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# 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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21	

# 22 ABSTRACT

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

41

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

# 45 **1. Introduction**

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

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, aphlebiae 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

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

92

### 2. Materials and Methods 93

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

108

109

107

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 m <sup>2</sup> , was systematically
112	excavated using the quantitative quadrat method, with a minimum resolution of $1 \times 1$ 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 $6 \times 7m$ ,
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.

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 ducurrent.
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 basiscopic subsidiary veins arise directly from the pinna axis
192	(Plate II, 2; Plate IV, 6).
193	

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

195

Some pinnules born on the common frond axis exhibit a variably smaller size (Plate IV, 3, 4).
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	

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 Callipteridum 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

- 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

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

253 The Wuda specimens of Yangopteris ascendens possess alethopterid pinnules that have acroscopically constricted and basiscopically decurrent bases (Plate V, 2, 6), and subsidiary veins 254 arising directly from the pinna axes (Plate II, 2; Plate IV, 6). Together with the distinctive venation 255 256 pattern, we are quite certain that the Wuda specimens are the same species as Halle's specimen, although the Wuda specimens were yielded from stratigraphically older strata from the Asselian aged 257 upper most part of the Taiyuan Formation where they represent the stratigraphically earliest 258 occurrence of the Yangopteris ascendens. The Wuda specimens are also comparable to Yang's 259 specimens based on their identical pinnules and hooked appendages, but display additional features 260 not present in the type and previously figured materials that are limited in number. 261 It is noteworthy that the terminal hooked structures in Yangopteris ascendens are extremely 262

similar to those in *Karinopteris* from the Indiana "Paper" Coal (DiMichele et al., 1984) in the

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

269

## 270 **4. Associated naked axes**

Previous accounts of *Yangopteris ascendens* documented the species from either pinnae (Halle,
1927; Kawasaki, 1934; Li, 1963; Xiao and Zhang, 1985; Zhao et al., 1987; He et al., 1995) or

bipinnate fronds (Gu and Zhi, 1974; Wang et al., 1982; Yang, 2006). The bipinnate nature is also

seen in the Wuda specimens, and the pinnae are commonly closely positioned (Plate I, 1; Plate III, 1–

3; Plate IV, 1). In a further investigation, bipinnate fronds of *Y. ascendens* were not found in organic

attachment to any stems. However, in the tuff bed there are several isolated, naked axes closely

associated with and in some cases overlapping fronds of *Y. ascendens*. Some are simple axes with

diameters varying from 11.4 to 32.3 mm (Plate I, 4; Plate III, 6; Plate V, 4), while others have

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).

Considering the affinity of the naked axes that are associated with specimens of *Yangopteris ascendens*, these all come from Site 1 (Fig. 2) that is a small area of the excavation ( $6 \times 7$  m). Site 1 has yielded numerous bipinnate fronds of *Y. ascendens* and associated naked axes described above. It 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 <i>N. haiwangii</i> , <i>Cladophlebis</i> sp. (Plate IV, 1) and species of <i>Sphenopteris</i> (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 <i>Cordaites</i> bore those naked axes, leaving only <i>Y</i> .
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

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

- 310
- 311

[Approximate position of Plate VIII]

312

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

314 Pteridosperms are a paraphyletic evolutionary grade of seed plants broadly united by the

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

scrambling/climbing plants (DiMichele et al., 2006). Previous accounts of medullosan pteridosperms

considered them to represent small trees with upright stems that could be self-supporting or growing

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 Blanzyopteris praedentata (Krings and Kerp, 1999), Medullosa steinii (Dunn et al., 2003) and

323 *Neuropteris attenuate* (Krings and Kerp, 2006).

Hooked prolongations in fossil plants were previously regarded as a specialized form to scramble (Schenk, 1892), but later were also considered to be sufficient for small to medium-sized

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,

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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597 Fig. 1 Location of the Wuda Tuff Flora in the Wuda Coalfield, Inner Mongolia, China. (A) Outline

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 $1 \text{ m} \times 1 \text{ m}$ quadrats (white lines).

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

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<sup>610</sup> Wuda excavation.



**Fig. 3.** Holotype of *Yangopteris ascendens*. (A) Gross form of the fragmental pinna. (B) Enlargement

- from (A) showing the pinnule form and venation pattern. Specimen S138136a (Swedish Museum of
- 616 Natural History).
- 617
- 618



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

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

- prolongation (white arrowhead). (4) Associated axes (simply branched) and *Cordaites* leaves, notice
- 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.



626

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



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. $C = Cortex$ , $H = Hair$ , $FA = Cortex$ , $FA = C$
636	Frond axis, PA = Pinna axis, PE = Petiole, PG = Parenchymatous ground tissue, VB = Vascular
637	bundle.
638	



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

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

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







649	bipinnate frond of <i>Cladophlebis</i> plant is preserved on the left, PB23172. (2) Diagram of the bipinnate
650	frond of <i>Y. ascendens</i> . (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).



Plate V. Pinnae of *Yangopteris ascendens*. (1) Two isolated pinnae, PB23173. (2) Enlargement of the
left white box in (1) showing a pinnule with acroscopically constricted and basiscopically decurrent

- 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
- box in (4) showing two falculate pinnules. Secondary veins extend at narrow angles (black
- arrowheads). (6) Another pinna of *Y. ascendens* showing the typical characters of pinnule base (white
- 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).
671	



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

- distal part of pinna axes. The frond axis is not visible, HEP 0350. (4) Enlargement of the left white
- box in (3) showing hooked spines on both sides of a pinna axis (white arrowheads). (5) Enlargement
- of right white box in (3) showing the hooked apices of two homolateral pinna axes (white
- 678 arrowheads).
- 679



Plate VIII. Field pictures of *Cordaites* branches in the same excavation. (1–3) Two-ordered branches
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,
- helical leaf scars (white arrowhead). CB = Cordaites branch; CL = Cordaites leaves.