Review of Palaeobotany and Palynology 221 (2015) 220–229

Contents lists available at ScienceDirect

Review of Palaeobotany and Palynology

journal homepage: www.elsevier.com/locate/revpalbo

Research paper

Additional observations on *Zosterophyllum yunnanicum* Hsü from the Lower Devonian of Yunnan, China

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ARTICLE INFO

Article history:
Received 11 December 2014
Received in revised form 10 March 2015
Accepted 18 March 2015
Available online 28 March 2015

Keywords:
Zosterophyllum yunnanicum
Sporangial border
Dehiscence
Early Devonian
Yunnan Province

ABSTRACT

Investigation of unfigured specimens in the original collection of *Zosterophyllum yunnanicum* Hsü, 1966 from the Lower Devonian (upper Pragian to basal Emsian) Xujiachong Formation, Qujing District, Yunnan, China has provided further data on both sporangial and stem anatomy. We show that the sporangia dehisced into more or less equal valves through a mechanism that involved the development of large thick-walled cells. Furthermore the coalified xylem is composed of tracheids with G-type thickenings (predominantly annular secondary thickenings with small circular to irregular perforations in the intervening wall), confirming the presence of this form of vascular element in the genus *Zosterophyllum*. The species diagnosis is emended. Characterisation of dehiscence mechanisms in fossil sporangia is complicated by their different modes of preservation. A brief critical survey of the marginal features in bivalved sporangia in zosterophylls and other selected species is followed by a discussion on their putative functional significance. Preservation notwithstanding, we identify clear differences in mechanisms related to the nature of the underlying cellular structure of the dehiscence feature. The distinctive groove present in many species might represent a mechanism for regulating the timing of dehiscence in response to atmospheric conditions.

1. Introduction

Specimens of *Zosterophyllum*, from the Xujiachong Formation in Yunnan Province, China, were described by the late Prof. J. Hsü in 1966 as a new species, *Zosterophyllum yunnanicum*, it being the first record of the genus in China. Subsequently, 29 species of *Zosterophyllum* were listed from Southwest China by Li and Cai (1977); seven were new (*Z. bifurcatum*, *Z. contiguum*, *Z. dushanense*, *Z. longhuashanense*, *Z.sinense*, *Z. spathulatum*, *Z. subverticillatum*), three were previously published (the type species *Z. myretonianum*, *Z. yunnanicum* and *Z. australianum*) and 19 of uncertain validity were left as *Z.* sp. and required more detailed evaluation (e.g., Cai and Schweitzer, 1983; Gensel and Andrews, 1984; Wang, 2007). Subsequently, investigation of additional collections in Yunnan Province has allowed reinterpretation of *Z. contiguum* and *Z. subverticillatum* (Li and Cai, 1977) and their assignation to new genera, *Demersatheca* (Li and Edwards, 1996) and *Adoketophyton* (Li and Edwards, 1992) respectively. *Zosterophyllum longhuashanense*, *Z. spathulatum* and *Z. bifurcatum* were all described from single and very fragmentary specimens and require more characters to establish even their generic identity. *Z. sichuanense* is being restudied and may be transferred to a new genus (work in progress). Better preserved material from various localities in Yunnan has since allowed the erection of a number of endemic species including Pragian *Z. ramosum* (Hao and Wang, 2000), *Z. minifertillum* and *Z. tenerum* (Hao and Xue, 2013), Lochkovian *Z. xishanense* (Hao et al., 2007), *Z. minorstachyum* (Xue, 2009) and *Z. shengfengense* (Hao et al., 2010), and extension of the range of the genus into the Silurian (*Z. qujingense*; Hao et al., 2007). *Z. yunnanicum* was revised from new material by Hao (1985), who added data on epidermal features and spores, and Wang (2007), who provided information on branching patterns and strobili.

This paper is based on unfigured material of *Z. yunnanicum* in the Institute of Botany, Chinese Academy of Science from the original collection made by Hsü (1966), and presents new data which further characterise the species.

2. Locality data, material and methods

The fossils were collected from the Xujiachong Formation in Qujing District, Yunnan, China. Details of the locality and stratigraphy are given in Hsü (1966) and Hao (1992). The age of the formation was estimated as late Pragian to early Emsian by Wang (2007) and the strata containing the plants described here, which were collected from the upper part of the formation, as early Emsian based on bivalves and comparative fossil plant assemblages (Wang, 2002), a biostratigraphic

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http://dx.doi.org/10.1016/j.revpalbo.2015.03.007
0034-6667/

coefficient based on plants (Gerrienne and Streel, 1994; Wang, 2007) and spores (Gao, 1981). More recently, Wellman et al. (2012) extracted well-preserved spore assemblages from the *Z. yunnanicum* horizons and placed them in the *polygonalis-emsiensis* Spore Assemblage Biozone (PE-SEB) of Richardson and McGregor (1986) of early Pragian to ?earliest Emsian age, but cautioned against correlation based on stratigraphic sequences alone especially between the distant Euromerica and the Chinese palaeocontinents in the absence of other biostratigraphically useful co-occurring fossils.

The fossils are coalified and preserved in grey to buff mudstones (Plate I). Fifteen specimens were investigated and nine illustrated. Standard palaeobotanical techniques were employed including maceration of fragments in Schulze's solution, and dégagement using tungsten steel needles (Leclercq, 1960; Fairon-Demaret et al., 1999). Coalified fragments were mounted on carbon discs on aluminium stubs and sputter coated with gold–palladium before viewing with an FEI (Philips, Eindhoven, The Netherlands) XL30 ESEM FEG scanning electron microscope at 20 kV.

3. Descriptions

3.1. Axes and strobili

The fragmentary smooth axes are up to 100 mm long and 0.6 to 1.7 mm wide. Branching is dichotomous or of the H- or K-type (arrowed in Plate I), but lacks the axillary structures noted by Wang (2007). An elongate strand (Plate II, 7,8–9) macerated from an axis contained tracheids, 13–15 μm wide with mainly annular, sometimes helical, secondary thickenings separated by a wall containing numerous small circular to irregularly shaped perforations (Plate II, 9)—organisation that typifies G-type thickenings (Kenrick and Edwards, 1988; Kenrick and Crane, 1991; Edwards, 2003).

Almost all the axes are fertile with the terminal strobili composed of helically arranged, closely packed sporangia. The more or less parallel alignment of the strobili and their proximity at the same level (Plate I) in an allochthonous assemblage suggest that all the strobili on this slab might have belonged to the same plant, although there remains the possibility of current alignment.

Strobili are 30 to 50 mm long and 4 to 6 mm wide. Individual strobili sometimes decrease in diameter distally because individual sporangia become smaller (Plate III, 1, 3). Strobilar appearance also varies depending on the preservation of the sporangia; some are folded laterally (Plate III, 1 lower left side; 6 right side) and others are compressed without distortion such that a dorsiventral view is seen (Plate III, 3, 7 middle row). Although superficially the sporangia appear to be attached in four rows (i.e., opposite and decussate; Plate III, 7), careful dissection indicates that individuals are inserted in a very low helix.

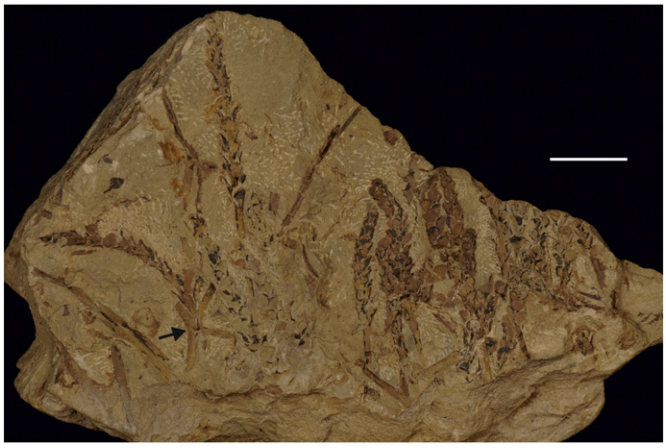

Plate I. Slab with aligned strobili of *Zosterophyllum yunnannicum* from the type locality in Qujing District, Yunnan. Arrow indicates H-branching typical of the genus. CBYn0302. Scale bar = 10 mm.

3.2. Sporangia and stalks

Each sporangium is borne on a short stalk inserted at an acute angle with only slight (Plate IV, 1, 2) or no (Plate III, 1, 5 lower arrow) adaxial curvature, such that the sporangium is held erect and almost parallel to the strobilar axis. The stalk gradually increases in width below the sporangium but there is no well-defined junction (Plates III, 8, 9; IV, 1, 2, 4) in dorsiventral view, The stalks are 0.8 to 1.2 mm high (n = 12) and 0.4 proximally to 0.8 mm wide distally (n = 10).

Each sporangium has two almost equal valves, and in face view, these may be circular or elliptical in outline with a gradual change in shape and often slight decrease in size from base to apex of a single strobilus. The diameter of the circular sporangia which ranges from 1.2 and 2.5 mm. These are usually located distally in the strobilus (Plate III, 2, 4). The height of the elliptical sporangia ranges from 1.2 to 2.5 mm, and their width from 1.7 to 3.3 mm The surface on the outside of a well preserved valve exhibits striations, probably representing epidermal cells, radiating without interruption from near the base of the sporangium to the convex margin (Plate III, 8, 9), and so a well-defined border is not obvious in this type of preservation and aspect. However when fragments of wall are missing its inner limits are marked by a coaly line or ridge which extends around the convex margin confirming the presence of a marginal feature which tapers towards the junction with the stalk (Plate IV, 3). Where the coaly wall is almost completely absent, the outer limit of the sporangium is also marked by a dark line (Plate III, 4) and a groove represents the inner limits of the border. In some specimens the junction between border and presumed sporogeneous area is marked by a gap in the coalified wall (Plate III, 9). The border itself is usually 0.3–0.4 mm wide (maximum width = 0.5 mm, n = 44) (Plate III, 4, 5 upper arrows, 7 arrows).

In sporangia compressed laterally or folded, the border is represented by two extended triangular areas that diverge at angles between 26 and 57° and taper from a broad base to a point (Plate IV, 7). In all such specimens the border of the abaxial valve is very slightly the longer and often wider at its base (Plates III, 1 arrows, IV, 1 arrow, 2 arrows, 5 arrows, 6–8,). This is confirmed by scanning electron micrographs of fractured fragments of sporangia (Plate II, 1, 2, 3 arrows, 4 arrows) where the base of the abaxial wall is thicker than the adaxial and contains some thick walled cells with rounded triangular lumina (Plate II, 1 arrow, 2 arrows; Text Fig. 1e). Where the two borders converge proximally, there is a narrow, apparently non-cellular, flat-topped band, about 25 μm wide (Plate II, 5, 6 arrows), which probably represents the dark ridges noted in light microscopy (Plate IV, 3 arrows). Here it is named the connecting band because it is a region of organic/cellular continuity between the valves. There is no evidence of further fusion between the borders of the two valves.

The sporangia are usually highly compressed dorsiventrally. In some examples the sporangial cavity is filled with a film of sediment on the surface of which, as well as on fragments of macerated sporangial wall, are occasional spores. These have been examined by scanning electron microscopy. They are smooth walled with very poorly preserved trilete marks (Plate II, 5 S-arrow, 10), but curvaturae were not observed. Spore diameter is 24 to 34 μm.

4. Systematic palaeobotany

Subdivision Lycophytina sensu Kenrick and Crane, 1997
Class Zosterophyllopsida Hao and Xue, 2013
Order Zosterophyllales Banks, 1968
Family Zosterophyllaceae Banks, 1968
Genus *Zosterophyllum* Penhallow, 1892
Zosterophyllum yunnanicum Hsü, 1966