# Quantitative climate reconstructions of the late Miocene Xiaolongtan megaflora from Yunnan, southwest China

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A B S T R A C T

The late Miocene Xiaolongtan megaflora from Kaiyuan in southeast Yunnan (23°48′45″N, 103°11′52″E, 1050 m a.s.l.) was chosen for palaeoclimatic reconstruction using three quantitative techniques, i.e. the Coexistence Approach (CA), Leaf Margin Analysis (LMA), and the Climate–Leaf Analysis Multivariate Program (CLAMP). The reconstructed climatic parameters are also compared with those of the two adjacent Miocene floras currently available in Yunnan, i.e. the early to middle Miocene carpological Mangdan flora (24°24′N, 97°49′E, 1620 m a.s.l.) and the late Miocene Lühe palynoflora (25°10′N, 101°22′E, 1930 m a.s.l.). Quantitative analyses of the Xiaolongtan flora supports the previous qualitative results of a southern, humid subtropical climate, being more humid and having a slightly higher mean annual temperature (MAT) than today. The MATs calculated by CA, LMA, and CLAMP overlap (16.7–19.2 °C, 22.3 ± 2.05 °C, 18.1 ± 1.2 °C, respectively) and are close to the present day value (19.7 °C). The overlapping of temperatures derived using the three techniques is unusual and probably related to the low latitude of the Xiaolongtan area and the southern subtropical nature of its vegetation. Both the mean temperatures of the warmest month (WMT) and of the coldest month (CMT) reconstructed by CA (WMT = 25.4–26.0 °C, CMT = 7.7–8.7 °C) and CLAMP (WMT = 25.9 ± 1.6 °C, CMT = 10.8 ± 1.9 °C) are similar to those of today (WMT = 24.3 °C, CMT = 12.8 °C), but great changes appear in the mean annual precipitation (MAP). The CLAMP results suggest a higher precipitation (1964 ± 335.9 mm) than CA (1215–1639 mm), but they are much higher than the present MAP (820.5 mm). This is consistent with results from the Lühe palynoflora, which also developed under a warmer subtropical climate with higher precipitation (803.6–1254.7 mm) than that of today (815.9 mm). In contrast, the Mangdan flora, situated in a more complicated topographic region to the west of Xiaolongtan and near the Sino-Myanmar border, implies a slightly lower precipitation (1170–1300 mm) than that of today (1300–1400 mm). Overall, the wetter climate during the late Miocene around the Xiaolongtan area suggests that the Himalayas had not yet uplifted to its present altitudes at that time.

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## 1. Introduction

Yunnan Province, located in southwestern China, is a mountainous plateau strongly affected by the Himalayan orogenic movement during the Cenozoic. It has developed a rich biodiversity during the dramatic climatic fluctuations particularly in the past 20 Ma (Xu et al., 2008). Detailed palaeoclimate studies are crucial (e.g. Bruch et al., 2002, 2007) for understanding the origin of biodiversity and also its evolution in a region. Throughout Yunnan there are well developed Neogene outcrops in the inter-mountain basins (Guo and Chen, 1989; Wang, 1990). By far, more than 20 Neogene micro- and mega-floras from various basins in Yunnan have been documented, making it one of the most important regions for research on Cenozoic climatic and floristic changes in East Asia (references cited in Xu et al., 2000; Sun et al., 2002; Liang et al., 2003; Wang and Shu, 2004; Xu et al., 2004, 2008; Sun and Wang, 2005; Zhao et al., 2004). Based on the shifts of species diversity of Fabaceae, Fagaceae, and Lauraceae, Xu et al. (2000) concluded that the general Neogene cooling in Yunnan was consistent with the Cenozoic global palaeoclimate change implied by the oxygen isotope records of benthic and planktonic foraminifera (Miller et al., 1987). However, quantitative palaeoclimate data for most of the Chinese Cenozoic floras are largely lacking, so that the conclusion of Xu et al. (2000) can still not be quantitatively testified.

The past decade witnessed a rapid development of approaches for quantitative palaeoclimate reconstructions by using fossil plants as

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proxy data (Uhl, 2006), which in turn has largely enhanced our understanding of terrestrial palaeoclimates and their evolution in geological history, particularly for the Neogene climates in Europe (e.g. Bruch et al., 2007). Chinese Neogene floras have seldom been used to test these approaches and thus, detailed Neogene climates in China are generally unexplored (Sun et al., 2002; Liang et al., 2003; Kou et al., 2006; Yang et al., 2007).

In this study, we chose the late Miocene Xiaolongtan megaflora from southeastern Yunnan for quantitative climate inferences. This flora was first reported by Colani (1920), and subsequently investigated taxonomically and floristically (Writing Group of Cenozoic Plants of China [WGCPC], 1978; Zhou, 1985; Wang, 1996). It is dominated by Fabaceae, Fagaceae, and Lauraceae. More than half (66%) of the genera are subtropical elements including *Desmos*, *Passiflora*, *Indigofera*, and *Smilax* etc. (Appendix A). Previous studies suggested that this Miocene flora, reflecting a subtropical evergreen broadleaved forest. Compared with the extant vegetations of China and the leaf physiognomic analysis on the Xiaolongtan megaflora, Zhou (1985, 2000) concluded that the Xiaolongtan fossil suggested a wetter climate, with an estimated MAP of 1000–1250 mm than today (820.5 mm at the present). The wetter palaeoclimate in Yunnan was likely due to the lower elevation of the Himalaya during the Miocene, which allowed more wet air to reach southwestern China from the Indian Ocean. However, this qualitative comparison provides limited information (see Mosbrugger, 1999). In a review of the development of the Neogene vegetation and the evolution of the Neogene climate throughout China, Liu and Zheng (1995) compared changes in the percentages of the entire-margined species in the Chinese Neogene floras, but the corresponding climatic parameters have not been calculated Recently, a quantitative palaeoclimate reconstruction on Xiaolongtan megaflora was performed using the Coexistence Approach (CA, Steppuhn et al., 2007). However, the results were only preliminary because the study was based on an outdated taxonomic list of the leaf fossil species provided by Guo (1993). A quantitative re-evaluation of the climate implications of Xiaolongtan megaflora is therefore needed.

The Xiaolongtan megaflora was chosen for the present study firstly because its taxonomy has been well studied in the Neogene assemblages of southwestern China (Colani, 1920; WGCPC, 1978; Zhou, 1985, 2000). This previous intensive taxonomic research permits us to apply the Coexistence Approach. Secondly, the Xiaolongtan megaflora represents the southernmost Neogene flora in Yunnan where the detailed knowledge of Neogene climates in the lower latitudes is lacking. A palaeoclimatic study on Xiaolongtan megaflora will help broaden our knowledge of the Neogene climate in low latitudinal regions of the Northern Hemisphere. Lastly, the geological age of the Xiaolongtan flora has been determined using mammalian fossils (see details below), and by a palynology survey (Wang, 1996). Although the palynology survey provides valuable information, we did not use these pollen data in our study because the fossil pollen were surveyed using light microscopy and the taxonomy supplied little information on botanical affinities and made the application of the Nearest Living Relatives approach almost impossible.

Our primary objective in this study is to quantitatively reconstruct the late Miocene climate in southwestern China by applying three quantitative methods to the Xiaolongtan megaflora, i.e. the Coexistence Approach (CA) (Mosbrugger and Utescher, 1997), Leaf Margin Analysis (LMA) (Wilf, 1997; Greenwood, 2007), and the Climate–Leaf Analysis Multivariate Program (CLAMP) (Wolfe, 1993; Wolfe and Spicer, 1999; Spicer, 2007) and use the obtained results to discuss the climatic evolution in the Miocene southwestern China.

## 2. Materials and methods

### 2.1. Study site and material

The Xiaolongtan Basin (103°12′–18′ E, 23°30′–38′N; 1030–1110 m a.s.l.) is located 16 km to the northwest of Kaiyuan city in Yunnan Province (Wang, 1996; Dong, 2001). It is an elliptical-shaped area about 21 km$^2$ containing the Xiaolongtan coal mine where Cenozoic lignite is exposed (Fig. 1). The detailed stratigraphy of the Xiaolongtan coal mine has been reported by Dong (1987). The lignite deposits in the mine, namely the Xiaolongtan Formation, have a rich plant and mammal record. The representative mammal fossils are *Sivapithecus*, Mustelidae indet., Castoridae gen. et sp. indet., *Tetralophodon*, *Gomphotherum*, *Zygolophodon*, *Tapirus*, *Propotamochoerus*, *Dicoryphochoerus*, *?Listriodon*, and *Paracervulus*
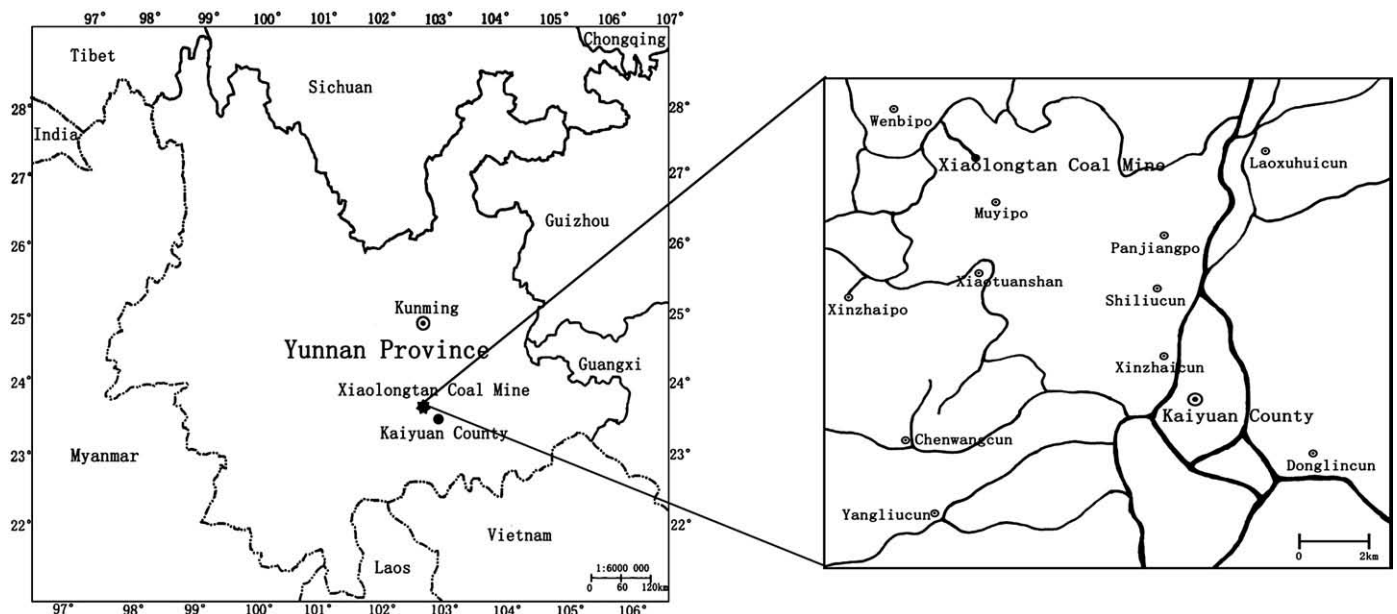


**Fig. 1.** Map of Yunnan province (left) showing the location of Xiaolongtan coal mine (right).

(Dong, 2001). These mammalian fossils are comparable to the late Miocene Vallesian in Europe (Dong, 2001). The geologic age of the Xiaolongtan Formation has also been confirmed by Wang's (1996) palynological study.

The Xiaolongtan flora was first studied by Colani (1920) but it is difficult to locate the depository of his original specimens. Starting in 1978, newly collected fossil plant material has formed the basis for subsequent taxonomic study of this flora (WGCPC, 1978; Zhou, 1985, 2000). More than 730 plant fossil specimens used in this study were originally collected by Zhou (1985) from the top layer of lignite in the coal mine (103°11′52″ E, 23°48′45″N; 1050 m a.s.l.; Fig. 1). These plant megafossils, all belonging to the Xiaolongtan flora, are mostly represented by leaf impressions, together with a small amount of seed and fruit impressions. These fossils represent 54 species (52 dicots and 2 monocots), belonging to 45 genera in 21 families (Appendix A). Although cuticles are rarely preserved (Guo and Zhou, 1992), the fossil leaves are well preserved with details of venation and tooth morphology, permitting a close comparison with the extant species (Zhou, 1985, 2000). In the present study, we follow the taxonomic treatment of Zhou (1985, 2000).

## 2.2. Methods

Three quantitative approaches were used to reconstruct the palaeoclimatic conditions of Xiaolongtan megaflora. The assumptions of these approaches and their procedures are outlined below.

Abbreviations of climate parameters used throughout the text include: 3-DRY, precipitation during the 3 consecutive driest months (mm); 3-WET, precipitation during the 3 consecutive wettest months (mm); CMT, mean temperature of the coldest month (°C); GRS, length of the growing season (months); GSP, growing season precipitation (mm); MAP, mean annual precipitation (mm); MAT, mean annual temperature (°C); MP-DRY, mean precipitation of the driest month (mm); MP-WET, mean precipitation of the wettest month (mm); MMGSP, mean monthly growing season precipitation (mm); RH, relative humidity (%); SH, specific humidity (%); and WMT, mean temperature of the warmest month (°C);

### 2.2.1. Coexistence Approach (CA)

The CA, following the principle of the classic Nearest Living Relative (NLR) method (Mosbrugger, 1999), was developed by Mosbrugger and Utescher (1997). It is based on the assumption that the climatic requirements of fossil species are similar to those of their NLRs (e.g. Mosbrugger and Utescher, 1997; Mosbrugger, 1999). It reconstructs the palaeoclimatic parameters for a given fossil flora using climatic intervals in which all of the NLRs of the fossil flora could coexist (Mosbrugger and Utescher, 1997; Mosbrugger, 1999). To facilitate the quantitative analysis, Utescher and Mosbrugger (1997–2006) have developed a database, PALAEOFLORA, which contains more than 4000 Cenozoic plant taxa, the corresponding NLRs, and about 1000 climatic data sets of these NLRs (T. Utescher, personal communications).

As discussed above, the majority of the fossils from Xiaolongtan are impressions. The determination of NLRs of these fossils is therefore mainly designated to the generic level. The only exception is applied to fagaceous leaves, to which specific NLRs are assigned through detailed leaf architectural comparisons (Jones, 1986; Zhou et al., 1995; Luo and Zhou, 2002). The climatic tolerances of these NLRs were queried from the PALAEOFLORA database. For some NLRs whose climatic tolerances were not available (e.g. *Abarema* sp., *Quercus pannosa*, and *Q. variabilis*), we determined their distribution ranges from Wu and Ding (1999) and estimated their climatic tolerances based on distribution ranges from the database of National Meteorological Bureau of China (1985) as outlined in Mosbrugger and Utescher (1997). Climatic intervals were calculated by the ClimStat program, provided by T. Utescher. In the

analysis of CA, several fossil taxa were excluded because they contributed little in determining climatic tolerances. These taxa include extinct taxon (*Podocarpium*), aquatics (*Typha*) and cosmopolitans (*Lespedeza*, *Salix*, and *Sophora*).

### 2.2.2. Leaf Margin Analysis (LMA)

LMA is based on the established positive relationship between the percentage of woody species in a given flora with entire-margined leaves and temperature (Bailey and Sinnott, 1915, 1916; Wolfe, 1979; Wing and Greenwood, 1993; Wilf, 1997; Greenwood, 2005, 2007).; The following regression equation, mainly based on the mesic vegetation of East Asia (Wolfe, 1979), was used to calculate MAT of the Xiaolongtan megaflora:

$$MAT = 1.14 + 0.306 \times p$$

where $p$ denotes the proportion of woody dicot species with entire-margined leaves in the flora. Teeth are defined as leaf margin sinuses less than 1/4 of the distance to the mid-vein or long axis of the leaf (Ash et al., 1999). A fossil species was scored 1 if all leaves were entire, 0.5 if only some leaves were entire and 0 when all leaves were toothed.

The MAT error was calculated using the equation of Wilf (1997):

$$\delta MAT = c\sqrt{\frac{p(1-p)}{r}}$$

where $c$ is the slope of the equation of the MAT regression,
where $p$ is defined as above, and $r$ is the number of total woody dicots studied in a fossil flora.

### 2.2.3. Climate–Leaf Analysis Multivariate Program (CLAMP)

The CLAMP uses a Correspondence Analysis to calculate the relationship between leaf physiognomy and climatic parameters (Wolfe, 1993; Wolfe and Spicer, 1999). This methodology is based on the assumption that there has been selection for those features of leaves that confer the maximum functional advantage under a variety of environmental conditions (Wolfe and Spicer, 1999). Herman and Spicer (1996) improved the accuracy of palaeoclimatic estimation by applying Canonical Correspondence Analysis (CCA), details of which are available on the CLAMP's official website (http://www.open.ac.uk/earth-research/spicer/CLAMP/Clampset1.html).

By using the calibration score sheet and definitions provided on the CLAMP website, 31 leaf characters for all the woody dicot fossils were scored. The PHYSG3BR/ Physg3br dataset, containing144 meteorological and leaf physiognomic data from the CLAMP website was chosen for our analysis. Climatic estimates were derived using CANOCO 4.5 and presented as a spreadsheet downloaded from the CLAMP website. Twelve climatic parameters were calculated, i.e., MAT, WMT, CMT, MAP, GRS, GSP, MMGSP, 3-WET, 3-DRY, RH, SH, and Enthalpy (Table 1).

## 3. Results

### 3.1. CA

Reconstructed climatic estimates using CA are MAT 16.7–19.2 °C, WMT 25.4–26.0 °C, CMT 7.7–8.7 °C, MAP 1215–1639 mm, MP-WET 224–248 mm, and MP-DRY 19–24 mm (Table 1). The ranges of the climatic parameters were determined by several climate-limiting species (Table 2). 95 to 100% NLRs could coexist in the obtained climate ranges. As the range of numerous climate parameters fell outside of most coexistence intervals, several outliers were identified: *Quercus monimotricha* for all the climatic parameters but CMT and MP-WET, *Laurus obovalis* and *Desmodium*

**Table 1**
The results of climatic parameters of the Miocene Xiaolongtan megaflora, reconstructed from CA, CLAMP, and LMA (the present study), vegetation comparison and leaf margin analysis (Zhou, 1985), and CA (Steppuhn et al. 2007).

| Climatic parameter | Xiaolongtan megaflora | | | | | Modern climate in Xiaolontan area | Lühe palynoflora | Mangdan carpoflora |
|---|---|---|---|---|---|---|---|---|
| | This study | | | Zhou (1985) | Steppuhn et al. (2007) | | | |
| | CA | CLAMP | LMA | | | | | |
| MAT (°C) | 16.7–19.2 | 18.1 ± 1.2 | 22.3 ± 2.05 | 20[a], 24[b] | 13.8–15.4 | 19.7 | 13.3–20.9 | 18.8–20.5 |
| WMT (°C) | 25.4–26.0 | 25.9 ± 1.6 | | 22–24[a] | | 24.3 | 22.5–27.5 | 27.6–28.0 |
| CMT (°C) | 7.7–8.7 | 10.8 ± 1.9 | | 10–20[a] | | 12.8 | 2.5–12.6 | 7.9–11.3 |
| MAP (mm) | 1215–1639 | 1964.8 ± 335.9[d] | | 1000–1200[a] | 996–1018 | 820.5 | 803.6–1254.7 | 1170–1300 |
| MP-WET(mm) | 224–248 | | | | | 153.5 | 179.4–249.6 | |
| MP-DRY(mm) | 19–24 | | | | | 11.4 | 10.2–18.5 | |
| GRS[c] (months) | | 10.1 ± 0.7 | | | | 12 | | |
| GSP[c] (mm) | | 1964.8 ± 335.9 | | | | 820.5 | | |
| MMGSP[c] (mm) | | 190.3 ± 36.9 | | | | 68.4 | | |
| 3-WET (mm) | | 854.4 ± 140.3 | | | | 439.4 | | |
| 3-DRY (mm) | | 312.2 ± 93.0 | | | | 42.2 | | |
| RH (%) | | 64.7 ± 7.4 | | | | 72 | | 70–74 |
| SH (%) | | 8.0 ± 0.9 | | | | | | |
| ENTHALPY | | 31.2 ± 0.3 | | | | | | |

For comparison, the modern climate in the Xiaolongtan area (Yunnan Meteorological Bureau, 1984) and the reconstructed palaeoclimates of two adjacent Miocene floras, the Lühe palynoflora (Xu et al., 2008) and the Mangdan carpoflora (Zhao et al., 2004) are also listed.
  [a] Indicates the results from comparison of vegetation types (Zhou, 1985).
  [b] Represents the MAT derived from Wolfe's (1979) graph showing the relationship between MAT and proportion of woody dicots with entire-margined species in East Asian vegetations (Zhou, 1985).
  [c] Denotes the data are summed up when the temperature > 10 °C.
  [d] The MAP value is roughly treated as being equal to the GSP value below, since the CMT obtained from CLAMP is about 10 °C.

*pulchellum* for MP-WET, and *Cyclobalanopsis praegilva* for MP-DRY (Appendix A).

### 3.2. LMA and CLAMP

The reconstructed MAT using LMA was 22.3 ± 2.05 °C, compared to 18.1 ± 1.2 °C obtained by using CLAMP and 3-DET was 845.4854.4 ± 140.3 and 3-DRY 312.2 ± 93.0 using CLAMP (Table 1). Other climatic parameters for the Miocene Xiaolongtan megaflora calculated using CLAMP and the corresponding statistics of leaf scorings were also present (Tables 1 and 3).

## 4. Discussion

A large number of tropical and subtropical genera, such as *Quercus*, *Cyclobalanopsis*, *Castanopsis*, *Lithocarpus*, *Cinnamomum*, *Machilus*, *Phoebe*, *Albizzia*, *Cassia*, *Desmos* and *Ficus*, and some temperate elements such as *Acer* and *Juglans*, suggest that the late Miocene Xiaolongtan flora must have grown in a humid subtropical climate (Zhou, 1985, 2000). Based on the similar vegetation and the leaf physiognomy of the fossil megaflora, Zhou (2000) concluded that the Xiaolongtan fossil megaflora presented a palaeoclimate similar to the southern subtropical climate currently in China with a slightly higher MAT and more humidity than the current climate in the Xiaolongtan area. Our more detailed quantitative parameters concur with Zhou's (2000) assessment.

**Table 2**
List of the climate-limiting NLRs in CA, which define the upper and lower limits of coexistence intervals for the Xiaolongtan megaflora.

| | Nearest Living Relative taxa | |
|---|---|---|
| | Min | Max |
| MAT (°C) | *Desmos* sp. | *Laurus* sp. |
| WMMT (°C) | *Ficus* sp. | *Nothaphoebe* sp. |
| CMMT (°C) | *Cassia* sp. | *Quercus pannosa* |
| MAP (mm) | *Phyllodium* sp. | *Jasminum* sp. |
| MP-WET (mm) | *Nothaphoebe* sp. | *Robinia* sp. |
| MP-DRY (mm) | *Machilus* sp. | *Laurus* sp. |

### 4.1. Temperature

In a previous analysis of the palaeoclimate of the Xiaolongtan fossil megaflora, Zhou (1985) estimated that the MAT was about 20 °C based on a comparison with China's modern vegetation, or 24 °C using Wolfe's (1979) graph of the linear relationship between MAT and the percentage of species with entire margins in modern mesic humid forests in Eastern Asia. Steppuhn et al. (2007) obtained an MAT of 13.8–15.4 °C (Table 1) for Xiaolongtan flora using CA, but

**Table 3**
The statistics of the leaf scorings for CLAMP on the Xiaolongtan megaflora.

| Leaf character | Percentage |
|---|---|
| Lobed | 3 |
| No teeth | 69 |
| Regular teeth | 26 |
| Close teeth | 24 |
| Round teeth | 11 |
| Acute teeth | 21 |
| Compound teeth | 0 |
| Nanophyll | 0 |
| Leptophyll 1 | 0 |
| Leptophyll 2 | 12 |
| Microphyll 1 | 28 |
| Microphyll 2 | 31 |
| Microphyll 3 | 24 |
| Mesophyll 1 | 7 |
| Mesophyll 2 | 4 |
| Mesophyll 3 | 1 |
| Emarginate apex | 13 |
| Round apex | 40 |
| Acute apex | 38 |
| Attenuate apex | 19 |
| Cordate base | 9 |
| Round base | 29 |
| Acute base | 63 |
| L:W < 1:1 | 1 |
| L:W 1–2:1 | 27 |
| L:W 2–3:1 | 38 |
| L:W 3–4:1 | 23 |
| L:W > 4:1 | 11 |
| Shape obovate | 14 |
| Shape elliptic | 54 |
| Shape ovate | 32 |

this was based on an outdated list of the fossil leaves cited in Guo (1993).

The MAT calculated by CA, LMA, and CLAMP, in the present study are 16.7–19.2 °C, 22.3 ± 2.05 °C, and 18.1 ± 1.2 °C respectively. The MAT from LMA is the highest but it doesn't follow a pattern obtained from a similar study of a middle Miocene Shanwang flora (Sun et al., 2002; Liang et al., 2003). Both Sun et al. (2002) and Liang et al. (2003) obtained higher temperatures using LMA than by using CLAMP, and the temperatures obtained from CA are the highest. The main difference between the two floras is that the Shanwang flora is located at the middle latitudes of eastern China. In general, the reconstructed Neogene climate estimated using fossil floras from the middle latitudinal eastern regions of China and from the European fossil floras had higher MATs when using CA and the coldest temperatures when using CLAMP (Mosbrugger and Utescher, 1997; Uhl et al., 2007). In a few cases, the results from the CA were similar to the results from LMA and the CLAMP (Uhl et al., 2003; Roth-Nebelsick et al., 2004). Being a single-character approach, LMA is likely affected by taphonomic distortions and collecting biases. It can provide a partial and possibly erroneous climatic signal (Herman and Spicer, 1997; Royer et al., 2005; Uhl et al., 2007). In lakeside and riparian floras, temperatures determined from leaf margins on woody plants are likely underestimated due to the high proportion of non-entire leaves resulting from constant water fluctuations (Burnham et al., 2001; Uhl et al., 2003). LMA tends to underestimate the MAT. In this study, LMA produced the highest MAT. Herman and Spicer (1997) reported that LMA can give an inflated value of MAT because drought can cause smaller leaves and teeth can be lost due to lack of precipitation, salinity or acidity of the ground water, or freezing. However, this does not seem to be the case with the Xiaolongtan megaflora, which represented the warm and wet climate. The comparatively constant results from all three approaches are probably related to the low latitude location of the fossil site, where more thermophilous elements grow and less species with toothed margins occur. Therefore significant underestimates of temperature caused by species with toothed margin were not evident. In Yunnan, only two Miocene floras, i.e. Mangdan and Lühe, have been quantitatively analyzed (Zhao et al., 2004; Xu et al., 2008) but neither was a leaf flora. It is not possible to verify whether this phenomenon is prevalent in the low latitude fossil leaf floras of Eastern Asia.

The current MAT in the Xiaolongtan area is about 19.7 °C (Table 1), and this is very similar to the palaeoclimate obtained in this study. Interestingly, the temperatures reported by Yang et al. (2007) study on the middle Miocene Shanwang flora from eastern China were not significantly different from current temperatures. Our result is also in correspondence with the conclusions of Micheels et al. (2007). These researchers performed a model simulation using the atmospheric general circulation model (AGCM) ECHAM4 coupled to a mixed-layer (ML) ocean model for the Tortonian (late Miocene) and concluded that late Miocene experienced slightly warmer temperatures in a global average (+0.6 °C) than that of today. On the other hand, the WMT in the late Miocene Xiaolongtan area could be slightly higher than at present, but the palaeo-CMT appears somewhat lower than the present CMT of this area (Table 1). The similar MATs in the Miocene of Yunnan have also been reported from a study of Mangdan and Lühe Miocene floras from Yunnan (Zhao et al., 2004; Xu et al., 2008). But the latter had a higher WMT and similar CMT compared to the present temperatures (Xu et al., 2008).

### 4.2. Precipitation

Both CA and CLAMP produced a significantly higher MAP in the Xiaolongtan area than that of today (Table 1). The high precipitation in Central Europe and China during the Miocene has also been reported by others (e.g. Mosbrugger et al., 2005; Micheels et al, 2007; Yang et al., 2007; Xu et al., 2008). Palaeobotanical proxies from Central Europe suggest that the precipitation was more than 1000 mm throughout the Cenozoic and the MAP between the late Miocene and the earliest Pliocene still remained high at ca. 1250 mm (Mosbrugger et al., 2005). In eastern China, the palaeoclimate reconstructed from the Shanwang flora also implied higher MAP during the Miocene than that of today, with a range of 1107.3 to 1880.0 mm (Yang et al., 2007). In their Tortonian simulation, Micheels et al. (2007) proposed that the global precipitation indicates more humid conditions (+27 mm/a) than the PD control run. Therefore, the higher precipitation seems to be a general global trend in the late Miocene.

The higher MAP values from CLAMP than those from CA may be due to some limitations of CLAMP (Yang et al., 2007). Current methods do not provide accurate estimates of precipitation in a relatively wet regime, because water availability is not limiting to plant growth and leaf physiognomy constrained by factors other than precipitation (Yang et al., 2007). Therefore, in areas experiencing drought, precipitation estimate might be more precise (Yang et al., 2007). Our results for the precipitation of the 3-wet months (854.4 ± 140.3 mm) and of the 3-dry months (312.2 ± 93.0 mm) show that the seasonality with the rainy and dry seasons occurred in late Miocene but not as evident as today: 80–90% rainfall of per annum is in the rain season in Yunnan (Wang, 2006). In these conditions, a lush subtropical forest developed in the Miocene Xiaolongtan area and it provided plenty of food for many large herbivorous mammals (Dong, 2001).

The seasonality with the rainy and dry seasons in Yunnan is believed to be related to the Asia monsoon system (Wang, 2006). It may have been caused by the influence of the further uplift of the Himalaya–Tibetan plateau and then the intensification of the Asian monsoon system. The Himalaya–Tibetan plateau strongly affects atmospheric circulation over Asia, including the monsoon over South Asia and the South China Sea. Micheels et al. (2007) assumed that the palaeoelevation of the Tibetan Plateau in the late Miocene was about half of the present height and led to a weaker Asian monsoon in the Tortonian run. An et al. (2001) suggested that the East Asian monsoons occurred about 9–8 Ma ago but it was still weak. Its intensity developed to peak about 3.6–2.6 Myr ago (An et al., 2001). The wetter climate and weaker seasonality with the rainy and dry seasons during the late Miocene in Xiaolongtan area were consistent with the comparatively weaker monsoon system that time. It suggests that the Himalayas would have not yet been uplifted to its present altitudes.

### Appendix A

List of the fossil species in the Xiaolongtan megaflora, their corresponding NLRs and the climate tolerances of the NLRs. The climate data of NLRs were mainly derived from the PALAEOFLORA database, maintained by T. Utescher at the University of Bonn, Germany and supplemented by data from China (National Meteorological Bureau of China, 1985; Wu and Ding, 1999). The fossil species marked with asterisk (*) were excluded in the calculation of CA due to either of the following reasons, i.e. extinct, cosmopolitan, or aquatic taxa.

**Table A1**

| Fossil taxon | NLR | MAT (°C) | | WMAT (°C) | | CMAT (°C) | | MAP (mm) | | MMaP (mm) | | MMiP (mm) | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Magnolia miocenica | Magnolia | 6.2 | 27.0 | 19.6 | 28.6 | −10.2 | 25.9 | 578 | 3500 | 102 | 610 | 1 | 180 |
| Desmos kaiyuanensis | Desmos | 16.7 | 27.7 | 21.2 | 28.1 | 7.7 | 27.0 | 1055 | 3151 | 204 | 389 | 14 | 165 |
| Cinnamomum oguniense | Cinnamomum | 13.5 | 27.2 | 18.6 | 31.7 | 2.5 | 26.1 | 828 | 3293 | 160 | 988 | 3 | 135 |
| Cinnamomum sp.1 | | | | | | | | | | | | | |
| Cinnamomum sp.2 | | | | | | | | | | | | | |
| Laurus obovalis | Laurus | 12.5 | 19.2 | 23.8 | 29.7 | 5.6 | 11.7 | 160 | 1018 | 20 | 164 | 0 | 24 |
| Litsea grabaui | Litsea | 13.6 | 27.7 | 20.9 | 28.6 | 2.2 | 27.0 | 816 | 3151 | 109 | 389 | 7 | 165 |
| Machilus americana | Machilus | 11.5 | 23.9 | 21.8 | 29.4 | −0.2 | 19.4 | 950 | 1917 | 131 | 323 | 19 | 93 |
| Machilus ugoana | | | | | | | | | | | | | |
| Nothaphoebe precavaleriei | Nothaphoebe | 3.0 | 26.5 | 11.8 | 26.1 | −6.0 | 27.0 | 1175 | 2497 | 224 | 287 | 15 | 124 |
| Phoebe pseudolanceolata | Phoebe | 6.9 | 27.0 | 18.3 | 29.4 | −7.3 | 24.8 | 376 | 1900 | 92 | 354 | 1 | 54 |
| Ficus sp. | Ficus | 13.8 | 27.7 | 23.4 | 28.6 | 1.8 | 27.0 | 677 | 3151 | 125 | 389 | 7 | 165 |
| Castanea miomollissima | Castanea mollissima | 8.5 | 24.0 | 14.5 | 28.3 | −8.2 | 18.0 | 730 | 2073 | 113 | 387 | 2 | 41 |
| Cyclobalanopsis mandraliscae | Cyclobalanopsis myrsinaefolia | 3.0 | 21.8 | 11.8 | 29.3 | −6.0 | 13.3 | 802 | 1923 | 134 | 470 | 13 | 45 |
| Cyclobalanopsis praegilva | Cyclobalanopsis gilva | 15.0 | 22.2 | 23.4 | 28.8 | 3.0 | 14.9 | 1206 | 1998 | 196 | 332 | 31 | 73 |
| Lithocarpus sp. | Lithocarpus harlandii | 7.0 | 22.1 | 17.7 | 28.6 | −3.1 | 13.3 | 1115 | 2395 | 184 | 379 | 14 | 64 |
| Castanopsis predelavayi | Castanopsis delavayi | 15.0 | 22.0 | 12.7 | 28.3 | 4.8 | 13.4 | 818 | 2076 | 175 | 430 | 7 | 26 |
| Castanopsis miocuspidata | Castanopsis echinocarpa | 8.5 | 22.6 | 14.4 | 27.6 | −0.2 | 15.6 | 877 | 1784 | 185 | 349 | 5 | 25 |
| | Castanopsis carlesii | 11.5 | 21.8 | 22.5 | 29.3 | −0.2 | 15.6 | 1031 | 1918 | 184 | 294 | 11 | 56 |
| Quercus lahtenoisii | Cyclobalanopsis glauca | 8.5 | 22.2 | 16.4 | 28.2 | −0.2 | 14.9 | 878 | 1998 | 168 | 265 | 2 | 73 |
| Quercus monimotricha | Quercus pannosa | 4.7 | 15.1 | 11.7 | 20.1 | −3.0 | 8.7 | 474.4 | 1079 | 139 | 229 | 0 | 12 |
| Quercus sinomiocenica | Quercus variabilis | 4.7 | 22.2 | 11.7 | 28.6 | −8.7 | 15.6 | 590.9 | 1998 | 139 | 300 | 3 | 73 |
| Myrica longifolia | Myrica | −6.9 | 28.1 | 8.9 | 33.9 | −25.0 | 27.0 | 233 | 3151 | 51 | 508 | 0 | 165 |
| Myrica elliptica | | | | | | | | | | | | | |
| Juglans japonica | Juglans | 0.0 | 27.5 | 9.5 | 31.2 | −22.7 | 25.0 | 210 | 2617 | 28 | 582 | 1 | 114 |
| Pterocarya insignis | Pterocarya | 7.0 | 24.2 | 17.7 | 31.6 | −6.5 | 16.4 | 246 | 2648 | 46 | 424 | 1 | 64 |
| Salix miosinica* | | – | – | – | – | – | – | – | – | – | – | – | – |
| Passiflora sp. | Passiflora | 13.8 | 27.7 | 16.7 | 29.5 | 3.7 | 27.0 | 529 | 3151 | 116 | 401 | 0 | 165 |
| Albizia bracteata | Albizia | 14.8 | 28.0 | 19.8 | 32.5 | 2.5 | 27.0 | 307 | 3151 | 81 | 558 | 0 | 165 |
| Albizia miokalkaora | | | | | | | | | | | | | |
| Cassia suffruticosa | Cassia | 14.7 | 27.7 | 19.8 | 28.8 | 7.7 | 27.0 | 1007 | 3151 | 207 | 406 | 11 | 165 |
| Cassia oblonga | | | | | | | | | | | | | |
| Dalbergia lucida | Dalbergia | 12.0 | 28.1 | 21.4 | 35.3 | −1.2 | 27.0 | 631 | 3151 | 166 | 554 | 1 | 165 |
| Desmodium pulchellum | Phyllodium | 14.8 | 27.6 | 19.8 | 30.0 | 7.5 | 26.1 | 1215 | 3752 | 265 | 937 | 3 | 71 |
| Erythrophleum ovatifolium | Erythrophleum | 15.2 | 27.2 | 22.1 | 30.6 | 6.1 | 23.0 | 954 | 2073 | 241 | 390 | 1 | 45 |
| Gleditsia integra | Gleditsia | 5.7 | 21.7 | 14.5 | 28.9 | −8.1 | 14.8 | 644 | 2559 | 90 | 363 | 1 | 154 |
| Indigofera suffruticosa | Indigofera | 15.5 | 27.7 | 20.2 | 29.2 | 2.2 | 26.1 | 815 | 3370 | 60 | 479 | 9 | 165 |
| Lespedeza sp.* | | – | – | – | – | – | – | – | – | – | – | – | – |
| Abarema xiaolongtanensis | Abarema | 8.5 | 24.7 | 15.6 | 29.2 | 0.2 | 19.8 | 657.1 | 1998 | 175 | 343 | 1 | 73 |
| Ormosia xiaolongtanensis | Ormosia | 15.6 | 28.1 | 24.7 | 30.1 | 2.2 | 26.0 | 979 | 2823 | 164 | 582 | 7 | 56 |
| Robinia nipponica | Robinia | 3.4 | 20.8 | 17.2 | 28.8 | −12.9 | 13.3 | 63 | 1695 | 13 | 248 | 0 | 87 |
| Podocarpium podocarpum* | | – | – | – | – | – | – | – | – | – | – | – | – |
| Sophora miojaponica* | | – | – | – | – | – | – | – | – | – | – | – | – |
| Sophora paraflavescens* | | | | | | | | | | | | | |
| Dodonaea japonica | Dodonaea | 14.8 | 27.7 | 19.9 | 30.9 | 5.5 | 27.0 | 224 | 3151 | 25 | 389 | 6 | 165 |
| Acer sp. | Acer | 2.7 | 24.0 | 16.2 | 28.6 | −15.6 | 20.6 | 115 | 2559 | 19 | 370 | 1 | 135 |
| Acer macrophyllum | | | | | | | | | | | | | |
| Alangium aequalifolium | Alangium | 8.5 | 27.7 | 16.4 | 28.5 | −7.3 | 27.0 | 338 | 3151 | 92 | 389 | 1 | 165 |
| Berchemia miofloribunda | Berchemia | 7.0 | 24.0 | 16.4 | 28.6 | −7.3 | 17.2 | 396 | 2395 | 108 | 448 | 3 | 71 |
| Jasminum paralanceolarium | Jasminum | 5.7 | 27.1 | 16.1 | 29.9 | −6.9 | 23.5 | 164 | 1639 | 110 | 343 | 2 | 62 |
| Smilax sp. | Smilax | −1.1 | 27.7 | 15.1 | 33.1 | −25.8 | 27.0 | 37 | 3151 | 8 | 389 | 0 | 165 |
| Typha lesquereuxii* | | – | – | – | – | – | – | – | – | – | – | – | – |
| Rhamnella sp. | Rhamella | 10.0 | 26.5 | 20.2 | 28.5 | −7.3 | 25.0 | 396 | 2740 | 108 | 346 | 3 | 155 |
| Distylium sp. | Distylium | 13.8 | 27.7 | 22.1 | 29.0 | 1.8 | 27.0 | 974 | 3905 | 178 | 610 | 5 | 180 |
| Exbucklandia cenica | Exbucklandia | 15.0 | 27.7 | 22.8 | 29.3 | 4.3 | 27.0 | 816 | 3151 | 160 | 389 | 10 | 165 |

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