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Late Miocene wood flora associated with the Yuanmou hominoid fauna from Yunnan, southwestern China and its palaeoenvironmental implication

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Abstract The Upper Miocene Xiaohe Formation of the Yuanmou Basin in Yunnan Province, southwestern China, is famous for its hominoid fauna and is important for studying the Late Cenozoic human and mammal evolution. Abundant fossil wood was found associated with this fauna, which provided important evidence for palaeoenvironmental reconstruction of the basin. Among the fossil wood, two different taxa have been identified namely, *Quercoxylon* sp. (Fagaceae) and *Pterocarya* sp. (Juglandaceae). Based on the habitats of their Nearest Living Relatives (NRLs), it is suggested that upland subtropical evergreen broad-leaved forest dominated by *Quercus*/*Lithocarpus* was common around the basin, while a lowland deciduous broad-leaved forest dominated by *Pterocarya* was present on the river bank of the basin during the Late Miocene.

Key words fossil wood, *Quercoxylon*, *Pterocarya*, palaeovegetation, Late Miocene, Yuanmou Basin

1 Introduction

Several Miocene hominoid localities, namely Baoshan, Kaiyuan, Lufeng, Shangri-La, Yuanmou, and Zhaotong occur in Yunnan Province of southwestern China (Biasatti *et al.*, 2012). The fossil hominoids of Yunnan provide a unique temporal perspective on the evolutionary history of hominoids (Harrison *et al.*, 2002). Among these localities, the Yuanmou Basin is well known for its Pliocene fauna (Cheng *et al.*, 2005; Qian 1985; Qian and Zhou, 1991) and the Late Miocene hominoid fauna (He, 1997; Qi *et al.*, 2006), and might have been an important refuge for hominoids after they experienced extinction in the rest of Eurasia (Harrison *et al.*, 2002; Zhu *et al.*, 2005). The age and character of the Yuanmou hominoid fauna are similar to the Late Miocene Siwalik faunas of Pakistan, the Lufeng fauna of Yunnan and the Baode fauna of Shanxi, China (Johnson and Vondra, 1972; Flynn *et al.*, 1990; Pan and Zong, 1993; Quade and Cerling, 1995; Barry *et al.*, 2002).

The palaeoenvironment of the Yuanmou Basin has been reconstructed with the help of faunal statistics (Ni and Qiu, 2002; Qi *et al.*, 2006), palynological evidence (Qian and Ling, 1998) and stable carbon and oxygen isotopes (Biasatti *et al.*, 2012). According to the analysis of micromammals, the habitats of the Yuanmou hominoids and associated fauna were mainly mountainous forests, including some dense forests and transitional shrubberies, as well as some open flat valleys and rivers (Ni and Qiu 2002; Qi *et al.*, 2006). Palynological analysis indicates that the Yuanmou hominoid lived in sparse forest-grasslands in a

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warm and dry climate (Qian and Ling, 1998). Additionally, stable carbon and oxygen isotope studies show that a forest cover was present in the Yuanmou Basin during the Late Miocene (Biasatti *et al.*, 2012).

Although the aforementioned studies indicate the presence of either a dense or a sparse forest cover in the Yuanmou Basin, lack of direct plant megafossil evidence makes it difficult to decipher the faunal makeup of the forest.

According to geological and paleontological surveys (Qian and Zhou, 1991; He, 1997; Zhang *et al.*, 2002), abundant fossil wood fragments were discovered with the hominoid fauna in the Upper Miocene Xiaohe Formation of Leilao, Zhupeng and Xiaohe villages in the Yuannmou Basin, but the woods have not been previously investigated in detail. Based on a large number of fossil wood specimens, this study describes two taxa of fossil wood, viz., *Quercoxylon* sp. (Fagaceae) and *Pterocarya* sp. (Juglandaceae) from the Upper Miocene hominoid-bearing Xiaohe Formation of Leilao, Zhupeng and Xiaohe villages, Yuanmou County, Yunnan Province, China and throws light on the palaeovegetation and palaeoclimate of the region.

2 Materials and methods

The Yuanmou Basin, at an elevation of 1050 to 1380 m, is located approximately 110 km northwest of Kunming (provincial capital) in Yunnan Province of southwestern China (Figure 1). The north-south elongated basin is bordered by elevated regions of metamorphic rocks and granites of the Precambrian basement and Jurassic to Cretaceous sediments. The basin is mainly filled by a thick series of Late Cenozoic fluvial and lacustrine sediments that contain abundant mammalian fossils (Qian and Zhou, 1991; Pan and Zong, 1991; He, 1997; Harrison *et al.*, 2002; Qi *et al.*, 2006). The Upper Miocene hominoid-bearing Xiaohe Formation lies mostly in the northwestern section of the basin, and consists of 80 m of clays, silts, partially cemented fine sands, and gravels overlying the Jurassic to Cretaceous sediments. The formation also contains abundant hominoid and other mammalian fossils (He, 1997; Harrison *et al.*, 2002; Qi *et al.*, 2006) and fossil wood fragments (Qian and Zhou, 1991; He, 1997). This formation is dated between 7.2 and 8.1 Ma based on palaeomagnetic evidence (Qi *et al.*, 2006). Large fossil trunks were often found in association with gravels. The material for the present study was collected from the lower part of the Xiaohe Formation of Leilao, Zhupeng, and Xiaohe villages of Yuanmou County in Yunnan Province of southwestern China. Ground thin sections were prepared using standard techniques of cutting, grinding and polishing and different grades of carborundum powder were used for polishing (Hass and Rowe, 1999). Both the specimens and the slides have been deposited at the Geological Museum of China. Anatomical terms used in this paper follow the recommendations of the IAWA list of microscopic features for hardwood identification (IAWA Committee, 1989).

3 Systematic description

3.1 Fagaceae

Quercoxylon Kräusel, 1939

Quercoxylon sp. (Figure 2a−2e)

Growth rings are indistinct. Wood is diffuse porous. Vessels are exclusively solitary, circular to slightly oval in outline, showing a stream-like arrangement. The tangential diameters of the vessels range from 67 to 270 μm, with a mean of 196 μm, and the radial diameter of the vessels range from 55 to 229 μm, with a mean of 167 μm. The vessel frequency is 6−10 /mm^2. Perforation plates are simple. Intervessel pits were not observed. Vessel-ray parenchyma pits with reduced borders are horizontally to vertically elongate and variable. Tyloses are thin-walled and abundant. Vasicentric tracheids with distinctly bordered pits present around large vessels. Axial parenchyma is relatively abundant, diffuse to diffuse-in-aggregate, and also in 1−3 celled thick bands. Rays consist of two distinct types, uniseriate and multiseriate; multiseriate rays are exclusively compound, 289−833 μm, mean 516 μm wide, up to 6 mm high.

Samples: P2291 (ZP6), P2292 (ZP28), P2293 (LL22).

Locality: Zhupeng (ZP) and Leilao (LL), Yuanmou County, Yunnan Province, China.

Horizon and age: Lower part of the Xiaohe Formation, Late Miocene.

Repository: Geological Museum of China, Beijing, China.

Affinities: The important diagnostic features of the fossils, exclusively solitary vessels, vessel-ray parenchyma pits with reduced borders, horizontally to vertically elongate vasicentric tracheids, diffuse to diffuse-in-aggregate axial parenchyma, and uniseriate and compound rays, indicate its affinity with the Fagaceae, especially with evergreen species of *Quercus* L. and *Lithocapus* Bl. (Metcalfe and Chalk, 1950; Shimaji, 1962; Cheng *et al.*, 1992).

Kräusel (1939) instituted the genus *Queroxylon* to include fossil wood resembling *Quercus*/*Lithocarpus*. As reviewed by Kramer (1974a, 1974b), Wheeler *et al.* (1978), Gros

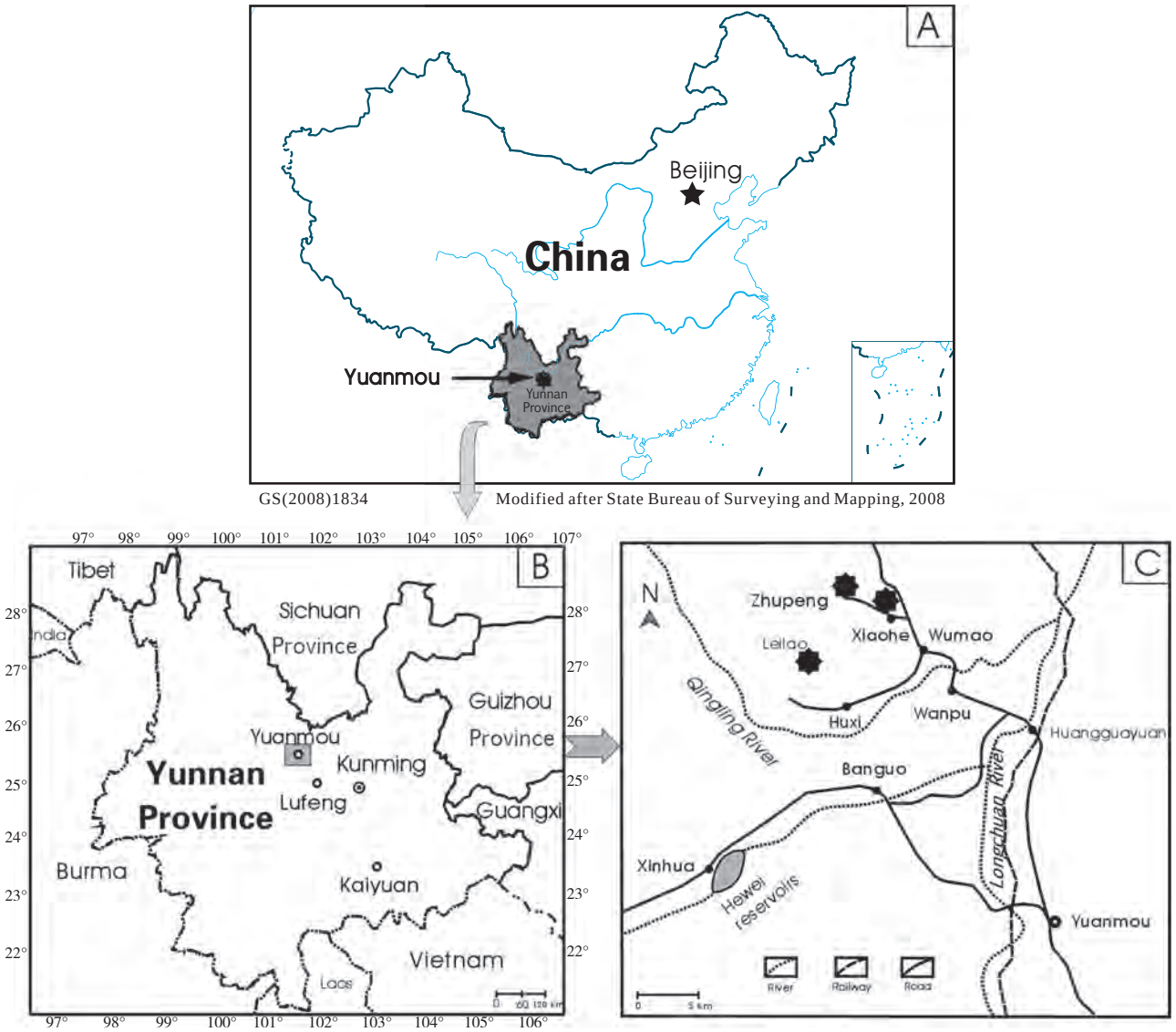

Figure 1 Map showing fossil collection localities of Yuanmou, Yunnan, China. ✹ Fossil site.

(1983), Suzuki and Ohba (1991), and Insidewood (http://insidewood.lib.ncsu.edu/search), a large number of fossil wood fragments belonging to *Quercus* and *Lithocarpus* are known from the Neogene of Europe, America and Asia. Most of them are ring porous, and only a few show diffuse and semi-ring porosity. Gros (1983) instituted the genus *Quercoxylon* to include fossil wood resembling *Quercus*/*Lithocarpus*. We assign the fossil to *Queroxylon* sp.

Evergreen species of *Quercus* and *Lithocapus* are distributed in tropical and subtropical regions of Asia and are important elements of the subtropical evergreen broad-leaved forest (Huang *et al.*, 1999).

3.2 Juglandaceae

Pterocarya Nutt. ex Moq.

Pterocarya sp. (Figure 3a−3e)

Growth rings are distinct, marked by radially flattened fibres near the growth rings, marginal parenchyma and difference in vessel diameter. Wood is diffuse porous. Vessels are mostly solitary or in radial multiples of 2−3 (−5), with a special diagonal arrangement. The tangential diameters of the vessels range from 67 to 248 μm, with a mean of 155 μm; and the radial diameters of vessels range from 57 to 260 μm, with a mean of 155 μm, their number ranges from 12 to 19 (mostly 14−16) /mm^2. Perforation plates are simple. Intervessel pits are alternate, and range from 8 to 14 μm, with a mean of 11μm in size. Vessel-ray parenchyma pits are similar to intervessel pits. Length of vessel elements is 245−600 μm, mean 429 μm. Helical thickening is absent. Thin-walled tyloses are abundant. The axial paren-

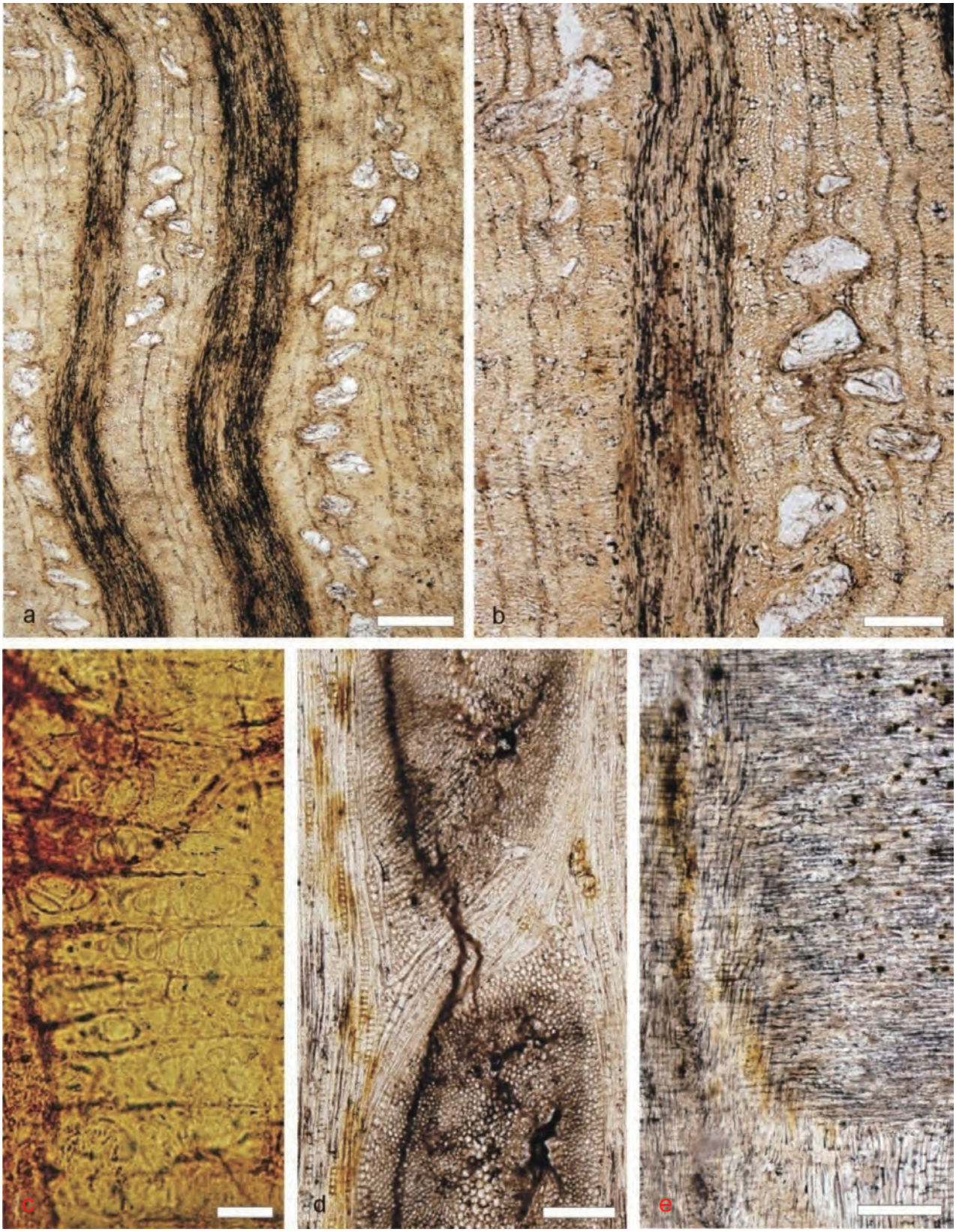

Figure 2 *Quercoxylon* sp. (Fagaceae) (P2291). a−Cross section showing diffuse porous wood and wide multiseriate ray. Scale bar = 500 μm; b−Another cross section showing diffuse to diffuse-in-aggregate axial parenchyma and thin-walled tyloses in vessels. Scale bar = 200 μm; c−Radial section showing vessel-ray parenchyma pits with reduced borders. Scale bar = 20 μm; d−Tangential section showing two types of rays, compound multiseriate and uniseriate. Scale bar = 200 μm; e−Radial section showing homocellular rays made up of procumbent cells. Scale bar = 200 μm.

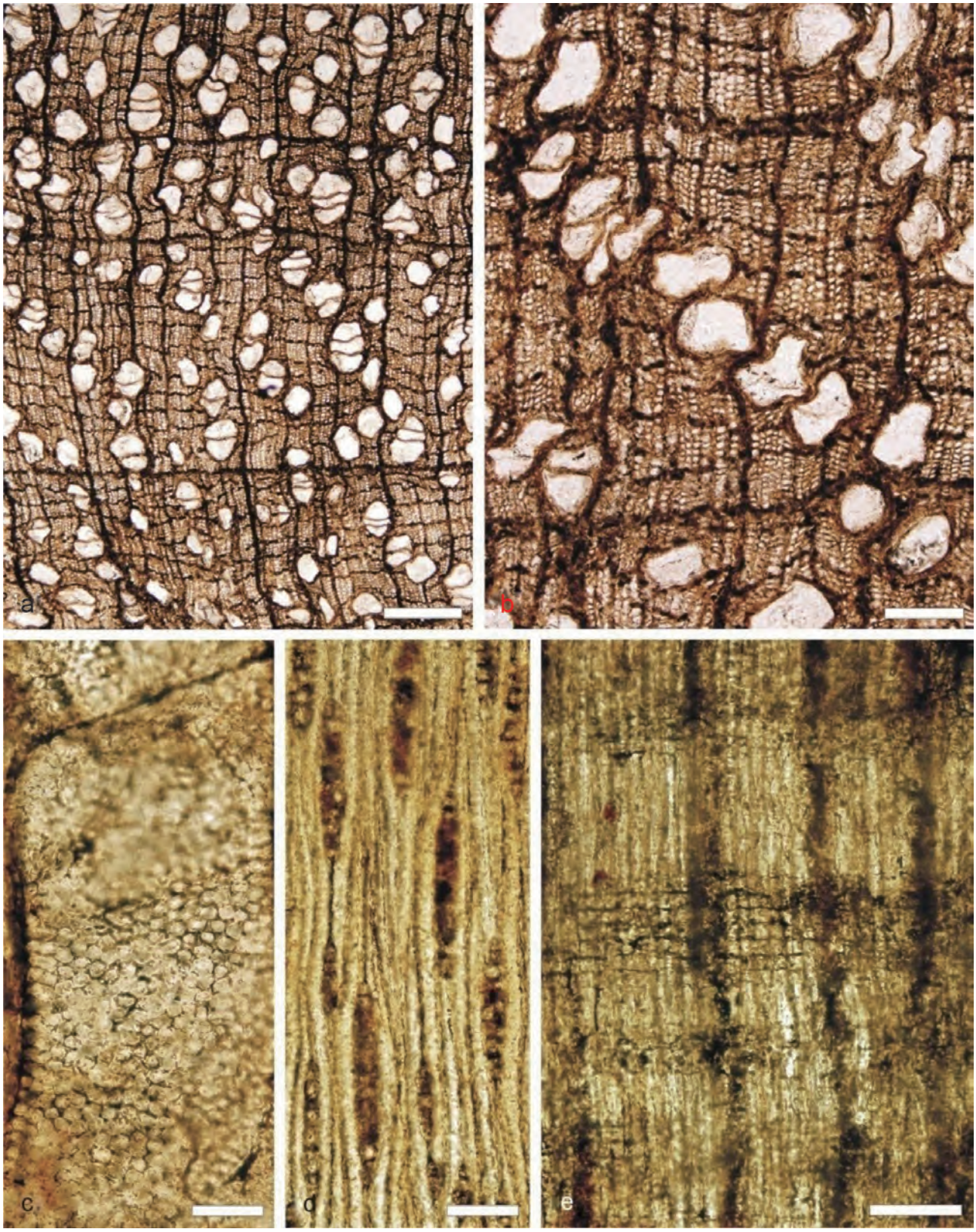

Figure 3 *Pterocarya* sp. (Juglandaceae) (P2302). a−Cross section showing distinct growth rings and diffuse porous wood. Scale bar = 500 μm; b−Another cross section showing long uniseriate lines of parenchyma. Scale bar = 200 μm; c−Tangential section showing alternate intervessel pits, and simple perforation plates. Scale bar = 50 μm; d−Tangential section showing width and height of rays. Scale bar = 100 μm; e−Radial section showing homocellular rays made up of procumbent cells. Scale bar = 100 μm.

chyma is in the form of long uniseriate lines, marginal and is closely spaced near the growth rings. Rays are 6−8 /mm, 1−3 (mostly 2) seriate, and homocellular; multiseriate rays are 3−22 cells or 48−358 (mean 191) μm in height.

Samples: P2302 (ZP 11), P 2294(LLTL5), P 2295 (ZP1), P 2296(ZP 2), P 2297 (ZP 3), P2298 (ZP 5), P 2299 (ZP 7), P 2300 (ZP 9), P2301 (ZP 10), P 2303 (ZP 12), P2304 (ZP 13), P2305 (ZP 14), P2306 (ZP 15), P2307 (ZP 16), P 2308 (ZP 17), P2309 (ZP 18), P 2310 (ZP 19), P2311 (ZP 23), P 2312 (ZP 24), P2313 (ZP 25), P 2314 (ZP 27), P 2315 (ZP 29), P2316 (XH3), P2317 (XH 4), P 2318 (XH 5), P 2319 (XH 6), P 2320 (LL20), P 2321 (LL 21), P2322 (LL25).

Locality: Zhupeng (ZP), Xiaohe (XH) and Leilao (LL) villages, Yuanmou County, Yunnan Province, China.

Horizon and age: Lower part of the Xiaohe Formation, Late Miocene.

Repository: Geological Museum of China, Beijing, China.

Affinities: The diagnostic characters of the present fossils, predominantly solitary vessels with a special diagonal arrangement, simple perforation plates, alternate inter-vessel pits, uniseriate and closely spaced axial parenchyma, and exclusively homocellular narrow rays were found in *Juglans* L. and *Pterocarya* Nutt. ex Moq. of the family Juglandaceae (Metcalfe and Chalk, 1950; Manchester, 1983). The wood of *Juglans* differs from the present fossil in having up to 4−celled wide rays and 2−3 celled thick axial parenchyma bands. The fossil in this study has a marked resemblance to *Pterocarya.*

Müller-Stoll et Mädel (1960) erected the genus *Pterocaryoxylon* for fossil wood resembling modern *Pterocarya*. To date, five species of *Pterocaryoxylon*, viz., *P. pannonicum* Müller-Stoll et Mädel from the Pliocene of Hungary (Müller-Stoll et Mädel,1960), *P. subpannonicum* Privé from the Pliocene of France (Privé, 1974), *P. knowltonii* Wheeler, Scott et Barghoorn from the Eocene of America (Wheeler *et al.*, 1978), *P. chinense* (Francini) Müller-Stoll et Mädel from the Tertiary of China (Francini, 1931; Dupéron, 1988), and *P. honshouense* (Watari) Müller-Stoll et Mädel from the Miocene of Japan (Müller-Stoll et Mädel, 1960) are known. Several fossil wood fragments have also been assigned to the extant taxon *Pterocarya parvipora* Terada et Suzuki from the Miocene of Japan (Choi *et al.*, 2010). Due to poor preservation of our fossil, we describe this fossil as *Pterocarya* sp.

Pterocarya consists of 6 species distributed in E and SW Asia, five of which are found in China and three of these in Yunnan. These are *P. stenoptera* C. DC., *P. tonkinensis* (Franch.) Dode, and *P. macroptera* Batalin, which often grow in wet places *i.e.*, rivulet, river bank, and hillside *etc.* (Lu *et al.*, 1999).

4 Discussion

The palaeoenvironment of the Late Miocene Yuanmou Basin has been reconstructed on the basis of palynological evidence (Qian and Ling, 1998), micromammalian studies (Ni and Qiu, 2002), analysis of the Yuanmou hominoids fauna (Qi *et al.* 2006), and stable carbon and oxygen isotope records (Biasatti *et al.*, 2012). None of these studies, however, show the type and composition of forest in any detail. The statistics (Qi *et al.*, 2006) show that 50% of the micromammals associated with the Yuanmou hominoids are strict forest habitat selectors, 18.4% are forest and relatively humid woodland margin habitat selectors, and only 5.3% are shrub and open grassland habitat selectors. The habitats of the Yuanmou hominoids and associated fauna are mainly mountainous forests, including some dense forests and transitional shrubberies, as well as some open flat valleys and rivers (Ni and Qiu 2002; Qi *et al.*, 2006). Palynological evidence suggests that the basin had sparse forest-grasslands and a warm, dry climate (Qian and Ling, 1998). Analysis of the stable carbon isotopes show that a largely forested environment existed at ~8 Ma in Yuanmou (Biasatti *et al.*, 2012).

A large number of fossil trunks found in the Xiaohe Formation indicate that dense forest was present around the Yuanmou Basin. This study describes evergreen *Quercus /Lithocarpus* (Fagaceae) and *Pterocarya* (Juglandaceae) wood fragments from the formation. The evergreen *Quercus /Lithocarpus* fossil wood is very common in the sediments of the Xiaohe Formation, and its NLR (Nearest Living Relative) is an element of upland subtropical evergreen broad-leaved forest. Fossil wood of *Pterocarya* is predominant in the assemblage and its NLR often grows on river banks. In addition to these fossils, fossil wood of *Pistacia* has recently been reported from the Xiaohe Formation of Leilao, Yuanmou (Cheng *et al.*, 2012). Based on the habitats of NRLs of the fossil wood, it is suggested that a subtropical evergreen broad-leaved forest of *Quercus / Lithocarpus* grew around the Yuanmou Basin, while the deciduous broad-leaved forest of *Pterocarya* and *Pistacia* occurred on the river bank within the basin, during the Late Miocene.

In Yunnan Province, two Late Miocene faunas, similar to the Yuanmou hominoid fauna in composition and characters, were obtained from the Kaiyuan and Lufeng Counties. The Kaiyuan and Lufeng faunas lived in an environment similar to that of the Yuanmou hominoid fauna.

Based on the analysis of fauna and flora, the Lufeng hominoids of the Shihuiba Formation lived in a woodland or forest environment with bush vegetation in a tropical or subtropical climate. Evidently, some lakes, ponds or swamps existed in or around the woodland. At the woodland edges and between the woodlands and wetlands, there was a variety of bush and grass (Qi, 1993). Both the Lufeng and Yuanmou localities must have had landscapes dominated by montane forests, with humid and luxuriant shrubs, and patches of open bush and grassland located in wide valleys with nearby rivers (Ni and Qiu, 2002).

According to palynological studies, the Kaiyuan Late Miocene vegetational type can be considered as an evergreen broad-leaved forest, predominantly composed of Fagaceae and accompanied by a few deciduous trees (Wang, 1996). A large number of tropical and subtropical genera such as *Albizzia*, *Cassia*, *Castanopsis*, *Cinnamomum*, *Cyclobalanopsis*, *Desmos*, *Ficus*, *Lithocarpus*, *Machilus*, *Phoebe*, and *Quercus*, and some temperate elements such as *Acer* and *Juglans* from the Late Miocene Xiaolongtan of Kaiyuan (Zhou, 1995; 2000), suggest that the Kaiyuan hominoid fauna must have lived in a humid subtropical climate. The above studies above indicate that the Kaiyuan hominoid fauna lived in mainly mountainous forests.

In addition to the three hominoid fauna localities, there are four representative Miocene sedimentary basins of Jianchuan, Tengchong, Jinggu, and Lincang in Yunnan Province. Abundant data on megafossils and spore-pollen fossils indicate that during the Miocene there was widespread distribution of tropical or subtropical evergreen broad-leaved forest or mixed deciduous-evergreen broad-leaved forest in Yunnan Province (Wu, 2010).

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