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Research paper

A new species of *Adoketophyton* from the Lower Devonian (Pragian) Posongchong Formation of Yunnan, China

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ABSTRACT

A new species of early vascular plant, *Adoketophyton parvulum* sp. nov., is described from the Lower Devonian (Pragian) Posongchong Formation of Yunnan, China. The plant is composed of main axes, lateral vegetative branches and isotomous or anisotomous fertile axes. The vegetative axes branch isotomously or pseudomonopodially in three dimensions, with some laterals ending in terminal circinately coiled tips. K-shaped branching and tubercles are preserved. Terminal strobili consist of four vertical rows of fertile units, arranged in opposite and decussate pairs. Each fertile unit comprises a fan-shaped sporophyll and a sporangium attached adaxially by a short stalk at the base of the sporophyll. The strobili and fertile units (sporophylls and associated sporangia) of this new species are much smaller than those of the type species, *Adoketophyton subverticillatum*, and the ratio of heights of sporangia to sporophyll laminae in the two species shows a large discrepancy. The affinity and evolution of *Adoketophyton* are discussed. The various leaf-like appendages in plants reported from the Early Devonian of South China are considered a phenomenon of convergent evolution.

1. Introduction

Up to now, more than 30 plants, many of which are endemic, have been reported from the Lower Devonian (Pragian) Posongchong Formation of Yunnan, China. They represent one of the best documented floras recording the diversification and disparities of early vascular plants during the Early Devonian period (Hao and Gensel, 2001). Among the reported plants, the genus *Adoketophyton* is of interest in that it differs strikingly from the contemporary plants commonly found in Lower Devonian sediments. *Adoketophyton* and the type species, *Adoketophyton subverticillatum*, were established by C.-S. Li and Edwards (1992) based on fossil materials originally named "*Zosterophyllum*" *subverticillatum* by X.-X. Li and Cai (1977) from the Posongchong Formation at Zhichang Village, Wenshan District, Yunnan. Li and Edwards (1992) gave a detailed description of the morphological characters of *A. subverticillatum*. Hao et al. (2003a) added some morphological features and revealed some anatomical information based on more extensive collections from three outcrops of this formation in Wenshan and Guangnan districts of Yunnan. The Early Devonian plants are generally regarded as simple in morphology and organization, only having terminal or lateral sporangia without leaves or leaf-like structures. However, *Adoketophyton* is characterized by a terminal strobilus, which consists of four vertical rows of fertile units arranged in opposite and decussate pairs. Each fertile unit is composed of a fan-shaped sporophyll and an adaxially attached, stalked sporangium. The sporangia are flattened, nearly round in shape and dehisce along the distally thickened margin into two equal valves (Li and Edwards, 1992). Anatomically, the axis has a columnar centrarch primary xylem with G-type tracheids and the sporophylls are possibly vascularized (Hao et al., 2003a). Here we report a new species of *Adoketophyton*, *A. parvulum* sp. nov., from the Posongchong Formation of Yunnan, which extends the character variation of this important genus and provides new data for understanding the diversity of strobilar structures during the Early Devonian.

2. Locality, material and methods

The plant fossils (designated as PKU-ZH-) were collected from the upper part of the sixth layer of the Posongchong Formation at Zhichang Village, Gumu Town, Wenshan District, Yunnan Province. The materials were originally collected by Z.F. Liu, D.M. Wang and S.G. Hao in 2005. Details about the geographic locality, stratigraphic range and lithological trait of the Posongchong Formation at the Zhichang section have been presented by Hao (1989), Hao and Beck (1991, 1993), Li and Edwards (1992) and Hao and Gensel (2001). This formation was considered Pragian in age based on marine faunal correlation (Liao et al., 1978; Hao, 1989), dispersed spore data (Wang, 1994) and plant assemblage characters (Gerrienne, 1996).

The specimens are usually black or yellowish brown in color, preserved as compressions and impressions in a 20-cm-thick bed of gray or dark gray mudstones. The GPS location of the locality is 23°17′ N, 104°15′ E. More than 20 specimens were prepared using steel needles

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under a binocular dissecting microscope, to show branching pattern, circinate tips and particularly architecture of the strobilar structure.

3. Systematics

Phylum Tracheophyta Sinnott, 1935 ex Cavalier-Smith, 1998
Order and Family Incertae Sedis
Genus *Adoketophyton* Li et Edwards, 1992
Type species *Adoketophyton subverticillatum* (X.-X. Li et Cai) Li et Edwards, 1992

Adoketophyton parvulum sp. nov. (Plates I–III)
Species diagnosis: Axes naked. Isotomously or pseudomonopodially branching, with vegetative ultimate tips circinately coiled. Fertile axes naked, dichotomously branching at angles of 25°–55°. Strobili parallel-sided, comprising four rows of oppositely and decussately inserted fertile units; the longest strobilus with more than 60 fertile units; each fertile unit consisting of a sporophyll and an adaxial sporangium. Sporophyll fan-shaped, with a short pedicel, and the laminar region partly enclosing the sporangium. Sporangia elliptical, attached to the adaxial base of the sporophyllous lamina by a short stalk, with distal dehiscence along convex margin. Height of sporophyll lamina and associated sporangium almost equal, 0.8–1.4 mm. Anatomy unknown.
Holotype: PKU-ZH01a (Plate I, 1).
Paratypes: PKU-ZH03b, 04a and 05b (Plate I, 2; Plate III, 1, 4).
Type locality: Zhichang Village, Gumu Town, Wenshan District, Yunnan Province, China (GPS location: 23°17′ N, 104°15′ E).
Horizon: Lower Devonian (Pragian) Posongchong Formation.
Etymology: From Latin "*parvulum*", referring to the small size of the plant.

4. Description

4.1. Branching architecture: vegetative and fertile axes

The plant is composed of main axes, lateral vegetative branches and isotomous or anisotomous fertile axes. Although the fertile and vegetative axes are not organically connected, this plant seems to be the only plant preserved in the horizon, based on the size of the axes, preservation pattern and surface color (Plate I, 1). The axes are slender and divide isotomously or anisotomously to produce lateral branches (Plate I, 2, 3). The vegetative axes have terminally coiled tips (Plate I, 1, arrows c, d) and the fertile ones are terminated by a distinctive strobilar structure (Plate I, 1, arrows e, f, and 2, arrow a).

The presumed main axes range from 1.0 mm to 1.7 mm in width. Lateral branches depart from the main axes at angles of about 40°–60°, but occasionally 70°–90° (Plate I, 3–6). The interval between two successive branches varies from 22 mm to 53 mm. The longest axis preserved is 8.5 cm long with two broken ends; it is 1.2 mm wide at the base and becomes gradually narrower towards the distal broken end. This longest axis is supposed to be a main axis. Proximally, the axis divides pseudomonopodially to produce a lateral branch (Plate I, 1, arrow a), and distally, it divides dichotomously (Plate I, 1, arrow b).

The vegetative axes divide isotomously or pseudomonopodially in three dimensions. The lateral branches are 0.8–1.1 mm in width (Plate I, 3–6; Plate II, 1–5). Some lateral branches are probably unbranched along the whole length, ending in circinately coiled tips (Plate I, 4). The largest branch with a coiled tip preserved in our specimens is about 27 mm long and 0.9 mm wide at the base, and tapers acropetally (Plate I, 4); the most distal part of this branch is a more than two evenly coiled circinate tip.

Some lateral branches are pseudomonopodially divided, irregularly or helically bearing ultimate branches with circinately coiled tips (Plate I, 3). The first ultimate branch generally occurs 1.5 mm distally to the branching point of the main axes and lateral branches (Plate I, 1, arrow a, and 5; Plate II, 2, 3). The mean interval between two ultimate branches is 24 mm (Plate I, 3, arrows). An axis (Plate II, 1), composed of two closely spaced dichotomies with circinately coiled tips, is considered as the most distal part of a vegetative branch.

Some lateral branches form a K-shaped branching configuration (Plate I, 6; Plate II, 4), possibly representing the basal region of the plant. The axes of the K-shaped lateral branch are up to 1.5 mm wide, departing from the main axes at angles of about 70°–90°. After departing, they extend for 3.0–4.0 mm and bifurcate once or twice at angles of 110°–150° (Plate I, 6; Plate II, 4).

In some examples, tubercles can be observed along the margins of isolated axes (Plate I, 6, arrow; Plate II, 5). The tubercles have a semi-circular dome shape, about 0.5 mm wide at the base and 0.3–0.4 mm high, probably representing aborted branches.

In the holotype specimen (Plate I, 1), numerous fertile axes, each of which has a terminal strobilus, lie approximately parallel on the bedding plane. These fertile axes are the results of dichotomies of lateral branches, or possibly the distal part of some main axes, representing the terminal part of the plant. They are generally 0.8–1.2 mm wide, divide dichotomously at least twice in three dimensions at angles about 25–55°. Successive branches are 2–19 mm apart.

Strobili are commonly found detached, with a short subtending axis (Plate I, 1; Plate II, 6–8; Plate III, 1), but occasionally some are clearly borne at terminal parts of fertile axes which dichotomously divide once or twice (Plate I, 1, arrows e, f, and 2, arrows b, c). The subtending axes of terminal strobili from the same dichotomy are generally equal in length, 9–17 mm long (from the branching point to the base of strobili), but in some examples, one subtending axis is extremely short, only 0.5–2.0 mm long, while the other is 9–14 mm long (Plate I, arrow f; Plate III, 1, arrow a). These subtending axes are generally slightly bent upward (Plate I, 1, 2; Plate III, 1).

4.2. Strobili

Most strobili are oriented parallel to each other on the bedding plane, generally cylindrical in shape with two parallel sides. Some strobili show a slight decrease in width from base to apex (Plate II, 6–8; Plate III, 1, 2). The strobili, 7–17 mm long and 2.2–2.8 mm wide, are composed of closely arranged fertile units which consist of sporophylls and adaxially attached sporangia (Plate III, 3, 4). The specimen in Plate III, 2 shows a complete strobilus being 7.0 mm long. The width of the strobilus is 2.2–2.7 mm. Strobilar axes are narrow (Plate III, 4), about 0.4–0.6 mm wide. The longest strobilus is up to 17 mm long, with more than 60 fertile units (Plate III, 1, arrow b).

The fertile units are arranged in four vertical rows, oppositely and decussately inserted on the strobilar axis, based on the observations of different orientations of compressions and planes of fracture (Fig. 1a). Both fan-shaped sporophylls (Plate II, 6, arrows, and 7, arrows d, e) and sporangia (Plate II, 7, arrows a–c) are arranged in vertical rows. Some strobili display three visible vertical rows, with two opposite rows of laterally preserved fertile units and one row of abaxially preserved units (Plate II, 8). The specimen in Plate III, 4 (arrows a, b) clearly shows the opposite arrangement of two fertile units, and a sporophyll of the third row (arrow c) is located above the former units. In Plate III, 5 (arrows a–d; Fig. 1b), the specimen demonstrates a more comprehensive configuration of strobilus; (a) is the abaxial surface of a sporophyll, (b) is an adaxial view of a sporophyll and an associated sporangium (Plate III, 5, small black arrows), (c) and (d) represent lateral views of two opposite sporangia. Fertile units (a) to (d) belong to four distinct vertical rows; (c) and (d) have an opposite arrangement; (a) is located below the level of (c) and (d), with its abaxial surface facing the observers, while its opposite counterpart is buried in the matrix; (b) is located above the level of (c) and (d). Thus, in this specimen the fertile units of two lateral rows are oppositely arranged, with the units of middle rows alternately inserted below or above, showing a decussate arrangement pattern. The intervals between adjacent fertile units in a vertical row are almost