Annals of Botany **115**: 1133–1148, 2015
doi:10.1093/aob/mcv049, available online at www.aob.oxfordjournals.org

ANNALS OF BOTANY
Founded 1887

Leaf evolution in early-diverging ferns: insights from a new fern-like plant from the Late Devonian of China

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Received: 28 January 2015 Returned for revision: 26 February 2015 Accepted: 13 March 2015

- **Background and Aims** With the exception of angiosperms, the main euphyllophyte lineages (i.e. ferns *sensu lato*, progymnosperms and gymnosperms) had evolved laminate leaves by the Late Devonian. The evolution of laminate leaves, however, remains unclear for early-diverging ferns, largely represented by fern-like plants. This study presents a novel fern-like taxon with pinnules, which provides new insights into the early evolution of laminate leaves in early-diverging ferns.
- **Methods** Macrofossil specimens were collected from the Upper Devonian (Famennian) Wutong Formation of Anhui and Jiangsu Provinces, South China. A standard degagement technique was employed to uncover compressed plant portions within the rock matrix.
- **Key Results** A new fern-like taxon, ***Shougangia bella* gen. et sp. nov.**, is described and represents an early-diverging fern with highly derived features. It has a partially creeping stem with adventitious roots only on one side, upright primary and secondary branches arranged in helices, tertiary branches borne alternately or (sub)oppositely, laminate and usually lobed leaves with divergent veins, and complex fertile organs terminating tertiary branches and possessing multiple divisions and numerous terminal sporangia.
- **Conclusions** *Shougangia bella* provides unequivocal fossil evidence for laminate leaves in early-diverging ferns. It suggests that fern-like plants, along with other euphyllophyte lineages, had independently evolved megaphylls by the Late Devonian, possibly in response to a significant decline in atmospheric CO_2 concentration. Among fern-like plants, planate ultimate appendages are homologous with laminate pinnules, and in the evolution of megaphylls, fertile organs tend to become complex.

Key words: Adventitious root, atmospheric CO_2, euphyllophytes, fern-like plants, ferns *sensu lato*, fertile organ, growth habit, Late Devonian, leaf evolution, monilophyte, *Shougangia bella*, stem, Wutong Formation.

INTRODUCTION

Euphyllophytina, the main clade of vascular plants, includes several extinct stem groups, moniliformopses and radiatopses (Kenrick and Crane, 1997). Moniliformopses or monilophytes (Pryer *et al*., 2004) refer to ferns, sphenopsids and their fossil relatives (i.e. ferns *sensu lato*), while radiatopses represent progymnosperms and spermatophytes (seed plants). The terms moniliformopses and monilophytes have been commonly used but essentially can be regarded as simply a synonym for ‘fern’ (Christenhusz and Chase, 2014). Early-diverging ferns include Middle Devonian–Early Carboniferous iridopteridaleans, pseudosporochnaleans, non-pseudosporochnaleans and rhacophytaleans, Late Devonian–Carboniferous stauropteridaleans, and sphenophyllaleans (sphenopsids traced to the Famennian of Late Devonian). Except for sphenophyllaleans, these groups without foliar-borne sporangia are called fern-like plants (Soria and Meyer-Berthaud, 2005; Taylor *et al*., 2009; Galtier, 2010).

Early Devonian *Eophyllophyton* has been placed at the most basal position within the euphyllophytes (Kenrick and Crane, 1997; Hao and Xue, 2013*a*, *b*), and its lobed megaphyll has been interpreted as a rare example of early adaptation to high atmospheric CO_2 concentration (Hao *et al*., 2003; Osborne *et al*., 2004). After a long delay, the rapid drop of CO_2 levels during the Middle to Late Devonian is proposed to have led to the initial widespread occurrence of laminate leaves of euphyllophytes in the Late Devonian and Early Carboniferous (Beerling *et al*., 2001). In the process of evolving megaphylls, the planation (i.e. transformation from three- to two-dimensional ultimate appendages) is followed by lamination (i.e. webbing in planate appendages) (Zimmermann, 1952). Leaf evolution of ferns with foliar-borne sporangia, and of radiatopses, has been studied or summarized in detail (Boyce and Knoll, 2002; Osborne *et al*., 2004; Phillips and Galtier, 2005; Sanders *et al*., 2009; Galtier, 2010; Corvez *et al*., 2012). Early-diverging ferns with planate appendages are central to our understanding of the evolution of laminate leaves (Corvez *et al*., 2012). However, fern-like plants, usually with terminal sporangia on branches, rarely bear laminate leaves. In this plant group, the homology between laminate leaves and planate appendages remains unclear, and the evolution of fertile organs is poorly known.

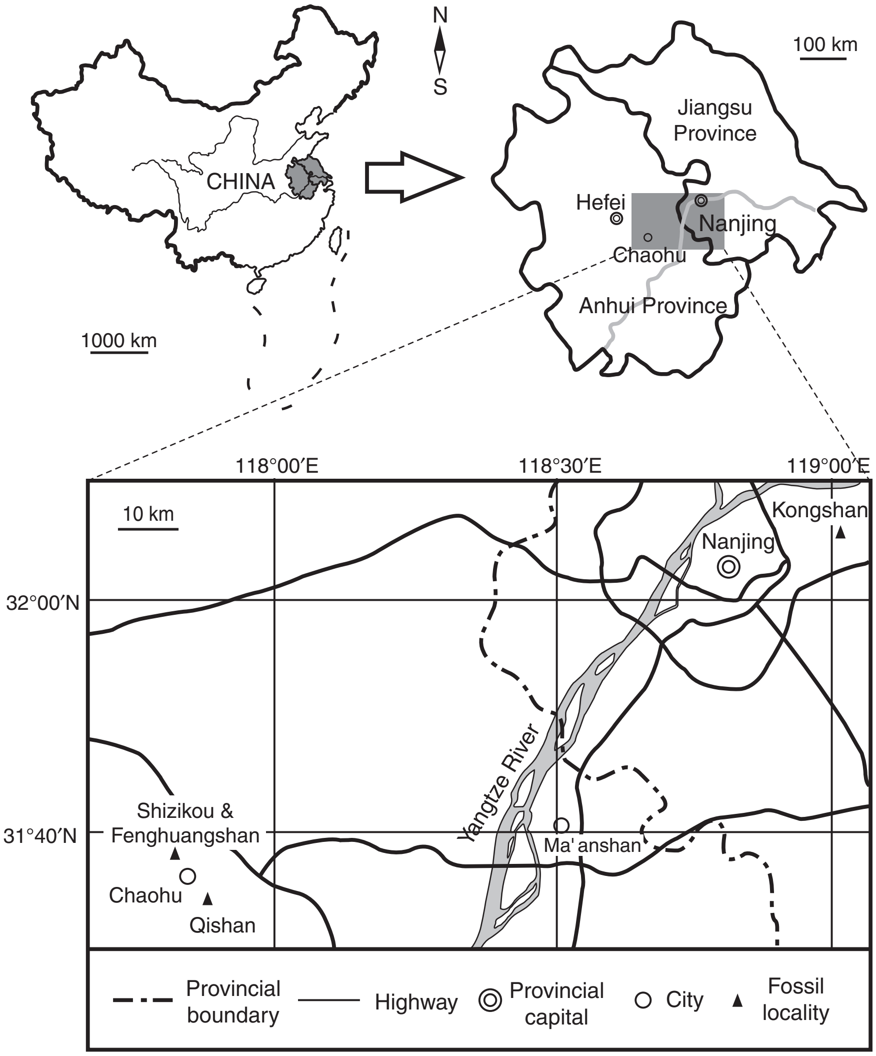

FIG. 1. Maps showing localities of Qishan and Kongshan, where the fossil plant ***Shougangia bella* gen. et sp. nov.** was collected.

Here, we report a new fern-like plant, ***Shougangia bella* gen. et sp. nov.**, from the Late Devonian in China. Known from vegetative and fertile morphology and growth habit, *Shougangia* provides definite evidence of laminate leaves for fern-like plants. The evolution of planate ultimate appendages toward laminate pinnules within fern-like plants is discussed in the background of CO_2 and fertile organs.

MATERIAL AND METHODS

The fossils of ***Shougangia bella* gen. et sp. nov.** were recovered from two localities in the Upper Devonian Wutong (Wutung) Formation of China. Over 300 specimens were collected from a hill named Qishan (GPS data: 31°35′04″N, 117°54′23″E), Chaohu City, Anhui Province (Fig. 1). About 80 specimens were obtained from Kongshan (32°4′37″N, 119°1′24″E), Jiangning County, Nanjing City, Jiangsu Province (Fig. 1). At both the Qishan and the Kongshan sections, the Wutong Formation includes the Guanshan Member lacking fossils and overlying fossiliferous Leigutai Member. At these localities, the Guanshan and Leigutai Members are characterized, respectively, by quartzose sandstone and by inter-beds of sandstone and silty mudstone (Cai *et al*., 1988; Hou and Qi, 2006). In the Chaohu area are several sections, such as Shizikou, Fenghuangshan and Qishan, which yield Late Devonian plants (Fig. 1). The Qishan section at Yafu County is represented in several quarries, where locals have excavated mudstone or clay for manufacturing pottery. Since 2006, we have visited this locality more than 15 times, keeping pace with the progress of clay exposure. Fieldwork at the Kongshan section has been systematically conducted by many geologists since the 1960s, with numerous plants including this new taxon continuously obtained.

At the Qishan section, the Guanshan Member is mainly covered by Quaternary sediments, and the exposed lower part of the Leigutai Member is 14 m thick. Here, *Shougangia bella* occurs at the lower to middle part of the Leigutai Member and near the horizon bearing two sphenopsids, *Hamatophyton verticillatum* (Wang and Guo, 2009) and *Eviostachya* sp. (Fig. 2). The plant bed is about 3·0 m thick and extends laterally for about 10 m.

At the Kongshan section, the Guanshan Member and lower to middle part of the Leigutai Member are 81·7 and 84 m thick,

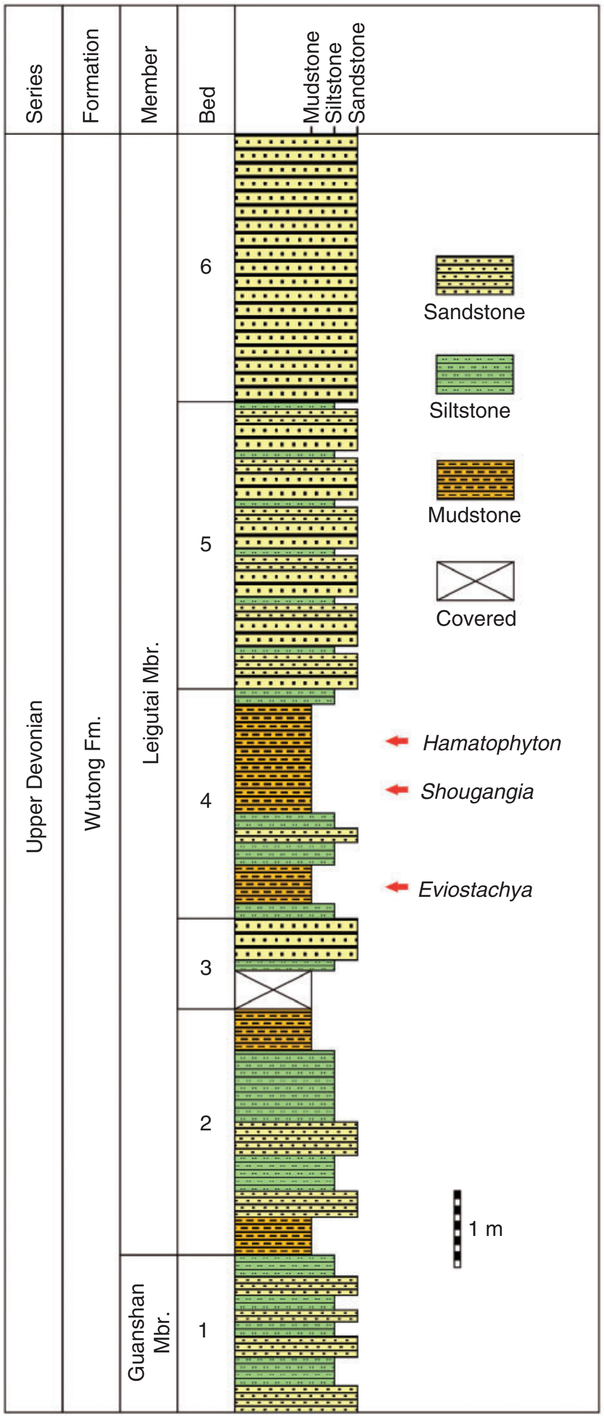

FIG. 2. Stratigraphic column at Qishan section, Chaohu City, Anhui Province, China, showing the bed within the Upper Devonian (Famennian) Leigutai Member that preserves plants including ***Shougangia bella*** **gen. et sp. nov**.

respectively (see stratigraphic column in Cai *et al*., 1988). At this section, the lower to middle part of the Leigutai Member contains seven plant beds of various thicknesses, in ascending order: (1) progymnosperm *Archaeopteris* sp., *Eviostachya hoegii*, fern-like plant *Rhacophyton*? sp. and sphenopsid *Sphenophyllum lungtanense* (2·7 m thick); (2) *Hamatophyton verticillatum* (5·2 m); (3) lycopsid *Sublepidodendron*? sp. (6·0 m); (4) *Hamatophyton verticillatum* (20 m); (5) lycopsid *Leptophloeum rhombicum* (3·4 m); (6) *Hamatophyton verticillatum*, and two lycopsids – *Sublepidodendron* sp. and *Stigmaria* sp. (9·2 m); (7) *Archaeopteris* (3·7 m). *Shougangia* occurs at the basal part (the first plant bed) of the Leigutai Member where *Eviostachya hoegii* (Wang, 1993) and the seed plant *Kongshania synangioides* (Wang, 2000) have been described. Cai *et al.* (1988) tentatively recognized limited fertile remains as '*Rhacophyton*? sp.' in the first plant bed, but morphological comparison leads us to conclude that these remains represent *Shougangia bella*.

Among the plants from the Qishan and Kongshan sections, *Hamatophyton* is widespread in Famennian deposits of South China (Wang and Guo, 2009) and *Eviostachya* is also present in coeval flora of Belgium (Leclercq, 1957). *Leptophloeum rhombicum* represents a Late Devonian element that is distributed worldwide (Cai *et al*., 1988; Wang *et al*., 2005). The Wutong Formation with Guanshan and Leigutai Members occurs in many localities of Anhui, Jiangsu and Zhejiang Provinces. In the Chaohu area of Anhui, the middle part of the Leigutai Member contains the LH spore assemblage (*Retispora lepidophyta* var. *minor* and *Apiculiretusispora hunanensis*) (Hou and Qi, 2006). *Retispora lepidophyta* has also been found in the middle part of the Leigutai Member, Kongshan section (Cai *et al*., 1988). On the basis of data from several localities, this spore assemblage at the lower to middle part of the Leigutai Member is interpreted as Famennian in age (Fa2d) (Chen and Ouyang, 1987; Ouyang, 2000).

Sedimentary and geochemical characteristics indicate that the Upper Devonian Wutong Formation in the above three provinces represents littoral rather than terrestrial deposits (Zhu *et al*., 1999). Plants, fish, conchostracans and trace fossils from the Leigutai Member in the Chaohu area and at the Kongshan section support this conclusion (Cai *et al*., 1988; Hou and Qi, 2006).

Shougangia is preserved as impressions and compressions in yellow–grey or red–purple silty mudstone. Many axes, leaves and fertile organs are coloured red, giving great contrast to the rock matrix. Under a microscope, the plant morphology was exposed with steel needles. A serial dégagement technique was used in some cases to show the complex branches within the fertile organs.

SYSTEMATICS

Order and Family: *Incertae sedis*
Genus: ***Shougangia*** **D.M. Wang** ***et al.*** **gen. nov.**
Type: ***Shougangia bella*** **D.M. Wang** ***et al.*** **sp. nov.**

Generic diagnosis. Adventitious roots occurring on only one side of horizontal portions of slender stem, with upright primary branches borne helically. Primary branches bearing secondary branches in irregular helices. Tertiary branches arranged alternately or (sub)oppositely, possessing basal fan-shaped pinnules in pairs, lateral alternate or subopposite *Sphenopteris*-like pinnules with three to six lobes, and either a terminal pinnule with two to four lobes or a terminal fertile organ. Fertile secondary branches also bearing basal fan-shaped pinnules. Pinnules laminate, with veins proximally parallel and then dichotomous.

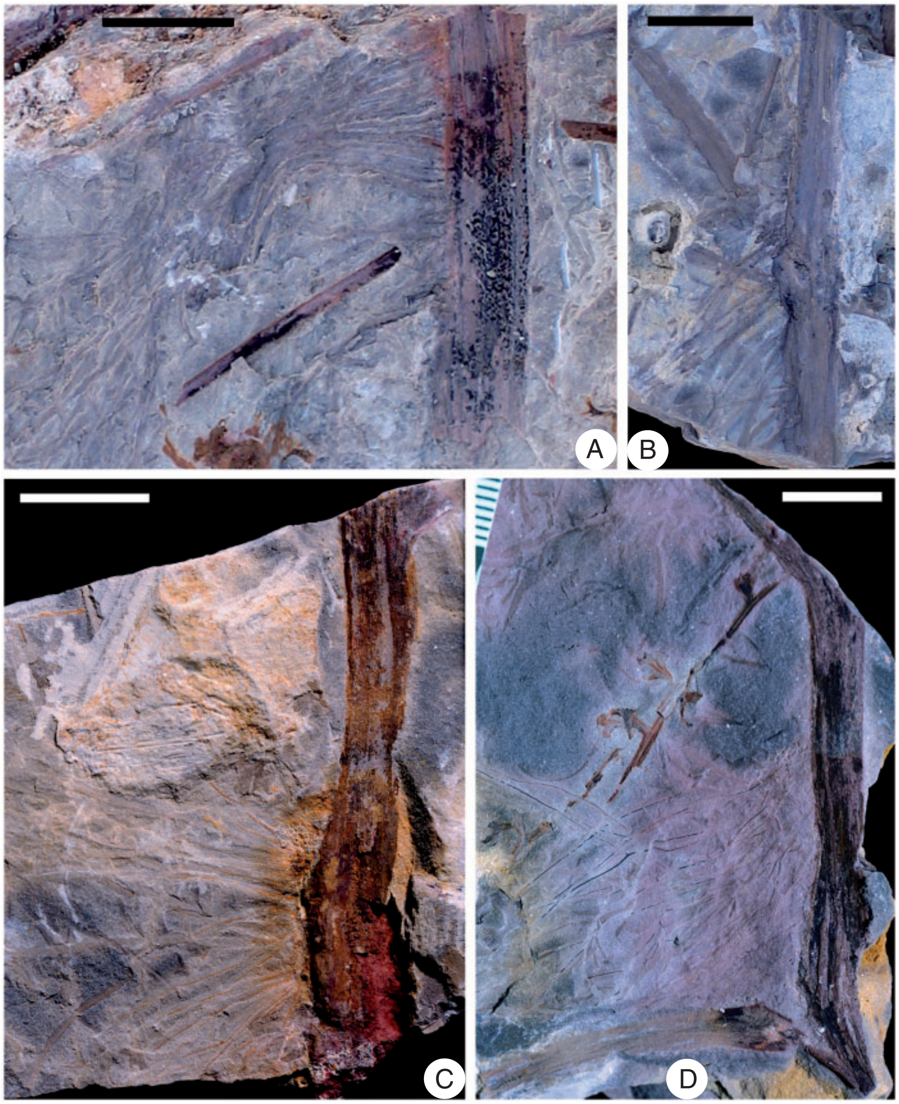

FIG. 3. ***Shougangia bella*** **gen. et sp. nov**. from Chaohu City, Anhui Province, China. (A–D) Stems with one side bearing adventitious roots, and showing several longitudinal grooves and ridges (PKUB14248, PKUB14247, PKUB14310, PKUB14313). (D) Primary branch and roots appearing to depart from the stem in the same direction, due to compression during fossilization. Scale bars = 1 cm.

Fertile organs complex, three-dimensionally dichotomous up to ten times and terminating in numerous sporangia. Sporangia paired, elongate and distally tapered.

Etymology. The generic name is dedicated to Professor Shou-Gang Hao (Peking University, Beijing) for his outstanding contributions to the study of early vascular plants.

Shougangia bella **D.M. Wang *et al.* sp. nov.**

(Figs 3A–D, 4A–J, 5A–E, 6A–F, 7A–G, 8A–I, 9A–C, 10A–G, 11A–E)

Specific diagnosis. As in the generic diagnosis. Stems up to 152 mm long and 4·5–7·8 mm wide, with adventitious roots departing at 60–90°. Primary branches up to 83 mm long and 2·6–4·8 mm wide; secondary branches up to 65 mm long and 1·0–4·0 mm wide; and tertiary branches 8·8–65 mm long and 0·4–1·6 mm wide. Basal pinnules 2·6–4·8 mm long and 2·8–4·8 mm wide and uneven at margin. Lateral pinnules of tertiary branches 2·8–14 mm long and 2·3–9·2 mm wide, with number of lobes decreasing acropetally. Terminal pinnules 1·5–2·6 mm long and 2·8–3·8 mm wide. Fertile organs pendulous, 7·5–16 mm long and 12–22·8 mm wide; axes comprising fertile organs 0·1–0·5 mm wide. Sporangia 2·7–3·8 mm long and 0·4–0·7 mm wide.

Etymology. The specific epithet is from the Latin *bellus*, beautiful, for the beautifully preserved laminate pinnules that characterize this plant.

Holotype. PKUB14229a, b (designated here; part and counterpart of a specimen; Fig. 7A, B), from Qishan section, Chaohu City, Anhui Province, China.

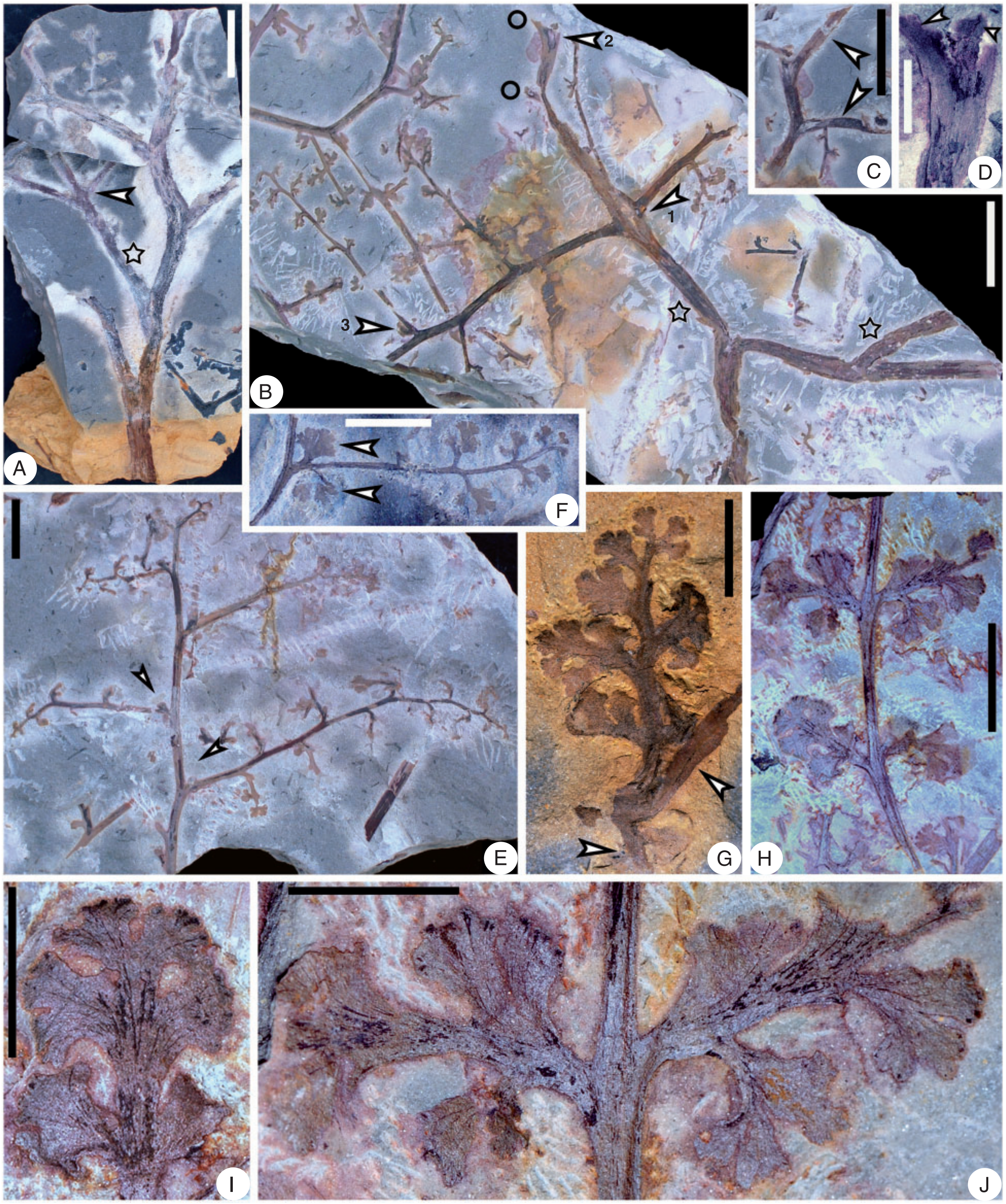

FIG. 4. ***Shougangia bella* gen. et sp. nov**. from Chaohu City, Anhui Province, China. (A) Stem with one primary branch (star) bearing two secondary branches (arrow) (PKUB14233a). (B) Markedly curved stem with primary, secondary and tertiary branches. One primary branch (right star) on stem. Another primary branch (left star) bearing two secondary branches (arrow 1) and bases of three additional secondary branches (arrow 2, circles). A pinnule at the base of a tertiary branch (arrow 3). Arrow 2 indicates the part enlarged in D (PKUB14232a). (C) Counterpart of portion in B (arrow 2, circles) showing primary branch bearing two secondary branches (arrows) which correspond to branch bases in B (circles) (PKUB14232b). (D) Enlargement of part in B (arrow 2) showing base of a secondary branch (left arrow) and base of another secondary branch extending into the rock matrix (right arrow). (E) Secondary branch with tertiary branches bearing basal (arrows), lateral and terminal pinnules (PKUB14234). (F) Tertiary branch with a pair of basal pinnules (arrows), and lateral and terminal pinnules (PKUB14231). (G) Secondary branch (upper arrow), base of a tertiary branch (lower arrow) and another tertiary branch above with laminate and lobed pinnules (PKUB14203). (H) Tertiary branch with laminate and lobed pinnules (PKUB14227). (I, J) Enlargement of lower left and upper parts of H, respectively, showing pinnules with veins. Scale bars = (A–C) 2 cm, (E, F, H) 1 cm, (D, G, I, J) 5 mm.

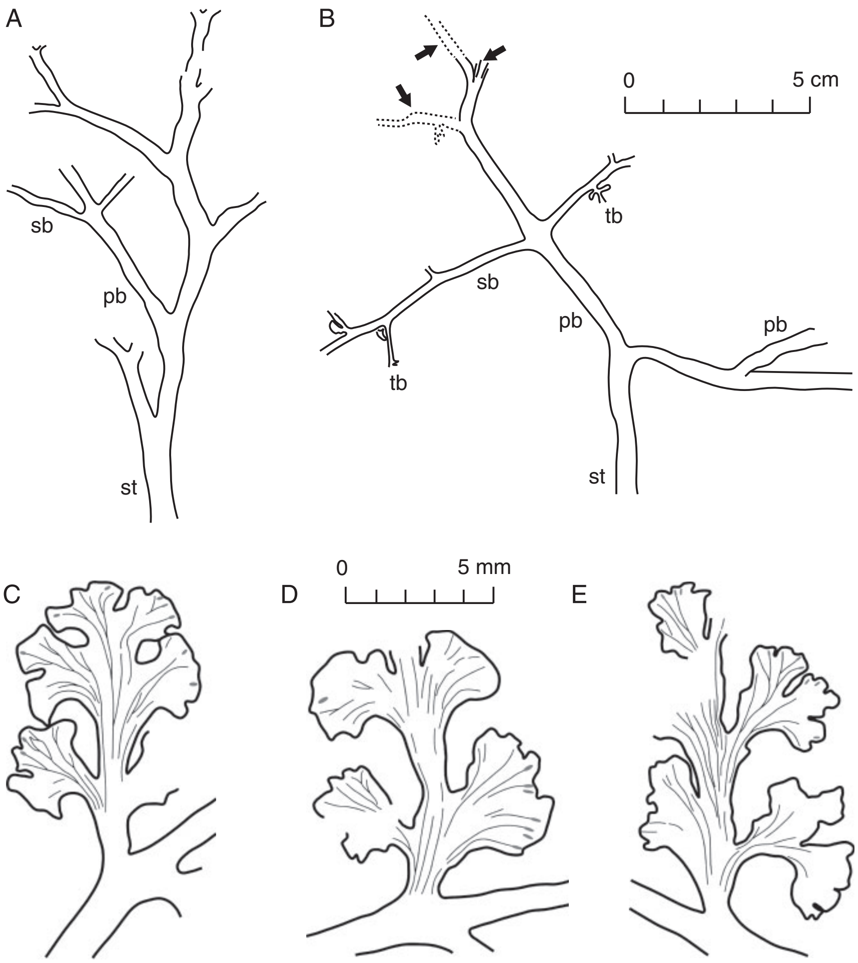

FIG. 5. ***Shougangia bella* gen. et sp. nov**. (A) Line drawing of Fig. 4A. (B) Combined line drawing of Fig. 4B–D showing three secondary branches (arrows). Dotted lines represent portions in Fig. 4C. (C–E) Line drawings of Fig. 4I and J, showing three pinnules with veins. st, stem; pb, primary branch; sb, secondary branch; tb, tertiary branch. Scale bars = (A, B) 5 cm, (C–E) 5 mm.

Paratypes. PKUB14213, PKUB14227, PKUB14232a, b, PKUB14234, PKUB14248, PB21952, PB21953 (designated here; Figs 3A, 4B, C, E, H, 8E, 10A, B).

Localities and horizon. Qishan in Chaohu City, Anhui Province, China; and Kongshan in Nanjing City, Jiangsu Province, China; Wutong Formation, Upper Devonian (Famennian).

Repository. The holotype and other specimens prefixed ‘PKUB’ (Figs 3, 4, 6A, B, 7, 8A, B, D, E, G–I) are deposited at Peking University, Beijing, China; specimens prefixed ‘PB’ (Figs 6C–E, 10) are housed at Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

RESULTS

Measurements of vegetative and fertile morphology are given in Table 1.

Stems and roots

Stems bear roots (Fig. 3), primary branches (Figs 4A, B, 5A, B) or both (Figs 7A, B, 8A). Adventitious roots depart from one side of the rhizomatous stem at 60–90° to form a dense mat (Figs 3, 7A, B, 8A). The stems lack spines or other ornamentation, have a few wide grooves and narrow ridges extending longitudinal, and sometimes curve (Figs 3D, 4B, 5B) or present a zigzag shape (Figs 4A, 5A). Probably owing to preservation, the roots sometimes curve (Fig. 3A) or extend in different directions (Fig. 3C). They are not branched and lack root hairs. An individual root contains a single vascular bundle (Fig. 3C, D).

Vegetative branches and laminate pinnules

A primary branch and roots occur on one side of the stem (Fig. 3D). Primary branches are borne helically at 35–90° on the stem (Figs 4A, B, 5A, B). The primary branch (Fig. 4A, star) is beneath the overlying stem and other three primary branches, and is attached at 45–90° by two opposite secondary branches (Fig. 4A, arrow). One primary branch departs from the front side of the stem (Fig. 4B, right star), below which occurs another primary branch (Fig. 4B, left star). On the latter primary branch, two secondary branches are oppositely placed at 90° (Fig. 4B, arrow 1). Further along this primary branch,

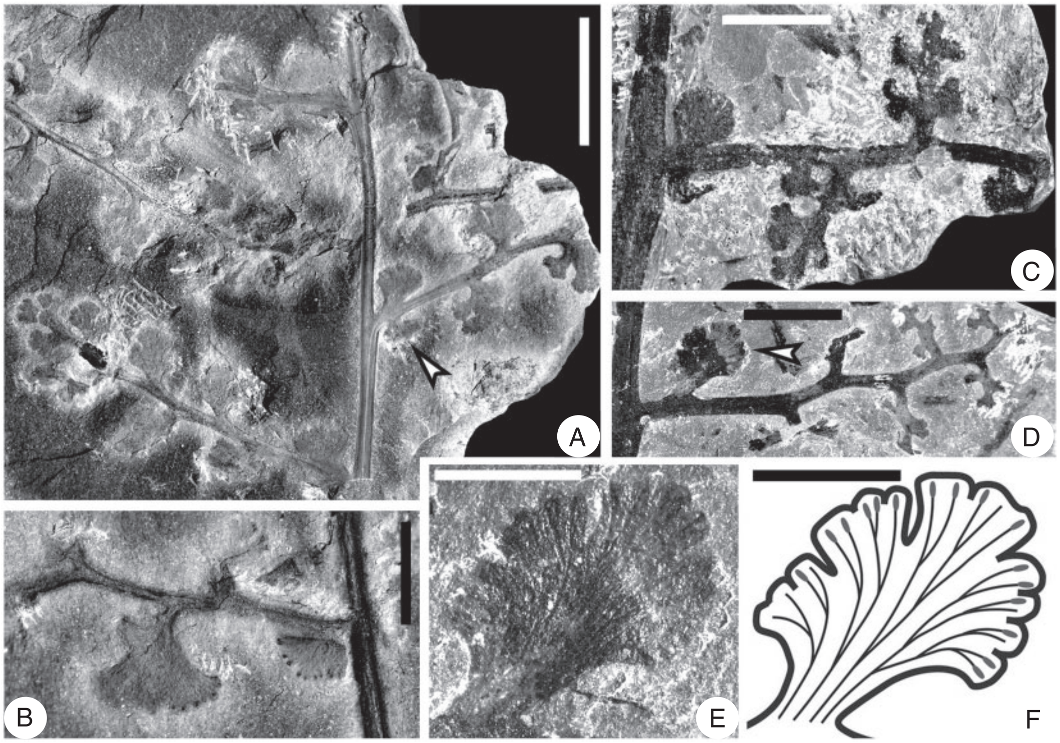

FIG. 6. ***Shougangia bella* gen. et sp. nov**. from Chaohu City, Anhui Province (A, B) and from Jiangning County, Nanjing City, Jiangsu Province (C–F), China. (A–D) Secondary branches with tertiary branches bearing pinnules (PKUB14307, PKUB14301b, PB21950, PB21951). (A) Paired pinnules at base of tertiary branch (arrow). (D) Single pinnule at base of tertiary branch (arrow). (E) Enlargement of D (arrow). (F) Line drawing of E. Scale bars = (A) 1 cm, (B–D) 5 mm, (E, F) 2 mm.

three secondary branches are closely arranged (Figs 4B, arrow 2 and circles, C, arrows, 5B, arrows), with one extending into the rock matrix (Fig. 4B, arrow 2, D, right arrow). Therefore, secondary branches are borne in an irregular helix. Tertiary branches are borne at 70–90°, and are alternately (Figs 4B, E, 6A) or suboppositely arranged (Fig. 4G). They are readily recognized by the characteristic pinnules (Figs 4B, E–H, 6A–D).

One pinnule (Figs 4B, arrow 3, E, arrows, 6B, D, arrow) or paired pinnules (Figs 4F, arrows, 6A, arrow, C) are present at the base of tertiary branches. Lateral pinnules are alternately or suboppositely arranged (Figs 4B, E–H, 6A–D). A single pinnule terminates the tertiary branches (Figs 4B, E–G, 6A). Pinnules are laminate and variously lobed. Basal pinnules are fan-shaped and uneven at the margin. Lateral pinnules are *Sphenopteris*-like and three- to six-lobed. Terminal pinnules are two- to four-lobed. One lateral pinnule, however, is fan-shaped (Fig. 6B). On a tertiary branch, the lobe number of lateral pinnules decreases acropetally (Fig. 4G). Pinnules at the lower part of tertiary branches may have what appears to be a ‘central axis’ (Figs 4E, 6C, D). Veins of pinnules appear parallel proximally (Figs 4J, left part, 5D, 6E, F), then dichotomize up to four times (Figs 4I, 5C) and finally terminate near the margin of leaf lobes rather than sinuses (Figs 4I, J, 5C–E, 6E, F). Some veins end in oval-like bodies, possibly representing glands or hydathodes.

Fertile branches and organs

Details of fertile branches are visible in part and counterpart of the holotype, which show five primary branches born helically at 45–90° (Fig. 7A, stars, B, stars). One primary branch (Fig. 7A, arrow 1) beneath another has been partially exposed through dégagement. Secondary branches depart at 60–90°. Three secondary branches are borne irregularly (potentially helically), with two bearing tertiary branches (Fig. 7A, arrows 2 and 3, B, arrows 1 and 2), and with one possibly being undeveloped and pendulous probably due to preservation (Fig. 7A, arrow 4, B, arrow 3). This possibly undeveloped secondary branch seems to show the base of a tertiary branch (Fig. 8B, arrow, C). Three tertiary branches are borne at 60–90°, with two being arranged alternately (Fig. 7A, arrows 2 and 3) and one singly (Fig. 7B, arrow 2). Among them, two branches are complete (Fig. 7A, arrow 2, B, arrow 2). One (Fig. 8G) or two opposite (Fig. 10A) or three alternate (Fig. 8E, F) tertiary branches occur at 45–90° on secondary branches.

One or two fan-shaped pinnules are present at the base of three secondary branches (Figs 7A, arrows 5 and 6, B, arrow 4, C, upper arrow, D, arrow, 8D), or several fragmentary pinnules along a secondary branch (Figs 7C, lower arrow, 8B, C). A pair of basal pinnules and two suboppositely arranged lateral pinnules occur on each tertiary branch (Figs 7A, arrow 3, E–G, 9). Paired basal pinnules, with one partly covered by a fertile organ (Fig. 7E, lower arrow, G, lower arrow), are fan-shaped, whereas two lateral pinnules, with one also partly covered by a fertile organ (Fig. 7E, upper arrow, G, upper arrow), are *Sphenopteris*-like and six-lobed. Sometimes, only one pinnule is visible at the base of a tertiary branch (Figs 8G, arrow, E, arrows, 10A, arrow).

A pendulous and complex fertile organ terminates each tertiary branch (Figs 7E–G, 8E–G, 9, 10A), and it may be

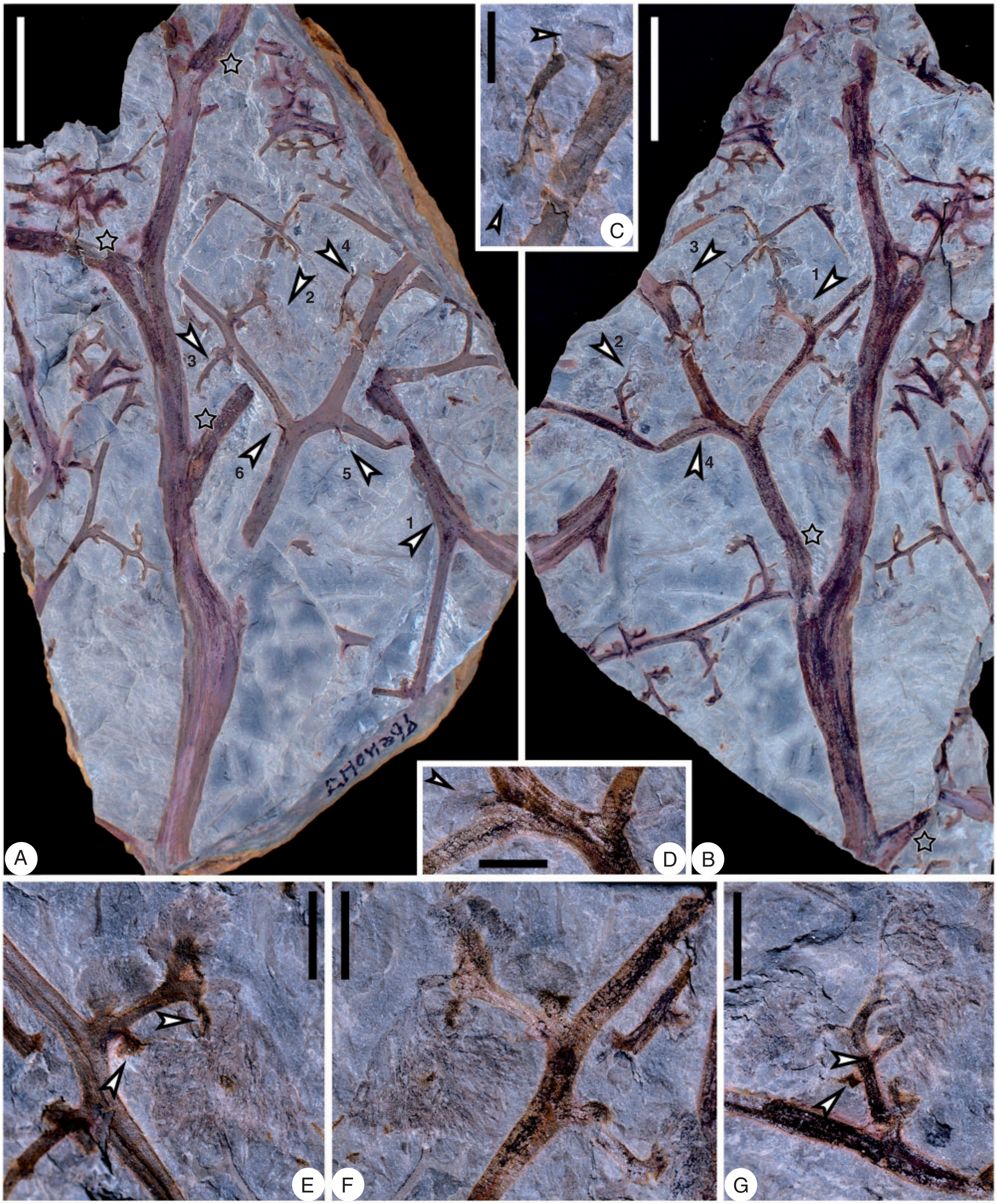

FIG. 7. ***Shougangia bella* gen. et sp. nov**. from Chaohu City, Anhui Province, China. (A, B) Part and counterpart of holotype showing stem, primary (stars), secondary and tertiary branches, and fertile organs (PKUB14229a, b). (A) One primary branch (arrow 1), tertiary branch with terminal fertile organ (arrow 2), tertiary branch incomplete distally (arrow 3), secondary branch (arrow 4), and pinnules at base of secondary branches (arrows 5 and 6). (B) Two tertiary branches with terminal fertile organs (arrows 1 and 2), secondary branch (arrow 3), and pinnule at base of secondary branch (arrow 4). (C) Enlargement of A (arrow 4) showing basal and lateral pinnules (arrows). (D) Enlargement of B (arrow 4) showing pinnule (arrow). (E–G) Enlargement of two tertiary branches in A (arrow 2) and B (arrows 1 and 2), respectively, showing pinnules and fertile organs. (E, F) Part and counterpart. (E, G) Lateral (upper arrows) and basal (lower arrows) pinnules partly covered by fertile organ. Scale bars = (A, B) 2 cm, (C–G) 5 mm.

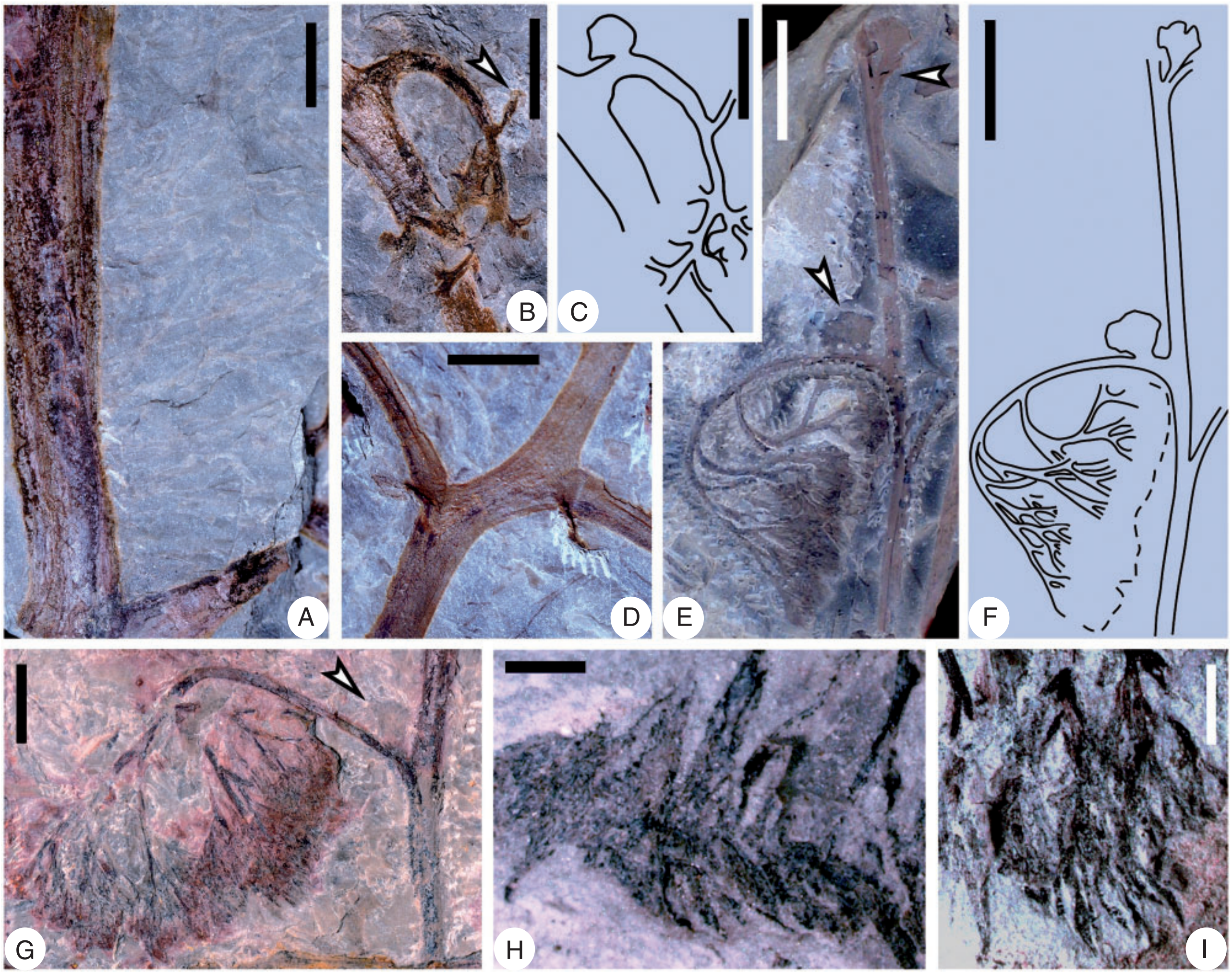

FIG. 8. ***Shougangia bella* gen. et sp. nov**. from Chaohu City, Anhui Province, China. (A) Enlargement of lower part of Fig. 7B showing adventitious roots on one side of stem. (B) Enlargement of Fig. 7B (arrow 3), arrow indicating base of a probable tertiary branch. (C) Line drawing of B. (D) Enlargement of Fig. 7A (arrows 5 and 6). (E) Secondary branch bearing three tertiary branches. A tertiary branch with basal pinnule (lower arrow) and terminal fertile organ. Pinnule at base of another tertiary branch (upper arrow) (PKUB14213). (F) Line drawing of E. (G) Tertiary branch with a basal pinnule (arrow) and terminal fertile organ (PKUB14206). (H, I) Sporangia within fertile organs (PKUB14210, PKUB14211). Scale bars = (A–D, G) 5 mm, (E, F) 1 cm, (H, I) 2 mm.

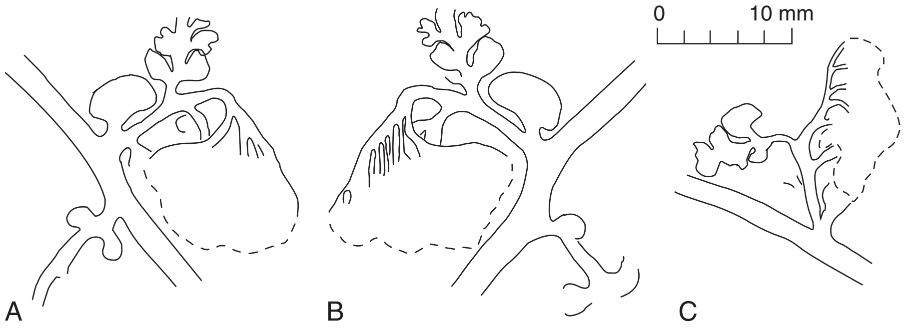

FIG. 9. ***Shougangia bella* gen. et sp. nov**. (A–C) Line drawings of Fig. 7E–G, respectively.

sometimes detached (Fig. 10B). One fertile organ (Fig. 10A) was treated using serial dégagement to show the multiple dichotomies in three dimensions (Figs 10D–G, 11A–D). The first dichotomy results in two major branches, each of which may then dichotomize up to nine times (Fig. 11A–D, a1–9, b1–9). The width of branches within the fertile organ decreases slightly with each dichotomy. The angles between two daughter axes are 30–90°. If all axes are equally dichotomous in this single fertile organ, the number of ultimate axes would be 2^{10}=1024, and as sporangia are borne in pairs at the tips of the

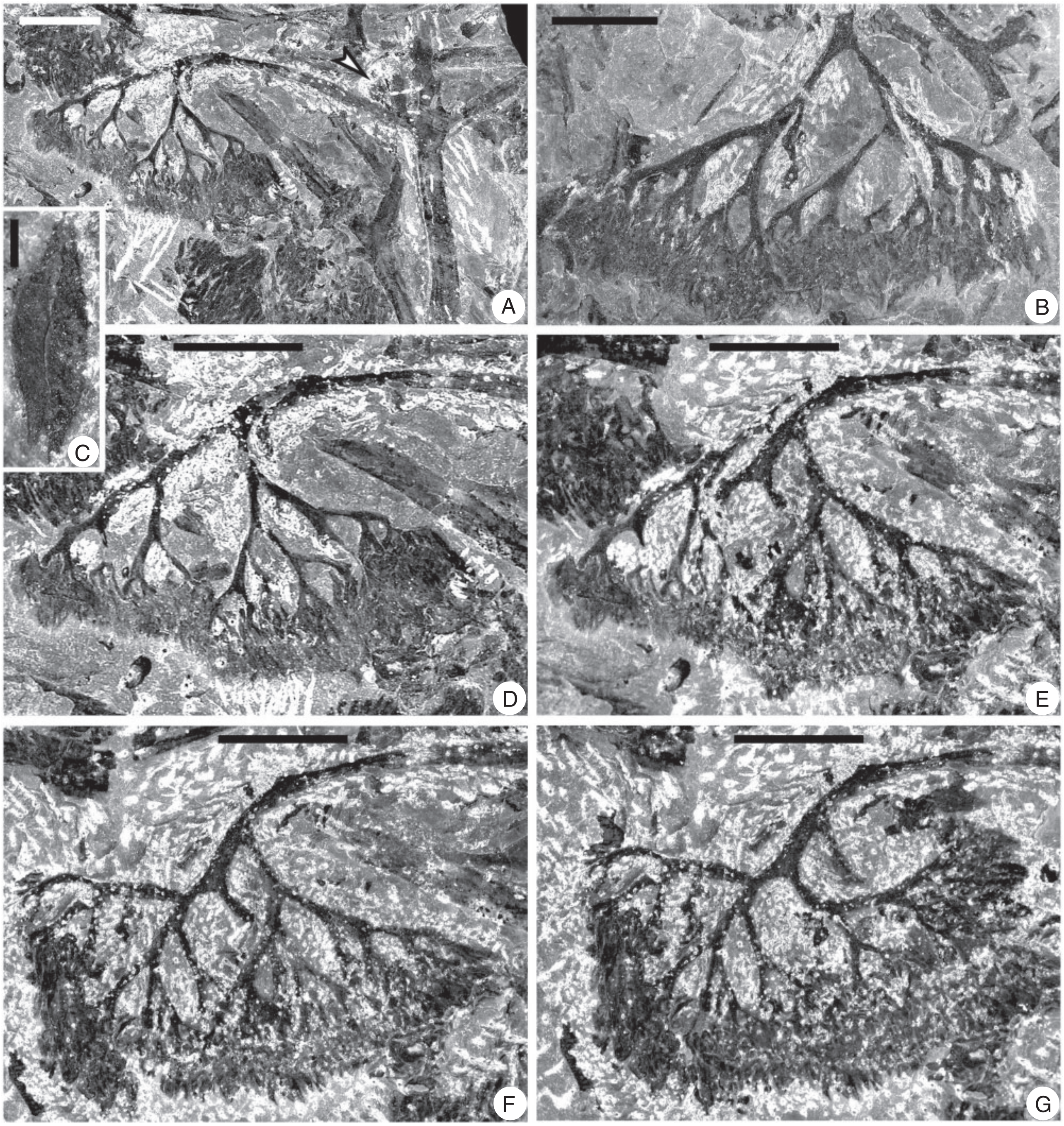

FIG. 10. ***Shougangia bella* gen. et sp. nov**. from Jiangning County, Nanjing City, Jiangsu Province, China. (A) Secondary branch with two tertiary branches, one of which bears a basal pinnule (arrow) and terminal fertile organ (PB21952). (B) Detached fertile organ (PB21953). (C) Sporangia in a pair (PB21954). (D–G) Serial dégagement of the fertile organ in A. Scale bars = (A, B, D–G) 5 mm, (C) 0·5 mm.

ultimate axes, there would be as many as 2048 elongate and distally tapered sporangia.

COMPARISONS

Table 2 presents a summary of comparisons between *Shougangia* and related plant groups or genera of Late Palaeozoic age. Comparisons include vegetative branching pattern, laminate leaves, planate vegetative ultimate appendages, basal aphlebiae and fertile organs (fertile ultimate appendages).

Iridopteridales, Pseudosporochnales and non-pseudosporochnaleans

Cladoxylopsida comprises Iridopteridales and Pseudosporochnales (Berry and Stein, 2000). In another

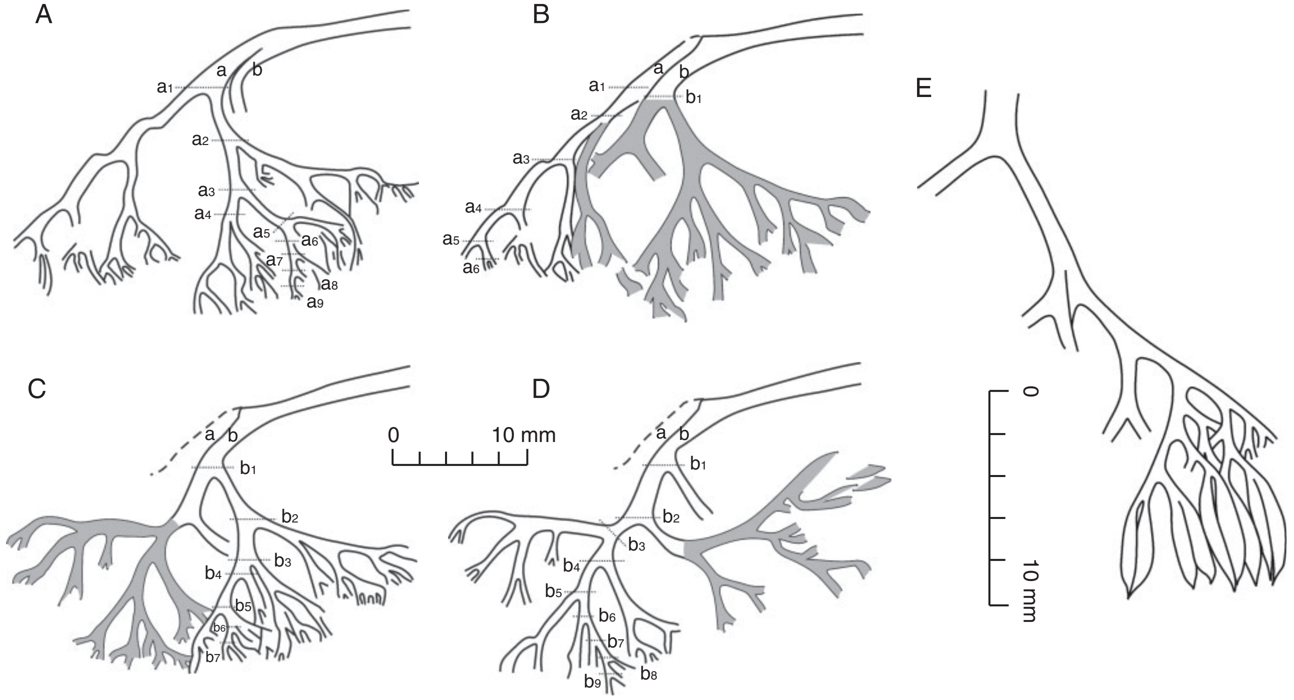

Fig. 11. ***Shougangia bella* gen. et sp. nov**. (A–D) Line drawings of Fig. 10D–G, respectively. a, b, two major axes within fertile organ; $a_{1–9}$, $b_{1–9}$, numbers of dichotomies of two major axes, respectively; shaded area, recovered axes following the former stage of dégagement. (E) Line drawing of right part of fertile organ in Fig. 10B, showing dichotomy and terminal elongate sporangia in pairs.

scenario, this class consists of Pseudosporochnales and an informal group of non-pseudosporochnaleans with taxa of unclear affinities at the ordinal level (Meyer-Berthaud *et al*., 2007). *Shougangia* resembles iridopteridaleans and most Pseudosporochnales and non-pseudosporochnaleans in having three-dimensionally dichotomous fertile branches terminated by elongate and paired sporangia, but fertile organs of *Shougangia* are unusual in that they terminate short tertiary branches bearing pinnules.

Laminate leaves are absent in iridopteridaleans [morphologically known genera such as *Anapaulia* (Berry and Edwards, 1996), *Compsocradus* (Fu *et al*., 2011), *Ibyka* (Skog and Banks, 1973) and possible iridopteridalean *Metacladophyton* (Wang and Lin, 2007)], Pseudosporochnales [*Calamophyton* (Leclercq and Andrews, 1960), *Lorophyton* (Fairon-Demaret and Li, 1993), *Pseudosporochnus* (Leclercq and Banks, 1962) and *Wattieza* (Berry, 2000)] and non-pseudosporochnaleans [e.g. *Denglongia* (Xue and Hao, 2008) and *Polypetalophyton* (Hilton *et al*., 2003)].

Whorled organs (branches and ultimate appendages) typify all iridopteridaleans but are absent in *Shougangia*. Pseudosporochnaleans with digitate branching are also distinguished from *Shougangia*. Late Devonian (Frasnian) *Polypetalophyton* with four orders of branches (Hilton *et al*., 2003) is very similar to *Shougangia* in the vegetative branching pattern; however, each fertile organ of *Polypetalophyton* is simpler and bears fewer sporangia (approx. 32). *Shougangia* and Late Devonian (Frasnian) *Denglongia* (Xue and Hao, 2008) share complex fertile organs which are pendulous and dichotomize into two major axes followed by many divisions. However, the vegetative branches of *Denglongia* occur in whorls; two major axes of fertile organs bear pinnate segments with each dichotomizing several times.

Rhacophyton and possibly related plants

Rhacophytales (*sensu* Taylor *et al*., 2009) consists of *Chlidanophyton* (Gensel, 1973), *Ellesmeris* (Hill *et al*., 1997), *Eocladoxylon* (Berry and Wang, 2006), *Protocephalopteris* (Schweitzer, 1968), *Protopteridophyton* (Li and Hsü, 1987) and *Rhacophyton* (Andrews and Phillips, 1968). *Chlidanophyton*, *Eocladoxylon* and *Protopteridophyton* are of unknown affinity at the ordinal level because they combine the morphological and/or anatomical features of multiple plant groups (Gensel, 1973; Li and Hsü, 1987; Berry and Wang, 2006). Here we consider these three genera as fern-like plants with terminal sporangia on branches. Based on branching pattern and stelar structure, *Ellesmeris* is regarded either as the earliest zygopterid fern (Hill *et al*., 1997) or as a fern-like taxon included within Rhacophytales (Phillips and Galtier, 2005; Taylor *et al*., 2009; Galtier, 2010). Where known, the fertile organs of the above plants, excluding *Rhacophyton*, possess elongate and sometimes paired sporangia terminating three-dimensionally dichotomous axes. However, fertile organs of *Shougangia* terminate tertiary branches with pinnules. Furthermore, *Rhacophyton* and related plants have a distinctive quadriseriate branching pattern (alternate pairs of branches) and/or bear dichotomous aphlebiae at the base of branches, and, except for *Ellesmeris*, they lack laminate pinnules.

The Late Devonian (Famennian) *Rhacophyton ceratangium* (Andrews and Phillips, 1968; Cornet *et al*., 1976) has paired fertile organs located at the base of quadriseriate secondary

TABLE 1. *Measurements of morphology of* Shougangia bella *gen. et sp. nov.*

Plant organ/tissue	Length (mm)	Width (mm)
Stems and roots		
Stems	up to 152	4·5–7·8
Root mats	up to 60	13·2–33
Individual root		0·4–1·0
Vascular bundle in root		approx. 0·1
Vegetative branches, laminate pinnules on vegetative tertiary branches		
Primary branches	up to 83	3·2–4·8
Secondary branches	up to 65	1·0–2·5
Tertiary branches	13·2–65	0·4–1·0
Basal pinnules	2·6–4·8	2·8–4·8
Lateral pinnules	2·8–14	2·3–9·2
Terminal pinnules	1·5–2·6	2·8–3·8
Pinnule veins		approx. 0·04
Glands terminating pinnule veins	0·2–0·3	0·1–0·2
Fertile branches and organs, laminate pinnules on fertile tertiary branches		
Primary branches	up to 68	2·6–3·8
Secondary branches	up to 50	1·5–4·0
Tertiary branches	8·8–18·8	0·8–1·6
Basal pinnules	approx. 3·0	approx. 4·7
Lateral pinnules	5·3–7·0	4·2–5·0
Fertile organs	7·5–16	12–22·8
Axes within fertile organs		0·1–0·5
Sporangia	2·7–3.8	0·4–0.7

branches. Each fertile organ dichotomizes several times to form many short and lateral segments terminated by dense masses of sporangia. Nevertheless, fertile organs of *Shougangia* are neither paired nor basal, but rather are terminal on tertiary branches. *Sphenopteris*-like laminate pinnules of Late Devonian (Frasnian) *Ellesmeris* (Hill *et al*., 1997) resemble those of *Shougangia*, but have fewer lobes and are arranged on secondary branches, as opposed to tertiary branches in *Shougangia*.

Stauropteridales

Stauropteridales (*sensu* Taylor *et al*., 2009) is represented by the Late Devonian *Gillespiea* (Erwin and Rothwell, 1989) as well as Carboniferous *Multifurcatus* (Wang, 2003), *Rowleya* (Long, 1976) and *Stauropteris* (Eggert, 1964). These differ from *Shougangia* in branching pattern, aphlebiae at the branch base, lack of laminate pinnules and simple fertile organs.

Zygopterid ferns

Shougangia and Carboniferous–Permian Zygopteridales [e.g. some species of *Zygopteris* (Phillips and Galtier, 2005)] share horizontal stems, upright primary branches (fronds or phyllophores or petioles in Zygopteridales) borne helically and laminate vegetative pinnules. However, fronds of many zygopterids possess quadriseriate and/or biseriate pinnae, sporangia are foliar-borne, and aphlebiae occur on stems or fronds or primary pinnae (Phillips and Galtier, 2005).

Triphyllopteris *and early seed plants*

Shougangia resembles Early Carboniferous *Triphyllopteris uberis* of uncertain affinity, in having fertile branches with laminate and lobed vegetative pinnules borne suboppositely, and a recurved and complex terminal fertile organ with sporangia of similar shape and size. Leaf veins of both plants are dichotomous and end near pinnule margins. Nevertheless, the branches of *T. uberis* are up to 130 mm long and 3·0–4·5 mm wide, pinnules are 10–40 mm long, and fertile organs are larger (approx. 80 mm long and 40 mm wide) and more closely resemble synangiate pollen organs (Skog and Gensel, 1980). This plant has been renamed as *Genselia uberis*, and the fertile organs interpreted as pollen organs of seed plants or sporangial masses of progymnosperms (Knaus, 1995). Notably, the Carboniferous spermatophyte (seed fern) *Polycalyx laterale* has *Triphyllopteris*-type foliage terminated by cupulate ovules (Vega and Archangelsky, 2001).

Early spermatophytes (e.g. Late Devonian *Elkinsia*) often have their fronds borne helically on the stem (Stewart and Rothwell, 1993), which conforms to the arrangement of primary branches in *Shougangia*. However, early seed plants are characterized by bipartite fronds with a proximally bifurcate rachis (Galtier, 1988). In contrast, the primary branches of *Shougangia* do not bifurcate proximally. As summarized by Wang *et al.* (2014), the spermatophyte pollen organs known from the Late Devonian are simple synangia often found in association with ovules. Furthermore, the microsporangia of early spermatophyte pollen organs are not borne in pairs. An individual fertile organ of *Shougangia* may have hundreds or even thousands of sporangia that are not basally fused, but are paired. Ovules have not been found in our large collection of over 380 specimens recovered over many years of meticulous fieldwork.

DISCUSSION

Affinity

Shougangia possesses fertile organs with three-dimensionally dichotomous axes bearing terminal elongate and paired sporangia, a feature also found in fern-like plants including iridopteridaleans, most pseudosporochnaleans, non-pseudosporochnaleans and possibly *Rhacophyton*-like taxa (*Chlidanophyton*, *Eocladoxylon* and *Protopteridophyton*). However, this newly described plant cannot be assigned to Iridopteridales with whorled organography, or to Pseudosporochnales with digitate branching. It differs from *Ellesmeris*, *Protocephalopteris*, *Protopteridophyton*, *Rhacophyton* and Stauropteridales, which typically have a quadriseriate branching pattern, and it differs significantly from zygopterid ferns characterized by foliar-borne sporangia and quadriseriate pinnae. *Shougangia* is then tentatively left as a fern-like genus of uncertain affinity at the order level, and is considered a derived taxon because of laminate pinnules and complex fertile organs. Amongst fern-like plants, *Shougangia* is more similar in branching pattern to *Polypetalophyton*, which has been described from the Late Devonian of China and allied with non-pseudosporochnaleans within Cladoxylopsida.

Growth habit

The stem of *Shougangia* may be prostrate where adventitious roots occur only on one side and at a wide angle (Figs 3, 7A, B).

Table 2. *Comparisons of* **Shougangia** ***gen. et sp. nov.*** *with related plants*

Taxon (reference*)	Vegetative branch			Laminate vegetative leaf	Planate ultimate appendage	Basal aphlebia	Fertile organ	
	Primary	Secondary	Tertiary				Arrangement; branching pattern	Sporangia
Shougangia	Helical	Irregularly helical	Alternate; (sub)-opposite	Present	Absent	Absent	Terminal on tertiary branch with pinnules; three-dimensionally dichotomous up to 10 times	Terminal, paired, elongate
Iridopteridales[1,2]	Whorled			Absent	Absent	Absent	Whorled; three-dimensionally dichotomous	Terminal, paired, elongate
Pseudosporochnales[1–3]	Digitate			Absent	Sometimes present	Absent	Usually irregular; mostly three-dimensionally dichotomous	Terminal, paired, elongate
Polypetalophyton[4]	Irregularly helical	Irregularly helical	Alternate; (sub)-opposite	Absent	Present	Absent	Alternate; three-dimensionally dichotomous about 6 times	Terminal, single, elongate
Denglongia[5]	Whorled			Absent	Present	Absent	Subopposite; three-dimensionally dichotomous many times	Along inner side of alternate segments, elongate
Rhacophyton[6–8]	Quadriseriate; helical	Quadriseriate; alternate	Alternate	Absent	Present	Present	Paired at secondary branch base; three-dimensionally dichotomous many times	Terminal on pinnate segments, elongate
Ellesmeris[9]	Quadriseriate; alternate	Alternate; subopposite	Absent	Present	Absent	Present	Unknown	
Chlidanophyton[10, 11]	Helical	Alternate	Alternate	Absent	Absent	Present	Paired at base of or alternate on secondary branch; three-dimensionally dichotomous 2–4 times	Terminal, elongate
Eocladoxylon[12]	Alternate			Absent	Present	Present	Paired at branch base or alternate on branch; three-dimensionally dichotomous 2–3 times	Terminal, paired, elongate
Protopteridophyton[13]	Helical; in two ranks	Quadriseriate	Quadriseriate	Absent	Absent	Absent	Quadriseriate; three-dimensionally dichotomous about 6 times	Terminal, paired, elongate
Stauropteridales[14,15]	Quadriseriate, trichotomous			Absent	Absent	Present	Few (single or paired) sporangia terminal on aphlebia-like branch or on branch node	
Zygopteridales[14,16]	Helical	Quadriseriate	Biseriate	Present	Absent	Present	Clusters of elongate sporangia on abaxial surface of laminate pinnule	
Triphyllopteris uberis (*Genselia uberis*)[17, 18]	Unknown			Present	Absent	Absent	Terminal on branch with pinnules; much divided with one-sided, unequal and pinnate dichotomies	Elongate
Early seed plants[19–22]	Helical; proximally bifurcate	Biseriate		Present	Present	Absent	Synangiate pollen organ with up to 8 elongate microsporangia fused at base	

*References: 1, Berry and Stein (2000); 2, Meyer-Berthaud *et al.* (2007); 3, Leclercq and Banks (1962); 4, Hilton *et al.* (2003); 5, Xue and Hao (2008); 6, Leclercq (1951); 7, Andrews and Phillips (1968); 8, Cornet *et al.* (1976); 9, Hill *et al.* (1997); 10, Gensel (1973); 11, Hilton (1999); 12, Berry and Wang (2006); 13, Li and Hsü (1987); 14, Taylor *et al.* (2009); 15, Wang (2003); 16, Phillips and Galtier (2005); 17, Skog and Gensel (1980); 18, Knaus (1995); 19, Galtier (1988); 20, Stewart and Rothwell (1993); 21, Wang *et al.* (2014); 22, Wang and Liu (2015).

Other portions of the same stem lacking roots imply an upturned and erect part (Fig. 7A, B). Long stems without any roots indicate an upright habit (Fig. 4A, B). The branching angles of primary branches also provide some evidence of habit, as they depart at about 90° from horizontal portions of stem (Figs 3D, 7A, B), but at 30–90° from upright portions (Figs 4A, B, 7A, B). The primary branch (Figs 3D, 7A, B), probably originally perpendicular or attached at a wide angle to the stem, may have been compressed so that the branch and roots seem to occur from the stem in the same direction. Because of its narrow stem and multiple orders of upright branches, the roots of *Shougangia* may function to anchor and support the plant body. Primary and secondary branches borne helically perhaps reduce self-shading of tertiary branches with pinnules and enhance the mechanical stability of the whole shoot system.

Evolution of laminate leaves and fertile organs

The emergence of laminate leaves, with an enhanced photosynthetic capability, is an evolutionary innovation in land plants and may represent a response to a major decline of atmospheric CO_2 levels during the Late Devonian (Beerling *et al*., 2001; Osborne *et al*., 2004). Early-diverging euphyllophytes usually have three-dimensionally dichotomous ultimate appendages rather than laminate leaves. Nevertheless, three lineages of euphyllophytes appear to have undergone convergent evolution, resulting in laminate leaves by the Late Devonian (Boyce and Knoll, 2002; Galtier, 2010): progymnosperms such as *Archaeopteris* (Taylor *et al*., 2009); spermatophytes such as *Elkinsia* and *Kongshania* (Serbet and Rothwell, 1992; Wang, 2000); and sphenopsids such as *Xihuphyllum* and *Sphenophyllum* (Chen, 1988; Wang *et al*., 2008). *Shougangia* clearly demonstrates both laminate pinnules and fertile organs characterizing fern-like plants. Another Late Devonian plant, *Ellesmeris*, also bears laminate pinnules, but unfortunately to the best of our knowledge there are no reports of fertile organs. *Shougangia* thus exhibits unequivocal evidence of laminate leaves for fern-like plants. This taxon and *Ellesmeris* indicate that the fourth lineage (fern-like plants largely representing early-diverging ferns) evolved laminate leaves similar to other early-diverging euphyllophytes. Therefore, laminate leaves appear to have independently evolved at least four times in euphyllophytes prior to the end of the Devonian.

The telome theory (Zimmermann, 1952) has long been accepted as orthodoxy for explaining megaphyllous leaf evolution. This theory holds that leaf evolution depends on essential processes of overtopping (anisotomous branching leading to determinate and three-dimensional ultimate appendages), subsequent planation, and final lamination. Molecular and cellular data recognize plausible mechanisms for overtopping and planation, but limited evidence for lamination (Beerling and Fleming, 2007). New data on fern-like plants are emerging to provide substantial support for the transformation of planation toward lamination. From the Middle (Givetian) to Late Devonian (Famennian), the planation of vegetative ultimate appendages (sometimes coupled with three-dimensional appendages) occurred to different degrees and repeatedly in fern-like plants (*Pseudosporochnus nodosus*, *Denglongia*, *Polypetalophyton*, *Eocladoxylon* and *Rhacophyton*), finally giving rise to fully laminate leaves (*Shougangia*, *Ellesmeris*). Additionally, during the evolutionary development of laminate leaves from homologous planate appendages, fertile organs of these plants trend toward increasing complexity. Each fertile ultimate appendage of Givetian *Eocladoxylon* and *Pseudosporochnus nodosus* divides only twice or three times (Leclercq and Banks, 1962; Berry and Wang, 2006). That of Frasnian *Polypetalophyton* and *Denglongia* divides five or six times (Hilton *et al*., 2003; Xue and Hao, 2008). Each fertile organ of Famennian *Rhacophyton* (Andrews and Phillips, 1968) and *Shougangia* has numerous divisions and hundreds or thousands of sporangia. The fertile organ of *Shougangia* terminates a branch that also bears pinnules, a highly derived character among early-diverging ferns. In light of geological age, branching pattern, planate ultimate appendages (resembling *Sphenopteridium*-type pinnules) and less complex fertile organs, the Frasnian *Polypetalophyton* may be the best candidate for the ancestor of *Shougangia*. These Devonian taxa suggest that early-diverging ferns present co-evolution of vegetative and fertile organs.

CONCLUSIONS

Shougangia is known from stems that are either prostrate with adventitious roots or upright and bear primary to tertiary branches, pinnules and fertile organs, and represents a derived taxon of fern-like plants. *Shougangia* reveals that fern-like plants, representing a major part of early-diverging ferns, had evolved laminate leaves during the Late Devonian, possibly coincident with rapidly declining levels of atmospheric CO_2. In this evolutionary scenario, their laminate pinnules are homologous with planate ultimate appendages, and fertile organs show an evolutionary increase in complexity and in the number of internal divisions and terminal sporangia.

ACKNOWLEDGEMANETS

We thank Professor James Basinger and Dr Yi Zhang for important discussions, and Dun-Lun Qi, Yi Wang, Pu Huang, Li Cui and Zhen-Zhu Wan for help with fieldwork. This study was supported by the National Basic Research Program of China (grant number 2012CB821900) of the Ministry of Science and Technology of China, and the National Natural Science Foundation of China (grant numbers 41172007 and 41272001).

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