

Earliest rooting system and root : shoot ratio from a new *Zosterophyllum* plant

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Summary

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- The enhanced chemical weathering by rooted vascular plants during the Silurian–Devonian period played a crucial role in altering global biogeochemical cycles and atmospheric environments; however, the documentation of early root morphology and physiology is scarce because the existing fossils are mostly incomplete.
- Here, we report an entire, uprooted specimen of a new *Zosterophyllum* Penhallow, named as *Z. shengfengense*, from the Early Devonian Xitun Formation (Lochkovian, c. 413 Myr old) of Yunnan, south China. This plant has the most ancient known record of a rooting system.
- The plant consists of aerial axes of 98 mm in height, showing a tufted habit, and a rhizome bearing a fibrous-like rooting system, c. 20 mm in length. The rhizome shows masses of branchings, which produce upwardly directed aerial axes and downwardly directed root-like axes.
- The completeness of *Z. shengfengense* made it possible to estimate the biomass allocation and root : shoot ratio. The root : shoot ratio of this early plant is estimated at a mean value of 0.028, and the root-like axes constitute only c. 3% of the total biomass. *Zosterophyllum shengfengense* was probably a semi-aquatic plant with efficient water use or a strong uptake capacity of the root-like axes.

Introduction

The origin and evolution of vascular plants were important evolutionary events affecting terrestrial ecosystems and all life on Earth. Current data indicate that the Late Silurian and Early Devonian periods were a critical interval during which the initial diversification of vascular plants began (Gensel & Andrews, 1984; Edwards, 1990; Kenrick & Crane, 1997). Although several important groups have been identified, we lack fundamental morphological data to achieve a better understanding of the physiology and ecology of early plants. In particular, the record of roots or rooting systems from Devonian deposits is unsatisfactory because of the scarcity and incompleteness of the fossils (Elick *et al.*, 1998; Gensel *et al.*, 2001; Raven & Edwards, 2001), hindering a better understanding of the crucial role played by the rooted vascular plants of the Devonian period in altering global biogeochemical cycles and atmospheric environments (Retallack, 1997; Algeo *et al.*, 2001).

Largely as a result of a lack of complete root fossils, the relationship between above-ground and below-ground

structures remains an enigma. The root : shoot ratio (R : S ratio) of extant plants has received much attention as a critical ecological parameter. Researchers have used this ratio to indicate the allocation of below-ground vs above-ground biomass, so that the functional balance between roots and shoots can be better understood in models of carbon and nutrient cycling (McConnaughay & Coleman, 1999; Mokany *et al.*, 2006). However, we know little about the R : S ratio in fossil plants; one exception is the shoot : root ratio of the debris of cordaitalean gymnosperms estimated by Raymond (1988) within Carboniferous coal-ball peats from Urbandale, Iowa, USA. In Devonian fossils, only a few root-like structures have been reported (Walton, 1964; Gensel *et al.*, 2001; Raven & Edwards, 2001; Kenrick, 2002), but they are fragmentary or strongly weathered, making detailed descriptions and further ecological interpretations difficult. Root traces found in Palaeozoic palaeosols gave only speculative information about the root morphology and taxonomic assignment of their parent plants (Retallack, 1992, 1997; Driese *et al.*, 1997; Elick *et al.*, 1998). Therefore, additional data on root structure in

Devonian fossils are necessary to understand the earliest root morphology and diversification, and to elucidate the change in the functional balance between above- and below-ground structures during the evolution of terrestrial ecosystems.

Here, we report a new *Zosterophyllum* plant showing a relatively complete rooting system from the Lower Devonian Xitun Formation (middle–upper Lochkovian) of Qujing City, Yunnan Province, south China. This find not only adds to our understanding of the morphology of early rooting systems, but also provides an opportunity to estimate the R : S ratio for an ecological interpretation in a fossil plant that lived during the Early Devonian period.

Materials and Methods

Material and stratigraphy

The plant fossils were collected from the middle–upper part of the Xitun Formation, at a building site excavated in Huguo Hill, Shengfeng District, c. 6 km west of the centre of Qujing City, Yunnan Province, China. The specimens are preserved as impressions and compressions of three dimensions in a c. 30-mm-thick horizon of grey to buff-coloured calciferous, sandy mudstone. The Xitun Formation consists mainly of continental deposits characterized by yellow sandstone and green calciferous mudstone and shale, with abundant bivalves and some plant fossils. The age of the strata is considered to correspond to middle–late Lochkovian of the Early Devonian (c. 413 Myr old), based on the correlation of spores with the upper part of the *Streelispora newportensis*–*Emphanisporites micromatus* (NM) and *Breconisporites breconensis*–*Emphanisporites zavallatus* (BZ) spore zones of the Lower Old Red Sandstone (Cai *et al.*, 1994) and macrovertebrate assemblage II, *Diabolepis*–*Nanpanaspis* (Zhu *et al.*, 2000).

R : S ratio estimation and measurements

The fossil material is an individual plant, which appears to be in its peak above-ground biomass, judging from the numerous mature and dehiscent, and immature sporangia borne along the axes. Assuming a constant tissue density, the R : S volume ratio can be considered to be equal to the R : S mass ratio. By making several assumptions, the R : S mass ratio can be calculated. Our assumptions were as follows. Firstly, because the fossil is preserved in three dimensions, in outline, the above-ground and below-ground parts of this plant, i.e. all erect and parallel shoot and root-like axes and their ‘airspaces’ (areas between two adjacent axes) approximately constitute a cylinder (Fig. 1a). The height of this cylinder, here symbolized as *H*, is the length of the axes, and the radius of this cylinder, symbolized as *R*, can be

defined by measuring the occupied area of the axes in the specimen (Fig. 1d).

Secondly, the volume of an individual aerial or root-like axis was obtained by assuming that each individual axis constitutes a thin, long cylinder. The aerial axes have an average diameter of 0.82 mm and a length of 98 mm; the root-like axes have an average diameter of 0.44 mm and a length of 19.5 mm (Table 1).

Thirdly, the distribution of axes has a constant density, or nearly so, along the diameter, i.e. each axis has a surrounding airspace equal to those of other axes. Here, we assumed this airspace to be a circle; its diameter was symbolized as *d* (Fig. 1d), which in value equals the distance of two adjacent axes. The measurement of the distance between two adjacent axes proceeded along a horizontal plane of the rock surface, being careful to avoid the overlap of axes from different planes.

Fourthly, the flattening during the preservation of compression fossils did not change the density of the axes in the matrix along the horizontal bedding planes (Fig. 1a–c) (Rex & Chaloner, 1983; Thomas, 2006). In our specimen, the axes are confined to at least a 30-mm-thick rock matrix, rather than just along the bedding plane, and so the axes are considered to basically retain their *in situ* density.

Finally, the biomass of sporangia was not considered in the present estimation. It was expected that the estimated ratio would be lower if the biomass of sporangia was taken into account. In addition, we did not consider the presence of root hairs, which were unrecognizable in this compression fossil, but would have great surface area and volume if they were present.

The total number of axes was obtained by the formula:

$$N = \left[\frac{0.785\pi R^2}{\pi(d/2)^2} \right] \quad \text{Eqn 1}$$

The constant, 0.785, is the occupation rate of high packing circles in a unit square (Fig. 1d), which approximately equals the occupation rate of *N* small circles in a large circle.

For aerial axes, the distance between two axes is 3.2–(4.36)–5.12 mm [*d*: minimum–(average)–maximum; the same blow] by measuring the compression specimen, and the radius of the axes of the cylinder is 41 mm (*R* = 41 mm). The ‘root-like axes’ cylinder has a radius of 5.1 mm (*R*) and the distance between two axes is 0.5–(0.77)–1.03 mm (*d*).

Results

Systematic palaeobotany

Genus: *Zosterophyllum* Penhallow 1892.

Type species: *Z. myretonianum* Penhallow 1892.

Zosterophyllum shengfengense sp. nov. (Figs 2–5).

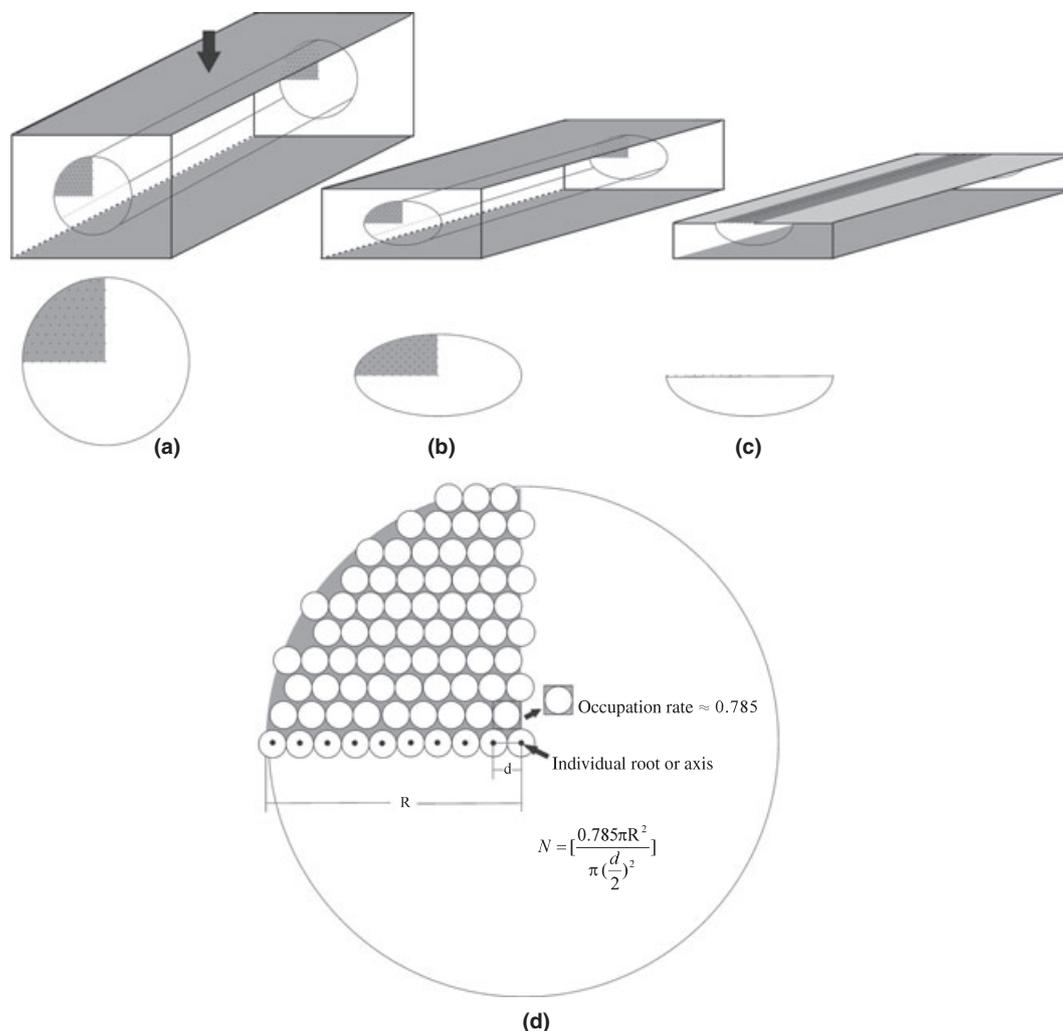


Fig. 1 Estimation of total numbers of axes. (a–c) Interpretative drawings of a cylinder (plant body) in a compression situation. Note that the fossil plant was preserved three-dimensionally in the rock matrix rather than in a bedding plane. Small points represent transverse sections of axes. Along a horizontal level, the number and density of axes or root-like axes will not change, accompanied by the compression and dehydration of sediments during the process of fossilization. (d) Maximum packing of cylinders with airspace surrounding each axis. Small circle, airspace of an individual axis; large circle, assumed cylinder composed of axes and their airspaces. For details, see Materials and Methods section.

Holotype PUH-QXI01-1, a nearly entire individual plant preserved as a compression, and its counterpart PUH-QXI01-1' (Fig. 2a,b).

Etymology The specific epithet is from the Shengfeng District of Qujing City, where the holotype was found.

Locality A building site at Huaguo Hill, Shengfeng District, Qujing City, Yunnan Province, China.

Horizon Middle–upper part of the Xitun Formation (middle–late Lochkovian age), Lower Devonian.

Specific diagnosis Plant small, with tufted habit. Compact rhizome area, at the centre of proximal part of the plant, *c.*

10.2 mm in diameter, formed by dense masses of branchings. Rhizome upwardly giving rise to naked aerial axes, and downwardly to a rooting system composed of numerous parallel axes. Each root-like axis, unbranched, sinuous, with smooth surface, and tapering to a distal apex, 0.29–0.66 mm wide and 17.0–22.0 mm long. Aerial axes extending upward, with horizontal or vertical 'K'- or 'H'-shaped branching at basal part and isotomous branching at middle–upper part. Axes widening upwardly, 0.48–1.45 mm in width, *c.* 98 mm high. Sporangia terminally borne on short stalks, departing from axis at an acute angle (*c.* 20–40°), scattered along the upper part of the axis. Sporangia, round to reniform in abaxial view, dorsiventrally flattened, 1.7–2.9 mm wide, 1.4–1.9 mm high and *c.* 0.6 mm thick. Sporangial stalk upright, 0.8–1.6 mm long and *c.* 0.6 mm

Table 1 Dimensions and volume estimation of root-like axes and shoots

	Numbers	Individual root/axis		Total volume (mm ³)	R : S ratio
		Width (mm)	Length (mm)		
Root-like axes	136 (76–326) ¹	0.44 (0.29–0.66)	19.5 (17.0–22.0)	403.25 (225.34–966.60)	0.028 (0.008–0.093)
Shoots	278 (201–515)	0.82 (0.48–1.45)	98 (82–106)	14387.64 (10402.57–26653.36)	

R : S ratio, root : shoot ratio.

¹Average (minimum–maximum estimation).

wide. Dehiscence, along a median line, dividing sporangium into two equal valves.

Morphology of *Zosterophyllum shengfengense*

The specimen of *Z. shengfengense* consists of below-ground and above-ground parts (Figs 2a,3,5). The below-ground part is a rhizome area bearing a downwardly directed rooting system. Arising from the rhizome area, the above-ground aerial parts show a tufted habit with a flat-bottomed

bowl shape (Fig. 5), *c.* 98 mm high and 100 mm wide. The flat-bottomed and convex lateral contour of the above-ground shoot system is outlined by horizontally, recumbently and upwardly extended axes and a nearly convex upper margin, with all erect axes terminating at slightly different levels. All erect axes (*c.* 278 axes) appear to be fertile and are densely aggregated parallel to the surface of the rock.

The rhizome area extends horizontally in a restricted region and consists of masses of branchings and intermingled

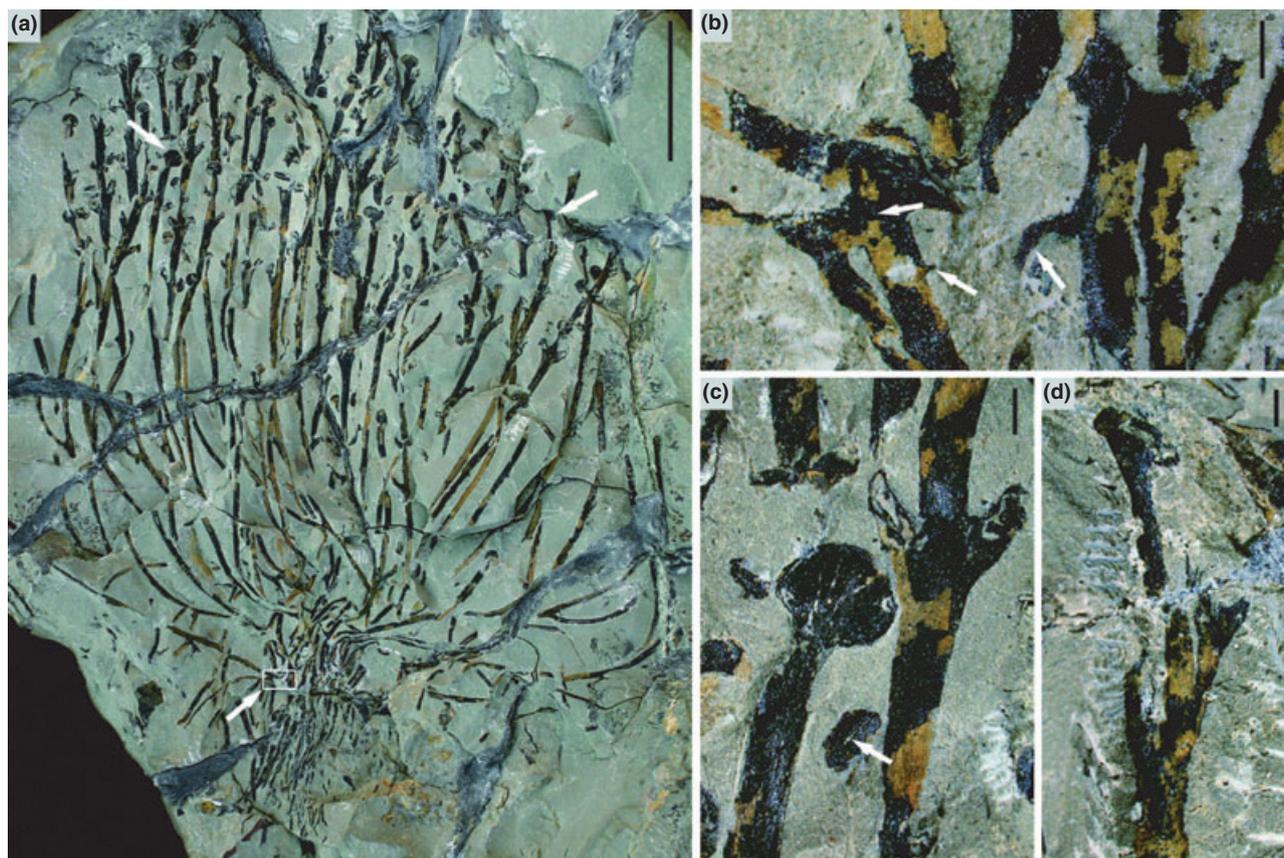


Fig. 2 *Zosterophyllum shengfengense*. (a) Holotype, PUH-QXI01-1. The plant shows a tufted habit of numerous aerial axes, which are supported by a rhizome area and shallow rooting system. The erect and basal horizontally extending axes exhibit 'K'- or 'H'-shaped branching. Top arrows point to the parts enlarged in (c) and (d). (b) Enlargement of the counterpart of the holotype, corresponding to the lower rectangle (bottom arrow) in (a). A small protuberance (see text, middle arrow) and a possible young root-like axis (right arrow) show lateral attachment and gravitropic growth. Left arrow indicates a part of the rhizome area with close branchings. (c) Lateral sporangia, showing sporangial shape and attachment. Arrow indicates dehiscence line. (d) An apparent terminal sporangium. Bars: (a), 20 mm; (b)–(d), 1 mm.



Fig. 3 Enlargement of the rhizome area in Fig. 2a, bearing a rooting system consisting of numerous downward-directed axes, after partial excavation. Note the rhizome area has many branchings and intermingled and intertwined axes (top arrow). Unfortunately, a crack just below the rhizome area has lost some material. The middle arrow points to sinuous and delicate root-like axes with longitudinal wrinkles, the bottom left arrow points to 'K'-shaped branching, and the bottom right arrow shows the delicate ends of the root-like axes. Bar, 4 mm.

and intertwined axes (Figs 2b,3,4). It is difficult to distinguish accurately the full extent of the axes and branching connections, because a further preparation by the micro-excavation of individual axes still hidden in the matrix would destroy the specimen. Only a few fragments of the apparent rhizome axes are found in the vertical plane at the margin of the region. They show a series of closely spaced and repetitive 'H-' or 'K'-shaped branchings, which differ from those more typical 'H'- or 'K'-shaped ones of the basal aerial axes by their repetitive close nature. They form creeping axes that produce upwardly directed shoot axes and downwardly directed root-like axes (Fig. 3). There are additional branches under the rhizome axis that extend into

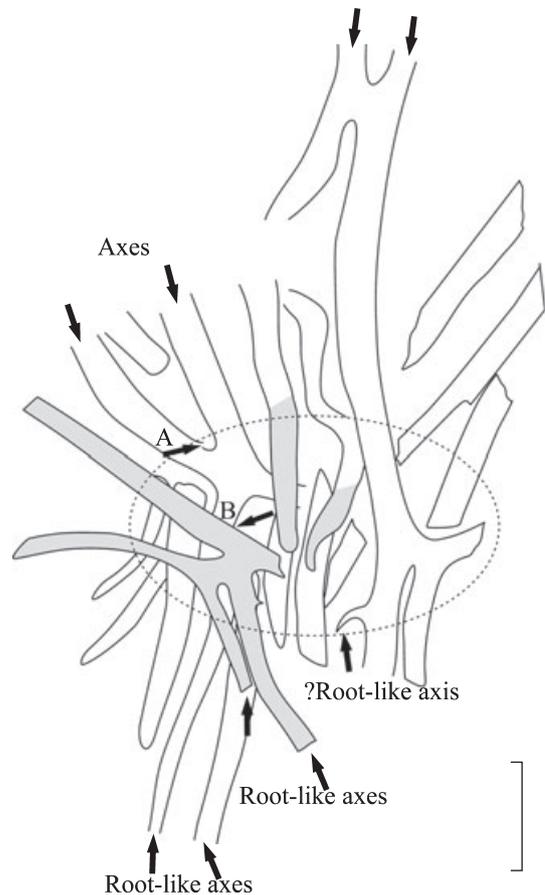


Fig. 4 Drawing of parts of the basal area of the plant, showing three-dimensional axes extending in different sedimentary planes. Parts within the dotted ellipse show the rhizome area from which upwardly and downwardly directed axes arise; parts in shadow, shown in Fig. 2b, were removed by *dégagement* (micro-excavation with needles). Arrow A indicates a branch extending into the matrix; arrow B shows a possible horizontal axis connecting to another part. Bar, 2 mm.

the matrix (Figs 2b,3). Although we have not followed these axes by micro-excavation, this suggests that rhizome axes branch in all directions. Thus, these creeping axes may overlap to form a dense mat. Root-like axes could be distinguished from shoot axes by their apparent gravitropic growth, sinuous course with smaller dimensions, less robust mummification with longitudinal wrinkles, distal taper to a pointed end, and restricted location in the lower part of the rhizome area at the centre of the basal part of the plant. The wrinkles may have resulted from compression and dehydration during death and burial, and may indicate a possibly parenchymatous cortex tissue. No evidence of mycorrhizal colonization was found as these axes have been largely compressed and carbonized. These root-like axes are similar in length, forming a fibrous-like type of rooting system, which consists of *c.* 136 individual root-like axes (Figs 2a,3; Table 1).



Fig. 5 Reconstruction of *Zosterophyllum shengfengense*. Bar, 20 mm.

A *c.* 0.1-mm-long protuberance with a tapering end (Fig. 2b, middle arrow) was seen in the rhizome axis, possibly representing an initial stage of the formation or abortion of a shoot branch (or root-like axis). A bud-like structure (Fig. 2b, right arrow) possibly represents a young shoot axis or 'root-like axis', and is only *c.* 0.3 mm (*c.* one-third of the attached axis diameter), which shows lateral attachment to the rhizome axis or to the base of an aerial axis. We speculate that it is a young root-like axis because of its tapering tip and apparent gravitropic growth that extends downwards and parallel to the mature root-like axes (Fig. 2b, right arrow). This type of protuberance has been observed in axes of the basal region of *Z. myretonianum* (Lele & Walton, 1961) and along the aerial axes of *Z. xishanense* (Hao *et al.*, 2007). The material of *Z. myretonianum* obtained by maceration revealed that there were lateral strands projecting into such protuberances, which were suggested to represent dormant lateral apices of branches (Lele & Walton, 1961, plate I, Figs. 4, 14). Bud-like structures occur at the bases of the aerial axes and rhizomes of other Early Devonian plants, such as *Aglaophyton major* and *Nothia aphylla* (Remy & Hass, 1996; Gensel *et al.*, 2001). These structures differ distinctly from an endogenous origin of roots of extant plants.

Typically, the roots of extant plants are characterized by a nonmedullated protostele, a root cap and root hairs (often supplemented by mycorrhizas), an endogenous origin of lateral roots, a gravitropic response and an absence of leaves (Gensel *et al.*, 2001; Raven & Edwards, 2001). We could

not determine the presence of a root cap and root hairs, which may not have evolved by that time or may be unrecognizable in compression fossils. We were also unable to determine the anatomy of the root-like axes. Although the rooting system shown here may lack the features of roots in extant plants, it seems to have been a below-ground structure that penetrated the substrate and performed the functions of roots, i.e. anchorage and the absorption of water and nutrients.

Discussion

Comparisons with related taxa

Zosterophyllum Penhallow and the type species *Z. myretonianum* are based on relatively well-preserved and rich compression fossils from the Early Devonian (Lochkovian) Dundee Formation, Lower Old Red Sandstone, UK (Lang, 1927; Edwards, 1975). This genus contains at least 18 species, which mainly occur in Late Silurian to Early Devonian strata (Hao *et al.*, 2007). In contrast with most species recorded (such as *Z. myretonianum*, *Z. rhenanum*, *Z. australianum*, *Z. yunnanicum*, *Z. qujingense*, etc.), which have radial spikes of laterally borne sporangia in a compact arrangement (Lang, 1927; Edwards, 1975; Hao, 1992), sporangia of *Z. shengfengense* are distributed loosely along the axis without forming a compact spike. The sporangia of *Z. myretonianum*, however, can be closely crowded in compact spikes or loosely arranged along the axis (Edwards, 1975).

Zosterophyllum deciduum from southern Belgium (Gerrienne, 1988) and *Wenshania zhichangensis* from the Early Devonian Pragian strata of south China (Zhu & Kenrick, 1999) have a more extended sporangial distribution, which resembles that of *Z. shengfengense*. However, their sporangia could be distributed over several orders of branching, which is distinctly different from that of *Z. shengfengense*. In addition, *W. zhichangensis* bears larger sporangia and long stalks, and the sporangia of *Z. deciduum* show developed basal lobes and wider angles (40–60°) of departure from the axis than do those of *Z. shengfengense* (20–40°).

Distichophytum (Rebuchia) ovatum (Schweitzer, 1979) from the Lower Devonian strata of Park County, Wyoming and *Hicklingia edwardii* (Kidston & Lang, 1923; Edwards, 1976) of the Middle Devonian in the UK show a similar tufted growth as well as lateral sporangia. Both show relatively complete aerial parts with a basal region, but the 'H'- or 'K'-shaped branching and descending rooting structures have not been distinguished from the close branching in the crowded basal region (Edwards, 1976). The sporangia of *Distichophytum* are arranged oppositely and/or suboppositely in two rows, and the sporangia of *Hicklingia* are large and oval in shape, whereas the sporangia of *Z. shengfengense* are loosely arranged and round to reniform in shape.

Rooting structures of early plants

The rooting structure of early vascular plants has been a topic of much ambiguity (Gensel *et al.*, 2001; Raven & Edwards, 2001; Kenrick, 2002). Here, we mainly discuss the difference in the basal parts and rooting structures of some related plants. *Zosterophyllum myretonianum* shows a basal dense branching region bearing downwardly directed and incomplete 'rooting' axes (Lang, 1927; Lele & Walton, 1961; Walton, 1964; Edwards, 1975). Recently, a few younger species of *Zosterophyllum* have been described from the Early Devonian Pragian strata of Bathurst Island, Arctic Canada (Gensel *et al.*, 2001). Gensel *et al.* indicated the downwardly directed, tufted axial structures as rooting structures, and illustrated that they arise in the same area as upwardly directed aerial axes. Here, *Z. shengfengense* demonstrates the more ancient and complete records of such structures in this genus. This suggests that the downwardly directed, fibrous-like rooting system is a potential synapomorphy of the genus *Zosterophyllum*, a group constituting the dominant vegetation of the Early Devonian. *Zosterophyllum myretonianum* and the Canadian *Zosterophyllum* specimens show fertile spikes, different from those of *Z. shengfengense*, where sporangia are in a loose arrangement, although this pattern could also be seen in *Z. myretonianum*. The Canadian specimens are incompletely preserved or were strongly weathered (i.e. *Zosterophyllum* sp. nov., fig. 5.11, 5.12a of Gensel *et al.*, 2001), making morphological, developmental and ecological interpretations difficult. A basal region of repetitive 'H'- or 'K'-shaped branching, as observed in *Z. shengfengense*, was not recognized in the Canadian specimens.

Generally, it has been suggested that many early vascular plants lack any kind of true rooting structure and that only the rhizome bears rhizoids, for which the rhyniophytes of the Rhynie Chert offer some evidence. The rhizomes of *Aglaophyton major* are more or less prostrate and contain localized clusters of nonseptate rhizoids (D. S. Edwards, 1986). *Rhynia gwynne-vaughanii* has clusters of rhizoids on the lower surface of a short presumed rhizome (D. S. Edwards, 1980). The rhizome of *Horneophyton lignieri* is a lobed parenchymatous structure and bears numerous nonseptate rhizoids (Eggert, 1974; El-Saadawy & Lacey, 1979). No rhizoids were found in the rhizome of the basal lycopsid *Asteroxylon mackiei*, which is also from the Rhynie Chert (Kidston & Lang, 1920). Of particular interest are two zosterophylls, *Trichopherophyton teuchansii* (Lyon & Edwards, 1991) and *Nothia aphylla* (Kerp *et al.*, 2001; Daviero-Gomez *et al.*, 2005), which were also reported to have rhizomes bearing rhizoids. The alternative suggestion is that such rhizomes may represent 'roots' and the rhizoids 'root hairs' (Lyon & Edwards, 1991; Edwards, 1994).

The measurements of the rooting structure of *Z. shengfengense* may provide some indications of the evolutionary

trajectory of the rooting depth. The fibrous-like rooting system of *Z. shengfengense* (Lochkovian, *c.* 413 Myr) appears to be only *c.* 2 cm in length, suggesting that it did not penetrate deeply into the soil. The zosterophyll species of Pragian age (410 Myr) also show a rooting depth of several centimetres (e.g. 3–5 cm) (Gensel *et al.*, 2001). However, within 3–6 Myr, the rooting structure of terrestrial plants had penetrated to 1 m in depth, as recorded by root traces from the Battery Point Formation (late Early Devonian, Emsian, 407 Myr) of Gaspé Bay, Québec, Canada (Elick *et al.*, 1998), suggesting a rapid development of both plant root systems and soil depth during this period.

R : S ratio of *Z. shengfengense*

The completeness of the *Z. shengfengense* specimen, although not fully micro-excavated, offers a unique opportunity to estimate the R : S volume ratio (Figs 1a–d, 2a; Table 1), which is equal to the R : S mass ratio, assuming constant tissue density between below- and above-ground parts. Although our calculation was based on volume, this ratio can still be compared with the R : S ratio of modern plants, which is based on dry weight, because the tissue density in modern plants is fairly constant among different plant organs (West *et al.*, 1997), and it is reasonable to assume a constant tissue density for a fossil plant such as *Z. shengfengense*.

The R : S ratio of *Z. shengfengense* is estimated at a mean value of 0.028 and the root-like axes constitute only *c.* 3% of the total biomass. Our estimation has a large value range, from 0.008 to 0.093 (Table 1), mainly resulting from the uncertainty of counting the number of aerial axes and root-like axes in compression fossils. Extant plants of small stature (thus excluding trees, which accumulate wood in their long-lived tissues) typically have smaller R : S values in annuals when comparing different life forms (0.13 in annuals relative to 4.0 in tree seedlings) (Monk, 1966), or in those found in wetter and hotter places when comparing different climatic conditions. Global analysis of R : S ratios in terrestrial biomes has shown that tropical–subtropical moist forest/plantation has the lowest value 0.092–0.253 (Mokany *et al.*, 2006). The R : S ratios of tropical–subtropical ferns (tree ferns, climbers and epiphytes) were calculated to range from 0.87 to 4.6 [from the data of tables 1 and 2 of Stewart *et al.* (1986); Andrade & Nobel, 1997]. Generally, one can reasonably assume that the lowest R : S ratio reported for extant terrestrial plants is *c.* 0.1, which is at the very highest end of the value range of *Z. shengfengense* and is *c.* four-fold higher than the mean value of this fossil plant.

The most reasonable explanation is that *Z. shengfengense* was probably a semi-aquatic plant. Extant aquatic and partially aquatic plants usually have lower root fractions; one example is the R : S ratio of *Egeria densa*

(Planch) (Hydrocharitaceae) which, in monocultures, reaches *c.* 0.03 (fig. 2 of Mony *et al.*, 2007). Some extant wetland plants subjected to experimental flooded treatments show low R : S ratios close to the value of *Z. shengfengense* (e.g. *Helianthus grosseserratus* Martens, *Eupatorium maculatum* L., *Solidago gigantea* Ait. in table 3 of Kercher & Zedler, 2004). However, the observation that the stomata are present at the middle–upper axes of the two *Zosterophyllum* species, i.e. *Z. myretonianum* and *Z. yunnanicum*, indicate that these axes are basically aerial (Walton, 1964; Hao, 1985), whereas the condition for the basal parts of these plants remains unclear. Mycorrhizal colonization might also contribute to the decrease in the R : S ratios (Marler *et al.*, 1999), although, in this study, we did not find any evidence of mycorrhizas in the specimen. However, Wang & Qiu (2006) reported that 80% and 92% of their surveyed land plant species and families (3617 species, 263 families) were mycorrhizal, implying that the mycorrhizal colonization may not necessarily relate to low R : S ratios.

The small rooting system of *Z. shengfengense* was able to supply sufficient nutrients to the relatively large shoot system by actively absorbing both nutrients and water, suggesting either a strong uptake capacity of these root-like axes or efficient water use by the shoots. The high water use efficiency is reasonable given the high levels of atmospheric CO₂ suggested for the Early Devonian (McElwain & Chaloner, 1995; Berner, 1997, 1998). The low R : S ratio of *Z. shengfengense* may also indicate a high temperature and high precipitation environment, enabling easier access to water and nutrients.

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