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Research paper

A new genus of Early Devonian plants with novel strobilar structures and vegetative appendages from the Posongchong Formation of Yunnan, China

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ABSTRACT

A new plant, *Dibracophyton acrovatum* gen. et sp. nov., is described from the Lower Devonian (Pragian) Posongchong Formation of Wenshan District, southeastern Yunnan, China. The plant has creeping axes from which arise vegetative and fertile axes. The vegetative axes helically bear lateral dichotomous appendages with curved or round tips. The fertile axes possess terminal strobili with numerous fertile units arranged in irregular helices. Each fertile unit consists of a stalked long-elliptical sporangium, with dehiscence into two equal valves, and two discrete long-ovate bracts covering sporangium from above–below directions. A new genus and species is thus established based on these characters and is temporarily regarded as incertae sedis of Tracheophyta, although it perhaps closes to the barinophytes in affinity. Detailed comparisons with other plants having a similar architecture, i.e., sporangia closely associated with modified vegetative structures, are made. The discovery of *D. acrovatum* further enriches the composition of the Posongchong flora and demonstrates great morphological disparity of the Early Devonian vascular plants.

1. Introduction

For the past several decades, much attention has been paid to the Early Devonian Posongchong flora from southeastern Yunnan, China, which has rich and diversified components compared to other coeval floras (Geng, 1983, 1985; Hao, 1989; Hao and Beck, 1991, 1993; Hao and Gensel, 1995, 1998; Hao et al., 2001, 2003, 2004; Li and Cai, 1977; Li and Edwards, 1992, 1997; Wang and Hao, 2002; Yang et al., 2009; Zhu et al., 2011). As currently known, there are at least 23 plant genera reported in this flora, representing a remarkably diverse assemblage of plants. Some plants show a combination of unusual characters in vegetative and fertile organs that are obviously advanced than those commonly attributed to early vascular plants, e.g., *Estinnophyton* (Fairon-Demaret, 1978; Hao et al., 2004), *Stachyophyton* (Geng, 1983), *Eophyllophyton* (Hao, 1988; Hao and Beck, 1993), *Adoketophyton* (Li and Edwards, 1992), *Celatheca* (Hao and Gensel, 1995) and *Polythecophyton* (Hao et al., 2001).

This paper describes a new plant, *Dibracophyton acrovatum* gen. et sp. nov., from the Posongchong Formation, which exhibits unusual vegetative appendages and unique strobilar structures composed of bracts and sporangia. The description of this plant further enhances the morphological disparity of the Posongchong flora with unique characters and is thus of significance in understanding both the evolution of plant organs and the Early Devonian (Pragian) radiation of plants.

2. Locality and material

The plant specimens described in this paper were collected from the Posongchong Formation outcropping in Wenshan Zhuang-Miao Autonomous Prefecture, southeastern Yunnan, China. This formation is considered to be Pragian in age based on marine fauna correlation (Hao, 1989; Liao et al., 1978), dispersed spore data (Wang, 1994) and plant assemblage characters (Gerrienne, 1996). In Wenshan district, there are two productive sections. One is at Zhichang Slope near Zhichang Village (Hao, 1989; Li and Edwards, 1992), about 16 km southwest of which is the other at Tiechan Slope near Changputang Village (Hao and Beck, 1991; Hao and Gensel, 1998). These two sections are well correlated on the basis of nearly similar lithologic features and plant compositions (Hao and Gensel, 1995, 1998). A few small-sized fertile fragments of the new plant (designated as PKU-Ch. Di-) were obtained by Hao S-G in 1987 from the eighth lithological unit of the Posongchong Formation at the Changputang section. The plant occurs in a thin-bedded (ca. 4–5 cm thick) layer of dark-gray arenaceous mudstone, which is about 1.5 m below the horizon of *Celatheca beckii* (Hao and Gensel, 1995) and about 0.5 m above the horizon of *Zhenglia radiata* (Hao et al., 2006) (see Hao and Gensel, 1998, their Fig. 1, p. 2). The subsequent productive collections, more than 20 specimens including the holotype (designated as PKU-Zh. Di-), were obtained from the fourth layer at the Zhichang section by Wang D-M and Hao S-G in 2004. Here, the plant occurs

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in a thin layer (ca. 5 cm thick) of dark gray arenaceous mudstone. This plant is well preserved near the bottom surface of the layer, showing a monospecific assemblage, but upwardly is mixed with fragments of some other plants. The specimens are preserved as impressions and compressions, commonly weathered to a yellow and brown color. Some specimens are casts or amorphous, carbonaceous films. Dégagement with steel needles under a binocular microscope and careful analysis of surface features of fertile axes were made to determine the arrangement of lateral bracts and sporangia.

3. Systematics

Phylum Tracheophyta Sinnott, 1935 ex Cavalier-Smith, 1998
Order and Family Incertae Sedis
Dibracophyton Hao, Xue, Zhu et Wang, gen. nov.
Type: *Dibracophyton acrovatum* Hao, Xue, Zhu et Wang, sp. nov.

Generic diagnosis: Plant with creeping axes, from which arise vegetative and fertile axes. Vegetative axes bearing lateral appendages in a helical arrangement; lateral appendages dichotomous, with curved, acuminate or round tips. Fertile axes terminated by strobili, which comprise fertile units arranged in irregular helices. Each fertile unit generally long-ovate in abaxial view, comprising a sporangium and two discrete bracts; sporangium being covered by two bracts from above and below directions. Sporangia stalked, long-elliptical in abaxial view, dehiscing along the whole margin into two equal valves.

Etymology: From Latin "*di-*", = two or two directions, "*brac*", = bract, and "*phyton*", = plant, in reference to the sporangium covered by upper and lower bracts.

Dibracophyton acrovatum Hao, Xue, Zhu et Wang, sp. nov. (Plates I–III)

Holotype: PKU-Zh. Di-01 (Plate I, 1).

Paratypes: PKU-Zh. Di-02-09 (Plate I, 2–4; Plate II, 1–7; Plate III, 1) and PKU-Ch. Di-01 (Plate II, 8–9).

Repository: School of Earth and Space Sciences, Peking University, People's Republic of China.

Type locality: Zhichang Village, Gumu Town, Wenshan District, Yunnan Province, China (GPS location: 23°17′50″N, 104°15′28″E).

Stratigraphic horizon: Lower Devonian (Pragian) Posongchong Formation.

Etymology: From Latin "*acro-*" and "*-ovatum*", referring to an ovate bract with a pointed tip.

Species diagnosis: Characters as for the genus. Basal axes creeping, thicker than the vegetative and fertile axes which arise at a nearly vertical angle. Vegetative axes branching dichotomously at angles ca. 40°; lateral appendages up to at least 16 mm long, departing at angles of 60°–90° from the vegetative axes at irregular intervals; lateral appendages not planated, once to thrice divided at angles of 70°–90°. A few lateral appendages, distributed on lower regions of fertile axes. Strobili, long-cylindrical in shape, up to 83 mm in length. Fertile units, ca. 6.7 mm long and ca. 2.8 mm wide, variable in shape, equal to the length of the bracts and equal to the width of sporangia when bracts are thinner than sporangia; fertile units loosely or moderately spaced at basal parts of strobili and densely spaced in the distal parts. Lower bracts long-ovate and distal bracts linear, folding inward to cover the sporangium. Sporangia long-elliptical, ca. 4.6 mm long and ca. 2.8 mm wide, with short stalks.

Plate I. *Dibracophyton acrovatum* gen. et sp. nov.

1. Holotype. Seven axes (axes a–g) lying approximately parallel on the bedding surface (PKU-Zh. Di-01). Note a piece of creeping axis at the bottom and one attached fertile axis (axis c, lower arrow); originally, axes a–g probably are attached on the same creeping axis; axis f is the preserved longest fertile axis but is incomplete in preservation. Also note vegetative appendages at basal parts of the fertile axes and the appearance of the first fertile unit (middle and upper arrows). Scale bar = 10 mm.

2–3. A piece of creeping axis with two incomplete vegetative axes (1: part, PKU-Zh. Di-02a; 2: its counterpart, PKU-Zh. Di-02b). Note a distal dichotomy of the right vegetative axis and lateral dichotomous appendages with recurved (upper arrow in 2) or upright tips (lower arrow in 2). Scale bar = 10 mm.

4. A vegetative axis arising from a creeping axis (PKU-Zh. Di-03). Note lateral appendages (most are once dichotomous) are inserted oppositely or alternately on the axis. Two white arrows indicate two stubs of lateral appendages, upper black arrow indicates a depression on the axis, and middle and lower black arrows indicate rounded tips. Scale bar = 10 mm.

Plate II. *Dibracophyton acrovatum* gen. et sp. nov. (see page 4)

1, 2. A piece of strobilus (1: part, PKU-Zh. Di-04a; 2: its counterpart, after removal of axial cast, PKU-Zh. Di-04b), showing basal parts of a strobilus, with two superficially and roughly subopposite or opposite rows of laterally preserved fertile units. See Fig. 1a, b for the line drawings, and Fig. 1c for a combined architecture of this piece. Arrows on axis in 1 indicate depressions marking the sporangia departing into the rock matrix, while arrows on axis in 2 represent sporangial bases which depart toward to the observer. A fertile unit (right arrow in 2) is enlarged in Plate III, 12. Scale bar = 3 mm.

3. A piece of strobilus (PKU-Zh. Di-05), showing probable basal parts of a strobilus with loosely arranged fertile units. A fertile unit (arrow) is enlarged in Plate III, 10. Scale bar = 5 mm.

4, 5. A relatively complete strobilus (4: PKU-Zh. Di-06a) and its slightly enlarged counterpart (5: PKU-Zh. Di-06b), showing an irregular arrangement of fertile units and thin longitudinal ribs on the strobilar axis. Note different development and arrangement pattern of fertile units from basal to distal parts of the strobilus. Scale bar = 10 mm.

6. Distalmost part or nearly so of a strobilus, showing a dense arrangement of fertile units (PKU-Zh. Di-07). Note a sporangium with weak-developed bract (arrow). Scale bar = 5 mm.

7. Basal part of a strobilus, showing a loose arrangement of fertile units (PKU-Zh. Di-08). A fertile unit (arrow) is enlarged in Plate III, 11. Scale bar = 5 mm.

8, 9. A piece of strobilus (8: part, PKU-Ch. Di-01a and 9: its counterpart, PKU-Ch. Di-01b), showing attachment and arrangement of fertile units. Fertile units (arrow in 8; upper and lower arrows in 9) are enlarged separately in Plate III, 2, 3 and 4. Scale bar = 5 mm.

Plate III. *Dibracophyton acrovatum* gen. et sp. nov. (see page 5)

1. Three fertile units (PKU-Zh. Di-09). Note long-ovate shape of a bract of the upper unit in abaxial view, with its largest width near and above the sharply contracted base and with a distal tip; long-elliptical shape of the sporangium of the middle unit in lateral–oblique view, outlined by black arrows, with staggered margin of bract (white arrow) and sporangial dehiscence. Scale bar = 2 mm.

2, 3. A fertile unit (part and counterpart) in lateral view. Note the upper/lower bracts separately derived from upper and lower epidermoid tissues of the strobilar axis (arrows in 2). After removal of the bracts, the sporangium (in 3) is exposed with two straight sides, a slightly decurrent stalk (arrow in 3) and dehiscence forming two equal valves. Scale bar = 1 mm.

4. A sporangium of a fertile unit, showing a decurrent stalk (arrow). Scale bar = 1 mm.

5. A fertile unit (PKU-Zh. Di-10) in lateral–oblique view, showing sporangial outline and bract. The bract folds inwardly to form a longitudinal ridge on the middle surface of sporangial valve. Scale bar = 1 mm.

6–8. Fertile units (PKU-Zh. Di-11, 12, 13) probably located at the upper parts of strobili, showing sporangia and narrow-linear bracts with long contracted tips. Note short stalks of the sporangia; remains of a bract on one valve of the sporangium (arrow in 6); bract beneath sporangium (in 7) or above sporangium (in 8). Scale bar = 1 mm.

9–12. Fertile units (9: PKU-Zh. Di-14; 10: PKU-Zh. Di-05; 11: PKU-Zh. Di-08; 12: PKU-Zh. Di-04b) probably located at the lower or middle-lower parts of strobili, showing long-ovate or even wide triangular bracts with curved tips. Note adaxial/abaxial bracts derived directly from upper and lower epidermoid tissues of the strobilar axis (arrows in 10, 11, 12) and different size of adaxial and abaxial bracts. Scale bars = 1 mm.

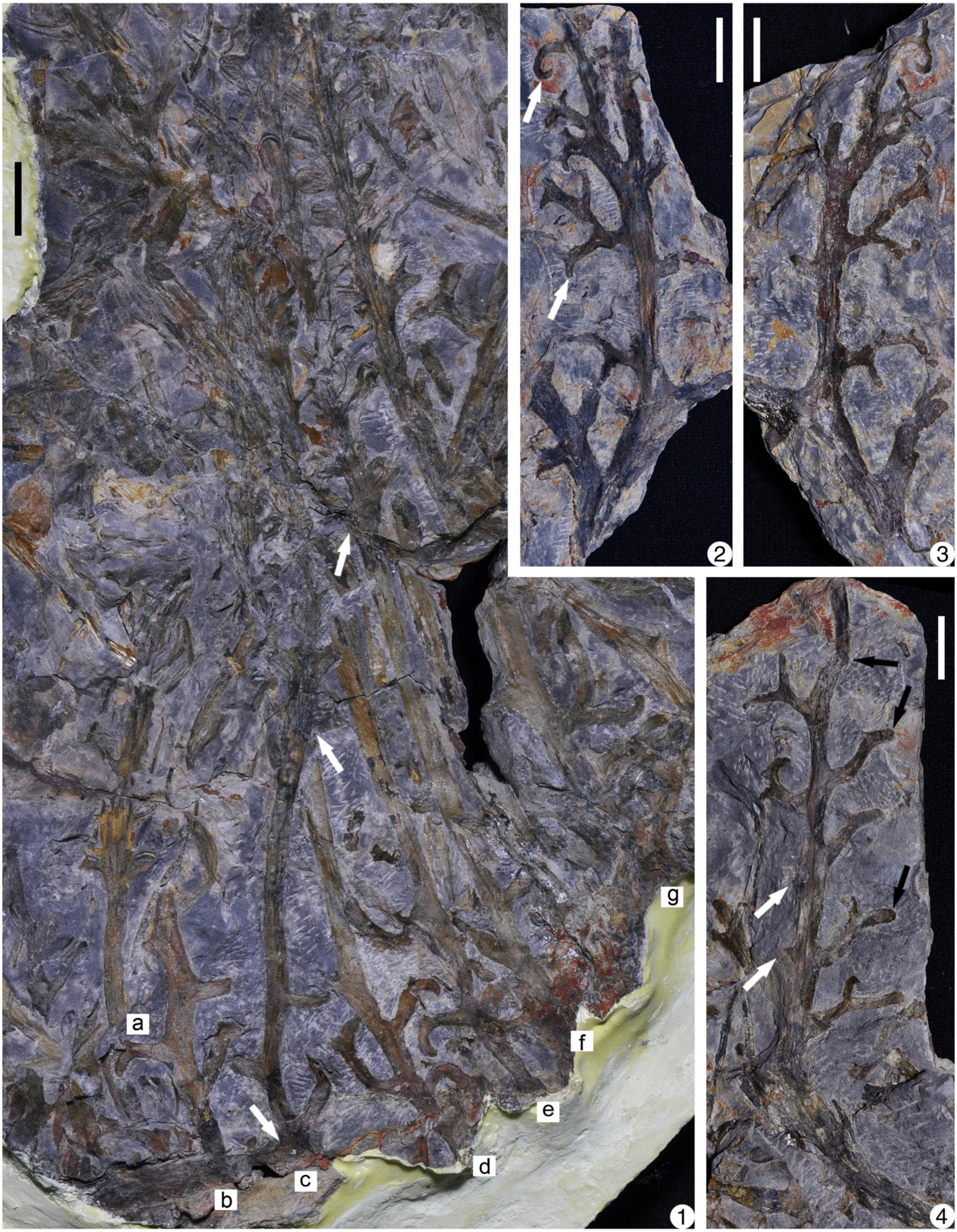

Plate I.

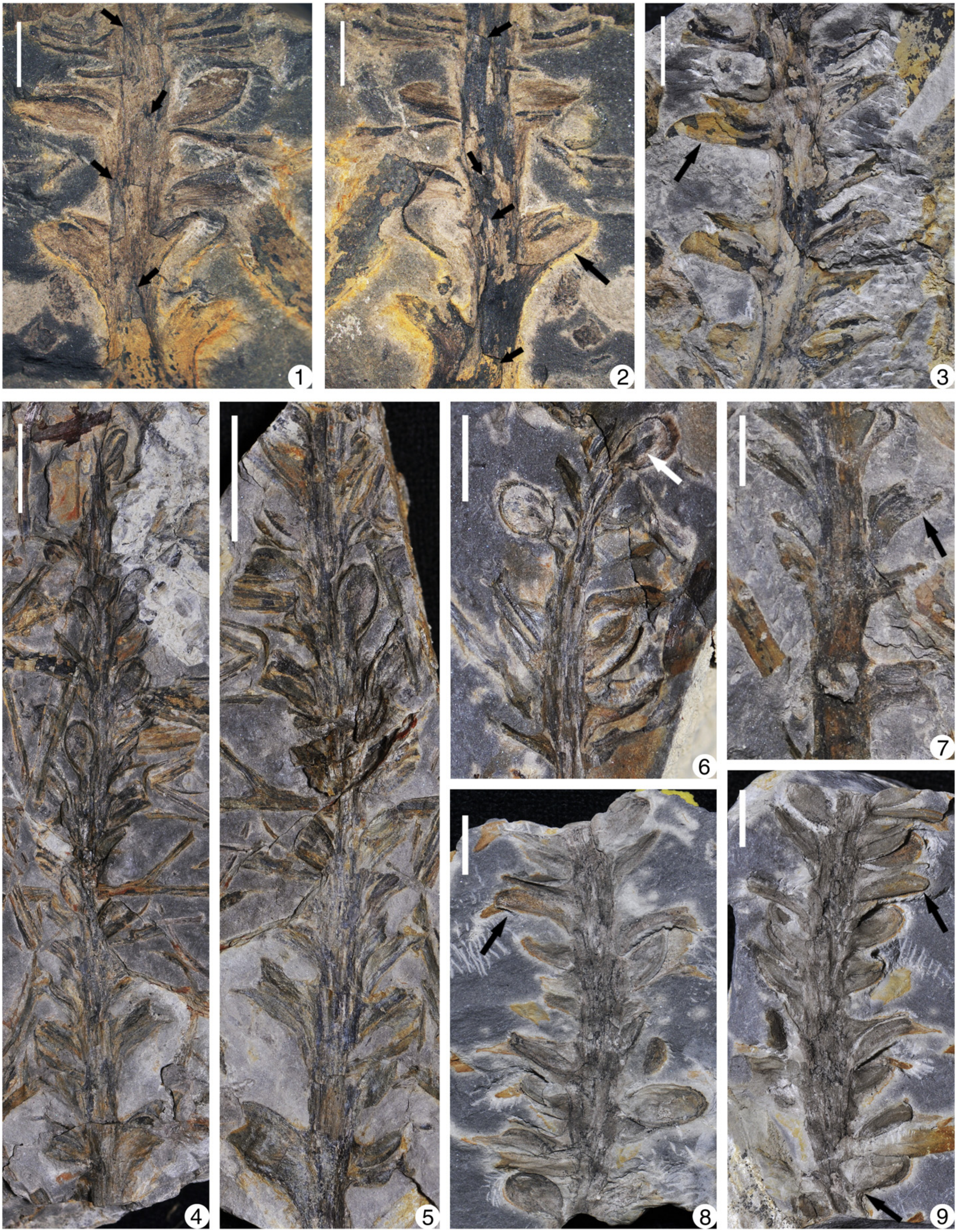

Plate II (*caption on page 2*).

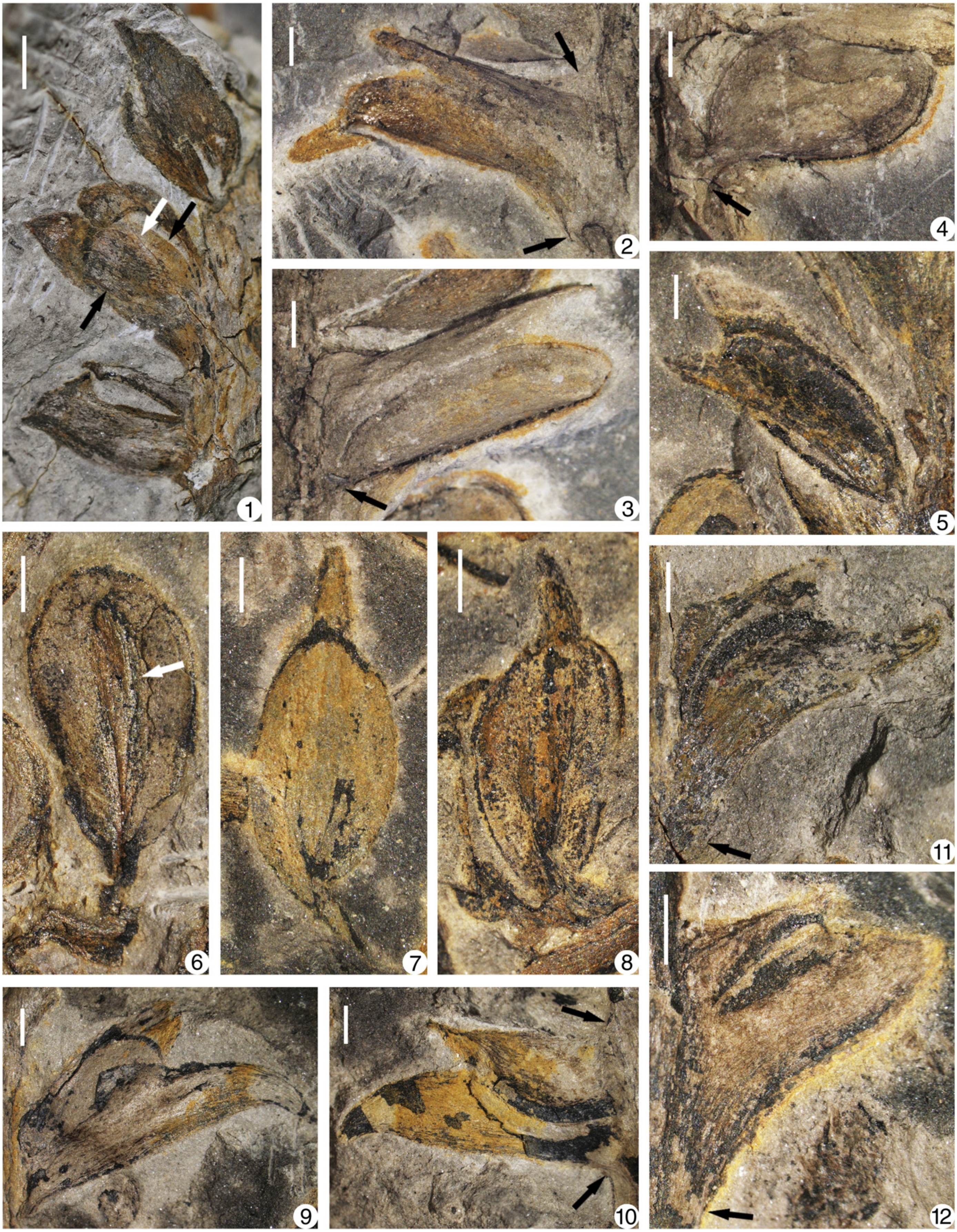

Plate III (*caption on page 2*).

4. Description

4.1. Branching architecture

4.1.1. Creeping axes, vegetative axes and lateral appendages

The holotype specimen shows seven upright axes (Plate I, 1, a–g) lying approximately parallel on the bedding plane. They are 5.8–21.6 mm apart from each other at the base, including four fertile axes with terminal strobili (i.e. Plate I, 1, a, c, f, g) and three other axes distally plunging downward into the matrix. These seven axes probably belong to the same plant. One of them (Plate I, 1, c, lower arrow) with a terminal strobilus arises directly at a vertical angle from a piece of creeping axis which is 3.0 cm long and ca. 5.2 mm wide. Another axis (Plate I, 1, b) is probably attached to this creeping axis either, but the connecting point is behind under the creeping axis. Other upright axes are not directly connected with the creeping axis, but they are distributed along the extending direction of the latter.

The specimen in Plate I, 2–3 (part and its counterpart) shows a piece of creeping axis extending obliquely; it is only 3.3 cm long and up to 7.4 mm wide, has two axes attached with an interval ca. 2.0 cm. The left axis is incomplete, only with the proximal part preserved. The right one is a vegetative axis, 6.1 cm long and 3.1–4.7 mm wide. On this axis, the first lateral appendage occurs at left side, 4.4 mm high above the departing point from the creeping axis; this appendage has a dichotomy of wide angle, about 12.6 mm long and 3.2 mm wide at the base, but its distal parts are broken. On the right side, the second appendage, with only the base preserved, occurs 13 mm above the first one. About 5.5 mm above the second appendage, the third one departs from the axis at an angle about 90° to the left side, 3.5 mm wide at the base; this appendage is relatively complete, showing a cuneate shape, and divides three times at angles of 60°–90°, with each terminal division bearing acuminate tips (Plate I, 2, lower arrow). The right vegetative axis dichotomizes at angles ca. 40° into two daughter axes. The daughter axes, extending parallel and broken distally, also bear lateral dichotomous appendages, most of which are incompletely preserved and have curved or strongly recurved tips (Plate I, 2, upper arrow; Plate I, 3).

Another vegetative axis, 8.0 cm long and 4.0 mm wide at the base and 2.1 mm wide distally, is borne on a piece of creeping axis, which is 4.4 cm long and 4.0–6.0 mm wide (Plate I, 4). Eight lateral appendages occur helically on the upright axis, four on the right side and four on the left (two are indicated by white arrows), and they appear to be rowed and more or less “pinnately” arranged in preservation. In addition there is a small depression on the distal part of the axis, marking the departure of another appendage into the rock matrix (Plate I, 4, upper black arrow). Thus a total of nine lateral appendages are inserted helically, but showing an apparent alternate arrangement, on the axis at angles of 60°–85°, with intervals of ca. 11.0 mm. Most of these lateral appendages are once dichotomous, dividing at angles of 90°–160°, probably nonplanated, 10–16 mm long and ca. 2.5 mm wide, with curved or round tips (Plate I, 4, lower and middle black arrows).

To sum up, the creeping axes reach up to 7.4 mm in width; the vegetative axes are 4.0–4.7 mm wide near the base and ca. 2.1 mm wide distally, and branch dichotomously at angles ca. 40°. The lateral appendages depart at wide angles from the vegetative axes with intervals of 4.4–11.0 mm, nonplanated and once to thrice divided.

4.1.2. Fertile axes

In the holotype specimen, four axes are terminated by strobili (Plate I, 1, a, c, f, g). The fertile axes are 7.9–14.6 cm long and generally 2.4–3.7 mm wide, unbranched along the whole length. A few lateral appendages occur at the basal parts of these axes, once dichotomous with curved tips, and they are alternately borne at angles of 40°–90°, with intervals of 4.4–10.2 mm. One fertile axis, 7.9 cm long and generally 2.8 mm wide, is directly connected to a creeping axis (Plate I, 1, c, lower arrow) and has three lateral vegetative appendages at the basal parts within a length of 24 mm. These appendages, 1.6–2.4 mm wide at the base, are inserted at angles of 50°–90° in an alternate pattern. Above them, a piece of unbranched axis, without any lateral appendages (also, no depressions or bumps representing departure points of laterals have been observed), extends 25 mm long up to the base of the strobilus (Plate I, 1, middle arrow).

The preserved longest fertile axis (Plate I, 1, f) is 14.6 cm long and 3.7 mm wide at the base. At the basal parts, three vegetative appendages are alternately attached within a length of 24 mm, and then a piece of naked axis extends 55 mm long up to the appearance of the first fertile unit (upper arrow). Other axes (Plate I, 1, b, d, e) also show such a distribution of vegetative appendages, probably implying that these axes are also fertile, although no terminal strobili have been observed. This condition is unlike that of vegetative axes, where vegetative appendages are evenly distributed along the whole length of the axes as shown in Plate I, 2–4.

4.2. Strobili

Except those shown in the holotype specimen, other strobili are incompletely preserved as small pieces (Plate II, 1–3). A complete strobilus with a short, broken subtending axis shows a long-

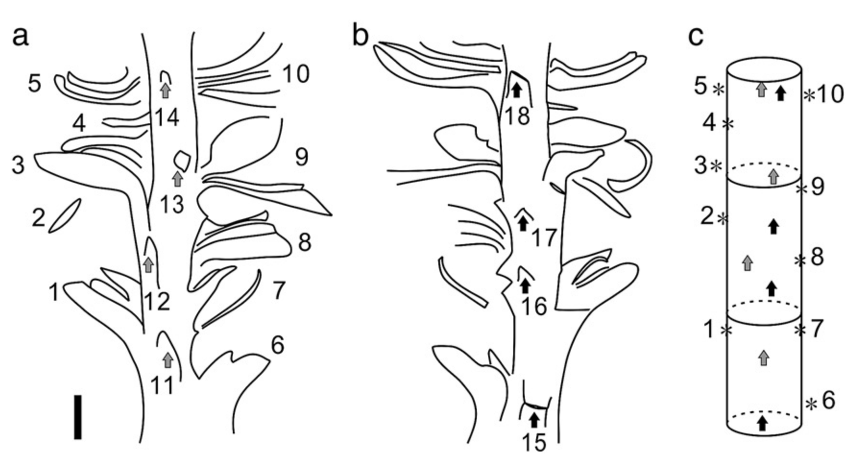

Fig. 1. *Dibracophyton acrovatum* gen. et sp. nov.(a), (b) Line drawings of the strobilus shown in Plate II, 1, 2 (part and counterpart). (c) Distribution of sporangia (corresponding to fertile units) on a supposed axis based on a combined architecture of (a) and (b), showing an irregular helical arrangement. A total of 18 fertile units are recognized: 14 ones shown in (a), and four other ones in (b). Fertile units 1–10 are laterally preserved (c, stars); units 11–14, departing into the rock matrix, are indicated by the depressions on the axis (a, c, light gray arrows); units 15–18, departing toward to the observer, are indicated by four step-like scars (b, c, dark gray arrows). Scale bar = 2 mm.

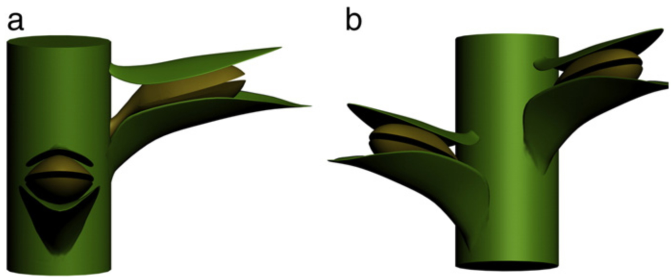

Fig. 2. *Dibracophyton acrovatum* gen. et sp. nov.Diagrammatic sketches showing two fertile units on a strobilar axis. (a) Lateral view. (b) Lateral-upward view.

cylindrical shape, gradually decreases in width distally, and measures 8.3 cm long and 9.5–14 mm wide (Plate II, 4, 5). The attaching angles of proximal fertile units are wider than those of distal ones. The strobilar axis, sometimes with several thin longitudinal ribs (Plate II, 4, 5), also shows a decrease of width, ca. 4.3 mm wide at the base and ca. 1.5 mm wide at the upper parts. The fertile units are distributed unequally around the strobilar axis and sometimes are grouped into a cluster (Plate II, 4), and their arrangement is suggested to be irregular, as is also demonstrated by the following analyses of sporangial attachments.

Detailed investigation on a piece of fertile strobilus, 2.5 cm long and 8.7–13.5 mm wide (Plate II, 1 and its diagram Fig. 1), was made. A total of 18 fertile units are recognized on this piece (Fig. 1a–c). Five units are respectively shown on the two sides of the strobilar axis, moderately spaced and with a superficially subopposite to opposite arrangement. Careful observation, however, indicates that these units are arranged irregularly. On the left side, unit 3 is above the axis, units 2 and 4 behind the axis, and units 1 and 5 to the lateral side (Fig. 1a), while on the right side, units 6 and 7 are above the axis, units 8 and 10 at the lateral side, and unit 9 is behind the axis. Moreover, there are four small longitudinal depressions on the mold of the axis (Plate II, 1, arrows; Fig. 1a,c, light gray arrows), representing the departures of sporangial stalks of the units 11–14 to the rock matrix. On its counterpart, after removing the muddy cast of the axis, four step-like scars can be observed on the axis surface (Plate II, 2, arrows on the axis; Fig. 1b,c, dark gray arrows), representing four sporangial bases of the units 15–18. Based on all these observations, the sporangia of this strobilus are shown to be in an irregular helical arrangement (Fig. 1c). This strobilus piece represents the lower parts of a strobilus, with a looser arrangement of fertile units proximally and a denser arrangement distally. Other strobili also demonstrate such a pattern (Plate II, 3, 6, 7). Specimen in Plate II, 6 shows the terminal part or nearly so of a strobilus, with fertile units more densely spaced, while specimens in Plate II, 3 and 7 show the basal parts of strobili, with fertile units in a looser arrangement. Another strobilus piece (part and counterpart; Plate II, 8, 9) is 3.5 cm long and 15 mm wide, with two broken ends. The fertile units are more densely arranged, superficially in a helical pattern, and depart at wide angles of 60°–90° from the axis.

4.3. Fertile units

Each fertile unit consists of a sporangium and two discrete bracts. Mature fertile units in abaxial view are usually long-ovate in shape (Plate III, 1). They are 5.1 (−6.7)–8.3 mm in length (n = 10) (equal to the length of bracts) and 2.1 (−2.8)–3.6 mm in width (n = 20) (equal to the width of sporangia when bracts are thinner than sporangia). In lateral view the mature units are cylindrical in shape and have two parallel sides (Plate III, 2, 3, 9, 10), ca. 5.3 mm wide, borne at angles of 60°–90° (measured according to the projecting direction of sporangium), and show two slightly divergent distal parts and expanded bases. An obvious variation of fertile units in

Fig. 3. *Dibracophyton acrovatum* gen. et sp. nov.Restoration of a part of the plant. Two pieces of creeping axes are shown. Three upright fertile axes are attached on the left creeping axis, with terminal strobili and a few lateral appendages on lower regions (based on Plate I, 1 and Plate II, 4, 5). Two vegetative axes are borne on the right one; both axes bear lateral appendages helically arranged, and the left axis dichotomizes once at the middle part (based on Plate I, 2–4). Scale bar = 10 mm.

morphology and dimensions occurs from the basal to distal regions of strobili (Plate III, 2–12), and different degree of maturity of fertile units, represented by sporangial shape and development of the associated bracts, is a main reason. Fertile units at the upper-middle parts of a strobilus are only outlined by their sporangial outline with projecting tips, because the bracts are thinner (i.e., poorly developed) than the sporangium (Plate III, 5–8), and these units are usually borne at narrow angles of 40°–60° (Plate II, 4–6).

On the strobilar axis, the bracts seem to be derived from the areas above and below the sporangial stalk and their epidermal cells appear to be continuous with the tissues of the strobilar axis (Plate III, 10–12). No veins have been observed in these bracts. Typical mature bracts are long-ovate in abaxial view, expand to their largest width just above their decurrent base, and decrease gradually in width to a distal convex tip. The sporangium and the associated bracts are separately attached at different levels along the strobilar axis (Plate III, 2, 3, arrows; Fig. 2a,b), with two bracts departing at 1.0–2.3 mm above and below the sporangium (Plate III, 2, 3, 9–11, arrows). And probably the sporangium is more close to the lower bract because of its decurrent stalk (Plate III, 2–4). In some specimens, the bracts are wide triangular in shape with a broad base (Plate III, 11, 12). Generally the lower bract is well developed and larger than the upper one (Plate III, 9–12). Lateral sides of bracts generally fold inward to cover the adaxial/abaxial valves of a sporangium from the above/below directions. Young bracts show a narrowly long-elliptical or linear shape (Plate III, 5–8), even less than 0.5 mm in width, and usually extend over the length of a sporangium to form a projected tip (Plate III, 7, 8). The bract tips are upwardly or downwardly curved (Plate III, 9–11). Narrow bracts, sometimes, fold inwardly to form a longitudinal ridge, shown on the middle surface of the sporangial valves (Plate III, 5). Fertile units located near the top of fertile axes appear to lack any bracts or their bracts are only very weakly developed (Plate II, 6, arrow; Plate III, 6, arrow).

After removal of a bract, or in fertile units without well-developed bract, the sporangial outline is exposed. In face view mature sporangia are long-elliptical with a rounded apex and often narrow toward the base (Plate III, 2, 3, 5–8), while young ones are oval or nearly round (Plate II, 6; Plate III, 4). They are 3.2 (−4.6)–6.3 mm long and 2.1 (−2.8)–3.6 mm wide (n = 20). Generally the length of a sporangium occupies 2/3-3/4 of its abaxial bract, and the width is equal to or slightly narrower than the adjacent bract. In lateral or lateral–oblique views, some sporangia show a long ovoid or columnar shape, with a slender stalk (Plate III, 6). The stalk is 0.6–1.0 mm long and ca. 0.8 mm wide, and has a slightly expanded and decurrent base at the attachment point to the axis (Plate III, 4, arrow). Some sporangia exhibit a peripheral dehiscence along the whole margin, which extends nearly from the base over the apex. Dehiscence separates the sporangia into two equal valves (Plate III, 1, 3, 8–12). No visibly thickened rims have been observed along the dehiscence margin. No spores were obtained. Based on the above description, a partial reconstruction of this plant is shown in Fig. 3.

5. Comparison and discussion

The presence of leaf-like structures (bracts, appendages, sporophylls or branching systems) associated with sporangia is a more advanced feature than is commonly encountered in the Early Devonian plants. Such structures were considered an adaption of convergence for protection and nutrition of the sporangium (Li and Edwards, 1992). Diversified and differently organized fertile structures occurred in many plants from the Posongchong flora (Early Devonian Pragian age) of southeastern Yunnan, China, implying an unusual condition of plants in this area. These plants include *Stachyophyton yunnanense* (Geng, 1983; Wang and Cai, 1996), *Eophyllophyton bellum* (Hao, 1988; Hao and Beck, 1993), *Adoketophyton subverticillatum* (Hao et al., 2003; Li and Edwards, 1992), *Adoketophyton parvulum* (Zhu et al., 2011), *Celatheca beckii* (Hao and Gensel, 1995), *Hedeia sinica* (Hao and Gensel, 1998), *Polythecophyton demissum* (Hao et al., 2001) and here the new plant *Dibracophyton acrovatum*. *Estinnophyton yunnanense* (Hao et al., 2004) also has a compound fertile structure. Moreover, *Bracteophyton variatum* from the Xujiachong Formation of Qujing, Yunnan (Pragian-lower Emsian) shows fertile structures with leaf-like bracts (Wang and Hao, 2004).

Most of these plants have nearly round to oval sporangia which are borne on or covered by a laminate leaf-like bract (appendage or sporophyll). Among them, in *Eophyllophyton*, multiple, nearly rounded sporangia are adaxially rowed on laminate fertile leaves, which form clusters terminally or laterally borne on axes. Leaf-like appendages of *Celatheca* enclose laterally positioned oval sporangia to constitute fertile structures which terminate at the tips of twice-forked axes (Hao and Gensel, 1995). *Estinnophyton* bears twice-bifurcate leaves, each with two stalked, recurved ovoid-elongate sporangia (Hao et al., 2004). Quite clearly, *Dibracophyton acrovatum* differs distinctly from the above plants in that its fertile units form a strobilar structure and each unit looks like a “soap box” with upper and lower bracts covering a sporangium inside. In addition, these bracts are probably unvascularized. These further demonstrate the disparity of vegetative structures associated with sporangia during the Early Devonian period.

Stachyophyton, *Adoketophyton*, and *Bracteophyton* resemble *Dibracophyton* in bearing terminal strobilus with lateral fertile units, but show differences in shape and organization of fertile units. *Stachyophyton* has a linear “sporophyll” with bifurcating tips, on which an elongate elliptic sporangium is adaxially attached (Geng, 1983; Wang and Cai, 1996). Fan-shaped sporophyll of *Adoketophyton* adaxially bears a globose-reniform sporangium (Hao et al., 2003; Li and Edwards, 1992; Zhu et al., 2011). Moreover, *Stachyophyton* has planar lateral vegetative branches with distally expanded divisions (Geng, 1983), and *Adoketophyton* has lateral branches with circinately coiled tips (Hao et al., 2003; Zhu et al., 2011). The fertile unit of *Dibracophyton acrovatum* is most similar to that of *Bracteophyton* (Wang and Hao, 2004). Terminal strobili of *Bracteophyton* consist of helically arranged fertile units, each of which comprises one or two elongate bracts and a long-ovate adaxial sporangium (Wang and Hao, 2004). Further observations on the specimens of *Bracteophyton* (deposited at Department of Geology, Peking University) confirm the presence of such structures, but the details of bract/sporangium organization, particularly the exact attachment of bract and sporangium are obscure. A main reason is that the fossils are preserved in a very rough matrix of siltstones and sandstones, which hampers a clear distinction between different structures. In comparison, however, *Bracteophyton* is distinct in that its strobili are very short (1.8 cm long) and are terminating the fertile axes at least thrice isotomously dichotomized. In *Dibracophyton*, the rather long strobili (8.3 cm long) are subtended by less branched axes which directly arise from creeping axes. The bracts of *Bracteophyton* have a uniform shape, unlike those of *Dibracophyton* which vary from long-ovate to narrow linear and show developmental variations. In addition, there is no information for vegetative organs of *Bracteophyton*.

As to sporangial morphology of *Dibracophyton acrovatum*, the somewhat flattened long-elliptical shape and dehiscing around the whole margin into two equal valves are superficially similar to those of zosterophylls, and *Yunia* of uncertain affinity. *Yunia* is characterized by centrarch primary xylem and complex protoxylem (parenchyma plus tracheids) (Hao and Beck, 1991). Current evidence indicates that nearly rounded sporangia with distal dehiscence may be plesiomorphic.

The lateral appendages of *Dibracophyton acrovatum* occur at the basal region of fertile axes and along the whole length of vegetative axes. Generally they are helically attached on the axes, once to thrice dichotomous at wide angles, with either recurved acuminate tips or upright round tips. They show an obvious similarity to the vegetative appendages of *Celatheca* (Hao and Gensel, 1995) and *Eophyllophyton* (Hao, 1988; Hao and Beck, 1993), although they are larger in dimensions than those of the latter two plants. *Celatheca*, *Eophyllophyton* and *Dibracophyton* show distinct differences in vegetative and fertile organs, but have similar dichotomous appendages, implying that this type of vegetative appendages may be plesiomorphic (Hao and Beck, 1993). Traditionally the presence of “pinnule-like vegetative appendages” (homologous to megaphylls, as a character of foliar structure) was regarded as one of the synapomorphies to define the euphyllophytes clade (Kenrick and Crane, 1997).

Several plants from the Laurussian Devonian deposits have strobilar structures comprising sporangia and associated leaf-like appendages (also called sporangiferous or sporangiophorous appendages). *Krithodeophyton* from the Early Devonian of South Wales (Edwards, 1968) and *Enigmophyton* from the Middle Devonian of Norway (Høeg, 1942) have two rows of possible bracts that alternate with the sporangia. In *Protobarinophyton* from the Late Devonian of America (Brauer, 1981), the strobilus consists of two rows of alternate bracts curving downward and back toward the strobilar axis. *Barinophyton* have laterally positioned sporangia and two alternate rows (clasping orientation) of bracts recurving adaxially. However, in *Barinophyton citrulliforme* from the Late Devonian of America, the exact attachment mode of the sporangium to the bract is undetermined (Brauer, 1980). *Barinophyton norvegicum* from the Middle Devonian of Germany shows that a stalked sporangium with a distal dehiscence is borne on the concave surface of the proximal part of a bract (see Fig. 9 of

Schweitzer and Giesen, 2008). *Dibracophyton* differs from these plants in that its fertile units have an irregular helical arrangement on the axes and each unit consists of a long-elliptical sporangium and two separate bracts.

In *Dibracophyton acrovatum*, from basal to distal parts of a strobilus, the different degrees of bract development are probably an abiding feature. The morphological variation exhibits a gradual transformation and is probably related to ontogenetic development. The most developed bracts at the basal parts of a strobilus are wide-ovate, more enveloping the sporangium (Plate III, 12); upwardly in the median region the bracts become long-ovate (Plate III, 9–11), and those of the distal region are narrow linear with tapering tips (Plate III, 7, 8). A few sporangia at the most distal parts of a strobilus appear to lack any bracts, or probably their bracts were not well-developed to extend over the length of sporangia (Plate II, 5, 6). It is interesting that parallel with these variations of bracts what would happen for the spores inside the sporangia? We presume that some degrees of differentiation might be present due to changes of the micro physiologic environments affected by the differentiation of their covering bracts, but this possibility cannot be confirmed in the absence of in situ spores.

6. Affinity

Compared to the previously described Early Devonian plants, *Dibracophyton* is distinct in that its fertile unit consists of a long-ovate sporangium and homogenized bracts covering sporangium from upper–lower (adaxial–abaxial) directions. The fertile units are attached irregularly on the axis to form a strobilus and lateral vegetative dichotomous appendages are more or less "pinnately" arranged. Such a combination of characters has not been found in any presently known taxa, indicating a status as a new genus and species. We presume, despite the absence of anatomy, that it is a tracheophyte plant and its affinity is perhaps close to the barinophytes, a group with an uncertain affinity or to the lycophyte lineage (Crane et al., 2004; Kenrick and Crane, 1997). A definite assignment needs more information, such as stelar architecture of the present plant, thus presently it is treated as Tracheophyta incertae sedis.

The evolution of fertile unit composed of sporangia and surrounding leaf-like structures probably implies the appearance of divergent lineages, such as *Adoketophyton*, *Bracteophyton*, *Celatheca*, *Eophyllophyton*, *Stachyophyton*, and the present plant *Dibracophyton*. Their sporangial shape and structure, as well as the position of sporangia relative to the leaf-like structures, are a very basic difference. The associated leaf-like structures are also particularly important for the distinction of different lineages in terms of their varied shape and organization (e.g., vascularized or not) and possibly different development (see Comparison and discussion). The bracts of *Dibracophyton* seem to be membranous-like structures derived from the extending epidermoid tissues (see Description) and probably are unvascularized. Such a bracteal structure strongly differs from those of vascularized leaf-like appendages of *Eophyllophyton* and *Adoketophyton*.

In *Dibracophyton acrovatum*, each fertile unit consists of a stalked long-elliptical sporangium and two discrete upper/lower long-ovate bracts. This resembles those of *Bracteophyton* (Wang and Hao, 2004), *Barinophyton* (Brauer, 1980; Schweitzer and Giesen, 2008) and *Protobarinophyton* (Brauer, 1981). Moreover, they share several characteristics, such as the presence of a strobilus and their sporangia having a short stalk, distal dehiscence and two sporangial valves (sporangial characters were demonstrated in *Barinophyton norvegicum* and the present plant). *Barinophyton* is characterized by the exarch protostele (Brauer, 1980). We suggest that these plants perhaps are related in affinity. Concerning other less well-known plants such as *Krithodeophyton croftii* (Edwards, 1968) and *Enigmophyton superbum* (Høeg, 1942) which were regarded as putative members of the barinophytes (Li and Edwards, 1992), their bract details and the exact relationship between the sporangia and bracts need further determination. Anyway, the discovery of *Dibracophyton acrovatum* further enriches the composition of the Posongchong flora and is of significance in understanding both the evolution of plant organs and the Early Devonian Pragian radiation (explosion) of plant diversity.

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