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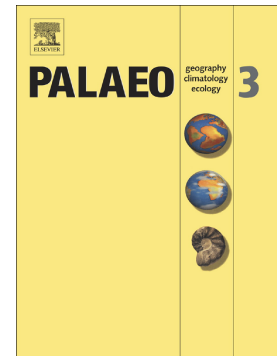
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Eocene – Early Oligocene climate and vegetation change in southern China: evidence from the Maoming Basin

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ABSTRACT

Although the Eocene-Oligocene climate transition marks a critical point in the development of the 'icehouse' global climate of the present little is known about this

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important change in the terrestrial realm at low latitudes. Our palynological study of the Shangcun Formation shows it to be early Oligocene in age: palyno-assemblages in the lower part of the formation indicate a cool interval dominated by conifer pollen in the earliest Oligocene followed by a warmer regime in the second half of the early Oligocene. To quantify middle Eocene to late early Oligocene climate conditions at low (~20 °N) palaeolatitudes in southern Asia several thousand leaf fossil specimens from the Maoming Basin, southern China, were subjected to a multivariate (CLAMP) analysis of leaf form. For terrestrial palaeoclimate comparisons to be valid the palaeoaltitude at which the proxy data are obtained must be known. We find that leaves preserved in the Youganwo (middle Eocene), Huangniuling (late Eocene) and Shangcun (early Oligocene) formations were likely to have been deposited well above sea level at different palaeoelevations. In the Youganwo Formation fine-grained sediments were deposited at an altitude of ~1.5 km, after which the basin dropped to ~ 0.5 km by the time the upper Huangniuling sediments were deposited. The basin floor then rose again by 0.5 km reaching an altitude of approximately 1 km in which the Shangcun Formation fine-grained sediments were accumulated. Within the context of these elevation changes the prevailing climates experienced by the Youganwo, Lower Huangniuling, Upper Huangniuling and Shangcun fossil floras were humid subtropical with hot summers and warm winters, but witnessed a progressive increase in rainfall seasonality. By the early Oligocene rainfall seasonality was similar to that of the modern monsoonal climate of Guangdong Province, southern China. All floras show leaf physiognomic spectra most similar to those growing under the influence of the modern Indonesia-Australia Monsoon, but with no evidence of any adaptation to today's South or East Asia Monsoon regimes. The Upper Huangniuling Flora, rich in

dipterocarp plant megafossils, grew in the warmest conditions with the highest cold month mean temperature and at the lowest altitude.

Key words: monsoon climate, plant fossils, CLAMP, altimetry

1. Introduction

The Eocene to Oligocene transition represents an important time in the history of global climate evolution because it witnessed a marked cooling towards modern 'icehouse' conditions, at least as recorded in deep ocean sediments (Zachos et al., 2001). What is less clear is what the terrestrial realm experienced at this time, especially at low latitudes. Southern China is particularly interesting in this respect because in this region today not only do different monsoon systems interact, but low latitude ecosystem evolution is archived in the form of rich palaeontological records.

Several thousand plant fossils studied here come from five opencast coal mines within the Maoming Basin located in southwestern Guangdong Province. Importantly, this region of southern China has remained more or less in the same geographic position since the Late Cretaceous (http://www.odsn.de), a period of at least 70 million years (Wakita and Metcalf, 2005) so palaeo-positional variations do not complicate the interpretation of palaeoclimatic change over time. However, correct interpretation of terrestrial palaeoclimate signals is critically dependant on understanding past land surface elevation and any changes that may have occurred during deposition of the sedimentary succession.

Our research is focused on the following topics: (1) altimetry and depositional environments of the Maoming Basin from middle Eocene to early Oligocene times;

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(2) palaeoclimate evolution over the same time interval as experienced by the plants of the Maoming Basin; (3) Eocene – early Oligocene changes in megathermal forest taxonomic composition. To facilitate this, new palynological data on the age of the Shangcun Formation are provided.

2. Materials and Methods

Our work utilises four plant megafossil assemblages of middle Eocene – early Oligocene age from the Maoming Basin, southern China (Fig. 1A). These assemblages were recovered from three formations within the Maoming Basin: one assemblage is from the lowermost Youganwo Formation, two are from the Huangniuling Formation, and one from the overlying Shangcun Formation. Fossil floras entombed within these formations are placed in a depositional context. Non-marine deposits belonging to the above formations were studied in five opencast coal mines within the Maoming Basin (Fig. 1B): the Zhenjiang opencast mine (21°52′47.5″ N; 110°40′06.3″ E), the Shigu opencast mine (21°50′44.9″ N; 110°45′40.7″ E), the Lishan opencast mine (21°50′39.22″ N; 110°46′42.8″ E), the Shangcun opencast mine (21°47′52.06″ N; 110°48′34.37″ E) and the Jintang opencast mine (21°42′33.2″ N; 110°53′19.4″ E). Deposits belonging to the Youganwo and Huangniuling formations were measured in the Zhenjiang, Jintang and Shigu opencast coal mines (Supplementary material-1; Aleksandrova et al., 2015; Spicer et al., 2016) and the Shangcun Formation was studied in the Shangcun and Lishan opencast coal mines (Fig. 3 and Supplementary material-2). The leaf fossils that form the basis of our work were recovered from the Jintang, Lishan and Shangcun opencast coal mines.

Recently these opencast coal mines have been abandoned as uneconomic and now are entirely or partially flooded.

Several thousand specimens from the Maoming Basin were collected and studied for this research. They are curated in the Museum of Biology, Sun Yat-sen University, Guangzhou with specimen numbers beginning MMJ1 and MMJ1U (the Youganwo Formation), MMJ2 (lower part of the Huangniuling Formation), MMJ3 (upper part of the Huangniuling Formation), and MSC, MMB, MMLS, MMCW and MM3a (Shangcun Formation).

To derive quantitative estimates of ancient temperature and precipitation, leaf trait spectra for the different floras are subjected to a CLAMP analysis (Climate Leaf Analysis Multivariate Program: Wolfe, 1993; Yang et al., 2011; http://clamp.ibcas.ac.cn/) using the PhysgAsia2 and high-resolution gridded climate calibration data sets HiResGRIDMetAsia2 of (Khan et al., 2014). We use this calibration because it incorporates leaf trait spectra from numerous vegetation types exposed to monsoon climates and, in terms of palaeoaltimetry, has been validated against an array of stable isotope palaeoaltimeters (Currie et al., 2016). CLAMP correlates 31 leaf characters of a minimum of 20 woody dicot morphotypes (species) with 11 climatic parameters providing quantitative estimates of palaeoclimate variables encoded in the morphology of leaves: mean annual temperature (MAT), warm month mean temperature (WMMT), cold month mean temperature (CMMT), length of the growing season (LGS), growing season precipitation (GSP), mean monthly growing season precipitation (MMGSP), precipitation during the three consecutive wettest months (3WET), precipitation during the three consecutive driest months (3DRY), relative humidity (RH), specific humidity (SH), and enthalpy (ENTHAL). We compare the climates derived from our fossil material with those

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recorded in the leaf architecture of modern vegetation from Guangdong Province, southern China.

3. Maoming Basin geological setting and age of the plant-bearing deposits

3.1. Maoming Basin stratigraphy

The Maoming sedimentary basin, located in southwestern Guangdong Province, southern China, is a NW-orientated graben-like structure approximately 50 km long and 10 km wide filled with Upper Cretaceous, Paleogene and Neogene non-marine sediments (Nan and Zhou, 1996; Ye et al., 1997) (Fig. 1). The basin infill consisting of a succession of approximately 2700 m of Paleogene fluvial and lacustrine sedimentary rocks has been divided into the Tongguling, Youganwo, Huangniuling, Shangcun, Laohuling, and Gaopengling formations. The plant megafossils studied were recovered from three of these: the Youganwo, Huangniuling and Shangcun formations.

The lower part of the Youganwo Formation, 70–150 m thick, consists of sandy conglomerates, sandstones, grey-green to purple-red clayey shales, and coal seams, while the upper part is dominated by dark grey to dark brown oil shales with subordinate yellowish brown mudstones alternating with coals (Aleksandrova et al. 2015). A lithostratigraphic log is given in Supplementary material-1 and a characteristic lithology in Figures 2A-B. The remains of fish, reptilians and mammals occur in the oil shales (for details see: Aleksandrova et al., 2015; Averianov et al., 2016). Two palynological assemblages recognised in the Yuganwo Formation are discussed in detail in Aleksandrova et al. (2015).

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The conformably overlying Huangniuling Formation, 60–200 m thick, consists of greyish yellow, grey-white, and pale red sandy conglomerates, sandstones, and greyish green mudstones, with intercalations of oil- and asphalt-bearing sandstones in the upper part (Aleksandrova et al., 2015). The succession is illustrated in a lithostratigraphic log in Supplementary material-1 and a characteristic lithology in Figures 2B-D. The Huangniuling pollen assemblages are found in clay lenses containing plant megafossils (for details see: Aleksandrova et al., 2015).

The overlying Shangcun Formation, 300–500 m thick, mostly consists of greyish brown and greenish grey compact mudstones, sandy shales, and siltstones with minor intercalations of oil shales and coal seams in the lower part. Lithostratigraphic units are given in Figure 3 and Supplementary material-2 and a lithologies characteristic of the formation are recorded in Figures 2E-F. Gastropod and fish remains are present in finer grained facies (Zhou and Chen, 1988; Aleksandrova et al., 2015).

3.2. Maoming floral assemblages

Based on taxonomic composition and the predominance of particular taxa, four plant megafossil assemblages, or floras, were distinguished from three formations within the Maoming Basin: one assemblage is from the lowermost Youganwo Formation, two are from the Huangniuling Formation and one from the overlying Shangcun Formation. Below is a short characterisation of these floras, for more detailed descriptions of the Youganwo and Huangniuling assemblages and a complete reference list see Aleksandrova et al. (2015) and Spicer et al. (2016). Taxonomic assignments were based on general morphology and in some cases cuticle analysis (e.g., as in Tang et al., 2016).

3.2.1. Youganwo Flora

Impressions and compressions of leaves and fruits and petrified wood remains are most abundant in the siltstones under the productive (main) coal seam in the basal part of the Youganwo Formation in the Jintang opencast coal mine of the Maoming Basin. The floral assemblage from this site consists of approximately 65 leaf, fruit and seed taxa representing ferns (Osmundaceae and Polypodiaceae) and angiosperms (Platanaceae, Fagaceae, Juglandaceae, Anacardiaceae, Fabaceae, Rhamnaceae, Ulmaceae, and others) dominated by deciduous dicotyledons. The most abundant plant remains are those of *Zelkova* Spach (Ulmaceae) and *Platimeliphyllum* N. Maslova (Platanaceae) leaves, *Paliurus* Miller (Rhamnaceae) leaves and fruits, and leaves of woody dicotyledons possibly belonging to the Anacardiaceae. *Leguminophyllum* A. Escalup-Bassi also occurs. The floral assemblage from grey mudstones of the coal-bearing unit in the lower part of the Youganwo Formation above the productive coal seam to-date consists of 31 leaf, fruit, rhizomes, and seed taxa representing horsetails (Equisetales), ferns (Salviniaceae and possibly Osmundaceae), conifers (Podocarpaceae), but the fossil assemblage is dominated by angiosperms (Nelumbonaceae, Lauraceae, Platanaceae, Fagaceae, Fabaceae, Anacardiaceae, Celastraceae, Rhamnaceae, Arecaceae, and others).

3.2.2. Lower Huangniuling Flora

The Lower Huangniuling Flora contains conifers (Pinaceae, Podocarpaceae, Taxaceae) and angiosperms belonging to at least 56 species assigned to the Lauraceae, Fagaceae, Altingiaceae, Myrtaceae, Juglandaceae, Aceraceae, Dipterocarpaceae, Rhamnaceae, Fabaceae and Celastraceae (?), together with some so

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far unidentified taxa. Conifers are represented by very rare podocarpaceous leaves (*Nageia* Gaertner), relatively abundant leaves possibly belonging to the Taxaceae, and *Pinus* L. reproductive and vegetative structure remains. The white pine *Pinus maomingensis* Xu et al. (*Pinus* subgenus *Strobus*) is described based on a compressed seed cone and cone scales. Fagaceae are the most diverse and abundant component of the Lower Huangniuling Flora comprising at least five taxa of the genera *Quercus* L., *Castanopsis* (D. Don) Spach and probably *Lithocarpus* Blume. Representatives of the Altingiaceae constitute a notable component of the flora. Woody dicots belonging to Myrtaceae and possibly Lauraceae and Fabaceae are less abundant.

3.2.3. Upper Huangniuling Flora

The Upper Huangniuling Flora contains ferns (Lygodiaceae), conifers (Pinaceae, Podocarpaceae, Taxaceae) and angiosperms so far assigned to Lauraceae, Fagaceae, Altingiaceae, Myrtaceae, Juglandaceae, Myricaceae, Dipterocarpaceae, Rhamnaceae and Fabaceae (75 fossil taxa in total). Ferns are extremely rare: only a few specimens of *Lygodium* Swartz fertile fronds have been found. Conifer abundance and diversity (*Pinus*, *Nageia* and cf. *Taxus* L.) are similar to those of the Lower Huangniuling Flora but these plants are dominated by *Pinus maomingensis*. The Podocarpaceae family is represented by the same species of the genus *Nageia* as in the Lower Huangniuling Flora. Representatives of Fagaceae dominate the Upper Huangniuling Flora in both diversity and abundance. This family comprises *Quercus*, *Lithocarpus* and *Castanopsis* genera. Altingiaceae (*Liquidambar* L.) and Myricaceae (*Myrica* L.) are represented by the most abundant plant megafossils of the Upper Huangniuling Flora, being accompanied by fewer numbers of Lauraceae, Myrtaceae, Dipterocarpaceae and Fabaceae. Winged fruits and associated leaves were assigned to *Shorea* Roxburgh ex

Gaertner (Dipterocarpaceae) (Feng et al., 2013). Representatives of the family Fabaceae include numerous large oblong pods assigned to *Leguminocarpon* Goeppert and leaflets possibly belonging to legumes.

3.2.4. Shangcun Flora

Fossil leaves are distributed not in dense leaf mats but isolated in greyish brown to light brown clays and siltstones representing a large lacustrine environment. The density and distribution of the leaves suggests that deposition was distant from the shoreline. Both impression and compression fossils occur, often with cuticles preserved. Detailed taxonomic analysis has yet to be completed but the Shangcun Flora contains at least 91 fossil taxa of leaves, stems, fruits, cones and seeds belonging to leafy bryophytes (Bryopsida), horsetails (Equisetaceae), ferns (Osmundaceae, Polypodiaceae), conifers (Pinaceae, Cupressaceae, Taxaceae) and angiosperms (Platanaceae, Lauraceae, Fagaceae, Malvaceae, Calophyllaceae, Juglandaceae, Fabaceae, Rhamnaceae, Cornaceae, Myricaceae, Menispermaceae?, Simaroubaceae and Palmae). Ferns are rare but relatively diverse; the most abundant fern is *Osmunda*, while mosses are represented by a few thin stems and horsetails are also few in number. In contrast to the earlier floras conifers are abundant and diverse, and are composed mainly of pinaceous and cupressaceous species. Angiosperms dominate both in terms of numbers of specimens and taxonomic diversity. Representatives of the Fagaceae and Lauraceae are the most abundant and diverse in the Shangcun Flora. The leaves of *Myrica* and woody dicotyledons of uncertain systematic affinity are also abundant.

3.3. Age of the plant-bearing deposits

3.3.1. Age of the Youganwo and Huangniuling formations

The Youganwo Formation has been considered to be of middle Eocene–early Oligocene age based on palynological data (Yu and Wu, 1983; Li et al., 2006), or late Eocene in age based on the presence of *Lunania* cf. *youngi* Chow mammal remains (Wang et al., 2007; Jin, 2008). The Youganwo Flora and the middle Eocene (Lutetian-Bartonian, 48–38Ma) Changchang Flora, Changchang Basin, Hainan Island, southern China, exhibit significant taxonomic similarity and share a number of taxa, for example *Osmunda lignitum* (Giebel) Stur and species assignable to *Nageia*, *Nelumbo*, *Laurophyllum*, *Quercus*, Celastraceae, Altingiaceae, *Podocarpium*. This allows them to be considered coeval (Kodrul et al., 2012 a, b; Spicer et al., 2014; Aleksandrova et al., 2015); a conclusion that is also supported by palynological observations (Lei et al., 1992; Yao et al., 2009; Aleksandrova et al., 2012).

The Huangniuling Formation was previously presumed to be Miocene in age (Nan and Zhou, 1996). However, Ye et al. (1997) regarded the sedimentary complex of the Maoming Basin, including the Youganwo, Huangniuling, Shangcun, and Laohuling formations, as being of middle to late Eocene age.

Palaeomagnetic data from boreholes in the Youganwo, Huangniuling, Shangcun, and the overlying Laohuling formations (Wang et al., 1994) show the succession to have been deposited during normal-polarity magnetic zones (C18n–C11n) of the geomagnetic polarity time scale (GPTS). This corresponds to an age range of 42 to 32 Ma (middle Eocene–early Oligocene) making the Maoming fossil plant assemblages featured in our study all middle Eocene to early Oligocene in age (Aleksandrova et al., 2015).

Palynological complexes from the Youganwo and Huangniuling formations indicate middle–late Eocene ages (Lutetian–Bartonian for the former and Priabonian

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for the latter) (Aleksandrova et al., 2015). Overall the Youganwo and Huangniuling palynological complexes are similar to those from middle to late Eocene sections of the South China Sporopollen Region (Ye et al., 1997), which comprise Yunnan, Guangxi, and Guangdong provinces as well as the South China Sea.

3.3.2. Palynological study and age of the Shangcun Formation

In the Shangcun Formation section near the Lishan village (Lishan opencast coal mine, Fig. 1A), three palynocomplexes (PCs) are distinguished (Fig. 3 and Supplementary material-2).

PC1 comes from Member 1 and the lowermost part of Member 2 (samples MML003 – MML013). It is characterised by a predominance of gymnosperm pollen (>70%) mostly representing different species of conifers, primarily pines with a subordinate amount of Taxodiaceae-Cupressaceae pollen. Taxodiaceae-Cupressaceae pollen, as well as fern spores, increase from the bottom to the top of the section. On average almost 25% of angiosperm pollen represents mostly temperate taxa such as *Corylopsis, Liquidambar, Hamamelis, Carya, Quercu*s, Fagaceae, with other taxa occurring sporadically. Finds of fresh water microplankton are frequent reflecting the lacustrine depositional environment.

PC2 comes from Members 2, 3 and 4 (samples MML015– MML044). In taxon counts, PC2 sharply differs from PC1, which points to some sediment erosion between PC1 and PC2. In PC2 angiosperm pollen predominates (>60%) represented mainly by *Quercus* including *Quercus Eotrigonobalanus*-type; *Castanopsis, Castanea,* and the *Rhoipites - Fususpollenites* pollen group is subdominant, while *Alnus* pollen has a constant background presence. Among gymnosperm pollen taxa coniferous Taxodiaceae-Cupressaceae grains prevail, but their abundance decreases

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towards the top of the section. No more than 10% of pollen represents pines. Judging from the composition of the organic matter (numerous small relatively rounded coaly particles and plant tissue fragments), as well as from the poor preservation of palynomorphs, the sediments were formed in well-oxygenated alluvial, or lacustrine-alluvial, depositional environments (Tyson, 1995).

PC3 comes from Members 5 and 6 (samples MML048 – MML2-22) and is characterised by the predominance of angiosperm pollen (>80% relative abundance) with *Quercus* pollen being again the most numerous. *Quercus Eotrigonobalanus*-type, *Castanopsis, Castanea,* and the *Rhoipites - Fususpollenites* group pollen become less abundant, but in general other taxa become more diverse and numerous. At this stratigraphic level the systematic composition of the microplankton assemblage changes reflecting the predominantly lacustrine origin of the sediments.

In terms of systematic composition and the quantitative proportions of different taxa, palynological spectra from the megafossils samples (Fig. 3 and Supplementary material-2) correspond to the same stratigraphic level as that of PC3 in the Lishan section.

Member 7 (samples MML2-27 – MML2-28) possesses sporadic grains of *Ephedra, Quercus, Liquidambar* and *Hamamelis*.

There is a good correlation between palynocomplexes in the Lishan section and Oligocene palynocomplexes. Complexes with a predominance of gymnosperm pollen, mainly belonging to Pinaceae, have been recognised in the lower part of the Lower Oligocene in many regions (Chateauneuf, 1980; Ollivier-Pierre et al., 1987; Zaporozhets, 1993; Fradkina, 1995; Cenozoic Climatic and Environmental Changes in Russia, 2005; Meyer et al., 2012; Kotthoff et al., 2014; and others). These complexes, unlike late Eocene palynocomplexes, are also characterised by a

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significant impoverishment in the angiosperm pollen systematic composition due to elimination of the most thermophillic genera. The most pronounced changes take place across the Eocene-Oligocene boundary and most likely reflect global cooling.

Many palynologists have interpreted a warming in the second half of the early Oligocene reflected by a reappearance of thermophilic elements (Chateauneuf, 1980; Zaporozhets, 1993; Fradkina, 1995; Oboh et al., 1996; Kuzmina, Volkova, 2008; and others). Thus palynocomplexes of this early Oligocene age appear similar to those of the late Eocene, but relictual Paleocene and early Eocene taxa are not reported. Palynomorphs representing these relictual Paleocene and early Eocene taxa do occur in the late Eocene samples.

A similar change was reported in the borehole 1148 (Deep Sea Drilling Programme) in the South China Sea (Wu et al., 2003). There the boundary between the early Oligocene "cold" and "warm" complexes is dated as 32 Ma. In the late Oligocene part of the borehole palynocomplexes reflect an even greater cooling than that seen across the Eocene–Oligocene transition.

In the Lishan section, PC1 can be correlated with the palynocomplexes of the early part of the early Oligocene due to the predominance of pine pollen and the presence of *Tsuga* spp., *Persicarioipollis* sp. pollen and grass pollen. *Persicarioipollis* sp., characteristic of the early Oligocene in Eastern Asia (Yu, 1983; Shaw, 1998; Yi et al., 2003), remains unknown in the Eocene. It is similar to the extant Polygonaceae pollen. PC2 and PC3 correspond with the "warm" palynocomplex of the second half of early Oligocene (Wu et al., 2003). The PC3 palynocomplex associated with the Shangcun megaflora therefore dates the studied megaflora to the second half of the early Oligocene.

4. CLAMP analysis

In the present study 49 dicot leaf morphotypes from the Youganwo Flora (illustrated in: Spicer et al., 2016), 46 morphotypes from the Lower Huangniuling Flora (illustrated in: Spicer et al., 2016), 53 morphotypes from the Upper Huangniuling Flora (illustrated in: Spicer et al., 2016), and 46 leaf morphotypes from the Shangcun Flora (Figs 4, 5) were scored for as many of the 31 characters as were preserved. The procedure follows the protocols given on the CLAMP website (http://clamp.ibcas.ac.cn/) and the scores are given in Table 1.

5. Results and discussion

Palaeoclimatic variables estimated for the Youganwo, Lower Huangniuling, Upper Huangniuling and Shangcun floras using CLAMP technique are shown in Table 2.

5.1. Palaeoaltimetry of Maoming Basin and depositional environment of the Youganwo, Huangniuling and Shangcun formations

Moist enthalpy, estimated using the CLAMP technique (Table 2, 3) can be used to reconstruct the palaeoelevation of a fossil site. The difference in moist enthalpy at a known elevation (such as sea-level) and a land-surface at an unknown height is given by the following equation (Spicer et al., 2003; Jacques et al., 2014; Khan et al., 2014):

$$Z = (H\text{sea level} - H\text{altitude}) / g \qquad (1)$$

where Z is the height difference, Hsea level is moist enthalpy at sea level, Haltitude is

moist enthalpy at the unknown altitude, g is the gravitational acceleration ($9.81m/s^2$).

Moist enthalpy at sea-level (MESL) can be obtained from a coeval locality at sea-level at the same latitude. Because we have no coeval sea-level assemblages for all the different Maoming floras we estimate MESL for each flora by simple time-weighted interpolation between the MESL for the Gurha-72m and Tirap floras (Fig. 6, Table 3). The Gurha-72m Flora is early Eocene in age (Shukla et al., 2014; Kumar et al., 2016) and the Tirap Flora is late Oligocene (Srivastava et al., 2012). Both floras existed in coastal lowlands near sea-level as evidenced by laterally equivalent marine units.

The values shown in Table 3 represent the most probable elevations of the Maoming Basin above sea level during deposition of the Youganwo, Huangniuling and Shangcun formations, assuming the interpolation we used is valid. During deposition of the Youganwo Formation the lake-side vegetation was at an elevation of ~ 1.5 km but during deposition of the Huangniuling Formation the area descended to ~0.5 km before rising again to ~1 km in the early Oligocene. However, these estimates carry uncertainties arising from the statistical nature of the method as well as those associated with geographic (palaeolatitude) and stratigraphic (age) positioning of the fossil floras analysed. The uncertainties given in Table 2 are derived from the scatter about the CLAMP moist enthalpy regression vector and equates to an elevational uncertainty of ~900 m (± 1s.d.), which is smaller than that associated with isotopic palaeoaltimetry against which the PhysgAsia2 calibration has been evaluated (Currie et al., 2016). Although large, these uncertainties do represent the most precise surface height estimates available. Surface height estimates should only be regarded as indicative of the sort of elevation changes that can complicate land surface temperature comparisons. A full treatment of CLAMP uncertainties is

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given on the CLAMP website (http://clamp.ibcas.ac.cn).

The composition of the Maoming Basin sediment fill also changed over time (Fig. 2). The lower part of the Youganwo Formation is characterised by the predominant occurrence of siltstones, shales and coal seams, while the upper part is characterised by the occurrence of oil shales. These deposits reflect intermittent swamp – shallow lake environments, which gave way to a deeper freshwater lake in which oil shales were formed. In the Huangniuling Formation relatively coarse sands and sandstones predominate with intercalations of silts and mudstones. These sediments were deposited in alluvial and fluvio-lacustrine deltaic environments that existed across a broad basin floor and its margins. The Shangcun Formation mostly consists of mudstones, siltstones and sandy shales, which were formed in a shallow freshwater lake. Hence the low-energy depositional environment of the Youganwo Formation gave way to a higher-energy environment of the Huangniuling Formation and further to a low-energy environment of the Shangcun Formation. These differences most probably are a reflection of relative height differences between the sediment sources and the depositional basin and the amount of accommodation space (Table 3). We estimate that the plants found in the Youganwo Formation grew around the margins of a lake at an elevation of ~1.5 km but during deposition the basin floor dropped thus deepening the lake. During deposition of the Huangniuling Formation the sediments become more fluvial in character, which may indicate the basin filled and the lake environment changed to one dominated by through-flowing rivers. However, our elevation estimates suggest that the surface on which the plants were growing descended by ~1 km, suggesting ongoing regional extensional tectonics and possibly higher local relief differences. Thus the deposition of coarser clastics could have been the result of high-energy run-off from a high surrounding hinterland. We see no major

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increase in precipitation that could otherwise account for higher run-off. By the time the Shangcun assemblages were deposited extension seems to have changed to compression and the land surface apparently rose by ~0.5 km reaching an altitude of approximately ~1 km at which the Shangcun Formation vegetation grew.

5.2. Maoming palaeoclimate as a precursor of the modern monsoon climate of southern China

Palaeoclimate variables experienced by the Youganwo, Lower Huangniuling, Upper Huangniuling and Shangcun floras derived using the CLAMP technique (Table 2) show that: (1) all four palaeoclimates were humid subtropical and were characterised by hot summers and warm winters; (2) the warmest climate was that experienced by the Upper Huangniuling Flora, with CMMT of this climate being the warmest; (3) WMMTs of these palaeoclimates were similar to each other and hot; (4) GSPs (which in this case are equivalent to the mean annual precipitation since the growing season was all year round) and MMGSPs of these palaeoclimates were high and more or less the same, with those of the Shangcun Flora being slightly lower; (5) there is an apparent trend in the 3WET/3DRY ratio from 3 in Youganwo time to ~5 in the Shangcun time reflecting increasing seasonal rainfall variations towards the kind of seasonality seen in modern monsoonal conditions.

According to the Köppen's classification of global climates (Köppen, 1936; Peel et al., 2007), modern climates of southern China are humid subtropical monsoon with hot wet summers and cool dry winters (Cwa), humid subtropical with hot wet summers and no dry season (Cfa), tropical rainy monsoon (Am) and tropical rainy savannah (with dry winter) (Aw). The Cwa and Cfa are widespread in the Guangdong

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Province and the northernmost part of the Hainan Island, while Am and Aw are present in the central and southern parts of the Hainan Island (Peel et al., 2007). Guangzhou city has a humid subtropical monsoon climate, characterised by hot summers and warm winters with little snow and frost.

The modern climate of southern China is exemplified by that of the Nankun Mountain (Nankun Mountain B site: 23°38'39.82"N; 113°50'06.17"E; altitude 744 m). The quantitative climate variables were estimated using CLAMP with the Nankun Mountain B floral sample physiognomy being treated as "passively" as if it were a fossil assemblage (Table 2, Nankun Mountain B estimated). The observed climatic parameters of the site were obtained from the University of Bristol BRIDGE website (Table 2, Nankun Mountain B measured). Both estimated and measured quantitative parameters show that the site climate is subtropical (with hot summer and warm winter) monsoon (humid with dry winter). In Köppen's classification it is climate Cwa. Figure 7 shows an example of a modern subtropical monsoon forest in the Dinghu Mountain, Dinghu Natural Reserve, Guangdong Province.

The palaeoclimates experienced by the Youganwo, Lower Huangniuling, Upper Huangniuling and Shangcun floras were all similar to that existing in Guangdong Province today. However, the observed palaeoclimate trend of increasing seasonality in precipitation from a non-monsoon (reflected by the middle Eocene Youganwo Flora) to a typical monsoon condition (experienced by the early Oligocene Shangcun Flora) makes the latter most similar to the modern regional climate of Guangdong Province.

Several modern monsoon systems are commonly recognised. The monsoon systems affecting Asia are divisible into the South Asia Monsoon (SAM) and the East Asia Monsoon (EAM) (Molnar et al., 2010). In adjacent regions outside of mainland

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Asia the Indonesia-Australia Monsoon (I-AM) is recognised (Zhang and Wang, 2008). The I-AM, which is largely zonal and controlled by the seasonal migrations of the Inter-tropical Convergence Zone, extends across parts of northern Australia to the south of the Indonesian main islands, e.g. Sumatra and Kalimantan.

Because leaf form adapts to the prevailing climate, particularly under the extreme seasonal stresses imposed by monsoons, fossil leaves carry a unique signature of past monsoon regimes. Previously we compared leaf form trait spectra obtained from Eocene fossils from the Maoming Basin with those seen in modern leaves growing under known climate regimes (Spicer et al., 2016). It appeared that the Eocene Youganwo, Lower Huangniuling and Upper Huangniuling fossil leaf trait spectra were most similar to those found in vegetation exposed to the modern I-AM. In the present research, we also include the early Oligocene Shangcun Flora in the physiognomic analysis. The results shown in Figure 8A clearly demonstrate that in Axes 1-2 space the position of the Shangcun fossil leaf assemblage appears to exhibit a physiognomic trait spectrum similar to modern vegetation sites experiencing the SAM, the transitional zone between the SAM and the EAM and the I-AM. However, in Axis 1–3 space (Fig. 8B) the Shangcun fossil assemblage is clearly allied more closely to the cloud of modern sites representing vegetation exposed to the I-AM and not the SAM nor the transitional area. Hence, as in the Eocene floras previously analysed (Spicer et al., 2016), the early Oligocene Shangcun Flora of the Maoming Basin exhibits a leaf physiognomic trait spectrum most similar to those seen in the modern I-AM with no clear evidence of any adaptation to today's EAM or SAM climate regime.

5.3. Youganwo, Huangniuling and Shangcun environment and the occurrence of dipterocarps

The Dipterocarpaceae are often considered as 'poster plants' for low latitude forests in Asia in that this family is currently distributed mainly in the Asian tropics and dominates the canopy of tropical lowland forests. The family comprises approximately 520 species in 17 genera and 3 subfamilies. These angiosperm trees contribute up to 30% of the total area of lowland evergreen forests in Southeast Asia (Dutta et al., 2011). A small proportion of dipterocarpaceous taxa (8%) grow in the tropics of Africa and South America (Zhang and Wang, 1985).

The earliest confirmed dipterocarp megaremains, represented by fossil leaves and fruits of *Shorea maomingensis* Feng, Kodrul et Jin (Fig. 9), are from the late Eocene of the Maoming Basin (Feng et al., 2013). The vast majority of these fossils come from the upper part of the Huangniuling Formation, while in the lower part of this formation they are of rare occurrence. They were not found in the Youganwo or Shangcun formations. Dipterocarpaceae pollen has been recorded from the Youganwo and Huangniuling formations (Aleksandrova et al., 2015) but not from the Shangcun Formation (Fig. 3 and Supplementary material-2).

Our estimates show that, in comparison to the other floras of Maoming Basin, the Upper Huangniuling Flora grew in the warmest climate conditions with the highest CMMT of 15°C (Table 2). This flora inhabited the lowest altitude compared with the other floras (Table 3). Hence, of the Maoming Basin floras discussed here, the Upper Huangniuling Flora growing conditions were probably the most favourable for *Shorea* given that today dipterocarps predominate in evergreen tropical lowland forests (Dutta et al., 2011).

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6. Conclusions

Leaf fossils from the Youganwo, Huangniulin and Shangcun formations record vegetation and changes in climate from middle Eocene to early Oligocene time in southern China. New analysis of pollen and spores in the Shangcun Formation shows it to be early Oligocene in age. Palyno-assemblages in the lower part of the formation indicate a cool interval dominated by conifers in the earliest Oligocene followed by a megathermal regime in the second half of the early Oligocene. During deposition of these leaf assemblages in the Maoming Basin the region underwent extensional and then compressional forces that resulted in surface elevation changes spanning ~ 1 km. The reconstructed Eocene tropical temperature regime was accompanied by an increase in rainfall seasonality so that by the early Oligocene the climate was similar to that seen in southern China today at elevations of ~ 750 m. However leaf form shows adaptations to conditions experienced by vegetation growing under the modern Indonesia-Australia monsoon climate, not those of the South or East Asia monsoons.

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Figure Captions

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Fig. 1. Geographic position of Maoming Basin (southwestern Guangdong Province): A – locations of Maoming Basin; B – locations of opencast coal mines within Maoming Basin.

Fig. 2. Lithology of the Youganwo and Huangniuling formations in the Jintang opencast coal mine (A–D) and Shangcun Formation in the Lishan opencast coal mine: A – Youganwo Formation, grey and dark grey coaliferous deposits in the lower part of the photograph and brown oil shales in the upper part; B – Youganwo (grey coaliferous deposits and brown oil shales) and Huangniuling (predominantly yellow orange sands) formations, the dotted line shows the boundary between the formations; C – Huangniuling Formation lower part (predominantly yellow-orange sands); the leaf symbol shows the place where plant megafossils of the Lower Huangniuling Flora were collected; D – Huangniuling Formation upper part (predominantly yellow-orange sands); a leaf symbol shows the place where plant megafossils of the Upper Huangniuling Flora were collected; E, F – Shangcun Formation, yellow-grey tabular silts and fine-grained sands.

Fig. 3. Lithostratigraphic units (members 1 to 7) and simplified palynological diagram of the Shangcun Formation in the Lishan opencast coal mine, Maoming Basin (see Supplementary material – 2 for the full version).

Fig. 4. Woody dicot leaf morphotypes of the Shangcun Flora, Maoming Basin, South China. Scale bar 1 cm.

A – morphotype 1, sample No MMC-004a;

B – morphotype 2, sample No MM3A-408b;

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C – morphotype 3, sample No MM3A-451b;

D – morphotype 4, sample No MM3A-470;

E – morphotype 5, sample No MMB-077;

F – morphotype 6, sample No MMLS-007;

G – morphotype 6, sample No MM3A-493;

H – morphotype 7, sample No MM3A-054a;

I – morphotype 8, sample No MMB-385;

J – morphotype 9, sample No MM3A-135;

K – morphotype 9, sample No MMLS-063a;

L – morphotype 10, sample No MMB-002a;

M – morphotype 11, sample No MMB-225b;

N – morphotype 12, sample No MM3A-080a;

O – morphotype 13, sample No MMB-194a;

P – morphotype 14, sample No MM3A-430;

Q – morphotype 14, sample No MMLS-160b;

R – morphotype 14, sample No MM3A-190;

S – morphotype 15, sample No MM3A-393-1;

T – morphotype 16, sample No MM3A-479a;

U – morphotype 17, sample No MMB-417;

V – morphotype 18, sample No MM3A-418;

W – morphotype 19, sample No MMLS-035;

X – morphotype 20, sample No MM3A-142a;

Y – morphotype 20, sample No MM3A-194a;

Z – morphotype 21, sample No MM3A-137a;

AA – morphotype 22, sample No MM3A-213;

AB – morphotype 23, sample No MM3A-465;

AC – morphotype 23, sample No MMB-239;

AD – morphotype 24, sample No MM3A-222;

AE – morphotype 24, sample No MM3A-172-2;

AF – morphotype 25, sample No MM3A-088a;

AG – morphotype 25, sample No MMB-094b.

Fig. 5. Woody dicot leaf morphotypes of the Shangcun Flora, Maoming Basin, South China. Scale bar 1 cm.

A – morphotype 26, sample No MM3A-133-1;

B – morphotype 27, sample No MM3A-463;

C – morphotype 28, sample No MMB-252;

D – morphotype 29, sample No MM3A-203b;

E – morphotype 30, sample No MM3A-235a;

F – morphotype 31, sample No MM3A-037b;

G – morphotype 32, sample No MM3A-492-3;

H – morphotype 32, sample No MM3A-109;

I – morphotype 33, sample No MM3A-452b;

J – morphotype 34, sample No MM3A-097a;

K – morphotype 35, sample No MM3A-210;

L – morphotype 35, sample No MM3A-225;

M – morphotype 36, sample No MM3A-060;

N – morphotype 37, sample No MMB-001a;

O – morphotype 38, sample No MMB-124;

P – morphotype 39, sample No MMB-302b;

Q – morphotype 40, sample No MM3A-084b;

R – morphotype 41, sample No MMB-081;

S – morphotype 42, sample No MMB-320;

T – morphotype 43, sample No MMLS-244a;

U – morphotype 43, sample No MMLS-244b;

V – morphotype 44, sample No MMLS-250;

W – morphotype 45, sample No MMLS-252;

X – morphotype 46, sample No MMB-228.

Fig. 6. Plot showing the interpolation used to estimate moist enthalpy at sea level for the Maoming Basin floras. Such an interpolation is not ideal but no coeval demonstrably sea level floras are known in southern China from which to obtain more reliable sea level data.

Fig. 7. Subtropical monsoon forest in the Dinghu Mountain, Dinghu Natural Reserve, Guangdong Province.

Fig. 8A, B. CCA plots showing the relationship between the leaf physiognomic traits exhibited in the Shangcun fossil assemblage (red filled circles) and those of modern vegetation exposed to different climate regimes. Coding for modern vegetation sites:

EAM – East Asia Monsoon, I-AM – Indonesia-Australia Monsoon, NAmM – North America Monsoon, NMS – no monsoon, SAM – South Asia Monsoon, TA – transition area based on monsoon types recognised by Wang and Ho, 2002.

Fig. 9. *Shorea maomingensis* Feng, Kodrul et Jin from the Upper Huangniuling Flora: A – collection MMJ3, sample No. 007a-2, leaf; B – collection MMJ3, sample No. 012, wing-like persistent calyx lobe; C – collection MMJ3, sample No. 011a, leaf; D – collection MMJ3, sample No. 009, winged fruit; E – collection MMJ3, sample No. 010a, winged fruit; scale bar 1 cm.

Table 1. The scoring results of the studied floras.

	Youganwo Flora	Lower Huangniuling Flora	Upper Huangniuling Flora	Shangcun Flora
leaves lobed	0	3	2	0
leaves with no teeth	65	60	68	79
teeth regular	23	36	12	21
teeth close	7	4	0	0
teeth round	10	18	7	6
teeth acute	25	22	25	17
teeth compound	0	0	0	2
nanophyll	0	0	0	0
leptophyll I	0	0	0	0
leptophyll II	1	1	0	0
microphyll I	10	9	0	10
microphyll II	43	36	24	33
microphyll III	34	30	38	32
mesophyll I	13	21	28	21
mesophyll II	0	1	8	3
mesophyll III	0	1	2	1
apex emarginate	3	0	0	3
apex round	4	7	11	6
apex acute	35	40	19	36
apex attenuate	58	54	69	55
base cordate	7	1	1	0
base round	31	29	12	30
base acute	62	71	87	70
l/w ratio less that 1:1	1	0	1	0
l/w ratio1:1 to 2:1	21	18	10	11
l/w ratio 2:1 to 3:1	50	46	53	22
l/w ratio 3:1 to 4:1	23	23	30	32
l/w ratio more that 4:1	5	12	6	35
leaves obovate	0	1	5	6
leaves elliptic	90	93	87	86
leaves ovate	10	5	7	8

Percentage of characters preserved is shown for the Youganwo, Lower Huangniuling, Upper Huangniuling and Shangcun floras, Maoming Basin. For detail see CLAMP website (http://clamp.ibcas.ac.cn/).

Table 2 Estimated and measured climatic and palaeoclimatic variables.

	MAT (°C)	WMMT (°C)	CMMT (°C)	LGS (months)	GSP (mm)	MMGSP (mm)	3WET (mm)	3DRY (mm)	3WET/3DRY ratio	RH (%)	SH (g/kg)	ENTHAL (kJ/kg)
Youganwo Flora	20.65	28.41	8.52	11.44	2362.6	260.7	1052.3	350.9	3.00	74.86	11.68	339.7
Lower Huangniuling Flora	20.68	28.4	8.86	11.42	2328.1	253.3	1045.9	326.5	3.20	75.04	11.79	340.2
Upper Huangniuling Flora	23.97	28.41	14.99	12.48	2404.5	252.8	1142.6	268.6	4.25	80.87	14.01	351.4
Shangcun Flora	23.1	28.18	12.01	12.32	2250.2	233.7	1037	200	5.19	70.79	12.57	345.4
Nankun Mt. B estimated	23.73	28.42	14.91	12.35	2273	228.7	1090.9	205.8	5.30	78.4	13.8	350.5
Nankun Mt. B measured	19.8	26.89	9.34	11.6	2145.4	184.6	1034.9	131.7	7.86	8.33	11.88	339.1
Uncertainty (±σ)	2.3	2.8	3.6	1.1	606	61	358	95	-	8.4	1.9	9

Palaeoclimatic variables estimated for Eocene and early Oligocene floras of the Maoming Basin using CLAMP and estimated and measured climate variables of the modern Nan Kun Shan B site.

Table 3. Estimated altitudes of the Maoming floras habitats.

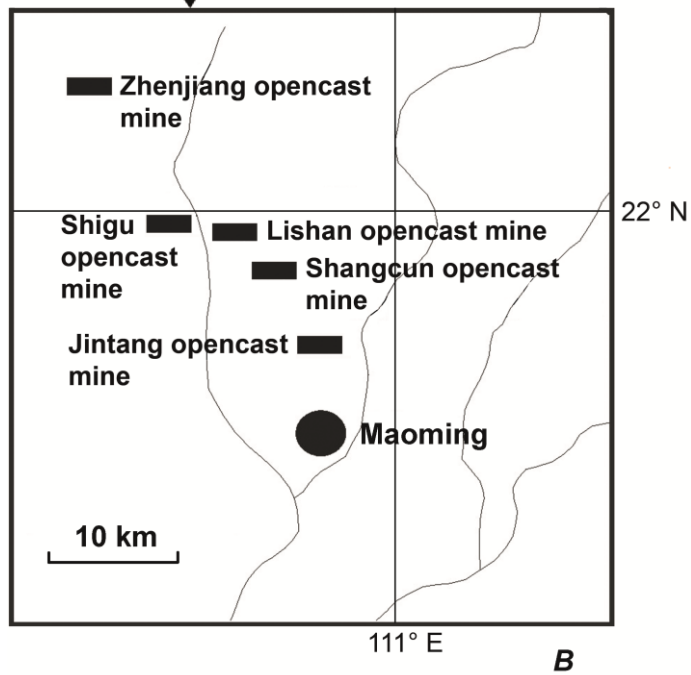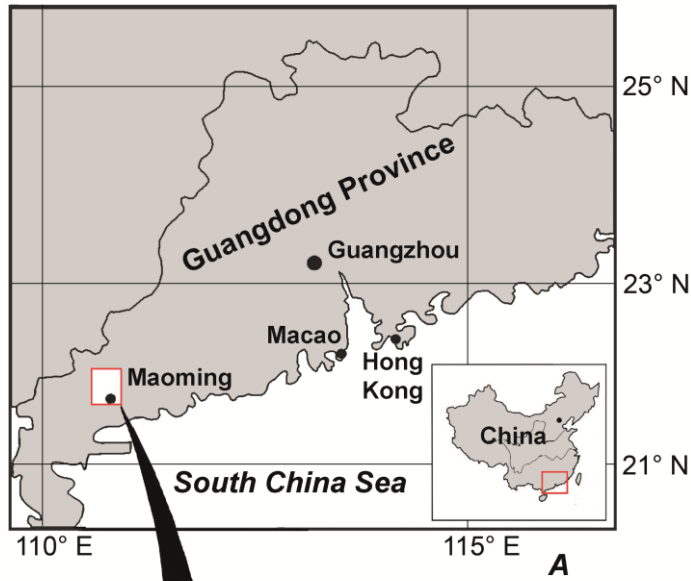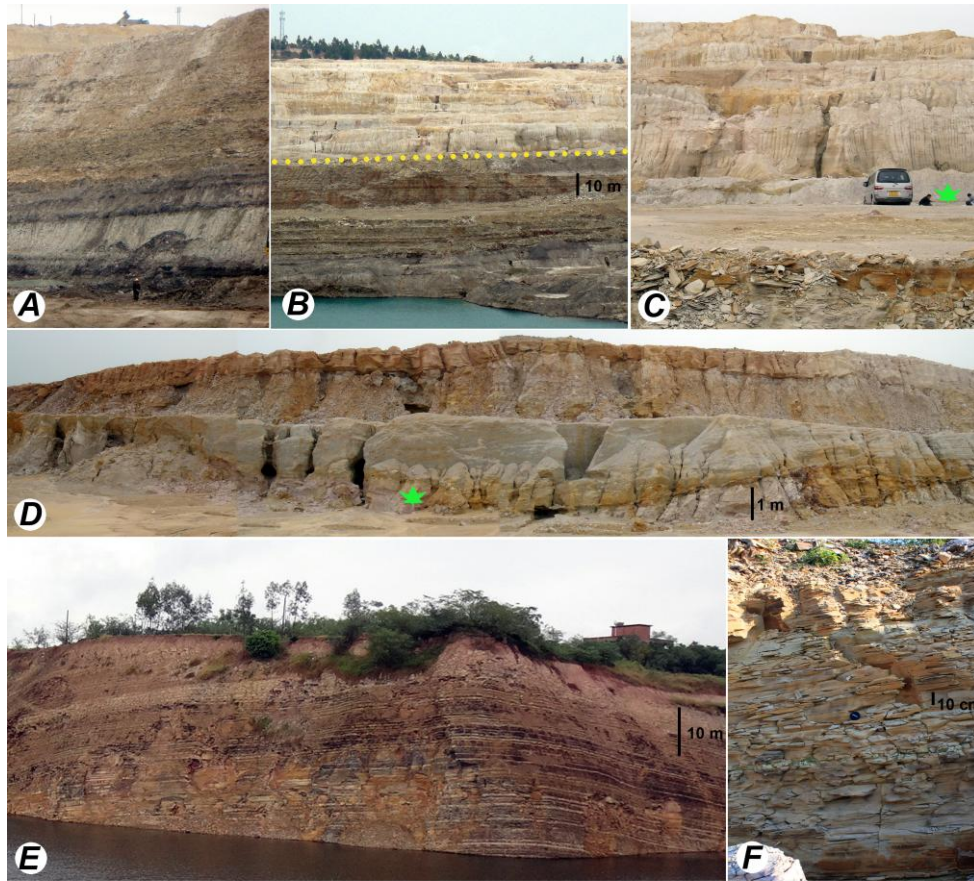|	Moist enthalpy (kJ/kg)	Altitude (km)
Youganwo Flora	340	1.60 (estimated)
Lower Huangniuling Flora	340	1.54 (estimated)
Upper Huangniuling Flora	351	0.40 (estimated)
Shangcun Flora	345	1.01 (estimated)
Gurha-39m (Early Eocene)	354	0
Tirap (latest Oligocene)	357	0

Uncertainty ($\pm\sigma$) is 9 kJ/kg
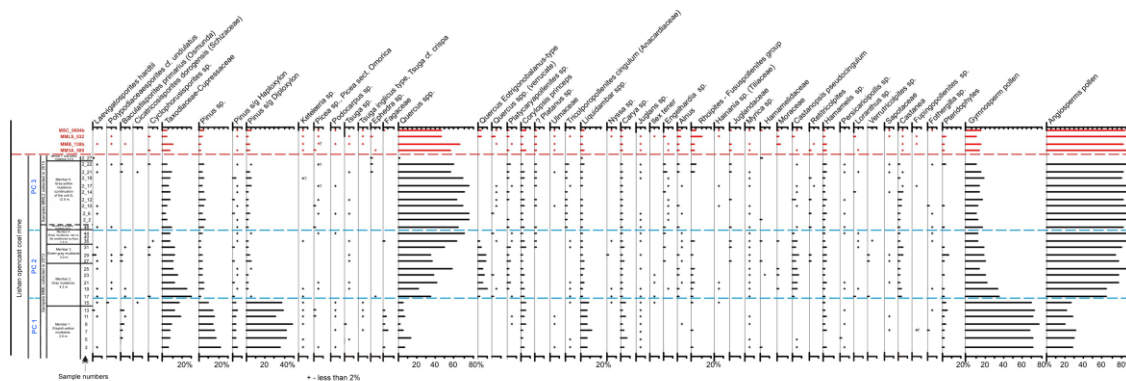
Figure 1

Figure 2

Figure 3

Figure 4

Figure 5

Figure 6

Figure 7
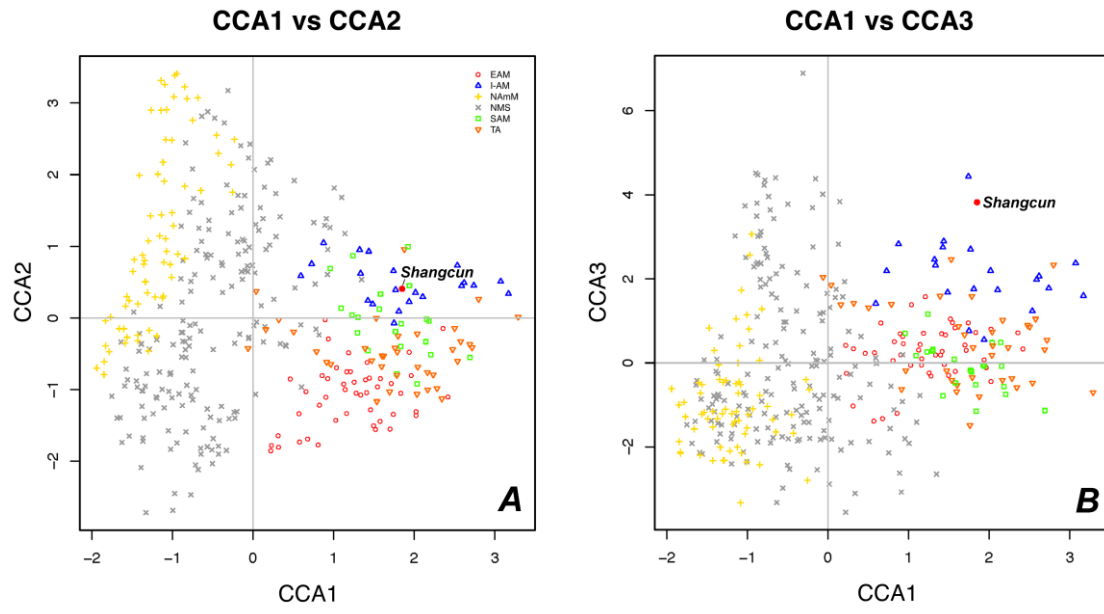
Figure 8
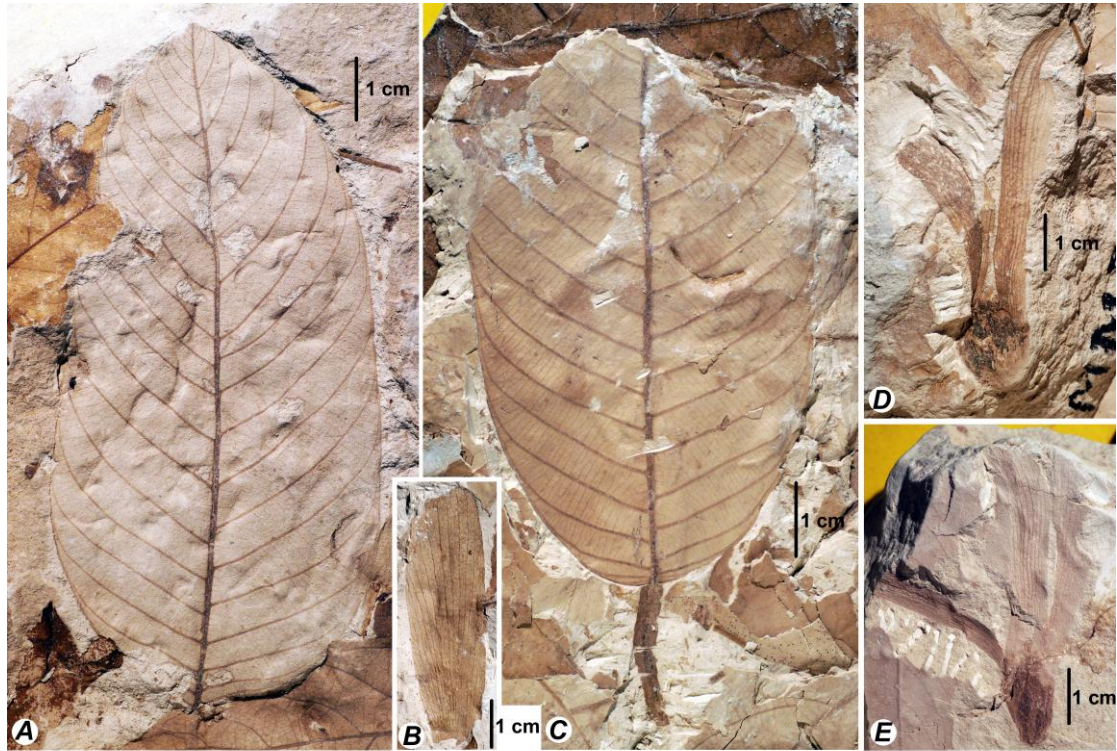
Figure 9

Highlights

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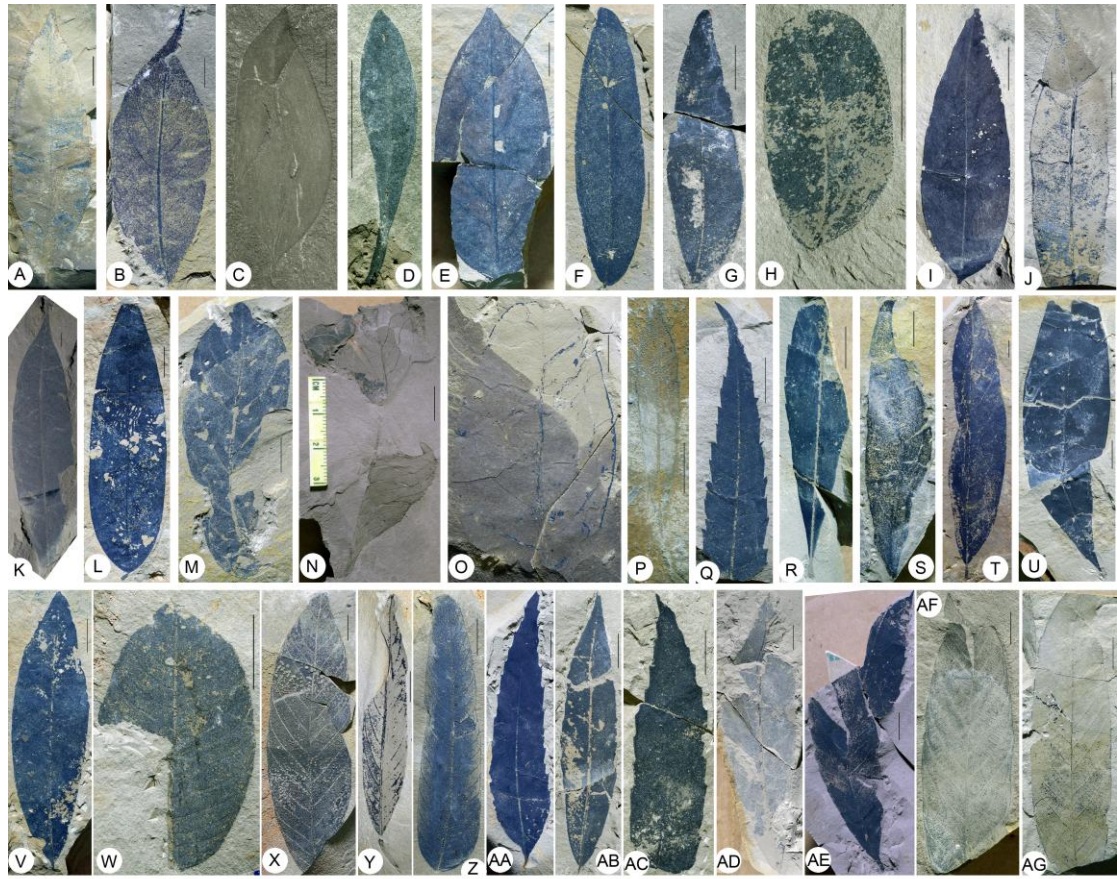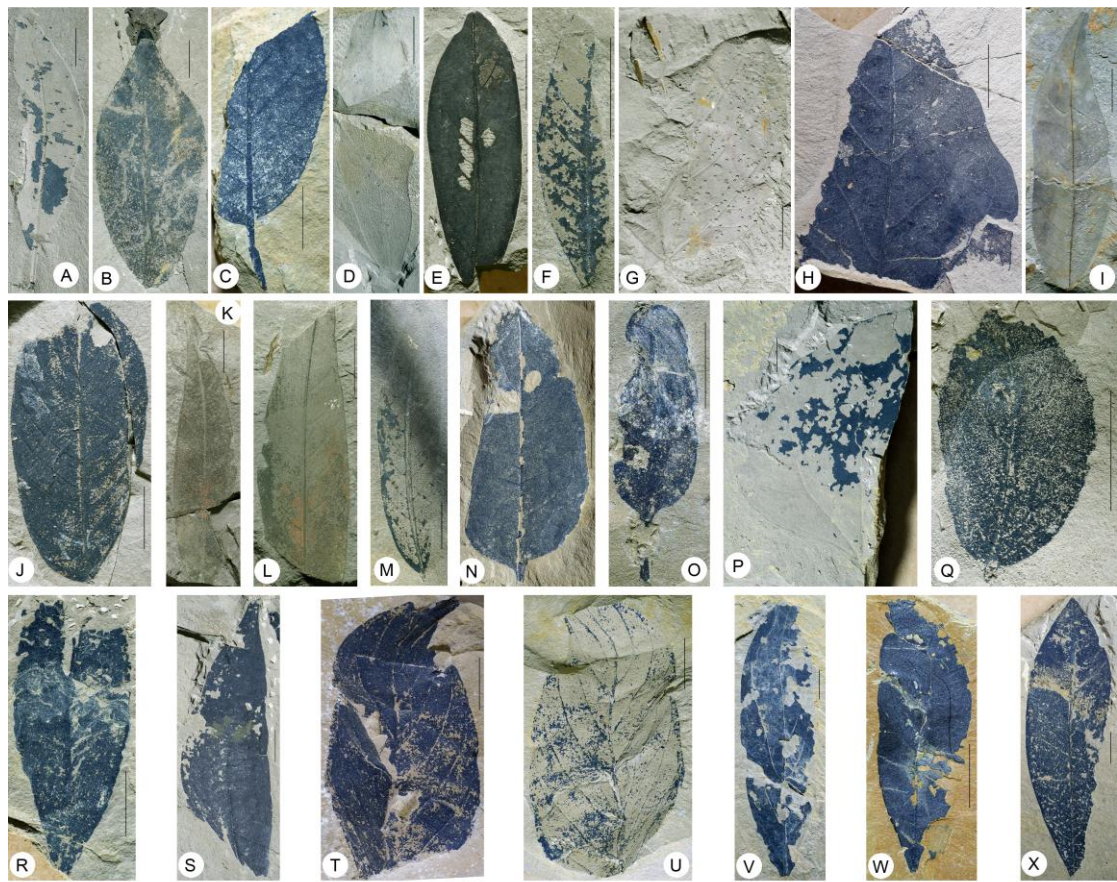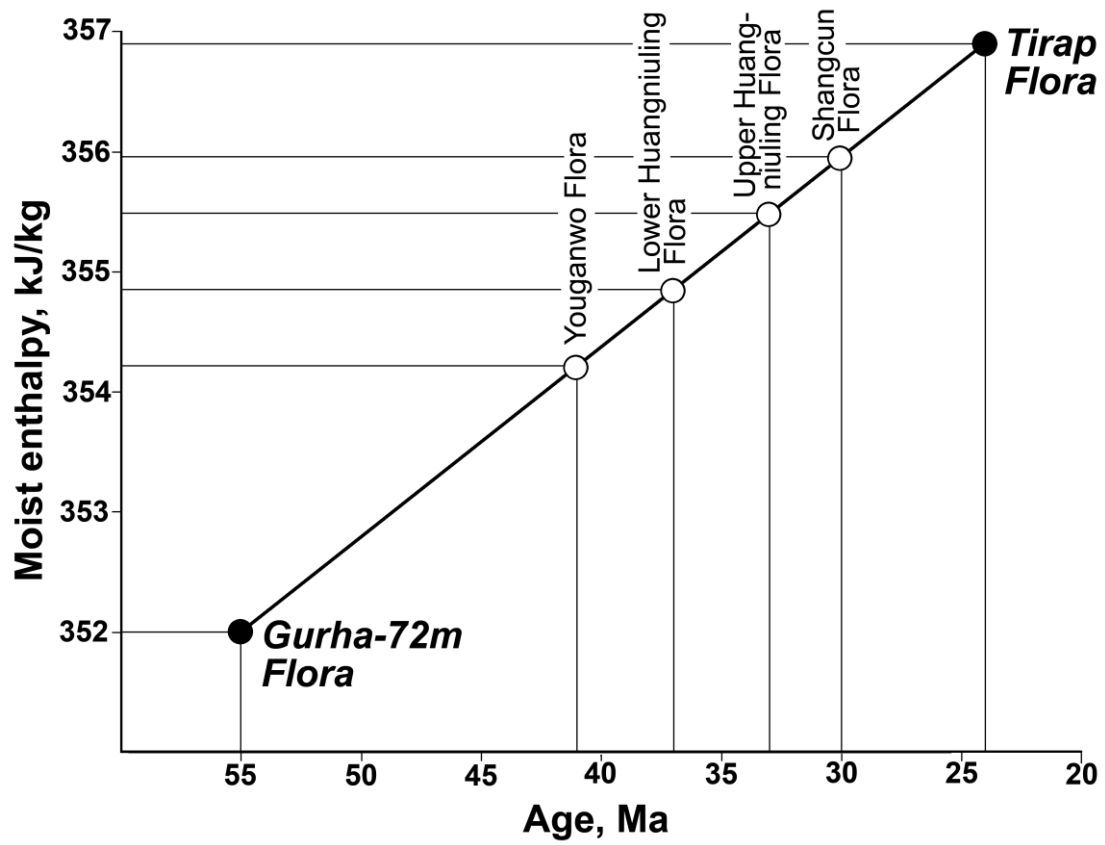
- Eocene and Oligocene plant fossils from southern China were subjected to a multivariate analysis of leaf form.

- Using CLAMP technique, we estimated that leaves were deposited at different palaeoelevations.

- The prevailing climates experienced by the fossil floras were humid subtropical with hot summers and warm winters.

- During middle Eocene - early Oligocene a progressive increase in rainfall seasonality is observed.

- By the early Oligocene rainfall seasonality was similar to that of the modern monsoonal climate of southern China.