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**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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25

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;

plant-insect interaction

Introduction

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

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

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

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

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

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

of the ecologic complexities in Permian terrestrial ecosystems.

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

Materials and methods

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

[Approximate position of Figure 1]

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

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

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

Results

Systematic palaeobotany

Family Gigantopteridaceae Koidzumi 1936

Genus *Filigigantopteris* gen. nov.

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

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

Etymology: “Fili-”, prefix for “filicales”, “-gigantopteris” the morphological genus originally applied in the gigantopterid leaves which are double-meshed. The new genus is named after its most typical morphological traits of fern-like leaf architecture and double-meshed venation pattern.

Remarks: The genus is restricted to the plant fossils of the Permian Period, in order to distinguish them from modern angiospermous leaves.

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

Holotype: PB23526

Paratype: PB23527

Type locality: Daha Coalfield, Qinghai Province, China

Stratigraphy: Bed 2 of the Nayixiong Formation

Age: Wuchiapingian (Lopingian, Permian)

Repository: Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China

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

Venation five orders. Tertiary veins anastomose. Quaternary veins form large polygonal meshes. Veinlets form small polygonal meshes with blind veins present inside.

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

Description

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

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

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

[Approximate positions of Figures 2, 3]

Species: *Filigigantopteris dahaia* sp. nov. (Figures 3(d), 4, 5, 6 (c-d))

Holotype: PB23528

Paratypes: PB23526 (the reverse side of Figures 2(a)), PB23529

Type locality: Daha Coalfield, Qinghai Province, China

Stratigraphy: Bed 2 of the Nayixiong Formation

Age: Wuchiapingian (Lopingian, Permian)

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

Sciences, Nanjing, China

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

Etymology: The new species is named after its locality.

Description

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

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

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

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

[Approximate positions of Figures 4, 5]

Discussion

Comparisons and systematic implications

Filigigantopteris dahaia clearly has a once-pinnate leaf architecture. The decurrently fused area between the coherent apex and first lateral pinnule (Figures 4(b), 5(b)) indicates the fronds form from a fern-like dissection mode that is dissected from a coherent pinna. Similarly, the holotype of *F. asymmetrica* (Figures 2(a)) shows it to be a deeply lobed pinnule. But it could also potentially be continuously dissected into a once-pinnate frond as indicated by the deep dissections (Figures 2(c), cf.

Auritifolia waggoneri in Chaney et al. 2009). Nevertheless, the coherent apices of *F.*

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

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

[Approximate positions of Table 1 and Figure 6]

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Leaf asymmetry of Filigigantopteris asymmetrica gen. et sp. nov.

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

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

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

Plant–insect interactions

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

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

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

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

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

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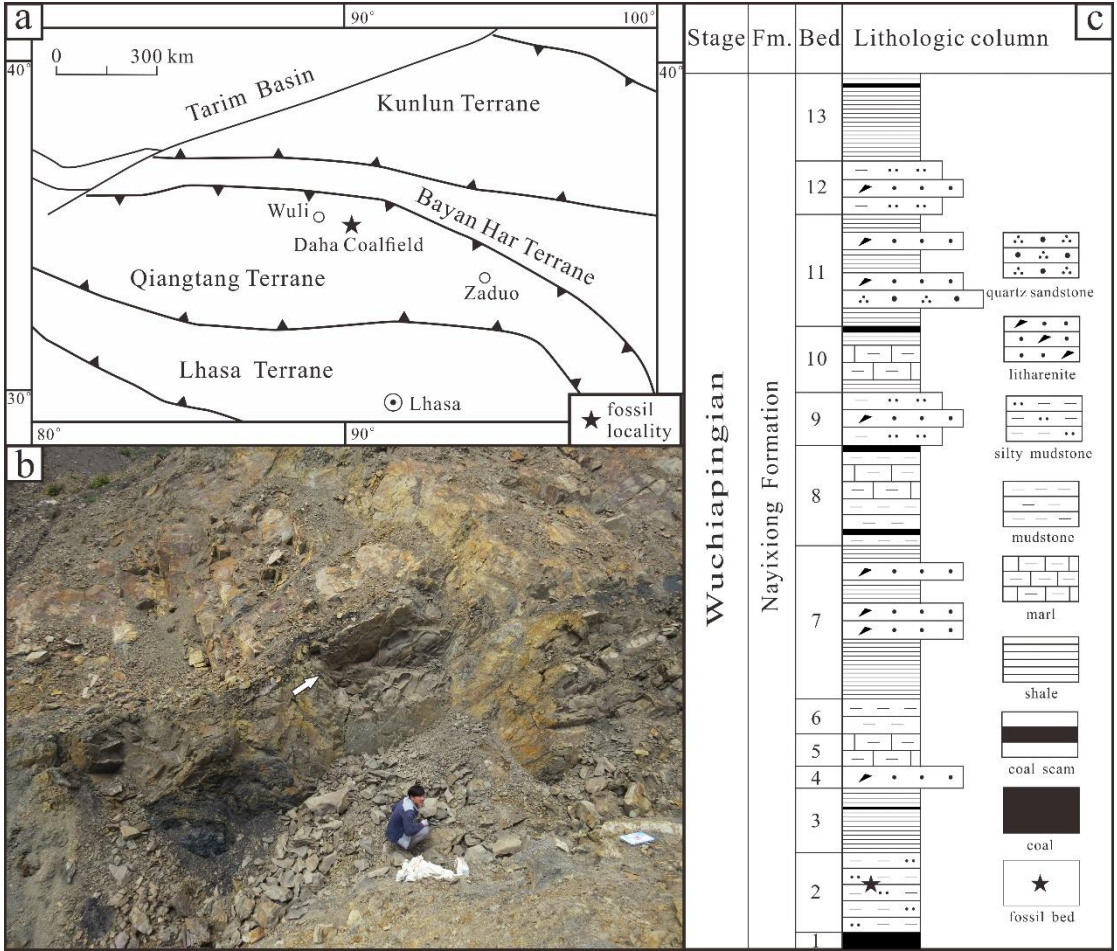
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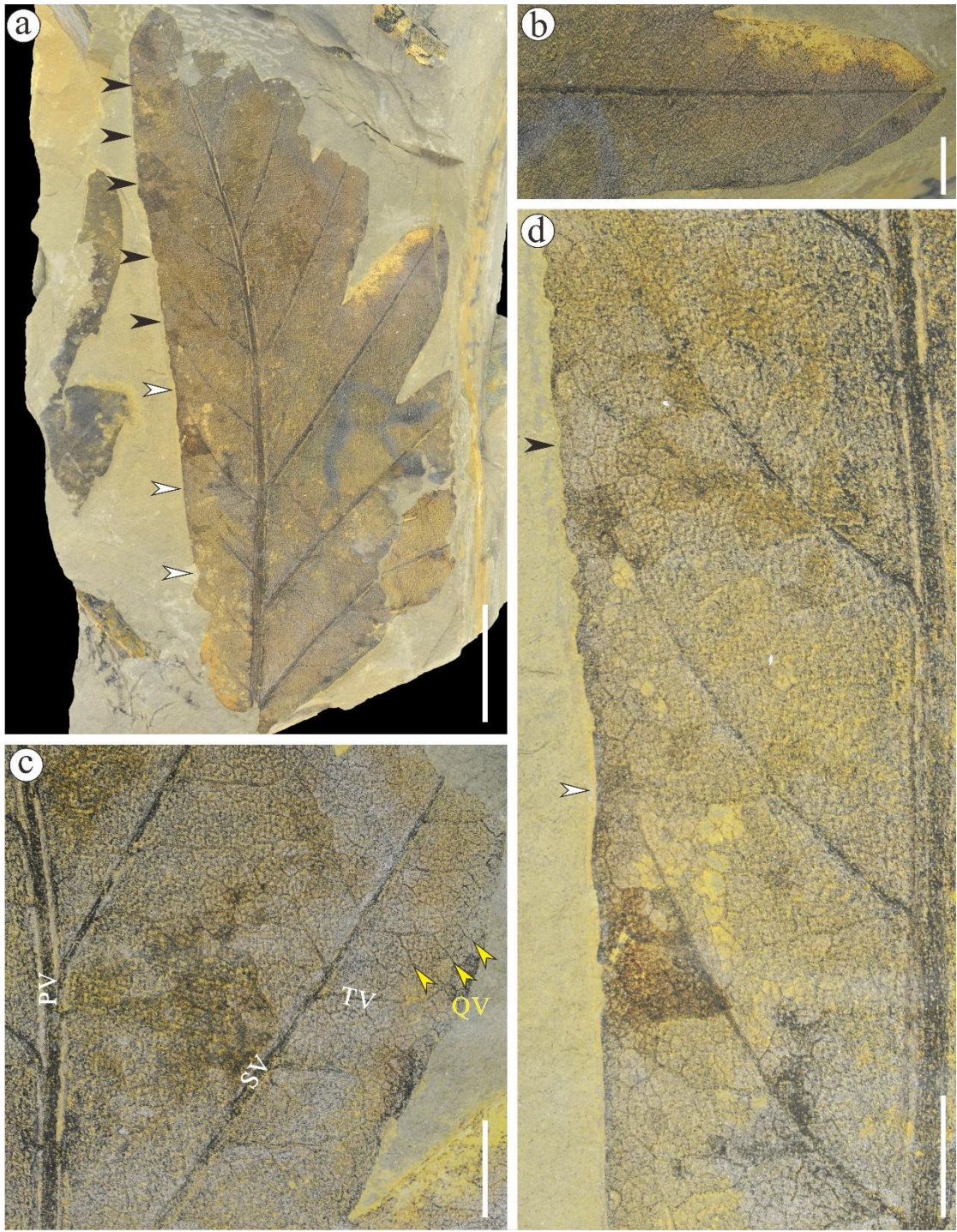
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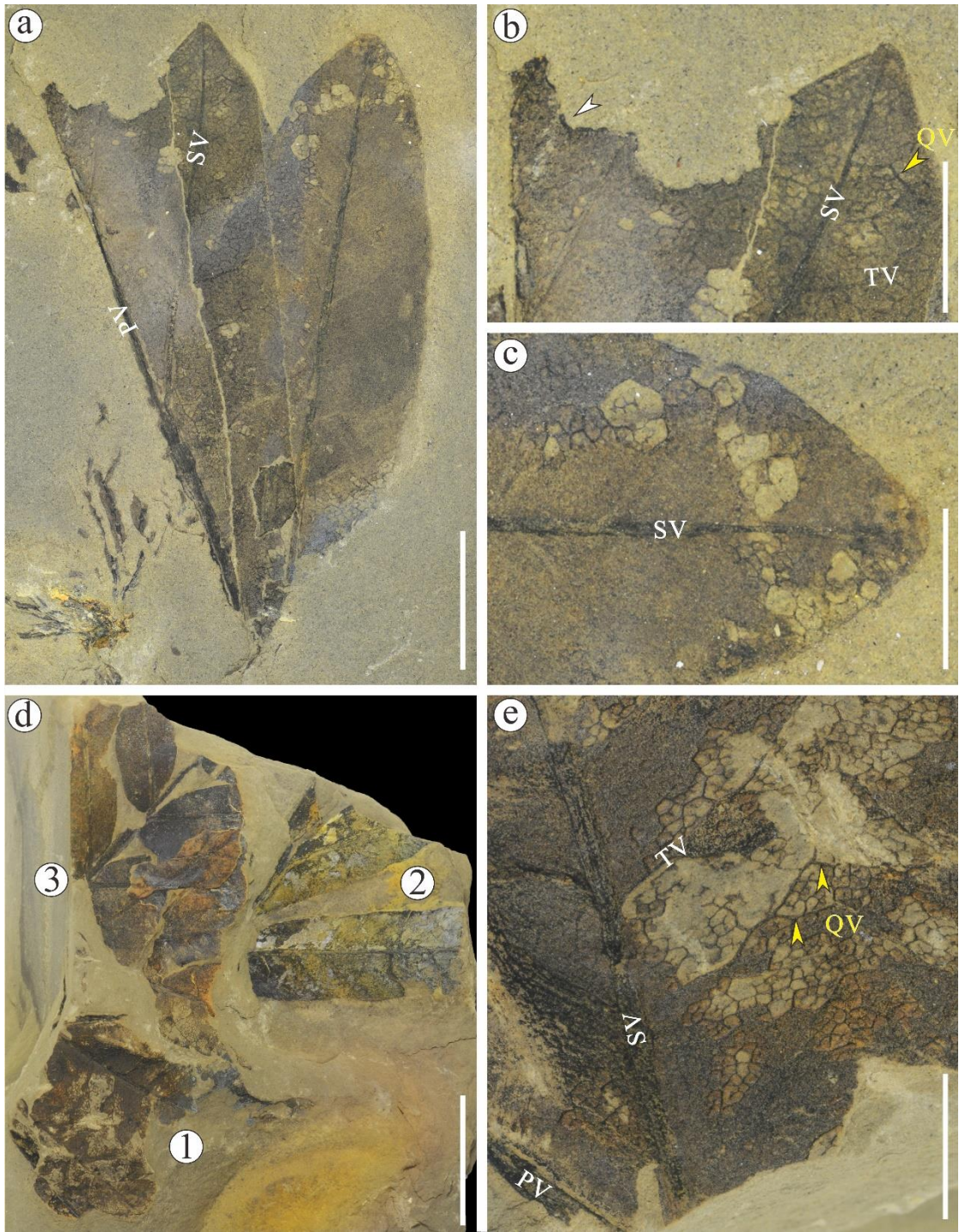
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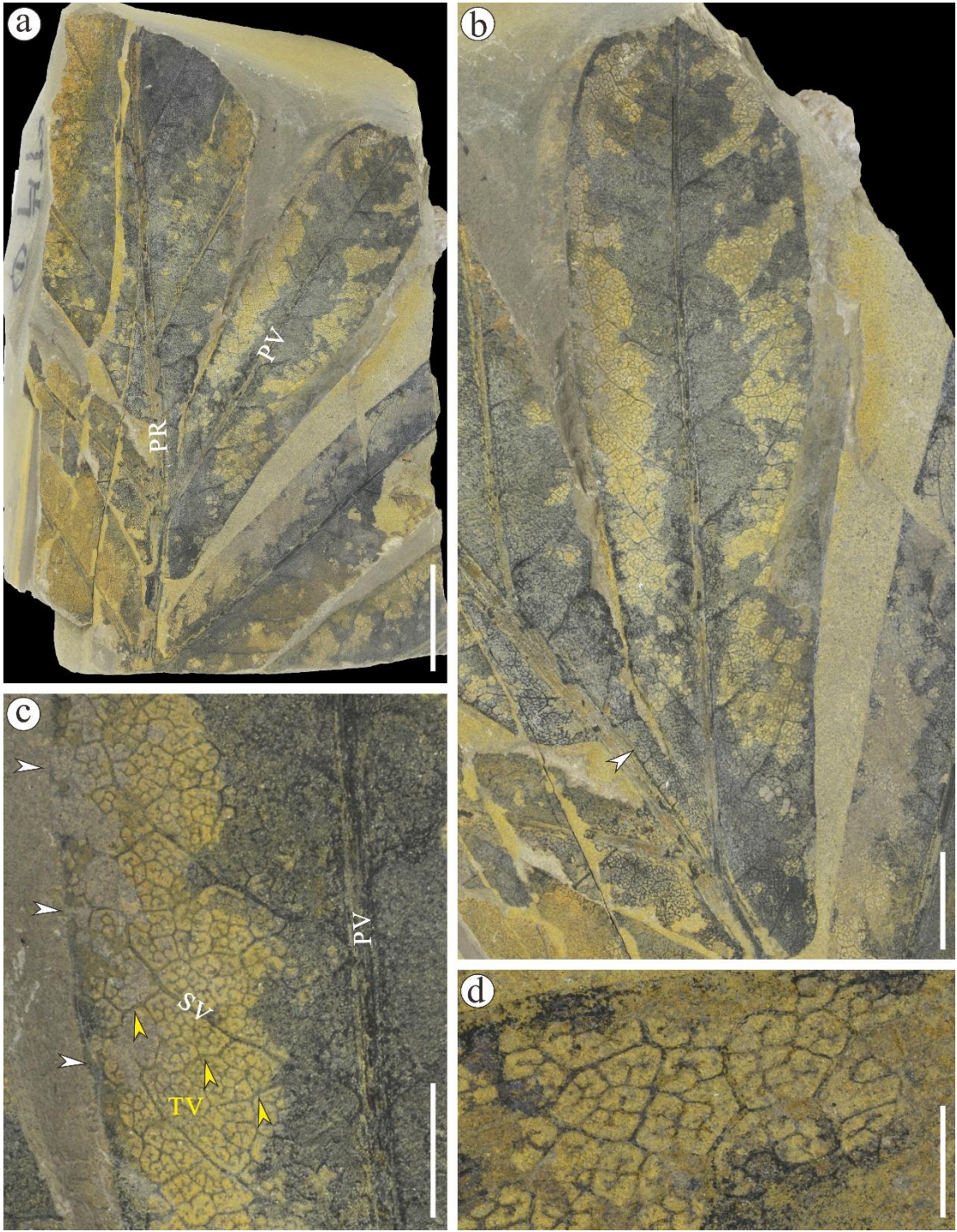




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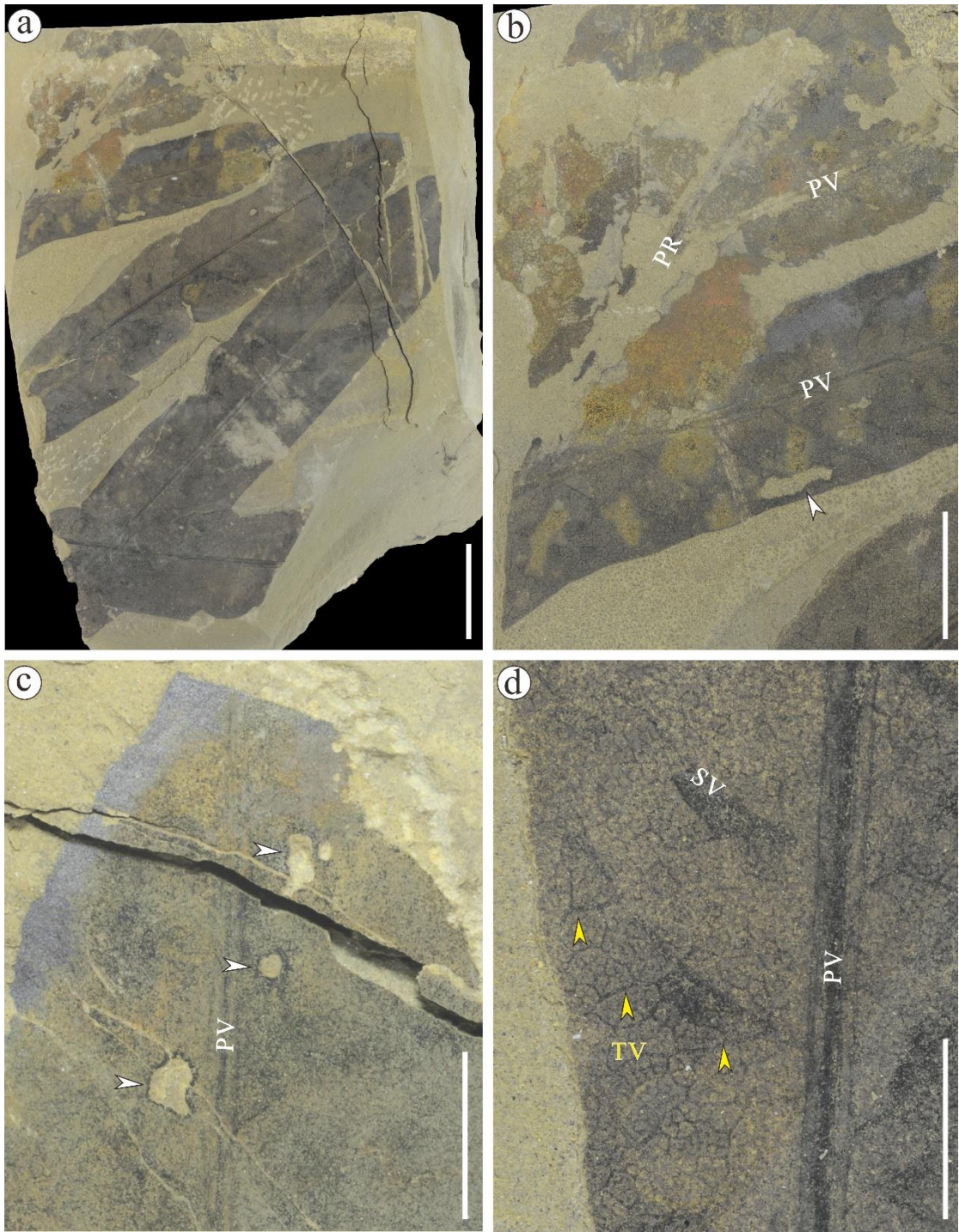
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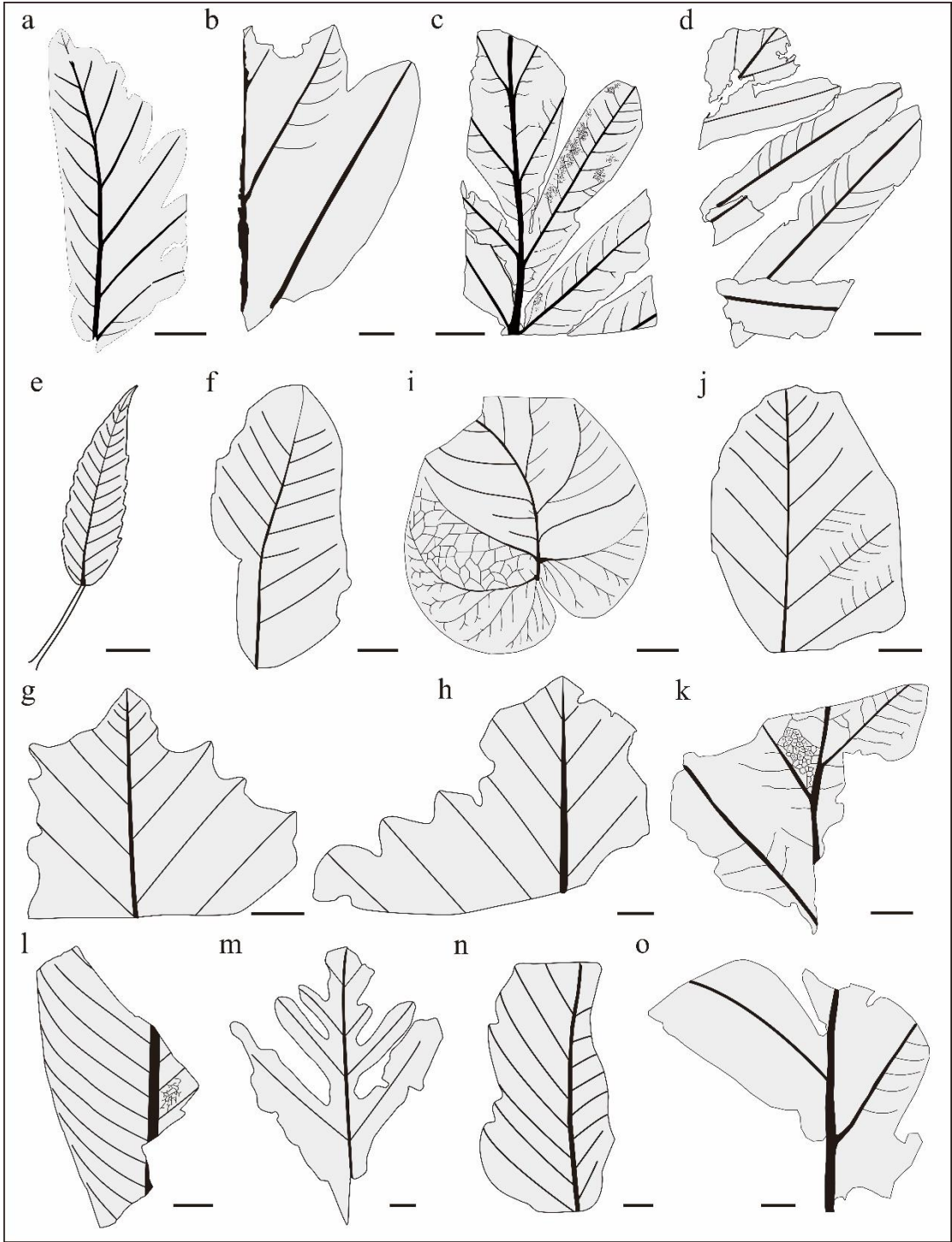
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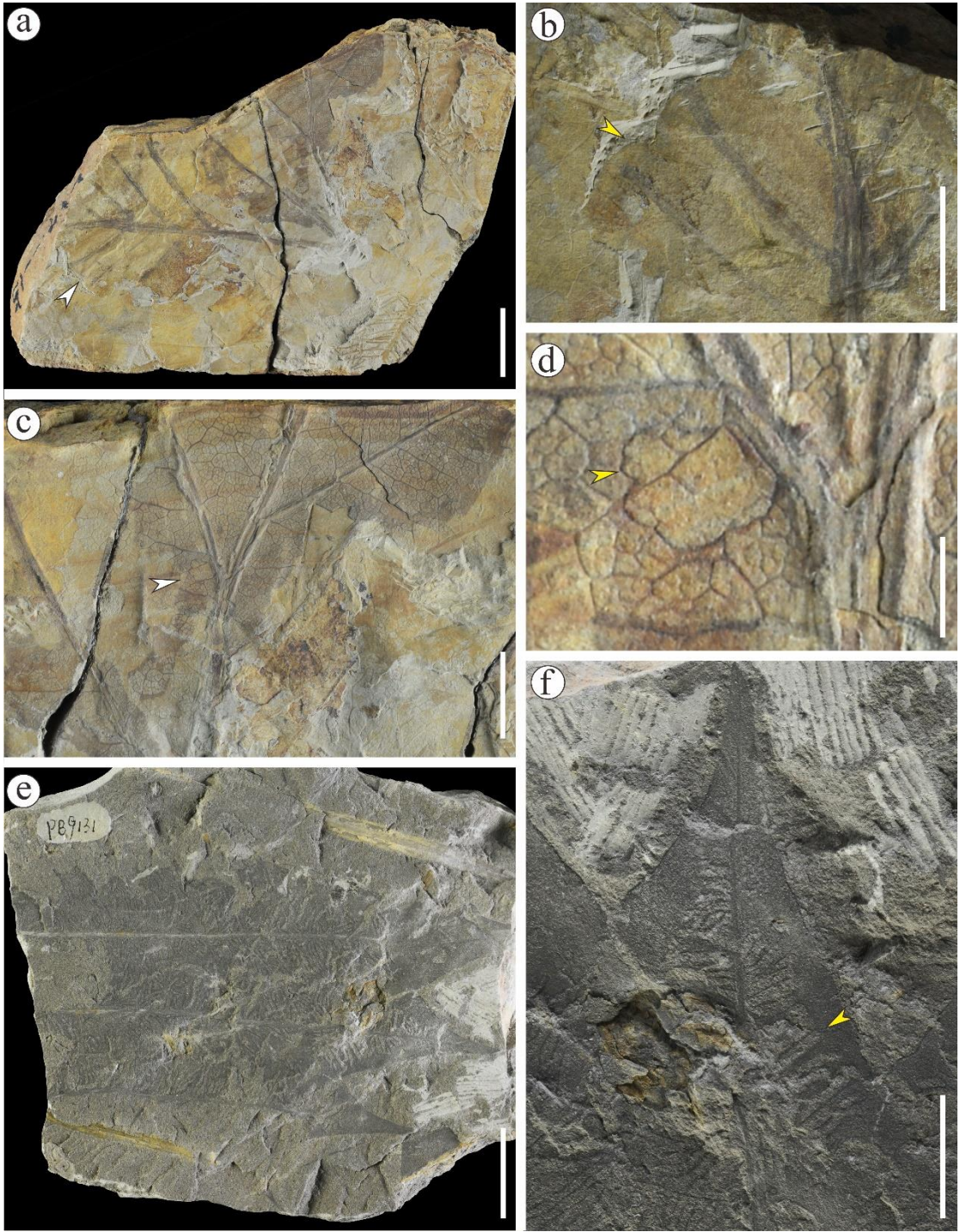
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680 Figure 7

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Table 1 Comparison of the leaf architecture and venation pattern between the two *Filigigantopteris* species and other double-meshed 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