



Fronde morphology and epidermal anatomy of *Compsopteris wongii* (T. Halle) Zalesky from the Permian of Shanxi, China

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Abstract

Compsopteris wongii (T. Halle) Zalesky is an enigmatic foliage type with unknown systematic affinities endemic to the Permian Cathaysia flora. Here we describe the frond morphology and epidermal anatomy of *C. wongii* based on material from the Palougou Section in Shanxi Province, China. Fronds are petiolate (i.e., possess a naked stipe), are once pinnate, and have alethopteroid, linear-oblong pinnules and a forked apex composed of two equally sized terminal pinnules. Fronds are amphistomatic, with haplocheilic, monocyclic to incompletely tricyclic stomata occurring on all parts. The epidermal anatomy, especially the distribution of stomata, and the lack of features suggestive of xeromorphy indicate that *C. wongii* had a high photosynthetic capacity and high assimilation rates, and was adapted to an everwet environment. With regard to frond morphology and epidermal anatomy, the species corresponds well to supposedly related peltasperms from Euramerica, such as *Glenopteris* Sellards and *Protoblechnum* Lesquereux. We attribute *C. wongii* to the glenopteroid group of peltasperms.

Keywords Cathaysia flora · *Protoblechnum wongii* · Peltaspermales · Cuticular analysis · Glenopteroids

Introduction

During the Permian, Earth underwent one of the most extreme climate transitions of the Phanerozoic, from ice-house conditions in the beginning to greenhouse conditions towards the end (Montañez et al. 2007; Montañez and Poulsen 2013). This change was caused by the formation of Pangaea in the Late Pennsylvanian, which had a significant impact on the worldwide climate. Four Late Paleozoic floral provinces have been defined: Gondwana, Angara, Euramerica, and Cathaysia. The Permian Cathaysia flora comprises

several elements known also from the Carboniferous of Euramerica, but, in addition, contains a number of interesting endemic taxa. Many of these Cathaysian taxa, however, are still known only from adpression fossils of sterile foliage that yield only information on vegetative gross morphology, and whose systematic relationships remain poorly resolved.

One such problematic Cathaysian foliage taxon is *Compsopteris wongii* (T. Halle) Zalesky 1934. Since its first description by Halle (1927) under the name *Protoblechnum wongii* Halle 1927, the relationships of this form to morphologically similar taxa from the Euramerican and Angara floral provinces, such as *Supaia* C. D. White 1929, *Glenopteris* Sellards 1900, *Protoblechnum* Lesquereux 1880, and *Compsopteris* Zalesky 1934, remain debated (DiMichele et al. 2005). Considerations with regard to the relationships between the different forms have hitherto been based exclusively on macromorphological features. Abundant foliage remains of *C. wongii* with well-preserved cuticles, including several near-complete fronds, have recently been recovered from the Guadalupian Lower Shihhotse Formation of the Palougou section in Northwest Shanxi (China). *Compsopteris wongii* fronds are amphistomatic, with abundant cyclocytic stomata present on the upper and lower surfaces of all frond parts. Our cuticular analysis provides further support to suggest a close relationship between *C. wongii*

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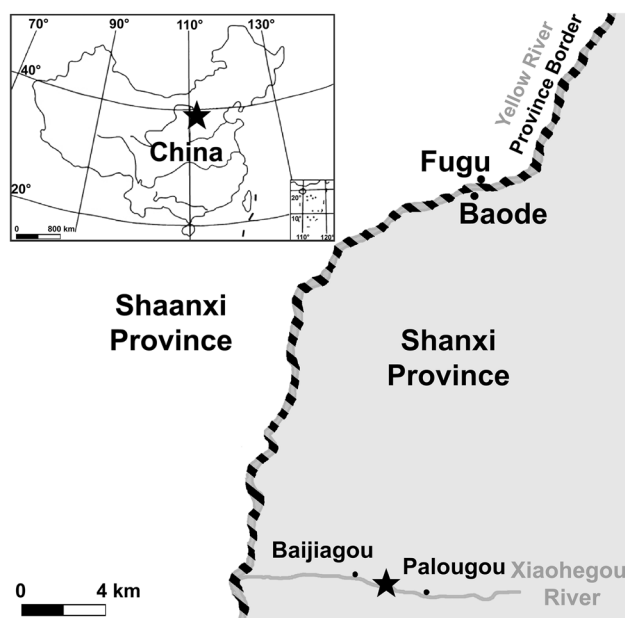


Fig. 1 Location of the Palougou section (black star) (redrawn after Liu et al. 2011 and Kaiser 1976)

and *Glenopteris* and *Nanshanopteris* Wan and Wang 2015. Furthermore, we identify *C. wongii* as a representative of the ‘glenopteroids,’ a group of putative peltasperms so far known only from the Lower Permian of Euramerica and the Upper Permian of Cathaysia.

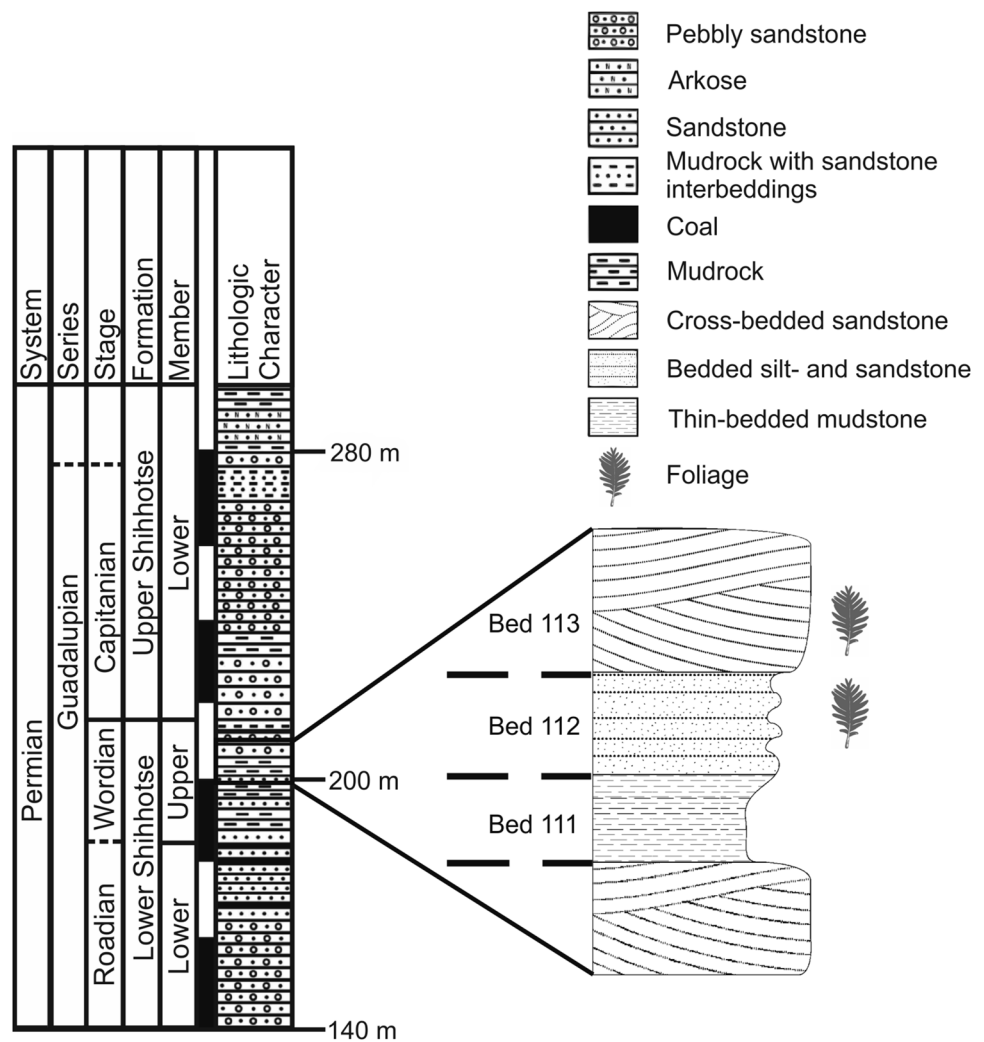
Geographical and geological setting and materials and methods

The Palougou section (or Baode section) is located in Baode County in the northwest of Shanxi Province (China), 30 km south of the county capital of Baode City (Fig. 1). In the valley of the Xiaohegou River, approximately 600-m-thick, slightly westward-dipping Pennsylvanian to Permian rocks are exposed that can be traced over a distance of approximately 6 km from Palougou village in the east to Baijiagou village in the west. The section comprises a continuous succession of all Pennsylvanian–Permian lithostratigraphic units of the North China block (Li 1995), including (in ascending order) the Benxi, Taiyuan, Shanxi, Lower Shihhotse, Upper Shihhotse, and Sunjagou formations. The Benxi Formation disconformably overlies the Ordovician Majiagou Formation. The Carboniferous Benxi and overlying Pennsylvanian to Permian Taiyuan formations represent marine to continental sediments, while the Shanxi Formation and younger sediments are deltaic and fluvial deposits of meandering river systems (Wang and Chen 2016). The Lower Shihhotse Formation comprises 78 m of fluvial sediments and is subdivided into two members. The basal

23 m of the lower member consist of thick-bedded, yellowish, quartzose sandstones overlain by beds of 1–3 m thick yellow-grayish sandstones alternating with thin-bedded, gray mudstone 1 m thick. Three coal seams, each less than 1 m thick, are intercalated between mud- and sandstones. The uppermost of these coal seams marks the boundary with the Upper Member. The Upper Member consists of up to 2-m-thick beds of massive brownish sandstone alternating with thin-bedded, gray silt- and mudstones. Plant macrofossils are abundant in the mudstone beddings, close to the erosional surface of the overlying sandstones. Samples were collected during field work in 2017 from outcrops 300 m southeast of the village of Liujiapocun in the Xiaohegou River valley, immediately to the north of a local coal mine (38°45′21.57″N; 111° 7′7.96″E). Bedding numbers, introduced by Liu et al. (2015), were adopted to define the exact stratigraphic provenance of samples. The samples described here were taken from the siltstone beddings 112 and the overlying sandstone beds 113 (Fig. 2). Besides *Compsopteris wongii*, the flora is rich in typical Cathaysian taxa such as *Tingia carbonica* (Schenk) T. Halle 1925, *Yuania chinensis* X. Du and J. Zhu 1982, *Mariopteris shanxiensis* H. C. Sze 1989, *Cladophlebis nystroemii* T. Halle 1927, *Protoblechnum contractum* S. W. S. Gu and W. S. Zhi 1974, and *Fasciapteris* sp., as well as species known from Euramerica including *Taeniopteris multinervis*, *Cordaites schenkii* T. Halle 1927, and *Cordaites principalis* (Germar) Geinitz 1855.

Specimens were manually prepared via *dégagement* using sewing needles, and macroscopic photographs were taken using a Canon EOS 7D digital SLR camera equipped with a Canon EFS 60-mm macro lens. Cuticle fragments were easily lifted off the adpression fossils using a preparation needle. Attempts were made to macerate selected cuticle fragments according to standard methods (Kerp 1990; Krings and Kerp 1997). Carbonaceous material was oxidized with Schulze’s reagent ($\text{HNO}_3 + \text{KClO}_3$) using concentrations increasing from 10 to 20% for 12 h, followed by treatment with a 5% potassium hydroxide solution. A 4% sodium hypochlorite solution was used for additional bleaching and cleaning. After each step, sample material was thoroughly rinsed in distilled water. For most of the cuticle material, however, even this gentle maceration method proved unsuccessful; most of the carbonaceous material completely decomposed after treatment with Schulze’s reagent, meaning that, in many cases, only cuticle fragments of the rachis remained sufficiently well preserved for mounting. Permanent microscopic slides were prepared using glycerine jelly. Instead, we analyzed and photographed the epidermal anatomy and cuticle morphology in situ via epifluorescence microscopy using a Leica DM 5500B research microscope equipped with transmitted and incident UV light and with a Leica DFC450 digital microscope camera. Composite

Fig. 2 Stratigraphy of the Shih-hotse Formation and provenance of the sampled sediments (stratigraphy modified after Wang et al. 2008)



images were produced by stacking and stitching individual images using Photoshop CC and Helicon Focus software. For cropping and conventional adjustments of contrast, brightness, and color, we used Photoshop CC and Corel Graphics Suite X6. Epidermal cells and stomata were measured with Leica LAS 4.5 software.

Systematic part

Class **Pteridospermatophyta**

Order **Peltaspermales** Delevoryas 1979

Genus *Compsopteris* (Zalessky) Naugolnykh 1999 emend. herein

Type species. Compsopteris adzvensis Zalessky 1934

Diagnosis. Fronds pinnate, petiolate, with prominent rachis. Pinnules oblong, straight or slightly curving, with entire margins and rounded apex; pinnules small and attached about perpendicular to rachis in the basal frond portion, becoming longer and arising at increasingly acute angles towards the apex; lowermost pinnules with a constricted base; towards the apex, pinnules becoming more broadly attached to decurrent or auriculate. Frond apex forked to form a single, basally confluent pair of terminal pinnules. Venation alethopteroid; midrib strong, reaching close to tip; secondary veins arising at acute angles, simple or forking up to four times. Wing-like decurrent basicopic pinnule portions with veins arising directly from rachis. Fronds amphistomatic; stomata haplocheilic, cyclocytic.

Remarks. The recent emendation of the genus (Naugolnykh 1999) lacked important information on cuticle features (see Meyen and Migdisova 1969) and included the following

Table 1 Simplified macroscopical comparison of *Compsopteris wongii* to possibly related pinnate taxa

Taxa	Frond architecture			Pinnules			Venation	
	Frond bifurcation	Petiolate	Apex forking	Apical pinnules connate	Adaxially attached	Pinnules auriculate	Midrib distinct	Bifurcations
<i>Compsopteris wongii</i> ^a	–	+	+	–	+	±	+	1–2
<i>Compsopteris adzvensis</i> ^b	–	?	+	–	?	±	+	1–4
<i>Glenopteris</i> ^c	–	+	–	+	+	+	–	0–1
<i>Supaia</i> ^d	+	+	–	+	?	±	+	1–2
<i>Megalopteris</i> ^e	?	?	+	+	?	+	+	1–3
<i>Nanshanopteris</i> ^f	–	+	–	+	–	+	–	4

^aHalle (1927); this study

^bZalessky (1934), Meyen and Migdisova (1969) and Naugolnykh (1999)

^cSellards (1900) and Krings et al. (2005)

^dWhite (1929)

^eDawson (1871) and Andrews (1875)

^fWan and Wang (2015)

problematic terms that we have omitted here. The frond architecture was described as ‘imparipinnate,’ whereas all sufficiently complete specimens instead show a forking apex with a terminal pinnule pair (Halle 1927; Meyen and Migdisova 1969; Naugolnykh 1999: Table 1). In addition, the terms ‘sphenopteroid’ and ‘pecopteroid’ were used to describe a constricted versus broadly attached pinnule base; these terms are, however, conventionally also used to describe venation and margin features, and are thus potentially misleading.

Compsopteris wongii (T. Halle) Zalessky 1934 emend. nov. Figures 3, 4, 5

Basionym. *Protoblechnum wongii* T. Halle 1927.

Syntypes. Ten specimens from the Shihhotse Formation, Shanxi Province, North China, described and figured in Halle (1927) as follows: Lower Shihhotse Formation, East Section, bed 18: specimen S138216 (apical frond fragment; pl. XXXV, fig. 1); Upper Shihhotse Formation, West Section, bed 25: specimen S138217 (basal petiolate frond fragment; pl. XXXV, fig. 2); Upper Shihhotse Formation, East Section, bed 21: specimen 138218 (frond fragment; pl. XXXV, fig. 3), specimen 138219 (frond fragment; pl. XXXV, fig. 4), specimen 138220 (basal frond fragment; pl. XXXV, fig. 5); Upper Shihhotse Formation, East Section, bed 21: specimen S138221 (frond fragment of lower part; pl. XXXVI, fig. 1), specimen 138222 (frond fragment near the base; pl. XXXVI, fig. 2); specimen 138223 (apical frond fragment with terminal bifurcation; pl. XXXVI, fig. 3); specimen 138224 (apical frond fragment with terminal bifurcation; pl. XXXVI, fig. 4); specimen 138225 (small, undeveloped fronds given off from rhizome; pl. XXXVI,

fig. 5); specimen S138380 (apical frond fragment with terminal bifurcation; pl. LXIV, fig. 12); all housed in the Palaeobiology Collections of the Swedish Museum of Natural History, Stockholm, Sweden.

Epitypes (designated here). Three specimens from the Lower Shihhotse Formation at the Palougou Section, NW Shanxi Province, North China, as follows: specimen PB22968, a complete frond with apex; specimen PB22972, large petiolate frond fragment; specimen PB22974, frond fragment with well-preserved venation and apex. All samples show cuticular preservation and are housed in the Palaeobotanical Collections of the Nanjing Institute of Geology and Palaeontology, Nanjing, China.

Additional material. Specimens housed in the Palaeobotanical Collections of the Nanjing Institute of Geology and Palaeontology, Nanjing, China: PB22966, PB22967, PB22969, PB22970, PB22971, PB22973, PB22975, PB22976, PB22977, PB22978, PB22979.

Locality of examined material. Bedding numbers 112 and 113, Lower Shihhotse Formation, Upper Member, Palougou Section, Shanxi Province, North China; coordinates: 38°45′21.57″N, 111°7′7.96″E.

Emended specific diagnosis. Fronds large (exceeding 40 cm in length), ovate in outline, petiolate, pinnate. Frond apex forking into two equally sized pinnules. Rachis prominent, channeled on upper side, keeled on lower. Pinnules closely spaced, arising at angles of 50–60° from the rachis in median portion of frond, in upper portion more oblique, in lower portion more extended, at the base commonly perpendicular or reflexed. Pinnules broadly attached, basally decurrent to

almost confluent with or slightly overlapping the subjacent pinnule margin. Decurrent wings wide, in the upper frond portion flat, in lower portion curving towards upper side of rachis in an auriculate manner, becoming gradually more indistinct towards frond base, lacking in lowermost pinnules. Pinnules linear, entire-margined, gradually tapering towards obtuse or subacute apex. Venation alethopteroid; midrib strong, reaching close to tip; secondary veins arising at narrow angle, arching, reaching margin at angles of 50–60° in median pinnule portion, usually forking once or twice, rarely simple. Veins in auricles directly arising from rachis, almost perpendicularly, bifurcating once. Fronds amphistomatic. Rachis, midrib, and pinnule lamina stomatiferous. Epidermal cells of rachis, midrib, and costal fields polygonal-elongate, epidermal cells of intercostal fields polygonal-isodiametric. Haplocheilic stomata longitudinally oriented on rachis and midrib, randomly oriented and distributed on lamina; monocyclic to incompletely tricyclic. Large multicellular trichomes randomly distributed on rachis.

Detailed description. Fronds are large, ovate, with alethopteroid pinnules and a basally widening petiole (Fig. 3a, b). The largest specimen at hand is an almost complete frond 44 cm long and 30 cm wide. The rachis is thick, marked by longitudinal striae, and attains a breadth of up to 6 mm on the impression of the pinnule-bearing portion. The petiole is basally widened and up to 14 mm wide (Fig. 3a). Two equally sized, small pinnules occur distally (Fig. 3a, b, d). Pinnules are linear-oblong, densely arranged, and decrease in size towards the base of the frond, attaining a maximum length of 17 cm and width of 4 cm. The auricle is variably well developed; in some specimens (Fig. 3e) it reaches or even slightly overlaps the subjacent pinnule; in other specimens with pinnules in a similar position on the frond, the leaf base is only slightly decurrent on the rachis. The wings are in many cases curving up on the upper side of the rachis and are absent in the lowermost, smallest pinnules (Fig. 3c, f). The auricle is widest in the two apical pinnules. The lamina of the pinnules is attached to the top of the midrib, which is generally 1 mm wide and reaches to near the pinnule apex. Lateral veins arise from the midrib at angles of 10–15°, gradually arch in an outward direction, and reach the margin at angles of ~50–60°. Veins usually fork once or twice in their course to the margin, or are rarely simple (Fig. 3e, f). In the decurrent wings, the lateral veins are given off directly from the rachis at angles of 80–90° and fork once to twice.

The fronds are amphistomatic, and stomata occur on all parts of the frond. Epidermal cells are generally elongate in the costal fields and isodiametric in the intercostal fields (Fig. 4a). Anticlinal walls are strongly cutinized, periclinal walls are smooth. Stomatal complexes are generally haplocheilic and monocyclic to incompletely tricyclic. The

upper surface of the rachis is obscured as pinnules are adaxially attached (Fig. 4b). On the lower surface of the rachis, cells are elongate, with straight lateral and oblique polar anticlinal walls, 48–(105)–236 µm long and 5–(16)–26 µm wide, and arranged in longitudinal rows (Fig. 4c, d). Stomatal complexes are longitudinally oriented, monocyclic, arranged parallel to the cells of the midrib, and 91–(103)–112 µm long and 50–(61)–72 µm wide. Large multicellular, truncate trichomes are randomly distributed, occur isolated or in pairs, and range in shape from slight swellings of the cuticle to thick cylindrical protrusions with an apical opening, measuring up to 340 µm in length and 214 µm in width (Fig. 4e). In many cases, the opening is filled with a black, amorphous substance (Fig. 4c, d).

Similar to the frond rachis, the upper side of the pinnule midrib is obscured because the pinnule lamina is adaxially attached. On the lower surface of the pinnule midrib, the epidermal pattern and stomata distribution are similar to those of the rachis, but trichomes are absent. On both sides of the lamina, the epidermis is only weakly differentiated into costal and intercostal fields (Fig. 4a). Cells in the intercostal fields are randomly oriented, isodiametric, 18–(41)–82 µm in diameter. Costal fields consist of undulating rows of elongate cells similar to those of the midrib and rachis; they are one or two cells wide on the upper pinnule lamina and three to five cells wide on the lower pinnule lamina. Stomatal complexes are distributed and oriented randomly in the intercostal fields, slightly sunken and monocyclic to incompletely tricyclic, with 6–8 subsidiary cells and up to 12 additional encircling cells. Stomatal complexes are 92–(120)–147 µm long and 80–(103)–126 µm wide (Fig. 4f–g).

Taxonomic remarks and comparisons. Halle (1927) erected the species *Protoblechnum wongii* based on pinnate fronds with a dichotomously forking tip and elongate, auriculate pinnules from the Shanxi Province in North China. However, *Protoblechnum* and its type species *P. holdenii* (E. D. Andrews) Lesquereux 1880 from the Pennsylvanian coal measures of Ohio, USA, are rather poorly known. The type material does appear superficially similar in overall gross morphology, but does not show unambiguous information on the diagnostic frond apex. No photographs are available, and in the single existing illustration of an apical frond portion (Andrews 1875: pl. LI, figs. 1, 2), the frond apex is covered by a thin layer of sediment on which an obviously separate leaf fragment is preserved. The arrangement of the central and apical portions of the apical pinnules is rather suggestive of the presence of just a single median pinnule instead of a true pair of terminal pinnules. This is further supported by the illustrations of an additional, near-complete frond that was collected in 1952 from the original type locality of *P. holdenii* (Cross et al. in Feldmann 1996: figs. 23–26:4, 5). This specimen also bears

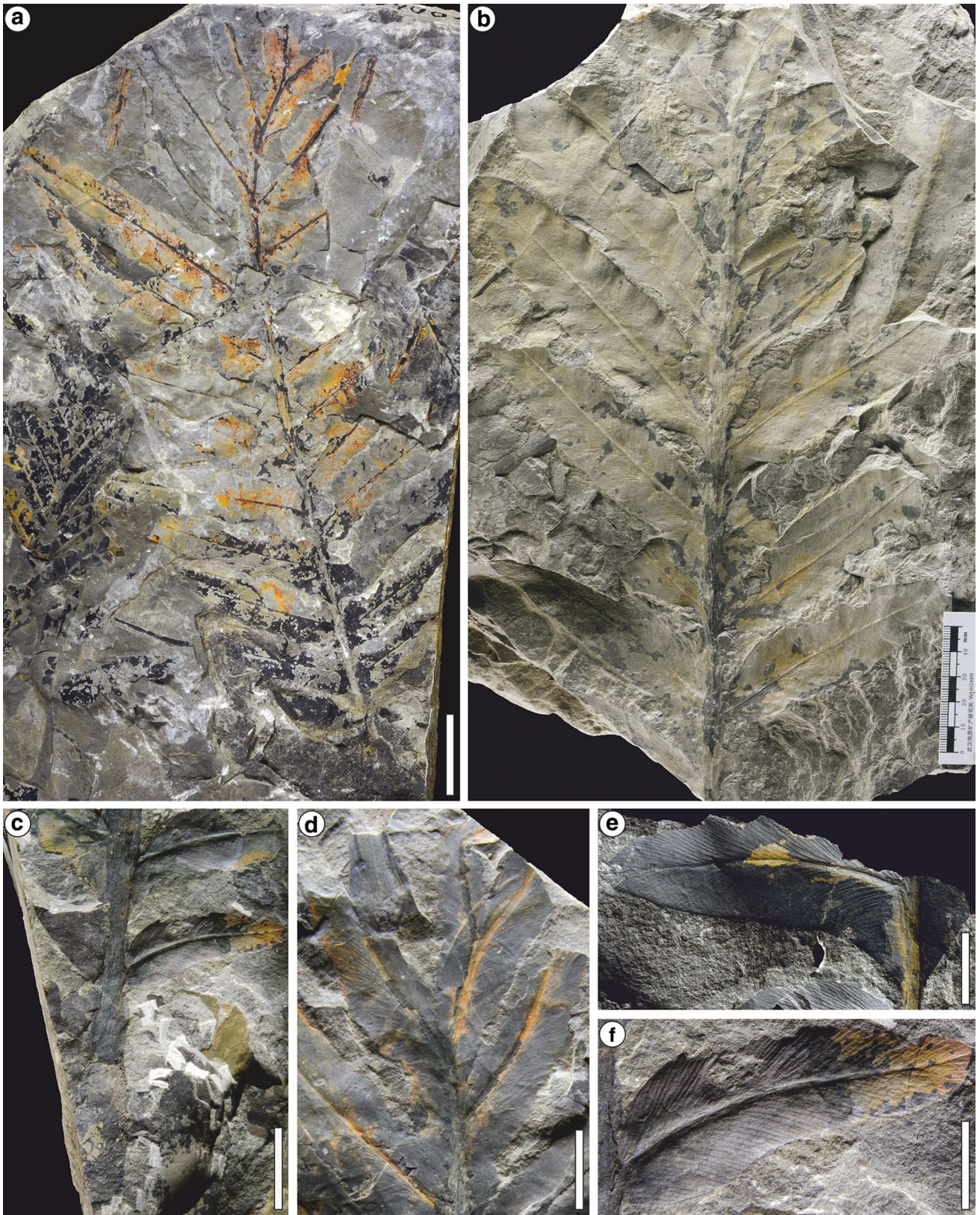


Fig. 3 Frond morphology of *Compsopteris wongii*. **a** Almost complete frond of *C. wongii* showing apical forking and petiole. Specimen PB22968, scale bar 5 cm. **b** Distal frond fragment with characteristic apical forking and slightly overlapping pinnules. Specimen PB22974, scale bar 5 cm. **c** Proximal portion with widened, scaly petiole. Specimen PB22972, scale bar 2 cm. **d** Apical frond fragment showing forking tip and overlapping pinnules. Specimen PB22969, scale bar 1 cm; **e** Pinnule in the lower part of the frond with decurrent leaf bases and secondary veins arising directly from rachis. Specimen PB22979, scale bar 1 cm. **f** Magnification from **c** showing details of lowermost pinnule without decurrent leaf base. Specimen PB22972, scale bar 1 cm

fused apical pinnules that decrease in size towards the apex and terminate in a single (i.e., non-dichotomizing) terminal pinnule. Altogether, there is thus good evidence that the frond architecture of the type species *Protoblechnum* is similar to that of *Glenopteris* and different from that of *Compsopteris*, including *C. wongii*.

Later, Zalesky (1934) erected the genus *Compsopteris* for similar fossils from the Petchora Basin in Russia and included the Chinese fronds in this genus. Several authors adopted Zalesky's new combination and used the name *Compsopteris wongii* (e.g., Gu and Zhi 1974; Naugolnykh and Kerp 1996; Sun 2006); others continued to use Halle's *Protoblechnum wongii* and pointed out the need for epidermal studies on the Chinese material for detailed comparisons of the two genera (e.g., Chow 1955; Liu 1989; Krings et al. 2005; Taylor et al. 2009; Wan and Wang 2015). Our results now show that the type species of *Compsopteris*, *C. adzvensis* Zalesky 1934 from the Angaran realm, is macroscopically and microscopically very similar to *C. wongii*. Fronds possess a distinct petiole, a dichotomously forking tip, elongate pinnules with a more or less well-developed auricle, and amphistomatic pinnules with cyclocytic stomatal complexes (Zalesky 1934; Meyen and Migdisova 1969). It is distinct from *C. wongii* in the significantly smaller size of the frond, with more repeatedly forking secondary veins, monocyclic to dicyclic (as opposed to mono- to incompletely tricyclic) stomatal complexes, papillate subsidiary cells, but without trichomes. *Compsopteris olgae* Naugolnykh 1999 and *C. tchirkovae* Zalesky 1934 are very similar to *C. wongii* but poorly defined, and may need to be synonymized with *C. wongii*.

Discussion

Comparisons

Compsopteris wongii belongs to a group of foliage genera from the Late Palaeozoic, such as *Glenopteris*, *Nanshanopteris*, *Supaia*, and *Megalopteris* Dawson 1871 (Tables 1, 2).

Glenopteris from the Lower Permian of Euramerica has often been proposed as a close relative of *Compsopteris*

wongii (e.g., Halle 1927; White 1929; Krings et al. 2005; Sun and Shen 1999a, b). The type species *Glenopteris splendens* Sellards 1900 shares many similarities in macromorphology and especially epidermal anatomy with *C. wongii*; the main differences concern the architecture of the frond tip and the simple, indistinct venation in the former (Table 1). Furthermore, cuticles of *C. wongii* do not show the peg-like projections in the anticlinal walls that are a typical feature of *G. splendens* (Krings et al. 2005), although anticlinal walls are thickened. Differences from the second glenopteroid species *Nanshanopteris nervosa* Wan and Wang 2015 from China are mainly the same as from *G. splendens*, with the addition that epidermal cells of the former bear papillae (Wan and Wang 2015). However, papillae are not necessarily of high taxonomic relevance; they may instead reflect paleoecological adaptation (Poort and Kerp 1990). Both of these glenopteroids occurred in seasonal Permian environments: *G. splendens* from the Artinskian of Euramerica in a coastal environment periodically affected by seasonality and soil and ground water salinity (Krings et al. 2005), and *N. nervosa* from the Changhsingian of China on a well-drained lacustrine shore under a seasonally wet climate (Wan and Wang 2015). *C. wongii* from the Guadalupian of China clearly lived in a tropical, everwet environment close to a meandering river system (Liu et al. 2015). It is therefore not surprising that epidermal features such as papillae, peg-like projections, or other supposedly xerophytic adaptations are absent.

Another interesting genus is *Supaia*, initially described from the Permian of Euramerica (White 1929). It differs from *Compsopteris* in its bipartite, imparipinnate frond architecture. Wang (1997) recorded *Supaia* fronds from the Capitanian Tianlongsi Formation (another name for the Upper Shihhotse Formation) of Shanxi and proposed it might represent a descendent of *Compsopteris wongii* that is morphologically adapted to a semi-arid environment. Pinnules of *S. contracta* Wang 1997 are amphistomatic, with monocyclic to dicyclic and slightly sunken stomata somewhat comparable to those of *C. wongii*. These similarities in the epidermal anatomy to *C. wongii* suggest a close relationship, with the main differences being the architecture, the contracted leaf bases, and the papillae on the cells of lower leaf sides of *S. contractum*.

Megalopteris from the Pennsylvanian of Euramerica is superficially similar, but most species were described based on small fragments, yielding limited information on frond architecture and morphology that is insufficient for detailed comparison (Table 1). Moreover, those three species for which cuticles have been described differ from *Compsopteris wongii* in that they are indicative of hypostomatic leaves (Florin 1933).

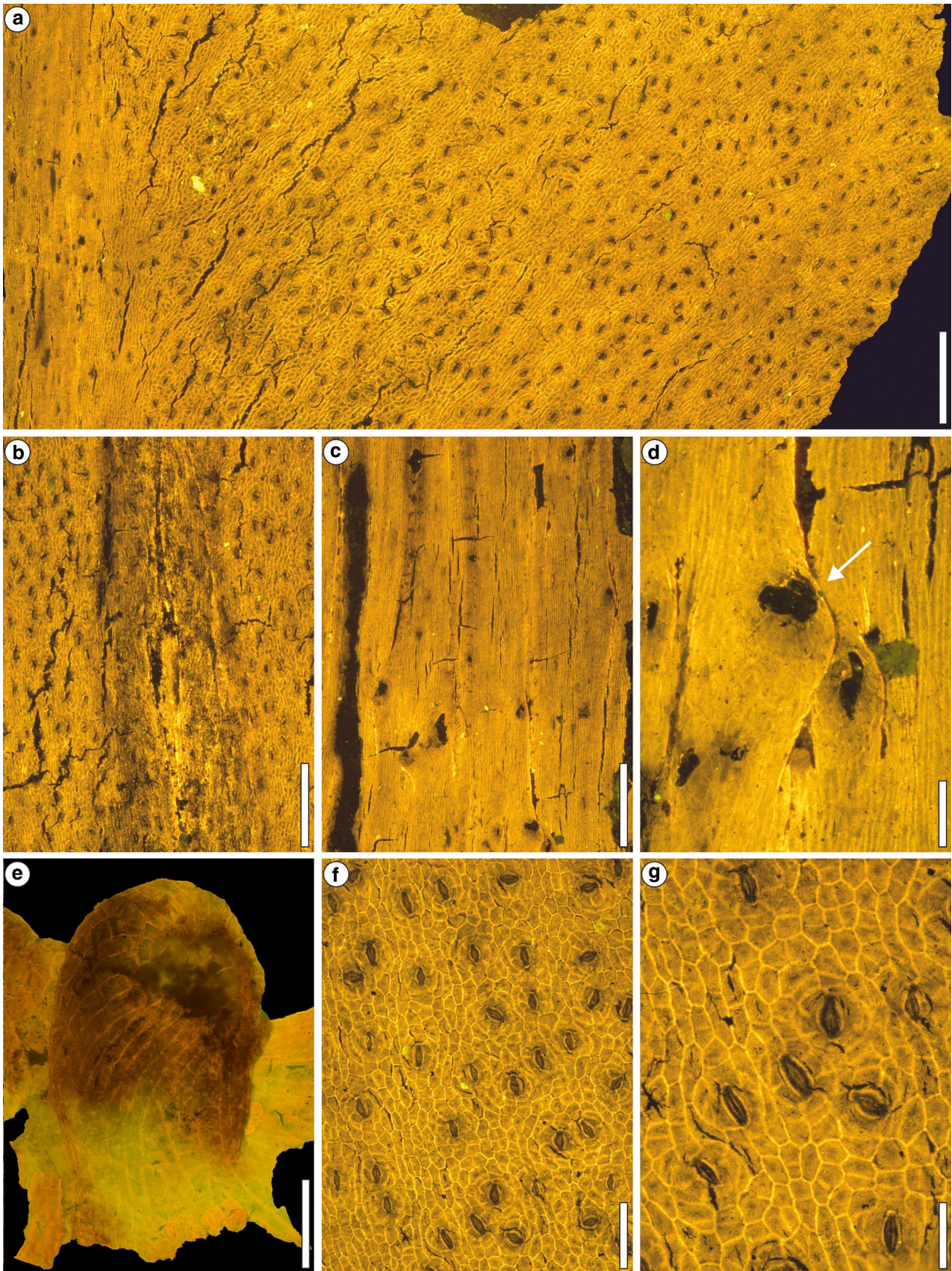


Fig. 4 Epifluorescence images of epidermal anatomy of *Compsopteris wongii*. **a** Lower pinnule surface with longitudinally arranged cells and stomata on midrib (left) and lamina with ill-defined costal and intercostal fields and high densities of randomly oriented stomata. Specimen PB22968, scale bar 100 μm . **b** Upper view showing the adaxial attachment of lamina to midrib, which is only visible as a cleft. Specimen PB22978, scale bar 500 μm . **c** Lower view of the rachis showing longitudinally oriented cells and randomly distributed glandular trichomes. PB22979, scale bar 500 μm . **d** Close-up of two trichome bases with truncate apex and opaque filling (arrow). Specimen PB22978, scale bar 100 μm . **e** Macerated trichome with apical opening. Specimen PB22978, scale bar 100 μm . **f** Intercostal field with randomly oriented, cyclocytic stomata. PB22979, scale bar 200 μm . **g** Group of mono- to dicyclic stomata in an intercostal field. PB22979, scale bar 100 μm

Paleobiology and paleoecology

The paleoenvironment of the Lower Shihhotse Formation in Shanxi was interpreted as a fluvial system with meandering rivers and a tropical, humid climate with no periods of seasonal dryness (Liu et al. 2015; Wang and Chen 2016). Specimens of *Compsopteris wongii* from this site are usually large fragments, including almost complete fronds more than 20 cm in size. Thus it is unlikely that they were transported over long distances; they were probably deposited close to their habitat. The associated flora in this habitat is rich in Noeggerathiales such as *Tingia carbonica*, Cordaitales as *Cordaites principalis* and *Cordaites schenkii*, and putative cycads such as *Taeniopteris* cf. *multinervis*. All these species have amphistomatic leaves with no xeromorphic adaptations and are typical coal-forming elements in Cathaysian floras. For instance, these genera have all been found to be very common elements in the peat-forming swamp forest of the Asselian (Early Permian) Wuda Tuff Flora (Chinese “vegetational Pompeii”) (Wang et al. 2012).

The epidermal anatomy of *Compsopteris wongii* also shows distinct adaptations to this environment, as pinnules are amphistomatic and do not show xeromorphic adaptations such as papillae, strongly sunken stomata, or trichomes. Furthermore, the high density of stomata on both sides of leaves, the midrib, and rachides indicate an adaptation to allow high photosynthetic capacities and assimilation rates (Mott et al. 1982; Smith et al. 1997; Bomfleur and Kerp 2010). This effect may have been enhanced by the attachment of the lamina to the very top of the midrib, which additionally increased the upper (sun-facing) surface of the lamina. Another interesting feature is that cuticles of *C. wongii* commonly show intense fracturing even in freshly split material, which may result from shrinkage and compaction of a particularly thick leaf substance. Fleishy or succulent pinnules can be an adaption to water stress or soil and groundwater salinity (Krings et al. 2005), but both of these interpretations are unlikely as *C. wongii* lived neither in a (seasonally) dry environment nor in a coastal habitat (Liu et al. 2015).

Another interpretation could be that the thickened pinnules were another adaptation to the high assimilation rates of *C. wongii*, in that the increased pinnule thickness would have substantially increased the mesophyll cell-surface area available for carbon dioxide absorption (Smith et al. 1997).

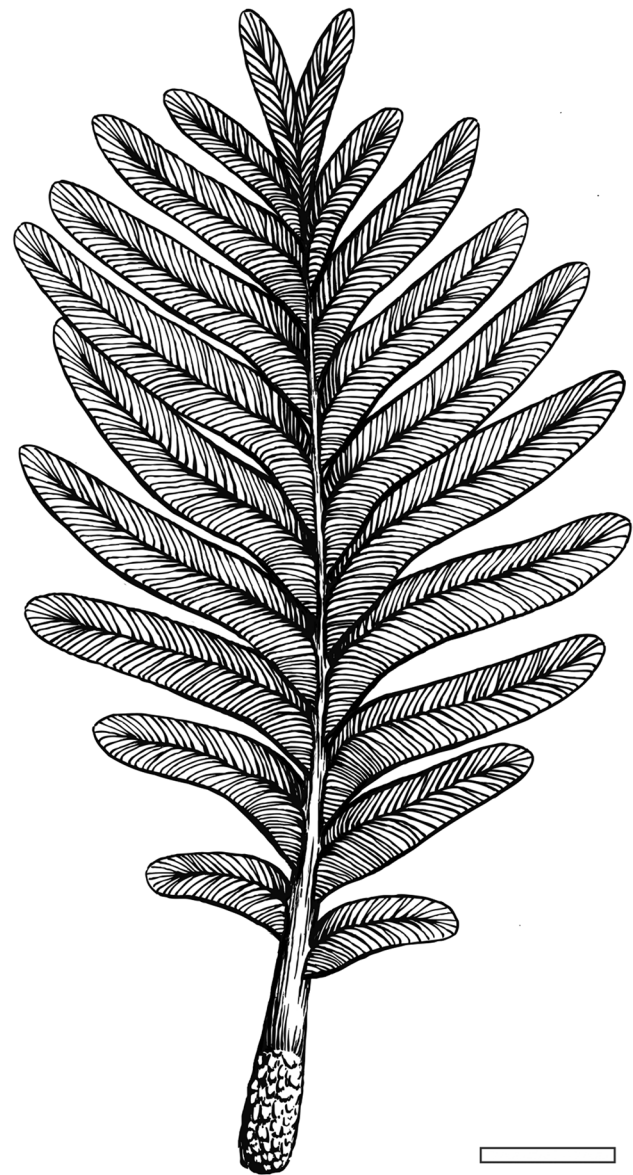
The distribution of trichomes in *Compsopteris wongii* is limited to the rachis, and their low density indicates that they did not have a defence function as a mechanical barrier against predators. Their shape and especially the opaque filling of their apical opening suggest that they were glandular structures, very similar to specimens of the peltasperm *Autunia conferta* that were recovered from peat-forming environments (Kerp 1996). Remarkably similar glandular trichomes also occur in extant plants, e.g., Lamiaceae or Cannabaceae (e.g., Werker 2000; Andre et al. 2016). In modern plants, such trichomes have different functions, depending on their location and the substance they secrete (Werker 2000). They can store and excrete lipophilic or hydrophilic secondary metabolic products as oils or mucilage, or excrete excessive nutrients as salts (Krings and Kerp 1998; Werker 2000). Without knowing which of these substances the trichomes of *C. wongii* secreted, however, we cannot identify their function precisely.

Reconstruction of the frond

Different frond fragments of *Compsopteris wongii* could be unequivocally correlated to the same plant based on similarities in macromorphology and especially epidermal anatomy. Fronds are simple pinnate with a forking tip, distinct petiole, and more or less auriculate, alethopteroid pinnules (Fig. 5). Features consistent among specimens are the typical dichotomous branching of the frond tip, the absence of auricles in the lowermost small pinnules, and the distinct, widened petiole of the frond. A certain degree of variability between individual fronds occurs with regard to the manifestation of the auricles and the level of overlap of superimposing pinnules, with both features well-developed to inconspicuous. Furthermore, our results show that fronds of *C. wongii* were monopodial rather than forked, a feature already recognized by Halle (1927). We restudied samples of supposedly forked fronds of *C. wongii* from the Upper Shihhotse Formation of southeast Shanxi (Chow et al. 1955; Sze 1955), but these samples are questionable as they are either two superimposed fronds or frond fragments that are quite different in shape and venation from those of *C. wongii*. The reports of supposedly bipinnate fronds—including specimens of *C. wongii* (Liu 1989) and of *P. contractum* (Gu and Zhi 1974; Sun and Shen 1999a, b)—remain doubtful, as the fronds are linear and pinnules are uniformly sized and broad with an indistinct midrib (Liu 1989). Unfortunately, none of these samples has a preserved frond tip. Another very interesting specimen in regard to the growth habit of *C. wongii*

Table 2 Simplified comparison of *Compsopteris wongii* to possibly related pinnate taxa in terms of epidermal anatomy

Taxa	Epidermal pattern		Stomata		Randomly oriented	On rachis	Number of subsidiary and encircling cells	Papillae		Trichomes	
	Amphistomatic	CF/ICF differentiated	Strictly monocyclic type					Rachis	Epidermal cells	Rachis	Midrib
<i>Compsopteris wongii</i> ^a	+	±	-	+	+	6–20	-	-	+	-	
<i>Compsopteris adzvensis</i> ^b	+	+	-	±	?	4–7	?	?	?	?	
<i>Glenopteris</i> ^c	+	±	-	+	+	6–15	-	-	-	-	
<i>Supaia</i> ^d	+	±	+	+	+	4–6	+	+	?	?	
<i>Megalopteris</i> ^e	-	±	-	-	?	4–7	-	+	?	?	
<i>Nanshanopteris</i> ^f	+	+	-	+	+	3–6	+	+	-	-	

^aThis study^bMeyen and Migdisova (1969)^cKrings et al. (2005)^dWang (1997)^eFlorin (1933)^fWan and Wang (2015)**Fig. 5** Reconstruction of a *Compsopteris wongii* frond based on specimens PB22968 and PB22972, scale bar 5 cm

was shown by Halle (1927: pl. XXXVI, fig. 5). This sample shows several juvenile fronds that arise from a rhizome, indicating that *C. wongii* might have had a shrub-like growth habit. However, this specimen is not well preserved, and the widened bases of several complete fronds in our collection indicate that they might have been shed from a major stem or branch of a tree.

Conclusions

Cuticles of *Compsopteris wongii* from the Permian of Shanxi provide the first information on the epidermal anatomy of this enigmatic Cathaysian foliage taxon. Our results provide sound arguments for proposing an affinity of *C. wongii* to the seed fern order Peltaspermales, which are generally characterized by amphistomatic fronds with alethopteroid pinnules, callipterid venation, and haplocheilic stomata surrounded by one to three rings of subsidiary cells (Taylor et al. 2009; Retallack 1981; Bomfleur et al. 2011). Furthermore, our results allow a detailed comparison with possibly related peltaspermean genera (Tables 1, 2). The similarities, especially with regard to the so-called glenopteroids *Glenopteris* and *Nanshanopteris* are sound enough to affiliate *C. wongii* with this group of putative Peltaspermales, as was previously proposed by Wan and Wang (2015). Due to the clear similarities of *C. wongii* to *C. adzvensis* and the problematic circumscription of *Protoblechnum* fossils from America, we follow Zalesky (1934) and include the Chinese material in the genus *Compsopteris*. Moreover, the limitation of *Compsopteris* to the Angaran realm (Naugolnykh 1999) is not in accordance with paragraph 38.3 of the International Code for Nomenclature for algae, fungi, and plants (Turland et al. 2018), which states that geographic features alone do not qualify as valid differentiating diagnostic criteria.

The depositional environment and epidermal anatomy indicate that *Compsopteris wongii* was an element of the peat-forming vegetation, along with noeggerathialeans, cordaitaleans, cycads, and other pteridosperms, confirming previous suggestions that peltasperms also inhabited everwet environments of Cathaysian coal swamps (Wang et al. 2014). *Supaia* and *Nanshanopteris* may be closely related forms that were adapted to more seasonally dry environments.

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during field work in 2012 and proposed this section for a Sino-German joint PhD project.

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