JOURNAL OF
PALEONTOLOGY
A PUBLICATION OF THE
Paleontological
SOCIETY

New material of the zosterophyllopsid *Gosslingia* from the Lower Devonian of Guizhou, southwestern China

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Non-technical Summary.—Zosterophyllopsids have a rich fossil record and represent one of the dominant components in Early Devonian plant assemblages around the world. However, knowledge about the paleogeographic distribution of different groups of zosterophyllopsids remains incomplete. In this article, we describe new plant macrofossils assignable to the genus *Gosslingia*, which was previously only known from the Lower Devonian of Europe. Our fossils show considerable similarities with the type species of *Gosslingia*, *Gosslingia breconensis*, and thus represent the first report of *Gosslingia* in the South China Block and the most convincing occurrence of this genus outside of Europe. The discovery of *Gosslingia* and other cosmopolitan genera in South China indicates that the dispersal of early vascular plants across different paleocontinents was more common than previously appreciated.

Abstract.—The zosterophyllopsids had a widespread distribution and constituted a dominant component in many plant assemblages during the Early Devonian. Although a large number of zosterophyllopsids have been documented, knowledge about the paleogeographic distribution of different genera/species remains to be expanded by further fossil evidence. In this article, new material assigned to the genus *Gosslingia* Heard, 1927 and designated as *Gosslingia* cf. *G. breconensis* Heard, 1927 is described from a new locality of the Lower Devonian of Guizhou Province, China. The Guizhou material shows main axes that are pseudomonopodially branched, pseudomonopodial lateral branching systems, subaxillary tubercle branches, circinate apices, elliptical xylem strand, exarch maturation of xylem, and G-type tracheids, and exhibits considerable similarities with the type and only species of *Gosslingia*, *Gosslingia breconensis*. Our finding represents the first report of *Gosslingia* in the South China Block and the most convincing occurrence of this genus outside of Wales, UK. *Gosslingia* adds to the diversity of genera shared among the Early Devonian floras of South China, western Europe, and North America, along with *Distichophytum* Mägdefrau, *Estinnophyton* Fairon-Demaret, *Zosterophyllum* Penhallow, and others, and indicates that the dispersal of early vascular plants among different paleocontinents was more common than previously appreciated.

Introduction

Early vascular plants diversified rapidly and evolved significantly in terms of morphological complexity during the Early Devonian, as evidenced by numerous macrofossil plants from the Lower Old Red Sandstone, the Rhynie Chert, the Lower Devonian siliciclastic sequence of North America (e.g., Gaspé), the Posongchong Formation of South China, and many others (Gensel and Andrews, 1984; Knoll et al., 1984; Kenrick and Crane, 1997; Hao and Xue, 2013; Edwards et al., 2014; Gensel and Berry, 2016; Xue et al., 2018; Niklas and Crepet, 2020; Toledo et al., 2021; Capel et al., 2022). The zosterophyllopsids had a widespread distribution around the world and constituted a dominant component in many Early Devonian assemblages, in particular in the South Chinese floras (Hao and Xue, 2013). Although a large number of species of zosterophyllopsids have been documented, the phylogenetic relationships among the known species remain to be resolved (Gensel, 1992; Kenrick and Crane, 1997; Hao and Xue, 2013; Gensel and Berry, 2016; Nibbelink and Tomescu, 2022) and knowledge about the paleogeographic distribution of different genera/species, to be documented by further fossil evidence (Cascales-Miñana and Meyer-Berthaud, 2015; Capel et al., 2023).

In this paper, we describe new material of a zosterophyllopsid plant from the Lower Devonian of Guizhou Province, China. The fossils show morphology and well-preserved anatomical structures, justifying their assignment to the genus *Gosslingia* Heard, 1927, which was previously known only from the Lower Devonian of the Laurussian paleocontinent (Heard, 1927; Croft and Lang, 1942; Edwards, 1970; Kenrick and Edwards, 1988; Kenrick and Crane, 1997). Our discovery expands the diversity of the Early Devonian floras of South China and presents an opportunity to consider the floristic exchanges between South China and Laurussia.

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Geological setting and stratigraphy

The fossils were collected from a bed of gray muddy siltstone of the Mangshan Group at a locality near Dahe Village, Duyun City, Guizhou Province, China (Fig. 1, Dahe section). Recently, abundant plant fossils were obtained from the lower part of this group at the nearby Baoyang section (Fig. 1), including *Adoketophyton subverticillatum* (Li and Cai) Li and Edwards, *Hedeia* sp. (or *Yarravia* sp. based on the recent systematic treatment sensu McSweeney et al., 2021), *Teyoua antrorsa* Huang, Liu and Xue, and *Zosterophyllum australianum* Lang and Cookson (Huang et al., 2022; Zhou et al., 2022).

The lithology and age of the Mangshan Group at the Baoyang section was recently reviewed by Huang et al. (2022). Based on our observations, the lithology of this group is consistent at the Dahe and Baoyang sections. The lower part of this group consists mainly of gray massive quartz sandstone, with a small amount of gray siltstone and mudstone, and the upper part consists of gray fine sandstone and muddy siltstone, with oolitic hematite beds (Dai et al., 2017). A Pragian age has been suggested for the lower part of the Manshan Group, based on fossil plants including *Adoketophyton subverticillatum* and *Zosterophyllum australianum* (see Huang et al., 2022), two species also occurring in the Pragian-aged Posongchong Formation (Hao and Xue, 2013).

Material and methods

The specimens are preserved as impressions and compressions, as well as pyrite permineralizations. Morphologically preserved specimens were prepared with fine needles and photographed with a digital camera. Permineralized axes with internal cellular structures were prepared by the standard procedure of embedding, section, and polishing for examination by reflected light. Several pyritized axes without any acid treatment were observed with scanning electron microscopy (SEM) at the Key Laboratory of Orogenic Belts and Crustal Evolution, Peking University.

Repository and institutional abbreviation.—All specimens and slides in this study were deposited at the Geological Museum, School of Earth and Space Sciences, Peking University (specimens PKUB18001 through PKUB18054; and slides 18001-24 through 18001-53).

Systematic paleobotany

Class Zosterophyllopsida Bierhorst, 1971
Order Gosslingiales sensu Hao and Xue, 2013
Family Gosslingiaceae Banks, 1968
Genus *Gosslingia* Heard, 1927

Type species.—*Gosslingia breconensis* Heard, 1927, by original designation, from the Senni Formation at Brecon Beacons Quarry, South Wales, UK.

Diagnosis.—See Edwards (1970, p. 237).

Gosslingia cf. *G. breconensis* Heard, 1927
Figures 2–7

Occurrence.—Lower Devonian Mangshan Group, Dahe section, near Dahe Village, Duyun City, Guizhou Province, China (GPS data: 26°9′44″N, 107°28′15″E).

Description.—

Morphology.—The largest specimen shows a main axis that is ~3.5 mm wide at the basal position and up to 19.8 cm long (Fig. 2.1, 2.2). This main axis is pseudomonopodially branched to produce at least two lateral branching systems (Fig. 2.1, arrows lbs), within which first-order branches further divide pseudomonopodially and bear second-order branches. A third lateral branching system is probably present at a lower position (extending into the rock matrix), indicated by the twist of the main axis (Fig. 2.1, lower arrow). First-order branches, ~1.8 mm wide at the proximal position, depart from the main axis at angles of ~35°, with an interval of ~50 mm. Other specimens are preserved as small fragments. The specimen in Figure 2.3, interpreted as a lateral branching system, shows a first-order branch that appears to pseudomonopodially branch to produce a second-order branch (Fig. 2.3, arrow), which further divides twice and terminates in circinate apices. All axes are naked, with no spines or appendages on the surface. Unfortunately, no fertile axes with sporangia attached were found.

More than 23 circinate apices were found (Fig. 2.3–2.7), but only a few are attached to larger axes (Fig. 2.3). Some apices are oppositely recurved and paired, indicating that they resulted from the dichotomy of a parent axis (Fig. 2.5); many others are singly preserved and it is deduced that the other apex of each pair has been broken during preservation. From the branching point to the tapering tip, these apices are ~5–8 mm in length. Two apices are unique in showing two or more loops, reaching > 15 mm length and ~2.9 mm width in loop diameter (Fig. 2.6, 2.7), i.e., these looped apices are approximately twice as long as the above paired, recurved apices. Similar looped apices were also found occurring on fertile axes of *Gosslingia* (Edwards, 1970). Nevertheless, it is difficult to determine the distribution of these different types of circinate apices on the plant body, due to their fragmentary preservation.

Subaxillary tubercle branches can be seen through careful dégagement in some specimens (Fig. 3, arrows), although their complete morphology is difficult to determine. In our examples, such branches are located below or quite close to branching points of the main axes, extending into the rock matrix, and thus are oriented at right angles to the plane of the main branching system. The orientation of such subaxillary tubercles makes them difficult to observe in many compression specimens.

Anatomy.—The xylem strand is elliptical in transverse sections of pyritized axes and shows a consistent shape at different levels of the main axes (Fig. 4.1–4.9) and lateral branches (Fig. 4.10–4.12). Xylem strands of the main axes are ~1.6 mm wide along the long axis, 0.5 mm wide along the short axis, with a mean area of 0.6 mm^2 (n = 9); those of the lateral branches are 0.9 mm by 0.3 mm wide with a mean area of 0.2 mm^2 (n = 3). It should be noted that these axes are apparently compressed, so that the ratio between the measured long axis and short axis is larger than its actual value, whereas the area of xylem strand can little change.
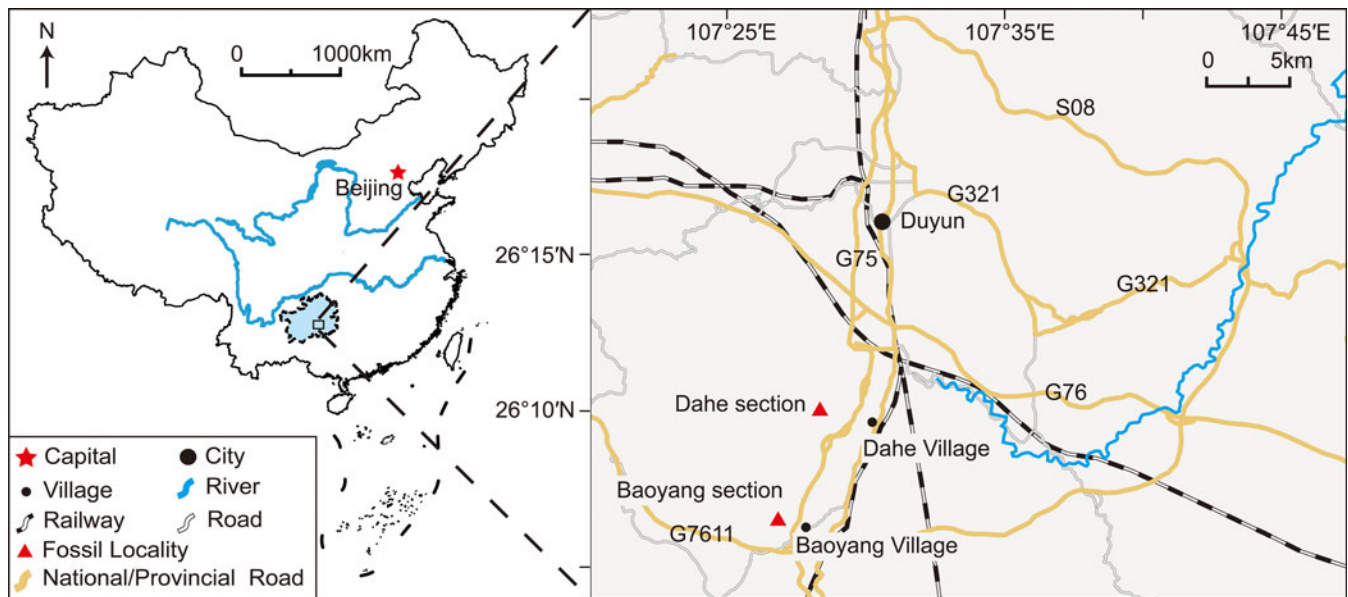
Figure 1. Maps showing the fossil locality (Dahe section) near Dahe Village, south of Duyun City, Guizhou Province, southwestern China. The location of the Baoyang section is also shown, where *Adoketophyton subverticillatum* (Li and Cai) Li and Edwards, *Hedeia* sp., *Teyoua antrorsa* Huang, Liu and Xue, and *Zosterophyllum australianum* Lang and Cookson were reported from the lower part of the Mangshan Group (Huang et al., 2022).

Tracheids show an obvious decrease in size toward the periphery (Figs. 4, 5), and thus maturation of the xylem is exarch. Tracheids at the periphery, interpreted as protoxylem, range from 9–13 μm wide (n = 13); and the other tracheids, interpreted as metaxylem, range from 34–65 μm wide (n = 123) in transverse sections. It appears that protoxylem is more prominent at the two ends of the elliptical strand (Fig. 4).

The cortex can be divided into two zones. Where preserved, the outer cortex is composed of two to four layers of thick-walled cells (Fig. 6.5). In transverse sections, the outer cortical cells are polygonal and measure 19–38 μm in width (n = 23; Fig. 6.5). Cells are rarely preserved in the region of the inner cortex. There are some poorly preserved cells surrounding the xylem strands (Fig. 5.2, 5.4, 5.6), probably representing the vestige of inner cortex tissues; these cells measure ∼14–28 μm wide (n = 36), and their cell walls appear thinner than those of the outer cortical cells.

In transverse sections, tracheids show a pyrite lumen cast and coalified remains of cell walls (Fig. 6.6, lc, wc; Fig. 6.7). Outside the coalified cell wall, the layer that corresponds in position to the middle lamella is heavily permineralized, showing as irregular crystals (Fig. 6.6, arrow ml). In transverse sections, coalified remains of cell walls are shown as thick, dark bands, often C-shaped and protruding into the lumen (Fig. 6.6, arrow wc), and these remains represent annular or helical thickenings of the cell walls (compare Kenrick and Edwards, 1988, fig. 5).

Lumen casts of tracheids are commonly seen in longitudinal sections, and protoxylem tracheids are located at the periphery of the xylem strand, confirming the exarch maturation pattern observed in transverse sections (Fig. 7.1). These lumen casts show grooves that are separated by a regular distance, indicating the position of annular and helical thickenings of cell walls. Coalified walls are also visible in longitudinal sections and show annular and helical thickenings (Fig. 7.2–7.8), corresponding well to the grooves in lumen casts (e.g., Fig. 7.7). In some longitudinal sections, coalified wall thickenings can be

seen forming fold-like structures, protruding into the grooves of lumen cast (i.e., protruding into the cell lumen; Fig. 7.7, arrows); the bar thickenings are uniform in thickness and there is a break inside of such fold-like structures. The mean height of the thickening bars is ∼3.7 μm and the mean distance between two annular bars is ∼6.6 μm.

The coalified walls between annular and helical thickenings are perforated. The perforations are circular and range from 1.0–2.0 μm in diameter. On lumen casts, there are some projections on the surface that might be formed during permineralization and cannot be considered to directly correspond to the perforations on coalified walls. Except for the perforated secondary walls, some coalified remains of cell walls show smooth surfaces in longitudinal section, and these remains are interpreted as possibly representing a part of the middle lamella without perforations (Fig. 7.4, 7.8).

The features of tracheids in our plant are consistent with the G-type tracheids, defined as having annular and helical thickenings, fine perforations between thickening bars, and two-layered cell walls comprised of a coalified inner layer and an outer layer that is usually heavily permineralized in fossils (Kenrick and Edwards, 1988; Kenrick et al., 1991; Kenrick and Crane, 1997; Wang et al., 2003).

Materials.—Fifty-four specimens with main axes and lateral branches, some of which are preserved by pyrite permineralization, and 30 slides produced from them.

Remarks.—Compared to other known early vascular plants, our plant is more similar to the genus *Gosslingia* (Edwards, 1970; Kenrick and Edwards, 1988; Kenrick and Crane, 1991), with the shared characters including pseudomonopodial branching of main axes, pseudomonopodial lateral branching systems, branches developed from subaxillary tubercles, circinate apices, elliptical xylem strand, exarch maturation of xylem, and G-type tracheids (Table 1). *Deheubarthia* Edwards,
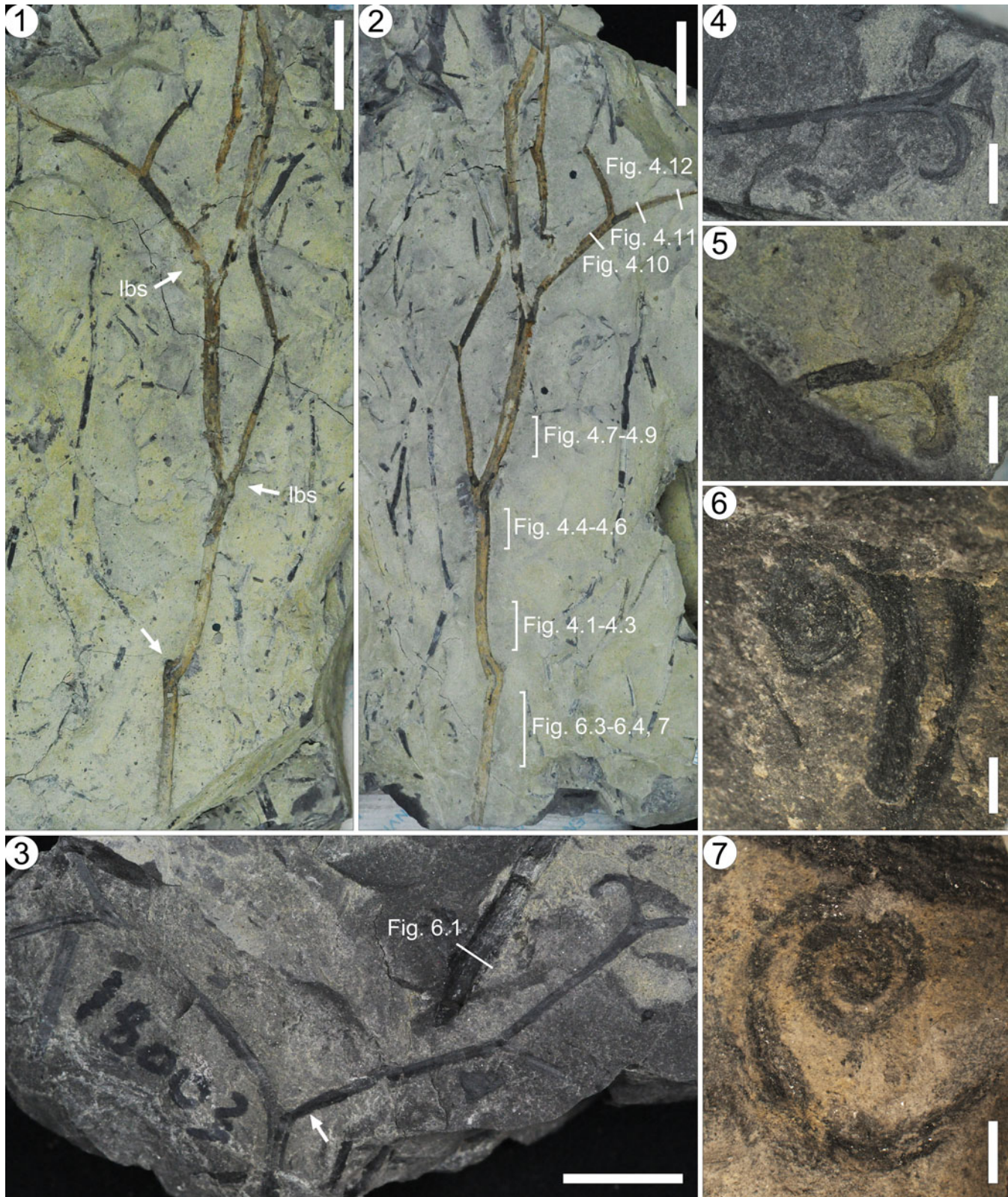
Figure 2. *Gosslingia* cf. *G. breconensis* Heard, 1927: (**1, 2**) part and counterpart, main axis pseudomonopodially branched, producing two lateral branching systems (arrow lbs) and a possible third lateral branch (lowermost arrow); the positions of anatomy illustrated in later figures are indicated; PKUB18001a, b; (**3**) a first-order branch, producing a second-order branch to the right (arrow), which is dichotomously divided twice and terminates in circination; the anatomy of the other first-order branch is shown in Fig. 6.1; PKUB18003; (**4–7**) circinate apices of different development degrees: (**4**) PKUB18028; (**5**) PKUB18018; (**6**) PKUB18010; (**7**) PKUB18002. Scale bars = 20 mm (**1, 2**); 10 mm (**3**); 3 mm (**4, 5**); 1 mm (**6, 7**).
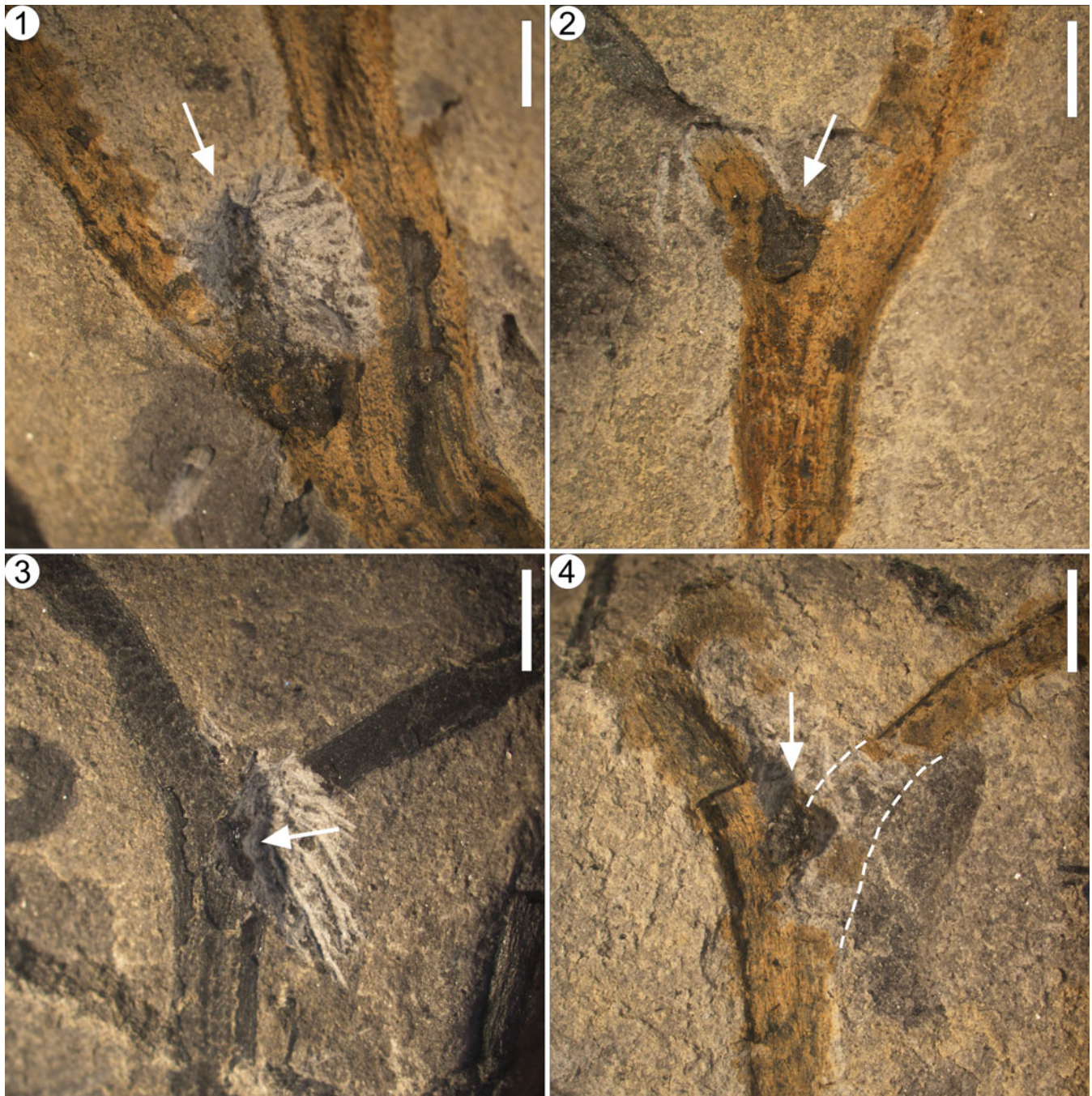
Figure 3. *Gosslingia* cf. *G. breconensis* Heard, 1927: (**1–4**) subaxillary tubercle branches (arrows) below or close to branching points of main axes: (**1, 3**) subaxillary branch extending into rock matrix; (**2**) subaxillary branch with only its base visible (as coalified compressions); (**4**) subaxillary branch with its base visible; dotted line indicates the base of a lateral branch, which has been partially removed through dégagement. (**1, 2**) PKUB18001; (**3**) PKUB18003; (**4**) PKUB18030. Scale bars = 2 mm.

Kenrick, and Carluccio also exhibits the above characters, but its axes are spiny (Edwards et al., 1989). In the type and only species of *Gosslingia*, *Gosslingia breconensis*, there are protuberances on the surface of axes (Edwards, 1970), whereas such structures are not present in our plant. The lack of fertile specimens in our material hinders further comparisons with *Gosslingia*, but the similarities demonstrated in both branching pattern and anatomical details of sterile axes strongly support the assignment of our plant to *Gosslingia*.

We further compare our plant with *Gosslingia breconensis* in terms of tracheid dimensions (Table 2; see Fig. 8 for compared parameters). Four parameters of tracheids are quite comparable between our plant and *Gosslingia breconensis*, including the maximum tracheid lumen diameter (W), thickening aperture diameter (D), thickness of annular bars (δ), and diameter of perforations (Dp). However, both the distance between annular bars (ε) and the distance of annular bars protruding into cell lumen (t) in our plant are significantly greater than in *Gosslingia breconensis*. Nevertheless, such differences
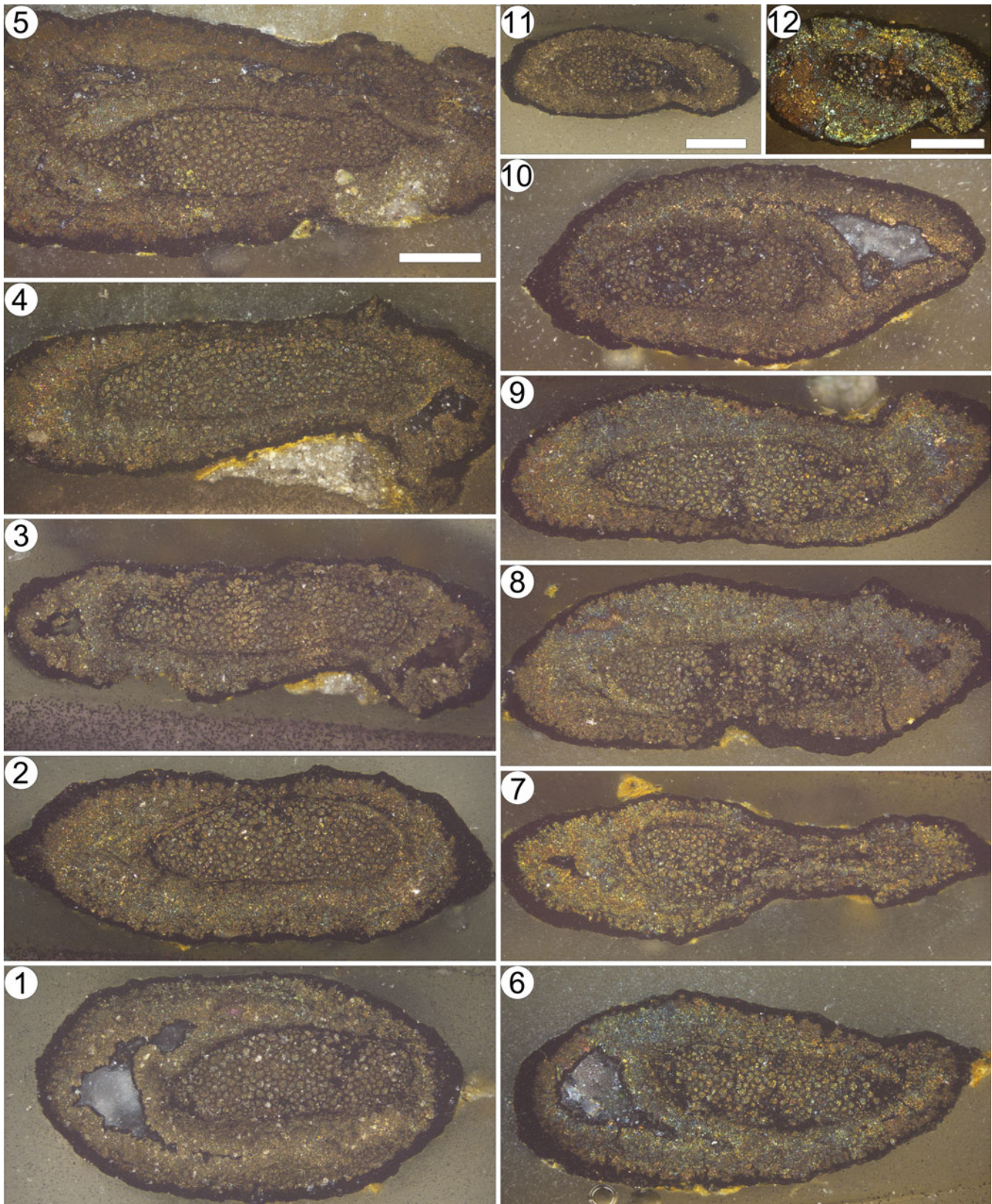
Figure 4. *Gosslingia* cf. *G. breconensis* Heard, 1927, successive transverse sections of the main axis and its branch shown in Figure 2.1 and 2.2, examined by light microscope with reflected light, showing variations in size and shape of xylem strand. Slides (**1**) 18001-24a; (**2**) 18001-26b; (**3**) 18001-28b; (**4**) 18001-30a; (**5**) 18001-31a; (**6**) 18001-36a; (**7**) 18001-40b; (**8**) 18001-44a; (**9**) 18001-44b; (**10**) 18001-46a; (**11**) 18001-51a; (**12**) 18001-48a. Scale bars = 500 μm; that in Figure 4.5 is for **1–10**.
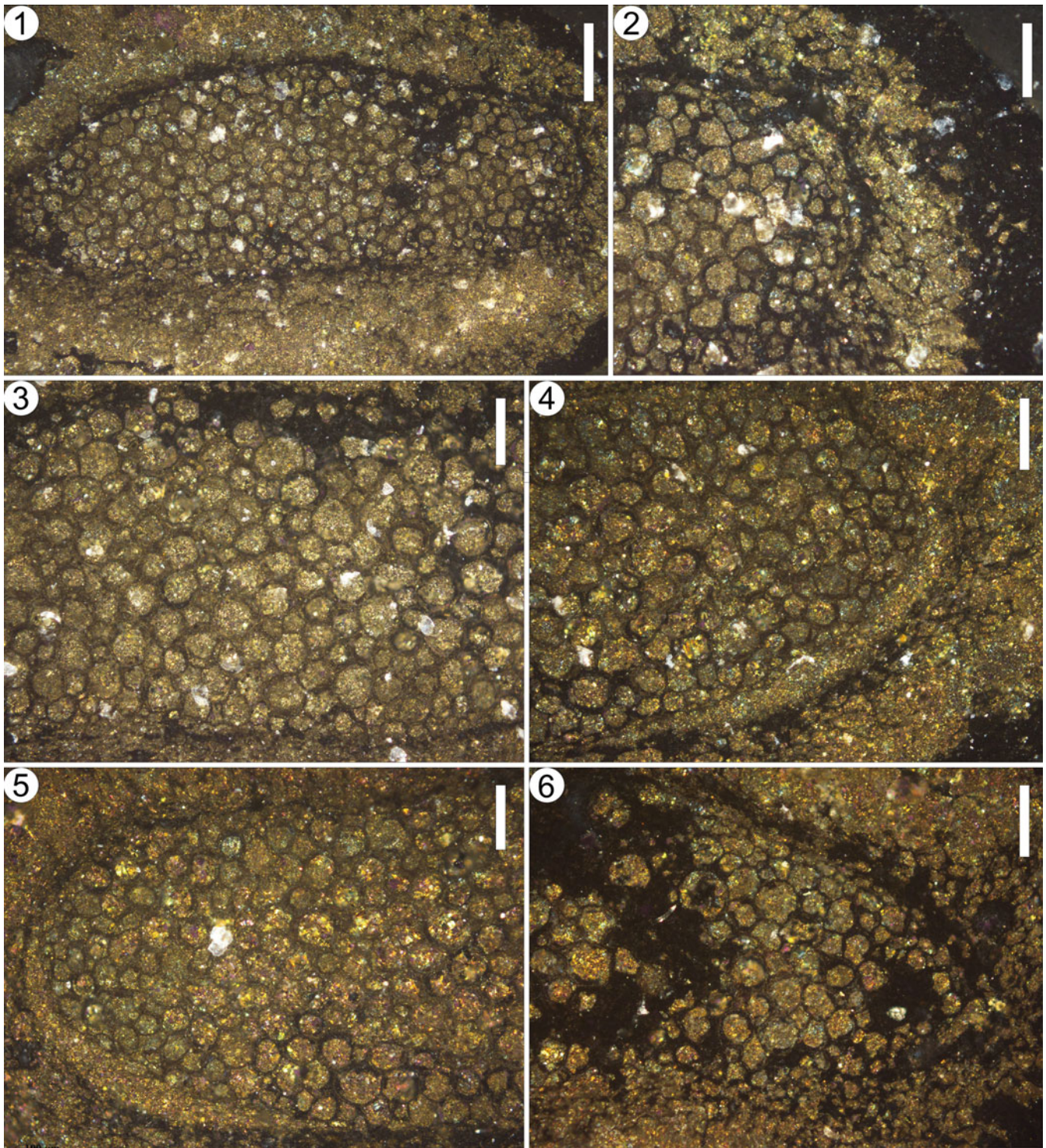
Figure 5. *Gosslingia* cf. *G. breconensis* Heard, 1927, enlarged views of transverse sections of main axis, examined by light microscope with reflected light: (**1**) elliptical xylem strand; slide 18001-24a; (**2**) enlarged view of xylem strand showing protoxylem tracheids; poorly preserved inner cortex cells are shown; slide 18001-24a; (**3–6**) enlarged views of protoxylem and metaxylem tracheids; slides (**3**) 18001-25a; (**4**) 18001-26b; (**5**) 18001-27a; (**6**) 18001-46b. Scale bars = 200 μm (**1**); 100 μm (**2–6**).

in tracheid features are to be expected as part of natural variability among plants of the same species, and at present it is appropriate to name our plant as *Gosslingia* cf. *G. breconensis.* An exact determination at the specific level needs further discovery of fertile specimens.

Discussion

Zosterophyllopsids were a prominent component of floras all around the world from the Silurian (Ludfordian) through the Devonian (Frasnian), including > 37 genera (Hueber and
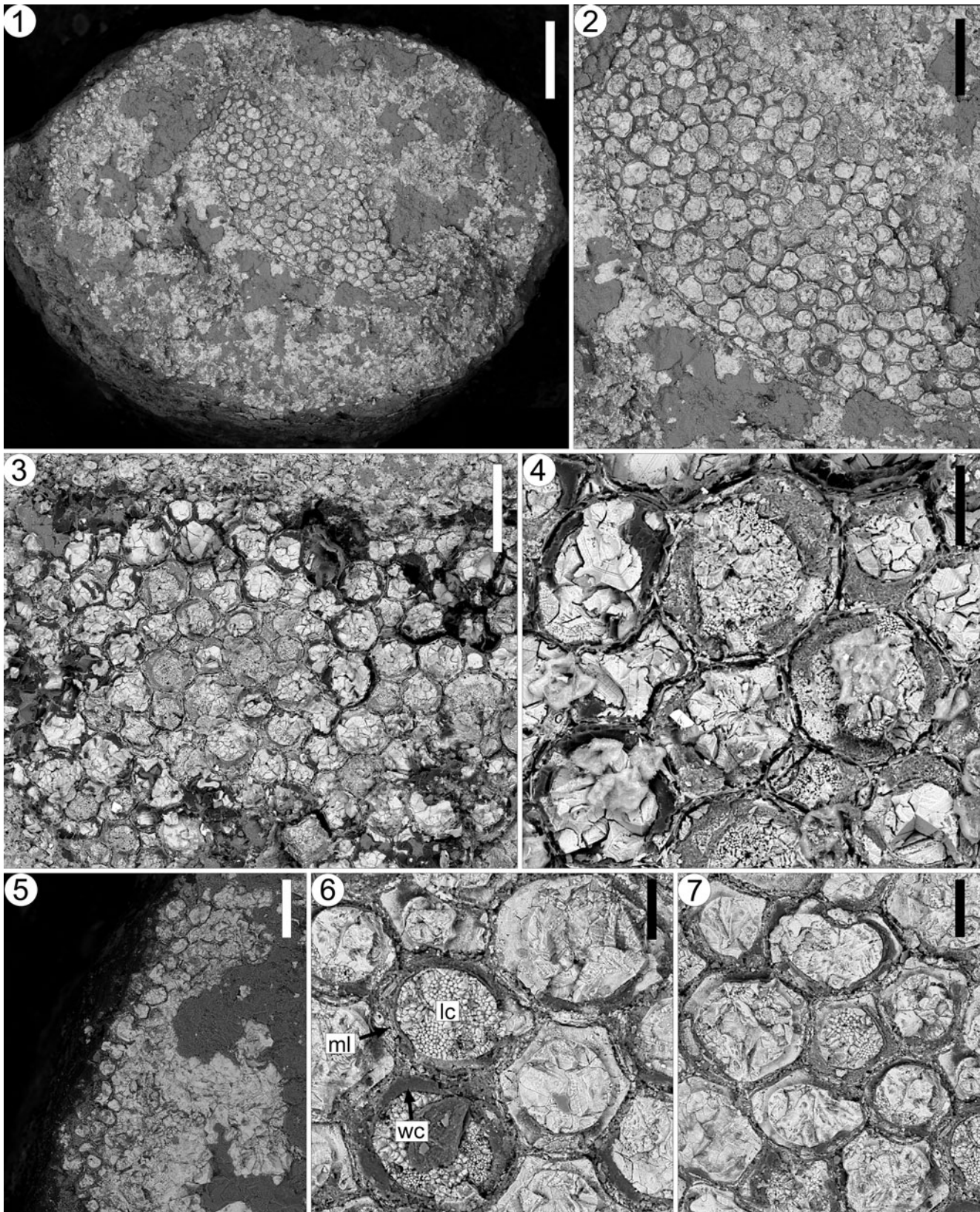
Figure 6. *Gosslingia* cf. *G. breconensis* Heard, 1927, transverse sections of main axes and lateral branches (SEM): (**1, 2, 5–7**) permineralized fragments from the upper first-order branch shown in Figure 2.3; PKUB18003-02: (**1**) first-order branch and its elliptical xylem strand; (**2**) enlarged view of xylem tracheids in (**1**); (**5**) epidermis and outer cortex tissue; (**6, 7**) detail of metaxylem tracheids, showing C-shaped coalified cell wall (arrow wc), middle lamella (arrow ml), and lumen cast (lc); (**3, 4**) permineralized fragments from the main axis shown in Figure 2.1; PKUB18001-23: (**3**) marginal region of xylem, showing pyritized tracheids; (**4**) detail of metaxylem tracheids. Scale bars = 200 μm (**1**); 150 μm (**2**); 100 μm (**3, 5**); 25 μm (**4, 6**); 30 μm (**7**).
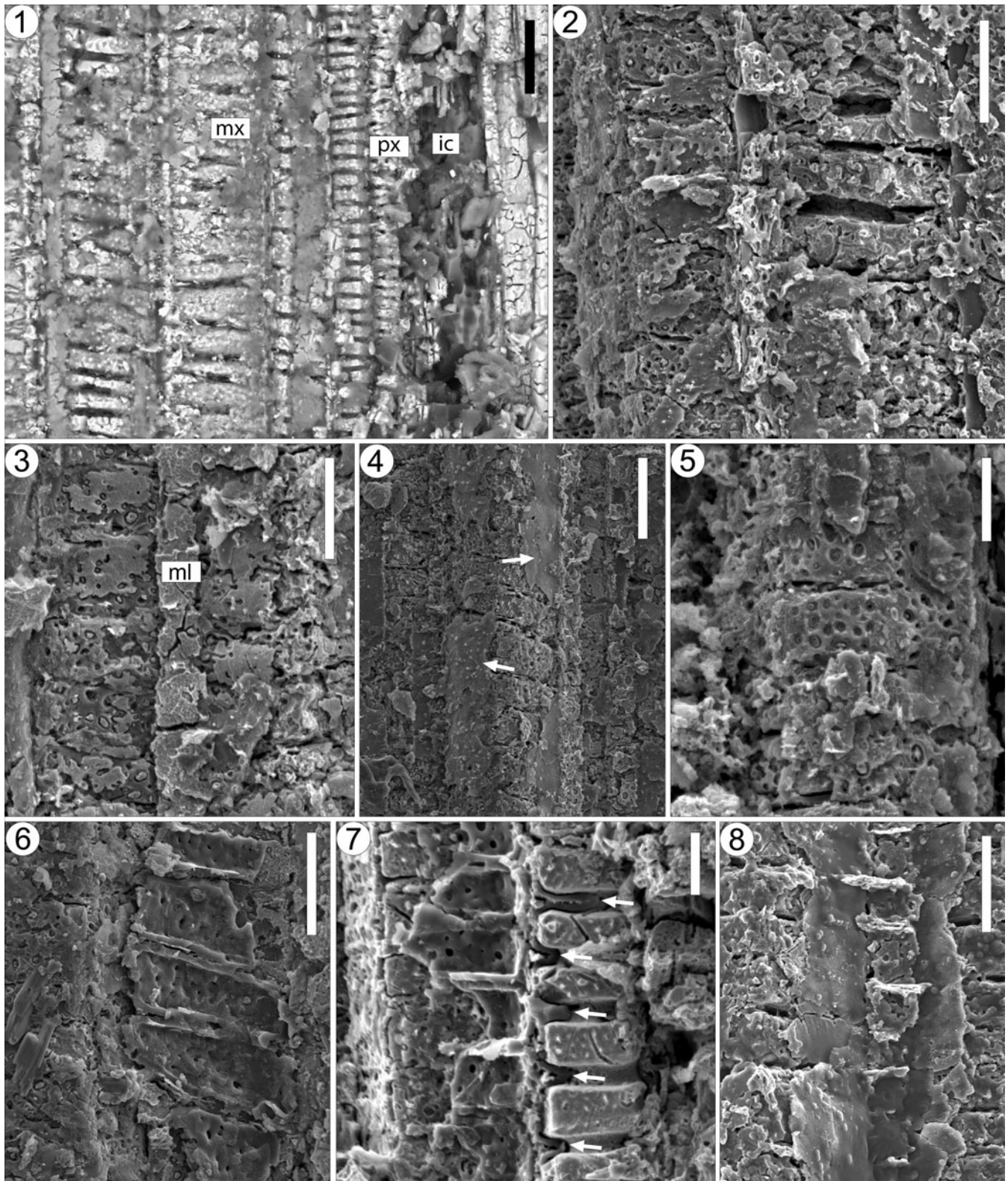
Figure 7. *Gosslingia* cf. *G. breconensis* Heard, 1927, longitudinal sections of tracheids of the main axis shown in Figure 2.1 (SEM): (**1**) lumen cast, showing interpreted protoxylem (px) and metaxylem (mx) tracheids, with annular thickenings (represented by grooves); note the changes in tracheid diameter; outside of the xylem strand is area of inner contex (ic); PKUB18001-22; (**2**) two trachieds of different preservation status; right tracheid shown as lumen cast, preserved by pyrite permineralization; left tracheid showing coalified cell walls with perforations; PKUB18001-02; (**3, 5, 7, 8**) PKUB18001-05: (**3**) coalified cell walls with perforations; middle lamella (ml) poorly preserved and featureless; (**5**) perforations on cell walls between thickening bars; (**7**) tracheids of different preservation status; left tracheid shows coalified cell walls with thickening bars and perforations; right tracheid shows both coalified cell walls and pyrite lumen cast; arrows indicate fold-like structures of coalified cell walls, which protrude into grooves of lumen cast; (**8**) smooth surfaces, probably of middle lamella remains; (**4**) smooth surfaces, probably of middle lamella remains; PKUB18001-02; (**6**) coalified cell walls with thickening bars (broken) and perforations; PKUB18001. Scale bars = 40 μm (**1**); 20 μm (**2, 3, 6, 8**); 30 μm (**4**); 10 μm (**5, 7**).

Table 1. Comparisons of our plant (*Gosslingia* cf. *G. breconensis* Heard, 1927) and the type species of *Gosslingia* (*Gosslingia breconensis*). Data for *Gosslingia breconensis* based on Edwards (1970) and Kenrick and Edwards (1988).

Characters	G. cf. G. breconensis	G. breconensis
Morphology		
Branching of main axes	pseudomonopodial	pseudomonopodial
Branching of first-order branches	pseudomonopodial	pseudomonopodial
Circinate vernation	present	present
Subaxillary tubercle	present	present
Width of axes	0.7–3.5 mm	0.5–4.0 mm
Protuberance	absent	present
Fertile region	unknown	lateral stalked sporangia
Anatomy		
Xylem strand shape	elliptical	elliptical
Protoxylem	exarch	exarch
Tracheid thickenings	annular and helical thickenings	annular and helical thickenings
Perforations between thickening bars	present	present
Density of perforations	11 per 100 square micrometers	9 per 100 square micrometers

Banks, 1979; Gensel and Andrews, 1984; Gensel, 1992; Kenrick and Crane, 1997; Kotyk et al., 2002; Hao and Xue, 2013; Gensel and Berry, 2016; Nibbelink and Tomescu, 2022). However, the phylogenetic relationships among these genera are controversial, and thus a consensus on the taxonomic treatment at the ordinal and family levels has not been reached. Niklas and Banks (1990) divided zosterophyllopsids into one group with 'terminate' (i.e., determinate) fertile axes (e.g., *Zosterophyllum* Penhallow and *Gumuia* Hao) and the other group with 'nonterminated' (i.e., indeterminate) fertile axes (e.g., *Gosslingia* and *Sawdonia* Hueber). In addition, sporangium orientation, sporangial arrangement, circinate apices, etc., have also been used for classification and phylogenetic inference (Gensel, 1992). The phylogenetic schemes of Kenrick and Crane (1997) and Nibbelink and Tomescu (2022) similarly recognized a 'large zosterophyll clade' (designated as the Sawdoniales by the former authors), which includes *Deheubarthia*, *Thrinkophyton* Kenrick and Edwards, *Gosslingia, Serrulacaulis* Hueber and Banks, *Sawdonia*, and *Crenaticaulis* Banks and Davis, among others. Hao and Xue (2013) divided the Zosterophyllopsida into two orders, the Zosterophyllales and the Gosslingiales. The latter order includes the Gosslingiaceae that is represented by *Gosslingia* and *Oricilla* Gensel (Hao and Xue, 2013).

The genus *Gosslingia* is monotypic and the type species, *Gosslingia breconensis*, has been extensively studied based on materials from the Lower Old Red Sandstone of Wales, UK (Heard, 1927; Croft and Lang, 1942; Edwards, 1970; Kenrick and Edwards, 1988; Kenrick and Crane, 1991). Thus *Gosslingia*

breconensis represents one of the best-characterized plants among zosterophyllopsids. However, the geographic distribution of this genus outside of Wales has been questionable until now. There have been some other records of *Gosslingia*, e.g., from Germany (Schweitzer, 1979, 1983, 1987), Belgium (Gerrienne, 1983, 1993), and the United States (Tanner, 1982), but these occurrences have been questioned due to the lack of clear diagnostic characters (e.g., Kenrick and Crane, 1997). Our material shows convincing evidence for the occurrence of *Gosslingia* in South China, although further efforts are still needed for collecting fertile specimens.

Capel et al. (2023) recognized two phytochoria units during the Pragian–Emsian periods based on paleogeographical distribution of plant genera, i.e., Equatorial to mid-latitudes and Northeast Gondwana. The Early Devonian floras of the South China Block, as a part of the Northeast Gondwana unit, show

Table 2. Comparisons of tracheid dimensions of our plant (*Gosslingia* cf. *G. breconensis* Heard, 1927) and the type species of *Gosslingia* (*Gosslingia breconensis*). See Figure 8 for the definition of compared parameters. All measurements in μm and shown as minimum value—mean—maximum value (n = number of measurements). Data for *Gosslingia breconensis* based on Kenrick and Edwards (1988, table 1), except for its Dp, which was obtained by measuring the illustrations of Kenrick and Edwards (1988, figs. 15, 16). - = unknown.

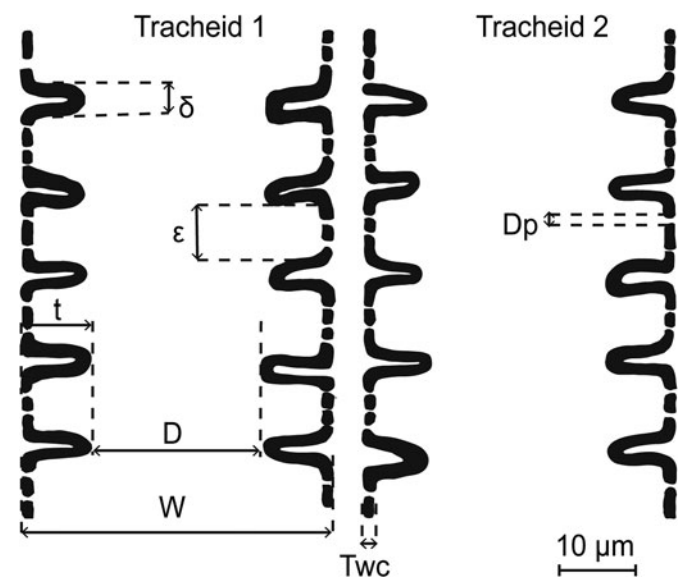| Parameters	G. cf. G. breconensis	G. breconensis
δ	2.3—3.7—5 (n = 23)	1.5—3.3—4.5 (n = 36)
ε	3.8—6.6—9.7 (n = 20)	1.0—2.8—5.3 (n = 33)
t	6.0—7.4—10.3 (n = 21)	1.5—3.6—6.1 (n = 16)
W	35.2—40.1—55 (n = 21)	? —29.6—50.0 (n = 23)
D	17.3—29.6—39.9 (n = 21)	? —22.4—37.8
Twc	0.6—1.1—1.5 (n = 36)	-
Dp	0.2—0.7—1.6 (n = 50)	0.6—0.9—1.2 (n = 12)

Figure 8. Diagrammatic longitudinal sections of two adjacent tracheids of *Gosslingia* cf. *G. breconensis* Heard, 1927, showing parameters for comparison of tracheid features in Table 2. Annular thickening bars protrude into the cell lumen. Black region = secondary cell walls. Diagram and parameter definition based on Kenrick and Edwards (1988, fig. 26). Measured parameters include: δ = thickness of annular bars; ε = distance between annular bars; t = distance of annular bars protruding into cell lumen; D = thickening aperture diameter; Dp = diameter of perforation; Twc = thickness of coalified wall; W = maximum tracheid lumen diameter.

high endemism at the generic level, and contain only a limited number of cosmopolitan genera. The latter belong to distinct lineages, including zosterophyllopsids (*Distichophytum* Mägdefrau, *Oricilla*, and *Zosterophyllum*), lycopsids (*Baragwanathia* Lang and Cookson and *Drepanophycus* Göppert) and euphyllophytes (*Estinnophyton* Fairon-Demaret, *Hedeia* Cookson, and *Psilophyton* Dawson) (Hao and Xue, 2013; Xue et al., 2018, and references therein). *Gosslingia* is a new addition to the list of cosmopolitan zosterophyllopsids. *Distichophytum* and *Oricilla* show rowed sporangia, like *Gosslingia*, indicating that zosterophyllopsids with rowed sporangia are not uncommon in South China. *Zosterophyllum* was widespread in western Europe, North America, and South China during the Early Devonian (Kenrick and Crane, 1997; Capel et al., 2022; Nibbelink and Tomescu, 2022), and the South Chinese species within this genus are predominantly those with helically arranged sporangia (Hao and Xue, 2013; Xue et al., 2018). The distribution of these cosmopolitan genera indicates that the dispersal of early vascular plants, which were relatively small and morphologically simple, among different paleocontinents was more common than previously appreciated.

It remains an open question about how early vascular plants migrated across areas that were separated by long distances and, usually, by geographic barriers, e.g., oceans. They might rely on spread by means of wind, ocean currents, or storms. Capel et al. (2023) proposed that spatial differentiation of early vegetation was controlled by both climatic conditions and geographical barriers. During the Pragian, the Equatorial to mid-latitudes phytochoria unit and the Northeast Gondwana unit were separated by apparently wide oceans in low to middle latitudes, but were probably connected in high latitudes, e.g., from west to middle Gondwana (Boucot et al., 2013; Huang et al., 2018). Thus, dispersal routes that connected the Equatorial to mid-latitudes and Northeast Gondwana might have been possible in high latitudes under warmer climatic conditions, but the paucity of paleobotanic data from west-middle Gondwana hinders a better understanding.

Acknowledgments

Declaration of competing interests

The authors declare none.

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