Review of Palaeobotany and Palynology 197 (2013) 253–265

Contents lists available at SciVerse ScienceDirect

Review of Palaeobotany and Palynology

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

Research paper

The earliest fossil bamboos of China (middle Miocene, Yunnan) and their biogeographical importance

Li Wang [a,c], Frédéric M.B. Jacques [a], Tao Su [a], Yaowu Xing [d], Shitao Zhang [e], Zhekun Zhou [a,b,*]

[a] Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences (CAS), Mengla 666303, China
[b] Key Laboratory of Biodiversity and Biogeography, Kunming Institute of Botany, CAS, Kunming 650204, China
[c] State Key Laboratory of Palaeobiology and Stratigraphy (Nanjing Institute of Geology and Palaeontology), CAS, Nanjing 210008, China
[d] Institute of Systematic Botany, University of Zürich, Zürich 8008, Switzerland
[e] Faculty of Land Resource Engineering, Kunming University of Science and Technology, Kunming 650093, China

ARTICLE INFO

Article history:
Received 15 February 2013
Received in revised form 22 June 2013
Accepted 25 June 2013
Available online 3 July 2013

Keywords:
bamboo fossil record
Bambusiculmus
Bambusium
biogeography
middle Miocene
Yunnan

ABSTRACT

Fossil bamboo leaf blades and culms from the middle Miocene deposits of Sanzhangtian, Zhenyuan County, Yunnan, Southwest China are reported for the first time. The distinctive pseudopetioles and parallelodromous venation patterns of the leaf blades and the nodal morphology of the culms support the placement of the fossils into Poaceae subfamily Bambusoideae. We describe one new genus and four new species. *Bambusium angustifolia* L. Wang et Z.K. Zhou, sp. nov. has leaf blades 0.7–1.6 (1.27) cm in width with 3–6 (4) lateral veins on both sides of the midrib. Leaf blades of *Bambusium latifolia* L. Wang et Z.K. Zhou, sp. nov. are 1.4–3.8 (2.16) cm wide with 4–7 (6) lateral veins on both sides of the midrib. Culms of *Bambusiculmus latus* L. Wang et Z.K. Zhou, sp. nov. have an internodal external diameter of 1.6–2.9 (2.5) cm, and more or less horizontal nodal line and supranodal ridge, while culm of *Bambusiculmus angustus* L. Wang et Z.K. Zhou, sp. nov. has an internodal external diameter of only 1.5 cm, and horizontal supranodal ridge and oblique nodal line. Our findings provide the earliest evidence of bamboo fossil leaf blades and culms with detailed external morphological characters in China. These fossils indicate that bamboos in Yunnan began to diversify no later than the middle Miocene. Because Yunnan is one of the biodiversity centres of modern bamboos, these fossils provide new insights into bamboo biogeography.

1. Introduction

Of the 12 Poaceae subfamilies, Bambusoideae is one of the largest (Soreng et al., 2012), and currently includes 115 genera with 1439 described species (Bamboo Phylogeny Group, 2006, 2012). The monophyly of Bambusoideae is supported by molecular phylogenetic studies and three tribes are recognized within the subfamily: Arundinarieae (temperate woody bamboos), Bambuseae (tropical woody bamboos), and Olyreae (tropical herbaceous bamboos) (BPG, 2012; Kelchner and BPG, 2013). Bamboos occur on all continents except Europe and Antarctica (Soderstrom and Calderon, 1979; Sungkaew et al., 2009). Temperate woody bamboos are highly diverse in East Asia with complex morphological features and diverse habitats (Li, 1999; Ohrnberger, 1999). Temperate woody bamboos exhibit a distribution typical of the eastern Asia–eastern North America disjunction (Triplett and Clark, 2010). New World and Old World tropical woody bamboos are recognized as independent clades according to molecular evidence (Kelchner and Clark, 1997; Guo and Li, 2002; Kelchner and BPG, 2013).

The diversity of woody bamboos in Yunnan Province, southwestern China, is one of the highest in the world, both at the community and species levels (Li and Xue, 1997; Yang et al., 2004). Most of the bamboo vegetation types, ranging from tropical to subtropical, temperate and alpine, are found in Yunnan (Hsueh and Jiang, 1986). Twenty-nine genera and 250 species of bamboos grow in Yunnan, which represent three quarters of all genera and half of all species of Chinese bamboos (Yang et al., 2004). Both Arundinarieae (for example, *Chimonobambusa* Makino, *Fargesia* Franchet) and Bambuseae (for example, *Cephalostachyum* Munro, *Dendrocalamus* Nees, *Gigantochloa* Kurz ex Munro, *Schizostachyum* Nees, *Thyrsostachys* Gamble) are represented in Yunnan (Li and Xue, 1997; Li et al., 2006).

The biogeography, diversification and origin of the Bambusoideae have been the subject of numerous studies (Clark, 1997; Bouchenak-Khelladi et al., 2010; Hodkinson et al., 2010; Triplett and Clark, 2010; Ruiz-Sanchez, 2011). Fossil evidence can provide new insights into the phylogeny and biogeography of Bambusoideae, but reliable fossil records of Bambusoideae are rare, especially in China despite their modern-day species richness and wide distribution. A long fossil history of bamboo exists in South America (Frenguelli and Parodi, 1941; Brea and Zucol, 2007). The earliest reliable macrofossil of bamboo is

* Corresponding author at: Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla 666303, China. Tel./fax: +86 871 5219932.
E-mail address: zhouzk@xtbg.ac.cn (Z. Zhou).

0034-6667/$ – see front matter © 2013 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.revpalbo.2013.06.004

from the Eocene of Argentina (Frenguelli and Parodi, 1941). The earliest evidence of bamboo phytolith is from the late Eocene deposit in North America (Strömberg, 2004, 2005). Worobiec and Worobiec (2005) summarized the occurrences of fossil bamboos in Europe: the earliest macrofossil of bamboos in Europe is from the Oligocene of Italy (Peola, 1900). There are no records of Bambusoideae fossils from Africa or from the Holocene of Europe. Bamboo fossils from Asia are reported from Nepal (Awasthi and Prasad, 1990), Japan (Miki, 1941; Ozaki, 1980) and Indonesia (Heer, 1883). There is only one unquestioned report of a bamboo fossil from China, a fusinized fossil culm from the Pliocene of Xundian County, central Yunnan (Li et al., 2008). Two bamboo fossils were recorded from Neogene floras in Zhejiang, eastern China (Li, 1984) and Taiwan (Chaney and Chuang, 1968), but without any detailed descriptions and figures to confirm their placement in Bambusoideae. It is not clear whether the prevalence of extant Chinese bamboos corresponds to a recent diversification event or whether bamboos have been present in China for a long time but without a clear fossil record.

Recently, numerous well-preserved leaf blades and culms were discovered from the middle Miocene deposits in Sanzhangtian Basin, Zhenyuan County, Yunnan, Southwestern China. The material described herein represents the earliest bamboo fossil leaf blades and culms from China, with detailed external morphologies. We propose one new genus and four new species, and the importance of these new findings on bamboo biogeographical history is discussed.

2. Material and methods

2.1. Fossil locality and geological settings

Specimens were collected from Sanzhangtian, Zhenyuan County, central Yunnan, Southwestern China (24°06′ N, 101°13′ E) (Fig. 1). The Neogene deposits in Sanzhangtian belong to the Dajie Formation, and this formation is dated as middle Miocene (Ge and Li, 1999; Zhang et al., 2012) based on stratigraphic studies. Two sedimentary facies are recognized in the fossil-bearing clay: a lower fluvial facies and an upper lacustrine facies (Figs. 2, 3). Most of the bamboo fossil leaf blades and culms were found in the grey-white or white layers at the upper part of the fluvial facies (Figs. 2, 3). The rests were found in the carbonaceous mudstones and calcareous mudstones in the lacustrine deposits (Figs. 2, 3).

2.2. Fossil materials and morphological measurements

Our descriptions are based on forty-four well-preserved compression and impression fossil leaf blades. These fossil leaf blades include 21 leaf blades from "layer 21" and 23 leaf blades from "layer 19" in the fluvial deposits (Fig. 3). The epidermis was preserved on almost all compression leaf blades, but lacked clear cell morphologies. Culms were mostly preserved as compressions. Some culms were preserved as cast.

Measurements were made using ImageJ (http://rsb.info.nih.gov/ij/) and a vernier calliper. If only half of a leaf blade is preserved, the width of the leaf blade is measured as twice the width of the half leaf blade. We measured vein density following Field et al. (2011) using the length of veins per unit of leaf blade area (mm mm^{-2}). Statistical analyses were carried out in the R package. The macromorphology and micromorphology of the fossils were photographed with a Nikon D700 camera, and studied under a stereo microscope (S8APO Leica) or a microscope (DM750 Leica) coupled with digital cameras. Some specimens were immersed in aviation fuel in order to enhance the contrasts. All fossil materials and epidermis slides are kept in Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences.

2.3. Terminology

Leaf blade and culm terminology of both fossil and living bamboos follows Metcalfe (1960), Wu (1961), Soderstrom and Young (1983), Worobiec and Worobiec (2005) and Brea and Zucol (2007) (Fig. 4).

3. Systematics

Order: POALES SMALL 1903
Family: POACEAE BARNHART 1895

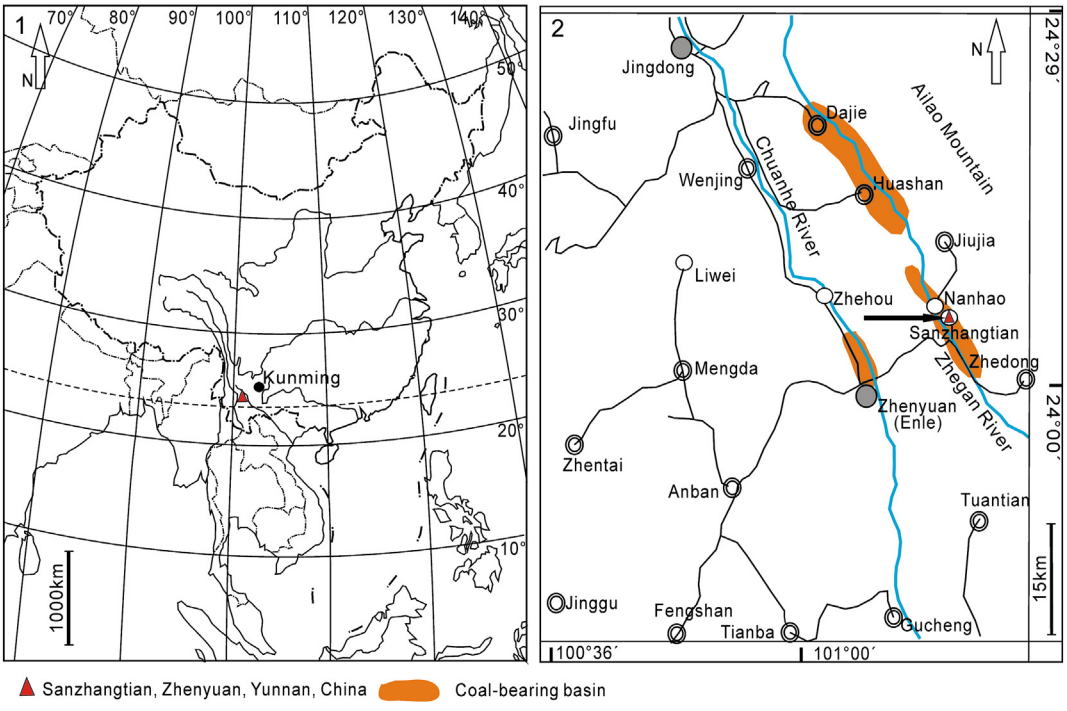

Fig. 1. 1, Study fossil locality; **2**, close-up of the site.