

A new gigantopterid genus from the late Permian of the Daha Coalfield, Tibetan Plateau and its implication on plant-insect interactions

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DOI:

[10.1080/08912963.2020.1860033](https://doi.org/10.1080/08912963.2020.1860033)

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Document Version

Peer reviewed version

Citation for published version (Harvard):

Zhou, W, Chen, B-Y, Sun, W, He, X, Hilton, J & Wang, J 2020, 'A new gigantopterid genus from the late Permian of the Daha Coalfield, Tibetan Plateau and its implication on plant-insect interactions', *Historical Biology*. <https://doi.org/10.1080/08912963.2020.1860033>

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1 **A new gigantopterid genus from the late Permian of the**
2 **Daha Coalfield, Tibetan Plateau and its implication on**
3 **plant-insect interactions**

4
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26 **ABSTRACT**

27 Gigantopterid plants share common traits of megaphyllous leaves with multi-ordered
28 venation and have a stratigraphic distribution restricted to the Permian Period. They
29 display a large variety of leaf morphologies which may indicate affinities from more
30 than one plant groups including ferns and pteridosperms such as the peltasperms. Here
31 we describe a new genus of gigantopterid with two species from the upper Permian
32 Nayixiong Formation in the Daha Coalfield, Qinghai Province, China. The new genus
33 *Filigigantopteris* is markedly different from other gigantopterid genera in having
34 fern-like leaf architecture with double-meshed venation. *Filigigantopteris*
35 *asymmetrica* gen. et sp. nov. is characterized by its asymmetric pinnules with
36 dissected lobes, while *Filigigantopteris dahaia* gen. et sp. nov. is characterized by its
37 once-pinnate frond. A gigantopterid leaf figured from the Lopingian of southwest
38 China that was previously incorrectly assigned to *Gigantopteris nicotianaefolia* may
39 represent a third species of *Filigigantopteris*. The new genus further emphasizes the
40 morphological diversity and obscure systematic position of the Permian
41 gigantopterids. In addition, three types of functional feeding groups, including hole
42 feeding, margin feeding and probably skeletonization, are present on laminae of
43 *Filigigantopteris*, suggesting frequent and diverse plant-insect interactions between
44 gigantopterid megaphylls and herbivorous insects in Cathaysia.

45

46 **KEYWORDS** Cathaysia; gigantopterids; *Filigigantopteris* gen. nov.; Tibetan Plateau;

47 plant-insect interaction

48

49 **Introduction**

50 Gigantopterids were important floral elements in parts of the Cathaysian and
51 Euramerican realms during the Permian Period (e.g., White 1912; Halle 1927; Mamay
52 1960; Li et al. 1983a; Booi et al. 2009; DiMichele et al. 2011; Yang 2006). They were
53 first documented from the Guadalupian of Hunan Province, China and assigned to
54 *Megalopteris nicotianaefolia* Schenk (Schenk 1883) but were later transferred to
55 *Gigantopteris* Schenk because the genus name *Megalopteris* Dawson had
56 nomenclatural priority. Since then numerous other gigantopterids have been reported
57 from China (e.g., Zeiller 1907; Halle 1927) as well as other countries including Japan
58 (Yabe 1904), Korea (Yabe 1908), America (White 1912) and Indonesia (Posthumus
59 1927). Early accounts placed all gigantopterids in the genus *Gigantopteris*, but
60 Koidzumi (1934) was first to recognize their morphological differences and
61 re-classified them into five subfamilies and eight genera (Koidzumi 1934, 1936). Up
62 to now, over 20 genera have been established within the gigantopterids (see Zhou et al.
63 2018 for recent review).

64 Although some accounts of gigantopterid plants include details of epidermal
65 (Wang 1999; Yao and Liu 2004; DiMichele et al. 2011), anatomical (e.g., Mamay et al.
66 1988; Li et al. 1996; Li and Taylor 1998, 1999) and alleged reproductive features (e.g.,
67 Li and Yao 1983b; Zhu and Zhang 1995; Wang 1999), their systematic affinity
68 remains uncertain. Current evidence suggests that gigantopterids are not a

69 monophyletic group but share convergent traits of megaphyllous leaves with
70 multi-ordered net venation (Glasspool et al. 2004a, 2004b; DiMichele et al. 2011;
71 Zhou et al. 2018). In terms of their morphology, several distinct evolutionary
72 pathways **have been proposed within gigantopterids** involving a theory termed
73 “Growth Retardation” in which gigantopterid leaves were assumed to have evolved by
74 the fusion of segments of more simple leaves into larger leaves with more complex
75 venation patterns (Asama 1959; Shen et al. 1977; Booi et al. 2009). However, this
76 concept has been widely discredited (e.g., Li and Yao 1983a; Yao 1983; Yang 1987).
77 For example, recent research documenting the genus *Gigantonoclea* in the earliest
78 Permian Asselian Stage of North China contradicts Asama’s growth retardation theory
79 in which this seemingly advanced genus occurs in the fossil record significantly
80 earlier than its suggested ancestors (Zhou et al. 2018).

81 Gigantopterids appeared to reach their peak of morphological diversity in Henan
82 Province (central China) during the early Guadalupian to early Lopingian (Yang
83 2006). From that **region** abundant well-preserved leaves were systematically
84 described and classified into 36 species from 12 genera based on their leaf
85 architecture and venation patterns. For instance, in the simple-meshed leaves of
86 *Gigantonoclea* (Koidzumi), those with fern-like compound architecture **with apically**
87 **fused laminae** which fit the original diagnosis of the genus were maintained in
88 *Gigantonoclea sensu-stricto*, whereas those with petiolate compound architecture with
89 **apically separated leaflets** or simple leaves and axillary buds present were transferred
90 to *Pinnagigantonoclea* Yang and *Monogigantonoclea* Yang respectively (Yang 2006;

91 Zhou et al. 2018). Similar categories have also been applied in the double-meshed
92 leaves of *Gigantopteris* where those with petiolate compound architecture and an
93 apical leaflet were transferred to *Pinnagigantopteris* Yang, while those with simple
94 leaves and axillary buds present were transferred to *Monogigantopteris* Yang (Yang
95 2006).

96 Gigantopterid leaves are frequently discovered with feeding traces preserved on
97 them. Plant–arthropod interactions were first evidenced in the fossil record during the
98 Early Devonian with coprolites containing plant spores (Edwards et al. 1995;
99 Habgood et al. 2004) and coprolites preserved in plant stems (Kidston and Lang 1921;
100 Kevan et al. 1975). Interactions between plants and arthropods were more diverse and
101 abundant during the latest Mississippian and Pennsylvanian as evidenced by the
102 consumption of various plant tissues including stems (Labandeira and Phillips 1996),
103 roots (Labandeira 2001), leaves (Iannuzzi and Labandeira 2007) and sporangia
104 (Labandeira 1998). Palaeogeographically, arthropod herbivory has been documented
105 from each of the global floral provinces during the Cisuralian including from
106 Euramerica (Beck and Labandeira 1988; Schachat et al. 2014, 2015), Angara
107 (Zherikhin 2002), Gondwana (Gallego et al. 2014; Schachat et al. 2014) and
108 Cathaysia (Hilton et al. 2002; Feng et al. 2020). Gigantopterids were restricted to the
109 Permian of Cathaysia and parts of Euramerica and appear to have been routinely
110 targeted by animals including insects (Yao et al. 1983; Beck and Labandeira 1998;
111 Glasspool et al 2003; Labandeira and Allen 2007; Zhou et al. 2018; Liu et al. 2020).
112 Studies of foliar feeding traces on gigantopterid plants will enhance our understanding

113 of the ecologic complexities in Permian terrestrial ecosystems.

114 In this paper we report a new genus and two new species of gigantopterid plant
115 from the Wuchiapingian (late Permian) of the Daha Coalfield in Qinghai Province,
116 southwest China that is part of the Tibet Plateau. The new genus has fern-like leaves
117 that are distinctly different from other double-meshed gigantopterid genera. In
118 addition, the leaves were targeted by three different kinds of functional feeding groups
119 including hole feeding, margin feeding, and probably surface feeding, providing
120 additional examples of insect predation of gigantopterids and suggesting similar
121 gigantopterid–insect component communities in both Euramerica and Cathaysia.

122

123 **Materials and methods**

124 Specimens were collected from mudstones of Bed 2 in the Nayixiong Formation
125 from the Daha Coalfield, Qinghai Province, China (Figure 1(b-c)). Tectonically, the
126 Daha Coalfield is within the Qiangtang Terrane and constitutes part of the central
127 Tibetan Plateau (Figure 1(a)). Biostratigraphically, the Nayixiong Formation is
128 approximately equivalent to the Longtan Formation in South China based on its
129 faunal and floral assemblages and is suggested to be Wuchiapingian (Longpingian,
130 late Permian) in age (He and Zhang 1984; Jin et al. 2000; Liao and Xu 2002).

131

132 [Approximate position of Figure 1]

133

134 Four specimens from the Daha Coalfield were studied in this paper. They were

135 first prepared by *dégagement* (Fairon-Demaret et al. 1999) to expose them from the
136 overlying sedimentary matrix. To enhance the contrast of the specimens to the matrix,
137 specimens were immersed in alcohol and photographed using a digital NIKON D-800
138 camera (Kerp and Bomfleur 2011). However, the mudstone matrix reacts and
139 becomes unconsolidated on contact with liquid, so immersion and photography were
140 undertaken quickly before allowing the specimen to air dry in a dry environment.
141 Specimens are deposited in the Nanjing Institute of Geology and Palaeontology,
142 Chinese Academy of Sciences (NIGPAS).

143 The terminology for the venation pattern mainly follows Hickey (1979), while
144 leaf morphology follows standard angiospermous leaf terminology as previously
145 applied in gigantopterid leaves by Glasspool et al. (2003), Booi et al. (2009) and
146 DiMichele et al. (2011). The central vasculature of a fused leaf is described as the
147 primary vein, whereas the central axis of once-pinnate leaf is considered to be a pinna
148 rachis and the primary vein is represented by the midrib of the lateral pinnule. The
149 difference of simple, odd-pinnate and fern-like leaves refers to Figure 4(a-c) of Zhou
150 et al. (2018).

151

152 **Results**

153 *Systematic palaeobotany*

154 Family Gigantopteridaceae Koidzumi 1936

155 Genus *Filigigantopteris* gen. nov.

156 Generic diagnosis: Fern-like pinnule or frond, deeply lobed or at least once-pinnate.

157 Venation four orders or higher, forming small meshes within large meshes.

158 Etymology: “Fili-”, prefix for “filicales”, “-gigantopteris” the morphological genus

159 originally applied in the gigantopterid leaves which are double-meshed. The new

160 genus is named after its most typical morphological traits of fern-like leaf architecture

161 and double-meshed venation pattern.

162 Remarks: The genus is restricted to the plant fossils of the Permian Period, in order to

163 distinguish them from modern angiospermous leaves.

164

165 Species: *Filigigantopteris asymmetrica* sp. nov. (Figures 2, 3, 6 (a–b))

166 Holotype: PB23526

167 Paratype: PB23527

168 Type locality: Daha Coalfield, Qinghai Province, China

169 Stratigraphy: Bed 2 of the Nayixiong Formation

170 Age: Wuchiapingian (Lopingian, Permian)

171 Repository: Nanjing Institute of Geology and Palaeontology, Chinese Academy of

172 Sciences, Nanjing, China

173 Specific diagnosis: Fern-like pinnule. Pinnule asymmetric, with one side of lobes.

174 Venation five orders. Tertiary veins anastomose. Quaternary veins form large

175 polygonal meshes. Veinlets form small polygonal meshes with blind veins present

176 inside.

177 Etymology: The new species is named after its asymmetric pinnule.

178

179 *Description*

180 Pinnule is asymmetrically elliptic in shape. As illustrated in the holotype
181 specimen PB23526 (Figure 2(a)), the right side of the pinnule possesses partly fused
182 lobes with acute apices and entire margins, while the left margin is almost straight.
183 The enlargement of the left margin shows that its upper part possesses an undulated
184 “fracture”, whereas its lower part has an obviously entire margin (Figure 2(d)).
185 Pinnule lobes encounter different degrees of dissection, with the deepest one
186 illustrated in Figure 2(a) dissected by nearly half of the lateral margin. Pinnule
187 laminae display five orders of venation (Figures 2(c), 3(b), 3(e)). The primary vein is
188 2 mm wide at the base and gradually taper towards the apex. Secondary veins are
189 generally sub-oppositely arranged, stretch out from the primary vein at angles of 30°
190 to 45°, and become gradually thinner when approaching the lobe apices. Secondary
191 veins from the asymmetric side of the pinnule are much weaker and slightly denser
192 than those from the other side that with normal lobes. Tertiary veins are alternatively
193 to sub-oppositely arranged. They stretch out from the secondary veins at an angle of
194 *ca.* 45°, bend upward and dissolve before reaching the pinnule margin (Figure 2 (c)),
195 or anastomose with the opposite tertiary veins in the adjacently fused area (Figure
196 3(e)). Quaternary veins are regularly arranged and form large polygonal meshes by
197 anastomosing with their opposite and adjacent quaternary veins (Figures 2(c), 3(b)).
198 Irregular veinlets form small meshes (Figure 3(c)). Blind veins are well developed
199 within the small meshes and are variable in their pattern (Figure 3(c)). Subsidiary
200 veins arise directly from the primary, secondary and tertiary veins (Figures 2(d), 3(e)).

201 The fragmentary pinnule illustrated in [Figure 3\(a\)](#) represents a nearly apical
202 portion of the pinnule. In this region the secondary veins stretch out from the primary
203 vein at an angle of *ca.* 30°. Tertiary and quaternary veins are less regularly arranged
204 towards the apices. Meshes, blind veins and shallowly dissected lobes with acute
205 apices and entire margins ([Figure 3\(b-c\)](#)) are generally identical to those of the
206 holotype.

207 The lower pinnule fragment illustrated in [Figure 3\(d\)](#) (the reverse side of
208 specimen shown in [Figure 2\(a\)](#)) clearly displays five orders of veins with distinct
209 double meshes and blind veins ([Figure 3\(e\)](#)). The angles between the primary and
210 secondary veins suggest this fragment may represent the middle to lower portion of a
211 complete pinnule of *Filigigantopteris asymmetrica*.

212

213 [Approximate positions of [Figures 2, 3](#)]

214

215 Species: *Filigigantopteris dahaia* sp. nov. ([Figures 3\(d\), 4, 5, 6 \(c-d\)](#))

216 Holotype: PB23528

217 Paratypes: PB23526 (the reverse side of [Figures 2\(a\)](#)), PB23529

218 Type locality: Daha Coalfield, Qinghai Province, China

219 Stratigraphy: Bed 2 of the Nayixiong Formation

220 Age: Wuchiapingian (Lopingian, Permian)

221 Repository: Nanjing Institute of Geology and Palaeontology, Chinese Academy of

222 Sciences, Nanjing, China

223 Specific diagnosis: Fern-like frond, at least once-pinnate. Pinna apex coherent. Lateral
224 pinnules shallowly fused or separated. Venation four orders. Secondary veins bend
225 upward and gradually diminished when approaching margin. Tertiary veins form large
226 polygonal meshes. Veinlets form small polygonal meshes with well-developed blind
227 veins.

228 Etymology: The new species is named after its locality.

229

230 *Description*

231 Fronds are at least once-pinnate (Figures 4(a), 5(a)). Pinna rachises are robust,
232 3.6 mm wide at the base and gradually taper towards the apex and are longitudinally
233 striated. Apices are coherent and obovate in form, with its basal part shallowly fused
234 with the first lateral pinnule (Figures 4(a), 5(b)). Lateral pinnules are non-fused,
235 ribbon-like with entire margins (Figures 4(b), 5(a)). The pinnule illustrated in Figure
236 4(b) is more than 8.3 cm long and 2.3 cm wide, and as the specimen is incomplete
237 (Figure 5(a)). Pinnule bases are decurrent with subsidiary veins arising directly from
238 the pinna rachis (Figures 4(b), 5(b)). Pinnule apices, although not preserved, are
239 inferred to be acute based on the morphology of the most complete preservation
240 (Figure 5(c)).

241 Pinnule lamina **display** four orders of venation. Primary veins are oppositely
242 arranged and stretch out from the pinna rachises at angles of 30° to 45°. Secondary
243 veins are prominent and extend from the primary veins at angles of 60° to 70°. They
244 bend upward at the halfway to the pinnule margin and dissolve before reaching the

245 pinnule margin. Tertiary veins are flexuous. They anastomose with the opposite and
246 adjacent ones forming regular, large, polygonal meshes (Figures 4(c)). Veinlets form
247 regular, small, polygonal meshes. Blind veins are well-developed within the small
248 meshes and highly variable in the pattern (Figures 4(d)).

249 The right upper frond illustrated in Figure 3(d) (the reverse side of Figure 2(a))
250 is once-pinnate and possesses ribbon-like pinnules with decurrent bases. In contrast,
251 the left upper frond is also once-pinnate but possesses shortly petiolate pinnules with
252 constricted bases. The venation is indistinct in both fronds. Nevertheless, the right
253 upper frond is perhaps assignable to *Filigiantopteris dahaia* on account of its
254 decurrent pinnules that are similar to those of the holotype.

255

256 [Approximate positions of Figures 4, 5]

257

258 Discussion

259 *Comparisons and systematic implications*

260 *Filigiantopteris dahaia* clearly has a once-pinnate leaf architecture. The
261 decurrently fused area between the coherent apex and first lateral pinnule (Figures
262 4(b), 5(b)) indicates the fronds form from a fern-like dissection mode that is dissected
263 from a coherent pinna. Similarly, the holotype of *F. asymmetrica* (Figures 2(a)) shows
264 it to be a deeply lobed pinnule. But it could also potentially be continuously dissected
265 into a once-pinnate frond as indicated by the deep dissections (Figures 2(c), cf.
266 *Auritifolia waggoneri* in Chaney et al. 2009). Nevertheless, the coherent apices of *F.*

267 *dahaia* are obovate in form and much larger (at least wider) than the lower lateral
268 pinnules (Figures 4(a), 5(b)), whereas in *F. asymmatica* the lobes are gradually
269 reduced in size towards the apex so that the apical lobe is the smallest one (Figures
270 2(a), 3(a)). In addition, the asymmetric feature is clearly illustrated in the holotype of
271 *F. asymmetrica* (Figures 2(a)) but is absent in *F. dahaia*. Collectively these features
272 reliably distinguish the two species of *Filigigantopteris*.

273 Gigantopterid species can be effectively distinguished from each other based on
274 their leaf architecture and venation pattern (Yang 2006; Zhou et al. 2018). In addition
275 to the two new gigantopterid species described in this paper, other gigantopterid
276 species have double-meshed venation and include *Gigantopteris nicotianaefolia*, *G.*
277 *dictyophylloides* Gu et Zhi, *G. cordata* Yabe et Ōishi emend. Tiang et Zhang, *G.*
278 *meganetes* Tian et Zhang, *G. paradoxa* Mo, *G. shuangquanensis* Yang,
279 *Monogigantopteris clathroreticulatus* Yang, *M. densireticulatus* Yang,
280 *Pinnagigantopteris lanceolatus* Yang et Xie and *P. oblongus* Chen (Yabe and Ōishi
281 1938; Gu and Zhi 1974; Tian and Zhang 1980; Zhao et al. 1980; Xiao and Zhang
282 1985; Yang 1985, 2006). Key features of these twelve species are compared in Table 1
283 and illustrated in Figure 6 to show their differences.

284

285 [Approximate positions of Table 1 and Figure 6]

286

287 *Monogigantopteris clathroreticulatus*, *M. densireticulatus*, *Pinnagigantopteris*
288 *lanceolatus* and *P. oblongus* (Figure 6(e–h)) are double-meshed gigantopterids from

289 the Permian Yuzhou Flora of Henan Province, North China (Yang 2006). *M.*
290 *clathroreticulatus* and *M. densireticulatus* are characterized by large, simple leaves
291 which are broadly oval shaped and commonly incompletely preserved. In contrast, *P.*
292 *lanceolatus* and *P. oblongus* are odd-pinnate fronds with long elliptical “leaflets”
293 (Table 1); the holotype of *P. lanceolatus* reveals that the “leaf” is an apical leaflet on a
294 pinna rachis. Similar leaf architecture is widely present in many *Gigantonoclea sensu*
295 *lato* species, with this leading Yang (2006) to establish the genus *Pinnagigantonoclea*
296 to accommodate them. The two new species documented here are distinct from the
297 four gigantopterids from the Yuzhou Flora as in the latter species apical leaflets are
298 the same as these lateral leaflets rather than being a coherent lamina (Table 1).

299 *Gigantopteris cordata* is known from the late Permian floras of Fujian Province,
300 South China (Yabe et Ōishi 1938) and has an elongate-reniform leaf (Figure 6(i)).

301 Although the original materials only displayed polygonal meshes and not
302 double-meshed venation (Gu and Zhi 1974), larger specimens of *G. cordata* from the
303 late Permian of Guizhou Province, South China (Tian and Zhang 1980) confirm the
304 presence of double-meshed venation in this species. *G. cordata* is remarkably
305 different from the two *Monogigantopteris* species and the two new *Filigigantopteris*
306 species described in this paper in terms of its elongate-reniform leaf shape (Table 1).

307 *Gigantopteris meganetes* was established based on two large leaves collected from
308 the late Permian of Guizhou Province, South China (Tian and Zhang 1980). The larger
309 leaf, although incompletely preserved, is broadly oval in shape, over 24 cm wide, with
310 a bicrenate margin (Figure 6(j)). The venation pattern including the presence of blind

311 veins and absence of accessory meshes in *G. meganetes* is similar to the specimens
312 described here but differs in lacking the fern-like leaf architecture that characterizes
313 the new genus established based on the material from the Nayixiong Formation ([Table](#)
314 [1](#)). Leaves of *G. meganetes* are more likely to be simple, and therefore may be
315 potentially transferrable to the genus *Monogigantopteris* (Yang [2006](#)).

316 *Gigantopteris dictyophylloides* is one of the most common gigantopterid species
317 in the Cathaysian floras (Gu and Zhi [1974](#)). This species is quite similar to
318 *Filigantopteris asymmetrica* from the Nayixiong Formation in its vein
319 characteristics such as having regular doubled-meshes and blind veins but lacking
320 accessory meshes ([Table 1](#); [Figures 6\(k\), 7\(a–d\)](#)). Leaves of *G. dictyophylloides*, if
321 capable of deep dissection, would be almost the same as the pinnule of
322 *Filigantopteris asymmetrica* from the Nayixiong Formation. However, the holotype
323 specimen of *G. dictyophylloides* contains several overlapped leaves on the bedding
324 surface that are suggested to belong to the same species. One of these leaves is broad
325 in shape with crenate margin ([Figure 7\(b\)](#)) and this characteristic has also been
326 included in the original and emended diagnosis of this species (Gu and Zhi [1974](#);
327 Glasspool et al. [2004a](#)). Moreover, this species has been widely reported from late
328 Permian strata of South China but no specimens show fern-like dissections to the leaf
329 (e.g., Li et al. [1982](#); Yu [2007](#)). Therefore, *Filigantopteris asymmetrica* is easily
330 distinguished from *G. dictyophylloides* in having fern-like leaf architecture and lobed
331 pinnule margin, while *F.dahaia* is also readily distinguished from *G. dictyophylloides*
332 in having ribbon-like decurrent pinnules with entire margin ([Table 1](#)).

333

334 [Approximate position of [Figure 7](#)]

335

336 *Gigantopteris nicotianaefolia* is perhaps the most typical and widely distributed
337 gigantopterid species in the Cathaysian floras (e.g., Schenk 1883; Yao 1983; Liu and
338 Yao 2009; Yang 2006). However, based on detailed examination of the type materials,
339 the precise leaf architecture of *G. nicotianaefolia* is uncertain (Glasspool et al. 2004a).
340 While some researchers believe that the leaves of *G. nicotianaefolia* should be simple
341 since they are commonly large in size and shortly petiolate (Gu and Zhi 1974; Yao
342 1983), Yang (2006) suggested that the “leaves” of *G. nicotianaefolia* could also be
343 leaflets of huge odd-pinnate fronds as their long, elliptic leaf shape ([Figure 6\(l\)](#)) is
344 similar to that of *Pinnagigantopteris lanceolatus* and *P. oblongus* ([Table 1](#)).
345 Nevertheless, neither of these possibilities is comparable to the fern-like leaves from
346 the Nayixiong Formation.

347 A large once-pinnate gigantopterid leaf with oppositely arranged and basally fused
348 pinnules ([Figure 6\(m\)](#)) identified as *Gigantopteris nicotianaefolia* from the Lopingian
349 of Guizhou Province, South China (Plate 15, fig. 1 in Tian and Zhang 1980) needs
350 further examination as it is distinct from other specimens of *G. nicotianaefolia* in
351 having a fern-like compound leaf architecture. The pinnate feature of this specimen
352 with five orders of veins distinguishes it from both of the two new species presented
353 in this paper ([Table 1](#)) but also make its assignment to *G. nicotianaefolia* unlikely. As
354 mentioned earlier, isolated leaves of *G. nicotianaefolia* are commonly petiolate,

355 indicating them to be either simple leaves or leaflets from odd-pinnate fronds.
356 Re-investigation of the specimen illustrated by Tian and Zhang (1980) is required as it
357 could more likely be a third species of *Filigigantopteris* rather than *G.*
358 *nicotianaefolia*.

359 *Gigantopteris paradoxa* Mo was established based on several isolated leaves from
360 the Lopingian of Yunnan Province, South China (Zhao et al. 1980). Leaves of *G.*
361 *paradoxa* are elliptic with serrate margins and probably blunt to cordiform bases
362 (Table 1; Figure 6(n)). They display four orders of venation with tertiary veins
363 forming indistinct large meshes, while the veinlets form small meshes. The leaf
364 architecture of *G. paradoxa* was suggested to be once-pinnate by (Zhao et al. 1980)
365 (in this case similar to *Filigigantopteris dahaia*), and the leaves are treated as
366 “pinnules” in the description. However, no specimens were illustrated to support the
367 pinnate interpretation, and such a pinnule form is more consistent with the concept of
368 *Monogigantopteirs* (Yang 2006). Even so, *F. dahaia* is readily distinguished from *G.*
369 *paradoxa* in possessing entirely margined and basally decurrent pinnules.

370 The holotype of *Gigantopteris shuangquanensis* Yang is a once-pinnate frond
371 from the Lopingian of Beijing, North China (Xiao and Zhang 1985; Chen 1990).
372 Pinnules of *G. shuangquanensis* are sub-oppositely arranged, with their basal lamina
373 entirely connected with the pinna rachis (Figure 6(o)). In terms of the venation pattern,
374 secondary veins stretch out at a very broad angle. Tertiary veins form irregular large
375 meshes. Veinlets are sparse and form indistinct small meshes, with possible glands
376 preserved inside. *G. shuangquanensis* differs from the species from the Nayixiong

377 Formation by its intermediate venation pattern (i.e., less-developed double meshes)
378 between the features of the genera *Gigantonoclea* and *Gigantopteris* which is now
379 commonly placed in the genus *Progigantopteris* Yang (Yang 1987, 2006).

380 In summary, both species from the Nayixiong Formation possess fern-like
381 pinnules or once-pinnate fronds, whereas previous accounts of other double-meshed
382 gigantopterids are mostly simple leaves or odd-pinnate fronds. The establishment of a
383 new genus for the specimens from the Nayixiong Formation is justified by the
384 essential difference of the fern-like leaf architecture that may suggest a distant
385 relationship to the previous double-meshed gigantopterids (Table 1; Figure 6).

386 Although the exact systematic position is unclear, the establishment of the new genus
387 *Filigigantopteris* further highlights the morphological disparity of gigantopterids and
388 lends additional support to the gigantopterids being unlikely to constitute a
389 monophyletic group (Glasspool et al. 2004a, b; DiMichele et al. 2011).

390

391 *Leaf asymmetry of Filigigantopteris asymmetric gen. et sp. nov.*

392 Specimen PB23526 of *Filigigantopteris asymmetrica* is unusual in showing an
393 asymmetric leaf of which the right half is broadly dissected but the left half is highly
394 restricted in vegetative growth (Figure 2(a, d)). Similar asymmetric leaves/leaflets are
395 present in some fossil taxa such as *Rhus asymmetrica* Tosal, Sanjuan et Martín-Closas,
396 a trifoliate leaf reported from the lower Oligocene of Spain (Tosal et al. 2019).

397 Different from the apical symmetric leaflet, the two lateral leaflets of *R. asymmetrica*
398 have different levels of asymmetry (Plate II in Tosal et al. 2019). The left leaflet in the

399 holotype of *R. asymmetrica* (Figure 2 in Tosal et al. 2019) is quite similar to the
400 asymmetric pinnule of *Filigigantopteris asymmetrica* (Figure 2(a)) in having one side
401 with an approximately straight margin. *Auritifolia waggoneri* Chaney, Mamay,
402 DiMichele et Kerp is a once-pinnate frond with possible affinity with the **Peltasperms**
403 reported from the lower Permian of Texas, USA (Chaney et al. 2009). Some
404 specimens of *A. waggoneri* display aberrant leaves, one of which as illustrated in the
405 Figure 8D of Chaney et al. (2009) possesses an asymmetric pinna lamina and is
406 comparable to the situation in *F. asymmetrica* (Figure 2(a)). However, we currently do
407 not have a second specimen to repeat the asymmetric nature of *F. asymmetrica* on
408 account of the limited collections available from the sampling locality. Therefore, the
409 causes of asymmetry of *F. asymmetrica* is still uncertain (e.g., developmental stages,
410 growth positions or local environmental stress).

411

412

413 *Plant–insect interactions*

414 In Euramerica, insect damage to gigantopterid leaves occur in *Zeilleropteris*
415 Koidzumi, *Gigantopteridium* Koidzumi and *Cathaysiapteris* Koidzumi emend. Yang
416 (Beck and Labandeira, 1988). By contrast, in Cathaysia insect damage on
417 gigantopterid leaves were previously only known in *Gigantonoclea* (Glasspool et al.
418 2003; Zhou et al. 2018) and *Gigantopteris* (Liu et al. 2020). Abundant feeding traces
419 in *Filigigantopteris* represent the third gigantopterid genus in Cathaysia to experience
420 insect damage.

421 Three different kinds of functional feeding groups are observed on the leaves of
422 *Filigigantopteris*, namely hole feeding, margin feeding and probably skeletonization.
423 In the largest specimen of *F. dahaia* (PB23527, [Figure 5\(b–d\)](#)), several holes are
424 identified as hole feeding damages on account of the unequivocal presence of
425 thickened wound reaction tissue ([Figure 5\(c\)](#)). According to the classification of
426 Labandeira et al. (2007), these damage types are classified as DT 1, DT 2 and DT 5
427 based on the size and shape of the holes. In specimen PB23529 of *F. asymmetrica*
428 ([Figure 3\(a\)](#)), a marginal cut is observed near the apex of the fragmentary pinnule.
429 This excision is identified as marginal feeding trace ([Figure 3\(b\)](#)) on account of the
430 partially preserved dark rim that represents wound reaction tissue. The damage type is
431 classified as DT 13 according to Labandeira et al. (2007) as the excision cuts the leaf
432 apex and primary veins. In addition, there are several small ovoid to circular holes
433 present in specimen PB23529 ([Figure 3\(a\)](#)). They do not possess the typical wound
434 reaction tissue seen in *F. dahaia* (i.e., [Figure 5\(b–d\)](#)), instead, they have some residual
435 veins within the holes.

436 The identification of these holes is perhaps controversial. In the literature, a
437 similar hole with residual veins was reported from a pinnule of the Cathaysian
438 gigantopterid *Gigantonoclea lagrelii* and suggested to be resulted from
439 skeletonization. However, such an interpretation is not accepted by some other
440 researchers (Labandeira and Allen, 2007) because the veins which should be retained
441 in that hole have already almost gone. In contrast, a few late Palaeozoic feeding traces
442 reported from Gondwanan Glossopteridales (Adami-Rodrigues et al. 2004) and

443 Euamerican gigantopterids (Beck and Labandeira 1998; Labandeira and Allen 2007)
444 and Medullosales (Xu et al. 2018) with completely preserved parallel veins were more
445 readily interpreted as the result of skeletonization.

446 Here we note some feeding traces within a gigantopterid leaf were also reported
447 from the Douling Formation (Guadalupian) of Hunan Province, China by Yao (1983).
448 Re-illustrating the specimen here in Figure 7(e–f) shows that the feeding traces are
449 very similar to those from Euramerican gigantopterids in retaining the whole and
450 parallel vasculature, suggesting a similar gigantopterid–insect component community
451 in both Euramerica and Cathaysia. Moreover, in re-investigating the holotype of
452 *Gigantopteris dictyophylloides* (Gu and Zhi 1974; see Figure 7(c)), a circular hole
453 with distinct wound reaction tissue is visible near its midvein. The quaternary vein
454 and veinlets, although still not completely reserved, were clearly retained in this hole
455 (Figure 7(d)). Therefore, the “skeletonized” behavior, if correctly interpreted by
456 previous researchers, appears more common in species of Cathaysian gigantopterids
457 than currently recognized. However, we still cannot exclude the possibility that all
458 these late Palaeozoic “skeletonizations” (in both the literature and this paper) were
459 actually surface feeding damages with one side of the epidermis decayed later before
460 preservation, resulting in an apparent “skeletonized” appearance due to taphonomy.

461

462 **Acknowledgements**

463 We thank Jing-jing Tang (Nanjing Institute of Geology and Palaeontology,
464 Chinese Academy of Sciences) for photographic assistance. This work is funded by

465 the Strategic Priority Research Program (B) of Chinese Academy of Sciences
466 (XDB18000000, XDB26000000), the National Natural Science Foundation of China
467 (41530101, 41702024 and 41802011), the Second Tibetan Plateau Scientific
468 Expedition and Research (2019QZKK0706), the projects of China Geological Survey
469 (DD20190116), and the State Key Laboratory of Palaeobiology and Stratigraphy
470 (NIGPAS) (20182114).

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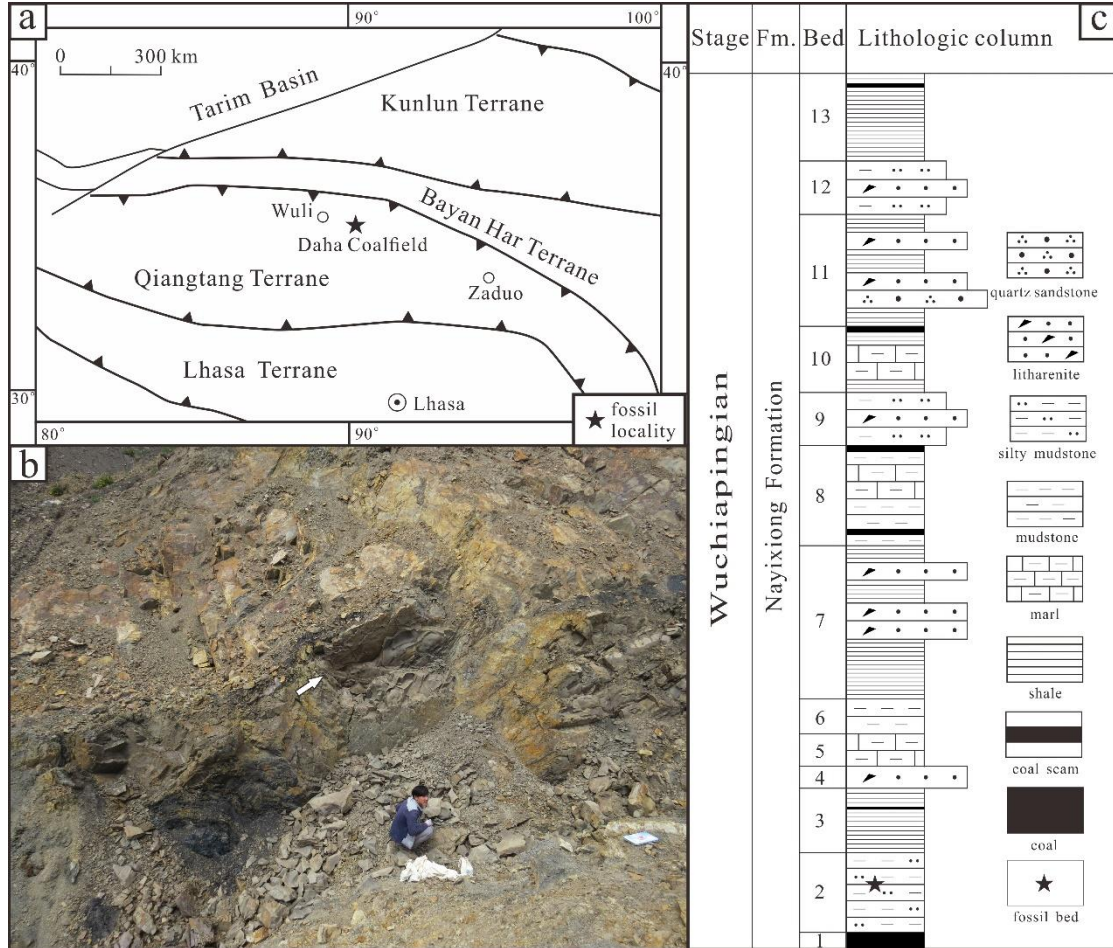
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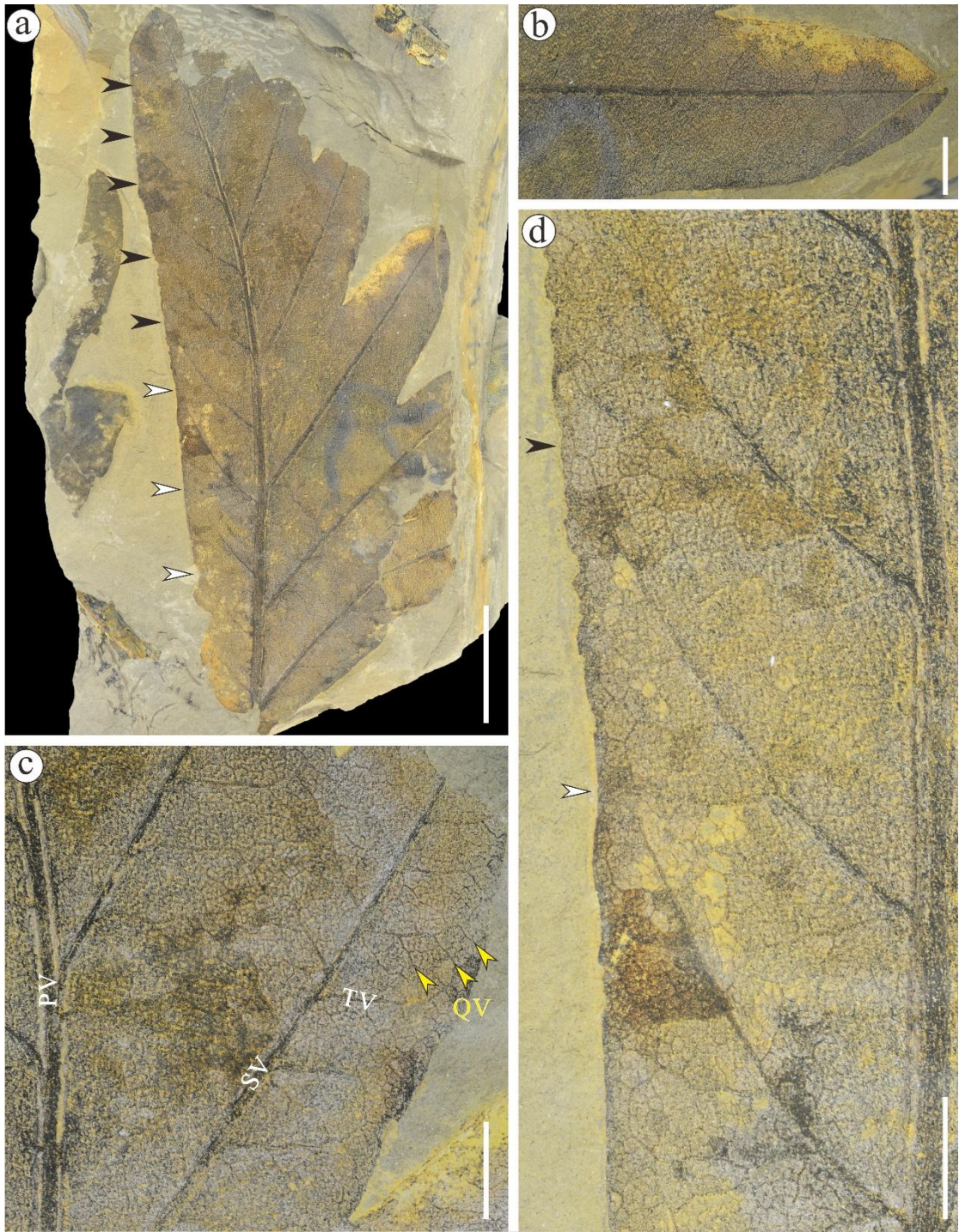
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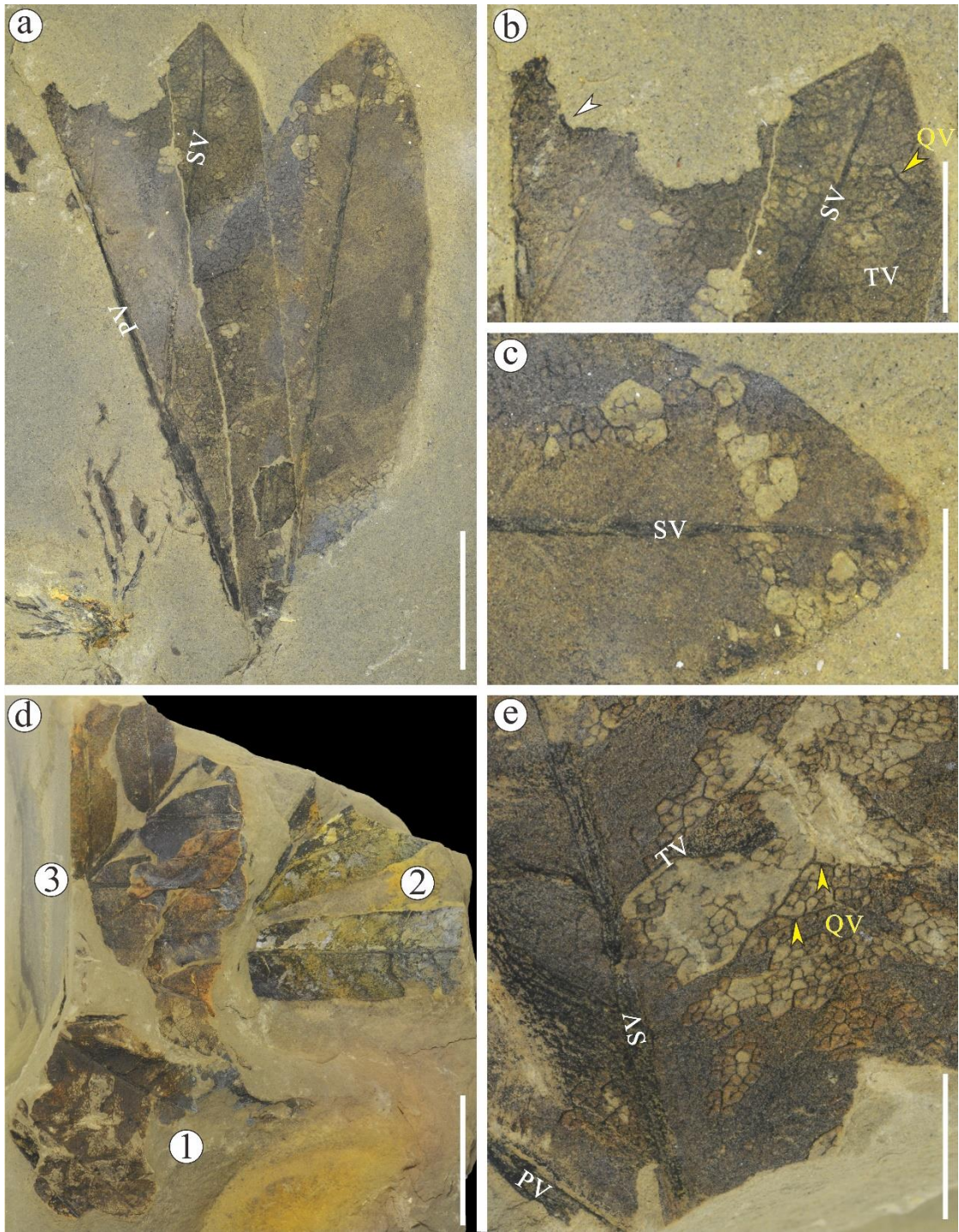
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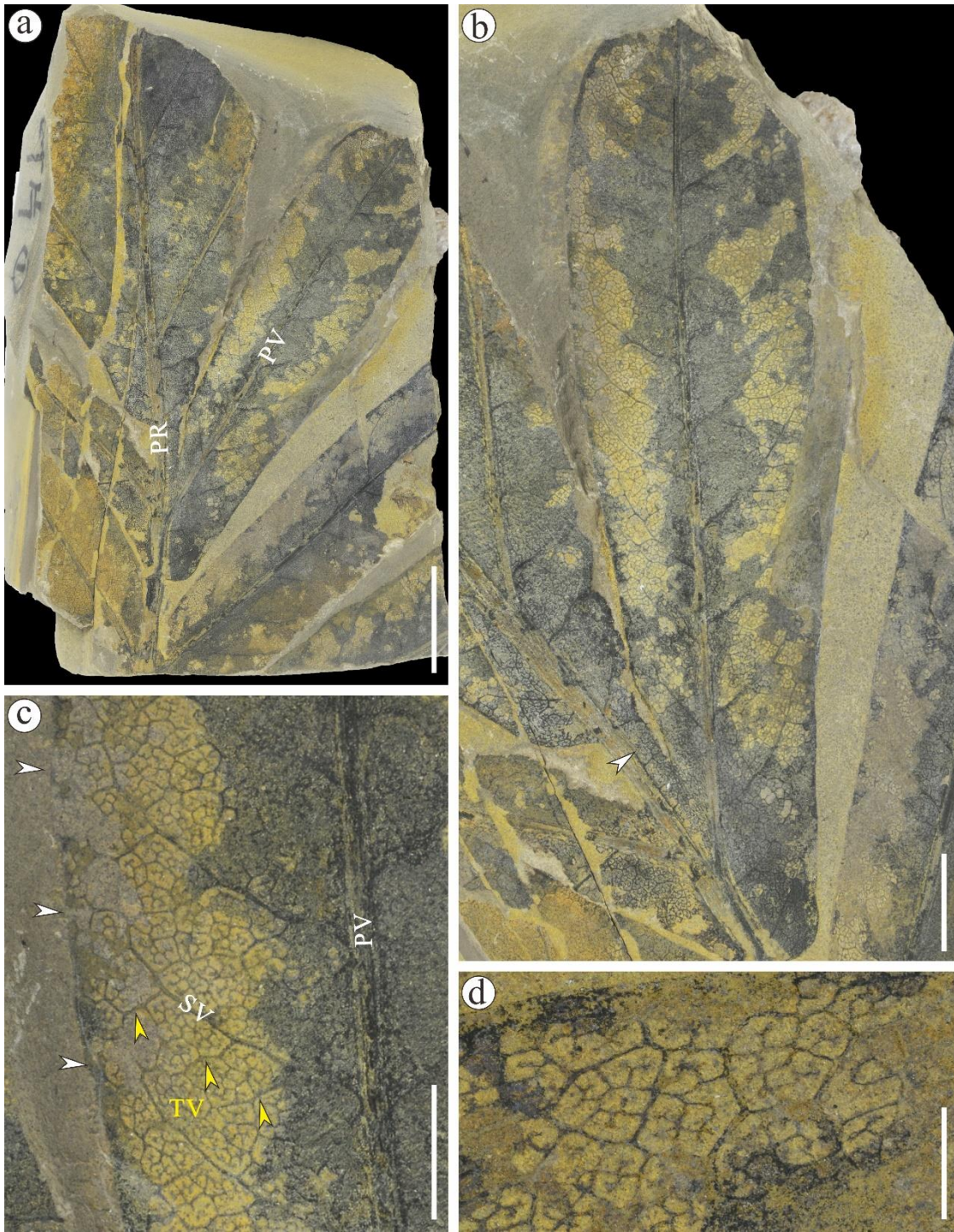
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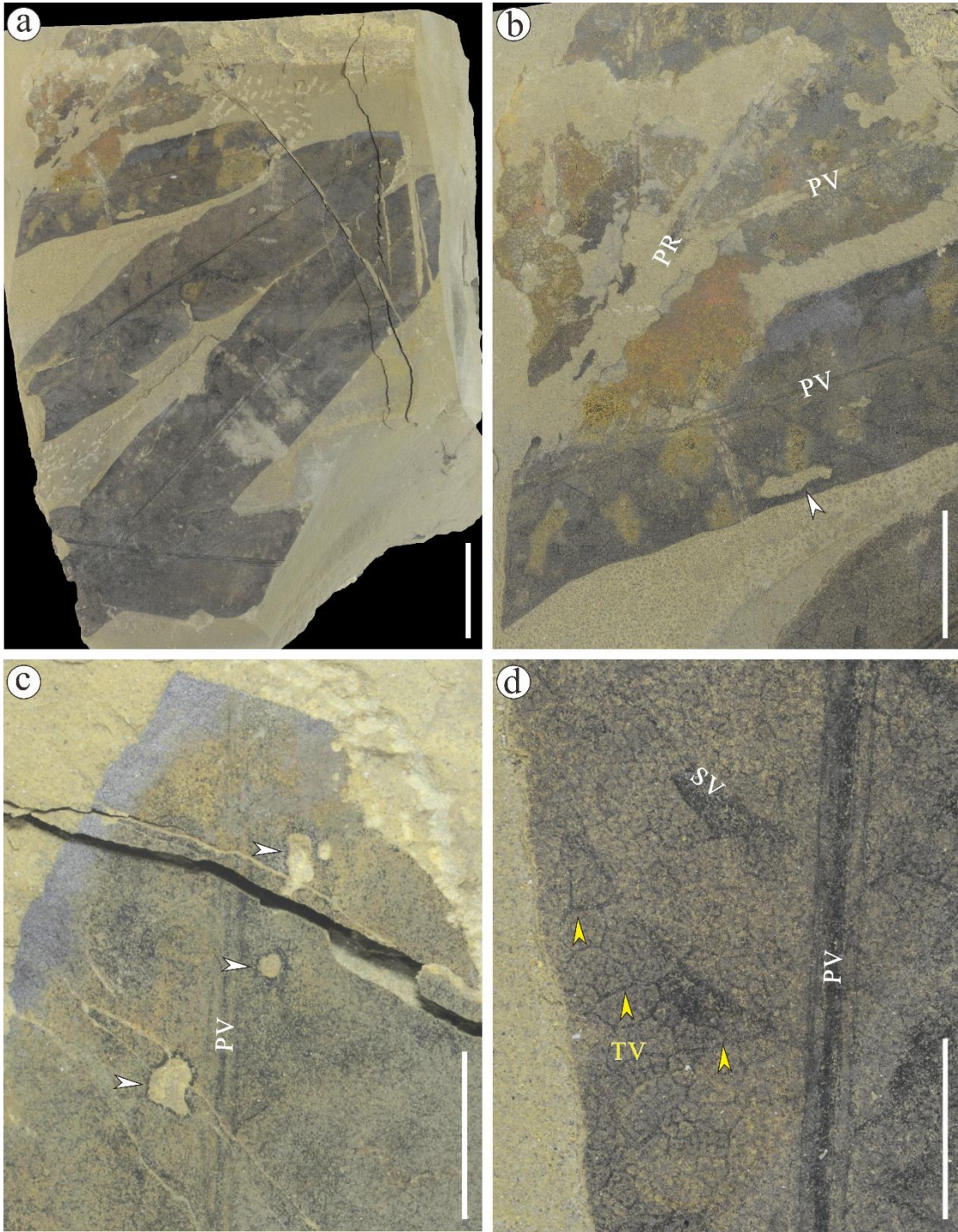
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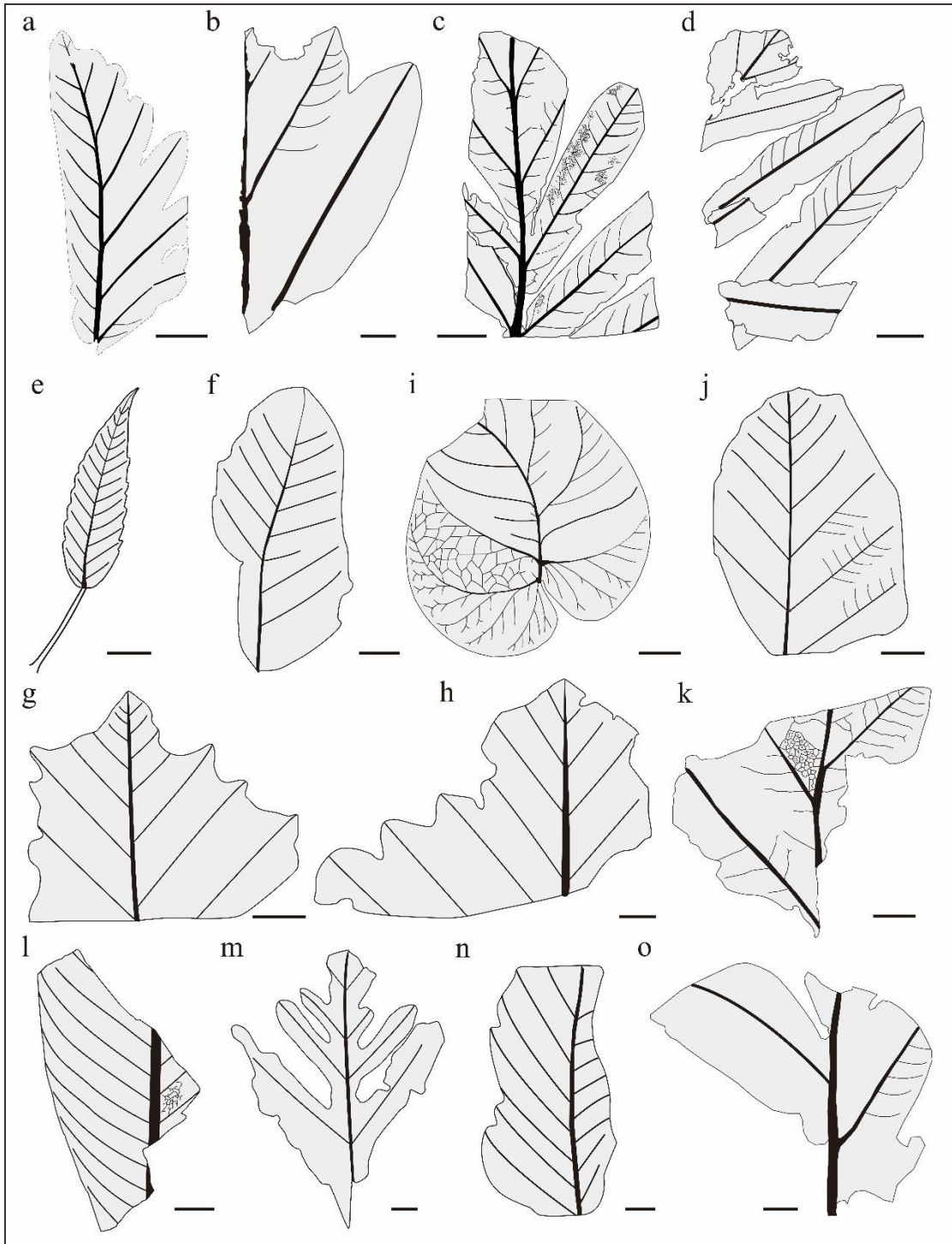


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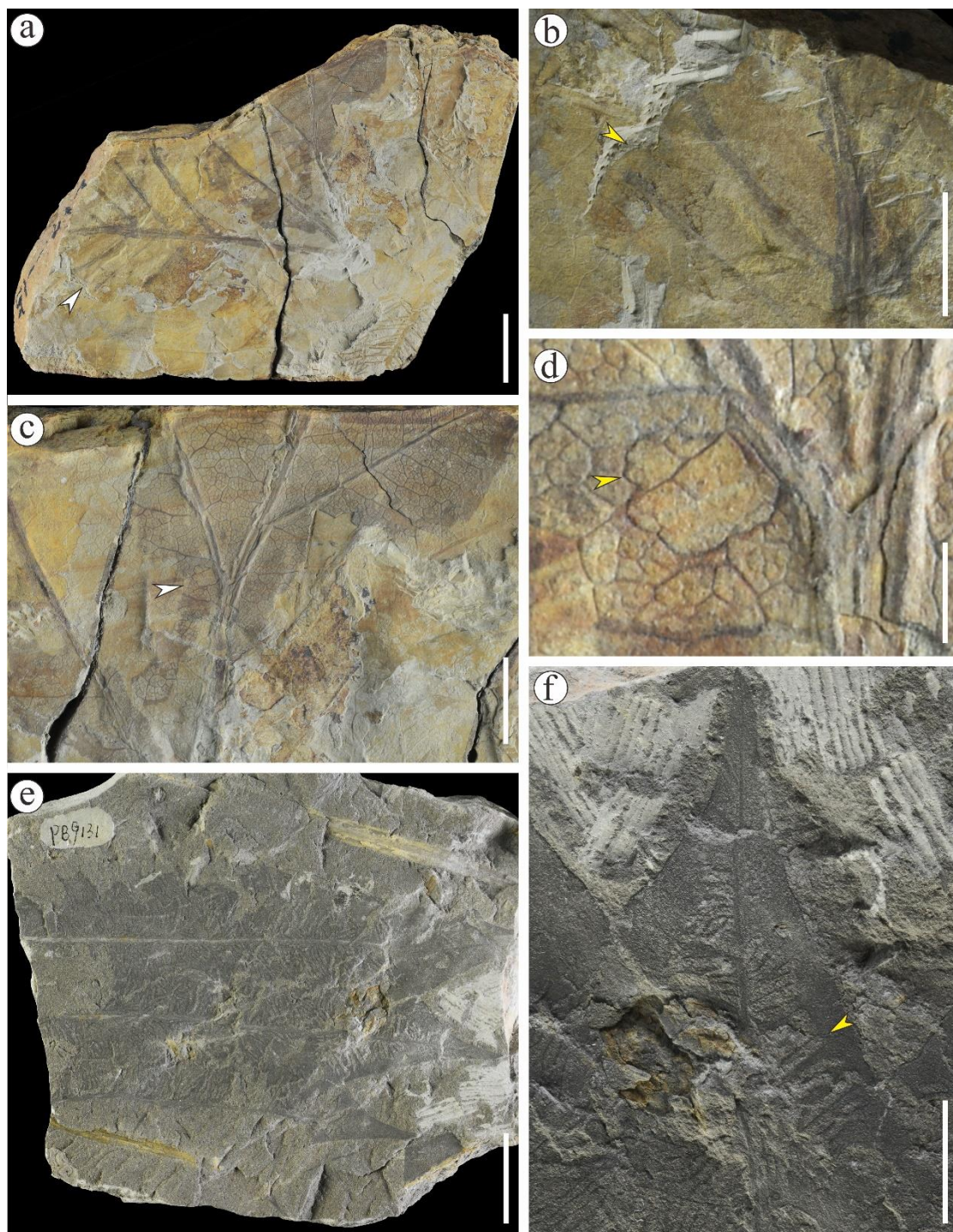
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680 Figure 7

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684 **Table 1** Comparison of the leaf architecture and venation pattern between the two *Filigigantopteris* species and other double-meshed
 685 gigantopterids. Conditions shared with *F. dahaia* are emphasized in boldface.

Species	Leaf architecture				Venation Pattern				Key reference
	Architecture	Foliage type	Shape	Margin	Order	Doubled-meshes	Accessory meshes	Blind veins	
<i>Filigigantopteris asymmetrica</i> gen. et sp. nov.	fern-like	pinnule	elliptic	lobed	5	distinct, regular	absent	present	this paper
<i>F. dahaia</i> gen. et sp. nov.	fern-like	frond	ribbon-like	entire	4	distinct, regular	absent	present	this paper
<i>Monogigantopteris clathroreticulatus</i> Yang	simple	leaf	uncertain	serrate	5	distinct, regular	absent	absent	Yang 2006
<i>M. densireticulatus</i> Yang	simple	leaf	uncertain	dentate	5	distinct, regular	absent	present	Yang 2006
<i>Pinnagigantopteris lanceolatus</i> Yang et Xie	odd-pinnate	leaflet	lanceolate	serrate	4	distinct, regular	absent	absent	Yang 2006
<i>P. oblongus</i> Chen	odd-pinnate	leaflet	elliptic	serrate	5	distinct, regular	absent	absent	Yang 2006
<i>Gigantopteris cordata</i> Yabe et Ōishi	simple	leaf	cordate	entire	5	indistinct, irregular	absent	absent	Yabe and Ōishi 1938
<i>G. meganetes</i> Tian et Zhang	simple	leaf	broadly oval	bicrenate	5	distinct, regular	absent	present	Zhang and Tian 1980
<i>G. dictyophylloides</i> Gu et Zhi	simple	leaf	uncertain	crenate	5	distinct, regular	absent	present	Gu and Zhi 1974
<i>G. nicotianaefolia</i> (Schenk)	simple or odd-pinnate	leaf or leaflet	elliptic	entire	5	indistinct, irregular	present	present	Schenk 1883
Gigantopterid identified as <i>G. nicotianaefolia</i>	fern-like	frond	ribbon-like	entire	5	indistinct, irregular	present	present	Zhang and Tian 1980
<i>G. paradoxa</i> Mo	simple or odd-pinnate	leaf or leaflet	elliptic	serrate	4	indistinct, irregular	present	present	Zhao et al. 1980
<i>G. shuangquanensis</i> Yang	fern-like	frond	long elliptic	entire	4	indistinct, irregular	absent	uncertain	Xiao and Zhang 1985

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