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

Li Wang\textsuperscript{a,c}, Frédéric M. B. Jacques\textsuperscript{a}, Tao Su\textsuperscript{a}, Yaowu Xing\textsuperscript{d}, Shitao Zhang\textsuperscript{e}, Zhekun Zhou\textsuperscript{a,b}\textsuperscript{*}

\textsuperscript{a}Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences (CAS), Mengla 666303, China

\textsuperscript{b}Key Laboratory of Biodiversity and Biogeography, Kunming Institute of Botany, CAS, Kunming 650204, China

\textsuperscript{c}State Key Laboratory of Palaeobiology and Stratigraphy (Nanjing Institute of Geology and Palaeontology), CAS, Nanjing 210008, China

\textsuperscript{d}Institute of Systematic Botany, University of Zürich, Zürich, 8008, Switzerland

\textsuperscript{e}Faculty of Land Resource Engineering, Kunming University of Science and Technology, Kunming 650093, China

\textsuperscript{*}Author for correspondence: Zhekun Zhou, zhouzk@xtbg.ac.cn

Tel and Fax: +86-871-5219932
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 centers of modern bamboos, these fossils provide new insights into bamboo biogeography.

**Keywords:** Bamboo fossil record; *Bambusiculmus; Bambusium*; biogeography; middle Miocene; Yunnan
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 (BPG), 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 Zuol, 2007). The earliest reliable macrofossils of bamboo are 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 are 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 (Fig. 2; Fig. 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 (Fig. 2; Fig. 3). The rests are found in the carbonaceous mudstones and calcareous mudstones in the lacustrine deposits (Fig. 2; Fig. 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

Subfamily: Bambusoideae Luerssen 1893

*Bambusium* Unger 1845

*Bambusium angustifolia* L. Wang et Z.K. Zhou, *sp. nov.*

*Holotype*: SZT0001-1 (Plate I, 1).

*Paratypes*: SZT0001-3, SZT0001-4, SZT0001-11, SZT0003-1, SZT0003-3, SZT0005-1 (Plate I, 3–6; Plate II, 1–3); slides: SZT-S-0001 (Plate II, 4).

*Repository*: Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, China.

*Type locality*: Sanzhangtian coal-bearing basin (24°06′ N, 101°13′ E), Zhenyuan County, central Yunnan, China.

*Type stratum*: Dajie Formation.

*Age*: middle Miocene.

*Etymology*: The specific epithet, *angustifolia*, was chosen for the narrow leaf blades.

*Diagnosis*: Leaf blades small and narrow; base cuneate; pseudopetiole narrow; leaf blade margin entire or loosely serrate with fine teeth; macro-hairs occasional; 3–6 (4) lateral veins on both sides of the midrib; 5–8 (6 or 7) third order parallel veins between lateral veins.

*Description*: The specimens are compression and impression fossil leaf blades (Plate I, 1, 3–6). Most leaf blades are incomplete. Leaf blades are linear, lanceolate to...
elongate, up to 10.5 cm long and 0.7–1.6 (1.27) cm wide. Two almost entire leaf blades are 8 and 9.5 cm long (Plate I, 3–4). The apex is attenuate (Plate I, 3–4).

Pseudopetioles are narrow and approximately 1 mm wide and 2 mm long (Plate I, 1). Leaf blade bases are cuneate, decurrent on pseudopetioles (Plate I, 1). Venation pattern is parallelodromous. Midrib is distinct, and generally projects on the abaxial surface. On both sides of the midrib there are 3–6 (4) less distinct lateral veins spaced 0.86–2.23 (1.27) mm apart (Plate I, 1, 3–4, 6; Plate II, 1). There are 5–8 (6 or 7) delicate, third order parallel veins spaced 0.12–0.27 (0.19) mm apart between adjacent lateral veins (Plate II, 1). Cross veins connect adjacent parallel veins (Plate II, 1). The cross veins and third order parallel veins form a tessellate venation pattern. Adjacent cross veins are spaced 0.35–1.07 (0.61) mm apart, slightly oblique or perpendicular to the third order parallel veins (Plate II, 1, 4). Vein densities are 5.78–10.11 (7.06) mm mm$^{-2}$. Leaf blade margins are entire or loosely serrate with fine teeth spaced 520–380 μm apart, at an angle of 45° or less from the margin (Plate II, 2). In some leaf blades, macro-hairs 82–141 μm long occur in the intercostal zones or near the third order parallel veins (Plate II, 3). Numerous small black dots with a diameter of 13.6–22.7 μm are more commonly found on both sides of the third order parallel veins (Plate II, 3); these dots are most likely prickle-hairs or prickle-hair bases. Bands of probable bulliform cells lie between two adjacent third order parallel veins (Plate II, 4).

There are also many larger dark spots with a diameter of 44–103 μm on the epidermis (Plate II, 1, 4). They are possible epiphyllous fungi. Leaf blade damage by pathogens (Plate I, 5) is similar to those found in modern samples (Plate IV, 7).
**Bambusium latifolia** L. Wang et Z.K. Zhou, *sp. nov.*

*Holotype*: SZT0009b-1 (Plate III, 1).

*Paratypes*: SZT0009a-7, SZT0009b-2, SZT0010a, SZT0010a-1, SZT0010a-2, SZT0010a-3, SZT0010a-5, SZT0010a-8, SZT0010a-10, SZT0010a-14, SZT0010b-8, SZT0010b-15, SZT0011-5 (Plate III, 2–6; Plate IV, 1–6).

*Repository*: Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, China.

*Type locality*: Sanzhangtian coal-bearing basin (24°06' N, 101°13' E), Zhenyuan County, central Yunnan, China.

*Type stratum*: Dajie Formation.

*Age*: middle Miocene.

*Etymology*: The specific epithet, *latifolia*, was chosen for the broad leaf blades.

*Diagnosis*: Leaf blades mostly large and wide; base cuneate or obtuse; pseudopetiole wide and long in branch leaf blades, very short in culm leaf blades; 4–7 (6) lateral veins on both sides of the midrib; 5–9 (7) or occasionally 3–5 third order parallel veins between lateral veins.

*Description*: The specimens are compression and impression fossil leaf blades (Plate III, 1–6). Most leaf blades are incomplete. Leaf blades are linear, lanceolate to elongate. The apex is attenuate (Plate III, 6). Leaf blade bases are cuneate or obtuse, decurrent on pseudopetioles (Plate III, 1–5). Venation pattern is parallelodromous.

Branch leaf blades are 1.4–3.8 (2.16) cm wide. Fragmentary leaf blades are up to 12.5 cm long. Pseudopetioles are about 2–4 mm long and 2 mm wide (Plate III, 1, 4).
Midrib is distinct, and generally projects on the abaxial surface. There are 4–7 (6) less distinct lateral veins on both sides of the midrib spaced 1.29–3.07 (1.87) mm apart (Plate III, 1, 4–6; Plate IV, 1). There are 5–9 (7) delicate, third order parallel veins spaced 0.18–0.42 (0.24) mm apart between adjacent lateral veins (Plate IV, 1–2, 6). Cross veins connect adjacent parallel veins. The cross veins and third order parallel veins form a tessellate venation pattern. Adjacent cross veins are spaced 0.26–1.02 (0.57) mm apart, oriented slightly oblique or perpendicular to the third order parallel veins (Plate IV, 1–2, 6). Vein density is 4.64–7.63 (5.84) mm mm^-2. The presence of teeth on leaf blade margins is not obvious. Numerous small black dots with a diameter of 17.6–25.7 (20.1) μm are more commonly found along the intermediate line of the intercostal zones between two adjacent third order parallel veins (Plate IV, 3). They are most likely prickle-hairs or prickle-hair bases.

There are also many larger dark spots with a diameter of 64.7–108.8 μm on the epidermis of branch leaf blades (Plate IV, 1, 6). They are possible epiphyllous fungi. Many pathogen-damaged areas were observed on some branch leaf blades (Plate III, 5–6; Plate IV, 5), and are similar to modern examples (Plate IV, 7).

Two culm leaf blades are 1 and 2.2 cm wide. Pseudopetioles are very short and wide, and about 1–1.5 mm long and 2–3 mm wide (Plate III, 2–3). Midrib is not distinct especially in the smaller leaf blade. On both sides of the midrib there are 6 less distinct lateral veins spaced 0.88–1.91 (1.42) mm apart (Plate III, 2–3). There are 3–5 (4–5) delicate, third order parallel veins spaced 0.22–0.34 (0.27) mm apart between adjacent lateral veins (Plate III, 2–3). Numerous small black dots with a
diameter of 12.8–19.2 (16.8) μm are found on both sides of the third order parallel
veins (Plate IV, 4). They are most likely prickle-hairs or prickle-hair bases.


*Type:* *Bambusiculmus angustus* L. Wang et Z.K. Zhou, *sp. nov.*

*Diagnosis:* Nodes and internodes conspicuous; nodal line and/or supranodal
ridge horizontal and/or oblique; remnant basal parts of the culm sheath sometimes on
odal line; surface smooth or sulcate.

*Etymology:* The new genus is named for bamboo fossil culms.

*Bambusiculmus latus* L. Wang et Z.K. Zhou, *sp. nov.*

*Holotype:* SZT0012a-1, SZT0012b-1 (Plate V, 1–4).

*Paratypes:* SZT0012a-2, SZT0012a-3, SZT0012b-2, SZT0012b-3 (Plate V, 1–2).

*Repository:* Xishuangbanna Tropical Botanical Garden, Chinese Academy of
Sciences, China.

*Type locality:* Sanzhangtian coal-bearing basin (24°06’ N, 101°13’ E), Zhenyuan
County, central Yunnan, China.

*Type stratum:* Dajie Formation.

*Age:* middle Miocene.

*Etymology:* The specific epithet “*latus*” refers to the wide feature of these fossil
bamboo culms.

*Diagnosis:* Culm thick; internodal external diameter around 2.5 cm; nodal line
and supranodal ridge both more or less horizontal; surface smooth.
**Description:** The specimens are compression, impression and cast of fossil culms (Plate V, 1–4). Culms are incomplete. Culms have conspicuous nodes and internodes. Each specimen has one conspicuous node and two incomplete internodes, with an internodal external diameter of 1.6–2.9 (2.5) cm. The nodes have a diameter of about 3 cm and a length of about 0.8 cm. Buds are not observed. The lowermost boundary of the node is the nodal line and the uppermost boundary of the node is the supranodal ridge (Plate V, 3–4). The nodal region is somewhat concave. The nodal line or sheath scar and the supranodal ridge are horizontal. The supranodal ridge area is more or less swollen. Culm surface is usually smooth. The incomplete internode is up to 14 cm long.

**Bambusiculmus angustus** L. Wang et Z.K. Zhou, *sp. nov.*

*Holotype:* SZT0013a, SZT0013b (Plate V, 5–8).

*Repository:* Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, China.

*Type locality:* Sanzhangtian coal-bearing basin (24°06' N, 101°13' E), Zhenyuan County, central Yunnan, China.

*Type stratum:* Dajie Formation.

*Age:* middle Miocene.

*Etymology:* The epithet “*angustus*” refers to the thin feature of these fossil bamboo culms.

*Diagnosis:* Culm thin, internodal external diameter about 1.5 cm; supranodal ridge more or less horizontal; nodal line oblique; remnant basal parts of the culm
sheath on nodal line; surface sulcate, especially on and above supranodal ridge.

**Description:** The specimens are compression and impression fossil culms (Plate V, 5–8). Culms are incomplete. The culm has conspicuous nodes and internodes. The culm is hollow in the internode area (Plate V, 5). The specimen has one conspicuous node and two incomplete internodes, with an internodal external diameter of about 1.5 cm of the culm. The node has a diameter of 1.6 cm and a length of 0.5 cm. Buds are not observed. The lowermost boundary of the node is the nodal line and the uppermost boundary of the node is the supranodal ridge (Plate V, 5–8). The nodal region is concave near the nodal line. The nodal line is oblique, bearing remnant basal parts of the culm sheath (Plate V, 7–8). The supranodal ridge area is swollen and the supranodal ridge is more or less horizontal. Culm surface is sulcate especially at and above the supranodal ridge (Plate V, 6–8). The incomplete internode is up to 8 cm long.

**4. Discussion**

**4.1. Fossil Taxonomy**

The presence of deciduous leaf blades and pseudopetioles is the synapomorphy of the woody bamboos (Soderstrom and Ellis, 1987; Geng and Wang, 1996; Grass Phylogeny Working Group (GPWG), 2001; Plate I, 2). The fossil leaf blades from the Miocene of Sanzhangtian are assigned to Bambusoideae due to the presence of a pseudopetiole along with the linear, lanceolate to elongate leaf blade shape and parallelodromous venation patterns.

In Poaceae, leaf blades of several genera such as *Phragmites* (subfamily
Arundinoideae), Arundo (subfamily Arundinoideae), Neyraudia (subfamily Chloridoideae) and Thysanolaena (subfamily Panicoideae) are similar to bamboo leaf blades in their general shape or venation pattern, but their leaf blades lack a pseudopetiole and pass directly into a sheath (Geng and Wang, 1996; personal observation).

Although pseudopetioles are also present in other Poaceae (GPWG, 2001), such as whole members of Anomochlooideae, Pharoideae and Puelioideae, some members of Ehrhartioideae and Panicoideae, and very few members of Pooideae (GPWG, 2001), these non-bambusoid grasses have leaf blades which lack the abscission layer in their pseudopetioles. For example, the leaf blade of Lophatherum Brongniart, a member of the Zeugiteae within the Panicoideae (Sánchez-Ken and Clark, 2010), has a pseudopetiole and leaf blade shape and venation pattern similar to those of Bambusoideae (personal observation), but Lophatherum is herbaceous and does not lose leaf blades due to the lack of an abscission layer between the leaf blade and leaf sheath and are unlikely to be preserved only as separated leaf blades, as is the case with our specimens. Moreover, the leaf blade vein density in Lophatherum (2.85 mm mm⁻²) is much lower than that of the fossils (5.9 to 6.99 mm mm⁻²).

Furthermore, these fossil bamboo leaf blades share other features with modern bamboos, including (1) minute teeth on the leaf blade margins (Plate II, 2, 6), (2) macro-hairs on the leaf blade epidermis (Plate II, 3, 5), (3) bands of bulliform cells between two adjacent third order parallel veins (Plate II, 4, 7) and (4) probable prickle-hairs or prickle-hair bases (Plate II, 3; Plate IV, 3–4). Among these features,
the presence of bulliform cells is a synapomorphy for the Poaceae family (Metcalf, 1960). The combined presence of pseudopetiole and such characteristics enables us to confidently assign the fossil presented here to Bambusoideae.

The fossil culms are identified as Bambusoideae because they share features characteristic of Poaceae stems and in particular Bambusoideae culms: they possess conspicuous nodes and internodes, and conspicuous nodal lines and supranodal ridges in the nodal regions. Although some non-bambusoid Poaceae genera have nodal lines and supranodal ridges, these structures are always less conspicuous than in bamboos (Keng, 1959).

Generic assignment of bamboo leaf blades based only on their morphological and anatomical characteristics is difficult (Metcalf, 1956; Soderstrom and Ellis, 1987; Worobiec and Worobie, 2005). Because the identification of bamboos based only on leaf blade or culm material is highly tentative, we place these fossil leaf blades in the fossil genus Bambusium and the culms in the fossil genus Bambusiculmus instead of assigning them to a specific modern genera.

Fossil bamboo culms are always preserved together with fossil bamboo leaf blades in the same sediment layers in Sanzhangtian. However, because there were no direct anatomic connections between the fossil leaf blades and culms described here, we prefer to describe them as separate species. New discoveries and further studies may help resolve their affinity.

4.2. Comparisons with other fossil species

The leaf blades of Bambusium angustifolia and B. latifolia differ remarkably
from *Bambusa ilinskiae* Shvareva from the Miocene of the Precarpatians (Shvareva, 1970): the latter has broader leaf blades, and more lateral veins (Table 1).

Leaf blades of *Sasa kodorica* Kolakovsky from the Neogene of Kodor in Abkhazia (Kolakovsky, 1964) are more than twice as wide as *Bambusium angustifolia*. *Sasa kodorica* has similar leaf blade width to *B. latifolia*, but lacks venation information. *Sasa lugdunensis* (Saporta) Givulescu, from a Neogene deposit in Chiuzbaia, Maramures, Romania (Givulescu, 1984), has narrow leaf blades, and is similar to *B. angustifolia* in size and the number of lateral veins, but has relatively fewer third order parallel veins.

*Bambusium* sp. A from the late Miocene flora of Tatsumitoge in Honshu, Japan (Ozaki, 1980) is not similar to the species from Sanzhangtian. It has larger leaf blades than *B. latifolia*, and far more lateral veins from 7 to 10). In the same deposit in Tatsumitoge, the size and numbers of veins in *Bambusium* sp. B are similar to *B. latifolia*, but whether cross veins are present in the former is unknown. *Bambusa* sp. from the Pliocene flora of Murat, Cantal, France (Roiron, 1991) has linear leaf blades with leaf blade base attenuate into short pseudopetioles, which are similar to those of Sanzhangtian fossil leaf blades, while the smaller leaf blades and fewer veins differ from those of *B. angustifolia*. Leaf blades of *Phyllostachys* sp. from the upper Miocene in Central Hondo, Japan (Miki, 1941) and *B. angustifolia* are similar in width, but no further venation information is available.

*Bambusium angustifolia* from Sanzhangtian is most similar to “*Bambusa* *lugdunensis*” Saporta (Worobiec and Worobiec, 2005) described from the upper
Miocene of the Belchatów Lignite Mine, Central Poland in size and vein numbers, except for the cross vein space. The cross vein space of *B. angustifolia* is over twice as long as “*Bambusa*” *lugdunensis*, thus the length/width ratio of the quadrangle formed by cross veins and third order parallel veins of *B. angustifolia* is higher than in “*Bambusa*” *lugdunensis*. *Bambusa lugdunensis* from the Pliocene of Asti, Piedmont, Italy, has abruptly narrowed leaf blade bases (Martinetto, 2003), which is different from our fossils which possess attenuate leaf blade bases into short pseudopetioles.

Few culm fossils with bambusoid affinities have been reported. Brea and Zucol (2007) reported the first fossil record of petrified bamboo culms *Guadua zuloagae* in the Pliocene Ituazaingó Formation, Argentina, which has both morphological and anatomical features. Its internodal external diameter is 3.0–3.5 cm, which is larger than in *Bambusicalmus latus*. Another fossil *Guadua* from the upper Pliocene–upper Pleistocene in the southwestern Peruvian Amazon (Olivier et al., 2009) differs from our fossil culms in its spiny or thorny structures at the node regions. The culm of *Phyllostachys* sp. from the late Miocene deposit in Central Hondo, Japan (Miki, 1941) is 1–1.4 cm broad, which is narrower than *B. latus* and *B. angustus*. The culm of Bambusoideae sp. from the Pliocene deposit in Xundian County, Yunnan, possesses Type-I vascular bundle (Li et al., 2008), but external morphological descriptions are not available. *Chusquea rolloti* from Cenozoic sediments of Colombia has relatively slender stems, large linear-lanceolate leaf blades and expanded rhizomal internodes (Berry, 1929). *Chusquea oxyphylla* has a 7 cm long leaf blade impression with a culm containing ten nodes covered by imbricated sheaths, where four leaf blades can be
observed (Frenguelli and Parodi, 1941). Both of these Chusquea culms bear leaf blades but have incomplete nodal and internodal information. In summary, based on the lack of morphological and anatomical similarities with other fossil and extant culms, we place fossil culms from Sanzhangtian into a new genus Bambusiculmus.

4.3. Biogeographical importance

Modern woody bamboos are distributed on all continents except Europe and Antarctica, and their greatest diversity is in Southeast Asia and South America, where they grow in various environments, such as tropical, subtropical, temperate and alpine zones (Hodkinson et al., 2010; Fig. 5). To date, there are about 43 localities around the world that have yielded fossil bamboos (Appendix; Fig. 5), though some fossils described from these localities may not be bamboos. Most fossil bamboo localities occur within the distributions of modern bamboos, especially in their greatest centers of diversity, Southeast Asia and South America. However, some fossil bamboos (e.g. European bamboo fossils) occur at latitudes further north than extant distributions (Fig. 5).

The earliest reliable bamboo macrofossils are found from the Eocene of Argentina (Frenguelli and Parodi, 1941), which is consistent with Clark’s (1997) hypotheses that the earliest bamboos were of Gondwanan origin (southern hemisphere). Consistent with the distribution of modern native bamboo taxa in South America, fossil bamboo genera in the region are mainly neotropical woody bamboos, such as Guadua (Brea and Zuco, 2007; Olivier et al., 2009; Brea et al., 2013). European bamboo fossils occur from the Oligocene to the Pleistocene (Peola, 1900;
Martinetto and Sami, 2001; Worobiec and Worobiec, 2005). The latest fossil bamboo record from Europe is from the Pleistocene of Italy (Martinetto and Sami, 2001). From then on, bamboos disappear from Europe, most likely because of Quaternary glaciations (Ehlers and Gibbard, 2008). In Asia, bamboo fossils are found mainly in the southern Himalayas to Japan from the late Miocene to Pliocene (Miki, 1941; Ozaki, 1980; Awasthi and Prasad, 1990; Li et al., 2008). These regions also have a rich diversity of modern temperate and paleotropical bamboos (Fig. 5). Pleistocene Arundinaria fossils were found in southeastern North America (Berry, 1910; Brown, 1938), consistent with the occurrence of extant Arundinaria in North America (Fig. 5). In Oceania, only two probable fossil bamboos are reported from the eastern coast of Australia (Ettingshausen, 1887a) and from New Zealand (Ettingshausen, 1887b). In these two areas there are no native modern bamboos. Modern Australian native bamboos only occur on the northern coast of Australia (Franklin, 2008) (Fig. 5). Although Africa has both modern palaeotropical and temperate woody bamboos (Bystriakova et al., 2004; Sungkaew et al., 2009), there are no fossil bamboo records. Our findings provide the earliest evidence of bamboo fossil leaf blades and culms in China. The presence of bamboo fossils in Sanzhangtian indicates that bamboos have occurred in Yunnan over a long geological history; a diversified fossil bamboo forest or bamboo understory was already present during the middle Miocene in Yunnan, the biodiversity center of modern bamboos in China. This ancient bamboo forest or bamboo understory in an evergreen–deciduous forest accompanied by taxa like Lauraceae, Alangium and Metasequoia (unpublished data) in Sanzhangtian
potentially represents the environment in which *Ailurarctos*, one of the basal members of the giant panda lineage found from the upper Miocene of Yunnan, China (Qiu and Qi, 1989; Abella et al., 2012), could have lived.

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Figures and plates captions:

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

Fig. 2. Stratigraphic section of the fossil locality in Sanzhangtian. The sketches of bamboo leaf blades and culms indicate the layers bearing fossils.

Fig. 3. Sedimentological stratigraphic section of the outcrop in Sanzhangtian. The sketches of bamboo leaf blades and culms indicate the layers bearing fossils. The Arabic numerals on the left of the two columns indicate the number of layers in each sedimentary facies.

Fig. 4. Line sketch of the typical leaf blade shape, venation pattern and culm morphology of modern bamboo. 1°, midrib, 2°, lateral vein, 3°, third order parallel vein, 4°, cross vein.

Fig. 5. Geographical distribution of fossil and modern woody bamboos. Dots represent fossil localities, and colours indicate geological ages (red, Paleogene; yellow, Miocene; green, Pliocene; blue, Pleistocene; grey, Neogene; dark black, Cenozoic). Modern wooly bamboo distribution in fill colours or outlines: pink, paleotropical woody bamboos; purple, neotropical woody bamboos; light blue outlines, temperate woody bamboos. Modern woody bamboo distribution map is modified from http://www.eeob.iastate.edu/research/bamboo/maps.html, with permission from Dr. Lynn Clark.

Plate I. Leaf blades of Bambusium angustifolia (1, 3-6) and Arundinaria gigantea
(Walt.) Muhl. (2).

1, Basal pseudopetiolate (black arrow) leaf portion, Holotype, SZT0001-1, scale bar = 10 mm;

2, *A. gigantea* leaf blade with a pseudopetiole (black arrow), KUN No. 0927028, scale bar = 10 mm;

3, a nearly entire leaf blade, Paratype, SZT0005-1, scale bar = 10 mm;

4, a nearly entire leaf blade, Paratype, SZT0003-1, scale bar = 10 mm;

5, Leaf fragment with damaged areas by pathogens (white arrow), Paratype, SZT0001-11, scale bar = 5 mm;

6, middle and basal part of a fossil bamboo leaf blade, Paratype, SZT0001-4, scale bar = 10 mm.

**Plate II.** Micromorphology of *Bambusium angustifolia* (1-4) and modern bamboos *Arundinaria gigantea* (5-6) and *Fargesia wuliangshanensis* T.P. Yi (7).

1, Amplification of a part of leaf blade, showing the venation pattern and epiphyllous fungi (indicated by white arrows), Paratype, SZT0001-3, scale bar = 5mm;

2, fine teeth (black arrow) on leaf blade margin, Paratype, SZT0003-3, scale bar = 200μm;

3, macro-hairs (white arrows) on epidermis, prickle-hairs or prickle-hair bases (black arrow) along the costal zones, Paratype, SZT0001-3, scale bar = 200μm;

4, separated leaf blade epidermis, showing epiphyllous fungi (black arrow), band of probable bulliform cells (white arrow), Paratype, SZT-S-0001, scale bar = 200μm;

5, macro-hairs (black arrows) on leaf blade epidermis of *A. gigantea*, Kun No.
0927028, scale bar = 200μm;

6, fine teeth (black arrow) on leaf blade margin of *A. gigantea*, Kun No. 0927028, scale bar = 200μm;

7, adxial leaf blade epidermis of a modern bamboo *F. wuliangshanensis*, showing bands of bulliform cells (black arrow) and the third order parallel veins (white arrow), ALS-S-0001, scale bar = 100μm.

Plate III. Branch leaf blades and culm leaf blades of *Bambusium latifolia* (1-6) and modern bamboo *Melocalamus arrectus* T.P. Yi (7).

1, Branch leaf blade with basal part with pseudopetiole (black arrow), Holotype, S0T0009b-1, Scale bar = 5 mm;

2, fragmentary basal part of culm leaf blade with short pseudopetiole (black arrow). Paratype, S0T0010b-8, scale bar = 5 mm;

3, fragmentary basal part of culm leaf blade with short pseudopetiole (black arrow). Paratype, S0T0010b-15, scale bar = 5 mm;

4, branch leaf blade with middle and basal part, showing broad leaf blade base (black arrow), Paratype, S0T0009b-2, Scale bar = 5 mm;

5, branch leaf blade with middle and basal part and an incomplete pseudopetiole (black arrow), Paratype, S0T0010a-1; black triangle indicate a damaged area by pathogens in another branch leaf blade, Paratype, S0T0010a-10, Scale bar = 5 mm;

6, fragments of fossil leaf blades (Paratype, S0T0010a) including branch leaf blades (black triangles: S0T0010a-3, S0T0010a-10, S0T0010a-14; white arrow: S0T0010a-2) and a basal part of culm leaf blade (black arrow: S0T0010a-8), white
arrow shows the attenuate leaf apex, black triangles indicate damaged areas by pathogens, scale bar = 10 mm;

7, leaf blade of modern bamboo *M. arrectus* on lower part of the culm, showing the short and wide pseudopetiole (black arrow), XTBG-0001, scale bar = 5 mm.

**Plate IV.** Micromorphology of *Bambusium latifolia* (1-6) with epiphyllous fungi and pathogen-damaged areas on the leaf blades and modern bamboo *Arundinaria fargesii* E.G. Camus (7).

1, Details of leaf blade venation, white arrows indicate epiphyllous fungi, Paratype, SZT0009a-7, scale bar = 2 mm;

2, details of leaf blade venation, Paratype, SZT0010a-3, scale bar = 2 mm;

3, prickle-hairs or prickle-hair bases (white arrow) in the intercostal zones, Paratype, SZT0010a-5, scale bar = 500μm;

4, prickle-hairs or prickle-hair bases (white arrow) along the costal zones, Paratype, SZT0010a-8, scale bar = 200μm;

5, enlargement of one damaged area by pathogens, Paratype, SZT0011-5, scale bar = 500μm;

6, part of leaf blade showing epiphyllous fungi (white arrow), Paratype, SZT0010a-10, scale bar = 500μm;

7, part of leaf blade of *A. fargesii* with damaged area by pathogens (white arrow), Kun No. 0384198, scale bar = 2mm.
Plate V. Culms of *Bambusiculmus latus* (1-4) and *Bambusiculmus angustus* (5-8).

1, three culms (a, b, c) of *B. latus*. a, Holotype, SZT0012a-1; b and c, Paratypes, SZT0012a-2, SZT0012a-3, scale bar = 5 cm;

2, three culms (a, b, c) that are counterparts of those in “1”. a, Holotype, SZT0012b-1, b and c, Paratypes, SZT0012b-2, SZT0012b-3, scale bar = 2 cm;

3, enlarged nodal region of one culm (a) in “1”, showing nodal line (triangle) and the supranodal ridge (arrow), Holotype, SZT0012a-1, scale bar = 1 cm;

4, enlarged nodal region of one culm (a) in “2”, showing nodal line (triangle) and the supranodal ridge (arrow), Holotype, SZT0012b-1, scale bar = 1 cm;

5, a part of culm of *B. angustus* with one node (arrow) and two incomplete internodes, noting the outer (white triangle) and inside (black triangle) surface of the impressed culm-wall, Holotype, SZT0013a, scale bar = 2 cm;

6, enlargement of the nodal region, showing the nodal line (triangle) and the supranodal ridge (arrow), Holotype, SZT0013a, scale bar = 1 cm;

7, enlarged nodal region of the counterpart of the culm in “6”, showing the nodal line (triangle) and the supranodal ridge (arrow), Holotype, SZT0013b, scale bar = 1 cm;

8, enlargement of the nodal region of the culm in “6”, showing the remnant basal parts of the culm sheath (triangle), Holotype, SZT0013a, scale bar = 5 mm.

Table captions:

Table 1. Comparison of Sanzhangtian fossil bamboo leaf blades with other fossils.
Figure 1

[Map showing locations and geological features]

▲ Sanzhangtian, Zhenyuan, Yunnan, China

Coal-bearing basin
Figure 2

Legend
- Bamboo fossils
- Carbonaceous mudstone
- Calcareous marl lens
- Silt mudstone
- Sandstone
- Finely conglomerate
- Coarse conglomerate

Lacustrine deposits

Fluvial deposits

80°

15m
Figure 3
Figure 4
Figure 5
Plate II
Plate III
Plate IV
Plate V
Table 1. Comparison of Sanzhangtian fossil bamboo leaves with other fossils.

<table>
<thead>
<tr>
<th>Fossil species</th>
<th>Leaf width (mm)</th>
<th>Lateral vein number</th>
<th>Third order parallel vein number</th>
<th>Lateral vein space (mm)</th>
<th>Third order parallel vein space (mm)</th>
<th>Cross vein space (mm)</th>
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<td>6-10</td>
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<td></td>
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<td><em>S. lugdunensis</em></td>
<td>6; 15</td>
<td>3; 5</td>
<td>5</td>
<td></td>
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<td>Givulescu, 1984</td>
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<td>7-10</td>
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<td>(0.61)</td>
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<td><em>B. latifolia</em></td>
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<td>5-9 (7)</td>
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* Branch leaves.
Highlights

• The earliest bamboo record of China was reported from the middle Miocene of Yunnan.

• Two genera with four new species were described by leaf blade and culm fossils.

• Bamboo had diversified in Yunnan as early as the middle Miocene.