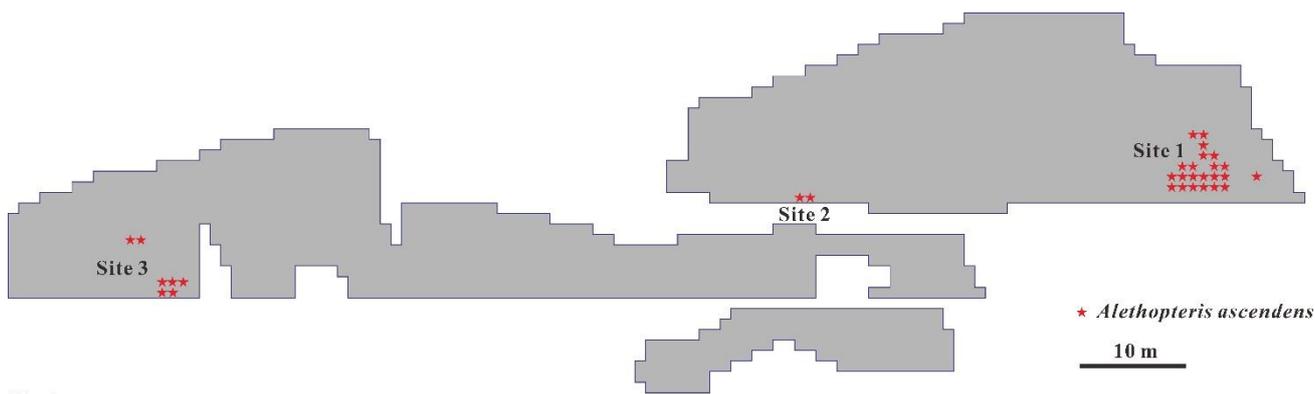


598 map of China with boxed area showing position of study area at the boundary of Inner Mongolia and
599 Ningxia provinces. (B) Enlargement of boxed area from (A) showing position of the study area (red
600 star) in Inner Mongolia. (C) Summary stratigraphic column of the Wuda section showing the position
601 of the four preserved floras. The volcanic tuff layer separates Coal No. 7 and Coal No. 6. Specimens
602 of *Yangopteris ascendens* are from Flora 2 (red star) and do not occur elsewhere in the profile. (D)
603 Excavation of the volcanic tuff bed, upper sediments have been removed and the surface was
604 mapped by 1 m × 1 m quadrats (white lines).

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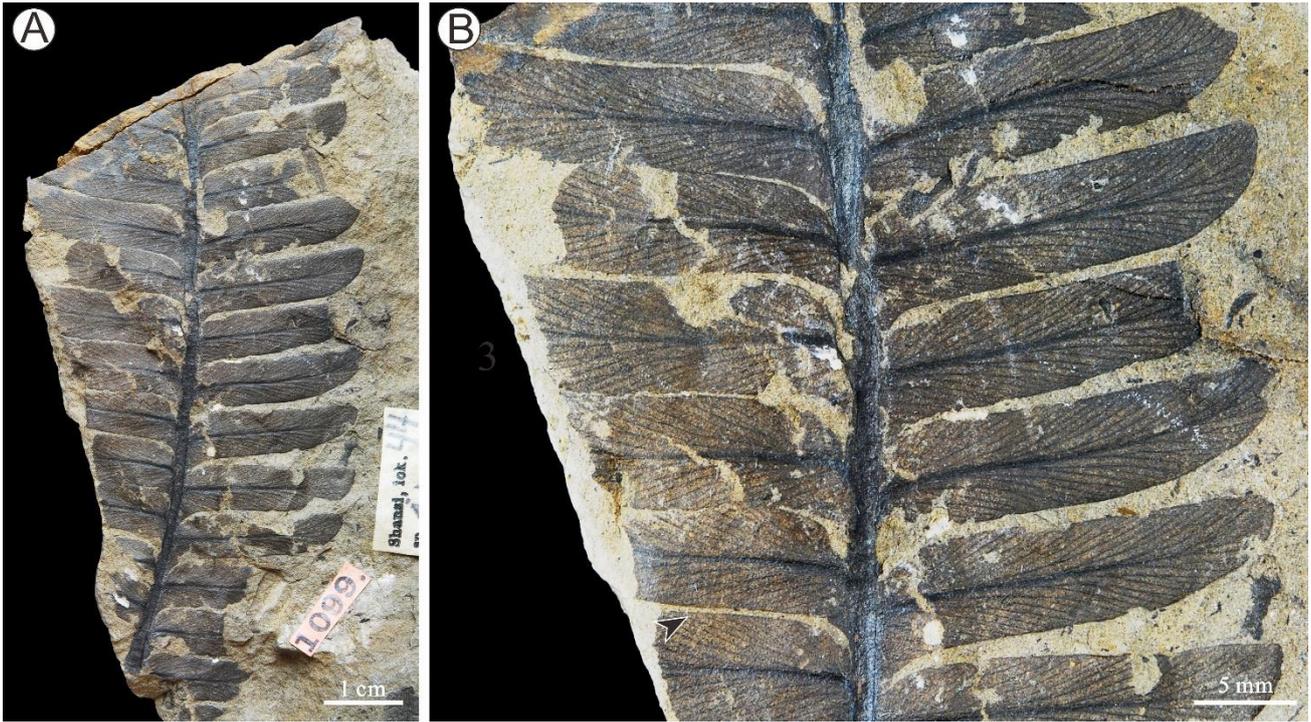
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609 **Fig. 2.** Distribution of specimens of *Yangopteris ascendens* and co-occurring plants in Site 1 of the

610 Wuda excavation.

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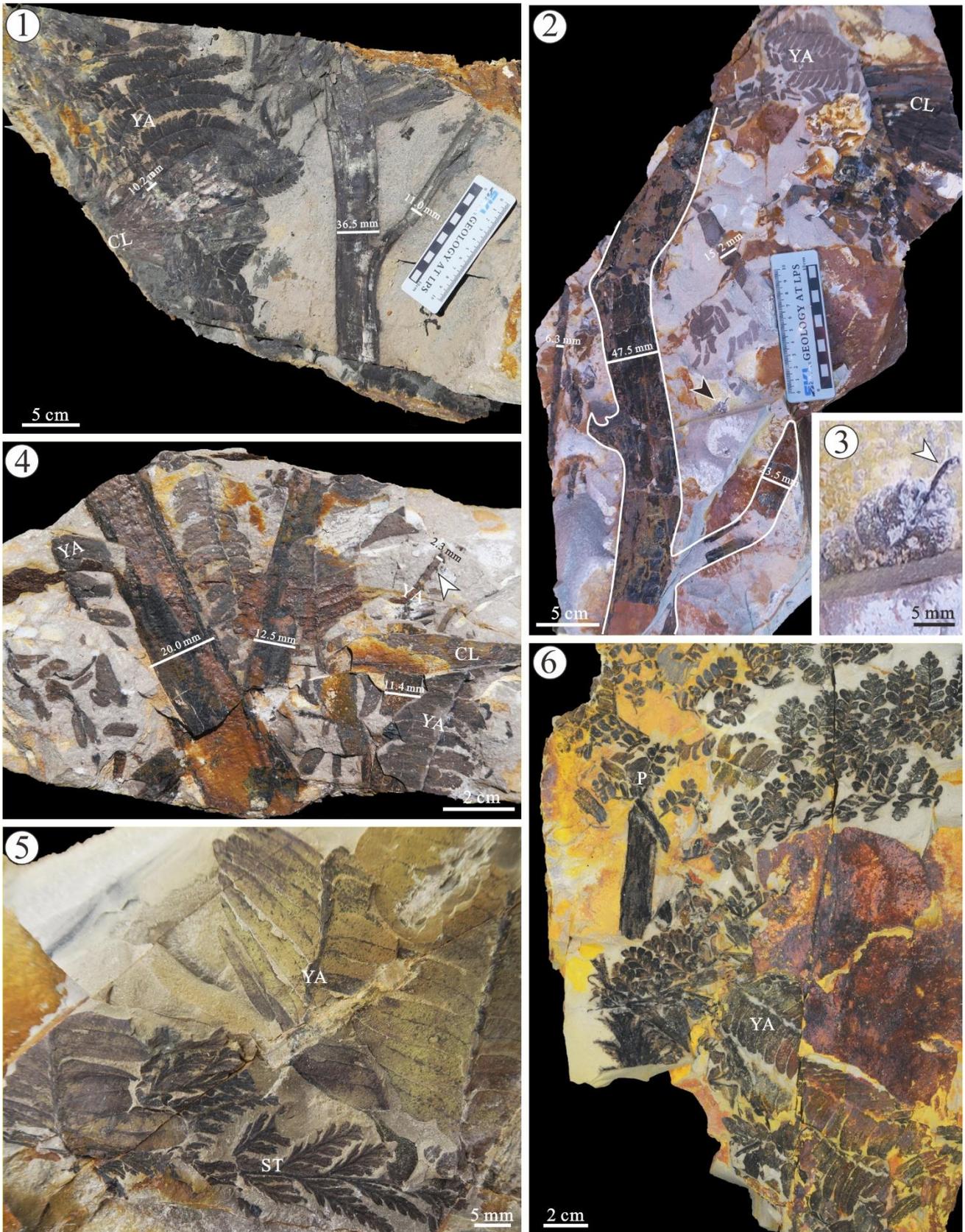


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614 **Fig. 3.** Holotype of *Yangopteris ascendens*. (A) Gross form of the fragmental pinna. (B) Enlargement
615 from (A) showing the pinnule form and venation pattern. Specimen S138136a (Swedish Museum of
616 Natural History).

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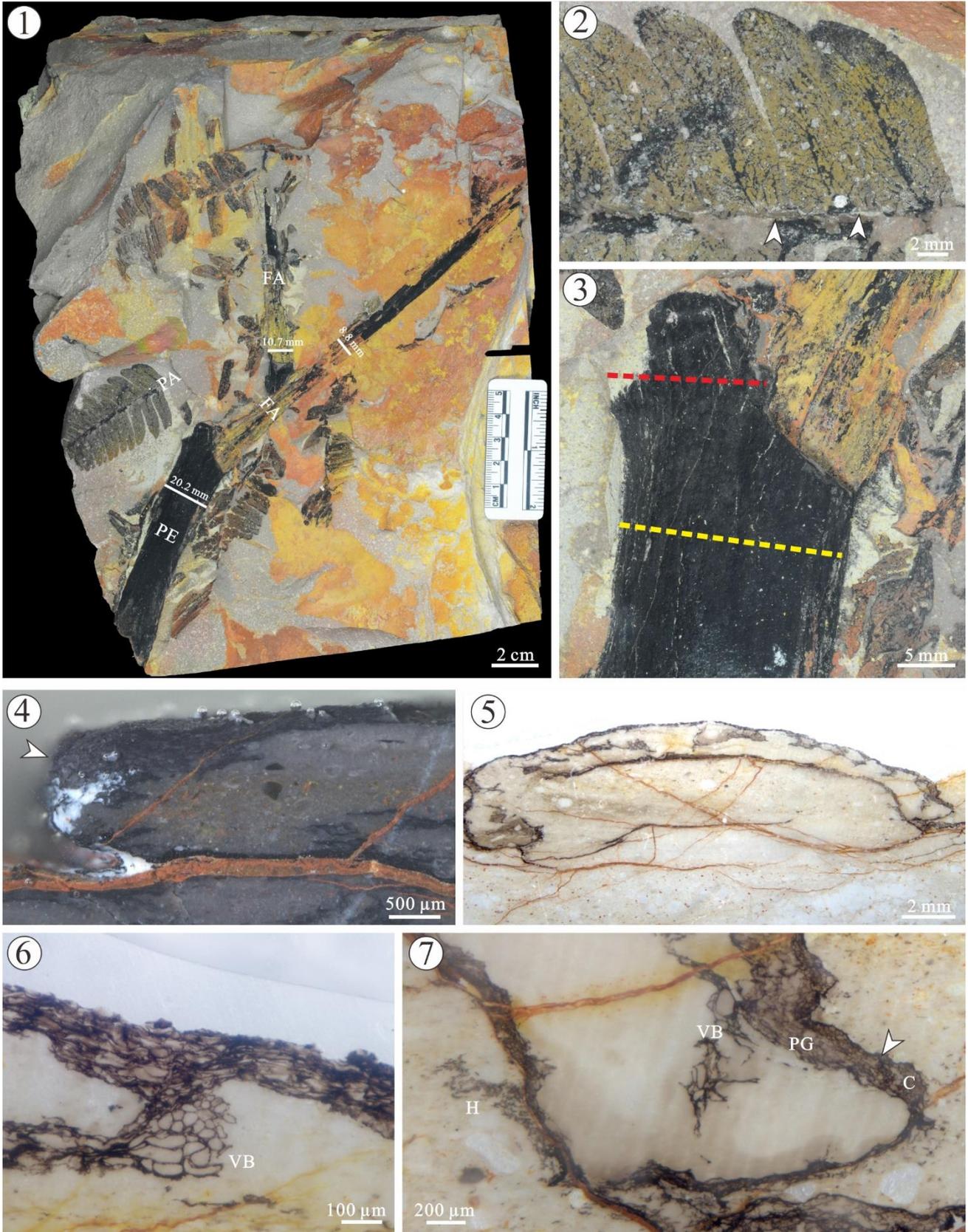


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620 **Plate I.** Plants associated with *Yangopteris ascendens*. (1, 2) Associated axes (two orders of

621 branching) and *Cordaites* leaves. (3) Enlargement from (2) showing a pinna with a short, naked

622 prolongation (white arrowhead). (4) Associated axes (simply branched) and *Cordaites* leaves, notice
623 a small rachis of *Y. ascendens* with two rows of hooked spines (white arrowhead). (5) Associated
624 *Sphenopteris* plants. (6) Associated *Pecopteris* fronds. CL = *Cordaites* leaves; P = *Psaronius*; ST =
625 *Sphenopteris tenuis*; YA = *Yangopteris ascendens*.



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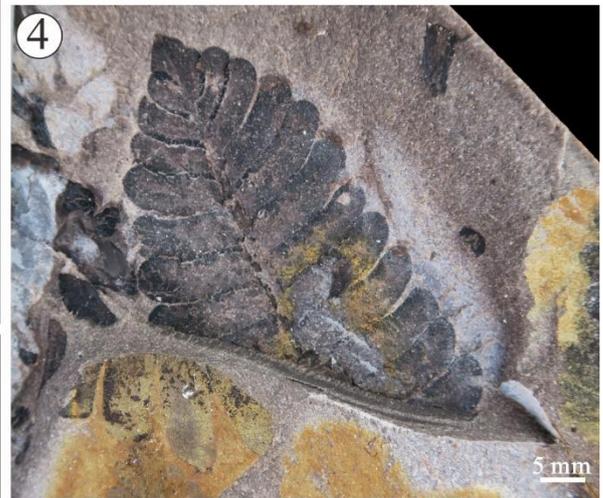
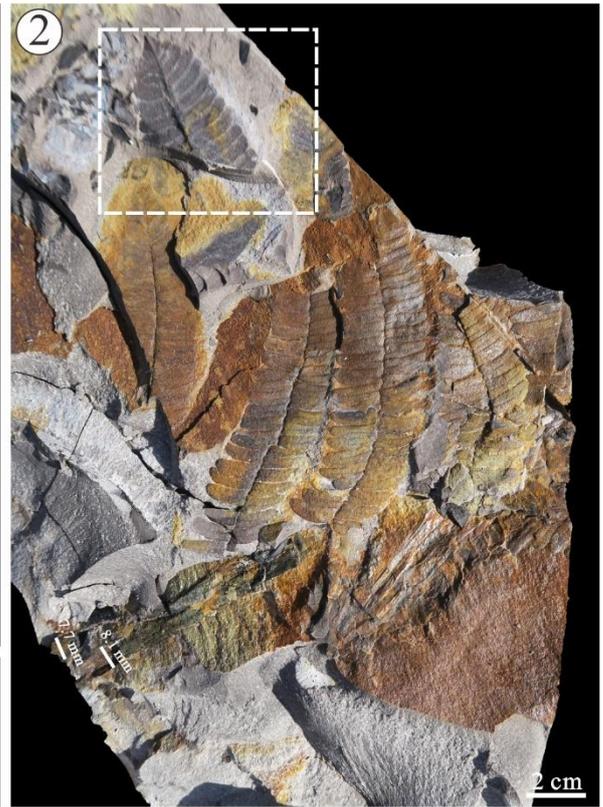
627 **Plate II.** Bipartite, bipinnate frond of *Yangopteris ascendens*. (1) The gross morphology, PB23171.

628 (2) Pinnules of *Y. ascendens* showing the subsidiary veins (white arrowheads) arising directly from

629 the pinna axis. (3) Enlargement of (1) showing the bifurcated portion. (4) Transverse section made
630 from the red dotted line in (3), the cortex boundary (white arrowhead) separates the petiole in the
631 middle thus demonstrates a bifurcation. (5) Transverse section made from the yellow dotted line in
632 (3), showing a number of scattered vascular bundles within the fairly compressed petiole. (6)
633 Enlargement of (5) showing a vascular bundle, notice the cells become larger towards the inner side.
634 (7) Enlargement of (5) showing the structures of cortex, parenchymatous ground tissue, vascular
635 bundle and hairs, white arrowhead indicates a band of sclerenchyma. C = Cortex, H = Hair, FA =
636 Frond axis, PA = Pinna axis, PE = Petiole, PG = Parenchymatous ground tissue, VB = Vascular
637 bundle.

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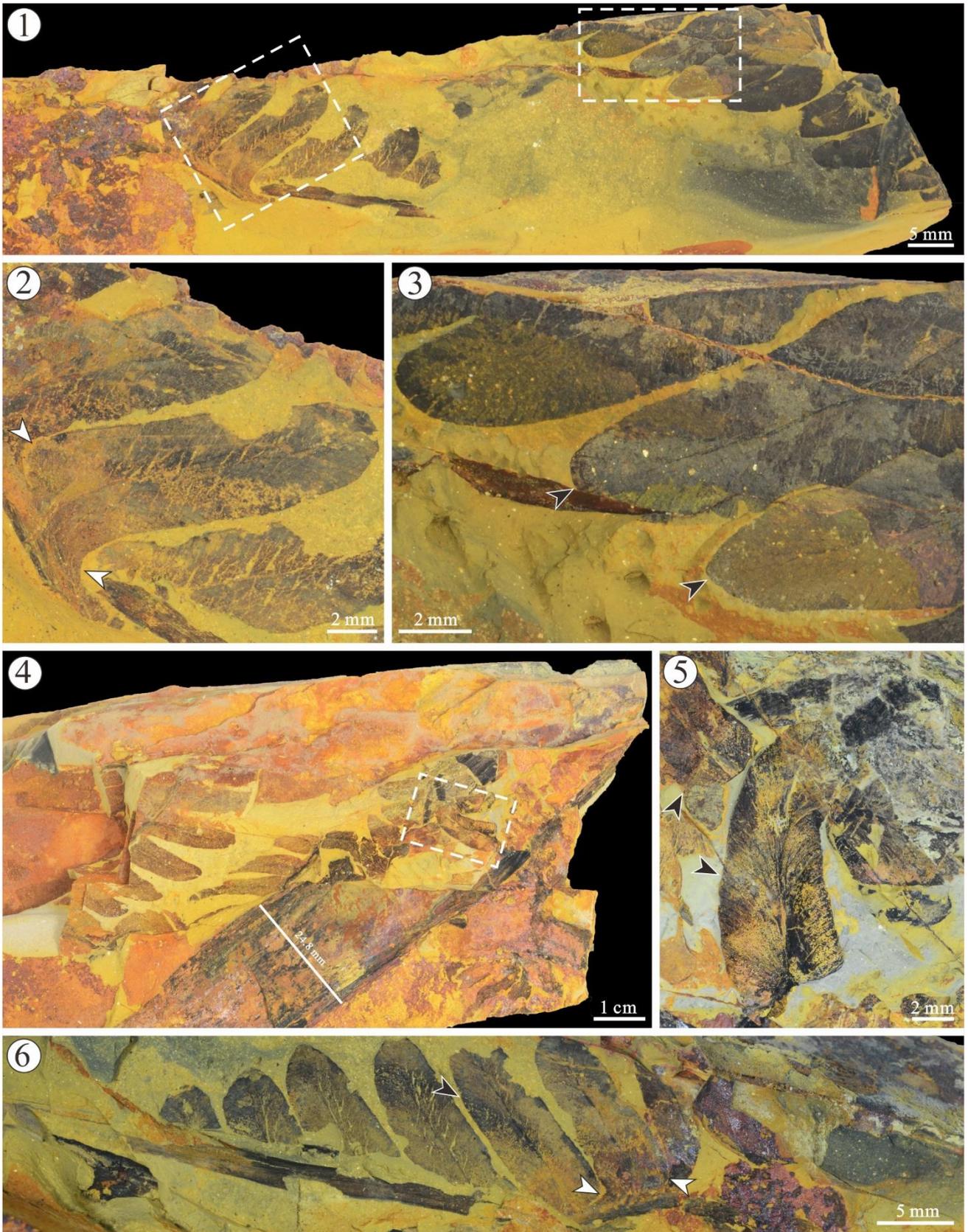


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641 **Plate III.** Field pictures of *Yangopteris ascendens*. (1) A bipinnate frond with pinna axes

642 sub-oppositely arranged. (2, 3) Two bipinnate fronds with long and crowded pinnae. (4) Enlargement

643 of (2) showing the imparipinnate pinna. (5) Three well-arranged pinnae each with one side of spines
644 suggests they derive from a bipinnate frond. (6) Fronds of *Y. ascendens* and associated simple
645 branches. YA = *Yangopteris ascendens*.

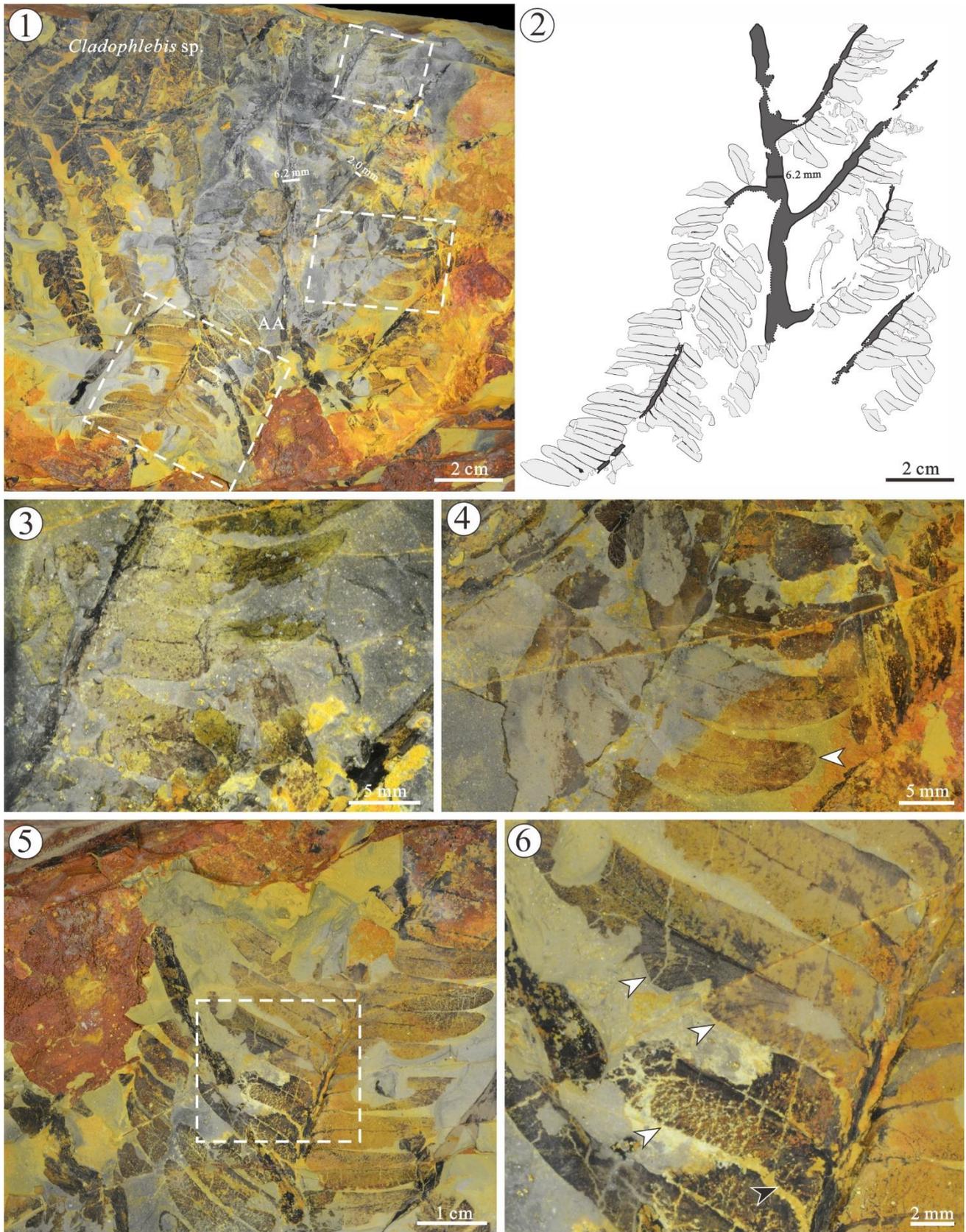


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648 **Plate IV.** A bipinnate frond of *Yangopteris ascendens*. (1) The general morphology, notice a

649 bipinnate frond of *Cladophlebis* plant is preserved on the left, PB23172. (2) Diagram of the bipinnate
650 frond of *Y. ascendens*. (3) Enlargement of the upper white box in (1) showing the small pinnules. (4)
651 Enlargement of the middle white box in (1) showing the small pinnules, white arrowhead indicates a
652 primary vein that tapers out before reaching the pinnule apex. (5) Enlargement of the lower white
653 box in (1) showing the large pinnules. (6) Enlargement of the white box in (5) showing the secondary
654 veins (white arrowheads) and subsidiary veins arising directly from the pinna axis (black arrowhead).

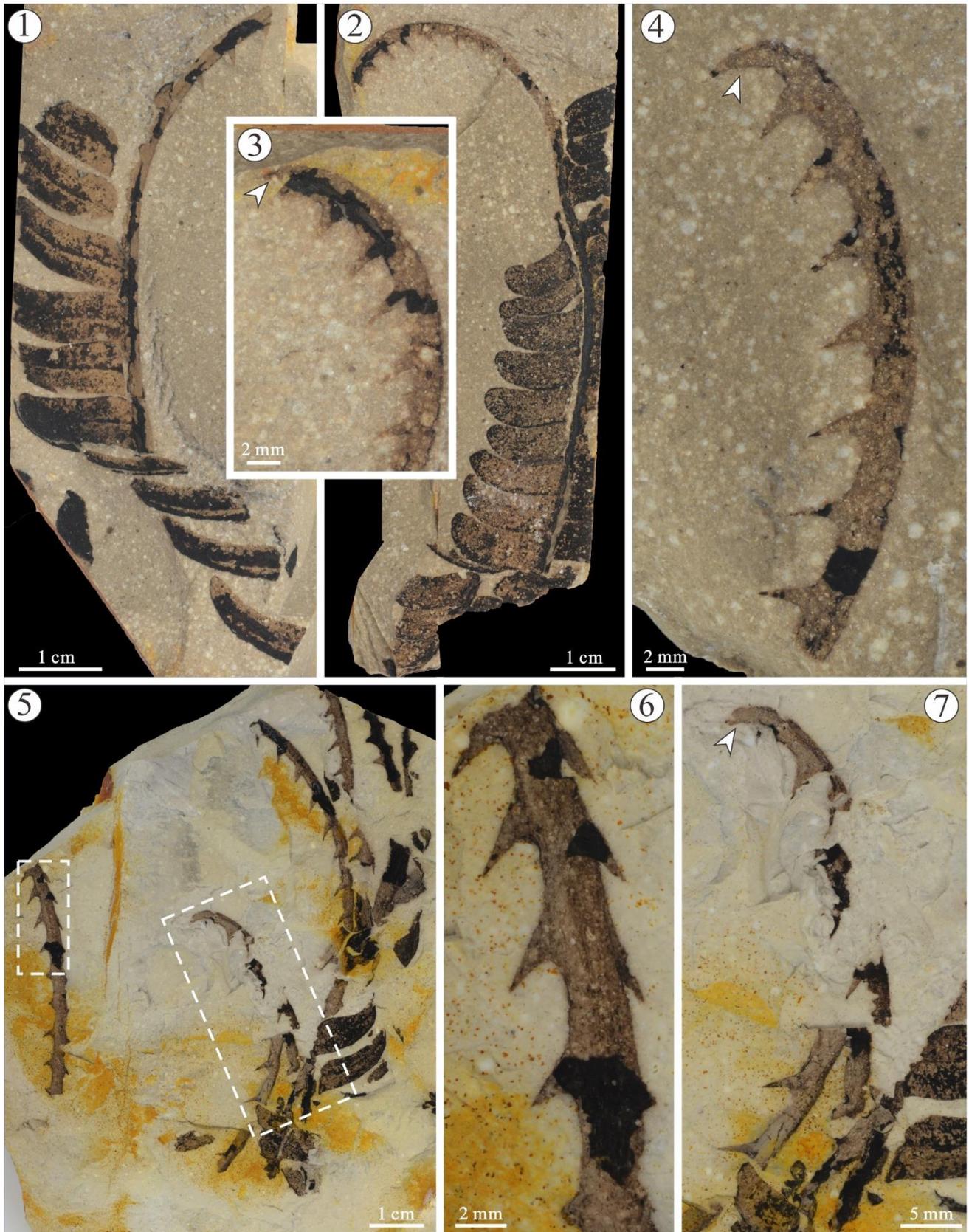


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656 **Plate V.** Pinnae of *Yangopteris ascendens*. (1) Two isolated pinnae, PB23173. (2) Enlargement of the

657 left white box in (1) showing a pinnule with acroscopically constricted and basiscopically decurrent

658 base (white arrowheads). (3) Enlargement of the right white box in (1) showing the pinnule venation
659 pattern. The primary veins dissolve before reaching the pinnule apices (black arrowheads). (4)
660 Fragments of *Y. ascendens*, associated with a simple axis, PB23174. (5) Enlargement of the white
661 box in (4) showing two falcate pinnules. Secondary veins extend at narrow angles (black
662 arrowheads). (6) Another pinna of *Y. ascendens* showing the typical characters of pinnule base (white
663 arrowheads) and secondary veins (black arrowhead), PB23175.



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Plate VI. The integrated structures of *Yangopteris ascendens*. (1-2) Two pinnae with hooked spines on the distal part of pinna axes, PB23176 and PB23177. (3) Enlargement of (2) showing the apex of

667 a pinna axis (white arrowhead). (4) An isolated integrated structure with a clear apex (white
668 arrowhead), PB23178. (5) Several well-oriented pinna axes with terminal integrated structures,
669 PB23179. (6) Enlargement of the left white box in (5) showing spines arranged on both sides of a
670 pinna axis. (7) Enlargement of the right white box in (5) showing the apex (white arrowhead).
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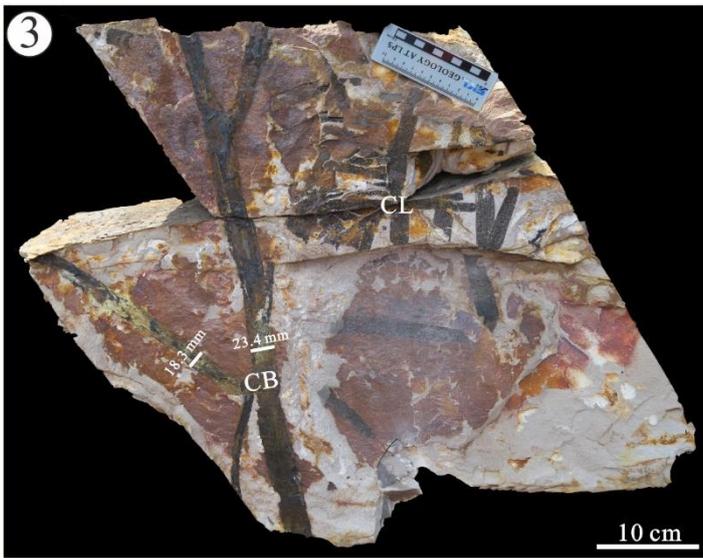
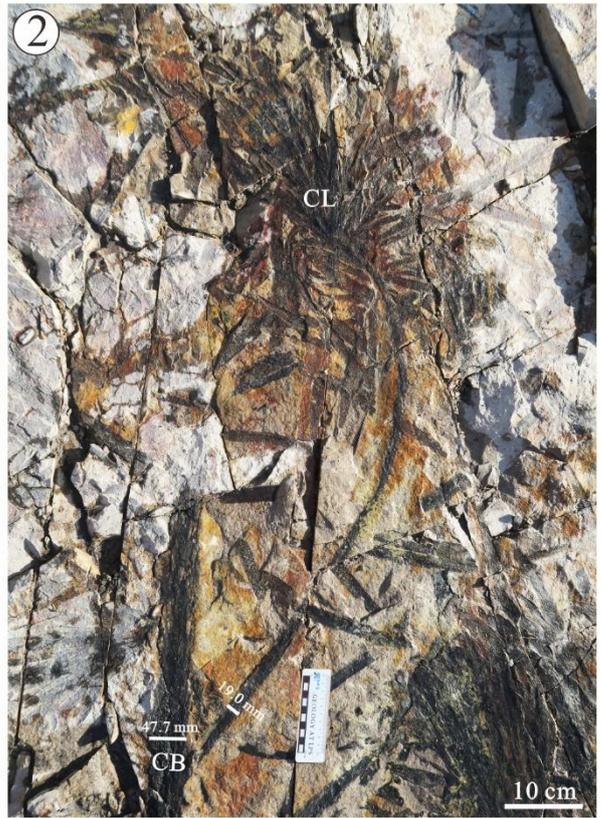
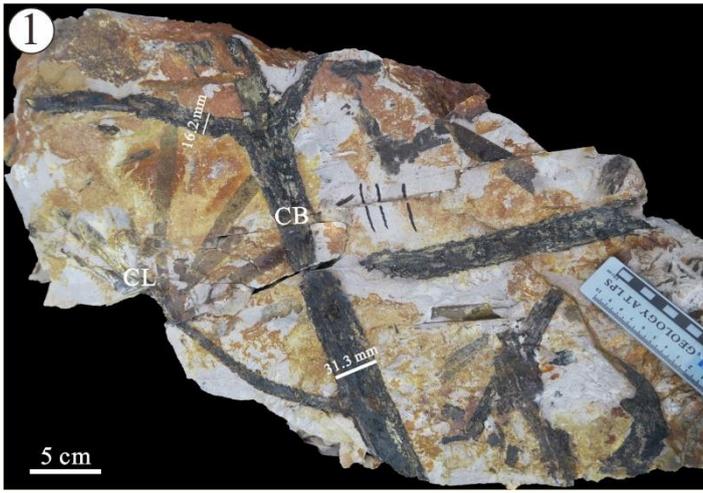


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673 **Plate VII.** Re-photographs of Yang (2006)'s specimens of *Yangopteris ascendens*. (1) A bipinnate
 674 frond, yyp. 003 (2) A long pinna, yyp. 004. (3) A bipinnate frond with hooked prolongations on the

675 distal part of pinna axes. The frond axis is not visible, HEP 0350. (4) Enlargement of the left white
676 box in (3) showing hooked spines on both sides of a pinna axis (white arrowheads). (5) Enlargement
677 of right white box in (3) showing the hooked apices of two homolateral pinna axes (white
678 arrowheads).

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681 **Plate VIII.** Field pictures of *Cordaites* branches in the same excavation. (1–3) Two-ordered branches

682 with leaves clustered on the distal part of a secondary branch. (4) An *Artisia*-type pith cast within a

- 683 *Cordaites* branch (white arrowhead). (5) Surface of a *Cordaites* branch showing the prominent,
- 684 helical leaf scars (white arrowhead). CB = *Cordaites* branch; CL = *Cordaites* leaves.