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# Asian Eocene monsoons as revealed by leaf architectural signatures

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ABSTRACT

The onset and development of the Asian monsoon systems is a topic that has attracted considerable research effort but proxy data limitations, coupled with a diversity of definitions and metrics characterizing monsoon phenomena, have generated much debate. Failure of geological proxies to yield metrics capable of distinguishing between rainfall seasonality induced by migrations of the Inter-tropical Convergence Zone (ITCZ) from that attributable to topographically modified seasonal pressure reversals has frustrated attempts to understand mechanisms underpinning monsoon development and dynamics. Here we circumvent the use of such single climate parameter metrics in favor of detecting directly the distinctive attributes of different monsoon regimes encoded in leaf fossils. Leaf form adapts to the prevailing climate, particularly under the extreme seasonal stresses imposed by monsoons, so it is likely that fossil leaves carry a unique signature of past monsoon regimes. Leaf form trait spectra obtained from fossils from Eocene basins in southern China were compared with those seen in modern leaves growing under known climate regimes. The fossil leaf trait spectra, including those derived from previously published fossil floras from northwestern India, were most similar to those found in vegetation exposed to the modern Indonesia–Australia Monsoon (I–AM), which is largely a product of seasonal migrations of the ITCZ. The presence of this distinctive leaf physiognomic signature suggests that although a monsoon climate existed in Eocene time across southern Asia the characteristics of the modern topographically-enhanced South Asia Monsoon had yet to develop. By the Eocene leaves in South Asia had become well adapted to an I–AM type regime across many taxa and points to the existence of a pervasive monsoon climate prior to the Eocene. No fossil trait spectra typical of exposure to the modern East Asia monsoon were seen, suggesting the effects of this system in southern China were a much later development.



## 1. Introduction

An annual reversal of surface winds underpins the basic definition of a monsoon (Ramage, 1971), but associated with such reversals are strong variations in rainfall (Wang and Ding, 2006). A global monsoon network arises from seasonal latitudinal excursions of the Inter-tropical Convergence Zone (ITCZ) (Webster and Fasullo, 2003) and in an ocean covered world the ITCZ monsoon would be global and straddle the equator. However, in reality this zonal pattern is disrupted, and in places amplified, by continental configuration and topography, no more so than in the case of the modern Asia monsoon systems.

The monsoon systems affecting Asia are divisible into the South Asia Monsoon (SAM), characterized by dry winters and wet summers with temperatures peaking in May/early June just before the sudden onset of the rainy season, and the East Asia Monsoon (EAM) (Molnar et al., 2010). The EAM is typified by a cold and dry winter that penetrates deeply across eastern Asia under the influence of air masses from the Siberian High, followed by heavy rain in late spring to early summer as a low pressure cell develops over the warming Siberia and allows moist air to penetrate from the south (Molnar et al., 2010). The mechanisms underpinning the EAM are clearly different from those of the SAM, which is strongly influenced by topography but in ways that are poorly understood (Boos and Kuang, 2010; Molnar et al., 2010). The characteristics of

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the EAM are so unusual that some authors question if it should be regarded as a monsoon at all (Molnar et al., 2010). The SAM is most strongly felt over northern India and the northeastern Indian Ocean, while the EAM most strongly affects China, the Korean Peninsula, and southern Japan. In parts of southern China these systems interact and Yunnan, Guangxi and Guangdong provinces experience a complex climate regime with considerable inter- and intra-annual variation (Wang and Ho, 2002).

Several other monsoon systems are commonly recognized outside of mainland Asia. Here we consider just two of them: the Indonesian–Australian Monsoon (I–AM) and the North American Monsoon (NAmM). The I–AM extends across parts of northern Australia to the south of the Indonesian main islands, e.g. Sumatra and Kalimantan. It is largely zonal and controlled by the migrations of the ITCZ. Because equatorial Indonesia experiences year-round high rainfall the seasonal contrasts in precipitation are muted and Indonesia is normally excluded from the region considered monsoonal (Zhang and Wang, 2008). In contrast to the humid I–AM the NAmM is experienced over a broad expanse of predominantly arid southwestern North America, encompassing much of the western United States and northwestern Mexico (Adams and Comrie, 1997).

Changes in Asian monsoon systems (including both SAM and EAM) over evolutionary timescales are poorly understood, as are the causes of these changes. Numerous studies have attempted to reconstruct the evolutionary history of Asian monsoon circulation (e.g. An et al., 2001; Passey et al., 2009; Wan et al., 2007) but because the drivers of the Asian monsoon systems are complex (e.g. Boos and Kuang, 2010; Molnar et al., 2010) and because there is no commonly applicable simple proxy to measure monsoon characteristics over evolutionary timescales, the developmental history of the Asian monsoon systems remains controversial and largely obscure. Indices to investigate short-term temporal changes in monsoon intensity have been based on either climatic parameters (e.g. Liu and Yin, 2002; Parthasarathy et al., 1992; Zhang and Wang, 2008; Zhao et al., 2009), or atmospheric circulation (e.g. Goswami et al., 1999; Wang and Fan, 1999), but these are not applicable to the geological record. For deep time monsoon development studies far less precise proxies such as those based on loess-paleosol successions, isotopic data (e.g. Licht et al., 2014), and terrestrial fossil records, usually translated via a variety of transfer functions into rainfall seasonality, have to be used (e.g. Shukla et al., 2014; Srivastava et al., 2012; West et al., 2015; Xing et al., 2012). Consequently the individual monsoon systems are hard to differentiate from each other and their origin and development are difficult to document.

Fundamental to understanding the history of monsoon dynamics is the ability to distinguish climate phenomena arising from ITCZ migration from those influenced by topography. In the context of the geological record metrics incorporating the ratio of wet to dry season rainfall are commonly used as indices of monsoon intensity (e.g. Jacques et al., 2014; Shukla et al., 2014; Spicer et al., 2014; West et al., 2015). However, rainfall patterns are strongly influenced by factors other than those associated with monsoon circulation, particularly at low latitudes such as in southern China. Here any changes in the seasonal latitudinal migration of the ITCZ, driven, for example, by changes in the latitudinal temperature gradient (e.g. Hasegawa et al., 2012), will affect the seasonal wet/dry precipitation ratio experienced at any given location. Indices that rely on such ratios must therefore be used with caution in low latitudes, making it particularly difficult to detect the onset, or changes in intensity, of topographically-modified monsoon circulation: a critical issue in understanding the drivers of the Asian monsoon systems.

Another factor that can confound the use of the rainfall regime as a monsoon indicator over geological time is that most preserved sediment and associated fossils, be they animal or plant, accumulated in depositional basins. This biases the climate signal towards that obtained where water also accumulates, which inevitably moderates the local environment either directly through evaporation to the atmosphere or through hysteresis in the water supply to the organism (e.g. the soil system in the case of plants).

The Eocene is an important time in the history of Asian monsoon systems because it was only recently that the existence of an Eocene SAM was postulated (Licht et al., 2014; Shukla et al., 2014) and, although climate modeling suggests that under elevated $pCO_2$ a strong Eocene SAM should exist irrespective of the height and extent of the Tibetan Plateau, the EAM is unlikely to have existed at that time (Huber and Goldner, 2012). Instead of using a monsoon index based around a proxy-derived single meteorological parameter such as rainfall, here we attempt to use leaf form (physiognomy) directly to detect and 'fingerprint' Eocene monsoon influence in southern China. As far as a leaf is concerned a monsoon is more than just variations in rainfall, but rather a combination of soil moisture availability, atmospheric humidity and temperature that fluctuate markedly throughout the lifetime of that leaf, and the leaf has to possess features (traits) that allow it to function effectively under those changing conditions.

Natural selection favors leaves that have architectures well adapted (optimized) to their immediate surroundings because such well 'tuned' leaves maximize photosynthetic return while minimizing structural and maintenance costs (e.g. Bloom et al., 1985; Givnish, 1984). Architectural trait spectra, not just from individual leaves but leaf aggregates across numerous taxa of woody dicotyledonous flowering plants (dicots) within stands of natural modern vegetation, show strong correlations with the local prevailing climate (Yang et al., 2015). Leaf form encodes a variety of climate signals simultaneously spanning temperature, precipitation and atmospheric moisture.

Southern China is particularly interesting because not only is it an area where today the SAM and EAM interact, but it is also an area potentially subject to the effects of ITCZ seasonal migration, and modeling suggests that ITCZ migration extended further poleward in the Eocene (Huber and Goldner, 2012). By comparing leaf physiognomic trait spectra from different climates, specifically different monsoon regimes, it should be possible to determine if fossil leaves possess characteristic climate signatures in their physiognomy that would allow atmospheric phenomena driven by ITCZ seasonal migrations to be distinguished from those arising from topographic modification of the climate system.

We use this approach to address the following questions:

1. Do the leaves of woody dicots posses leaf form signatures characteristic of different monsoon regimes?
2. Were any of these present in southern China during the Eocene?
3. If they were present, which modern monsoon leaf form signatures did they most closely resemble?
4. Did these monsoon signatures show any pattern of change over time?

## 2. Our approach

### 2.1. Modern leaf samples

To answer these questions we employed the global data set of present day leaf physiognomic traits (PhysgGlobal378) presented in Yang et al. (2015). This data set consists of leaf traits from 378 vegetation sites distributed across all continents except Antarctica. As such the vegetation sites represent regions of the globe subject not only to the SAM, EAM and non-monsoonal climates, but also other monsoon regimes such as that seen in southwestern North America. At each site the full morphological range displayed by

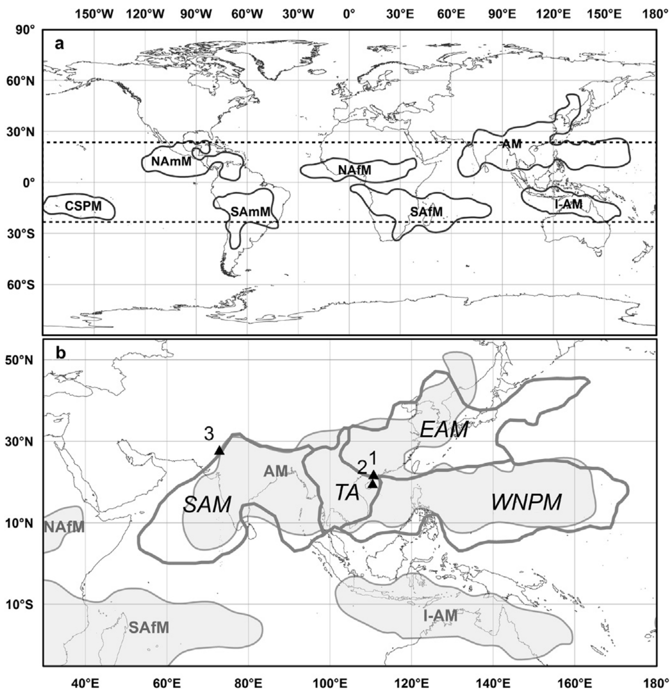


**Fig. 1. a** Map showing the location of the major monsoon areas based on summer monsoon rainy seasons as defined by Zhang and Wang (2008): CSPM – Central South Pacific Monsoon, NAmM – North American Monsoon, SAmM – South American Monsoon, NAfM – North African Monsoon, SAfM – South African Monsoon, AM – Asian Monsoon, I–AM – Indonesian–Australian Monsoon. **b** Shows the location of the fossil sites (black triangles: 1 – Maoming Basin, 2 – Changchang Basin) and areas in southern Asia experiencing influences of the South Asia Monsoon (SAM), East Asia Monsoon (EAM) and the transitional area (TA) where both monsoon systems affect the climate. The Western North Pacific Monsoon (WNPM) is the reciprocal of the Indonesian–Australian Monsoon (I–AM) both of which are largely a reflection of seasonal Inter-tropical Convergence Zone (ITCZ) latitudinal excursions. Delimitation of these areas is after Wang and Ho (2002).

leaves of at least 20 species of woody dicots was sampled in the field from natural or naturalized stands of vegetation using standard protocols (see http://clamp.ibcas.ac.cn for details). The leaves of each species were numerically scored for 31 physiognomic traits that can be obtained reliably from fossil leaf impressions even when no organic matter is preserved. These scores were then summarized into a string of 31 numbers describing the leaf physiognomic trait spectrum across all species observed at each site (see http://clamp.ibcas.ac.cn for details).

### 2.2. Fossil leaf material

The Maoming and Changchang sedimentary basins, located in southwestern Guangdong Province and on Hainan Island respectively, southern China (Fig. 1, S1), are situated in a region influenced today by both the SAM and EAM systems and close to the area dominated by the EAM. Importantly this region of southern China has remained more or less in the same geographic position since the Late Cretaceous (Spicer et al., 2014), a period of at least 70 million years. This means that plant fossil assemblages found in these basins should record vegetation changes linked to monsoon development without the complications associated with a changing paleogeographic location.

The lithology, stratigraphy and paleontology of the Maoming Basin, including age-diagnostic taxa, are reviewed in Aleksandrova et al. (2015). The Maoming Basin (Fig. 1b) is a NW-extending graben-like structure filled with Upper Cretaceous, Paleogene, and Neogene non-marine sediments and is approximately 50 km long and 10 km wide. Paleogene fluvial and lacustrine sedimentary rocks, approximately 2700 m thick, include the Youganwo and Huangniuling formations that are the subject of this study. The palynological material of Aleksandrova et al. (2015) was obtained from three quarries: the Zhenjiang quarry (21°52′47.5″N; 110°40′06.3″E), the Shigu quarry (21°50′44.9″N; 110°45′40.7″E), and the Jintang quarry (21°42′33.2″N; 110°53′19.4″E.), while the leaf fossils that form the basis of our work were recovered from only the Jintang quarry. Details of the sections are given in Aleksandrova et al. (2015).

Paleomagnetic data from boreholes through the Maoming Basin (Wang et al., 1994) show the sedimentary complex to have been deposited during normal-polarity magnetic zones (C18n–C11n) of the geomagnetic polarity time scale (GPTS), and the Maoming fossil assemblages that make up our study are all middle to late Eocene in age (Aleksandrova et al., 2015).

The Youganwo Formation (70–150 m thick) consists of sandy conglomerates, sandstones, gray–green to purple–red clayey shales, and coal seams in the lower part, while the upper part is dominated by dark gray 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 S1. For our analysis 626 fossil dicot leaf specimens belonging to 49 morphotypes (species) were collected from the Youganwo Formation. All specimens are curated in the Museum of Biology, Sun Yat-sen University with collection numbers beginning MMJ1 and MMJ1U. The traits scores are given in S2 and illustrations of specimens representative of the different morphotypes are given in S3–5.

The overlying Huangniuling Formation (60–200 m thick) is composed of grayish yellow, gray–white, and pale red sandy conglomerates, sandstones, and grayish 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 S1. For the analysis 421 fossil dicot leaf specimens representing 46 morphotypes (species) were recovered from the lower Huangniuling Formation. Several thousand specimens from the upper Huangniuling Formation were collected and from these 53 morphotypes were recognized. The leaf fossils occur in grey, beige, and white kaolinitic clay lenses within a predominantly fluvial succession of sands and gravels. They are curated in the Museum of Biology, Sun Yat-sen University with specimen numbers MMJ2 and MMJ3 respectively. The traits scores are given in S6 and 7 and illustrations of specimens representative of the different morphotypes are given in S8–11.

The Paleogene deposits of the Changchang Basin, Hainan Island, southern China (19.63°N, 110.45°E; Fig. 1b), are summarized in the lithostratigraphic log given in S1. The lower 52–54 m thick part of the Changchang Formation yields well-preserved plant megafossils from middle Eocene (Lutetian–Bartonian, 48.6–37.2 Ma) coaly shales, grey mudstones and siltstones that represent ancient mire and lake environments. This is overlain by 37–40 m of predominantly lacustrine and fluvial mudstones, siltstones and sandstones.

More than 5000 megafossil specimens were collected from the Changchang Formation and from these 135 morphotypes (species) represented by the most complete specimens of woody dicot leaves were used in our analysis. The material used is described and illustrated in Spicer et al. (2014). They are curated in the Museum of Biology, Sun Yat-sen University with specimen numbers preceded by the letters CC.

Physiognomic trait spectra from early Eocene fossil dicot leaves found in laminated lacustrine sediments exposed in the Gurha Mine, Rajasthan, India (for details of the section, age control and assemblages used see Shukla et al., 2014) are also included in our analysis for comparison purposes. The samples come from two stratigraphic levels separated by 33 m of lake clays and are dated as early Eocene based on regional geology and characteristic pollen taxa. The lower assemblage yielded 54 dicot morphotypes, while

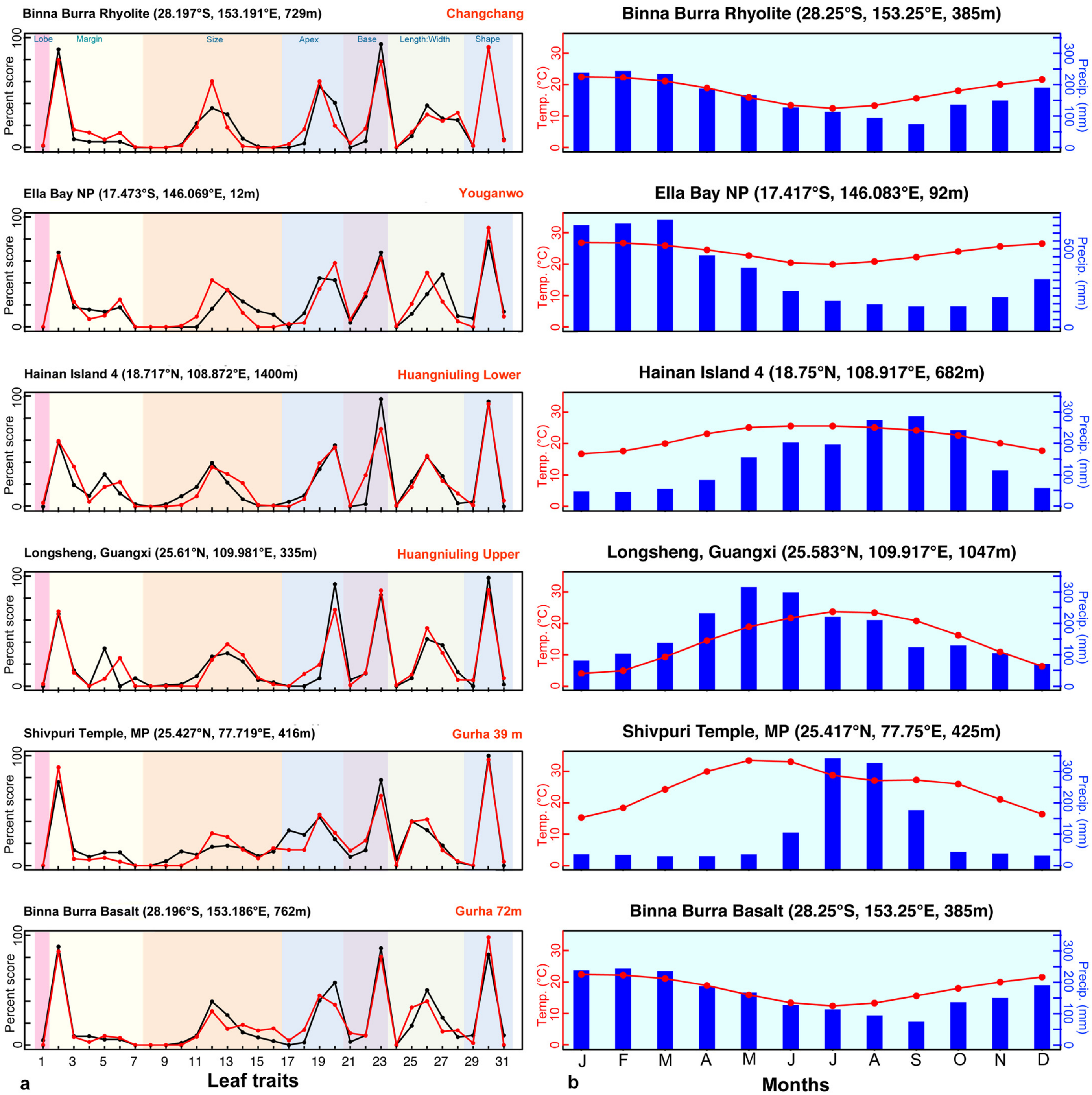


**Fig. 2. a.** Leaf physiognomic trait spectra for six modern vegetation sites growing under contrasting climates, here reduced to just thermal and precipitation regimes. These modern sites plot the closest to the fossil assemblages in Fig. 3a–c based on their leaf physiognomic trait spectra. Positioning is carried out in Axes 1, 2 and 3 space of a Canonical Correspondence Analysis. The spectra of the fossil assemblages are shown in red. Leaf traits are grouped and color-coded as in the score sheets (S2–4). Full details of the trait definitions and scoring protocols are given at http://clamp.ibcas.ac.cn. **b** Shows temperature and precipitation profiles derived from New et al. (2002) for the climate regimes experienced by each of the modern vegetation sites featured in **a**.

57 morphotypes were identified from the upper level. All specimens are curated in the collections of the Birbal Sahni Institute of Palaeobotany, Lucknow, India.

More detailed accounts of the taxonomic compositions of the various fossil floras are given in the Supplementary Material S12.

### 2.3. Physiognomic analysis

Leaf physiognomic trait spectra for both modern and fossil leaves were scored following identical standard protocols (http://clamp.ibcas.ac.cn). Graphical examples of such spectra for modern vegetation growing under the influence of the SAM, I–AM, NAmM and no monsoon climates are shown in Fig. 2 together with the distribution of rainfall and temperature throughout the year as derived from New et al. (2002) for those sites.

The full PhysgGlobal378 data set describing modern leaf physiognomy in the form of a data matrix of 378 sites × 31 trait scores was paired with a similar 378 × 11 matrix representing the same sites characterized by 11 meteorological variables observed at each vegetation site. The climate data were derived from

New et al. (2002) following the procedures given in Spicer et al. (2009). These two data sets were then subjected to a Canonical Correspondence Analysis (CCA) to explore similarities between the physiognomic trait spectra of the fossil leaves and those of modern vegetation, and specifically to see if any physiognomic trait spectra typical of vegetation exposed to modern monsoon climates were present in the Eocene vegetation of southern China. Using CCA modern vegetation sites were arranged in multidimensional space based on similarities in their leaf physiognomic trait spectra and coded as non-monsoonal or belonging to SAM, EAM, I-AM, NAmM or transitional monsoonal climates (TA) based on the summer precipitation criteria of Wang and Ho (2002) and Zhang and Wang (2008). Note that although these authors refer to summer monsoons, plants with a 12 month growing season, like those at low latitudes considered here, have to be adaptive to conditions year round and conditions during the dry season are as important, if not more so, as those in the wet season for constraining leaf physiognomy. The fossil sites were positioned passively within physiognomic space based on the leaf physiognomic trait spectral scores.

To obtain quantitative estimates of paleoclimate in terms of temperature and moisture parameters we performed a standard CLAMP analysis (Yang et al., 2011) using the smaller PhysgAsia2 and HiResGRIDMetAsia2 (Khan et al., 2014). This is because with the large 378 sample global dataset the structure of physiognomic space is complex, often highly contorted with respect to precipitation variables, and only summarized poorly by general trends. In a CLAMP analysis climate trends through this physiognomic space are determined from the associated meteorological data and represented as vectors. In the complex physiognomic space arising from large global data sets the predictive precision derived from such vectors is low compared to smaller data sets with a simpler calibration space (Yang et al., 2015). For enthalpy derived estimates of paleoaltitude this data set has been validated by multiple isotope studies (Currie et al., 2016).

## 3. Results

### 3.1. Physiognomic trait spectra

Figs. 3a–c show the results of the CCA. The symbols representing modern vegetation sites indicate their attribution to geographic areas experiencing different climatic regimes. For simplicity only monsoon regimes experienced in southern Asia (Fig. 1), following Wang and Ho (2002), Indonesia–Australia and North America are identified (Adams and Comrie, 1997; Anderson et al., 2000; Zhang and Wang, 2008). Also included are sites exposed to non-monsoonal climates. In Axes 1–2 space (Fig. 3a) the positions of the fossil leaf assemblages (red filled circles) indicate that they exhibit physiognomic spectra similar to those of modern vegetation sites experiencing the SAM, the transitional zone between the SAM and the EAM and the I-AM. None of our fossil sites plot clearly within the non-monsoonal or EAM cloud of sites. This shows that leaf physiognomic trait spectra typical of the modern EAM had not evolved by the Eocene in southern China, but those trait spectra found in today's SAM and IAM apparently had.

In Axis 1–3 space (Fig. 3b) the fossils sites, including the Gurha sites from northwestern India, are clearly allied more closely to the cloud of modern sites representing vegetation exposed to the I-AM than the SAM. The I-AM is largely a product of seasonal latitudinal migrations of the ITCZ and has quite different characteristics in terms of precipitation and temperature regimes to the SAM (Fig. 2a) suggesting that at the lower paleolatitude of the Gurha site in the early Eocene (≤10°N, Shukla et al., 2014) an ITCZ driven monsoon predominated rather than the topographically modified monsoon seen in the modern SAM.

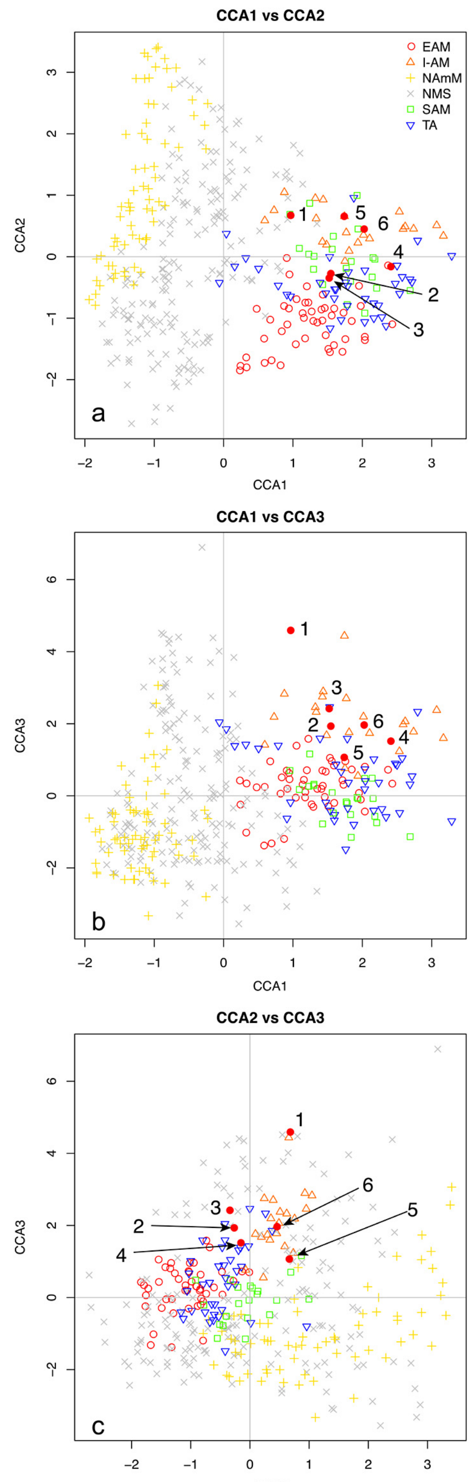


**Fig. 3.** CCA plots showing the relationship between the leaf physiognomic traits exhibited in the fossil assemblages (red filled circles) and those of modern vegetation exposed to different climate regimes. Coding for modern vegetation sites: EAM – East Asia Monsoon, I-AM – Indonesia–Australia Monsoon, NAmM – North America Monsoon, NMS – no monsoon, SAM – South Asia Monsoon, TA – transition area. Fossil assemblages are numbered as follows: 1 – Changchang, 2 – Youganwo, 3 – Huangniuling lower, 4 – Huangniuling upper, 5 – Gurha 39 m, 6 – Gurha 72 m.

Modern I-AM and SAM areas occur at low latitudes and hence warm climates, whereas the area affected by the EAM system extends as far north as northern China and is driven in part by the development an alternating strong winter high- and summer low-

**Table 1**
CLAMP climate retrodictions for southern Asia Eocene fossil assemblages using the PhysgAsia2 and high-resolution gridded calibration data. The Gurha mine assemblages are early Eocene in age, the Youganwo and Changchang are middle Eocene while Huangniuling are dated as late Eocene.

| | MAT (°C) | WMMT (°C) | CMMT (°C) | LGS (Months) | GSP (cm) | MMGSP (cm) | 3-WET (cm) | 3-DRY (cm) | 3Wet/3Dry | RH (%) | SH (g/kg) | ENTHAL (kJ/kg) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Changchang | 21.3 | 28.4 | 10.8 | 11.5 | 202.0 | 19.7 | 88.0 | 22.6 | 3.9 | 69.0 | 11.3 | 339.0 |
| Youganwo | 20.2 | 28.4 | 7.9 | 11.3 | 233.4 | 25.7 | 103.7 | 34.85 | 3.0 | 74.4 | 11.4 | 338.0 |
| Huangniuling Lower | 20.7 | 28.4 | 8.9 | 11.4 | 232.8 | 25.3 | 104.6 | 32.7 | 3.2 | 75.0 | 11.8 | 340.0 |
| Huangniuling Upper | 24.0 | 28.4 | 15.0 | 12.0 | 240.1 | 25.3 | 114.3 | 26.9 | 4.3 | 80.1 | 14.0 | 351.0 |
| Gurha 39 m (India) | 26.4 | 28.2 | 19.0 | 12.0 | 183.8 | 15.8 | 98.4 | 8.3 | 11.8 | 78.6 | 14.5 | 354.0 |
| Gurha 72 m (India) | 23.9 | 27.2 | 18.2 | 12.0 | 179.2 | 15.3 | 93.8 | 10.6 | 8.9 | 78.0 | 14.1 | 352.0 |
| Uncertainties (2 s.d.) | 4.7 | 5.6 | 7.2 | 2.1 | 122.0 | 12.2 | 71.6 | 18.9 | – | 16.7 | 3.7 | 17.0 |

pressure system over Siberia. Such alternations would not have been so strong in the globally warm Eocene and the southward winter penetration of cold air that is typical of the EAM would not have occurred. By comparison climates similar to those arising from the modern SAM and I–AM must have been in existence long enough for evolution to have favored physiognomic trait spectra specific to those regimes across numerous taxa.

Fig. 2 shows the physiognomic trait spectra for the fossil sites (in red) and climate summaries for those modern vegetation sites with leaf physiognomic spectra most similar to them (i.e. closest in physiognomic space).

### 3.2. Quantitative paleoclimatic interpretations

The quantitative paleoclimate interpretations of the Changchang, Youganwo and Huangniuling floras indicate a cool subtropical to tropical temperature regime (Table 1). In the Maoming Basin the temperatures of the cold month mean show a progressive rise over time and a possible increase in the wet/dry ratio. Accompanying this rise is the arrival of predominantly tropical trees belonging to the dipterocarps (family Dipterocarpaceae) in the upper Youganwo Flora followed by a progressive increase in dipterocarp leaf abundance through to the Upper Huangniuling Flora. This is matched by an increase in enthalpy, which may indicate a possible reduction in basin elevation. Deciduous oak pollen replaces evergreen oak pollen possibly as a result of stronger rainfall seasonality.

Table 1 presents the retrodicted paleoclimate for the fossil sites using the PhysgAsia2 and GRIDMetAsia2 datasets. The climate retrodictions for the fossil sites are derived from their positions along the vectors projected in four-dimensional space following the usual procedures for this kind of analysis. For details of the technique see Yang et al. (2011) and the CLAMP website (http://clamp.ibcas.ac.cn). As might be expected the temperature regime was typical of low latitudes, plant growth was year round (length of the growing season ∼12 months), and overall the climate was humid, consistent with the high taxonomic diversity, particularly among angiosperms, and the presence of tropical taxa such as those of the families Fabaceae, Anacardiaceae and Dipterocarpaceae.

With a mixture of tropical evergreen through to temperate taxa the compositionally unusual Changchang fossil assemblage possesses a leaf physiognomic spectrum that indicates a mean annual temperature of $21\text{–}22 \pm 4.6\,°\text{C}$ (2 sigma) with a minimum mean annual temperature range of around 20 °C (Spicer et al., 2014). This is a minimum estimate because the warm month mean temperature is likely to be lower than that actually experienced by the plants when alive due to the flattening of the calibration curve at higher temperatures (Srivastava et al., 2012) and evapotranspirational cooling (Spicer et al., 2011). Evapotranspirational cooling will be greatest in the dry season, which as a function of ITCZ migration coincides with the coolest part of the year. It is likely then that to some extent the reconstructed CMMT's reflect this phenomenon. Nevertheless overall temperatures are cool given the low paleolatitude (∼20°N) at a time of globally warm Eocene paleoclimate. High paleoelevation can be discounted as a possible cause because the high enthalpy values mean that the Changchang forests were unlikely to have been much more than 1.3 km above sea level (Spicer et al., 2014). However, these cool Eocene temperatures are not unique and are similar not only to those given by other leaf physiognomic analyses (e.g. Shukla et al., 2014), but an array of isotope systems from shallow marine sediments at low latitudes in North America (Keating-Bitonti et al., 2011), suggesting enhanced heat transport to higher latitudes in the Eocene 'hothouse' world.

## 4. Discussion

The inability of simple climate metrics to properly characterize the complex atmospheric phenomena that are monsoons has hampered our understanding of monsoon history, the mechanisms underlying monsoon dynamics and hence the vulnerability of monsoon systems to future climate change. Unlike meteorological instruments the leaves of woody dicot plants reflect atmospheric conditions across all climate variables simultaneously and where vegetation is predominantly evergreen, and leaves have to function well all year round, they are likely to capture well seasonal variability typical of monsoon climates.

Fig. 3 clearly shows that modern vegetation sites exposed to individual monsoonal regimes group together demonstrating that each monsoon region gives rise to vegetation possessing distinctive and characteristic leaf physiognomic trait spectra. Not all monsoon regions recognized by some authors (e.g. Zhang and Wang, 2008) are present in Fig. 3 due to limitations in geographic coverage within the data set of 378 vegetation stands worldwide that we used as the basis of our analysis. However, those that are represented (NAmM, I–AM, SAM and EAM) are distinctive in terms of leaf traits. The more arid NAmM stand sites are separated from those of the humid Asia/Australia monsoons by sites exposed to non-monsoonal climates, while the EAM sites are distinct from the I–AM and SAM sites. These overlap in CCA Axes 1–2 space (Fig. 3a) but are separated on CCA Axis 3 (Fig. 3b). Moreover, where the SAM and EAM systems interact today the physiognomic traits in that area are also distinctive (the transitional sites).

Our fossil material was derived from the Eocene Changchang, Youganwo and Huangniuling formations with comparator Eocene samples from the Gurha Mine of northwestern India. Within the limits of dating resolution the Changchang and Youganwo formations are age equivalent (middle Eocene, Lutetian–Bartonian, 48.6–37.2 Ma) while the Huangniuling Formation is slightly younger (late Eocene, Priabonian ∼37.2–33.0 Ma) (Aleksandrova et al., 2015). The Gurha mine samples are early Eocene in age (Ypresian).

Canonical Correspondence Analysis of the fossil assemblages within the context of the global dataset (Figs. 3a–c) clearly shows that Eocene vegetation of southern China had developed leaf physiognomic trait spectra similar to those seen in vegetation exposed to the modern SAM and I–AM, but not the EAM. This finding supports other evidence that a monsoon system was already well established in Asia in the Eocene (Licht et al., 2014; Shukla et al., 2014). Geologic and paleoaltimetric studies show that parts of the Tibetan Plateau were already elevated, some even to near their present height, as early as the Eocene (e.g. Burg and Chen, 1984; Ding et al., 2014; Dupont-Nivet et al., 2008; England and Searle, 1986; Kapp et al., 2003, 2005; Murphy et al., 1997) providing a mechanism for enhancing monsoonal air circulation across southern Asia that should have existed, albeit in a weaker form, for much of the Mesozoic and Cenozoic because of regional land/sea contrasts (Parrish et al., 1982). The mechanism for this enhancement is likely to have been through deflecting airflow (Boos and Kuang, 2010; Molnar et al., 2010) or from an elevated 'heat pump' (e.g. Yanai and Wu, 2006) or both. However, such topographic enhancement may not be essential for developing a strong Eocene Asia monsoon system (Huber and Goldner, 2012).

In Axis 1–2 space (Fig. 3a) it would appear that a monsoon leaf form signature was already present in the vegetation of southern China at ∼40 Ma and most likely a monsoon climate had been a dominant factor in the evolution of the flora long before that. Close inspection of Fig. 3b shows that the fossil sites are embedded within the physiognomic space occupied by the modern I–AM and not the SAM. The samples in the PhysgGlobal378 database representing the I–AM are all from northern Australia, which experiences a more gradual onset of the wet season than sites under the SAM, largely as a result of seasonal latitudinal migrations of the ITCZ. The fossil sites most strongly associated with the I–AM are those from the Gurha Mine, India, which, at the time they were being deposited, were situated at a paleolatitude of ∼10°N or less (Shukla et al., 2014). At this position the effect of seasonal ITCZ migrations would have been strongly felt even without amplification from an already high Tibetan Plateau, or greater latitudinal excursions of the ITCZ in a warm world (Huber and Goldner, 2012). We suggest that across southern Asia monsoon-adapted physiognomic spectra had their origin in climates arising from ITCZ migration and only later became further modified to specific Asian monsoon regimes as they developed.

None of our fossil assemblages reveal leaf physiognomic trait spectra typical of today's EAM and so the influence of the EAM appears to have been either non-existent or very weak in southern China during the Eocene. A diversity of geologic proxies point to the Paleogene climate of central China being arid across a broad central belt before increasing penetration of moisture in the Neogene confined the arid zone to the northwest, where it persists today. This has been interpreted as resulting from the establishment of the EAM around 23 million years ago, approximately at the Oligocene/Miocene boundary (Sun and Wang, 2005). Paleobotanical evidence for the existence of seasonal rainfall in northeastern China suggests a possible development of the EAM in the late Eocene, perhaps as early as ∼40 Ma (Quan et al., 2011), but if this interpretation is correct the strength of the EAM was insufficient to re-organize the major climatic zones in China, as identified by Sun and Wang (2005), until some 17 million years later. In a world in which latitudinal temperature gradients were shallower than now any EAM would be fundamentally different because a winter Siberian High would have been much weaker or non-existent. Importantly, prior to 23 Ma there is no evidence of the strong reversal in wind patterns seen today that produce dry cold conditions in winter but draw in moist air from the south in summer. However, because the Eocene central belt of China was moderately moist (Quan et al., 2011), and not arid, such a reversal may be difficult to detect using conventional proxies.

The quantitative paleoclimate estimates given in Table 1 circumscribe a climate conducive to the development of subtropical to tropical seasonally moist forest as corroborated by the systematic compositions of the megafloral and palynological fossil assemblages. Often such forests are characterized by the presence of genera such as *Shorea*, a member of the Dipterocarpaceae family. Today dipterocarps are confined to the tropics of Asia, Africa, and South America and in Southeast Asia, where most (90%) of their living species occur. Our results suggest that dipterocarps had an early exposure to conditions found today in the I–AM and SAM.

Within uncertainty leaf physiognomic spectra temperatures compatible with year-round growth and productivity was not limited by aridity because the mean annual precipitation was ∼2 m and the dry season precipitation was ∼1 m. All plant-based paleoprecipitation proxies lose precision in wet regimes because leaf form is not constrained by lack of water. Inevitably uncertainties are high but none of the floras suggests rainfall seasonality typical of strong monsoons.

## 5. Conclusions

In answer to the questions posed in the introduction we conclude the following:

1. In modern vegetation leaves of woody dicots display distinctively different physiognomic spectra under different climate conditions, and in particular leaves exposed to NAmM, I–AM, EAM and SAM regimes develop recognizable leaf trait spectral signatures characteristic of those regimes.
2. Woody dicot leaf physiognomic spectra superficially similar to today's SAM, but more characteristic of the I–AM, were present in the Eocene floras of southern China and northwest India, but we found no clear evidence of any adaptation to today's EAM regime.
3. The Eocene fossil floras of southwest China and northern India exhibit leaf physiognomic spectra most similar to those seen in the modern I–AM, which is probably more a reflection of wider latitudinal migrations of the ITCZ than to an enhanced SAM regime. In southern China no marked dry season was in evidence and the overall humid climate regime would not be considered monsoonal if only seasonal precipitation ratios were used as a measure of monsoon strength. The Gurha sites from northwestern India, paleolatitude ≤10°N, point to a strong monsoonal signature more similar to that seen in northern Australia today under a strong ITCZ influence rather than that of the modern SAM.
4. Leaf physiognomic spectra obtained from fossils collected from the Youganwo and Huangniuling formations indicate a progressive warming over time; particularly in terms of the cold month mean temperature. There is also an increase in the wet/dry season precipitation ratio when the Huangniuling Formation was laid down, although uncertainties are large. Future analysis of the flora contained in the overlying Shangcun Formation is required to determine if this trend marks the transition from a climate predominantly influenced by seasonal migrations of the ITCZ to one influenced by a strengthening SAM.

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## Appendix A. Supplementary material

Supplementary material related to this article can be found online at http://dx.doi.org/10.1016/j.epsl.2016.05.036.

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