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Late Miocene southwestern Chinese floristic diversity shaped by the southeastern uplift of the Tibetan Plateau

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ABSTRACT

In southwestern China and Southeast Asia modern geology and topography have been influenced strongly by the collision between the Indian and Eurasian plates. The southeastern margin of the Tibetan Plateau is well known for its high biodiversity and diverse vegetation types. While the present diversity is explained by the geological history of this region, to date no study has looked at how past vegetation was shaped by geological and topographical history. In this study, we focus on three coeval late Miocene leaf assemblages from Yunnan: Lincang, Xiaolongtan and Xianfeng. The palaeoelevation of these three sites is reconstructed using enthalpy as a palaeoaltimeter. Enthalpy at the fossil site is reconstructed based on leaf physiognomy; the difference between this enthalpy and enthalpy at sea-level is used as a proxy for altitude. The palaeoaltitudes are resolved as 214 ± 901 m asl for Lincang, 530 ± 901 m asl for Xiaolongtan, and 1936 ± 901 m asl for Xianfeng. The floristic components of these floras are analysed for their geographical elements. There is a gradient in the percentage of tropical genera between the three floras from Lincang, at the lowest elevation, to Xianfeng, at the highest level. For Lincang, this percentage exceeds the threshold used to define present day tropical regions. Our results demonstrate that there was already a floristic differentiation in Yunnan during the late Miocene. Floras with tropical affinities were at low altitude, whereas floras with temperate affinities were at high altitude. With the later uplift of southern Yunnan, floras with tropical affinities retreated to the south where they are still present. The uplift framework reconstructed in this paper gives a tectonic context for further studies on the impact of uplift on biodiversity.

1. Introduction

In recent years many studies have focused on the southeastern extension of the Qinghai–Tibetan Plateau (Clark and Royden, 2000; Schoenbohm et al., 2004; Clark et al., 2005a,b; Shen et al., 2005; Schoenbohm et al., 2006a,b; Westaway, 2009; Bai et al., 2010; Searle et al., 2011; Wang et al., 2011). This southeastern Tibetan borderland is mostly situated in Yunnan, southwestern China (Fig. 1) and has been studied extensively because important mechanisms of the India–Eurasia collision, such as the extrusion of Indochina, took place in this region (Tapponnier et al., 1990; Leloup et al., 1995; Replumaz et al., 2001; Replumaz and Tapponier, 2003). The impact of the regional tectonics on past climates has been studied in several papers: Kou et al. (2006) demonstrated the influence of the uplift of mountain ranges on Yunnan precipitation; Zhang et al. (2012) demonstrated how the uplift of the Ailao mountains influenced the winter monsoon; Xie et al. (2012) and Su et al. (2013) showed how the uplift of Gaoligong and Nu mountains influenced precipitation in western Yunnan. Several palaeobotanical studies have provided a detailed palaeoclimatic background for this province during the late Cenozoic (Wu et al., 2009; Xia et al., 2009; Jacques et al., 2011a; Sun et al., 2011, 2012; Xing et al., 2012; Zhang et al., 2012; Su et al., 2013). The modern diverse floristic composition of Yunnan province has been explained by the geological history of the province (Zhu, 2012, 2013a). Palaeovegetation reconstructions of China show an imbrication of several vegetation types in Yunnan since the late Miocene (Jacques et al., 2011c, 2013) hypothetically linked to a complex landscape (Jacques et al., 2011c). However, no study has really looked at the impact of the local geology on the floristic differentiation of Yunnan in the past.

Several phylogeographic studies based on molecular sequences have demonstrated the importance of the geological history of Yunnan on the plant population and diversification in this region. For example, the evolution of the drainage system influenced the diversity pattern of *Terminalia franchetii* (Zhang and Sun, 2011) and *Buddleja crispa* (Yue et al., 2012), while the uplift of the Qinghai–Tibet Plateau can explain the floristic evolution of the region and its origin from a Tethysian flora (Sun and Li, 2003) and tectonic movement and river dynamics the formation of endemic species in Yunnan (Qiu et al., 2011). Yunnan

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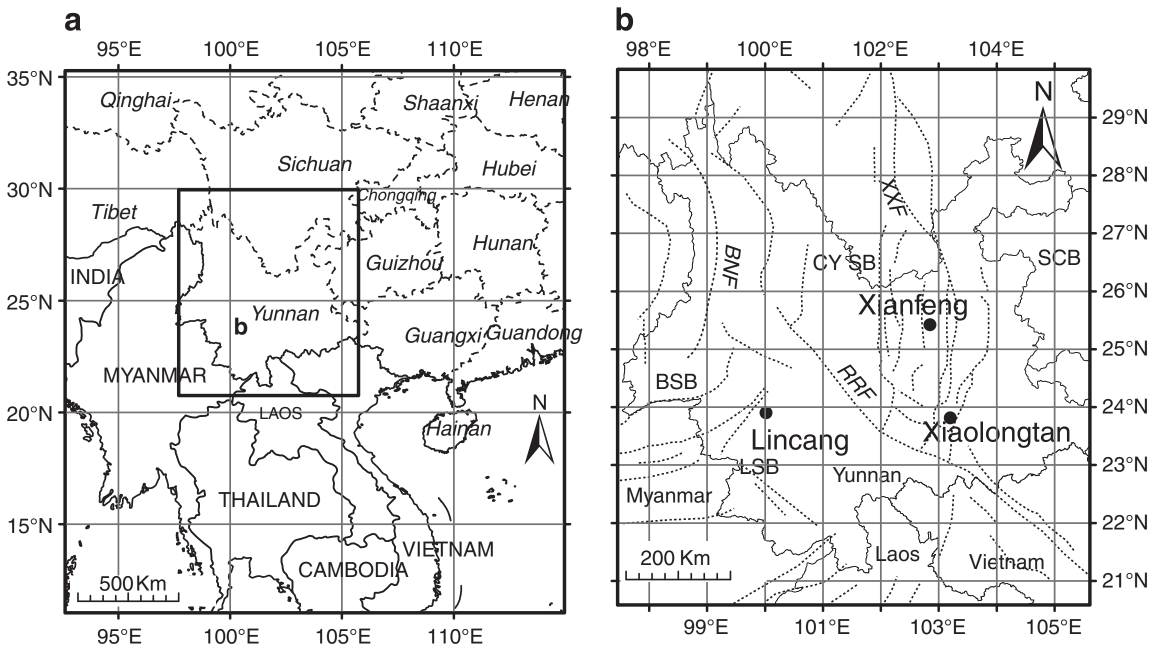

Fig. 1. Location of the three fossil sites. a. General map of Southeast Asia. b. Location of the three fossil sites in Yunnan and main fault systems (dashed lines) of the region. BNF, Bangong–Nujiang Fault; BSB, Baoshan Sub-block; CY SB, Central Yunnan Sub-block; LSB, Lincang Sub-block; RRF, Red River Fault; SCB, South-China Block; XXF, Xianshuihe–Xiaojiang fault system.

is one of China's biodiversity 'hotspots': its surface only accounts for 4% of the Chinese territory, but supports half the species of vascular plants, birds and mammals present in China (Wu and Zhu, 1987). Moreover, most vegetation types of China can be found in this province. Consequently, Yunnan is an ideal region to study the impact of tectonics on floristic composition and structure because: (1) the diversity of vegetation types occurring in Yunnan ranges from tropical forest in the south to alpine meadow in the northwest (Li and Walker, 1986); (2) the complex tectonic history of the province, where modern altitudes range from almost sea level to more than 6000 m asl within a distance of approximately 850 km. These marked vegetation and altitude differentiations can enhance the visibility of the changes.

Despite the important relationship between uplift and biodiversity, research in this field lacks a good time and space framework for the uplift. Several studies provide insight into the uplift history of Yunnan (Schoenbohm et al., 2004, 2006a; Cao et al., 2011), but they all give relative, instead of absolute, altitude. In this paper, we propose an original approach: reconstruct absolute palaeoaltitudes of the studied fossil sites in order to discuss Yunnan floristic changes in a strong tectonic context. Using enthalpy as a palaeoaltimeter (Forest et al., 1999) gives the palaeoaltitude at a fossil site, and palaeoenthalpy is obtainable from fossil leaf assemblages.

Here we focus on the late Miocene. The Miocene is a critical time slice to investigate because the modern tectonic regime in Yunnan province was established by around 8 to 10 Ma (Royden et al., 2008), as a result of a long period of extrusion of Indochina (Replumaz and Tapponier, 2003; Royden et al., 2008; Yang and Liu, 2009). First we reconstructed the geological and tectonic context of the three fossil sites in terms of palaeoaltitude. We then analysed the floristic differences between three late Miocene floras of Yunnan. Finally, we looked at possible links between geological patterns and floristic patterns.

2. Material and methods

2.1. Geological settings

The major tectonic structures in Yunnan Province (Fig. 1) are the Red River Fault, which shows minor activity in the late Cenozoic (Schoenbohm et al., 2006a), and the Xianshuihe–Xiaojiang fault system (Shen et al., 2005; Royden et al., 2008; Taylor and Yin, 2009), which became active at around 8 to 10 Ma (Royden et al., 2008). In the Neogene, the tectonic activity of Yunnan Province is characterised by a general extensional context (Schoenbohm et al., 2006a). Modern GPS velocity data indicate a surface regional clockwise rotation around the eastern Himalayan syntaxis (Shen et al., 2005). The geological structures of Yunnan have sometimes been used to explain the modern phytogeography of Yunnan: the geological structures correspond to the accretion of different geological blocks or terranes, the two major ones being the Yangtze Block and the Lincang Terrane. According to Zhu (2013a), there is a biogeographical line at the border between these two blocks.

2.2. Palaeofloras

The three leaf assemblages studied here are: the Lincang flora (Guo, 2011; Jacques et al., 2011a), the Xiaolongtan flora (Zhou, 1985; Tao et al., 2000; Xia et al., 2009) and the Xianfeng flora (Xing et al., 2012) (Fig. 1). The Lincang flora is situated on the Lincang Terrane, whereas Xiaolongtan and Xianfeng are both situated on the South China Terrane, or Yangtze Block, north of the Red River Fault (RRF; Fig. 1). The coordinates of the studied sites are indicated in Table 1. The Lincang flora belongs to the Bangmai Formation, which is dated as being of late Miocene age by stratigraphic correlation between sediment deposits in Yunnan and the plant fossil composition of these layers (Guo, 2011; Jacques et al., 2011a), while both the Xiaolongtan and Xianfeng floras belong to the Xiaolongtan Formation, also dated as late Miocene by mammal fossils (Dong, 2001) and palynology (Wang, 1996). Thus, both the Bangmai Formation and the Xiaolongtan Formation are considered as late Miocene; and, according to the available geological and stratigraphical evidence (Group of the Regional Stratigraphic Table of Yunnan, 1978; Bureau of Geology and Mineral Resources of Yunnan Province, 1990; Zhang, 1997), the three floras are considered as coeval.

These three floras yielded rich fossil assemblages with Fagaceae and Lauraceae as dominant families (Zhou, 1985; Xia et al., 2009; Guo, 2011; Xing et al., 2012). Overall, 73 morphotypes were recognised from the Lincang flora, 54 from Xiaolongtan and 54 from Xianfeng. Compositionally, they reflect a warm and humid late Miocene climate in Yunnan (Xia et al., 2009; Jacques et al., 2011a; Xing et al., 2012). CLAMP palaeoclimate reconstructions give mean annual temperatures (MATs)

Table 1
Palaeoclimate reconstructions of three late Pliocene floras in Yunnan.

Site		Lincang		Xiaolongtan		Xianfeng	
Age		Late Miocene	Present day	Late Miocene	Present day	Late Miocene	Present day
Location	Latitude		23.9		23.81		25.42
	Longitude		100.02		103.2		102.85
CLAMP results	MAT (°C)	19.8 ± 1.25	17.3	19.9 ± 1.25	19.7	15.4 ± 1.25	14.9
	WMT (°C)	27.3 ± 1.51	21.3	26.7 ± 1.51	24.3	26.8 ± 1.51	19.7
	CMT (°C)	11.2 ± 2.57	10.8	12.5 ± 2.57	12.8	6.2 ± 2.57	7.6
	GSP (mm)	2269.7 ± 217.7	1178.7	1970.3 ± 217.7	820.5	1908.7 ± 217.7	1003.2
	SH (g/kg)	13.15 ± 1.09	10.9	12.58 ± 1.09	11.7	9.67 ± 1.09	9.57
	Enthalpy (kJ/kg)	344.1 ± 5.4	325.3	342.3 ± 5.4	333.1	327.0 ± 5.4	318.3
Enthalpy at sea-level (kJ/kg)		346.2 ± 7.0		347.5 ± 7.0		346.0 ± 7.0	
Altitude (m)		214 ± 901	1600	530 ± 901	1050	1936 ± 901	2200

between 15 and 19 °C and growing season precipitation (GSP) estimates between 1900 and 2300 mm for these three sites, confirming warm and humid palaeoclimates (Xia et al., 2009; Jacques et al., 2011a; Xing et al., 2012).

2.3. Palaeoelevation analysis

The enthalpy palaeoaltimeter is based on physical properties of the atmosphere. The difference in enthalpy at a known elevation (such as sea-level) and a land-surface at an unknown height is given by Eq. (1) (Forest et al., 1999):

$$Z = \frac{H_{\text{sea level}} - H_{\text{altitude}}}{g} \tag{1}$$

where Z is the height difference, $H_{\text{sea level}}$ is enthalpy at sea level, H_{altitude} is enthalpy at the unknown altitude, and g is the acceleration due to gravity (9.81 m s^{-2}).

In order to reconstruct the palaeoelevation of fossil sites, enthalpy both at the fossil site and at a known height such as sea-level is required (Forest et al., 1999; Spicer et al., 2003). Enthalpy is strongly coded in leaf form (physiognomy) and is routinely estimated using CLAMP (Climate Leaf Analysis Multivariate Program) (Wolfe, 1993). CLAMP traditionally correlates 31 leaf characters of woody dicots with 11 climatic parameters, including enthalpy (Herman and Spicer, 1996), is robust to taphonomical bias (both species and character loss) (Spicer et al., 2011), gives estimates of elevation comparable with those obtained by isotopic methods and with quantifiable uncertainties (Spicer and Yang, 2010). This empirical multivariate relationship is universal and robust worldwide in contrast to univariate relationships, and has therefore been used widely for climatic reconstructions ranging in age back to the mid Cretaceous (Herman and Spicer, 1996). A CLAMP analysis was carried out for each site. The physiognomic scores of each site are given in Supplementary Information 1; the scores used in this study are those used in the original publication (Xia et al., 2009; Jacques et al., 2011a; Xing et al., 2012). CLAMP is calibrated using modern vegetation and several such datasets are available. Here we use the PhysgAsia1–GridMetAsia1 calibration because it is the one that is most appropriate for the monsoon climates of China (Jacques et al., 2011b). Canonical correspondence analysis was performed using CANOCO 4.5. The procedure follows the protocols given on the CLAMP website (http://clamp.ibcas.ac.cn/). The calibration used for this study is appropriate because all the fossil floras used here plot within the cloud of modern Asian (Chinese and Japanese) sites in physiognomic space (Fig. 2).

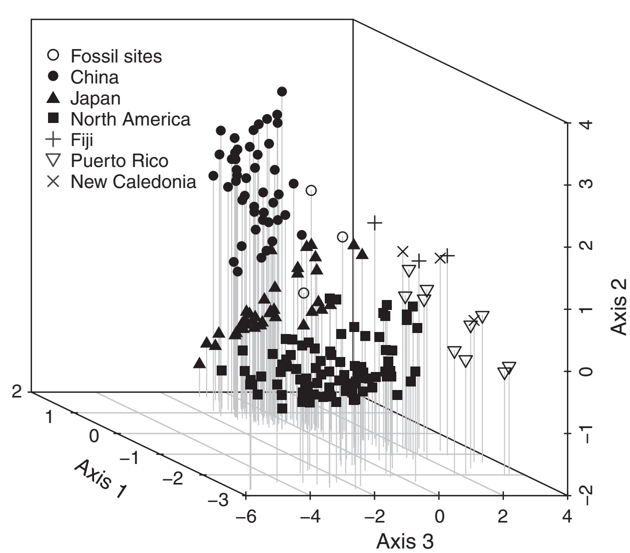

Fig. 2. Position of the three fossil assemblages in physiognomic space. Physiognomic space is constructed using canonical correspondence analysis based on the PhysgAsia1 CLAMP calibration. LC, Lincang; XF, Xianfeng; XLT, Xiaolongtan. Lincang plots within the Chinese cloud; Xiaolongtan plots between the Chinese and Japanese clouds; Xianfeng plots within the Japanese cloud.

Enthalpy at sea-level can be obtained from a coeval locality at sea-level and at the same latitude or from palaeoclimate modelling (Spicer et al., 2003). In this study, a projected value for sea level enthalpy for the same location as the fossil sites was retrieved from a Hadley Centre numerical model for the late Miocene (xakf), available from the BRIDGE website (http://www.bridge.bris.ac.uk/resources/simulations).

The uncertainty of the palaeoaltitude reconstruction has two components: uncertainty of the enthalpy at the fossil site reconstructed by CLAMP (5.4 kJ.kg^{-1}) and uncertainty of the enthalpy at sea level from the model (7.0 kJ.kg^{-1}; Spicer et al., 2003). There is an 8.84 kJ.kg^{-1} uncertainty in the enthalpy difference, which results in a ±901 m uncertainty of elevation when dividing by gravitational acceleration.

2.4. Floristic analysis

The three palaeofloras have been well studied. Their floristic composition was retrieved from the original descriptions (Zhou, 1985; Xing, 2010; Guo, 2011). Complete species lists for these sites are given in Appendix 1. The APG3 classification was used for each taxon in this study. Only the angiosperms were considered.

For the floristic analysis, we followed the method of Wu (1991), which was also used by Zhu (2012, 2013a) for modern biogeographic studies in Yunnan. The distribution patterns of the floristic elements of these three floras were evaluated at the generic level based on Wu (1991) and at the family level based on Wu et al. (2003). This method recognises 18 major areal types for Chinese plants (the last three types are not naturally occurring in China):

1. Cosmopolitan;
2. Pantropic;
3. Tropical and subtropical East Asia and tropical, subtropical America disjunct;

4. Old World Tropics;
5. Tropical Asia to tropical Australasia and Oceania;
6. Tropical Asia to tropical Africa;
7. Tropical Asia;
8. North Temperate;
9. East Asia and North America disjunct;
10. Old World Temperate;
11. Temperate Asia;
12. Mediterranean and West to Central Asia;
13. Central Asia;
14. East Asia;
15. Endemic to China;
16. Extratropical South Hemisphere disjunct or dispersed;
17. Tropical Africa and Tropical America disjunct;
18. Holantarctic.

We performed a comparison between the three palaeofloras based on the floristic composition and the geographical patterns of these elements. This method indicates the areal type of each floristic element, i.e. its distribution around the globe.

2.5. Independence of the methods

Our study reconstructs both palaeovegetation and palaeoaltitude from plant mega-fossil data. However, the two reconstructions are methodologically independent, because they use different information from the fossils. The palaeovegetation is reconstructed based on the taxonomy of the fossils whereas the palaeoaltitude is reconstructed using the physiognomy of the fossils.

3. Results

3.1. Palaeoaltitude analysis

The complete CLAMP results are available in Supplementary Information 2. Our results show that in late Miocene times both Lincang and Xiaolongtan were at low altitude (214 m and 530 m asl, respectively), whereas Xianfeng was at almost 2000 m asl (Table 1). Xianfeng was close to its present altitude, whereas Lincang and Xiaolongtan were both at a lower altitude than present.

3.2. Floristic analysis

The family composition of each palaeoflora is given in Table 2. Fagaceae and Lauraceae, the two major components of all three floras, are represented by up to 20% of morphotype diversity in these floras. Fabaceae are major elements in Lincang and Xiaolongtan (up to 30% in Xiaolongtan). The biodiversity at the family level is the highest in Lincang. The generic composition of each palaeoflora is given in Table 3. Details of the assignments are indicated in Supplementary Information 3.

The geographical elements at family level are given in Table 4. The three fossil sites have clearly different compositions in areal types at the family level (Fig. 3A). Pantropical families represent almost half of the families present in Lincang, whereas they represent only a quarter of the families in Xiaolongtan and Xianfeng. The temperate families are important in Xianfeng, with almost half of the families having temperate biogeographic affinities. In Xiaolongtan, the cosmopolitan families are the major component, representing almost one half of the families.

The geographical elements at generic level are given in Table 5. The three fossil sites have clearly different compositions in areal types at the genus level (Fig. 3B). Pantropical genera are the most abundant in Lincang and Xiaolongtan: more than 30% of all genera in Lincang and 22% in Xiaolongtan. North temperate genera are the most abundant in Xianfeng, representing more than one third of the total. Seven genera occur at all the three studied sites: *Albizia*, *Castanopsis*, *Cinnamonum*, *Cyclobalanopsis*, *Lithocarpus*, *Litsea*, *Quercus*.

4. Discussion

4.1. Geological implications

In this study, the uncertainty in palaeoaltitude is ±901 m. The enthalpies at sea-level for the different sites are very similar, which is not surprising for sites that are not separated by large distances. However, the enthalpies at the fossil sites are very different: both Lincang and Xiaolongtan have high values while Xianfeng is much lower. This is an important result because even if the precision of the palaeoaltimetry can be criticised, the difference in altitude between Lincang–Xiaolongtan and Xianfeng is still significant and robust. If the altitude difference between sites is calculated directly from their palaeoenthalpies, we get: 1745 ± 764 m between Lincang and Xianfeng and 1561 ± 764 m between Xiaolongtan and Xianfeng, the difference between Lincang and Xiaolongtan is not significant. Irrespective of the uncertainty, the diachronous uplift of Yunnan Province is statistically significant.

The palaeoclimate reconstructions also indicate that the low altitude sites of Lincang and Xiaolongtan differ from the high altitude site of Xianfeng by having higher mean annual temperatures (MATs), mainly due to higher cold month mean temperatures (CMMTs), i.e. winter temperatures, and by a higher relative humidity (RH), i.e. higher humidity (Table 1). The differences in altitudes readily explain differences in climate in Yunnan during the late Miocene. Global cooling occurred in late Cenozoic (Zachos et al., 2001). This cooling is more marked at high latitudes than at low latitudes (Bruch et al., 2006; Steppuhn et al., 2006, 2007), and was not conspicuous in South China (Jacques et al., 2013). Because the three studied sites are close to each other, the effect

Table 2
Family composition of Lincang, Xianfeng and Xiaolongtan palaeofloras. Only families with two or more species are indicated.

Flora of Lincang			Flora of Xiaolongtan			Flora of Xianfeng		
Family	No. sp.	Sp.%	Family	No. sp.	Sp.%	Family	No. sp.	Sp.%
Fagaceae	13	19.4	Fabaceae	16	29.6	Fagaceae	14	18.5
Fabaceae	10	14.9	Fagaceae	10	18.5	Lauraceae	6	11.1
Lauraceae	5	7.46	Lauraceae	9	16.7	Betulaceae	2	3.70
Anacardiaceae	4	5.97	Sapindaceae	3	5.56	Anacardiaceae	2	3.70
Rosaceae	3	4.48	Hamamelidaceae	2	3.70	Sapindaceae	2	3.70
Juglandaceae	2	4.48	Myricaceae	2	3.70			
Malvaceae	2	4.48	Rhamnaceae	2	3.70			
Meliaceae	2	4.48						
Myrtaceae	2	4.48						
Rutaceae	2	4.48						

Table 3
Generic composition of Lincang, Xianfeng and Xiaolongtan palaeofloras. The numbers indicate the number of species belonging to each genus for each site.

Genus	Family	Lincang	Xiaolongtan	Xianfeng
Abarema	Fabaceae		1	
Acer	Sapindaceae		3	2
Alangium	Cornaceae		1	1
Albizia	Fabaceae	1	2	1
Alnus	Betulaceae			1
Aphanamixis	Meliaceae	1		
Berchemia	Rhamnaceae	1	1	
Betula	Betulaceae	1		
Capparis	Capparaceae	1		
Carpinus	Betulaceae			1
Cassia	Fabaceae		2	
Castanea	Fagaceae		1	
Castanopsis	Fagaceae	2	2	4
Celtis	Cannabaceae	1		
Chrysophyllum	Sapotaceae	1		
Cinnamomum	Lauraceae	3	3	1
Cyclobalanopsis	Fagaceae	2	2	4
Dalbergia	Fabaceae	1	1	
Desmodium	Fabaceae	1	1	
Desmos	Annonaceae		1	
Distylium	Hamamelidaceae		1	
Dodonaea	Sapindaceae		1	
Dryophyllum	Fagaceae			1
Engelhardia	Juglandaceae	1		
Erythrophleum	Fabaceae		1	
Exbucklandia	Hamamelidaceae		1	
Ficus	Moraceae	1	1	
Gleditsia	Fabaceae	1	1	
Helicteres	Malvaceae	1		
Hydrangea	Hydrangeaceae	1		
Ilex	Aquifoliaceae	1		
Indigofera	Fabaceae		1	
Jasminum	Oleaceae		1	
Juglans	Juglandaceae		1	
Laurus	Lauraceae		1	
Lespedeza	Fabaceae		1	
Lithocarpus	Fagaceae	5	1	2
Litsea	Lauraceae	1	1	2
Machilus	Lauraceae		2	1
Magnolia	Magnoliaceae		1	
Millettia	Fabaceae	1		
Mucuna	Fabaceae	1		
Murraya	Rutaceae	1		
Myrica	Myricaceae		2	
Neocinnamomum	Lauraceae	1		
Nothaphoebe	Lauraceae		1	1
Ormosia	Fabaceae	1	1	
Passiflora	Passifloraceae		1	
Phoebe	Lauraceae		1	1
Photinia	Rosaceae	1		
Piper	Piperaceae	1		
Pistacia	Anacardiaceae	1		1
Pittosporum	Pittosporaceae	1		
Platycarya	Juglandaceae			1
Podocarpium	Fabaceae		1	
Populus	Salicaceae	1		
Pterocarya	Juglandaceae		1	
Quercus	Fagaceae	4	3	3
Reevesia	Malvaceae	1		
Rhamnella	Rhamnaceae		1	
Rhododendron	Ericaceae			1
Rhus	Anacardiaceae	1		1
Robinia	Fabaceae		1	
Salix	Salicaceae		1	
Schisandra	Schisandraceae	1		
Schoepfia	Olacaceae	1		
Shuteria	Fabaceae	1		
Sinosideroxylon	Juglandaceae	1		
Smilax	Smilacaceae	1	1	
Sophora	Fabaceae	1	2	
Sorbus	Rosaceae	1		
Stranvaesia	Rosaceae	1		
Styrax	Styracaceae	1		
Syzygium	Myrtaceae	2		
Terminalia	Combretaceae	1		
Ternstroemia	Theaceae	1		
Tetragonia	Aizoaceae	1		
Toona	Meliaceae	1		
Toxicodendron	Anacardiaceae	2		
Trapa	Lythraceae	1		
Typha	Typhaceae		1	
Viburnum	Adoxaceae	1		
Zanthoxylum	Rutaceae	1		

of general cooling can be excluded to explain the strong differences observed.

Our results are congruent with a diachronous uplift of Yunnan province during the Neogene. Results derived from incision of the Red River also favour a diachronous uplift: uplift is greater south of the Red River and in the southeast areas north of the Red River, whereas uplift is limited in northern areas north of the Red River (Schoenbohm et al., 2004). The diachronous uplift is also consistent with the exhumation of the metamorphic massifs of Yunnan (Cao et al., 2011). An early uplift of northern Yunnan is suggested by thermochronological results that indicate that large regions of eastern Tibet already had significant elevation before the late Miocene (Wang et al., 2012). Results from several disciplines agree an early uplift of northern Yunnan and a late uplift of southern Yunnan.

4.2. Floristic implications

The three palaeofloras clearly show different geographical affinities. Lincang in the south is characterised by a high level of tropical elements, Xianfeng in the north shows a high level of warm temperate elements, and Xiaolongtan features cosmopolitan to tropical elements. Zhu (2013b) defined some floristic thresholds for the tropical flora in China. He looked at the total percentage of tropical elements (pantropical, tropical and subtropical East Asia and tropical America disjunct, Old World tropics, tropical Asia to tropical Australasia, tropical Asia to tropical Africa, tropical Asia) in different regions of China, and compared them with the boundary generally attributed to tropical regions. The 60% tropical genera threshold marks the limit of the tropical area. For the three studied palaeofloras, Lincang has 64.1% of tropical genera, Xiaolongtan 53.7% and Xianfeng 47.1%. Lincang corresponds to a tropical flora under this definition, whereas the level of tropical elements gradually decreases from Xiaolongtan to Xianfeng.

There are also seven genera in common between the three studied sites. At the present day, these seven genera are common and widespread in regions south of the Yangtze River. Their occurrence in the three studied sites indicated that they were also widespread in different vegetation types during the late Miocene.

Table 4
Geographical elements of angiosperm families occurring in the three palaeofloras.

Geographical elements	Lincang		Xiaolongtan		Xianfeng	
	No. of families	%	No. of families	%	No. of families	%
Cosmopolitan	6	19.4	8	47.1	3	33.3
Pantropical	15	48.4	4	23.5	2	22.2
Tropical & Subtropical E Asia & Tropical America disjunct	2	6.45				
Old World Tropics	1	3.23				
North Temperate	2	6.45				
North South Temperate disjunct	4	12.9	4	23.5	4	44.4
East Asia & North America disjunct	1	6.45	1	5.88		

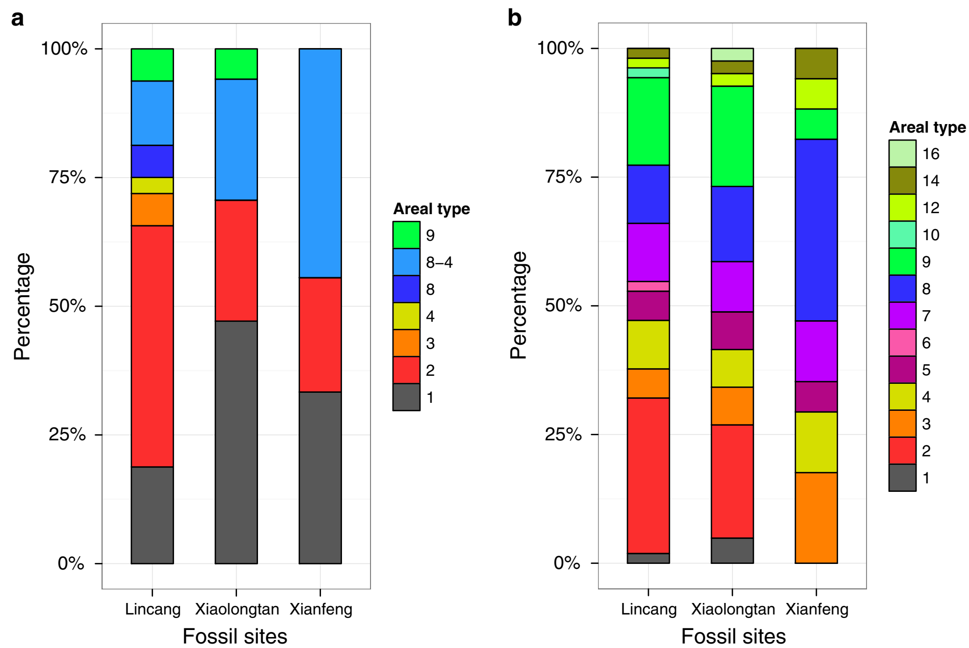

Fig. 3. Areal type composition of the three fossil sites. A, Family level; B, genus level. Codes for areal types are those used by Wu et al. (2003). 1, Cosmopolitan; 2, Pantropical; 3, Tropical and subtropical East Asia and tropical America disjunct; 4, Old world tropics; 5, Tropical Asia to tropical Australasia Oceania; 6, Tropical Asia to tropical Africa; 7, Tropical Asia; 8, North temperate; 8–4, North temperate and South temperate disjunct; 9, East Asia and North America disjunct; 10, Old world temperate; 12, Mediterranean, West to central Asia; 14, East Asia; 16, Australia.

In Yunnan today there is a marked altitudinal separation between vegetation types from tropical evergreen rainforest to alpine meadow (Li and Walker, 1986). The tropical evergreen forest is restricted to south Yunnan and only below 1800 m asl. Predominant families, such as Combretaceae, Meliaceae and Sapotaceae (Li and Walker, 1986) are also found in the Lincang palaeoflora. The subtropical evergreen broad-leaved forest is widespread in modern Yunnan, occurring mostly between 1000 and 2500 m asl, but sometimes up to 2800 m asl, the predominant families in this forest type are: Fagaceae, Theaceae, Lauraceae and Magnoliaceae (Wu and Zhu, 1987).

There is a gradient in the percentage of tropical genera between the three floras from Lincang, with the highest level, to Xianfeng, with the lowest level. The late Miocene palaeoenvironments of Yunnan clearly show a diversity of vegetation types. The present day differentiation of vegetation types in Yunnan was already present during the late Miocene. Therefore, our results indicate that the diversification of vegetation types in Yunnan occurred before the late Miocene.

Table 5
Geographical elements of angiosperm genera occurring in the three palaeofloras.

Geographical elements	Lincang		Xiaolongtan		Xianfeng	
	No. of genera	%	No. of genera	%	No. of genera	%
Cosmopolitan	1	1.89	2	4.88		
Pantropical	16	30.2	9	22.0		
Tropical & Subtropical E Asia & Tropical America disjunct	3	5.66	3	7.32	3	17.6
Old World Tropics	5	9.43	3	7.32	2	11.8
Tropical Asia to Tropical Australasia	3	5.66	3	7.32	1	5.88
Tropical Asia to Tropical Africa	1	1.89				
Tropical Asia	6	11.3	4	9.76	2	11.8
North Temperate	6	11.3	6	14.6	6	35.3
East Asia & North America disjunct	9	17.0	8	19.5	1	5.88
Old World Temperate	1	1.89				
Mediterranean, W Asia to C Asia	1	1.89	1	2.44	1	5.88
East Asia	1	1.89	1	2.44	1	5.88
Australia			1	2.44		

4.3. Altitudinal differentiation of late Miocene floras

At the present day, Lincang, Xiaolongtan and Xianfeng have a subtropical evergreen broad-leaved forest (Li and Walker, 1986). But Lincang and Xiaolongtan palaeofloras had more affinities with tropical evergreen forest in the late Miocene. Xianfeng was already at a high altitude during the late Miocene, whereas Lincang and Xiaolongtan went through a major uplift between the late Miocene and the present day (1386 m and 520 m, respectively). Our results suggest that the distribution of tropical taxa in Yunnan has been highly impacted by the regional uplift: these taxa have been progressively restricted to more southern regions. The subtropical evergreen broad-leaved forest expanded to the south into regions previously occupied by tropical taxa.

During the Neogene, the eastward expansion of the Qinghai–Tibet Plateau resulted in the uplift of parts of Yunnan. Along with the well-studied effect of this uplift on the local climate, our study demonstrates that the uplift resulted in a southward retreat of the vegetation belts. In their survey of the plant geography of Yunnan, Li and Walker (1986) discussed how the uplift of Yunnan might have impacted the local vegetation structure; however, they pointed out that only the fossil record could test their ideas. Our results confirm the southward movement of the floras. We have even shown that, during late Miocene times, northern Yunnan was already at a high altitude, whereas southern Yunnan was still at a low altitude. This diachrony is very important because it gives time for the plant species to migrate and evolve: the uplift of different parts of Yunnan at different times creates new environments favourable for speciation. This, combined with the presence of biogeographic barriers, explains the extant of high plant diversity and endemism found in Yunnan (López-Pujol et al., 2011).

Previous studies demonstrated that geological boundaries between terranes can explain floristic differences at taxonomic level in Yunnan (Zhu, 2011). In this work, the geology is shown to have another impact on Yunnan vegetation: the uplift influenced the tropical to temperate character of the flora. These two results are complementary because they look at the vegetation at two different levels. Therefore, we can say that geological boundaries explain biogeographic boundaries in terms of floral composition at several taxonomic levels, while the change from the tropical to temperate character of the vegetation responds to geological movements such as uplift.

In conclusion, the uplift of Yunnan during the Neogene shaped the present vegetation: it restricted the tropical taxa to the southernmost areas and induced the expansion of subtropical and warm temperate vegetation. The geological history of Yunnan is a key component for understanding the present plant distribution in this province, and for understanding the evolution of its biodiversity. The uplift framework reconstructed in this paper suggests that tectonic context is important in understanding present day biodiversity and the biological characteristics of the component taxa.

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Appendix 1. List of species occurring at the three studied fossil localities

List of species occurring in Lincang:

Albizia scalpelliformis, *Aphanamixis* sp., *Berchemia calymmatophylla*, *Betula mioluminifera*, *Capparis lincangensis*, *Castanopsis brevijucunda*, *Castanopsis gemmifolia*, *Celtis miobungeana*, *Chrysophyllum sinicum*, *Cinnamomum naitoanum*, *Cinnamomum scheuzeri*, *Cinnamomum versutifolium*, Cyclobalanopsis mandraliscae, *Cyclobalanopsis paraschottkyana*, *Dalbergia sigillata*, *Desmodium praegyroides*, *Engelhardtia sclerophylla*, *Ficus proreligiosa*, *Gleditsia miosinensis*, *Helicteres callineura*, *Hydrangea lanceolimba*, *Ilex ornatinervosa*, *Lithocarpus flexicostatus*, *Lithocarpus ravidifolius*, *Lithocarpus reniifolius*, *Lithocarpus* sp., *Lithocarpus validifolius*, *Litsea grabaui*, *Loranthus palaeoeuropaeus*, *Lumnitzera pseudoracemosa*, *Maackia* sp., *Millettia* sp., *Mucuna leiophylla*, *Murraya* sp., *Neocinnamomum fuscatifolium*, *Ormosia* sp., *Photinia* sp., *Piper lincangense*, *Pistacia miochinensis*, *Pittosporum lincangense*, *Populus glandulifera*, *Quercus latifolia*, *Quercus mutilatifolia*, *Quercus simulata*, *Quercus* sp., *Reevesia* sp., *Rhus mortinerva*, *Schisandra splendinervosa*, *Schoepfia elegantifolia*, *Shuteria* sp., *Sinosideroxylon lincangense*, *Smilax grandifolia*, *Sophora miojaponica*, *Sorbus* sp., *Stranvaesia cosmophylla*, *Styrax pulchellus*, *Syzygium lincangense*, *Syzygium poecilophyllum*, *Terminalia lincangensis*, *Ternstroemia maekawai*, *Tetragonia ovatifolia*, *Toona bienensis*, Toxicodendron *inaequilaterum*, *Toxicodendron miosuccedaneum*, *Trapa* sp., *Viburnum validum*, *Zanthoxylum refractifolium*.

List of species occurring in Xiaolongtan:

Abarema xiaolongtanensis, *Acer macrophyllum*, *Acer* sp., *Alangium aequalifolium*, *Albizia bracteata*, *Albizia miokalkaora*, *Berchemia miofloribunda*, *Cassia oblonga*, *Cassia suffruticosa*, *Castanea miomollissima*, *Castanopsis miocuspidata*, *Castanopsis predelavayi*, *Cinnamomum oguniense*, *Cinnamomum* sp1, *Cinnamomum* sp2, *Cyclobalanopsis mandraliscae*, *Cyclobalanopsis praegilva*, *Dalbergia lucida*, *Desmodium pulchellum*, *Desmos kaiyuanensis*, *Distylium* sp., *Dodonaea japonica*, *Erythrophleum ovatifolium*, *Exbucklandia cenica*, *Ficus* sp., *Gleditsia integra*, *Indigofera suffruticosa*, *Jasminum paralanceolarium*, *Juglans japonica*, *Laurus obovalis*, *Lespedeza* sp., *Lithocarpus* sp., *Litsea grabaui*, *Machilus americana*, *Machilus ugoana*, *Magnolia miocenica*, *Myrica elliptica*, *Myrica longifolia*, *Nothaphoebe precavaleriei*, *Ormosia xiaolongtanensis*, *Passiflora* sp., *Phoebe pseudolanceolata*, *Podocarpium podocarpum*, *Pterocarya insignis*, *Quercus lantenoisii*, *Quercus monimotricha*, *Quercus sinomiocenica*, *Rhamnella* sp., *Robinia nipponica*, *Salix miosinica*, *Smilax* sp., *Sophora miojaponica*, *Sophora paraflavescens*, *Typha lesquereuxii*.

List of species occurring in Xianfeng:

Acer cf. *paxii*, *Acer florinii*, *Alangium* cf. *chinensis*, *Albizzia* sp., *Alnus nepalensis*, *Carpinus* sp., *Castanopsis* cf. *calathiformis*, *Castanopsis* cf. *delavayi*, *Castanopsis* cf. *tibetana*, *Castanopsis praedelavayi*, *Cinnamomum scheuchzeri*, *Cyclobalanopsis praegilva*, *Cyclobalanopsis preglauca*, *Cyclobalanopsis preoxyodon*, *Cyclobalanopsis xianfengensis*, *Dryophyllum yunnanense*, *Lithocarpus* cf. *fordianus*, *Lithocarpus lancifolius*, *Litsea* cf. *yunnanensis*, *Litsea grabaui*, *Machilus leptophylla*, *Nothaphoebe precavaleriei*, *Phoebe* cf. *yunnanensis*, *Pistacia paraweinmannifolia*, *Platycarya* sp., *Quercus miovariabilis*, *Quercus preguyavaefolia*, *Quercus wulongensis*, *Rhododendron* sp., *Rhus* sp.

References

Bai, D.H., Unsworth, M.J., Meju, M.A., Ma, X.B., Teng, J.W., Kong, X.R., Sun, Y., Sun, J., Wang, L.F., Jiang, C.S., Zhao, C.P., Xiao, P.F., Liu, M., 2010. Crustal deformation of the eastern Tibetan plateau revealed by magnetotelluric imaging. Nat. Geosci. 3, 358–362.

Bruch, A.A., Utescher, T., Mosbrugger, V., Gabrielyan, I., Ivanov, D.A., 2006. Late Miocene climate in the circum-Alpine realm — a quantitative analysis of terrestrial palaeofloras. Palaeogeogr. Palaeoclimatol. Palaeoecol. 238, 270–280.

Bureau of Geology and Mineral Resources of Yunnan Province, 1990. Regional Geology of Yunnan Province. Geological Publishing House, Beijing (in Chinese).

Cao, S.Y., Neubauer, F., Liu, J.L., Genser, J., Leiss, B., 2011. Exhumation of the Diancang Shan metamorphic complex along the Ailao Shan–Red River belt, southwestern Yunnan, China: evidence from $^{40}Ar/^{39}Ar$ thermochronology. J. Asian Earth Sci. 42, 525–550.

Clark, M.K., Royden, L.H., 2000. Topographic ooze: building the eastern margin of Tibet by lower crustal flow. Geology 28, 703–706.

Clark, M.K., House, M.A., Royden, L.H., Whipple, K.X., Burchfiel, B.C., Zhang, X., Tang, W., 2005a. Late Cenozoic uplift of southeastern Tibet. Geology 33, 525–528.

Clark, M.K., Bush, J.W.M., Royden, L.H., 2005b. Dynamic topography produced by lower crustal flow against rheological strength heterogeneities bordering the Tibetan Plateau. Geophys. J. Int. 162, 575–592.

Dong, W., 2001. Upper Cenozoic stratigraphy and paleoenvironment of Xiaolongtan Basin, Kaiyuan, Yunnan Province. Proceedings of the Eighth Annual Meetings of Chinese Society of Vertebrate Paleontology, 8 (in Chinese).

Forest, C.E., Wolfe, J.A., Molnar, P., Emanuel, K.A., 1999. Paleoaltimetry incorporating atmospheric physics and botanical estimates of paleoclimate. Geol. Soc. Am. Bull. 111, 497–511.

Group of the Regional Stratigraphic Table of Yunnan, 1978. Regional Stratigraphic Table of SW China: Yunnan Volume. Geological Publishing House, Beijing (in Chinese).

Guo, S.X., 2011. The late Miocene Bangmai flora from Lincang County of Yunnan, Southwestern China. Acta Palaeontol. Sin. 50, 353–408 (in Chinese).

Herman, A.B., Spicer, R.A., 1996. Palaeobotanical evidence for a warm Cretaceous Arctic Ocean. Nature 380, 330–333.

Jacques, F.M.B., Guo, S.X., Su, T., Xing, Y.W., Huang, Y.J., Liu, Y.S.C., Ferguson, D.K., Zhou, Z.K., 2011a. Quantitative reconstruction of the Late Miocene monsoon climates of southwest China: a case study of the Lincang flora from Yunnan Province. Palaeogeogr. Palaeoclimatol. Palaeoecol. 304, 318–327.

Jacques, F.M.B., Su, T., Spicer, R.A., Xing, Y.W., Huang, Y.J., Wang, W.M., Zhou, Z.K., 2011b. Leaf physiognomy and climate: are monsoon systems different? Glob. Planet. Chang. 76, 56–62.

Jacques, F.M.B., Shi, G.L., Wang, W.M., 2011c. Reconstruction of Neogene zonal vegetation in South China using the Integrated Plant Record (IPR) analysis. Palaeogeogr. Palaeoclimatol. Palaeoecol. 307, 272–284.

Jacques, F.M.B., Shi, G.L., Wang, W.M., 2013. Neogene zonal vegetation of China and the evolution of the winter monsoon. Bull. Geosci. 88, 175–193.

Kou, X.Y., Ferguson, D.K., Xu, J.X., Wang, Y.F., Li, C.S., 2006. The reconstruction of paleovegetation and paleoclimate in the late Pliocene of west Yunnan, China. Clim. Chang. 77, 431–448.

Leloup, P.H., Lacassin, R., Tapponnier, P., Schärer, U., Zhong, D.L., Liu, X.H., Zhang, L.S., Ji, S.C., Trinh, Phan Trong, 1995. The Ailao Shan–Red River shear zone (Yunnan, China), Tertiary transform boundary of Indochina. Tectonophysics 288, 3–84.

Li, X.W., Walker, D., 1986. The plant geography of Yunnan Province, southwest China. J. Biogeogr. 13, 367–397.

López-Pujol, J., Zhang, F.M., Sun, H.Q., Ying, T.S., Ge, S., 2011. Centres of plant endemism in China: places for survival or for speciation? J. Biogeogr. 38, 1267–1280.

Qiu, Y.X., Fu, C.X., Comes, H.S., 2011. Plant molecular phylogeography in China and adjacent regions: tracing the genetic imprints of Quaternary climate and environmental

change in the world's most diverse temperate flora. Mol. Phylogenet. Evol. 59, 225–244.
Replumaz, A., Tapponier, P., 2003. Reconstruction of the deformed collision zone between India and Asia by backward motion of lithospheric blocks. J. Geophys. Res. 108, 2285.
Replumaz, A., Lacassin, R., Tapponnier, P., Leloup, P.H., 2001. Large river offsets and Plio-Quaternary dextral slip rate on the Red River fault (Yunnan, China). J. Geophys. Res. 106, 819–836.
Royden, L.H., Burchfiel, B.C., van der Hilst, R.D., 2008. The geological evolution of the Tibetan Plateau. Science 231, 1054–1058.
Schoenbohm, L.M., Whipple, K.X., Burchfiel, B.C., Chen, L.Z., 2004. Geomorphic constraints on surface uplift, exhumation, and plateau growth in the Red River region, Yunnan Province, China. Geol. Soc. Am. Bull. 116, 895–909.
Schoenbohm, L.M., Burchfiel, B.C., Chen, L.Z., 2006a. Propagation of surface uplift, lower crustal flow, and Cenozoic tectonics of the southeast margin of the Tibetan Plateau. Geology 34, 813–816.
Schoenbohm, L.M., Burchfiel, B.C., Chen, L.Z., Yin, J.Y., 2006b. Miocene to present activity along the Red River fault, China, in the context of continental extrusion, upper-crustal rotation, and lower-crustal flow. Geol. Soc. Am. Bull. 118, 672–688.
Searle, M.P., Elliott, J.R., Phillips, R.J., Chung, S.L., 2011. Crustal–lithospheric structure and continental extrusion of Tibet. J. Geol. Soc. 168, 633–672.
Shen, Z.K., Lü, J., Wang, M., Bürgmann, R., 2005. Contemporary crustal deformation around the southeast borderland of the Tibetan Plateau. J. Geophys. Res. 110, B11409.
Spicer, R.A., Yang, J., 2010. Quantification of uncertainties in fossil leaf paleoaltimetry: does leaf size matter? Tectonics 29 (TC6001), 1–13.
Spicer, R.A., Harris, N.B.W., Widdowson, M., Herman, A.B., Guo, S.X., Valdes, P.J., Wolfe, J.A., Kelley, S.P., 2003. Constant elevation of southern Tibet over the past 15 million years. Nature 421, 622–624.
Spicer, R.A., Bera, S., Bera, S.D., Spicer, T.E.V., Srivastava, G., Mehrotra, R., Mehrotra, N., Yang, J., 2011. Why do foliar physiognomic climate estimates sometimes differ from those observed? Insights from taphonomic information loss and a CLAMP case study from the Ganges Delta. Palaeogeogr. Palaeoclimatol. Palaeoecol. 302, 381–395.
Steppuhn, A., Micheels, A., Geiger, G., Mosbrugger, V., 2006. Reconstructing the Late Miocene climate and oceanic heat flux using the AGCM ECHAM4 coupled to a mixed-layer ocean model with adjusted flux correction. Palaeogeogr. Palaeoclimatol. Palaeoecol. 238, 399–423.
Steppuhn, A., Micheels, A., Bruch, A.A., Uhl, D., Utescher, T., Mosbrugger, V., 2007. The sensitivity of ECHAM4/ML to a double CO_2 scenario for the Late Miocene and the comparison to terrestrial proxy data. Glob. Planet. Chang. 57, 189–212.
Su, T., Jacques, F.M.B., Spicer, R.A., Liu, Y.S., Huang, Y.J., Xing, Y.W., Zhou, Z.K., 2013. Post-Pliocene establishment of the present monsoonal climate in SW China: evidence from the late Pliocene Longmen flora. Clim. Past 9, 1911–1920.
Sun, H., Li, Z.M., 2003. Qinghai–Tibet Plateau uplift and its impact on Tethys flora. Adv. Earth Sci. 18, 852–862.
Sun, B.N., Wu, J.Y., Liu, Y.S., Ding, S.T., Li, X.C., Xie, S.P., Yan, D.F., Lin, Z.C., 2011. Reconstructing Neogene vegetation and climates to infer tectonic uplift in western Yunnan, China. Palaeogeogr. Palaeoclimatol. Palaeoecol. 304, 328–336.
Sun, B.N., Ding, S.T., Wu, J.Y., Dong, C., Xie, S.P., Lin, Z.C., 2012. Carbon isotope and stomatal data of late Pliocene Betulaceous leaves from SW China: implications for palaeoatmospheric CO_2-levels. Turk. J. Earth Sci. 21, 237–250.
Tao, J.R., Zhou, Z.K., Liu, Y.S., 2000. The Evolution of the Late Cretaceous–Cenozoic Floras in China. Science Press, Beijing, pp. 1–282.
Tapponnier, P., Lacassin, R., Leloup, P.H., Schärer, U., Zhong, D., Liu, X., Ji, S., Zhang, L., Zhong, J., 1990. The Ailao Shan/Red River metamorphic belt: Tertiary left-lateral shear between Indochina and south China. Nature 343, 431–437.
Taylor, M., Yin, A., 2009. Active structures of the Himalayan–Tibetan orogen and their relationships to earthquake distribution, contemporary strain field, and Cenozoic volcanism. Geosphere 5, 199–214.
Wang, W.M., 1996. A palynological survey of Neogene strata in Xiaolongtan basin, Yunnan Province of South China. Acta Bot. Sin. 38, 743–748 (in Chinese with English abstract).
Wang, Z., Huang, R.Q., Wang, J., Pei, S.P., Huang, W.L., 2011. Regional flow in the lower crust and upper mantle under the southeastern Tibetan Plateau. Int. J. Geosci. 2, 631–639.
Wang, E., Kirby, E., Furlong, K.P., van Soest, M., Xu, G., Shi, X., Kamp, P.J.J., Hodges, K.V., 2012. Two-phase growth of high topography in eastern Tibet during the Cenozoic. Nat. Geosci. 5, 640–645.
Westaway, R., 2009. Active crustal deformation beyond the SE margin of the Tibetan Plateau: constraints from the evolution of fluvial systems. Glob. Planet. Chang. 68, 395–417.
Wolfe, J.A., 1993. Method of obtaining climatic parameters from leaf assemblages. U.S. Geol. Surv. Bull. 2040, 1–71.
Wu, Z.Y., 1991. The areal-types of Chinese genera of seed plants. Acta Bot. Yunnanica (Suppl. 4), 1–139.
Wu, Z.Y., Zhu, Y.C. (Eds.), 1987. Vegetation of Yunnan. Science Press, Beijing (in Chinese).
Wu, Z.Y., Zhou, Z.K., Li, D.Z., Peng, H., Sun, H., 2003. The areal-types of the world families of seed plants. Acta Bot. Yunnanica 25, 245–257.
Wu, J.Y., Sun, B.N., Liu, Y.S., Xie, S.P., Lin, Z.C., 2009. A new species of *Exbucklandia* (Hamamelidaceae) from the Pliocene of China and its paleoclimatic significance. Rev. Palaeobot. Palynol. 155, 32–41.
Xia, K., Su, T., Liu, Y.S.C., Xing, Y.W., Jacques, F.M.B., Zhou, Z.K., 2009. Quantitative climate reconstructions of the late Miocene Xiaolongtan megaflora from Yunnan, southwest China. Palaeogeogr. Palaeoclimatol. Palaeoecol. 276, 80–86.
Xie, S.P., Sun, B.N., Wu, J.Y., Lin, Z.C., Yan, D.F., Xiao, L., 2012. Palaeoclimatic estimates for the late Pliocene based on leaf physiognomy from western Yunnan, China. Turk. J. Earth Sci. 21, 251–261.
Xing, Y.W., 2010. The Late Miocene Xianfeng flora, Yunnan, Southwest China and its quantitative palaeoclimatic reconstructions(Ph.D. Thesis) Kunming Institute of Botany, Chinese Academy of Sciences, China (in Chinese with English abstract).
Xing, Y.W., Utescher, T., Jacques, F.M.B., Su, T., Liu, Y.S.C., Huang, Y.J., Zhou, Z.K., 2012. Palaeoclimatic reconstructions reveal weak precipitation seasonality in southwestern China during the late Miocene: evidence from plant macrofossils. Palaeogeogr. Palaeoclimatol. Palaeoecol. 358–360, 19–26.
Yang, Y.Q., Liu, M., 2009. Crustal thickening and lateral extrusion during the Indo-Asian collision: a 3D viscous model. Tectonophysics 465, 128–135.
Yue, L.L., Chen, G., Sun, W.B., Sun, H., 2012. Phylogeography of *Buddleja crispa* (Buddlejaceae) and its correlation with drainage system evolution in southwestern China. Am. J. Bot. 99, 1726–1735.
Zachos, J.C., Pegani, M., Stone, L., Thomas, E., Billups, K., 2001. Trends, rhythms, and aberrations in global climates 65 Ma to present. Science 292, 686–693.
Zhang, Y.Z., 1997. Lithostratigraphy in Yunnan Province. China University of Geosciences Press, Wuhan (in Chinese).
Zhang, T.C., Sun, H., 2011. Phylogeographic structure of *Terminalia franchetii* (Combretaceae) in southwest China and its implications for drainage geological history. J. Plant Res. 124, 63–73.
Zhang, Q.Q., Ferguson, D.K., Mosbrugger, V., Wang, Y.F., Li, C.S., 2012. Vegetation and climatic changes of SW China in response to the uplift of Tibetan Plateau. Palaeogeogr. Palaeoclimatol. Palaeoecol. 363-364, 23–36.
Zhou, Z.K., 1985. The Miocene Xiaolongtan fossil flora in Kaiyuan, Yunnan, China(M.Sc. Thesis) Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (in Chinese).
Zhu, H., 2011. A new biogeographical line between South Yunnan and Southeast Yunnan. Adv. Earth Sci. 26, 916–925 (in Chinese with English abstract).
Zhu, H., 2012. Biogeographical divergence of the flora of Yunnan, southwestern China initiated by the uplift of Himalaya and extrusion of Indochina block. PLoS ONE 7, e45601.
Zhu, H., 2013a. The floras of Southern and Tropical southeastern Yunnan have been shaped by divergent geological histories. PLoS ONE 8, e64213.
Zhu, H., 2013b. Geographical elements of seed plants suggest the boundary of the tropical zone in China. Palaeogeogr. Palaeoclimatol. Palaeoecol. 386, 16–22.