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Paleogene Monsoons across India and South China: Drivers of Biotic Change

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Abstract

Monsoonal climates at low latitudes (<32 °N) are an inevitable consequence of seasonal migrations of the Inter-tropical Convergence Zone (ITCZ), but the character of these monsoons depends on continental configuration, orographic expression and the strength of Hadley circulation. To explore the evolution of monsoon systems across southern Asia we compare climate signatures archived in ten Paleogene floras from northern India, Tibet and southern China, occupying low palaeolatitudes at a time of extreme global warmth and elevated CO_2. Fossil leaf form reveals that under such 'hothouse' conditions megathermal early Eocene to earliest Miocene forests were exposed to strong monsoonal climates typical of those experienced today arising from annual migrations of the ITCZ, possibly enhanced by a lower equator-to-pole temperature gradient. Throughout the Paleogene an elevated Tibetan highland produced no discernable modification of this ITCZ monsoon, although rainfall seasonality similar to that of the modern South Asia Monsoon (SAM) is observed in northern India as early as the beginning of the Eocene, despite its near-equatorial palaeoposition. In South China rainfall seasonality increased progressively achieving modern monsoon-like wet season/dry season precipitation ratios by the early

Oligocene. Despite evidencing weak rainfall seasonality overall, fossil leaves from South China have exhibited monsoon-adapted morphologies, comparable to those seen in today's Indonesia-Australia Monsoon, for at least 45 million years. Together, the Indian and South China fossil leaf assemblages show that the evolution of megathermal ecosystems across southern Asia has been influenced profoundly by monsoonal climates for at least the last 56 million years. The Paleogene ITCZ-driven monsoon system strongly impacted India as it transited the Equator likely eliminating Gondwanan taxa not able to adapt to seasonal precipitation extremes. Furthermore, powerful seasonally-reversing winds, and associated surface ocean currents, are likely to have facilitated two-way biotic transfer between India and Eurasia long before closure of the Tethys Ocean.

Keywords: Plant evolution, ITCZ, Eocene, Oligocene, climate, Tibet

1. Introduction

Southern Asia hosts one of the world's great biodiversity 'hotspots' (Myers et al., 2000) and large parts of it experience an intense monsoonal climate. The links between biodiversity and marked seasonal variations in rainfall, topographic complexity (resulting in niche diversity) and long term climate change are not well understood, however the evolution of Asian monsoon systems is likely to have been an important factor in the development of the southern Asia biodiversity hotspot.

The word 'monsoon' originally referred to seasonal prevailing winds and relates to reversals in airflow often, but not exclusively, accompanied by seasonal variations in rainfall (Ramage, 1971). However, amongst atmospheric scientists there is no universally accepted definition of what constitutes a monsoon climate. Because seasonal variations in precipitation have marked social and economic consequences rainfall has become an essential component in the recognition of a monsoon climate (Wang and Ho, 2002). Zhang and Wang (2008) recognised six major summer monsoon rainy season domains characterised by the mean dates of the local onset, peak and withdrawal of the rainy season, coupled with wind parameters. The thresholds for these meteorological parameters were in part chosen to differentiate what here we will refer to as 'enhanced' monsoon climates from rainfall seasonality associated with latitudinal migrations of the Inter-tropical Convergence Zone (ITCZ), which we will call 'ITCZ monsoons'. These thresholds, although useful, are somewhat arbitrary. For example "the domain of the summer rainy season is where the summer (May to September in the Northern hemisphere and November to March in the Southern Hemisphere) rainfall equals or exceeds 3 mm/day and the ratio of summer rainfall to annual rainfall must be greater than 55%" (Zhang and Wang, 2008, p. 1566). However, even when using these criteria different sets of modern observational data yield different spatial distributions of modified monsoon climates (Zhang and Wang, 2008, their Fig. 9). The boundaries of modified monsoon climates areas as shown in Figure 1 must, therefore, be regarded as indistinct.

Unfortunately these meteorological criteria are also difficult to apply to the geological record, which does not routinely record annual repeating patterns of wind strength and direction, and rainfall proxies lack the required precision. Often the best that can be achieved through proxies is the detection of qualitative, or semi-quantitative, signals of rainfall seasonality. This can lead to problems in recognising and characterising ancient monsoon systems, which in turn colours our understanding of monsoon evolution.

In this work we use plant morphological environmental adaptations as archived in fossil leaf assemblages to investigate the signatures of ancient monsoon climates. Leaf form trait spectra record adaptations to a range of seasonally fluctuating temperature and moisture regime variables that collectively represent monsoon conditions.

1.1 ITCZ monsoons

In a hypothetical ocean-covered Earth seasonal migrations of the thermal equator and associated low-pressure systems, the Inter-tropical Convergence Zone (ITCZ), would create global monsoon belts symmetrical about the Equator. Either side of an ever-wet equatorial zone, the width of which would depend upon the width of the ITCZ and the extent of ITCZ latitudinal migrations, there would be seasonally wet/dry subequatorial belts. Using geological rainfall proxies these belts are monsoonal. The latitudinal range of the ITCZ excursion and associated rainfall patterns appears sensitive to the behaviour of Hadley circulation in relation to the equator-to-pole temperature gradient (Hasegawa et al., 2012). In a warm world such as existed during the Paleogene, the excursion of the thermal equator may have been several degrees greater than now, reaching latitudes as high as 25° (Huber and Goldner, 2012) and bringing seasonal rainfall to latitudes of ~30°.

Given this ITCZ-related monsoon driving mechanism it is no surprise that low latitude monsoonal climates have been reported from the Paleogene of Asia (Licht et al., 2014; Shukla et al., 2014) because near-tropical ITCZ monsoons should have been present throughout Earth history. However the criteria for recognising monsoon climates in these studies fall far short of the those used in the meteorological definitions proposed by Zhang and Wang (2008).

1.2. Enhanced monsoons

In the real world, past and present, the distribution of continents and topography disrupts, and in places may enhance, the ITCZ-related global monsoon belts (Alisov, 1950; Wang and Ho, 2002; Khromov and Petrosiants, 2006; Zhang and Wang, 2008) (Fig. 1) and in today's world the strongest monsoon modification is seen over Asia. The precise mechanism for this enhancement is poorly understood but is often attributed to a combination of the Tibetan Plateau acting both as a high elevation 'heat pump' and as a deflector of airflow (Molnar et al., 2010), while the high Himalaya block and redirect north-south air streams (Boos and Kuang, 2010).

[Fig. 1 near here]

Studies using General Circulation Models (GCM) (reviewed in Huber and Goldner, 2012) generally confirm the apparent relationship between topographic expression and monsoon enhancement, but also point to other palaeogeographic boundary conditions, temperature in particular (Washington and Meehl, 1983; Anderson et al., 2002; Neelin, 2007; Anderson et al., 2010; Cherchi et al., 2010), as having a strong influence on monsoon systems. Notably, GCM modeling of the Eocene world generates a global monsoon system regardless of plateau surface elevation and changing plateau height results in only minor effects on large-scale atmospheric circulation (Huber and Goldner, 2012), which underlines the ubiquitous influence of the ITCZ. It seems that at low latitudes in a warm world strongly seasonal fluctuations in rainfall would arise from enhanced ITCZ annual migration, and that the presence of a Tibetan Plateau, or a Himalayan mountain chain, may not be a prerequisite for developing monsoon climates over southern Asia. However ITCZ monsoons may well be modified by orography, raising questions as to the relative roles of the Tibetan Plateau and the Himalaya in such modifications.

The roles of topography, continental configuration and temperature regime in modifying ITCZ monsoon characteristics, are clearly difficult to disentangle and undoubtedly change over time in response to changing geographical configurations, surface uplift, and global thermal regimes. This frustrates attempts to understand the underpinning mechanisms and evolution of modern modified monsoon systems across Asia, and thus their vulnerability to change in a warming world. However, modeling shows that plateau height may have significant effects on Tibetan Plateau vegetation biome types, and to some extent vegetation in surrounding regions in terms of the positions of biome boundaries (Lunt et al., 2010). If the models are correct in predicting changes at the biome level the vegetation of Asia, particularly in physiognomic terms, is likely to be sensitive to changes in climate associated with orographic development and those changes should be recorded in plant fossils.

1.3 Research questions

Given this background, here we attempt to address important questions concerning the evolution of the Asian monsoon systems. Questions of immediate concern are:

1) Are the observed Paleogene Asian monsoonal regimes solely a reflection of ITCZ migrations?

2) If not, can we determine if they reflect geographically/topographically modified monsoons?

3) What roles might particular palaeo-monsoon regimes have had in shaping early Cenozoic biotas across southern Asia?

In this exploratory study we compare ten fossil floras from across southern Asia that record environmental conditions throughout the Eocene and Oligocene, looking specifically for telltale monsoon signatures as recorded by leaf form. Once characterised we then speculate on the possible role that monsoons had in shaping the biotas of southern Asia.

2. Materials and Methods

Our work brings together three leaf fossil assemblages from India, two from southern Tibet and five from two depositional basins in South China (Fig. 1). Nine of these fossil floras are of Paleogene age and one is from the beginning of the Neogene (earliest Miocene) (Figure 2). The compositions of these floras and how they are dated are given below (Section 2.2). These diverse megafloras, spanning the early Eocene to the earliest Miocene, capture environmental change across a key interval in the development of the modern geography and vegetation of southern Asia. We focus on megafossils (leaves, seeds/fruits, and wood) rather than microfossils (assemblages of spores and pollen) because megaremains are seldom transported far from their origin, are largely immune to reworking from older to younger sediments, and so offer good spatial and temporal resolution.

[Fig. 2 near here]

The Indian fossil material comes from the Gurha Mine in Rajasthan, northwestern India (Fig. 1, Fossil site 1), and the Tirap mine in Assam, northeastern India (Fig. 1, Fossil site 2). Today both locations are exposed to the SAM but the Gurha mine area experiences a semi-arid climate while the Tirap mine experiences far wetter conditions. At the time they were deposited the Gurha assemblages were located close to the Equator (6–12 °N, Shukla et al., 2014), while the Tirap palaeoforests were close to 15 °N (Srivastava et al., 2012). In both cases the ancient vegetation grew within the normal latitudinal range of the ITCZ and therefore should exhibit leaf forms adapted accordingly. However the question is whether or not the fossil leaves show any evidence of conditions like that of an enhanced monsoon similar to that of the modern SAM.

The fossil localities we sampled in Tibet (Fig. 1, Fossil sites 3 and 4) today experience semi-arid conditions with some SAM influence. Overall rainfall is low because today the fossil sites sit in the summer rainshadow of the Himalaya. In the Paleogene the forests the fossils represent were located on the southern flank of a high (>4 km) proto-Tibetan Plateau (Ding et al., 2014, 2017; Wang et al., 2014), much as today's monsoon forests of the northern Gangetic plain and Siwaliks clothe the southern flank of the modern Himalaya. If a Paleogene SAM existed we should see strong evidence for it in the Tibetan fossil assemblages.

The Changchang Basin, Hainan Island (Fig. 1, Fossil site 5), and the Maoming Basin (Fig. 1, Fossil site 6) located in southwestern Guangdong Province, South China, are close to that region of China that today is influenced predominantly by the East Asia Monsoon (EAM). Bearing in mind that the boundaries shown in Figure 1 are gradational, despite this proximity they actually lie in an area Wang and Ho (2002) term a Transitional Area (TA). The TA experiences the effects of both the South Asia Monsoon (SAM) and the Western North Pacific Monsoon (WNPM)

(Wang and Ho, 2002) (Fig. 1). The WNPM is mirrored in the Southern Hemisphere by the Indonesia-Australia Monsoon (I-AM) and both the WNPM and the I-AM are expressions of seasonal migrations of the ITCZ. The monsoon climates they experience are shaped to some extent by land-sea contrasts, but are virtually unmodified by orography.

Unlike sites in India, the Chanchang and Maoming Basins in South China have remained more or less at the same latitude (~23 °N) for at least 70 million years (Wakita and Metcalf, 2005; Spicer et al., 2014) meaning that changes in monsoon characteristics are likely to reflect changes in monsoon dynamics rather than palaeogeographic position, and thus provide a useful comparator with perceived monsoon changes over India. The research question here is 'do the ancient leaf forms exhibit the signature of the TA, or any of the other Asian monsoon climates, or can the ancient climate be regarded as a simple reflection of seasonal ITCZ migration?'

2.1. Analysis of leaf form

As would be expected in humid megathermal environments all our studied floras (both fossil and modern) are highly species rich and a full systematic analysis of the megafossils is ongoing. However no taxonomic identification is required for extracting climate signals from leaf form using the technique known as Climate Leaf Analysis Multivariate Program (CLAMP) (Yang et al., 2011; Yang et al., 2015). CLAMP uses a numerical description of 31 leaf character (trait) states found in at least 20 morphotypes (a morphotype being a morphologically distinct group of specimens thought to be representative of a biological species) of woody (trees, shrubs and vines) dicot leaves at a given location to create a 'physiognomic leaf trait spectrum' characteristic of vegetation growing at that site. By means of these leaf trait spectra modern day reference vegetation sites growing under a variety of different climate regimes are positioned in multidimensional space using Canonical Correspondence Analysis (ter Braak, 1986). Sites that plot close together in multidimensional space are more similar in their leaf physiognomic trait spectra than sites that plot further apart. Trends through this space, summarised by vectors calibrated using modern climate data, reveal the relationship between overall leaf form and a range of climate variables. Fossil leaf assemblages, the traits of which are numerically described the same way, are positioned passively within this calibrated multidimensional cloud of modern reference sites (known as physiognomic space). The conditions under which the fossils once grew can be estimated from the positions of the fossil sites within physiognomic space and their location along the climate vectors.

In addition to obtaining quantitative estimates of past climate variables the relative position of fossil samples within physiognomic space captures overall past leaf form adaptation to the ancient prevailing climate. Spatial distributions of modern vegetation samples may be used to characterise adaptations to particularly demanding environmental regimes such as those associated with monsoon systems (Spicer et al., 2016) and the relative positions of fossil sites within physiognomic space reveal whether or not ancient vegetation was adapted to monsoon conditions.

It could be argued that this methodology simply reflects climate selection for species that have appropriate leaf forms and not selection within lineages for the capacity to produce climate-appropriate foliar physiognomy. If leaf trait spectra are simply a reflection of species selection by climate then the CLAMP approach would, like other palaeobotanical climate proxies based on the properties of extant species, be restricted to Neogene or younger fossil assemblages because older assemblages would contain taxa so different from the modern that the technique would be unreliable. If the leaf trait spectra are an expression of convergent adaptation to climate then CLAMP should be robust over virtually all woody angiosperm evolutionary history. Of course these two processes by which leaf form in a stand of vegetation becomes 'tuned' to the prevailing climate are not mutually exclusive. Species selection no doubt occurs over short timescales (decades to millenia) but evolutionary adaptation must also occur. This is evidenced by the finding of Yang et al. (2015) that stands of vegetation in highly endemic and compositionally distinct floras such as those of South Africa, New Zealand and Japan, all of which due to latitude and altitude grow under similar climates, have leaf trait spectra more similar to one another than those of other stands that experience different climates (Yang et al., 2015, Figs. 3 and S2). In the case of New Zealand a unique degree of genetic isolation since the Late Cretaceous has resulted in a distinctive flora, but one still displaying high levels of leaf trait spectral similarities to those growing elsewhere in similar climates. It therefore follows that leaf form adaptation to the extreme seasonal climate variability typical of monsoons should be largely taxon independent and thus useful for the characterisation of monsoon climates in deep time.

To derive quantitative estimates of ancient temperature and precipitation leaf form trait spectra for the ten fossil floras considered here were subjected to a CLAMP analysis (Yang et al., 2011) using the PhysgAsia2 and high-resolution gridded climate (HiResGRIDMetASia2) calibration data sets of Khan et al. (2014). Although Jacques et al. (2015) first demonstrated the utility of CLAMP to investigate monsoon climates in China, we use the Khan et al. (2014) calibration because it additionally incorporates leaf trait spectra from vegetation exposed to monsoon climates in India and Thailand, and in terms of palaeoaltimetry has been validated against an array of stable isotope palaeoaltimeters (Currie et al., 2016). We compare the climates derived from our fossil material with those recorded in the leaf architecture of modern vegetation from India and South China, and examine these leaf trait spectra for different monsoon signatures using the global dataset of Yang et al. (2015).

2.2 Fossil material: context and composition

2.2.1. Gurha Mine Section, northwestern India

Laminated lacustrine sediments overlying lignites in the Gurha Mine (27.87398 °N, 72.86709 °E), Rajasthan, India (Fig. 1, Fossil site 1) yield a diversity of fossil leaves, flowers, fruits, seeds and insects. Lapilli tuffs occurring below the lignite proved to be altered to clay and were not dateable.

Based on characteristic pollen taxa the Gurha lignites appear coeval with those of the early Eocene Cambay Basin (~55–52 Ma), some 700 km to the south in Gujarat, which inter-finger with well-dated marine units (Sahni et al., 2004; Prasad et al., 2013; Shukla et al., 2014; Kumar et al., 2016). The Gujarat Vastan lignite successions are highly fossiliferous having yielded pollen (Samant and Tapaswi, 2000, 2001), plant remains (Sahni et al., 2006), dinoflagellates (Garg et al., 2008), marine ostracodes (Bhandari et al., 2005), marine fish (Samant and Bajpai, 2001; Rana et al., 2004; Nolf et al., 2006) and mammals (Sahni et al., 2004; Rose et al., 2006) including bats (Rana et al., 2005). In the Gurha Mine abundant leaves, flowers, wood, pollen and insects appear to have been deposited in a poorly oxygenated lacustrine environment represented by laminated clays and sands of the Palana Formation (Fig.

2). The ancient lakes were saline at times, possibly due to groundwater seepage of marine waters or evaporation (Shukla et al., 2014).

A comprehensive inventory of the Gurha megaflora has yet to be completed but those forms so far identified include *Uvaria* (Shukla and Mehrotra, 2014), *Aporosa* (Shukla et al., 2016), *Saraca*, *Cajanus* (Shukla and Mehrotra, 2016), *Sterculia*, *Gardenia*, *Eucalyptus*, *Putranjiva*, *Terminalia*, *Miliusa*, *Syzygium* and *Astronium*, together with members of the Lauraceae and Fabaceae. The flora is extremely rich and the plant fossils are well preserved. All taxa are characteristic of humid tropical and paratropical evergreen forests, and although megafossils of palms are lacking this group is well represented in the pollen record (Shukla et al., 2014; Kumar et al., 2016).

For the CLAMP analysis 54 woody dicot leaf morphotaxa from a lower assemblage (Gurha 39) and 57 morphotaxa from an assemblage 33 m higher in the section (Gurha 72) (Shukla et al., 2014) were used.

2.2.2. Tirap Mine, northeastern India.

Some 200 m of the Upper Oligocene Tikak Parbat Formation (Fig. 2) are exposed in the Tirap opencast coalmine (27.28889 °N, 95.77083 °E) (Fig. 1, Fossil site 2) situated within the Makum Coalfield of northeastern India. The sediments reflect a fluvio-marine deltaic environment within the Barail Group.

Throughout the Barail Group sediments trend from predominantly marine to predominantly non-marine upsection filling a linear basin on the eastern edge of the Indian Plate. The lower part of the Tirap mine section represents a lower delta plain environment with topogenous, or perhaps ombrogenous swamps, lacustrine and fluvial environments and floodplain interfluves. A sedimentary log of the section is given in Srivastava et al. (2012) and the palynofacies are described in Kumar et al. (2012). The late Oligocene age for the sediments places the palaeolatitude of the contained plant fossils at ~10–15 °N (Srivastava et al., 2012).

Megafossil remains are abundant in the Makum Coalfield (Seward, 1912; Awasthi and Mehrotra, 1995). Collections from coeval sediments in the Baragolai, Ledo, Tirap and Tipongpani mines have yielded dicotyledonous leaf taxa belonging to the genera *Calophyllum*, *Garcinia*, *Kayea* (Calophyllaceae), *Garcinia,Pterygota* (Malvaceae), *Santiria* (Burseraceae), *Heynea* (Meliaceae), *Nephelium* (Sapindaceae), *Lannea, Mangifera, Parishia* (Anacardiaceae), *Rhizophora* (Rhizophoraceae), *Terminalia* (Combretaceae), *Memecylon* (Memecylaceae), *Avicennia* (Avicenniaceae), *Alstonia* (Apocynaceae), *Myristica* (Myristicaceae), *Apollonias* (Lauraceae) and *Bridelia* (Phyllanthaceae), together with fruits/seeds of *Dalbergia* and *Entada* (Fabaceae). Subsequently a leaf and a fruit of *Mesua* (Clusiaceae) (Awasthi et al., 1992), leaves assigned to *Daphnogene* (Lauraceae) (Mehrotra et al., 2009), *Alphonsea* (Annonaceae) (Srivastava and Mehrotra, 2013a), *Poeciloneuron* (Calophyllaceae) (Srivastava and Mehrotra, 2013b), *Firmiana* (Malvaceae), *Paranephelium*, *Sapindus* (Sapindaceae) (Srivastava and Mehrotra, 2013c), fruits of *Barringtonia* (Lecythidaceae) and *Sterculia* (Malvaceae) (Mehrotra, 2000) and legumes (Fabaceae) assigned to the genera *Buteocarpon* and *Luguminocarpon* (Srivastava and Mehrotra, 2010) were added to the flora. Palms, including *Nypa*, are a significant component of the Tirap megafossil flora (Mehrotra et al., 2003; Srivastava et al., 2012). Conifers such as *Podocarpus* (Podocarpaceae) (Awasthi et al., 1992) are very rare as is the horsetail *Equisetum* (Mehrotra et al., 2009), although rooting systems possibly belonging to *Equisetum* are common throughout the section.

In a CLAMP analysis of 80 woody dicot morphotypes from the Tirap mine, Srivastava et al. (2012) used a modern data set called PhysgIndia for their calibration. Here we use PhysgAsia2 for all our analyses because it contains a greater representation of modern megathermal vegetation, including that exposed to monsoon climates.

2.2.3. Liuqu Flora, southern Tibet.

This flora is preserved within siltstone lenses forming parts of the Liuqu conglomerate, exposed near Liuxiang to the south of the Yarlung-Zangpo suture zone, southern Tibet (29.197 °N, 87.832 °E) (Fig. 1, Fossil site 3). As evidenced by its overall coarse nature and composition the Liuqu conglomerate accumulated rapidly in a sedimentary wedge in the Yarlung-Zangpo foredeep located along the base of the southern flank of the high (>4 km) Gandese Mountains. The flora is dated as late Paleocene to early Eocene (~56 Ma, Thanetian–Ypresian, Fig. 2) based on detrital zircons and depositional context. This age is consistent with that deduced from the component taxa (Fang et al., 2005; Ding et al., 2017). Palaeoenthalpy measurements place the depositional site at ~1 km above sea level (Ding et al., 2017).

Leaf fossils are quite diverse, if fragmentary, from which 36 woody dicot morphotypes have been recognised. Formal taxonomic identification has not yet been completed and is frustrated by a lack of preserved leaf cuticles. Most leaves are entire-margined and coriaceous, typical of what might be found in a modern megathermal forest. Particularly notable are impressions of large fragments of fan palms, together with palm trunks (Ding et al., 2017).

2.2.4. Qiabulin Flora, southern Tibet

The Qiabulin flora (29.335 °N, 88.507 °E) (Fig. 1, Fossil site 4) comes from just west of Xigatze and is preserved in the Qiuwu Formation, a unit about 280 m thick comprised of 10 m of volcanic and granitic pebbly conglomerate beds at the base overlain by grey interlayered sandstones, coarse sandstones and mudstones with locally thinly-bedded coals. The leaf fossils are found in cross-bedded sandstones where bedding geometry indicating a southward flow. The Qiuwu is disconformably overlain by the ~1060 m thick Dazuqu Formation, composed of mottled conglomerates, grey-yellow coarse sandstones, medium sandstones, purple mudstones and shale.

The youngest U-Pb ages of detrital zircons of the Qiuwu Formation are 26-21 Ma (Ding et al., 2017). These ages are also consistent with the Qiuwu Formation at Angrento to the west and the equivalent unit of the Luobusha Formation at Zedong to the east (Li et al., 2015). The age of the overlying Dazuqu Formation is regarded as being no older than ~19 Ma at the Qiabulin locality as determined by U-Pb ages of detrital zircons and $^{40}Ar/^{39}Ar$ analyses of laterally equivalent tuffs (Aitchison et al., 2009) constraining the age of the Qiabulin flora to be 21-19 Ma (earliest Miocene) (Fig. 2).

The Qiabulin flora lacks palms and like the Liuqu flora is fragmentary. Overall it appears to be composed of warm temperate taxa but a full taxonomic investigation is not yet complete. However, 26 morphotypes have been recognised for our CLAMP analysis.

2.2.5. Changchang Basin, Hainan Island.

The Paleogene deposits of the Changchang Basin, Hainan Island, South China

(19.63 °N, 110.45 °E) (Fig. 1, Fossil site 5) are divisible into three formations; the Changtou Formation (Paleocene) is overlain by the Changchang Formation (Eocene), above which occurs the Wayao Formation (Eocene) (Zhou and Chen, 1988; Lei et al., 1992). The lower 52–54 m of the Changchang Formation yields well-preserved plant megafossils from middle Eocene (Lutetian–Bartonian, 48.6–37.2 Ma; Fig. 2) within 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.

The Changchang Flora contains a mixture of evergreen and deciduous plants (Zhang, 1980) encompassing horsetails, ferns, conifers and angiosperms belonging to over 200 species (morphotaxa) and is comparable to the richest Eocene floras known. However, it is an unusual assemblage in that it contains angiosperm taxa, including palms, typical of tropical, subtropical and even temperate vegetation (Spicer et al., 2014).

Angiosperms, both dicots and monocots, dominate in terms of diversity and it is likely that they contributed the greatest biomass in the ancient vegetation. The families Lauraceae, Fagaceae, Altingiaceae, Myricaceae, Fabaceae, Malvaceae, Juglandaceae and Ulmaceae are well represented and Lauraceae is an almost ubiquitous component. The Fagaceae are present in the form of *Castanopsis*, *Lithocarpus* and *Quercus*, while the Altingiaceae is represented by three-lobed *Liquidambar* leaves. A single species of *Myrica* represents the Myricaeae and the Changchang Flora contains numerous members of the Fabaceae (e.g. *Podocarpium*) (Xu, 2015). For the CLAMP analysis 135 woody dicot leaf morphotypes were used. A more complete description of the Changchang Flora, including illustrations of the leaf morphotypes, is given in (Spicer et al., 2014).

2.2.6 Maoming Basin, South China

The Maoming Basin (Fig. 1, Fossil site 6) is a NW-orientated graben-like structure filled with Upper Cretaceous, Paleogene, and Neogene non-marine sediments (Nan and Zhou, 1996; Ye et al., 1996), approximately 50 km long and 10 km wide. A succession of approximately 2700 m of Paleogene fluvial and lacustrine sedimentary rocks is divisible into the Tongguling, Youganwo, Huangniuling, Shangcun, Laohuling, and Gaopengling formations. Palaeomagnetic data from boreholes in the Youganwo, Huangniuling, Shangcun, and 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. This corresponds to an age range of 42 to 32 Ma (middle Eocene–early Oligocene) making the Maoming fossil assemblages featured in our study all middle Eocene to early Oligocene in age (Aleksandrova et al., 2015) (Fig. 2).

The leaf fossils that form the basis of our work were recovered from Youganwo, Huangniuling and Shangcun formations exposed within quarries at Jintang (21.70917 °N; 110.8886 °E.), Shangcun (21.79778°N; 110.8094°E) and Lishan (21.84417 °N; 110.7786 °E).

2.2.6.1. Youganwo Formation, Maoming Basin, South China

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). The remains of fish (*Cyprinus maomingensis* Liu), reptilians (*Anosteria* *maomingensis* Chow et Liu, *Isometremys lacuna* Chow et Yeh, *Aspideretes impressus* Yeh, *Adocus inexpectatus* Danilov, Syromyatnikova, Skutschas, Kodrul et Jin, *Tomistoma petrolica* Yeh, Alligatoridae gen. et sp. indet.), and mammals such as *Lunania* cf. *youngi* Chow and *Maofelis cantonensis* Averianov, Obraztsova, Danilov, Scutschas et Jin occur in the oil shales (Chow and Liu, 1955; Liu, 1957; Yeh, 1958, 1963; Chow and Yeh, 1962; Li, 1975; Wang et al., 2007; Tong et al., 2010; Danilov et al., 2013; Skutschas et al., 2014; Averianov et al., 2016).

For our analysis 626 fossil dicot leaf specimens belonging to 49 morphotypes (species) were collected from throughout the Youganwo Formation. All specimens are curated in the Museum of Biology, Sun Yat-sen University with collection numbers beginning MMJ1 and MMJ1U. Impressions and compressions of leaves, 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 exposed in the Jintang section, and this assemblage was used for our analysis.

The Lower Youganwo megaflora comprises impressions and compressions of leaves and fruits and petrified wood remains found in siltstones underlying the primary coal seam in the Jintang quarry of the Maoming Basin. The floral assemblage 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 remains are those of *Zelkova* (Ulmaceae) and *Platimeliphyllun* (Platanaceae) leaves, *Paliurus* (Rhamnaceae) leaves and fruits, and leaves of woody dicotyledons possibly belonging to the Anacardiaceae. *Leguminophyllum* also occur.

The floral assemblage from the grey mudstones above the productive coal seam to-date has yielded 31 leaf, fruit, rhizome and seed taxa representing horsetails (Equisetales), ferns (Salviniaceae and possibly Osmundaceae), and conifers (Podocarpaceae), but by far the most common remains are those of angiosperms belonging to the Nelumbonaceae, Lauraceae, Platanaceae, Fagaceae, Fabaceae, Anacardiaceae, Celastraceae, Rhamnaceae, and Arecaceae. However the number of woody dicot morphotypes is so far insufficient for a reliable physiognomic analysis.

Petrified wood is common in the localities including *Bischofia maomingensis* Feng et Jin (Euphorbiaceae) and *Myrtineoxylon maomingensis* Oskolski, Feng et Jin (Myrtaceae) (Feng et al., 2012; Oskolski et al., 2013).

Several characteristic species of the genera *Osmunda*, *Salvinia*, *Nelumbo*, *Laurophyllum*, *Platimeliphyllum*, cf. *Celastrus*, *Palaeocarya*, *Leguminophyllum*, *Podocarpium*, *Sabalites*, and *Davidocarpon* from the Youganwo Flora are also found in the Changchang Flora from Hainan Island (Spicer et al., 2014).

2.2.6.2. Huangniuling Formation, Maoming Basin, South China

The 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 Huangniuling megaflora includes at least 150 morphotaxa. Ferns are extremely rare in the Huangniuling Flora: only single specimens of fertile fronds belonging to the genus *Lygodium* have been found. Conifers, represented by the genera *Pinus*, *Nageia*, and cf. *Taxus*, are more abundant and diverse than in the Youganwo Flora. The white pine, *Pinus maomingensis* Xu et al. (*Pinus* subgenus *Strobus*), is represented by a single compressed cone. *Pinus* sp. is also represented by fascicles of needle leaves with deciduous sheaths and bulbous bases indicative of *Pinus* subgenus *Strobus* (Xu et al., 2015). The Podocarpaceae in both Youganwo and Huangniuling floras are represented by the genus *Nageia* (Liu et al., 2015), with different macromorphological and epidermal leaf features from those of the Eocene species *Nageia hainanensis* Jin, Qiu, Zhu et Kodrul from the Changchang Formation (Jin et al., 2010).

Angiosperms dominate the Huangniuling megafloral assemblage in both diversity and abundance and include representatives of the Fagaceae, Lauraceae, and Fabaceae, accompanied by subordinate Altingiaceae (Maslova et al., 2015), Hamamelidaceae, Myricaceae, Juglandaceae, Rhamnaceae (*Paliurus*) and Dipterocarpaceae represented by fruits and leaves of *Shorea* (Feng et al., 2013). The family Fagaceae is represented by the genera *Quercus, Lithocarpus* and *Castanopsis*.

For our climate analysis 421 fossil dicot leaf specimens representing 46 morphotypes (species) were recovered from the lower Huangniuling Formation, while several thousand specimens from the upper Huangniuling Formation yielded 53 morphotypes. The two assemblages, lower and upper, were treated separately in our analysis.

The Lower Huangniuling Flora contains conifers represented by very rare podocarpaceous leaves (*Nageia*), relatively abundant leaves possibly belonging to the Taxaceae, and *Pinus* reproductive and vegetative remains. The white pine, *Pinus maomingensis* Xu et al. (*Pinus* subgenus *Strobus*) has been described based on a compressed seed cone and cone scales.

Angiosperms are also present in abundance with members of the Fagaceae being the most diverse and abundant component of the Lower Huangniuling Flora. At least five species of the genera *Quercus*, *Castanopsis* and probably *Lithocarpus* have so far been identified. Representatives of the Altingiaceae constitute a notable component of the flora while woody dicots belonging to Myrtaceae and possibly Lauraceae and Fabaceae are less abundant.

The Upper Huangniuling Flora contains extremely rare ferns (Lygodiaceae), conifers (Pinaceae, Podocarpaceae, Taxaceae) in similar abundance to the Lower Huangniulin but dominated by *Pinus maomingensis*, and angiosperms assigned to Lauraceae, Fagaceae, Altingiaceae, Myrtaceae, Juglandaceae, Myricaceae, Dipterocarpaceae, Rhamnaceae and Fabaceae (over 75 fossil taxa in total). Not all specimens have been identified. Representatives of Fagaceae (*Quercus*, *Lithocarpus*, and *Castanopsis*) dominate the Upper Huangniuling Flora in both diversity and abundance. Altingiaceae (*Liquidambar*) and Myricaceae (*Myrica*) are also abundant accompanied by subordinate representatives of the Lauraceae, Myrtaceae, Dipterocarpaceae and Fabaceae. Specimens assigned to the Fabaceae include numerous large oblong pods of *Leguminocarpon* and possible legume leaflets.

The leaf fossils occur in grey, beige, and white kaolinitic clay lenses within sands and gravels of a predominantly fluvial origin. They are curated in the Museum of Biology, Sun Yat-sen University with specimen numbers MMJ2 (Lower Huangniuling) and MMJ3 (Upper Huangniuling).

2.2.6.3. Shangcun Formation, Maoming Basin, South China

The 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. Gastropods (*Viviparus* sp., *Tulotomoides kuangsiensis* and *Melania* sp.) as well as fish (*Pychodus*) (Zhou and Chen, 1988; Aleksandrova et al., 2015) are present in finer grained facies.

Pollen analysis positions the Eocene-Oligocene transition near the base of the Lishan section as marked by a sudden increase in the proportion of conifers and loss of megathermal angiosperm taxa consistent with the observed marked cooling at the beginning of the Oligocene. Higher in the section megathermal angiosperms recover in terms of abundance and diversity, but lack key taxa typical of the Eocene. A similar pattern of change was reported in 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. Although many of the Shangcun megafossils were not collected *in situ,* the pollen spectra within the matrix entombing the leaf fossils is similar to that above the conifer-rich horizons and so the leaf assemblage used in our analyses represent conditions in the later part of the early Oligocene (late Rupelian) (Fig. 2).

Unlike in the Youganwo and Huangniuling formations leaves are distributed not in dense leaf mats but isolated in greyish brown to light brown clay and siltstones representing a large lacustrine environment. The density and distribution of the leaves suggest that deposition was distant from the shoreline. Detailed taxonomic analysis has yet to be completed, but the Shangcun megaflora contains at least 91 fossil taxa of leaves, stems, fruits, cones, and seeds belonging to leafy bryophytes, horsetails, ferns, conifers and angiosperms.

Ferns are scarce, but relatively diverse. The most abundant fern is *Osmunda*, while mosses are represented by a few thin stems and horsetails are rare. In contrast to the older floras conifers are relatively abundant and diverse in the Shangcun Formation, and are composed mainly of pinaceous and cupressaceous species.

As with the previous floras in the Maoming Basin angiosperms dominate both in terms of numbers of specimens and taxonomic diversity and for our analysis have been divided into 46 morphotypes. Representatives of the Fagaceae and Lauraceae are the most abundant and the most diverse. The leaves of *Myrica* and woody dicotyledons of uncertain systematic affinity are also abundant.

The preliminary list of the Shangcun plants at family level is as follows: Bryopsida, Equisetaceae, Osmundaceae, Polypodiaceae, Pinaceae, Cupressaceae, Taxaceae, Platanaceae, Lauraceae, Fagaceae, Malvaceae, Calophyllaceae, Juglandaceae, Fabaceae, Rhamnaceae, Cornaceae, Myricaceae, Menispermaceae?, Simaroubaceae and Palmae. Genera include*Pinus* (Pinaceae),*Calocedrus* (Cupressaceae), *Quercus* (Fagaceae) (leaves and fruits), *Castanopsis* (Fagaceae), *Burretiodendron* Rehder (Malvaceaes.l.) (fruits), *Calophyllum* (Calophyllaceae), *Palaeocarya* (Juglandaceae), *Paliurus* (Rhamnaceae), *Myrica* (Myricaceae) and *Ailanthus* (Simaroubaceae) (fruits). Specimens are curated in the Museum of Biology, Sun Yat-sen University with specimen numbers beginning MSC, MMB, MMLS, MMCW and MM3A.

3. Results

Figures 3–5 illustrate the mean annual and annual variation in temperature, as well as rainfall seasonality experienced across all fossil assemblages. Some representative modern sites from across southern Asia and Australia (exposed to today's I-AM) are also shown for comparison purposes. Leaf trait spectra for the modern sites were entered into the analysis as if they were fossil assemblages (i.e. passively), ensuring that the fossil and modern climate estimates are directly comparable.

3.1 Temperature regimes

As would be expected the palaeotemperature regimes are all indicative of megathermal conditions, consistent with what we observe from the taxonomic compositions of the fossil assemblages. Figure 3 shows the cold month mean temperatures (CMMTs) and mean annual temperatures (MATs) for the fossil sites as determined by CLAMP using the PhysgAsia2 and high-resolution gridded climate calibration. Because the warm month mean temperatures (WMMTs) can be under-estimated in CLAMP due to the curvature of the calibration regression at high temperatures and evaporative cooling (Spicer et al., 2011; Srivastava et al., 2012) the annual variation is calculated by simply doubling the difference between the CMMT and MAT.

[Fig. 3 near here]

3.2. Precipitation

Figure 4 shows the ratios of precipitation during the three consecutive wettest months to the three driest months as estimated by CLAMP using the PhysgAsia2 and high-resolution gridded climate calibration (HiResGRIDMetASia2). By themselves such ratios do not define monsoonal climates, but because rainfall seasonality is a favourite (but flawed) proxy for detecting monsoons in deep time studies we present them here for comparison purposes.

[Fig. 4 near here]

The record of precipitation seasonality in the Maoming Basin is muted and only that of the early Oligocene Shangcun assemblage approaches the degree of seasonality seen today in monsoon climates. The Tibet assemblages also show some precipitation seasonality but less than half as strong as than that seen in the Himalayan Foreland Basin today (e.g. Kheri Riverside and Manas). The most marked seasonal differences in rainfall are those of the Indian fossil sites with wet/dry ratios typical of those seen in SAM regions today. Unfortunately rainfall seasonality is a poor way of detecting monsoons because high seasonality can occur in non-monsoonal areas such those surrounding the Mediterranean and along the California coast. Added to this, geological and palaeontological proxies for precipitation overall, and rainfall seasonality in particular, tend to be compromised because they reflect conditions where sediments and water accumulate, thereby buffering and biasing the perceived precipitation regime. A more sensitive way of detecting monsoons is by using leaf form. Leaves have to be adapted to extreme variations in a range of climate variables including atmospheric temperature, humidity and evaporative stress.

3.3. Monsoon signatures

Figures 5a, b and c show the positions of the fossil sites in three Axes 1-3 space of a CLAMP plot using the PhysgGlobal378 dataset of Yang et al. (2015) with the modern vegetation sites coded for the modern monsoon attribution using the spatial spread of different monsoon types designated on the meteorological criteria of Wang and Ho (2002).

[Fig. 5 near here]

In the Axis 1-2 plot (Fig. 5a) most fossil sites appear to be grouped in an area of physiognomic space occupied today by leaves exposed to the I-AM or the SAM indicating a strong adaptation to the kind of marked seasonal climate variability seen in modern Asian monsoon systems. The Changchang site sits closest to the non-monsoonal area of physiognomic space. The Qiabulin, Youganwo and both

Huangniuling assemblages also appear to show some affinity with the transitional monsoon area (TA) between the modern I-AM and the SAM.

In the Axes 1-3 plot (Fig. 5b) it is clear that most fossil sites are not in fact associated with SAM space, but instead possess leaf trait spectra more similar to those of the I-AM. Two fossil samples (Gurha 72 and Qiabulin) also plot close to the cloud of modern sites exposed to the EAM. The late Oligocene Tirap assemblage is the only exception, plotting away from the other fossil sites in an area of physiognomic space reflecting adaptation to both the TA and the SAM.

Fig. 5c shows the Axes 2-3 plot and here it becomes clear that the only fossil assemblage showing the kind of leaf adaptations to the extreme conditions of the modern SAM is from the Tirap mine. All other fossil assemblages show adaptations to the I-AM conditions. This is also the case for Gurha 72 and Qiabulin that from Fig. 5b appear to show an EAM adaptation signature.

Taken together these plots show that all the fossil sites we examined archived leaves with leaf trait spectra similar to those adapted to the modern I-AM. Only one assemblage, that from the Tirap mine, displayed a leaf physiognomic trait spectrum with any affinity to conditions today seen in the SAM, but even here in Axes 1-2 space it is clear that the ancient climate of the Tirap area was more like the modern I-AM than the SAM. It may indicate, however, that by the late Oligocene the modern SAM was beginning to emerge as a distinct monsoon system.

4. Discussion

4.1. The Paleogene climate of southern Asia

The early Eocene Gurha assemblages, northwestern India, archive strong rainfall seasonality, comparable to that seen under the influence of today's SAM across many parts of the subcontinent (Fig. 4), but the overall climate signature (Fig. 5) is one more similar to that of the modern I-AM. This shows that as India traversed the equator it was exposed to ITCZ-driven seasonality with no sign of orographically modified monsoon circulation. However, we also see no evidence that ever-wet conditions existed during the deposition of either Gurha assemblage. It is possible that under the lower equator-to-pole thermal gradient of the early Eocene (Greenwood and Wing, 1995) a wider ITCZ latitudinal migration (Huber and Goldner, 2012) may have reduced the width of, or even eliminated, the Equatorial ever-wet zone. Unfortunately, with uncertainty in the palaeolatitudinal position for the Gurha site of several degrees (Molnar and Stock, 2009) interpreting the Gurha climate in terms of its position in relation to the possible widths and positions of the palaeo-ICTZ rainfall belts is fraught with problems.

At the start of the Eocene the proto-Tibetan Plateau/Gangdese Massif was already high (>4 km) (Wang et al., 2014; Ding et al., 2014) and on its southern flank the megathermal, palm-rich, Liuqu flora indicates a far weaker contrast in seasonal rainfall than the approximately contemporary Gurha floras ~20° further south on the Indian Plate. If the proto-Tibetan Plateau had been playing a key role in monsoon dynamics we would expect a higher wet quarter/dry quarter precipitation ratio in the Liuqu flora. We should expect a ratio similar to those experienced along the modern southern flank of the Himalaya, and evidence of a leaf physiognomic trait spectrum approaching that of the modern SAM. Even by the earliest Miocene the Qiabulin flora which was also deposited on the southern flank of the proto-Tibetan Plateau, albeit at a higher elevation of ~2.3 km (Ding et al., 2017), still does not display a typical SAM physiognomic trait spectrum and only relatively weak rainfall seasonality.

The late Oligocene Tirap section of northeastern India at a palaeolatitude of ~10–15 °N displays rainfall seasonality similar to that of the Gurha assemblages (Fig. 4), and more extreme than that seen in the modern Sunderbans (22.101389 °N, 88.810278 °E). Comparison with the Sunderbans is relevant because both the Tirap and Sunderbans floras are from similar depositional settings and both represent vegetation exposed to fluctuating root zone salinities. Of all the fossil floras considered here the Tirap shows the strongest monsoon influence and although it displays features similar to today's vegetation exposed to the modern I-AM it plots close to the SAM area of physiognomic space.

In the middle Eocene of South China (palaeolatitude ~20 °N) both the Changchang and Youganwo leaf fossil assemblages suggest only very weak rainfall seasonality; far weaker than can be considered indicative of a monsoon climate (Fig. 4). Overall the climates were humid and display adaptive leaf form signatures similar to those seen today in the Indonesian-Australian region where, for the most part, conditions are humid due to oceanic influence and proximity to the Equatorial ever-wet belt. Later in the Eocene the Huangniuling assemblages document a progressive increase in rainfall seasonality until, in the late early Oligocene, the leaves from the Shangcun flora indicate rainfall seasonality approaching that seen in South China today. However the overall climate signature (Fig. 5) is still one of the I-AM rather than that seen on Hainan Island today, which is influenced by both the Northern Hemisphere mirror of the I-AM (the WPM) and also by the SAM (Fig. 1).

Taken together the Paleogene floras of India, Tibet and South China display overall palaeoclimate signatures typical of an ITCZ-driven monsoon system apparently unmodified by orographic highs, and because such a monsoon system is independent of an elevated Tibet it must have been in operation across southern Asia prior to the Cenozoic. The first indication that an orographic modification of the ITCZ monsoon might be taking place is in the late Oligocene as evidenced by the Tirap assemblage, but even here the leaf trait spectrum shows leaf form adapted to a monsoon more like the I-AM than the SAM. Evidence for the development of a distinct SAM is also lacking in the earliest Miocene of southern Tibet (the Qiabulin flora).

It is clear from our analyses that the development of the modern SAM was a Neogene phenomenon. Exactly when it occurred, how and what caused it await similar analyses on numerous Neogene floras across southern Asia, correcting where necessary for local differences in surface elevation that would otherwise invalidate site comparisons. However, it is likely that if the modeling of Boos and Kuang (2010) is correct the SAM arose as a result of the Himalaya achieving elevations in excess of those of the proto-Tibetan Plateau and this is most likely to have occurred after mid Miocene time (Ding et al., 2017).

4.2. Monsoons as drivers of biotic pre-collisional exchange between India and Eurasia

The exact timing of first contact between India and Asia remains controversial but it most likely occurred ~55 ± 10 Ma (Beck et al., 1995; Rowley, 1996; Acton, 1999; de Sigoyer et al., 2000; Aitchison et al., 2002; Ding et al., 2005; Leech et al., 2005; Zhu et al., 2005; Garzanti, 2008; Guillot et al., 2008; Copley et al., 2010; Liebke et al., 2010; St-Onge et al., 2010; Cai et al., 2011; Wang et al., 2011; Hu et al., 2012; Meng et al., 2012; White et al., 2012; Zahirovic et al., 2012; Zhang et al., 2012; Bouilhol et al., 2013; Li et al., 2013; Wang et al., 2014). Although to some extent

India acted as a kind of 'Noah's Ark' (Axelrod, 1971; McKenna, 1973; Morley, 2000; Conti et al., 2002), the effects of the Deccan Traps eruptions (69 Ma to 63 Ma with peak intensity at 66.9 ± 0.2, Pande, 2002), and passage across the equator after rapid transit from high to low latitudes must have resulted in substantial biotic selection and affected plant and animal diversity on the Indian raft (e.g. Samant et al., 2013).

The extent to which India was biologically isolated during its passage northwards is a topic hotly debated (Chatterjee and Scotese, 1999; Prasad and Sahni, 1999; Whatley and Bajpai, 2000, 2006; Briggs, 2003; Sahni and Prasad, 2008; Samant et al., 2013; Klaus et al., 2016) but it is clear that even Indian Late Cretaceous deposits contain a mixture of Laurasian (Jaeger et al., 1989; Sahni and Bajpai, 1991; Prasad and Sahni, 1999; Samant et al., 2013), Gondwanan (Krause et al., 1997; Prasad and Sahni, 1999, 2009; Sahni and Prasad, 2008) and endemic (Whatley and Bajpai, 2006) fossil taxa. In the early Eocene (Ypresian) the Cambay Shale Formation exposed in the Vastan and Mangrol lignite mines, Gujarat, western India, reveals a mixed vertebrate fauna of both European and Gondwanan affinities (Smith et al., 2016).

Although the arrival of India undoubtedly introduced new taxa to Asia, there must have been transfer of taxa between Asia and India long before a land connection was established, even as early as the Late Cretaceous and therefore long before final closure of the Tethys Ocean. For example palms preserved as megafossils are present in the Inter-trappean beds of India (Bonde, 1986, 1987, 1990, 1996; Bonde et al., 2000; Cripps et al., 2005; Samant et al., 2013) and such taxa, the first records of which are in the mid Late Cretaceous in North America and Europe (Harley, 2006), would not have been present when India detached from Gondwana in high southern latitudes at ~85 Ma. Moreover, typically northern hemisphere pollen taxa (e.g.

Aquillapollenites: Herngreen et al. 1996) are present in some abundance in India during the Late Cretaceous, well before the likely onset of collision (Samant et al., 2013).

Samant et al. (2013) recognise three models of biotic exchange: 1) India and Africa were in close proximity during the Late Cretaceous (Briggs, 2003), 2) the India-Asia collision took place during the Deccan Traps eruption phase and therefore earlier than most geological evidence suggests (Jaeger et al., 1989; Sahni and Prasad, 2008), and 3) transoceanic rafting took place from Asia to India (Ali and Aitchison, 2008). With most geological, geophysical and geochemical data indicating that the leading edge of the Indian subcontinent (i.e. Greater India) made initial contact with the southern margin of Asia at ~65 Ma at the earliest, it would seem that abundant biotic exchange preceded the establishment of a land connection, implying an effective transoceanic transfer of propagules, possibly aided by island arc or microcontinent 'stepping stones' now subducted or accreted into the Himalaya-Karakoram mountain belts (van Hinsbergen et al., 2012).

Seeds, fruits and vegetative propagules can be dispersed across oceans by floating or by aerial transport suspended within air currents or attached to birds/bats etc. The Paleogene, and most probably pre-Paleogene presence of a strong monsoon system, with seasonally reversing cross-equatorial winds at a time when India was at low latitudes, would undoubtedly have facilitated bidirectional propagule exchange between India and Asia long before 'hard contact' and ocean closure. In a Paleogene world with low equator-to-pole temperature gradients transport of Gondwanan taxa on the Indian 'Noah's Ark' raft across latitudes was minimally affected by temperature regimes; being able to tolerate seasonality in the availability of moisture would have been more of a limiting factor. As India transited the ITCZ strong rainfall seasonality would have selected for plants and animals able to tolerate drought as well as saturated soils. It was primarily those Gondwanan taxa that survived the monsoon 'filter' that contributed to the already diverse monsoon-adapted Paleogene forests of southern Asia.

Today, globally, the greatest biodiversity and speciation rates are associated with ever-wet megathermal climates (e.g. Gentry, 1988; Allen et al., 2006; Wright et al., 2006). However in Asia high biodiversity such as is found in the Indo-Burma and South Central China 'hotspots' (Myers et al., 2000) is associated with mountainous terrains and monsoonal climates Although many Asian molecular phylogenies are unreliably dated due to erroneous assumptions about the timing of the uplift of Tibet and its consequences (Renner, 2016), Klaus et al. (2016) show, based on dated phylogenies, limited overall dispersal rates from India to Asia compared to those from Asia to India. This may be due to the limited size of India compared to Asia (smaller ecological space and thus intrinsic diversity) and/or the strength of the ITCZ climate filter.

Between 70 and 65 Ma, before closure of the Tethys Ocean, the maximal number of dispersal events per million years from Asia to India is more or less the same as those from India to Asia, but clearly bidirectional exchange was occurring and rising over time. After 65 Ma immigration to India exceeded that from Asia and remains so. The most rapid period of biotic export from India to Asia occurred between 50 and 35 Ma, and this is associated with a reduction in dispersal from Asia to India. Klaus et al. (2016) suggest that this might be due to aggressive competition from the Indian biota on the assumption that the Indian biota was already adapted to hot and humid conditions. However, this is precisely the time when the northern Indian biota was experiencing seasonally arid climates as evidenced by the Gurha assemblages. It is more likely that adaptation to survive seasonal variations in moisture availability allowed migration to, and occupation of, a range of environmental niches that presented themselves in the topographically varied terrain that existed along the southern margin of the Eocene proto-Tibetan uplands.

Klaus et al. (2016) also show maximum dispersal events from Asia to India in the Miocene and interpret this to be a consequence of the Mid Miocene Climatic Optimum (MMCO). Part of this peak may be related to the MMCO, but part may be a function of erroneously inflated Miocene Asian phylogenetic diversification (Renner, 2016). Assuming this peak to be real, perhaps the greatest cause was due to the elevation of the Himalaya above 5 km (with associated topographic niche partitioning and speciation) and the development of the SAM with its enhanced seasonal precipitation regime.

5. Conclusions

Our analyses of Paleogene plant fossils across South China, India and Tibet reveal a megathermal regime under a monsoon influence similar to that found today in the Indonesia-Australian Monsoon system. This system is a reflection of seasonal latitudinal migrations of the Inter-tropical Convergence Zone. We see no evidence that the modern South Asia Monsoon, the characteristics of which are thought to be influenced by the Himalaya-Tibet orogen, existed in the Paleogene despite abundant evidence that a high (>4 km) proto-Tibetan plateau existed at that time. The lack of a SAM signature along the southern flank of this upland until beginning of the Neogene is particularly telling. This suggests that the modern South Asia Monsoon evolved in the Neogene, and most probably became established as a stable system in mid Miocene time as a result of the Himalaya exceeding the surface height of the Tibetan Plateau.

The leaf physiognomic trait spectra we use to characterise palaeo-monsoons are necessarily derived from living vegetation, so we view ancient climates through the lens of what exists now. Ancient monsoons may not have been identical to those of today, but what we can say is that fossil leaves were adapted to similar climatic constraints as we see in today's monsoon systems.. Using this technique it is difficult to detect directly monsoon signatures that might arise from a modification of Hadley circulation in a warm world. However, as more fossil data with better temporal and spatial resolution are amassed it may be possible to detect variations in the width of ITCZ migration and associated precipitation patterns.

The presence of an ITCZ type monsoon system across southern Asia throughout the Paleogene means that as India transited this system resident, predominantly Gondwanan, taxa would have been filtered to favour those capable of thriving under strongly seasonal drought as well as a tropical temperature regime. The seasonally reversing air-flow would have facilitated biotic exchange between India and Eurasia long before closure of the Tethys, and it would have been an exchange mechanism far more effective than that seen today between the Galapagos and South America. This exchange is evidenced by the mix of Gondwanan and Eurasian taxa found in Indian fossil assemblages as early as the Late Cretaceous.

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Figure Captions

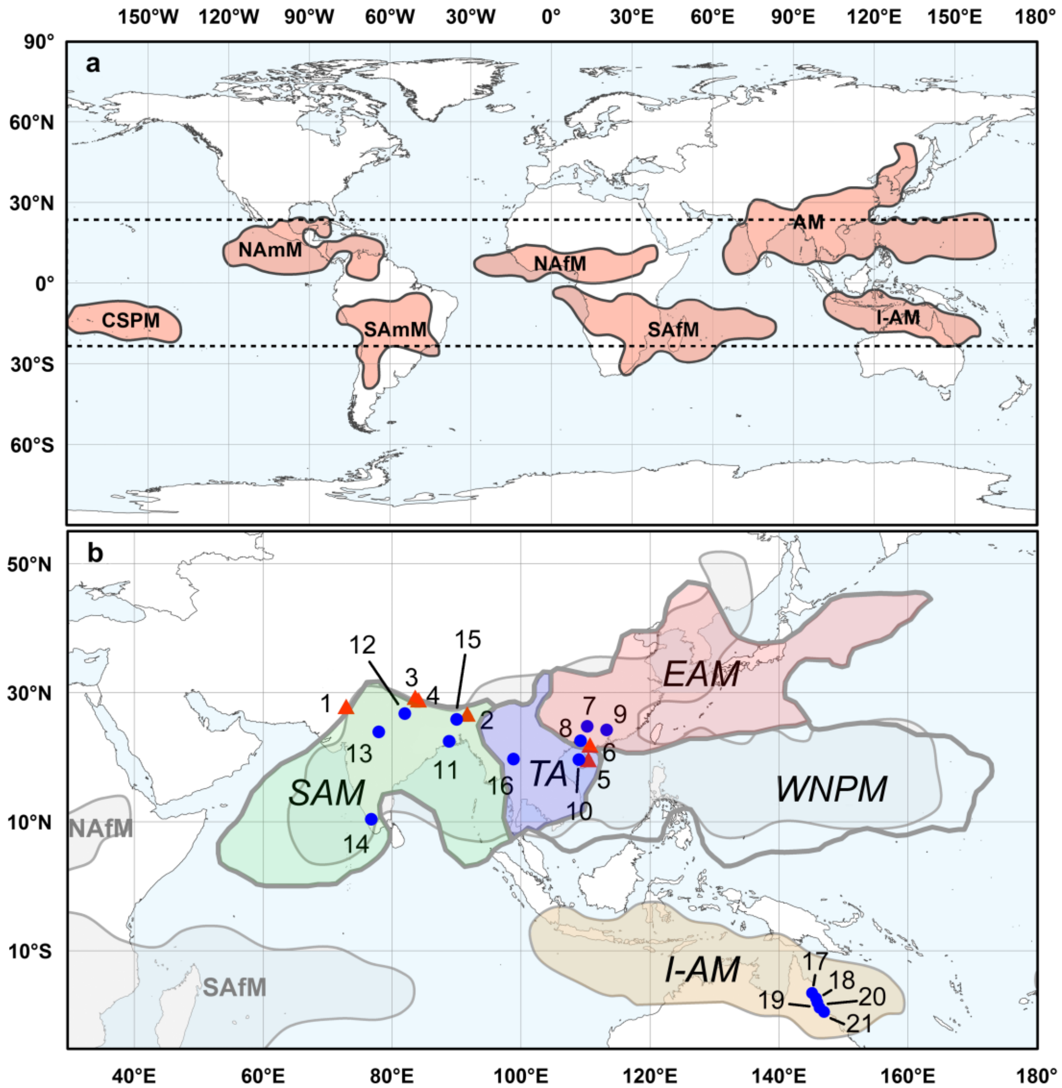
Figure 1. a) Map showing the positions and aerial extent of monsoons as defined by the meteorological parameters of Zhang and Wang (2008). CPSM - Central Pacific Summer Monsoon, NAmM - North America Monsoon, SAmM - South America Monsoon, NAfM - North Africa Monsoon, SAfM - South Africa Monsoon; AM - Asia Monsoon, I-AM Indonesia-Australia Monsoon. b) Map of southern Asia showing the positions of the fossils assemblages (red filled triangles), together with the modern comparison sites (blue filled circles). Fossil sites: 1 - Gurha 38 and Gurha 72, 2 - Tirap, 3 - Liuqu, 4 - Qiabulin, 5 - Changchang, 6 - Maomin Basin (Youganwo, Huangniulin Lower, Huangniulin Upper, Shangcun). Modern sites: 7 - Lingchuan, 8 - Wuming, 9 - Zaoqing and Nankun Mountain, 10 - Hainan Island (Baisha, Mangrove, Wuzhshan), 11 - Sunderbans and Green Island, 12 - Kheri River, 13 - Shivpuri Temple, 14 - Thekkady, 15 - Manas, 16 - Sakaerat Reserve. 17 - Daintree, 18 - Kurunda, 19 - Wooroonoran, 20 - Hull River, 21 - Bowling Green bay. The modern monsoon areas are those recognised by Wang and Ho (2002), SAM - South Asia Monsoon, TA - Transitional Area, EAM - East Asia Monsoon, I-AM - Indonesia-Australia Monsoon, WNPM - Western North Pacific Monsoon.

Figure 2. Chart showing the ages of the different fossil assemblages used in our analysis. The numbers in parentheses refer to the fossil localities in Fig. 1, while red italicised numbers give the numbers of woody dicot leaf morphotypes analysed in each assemblage.

Figure 3. Estimated temperature regimes based on a CLAMP analysis of fossil and modern leaf trait spectra. Histogram column heights indicate the mean annual temperature (MAT) while the vertical bars indicate the mean annual range of temperature. The Warm Month Mean Temperature (WMMT) is represented by the top of the range bar, and the Cold Month Mean Temperature (CMMT) the bottom of the range bar. MAT uncertainties (σ) 2.3 °C.

Figure 4. Estimated rainfall seasonality based on a CLAMP analysis of fossil and modern leaf trait spectra. Rainfall seasonality above 5 (red line) is typical for modern monsoonal climates using this CLAMP calibration (PhysgAsia2). Precipitation estimates have large uncertainties due in part to buffering by the soil moisture reservoir. For the calibration used here the statistical uncertainty (σ) in estimating precipitation during the three wettest months is 35.8 cm and that for the 3 driest months is 9.8 cm.

Figure 5 a-c. CLAMP plots showing the distribution of modern vegetation sites coded for the monsoon type to which they are exposed (EAM - East Asia Monsoon, I-AM - Indonesia-Australia Monsoon, NAmM - North America Monsoon, NM - No Monsoon, SAM - South Asia Monsoon, TA - Transitional Area) and the positions of the fossil assemblages (numbered filled red circles). 1 - Gurha 72, 2 - Gurha 32, 3 - Tirap, 4 - Liuqu, 5 - Qiabulin, 6 - Changchang, 7 - Youganwo, 8 - Huangniuling Lower, 9 - Huangniuling Upper, 10 - Shangcun.


a
b
150°W
120°W
90°W
60°W
30°W
0°
30°E
60°E
90°E
120°E
150°E
180°
90°
60°N
30°N
0°
30°S
60°S
CSPM
NAmM
SAmM
NAfM
SAfM
AM
I-AM
50°N
10°N
10°S
40°E
60°E
80°E
100°E
120°E
140°E
160°E
SAM
TA
EAM
WNPM
1
2
3
4
5
6
7
8
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11
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14
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16
17
18
19
20
21

Fig. 1

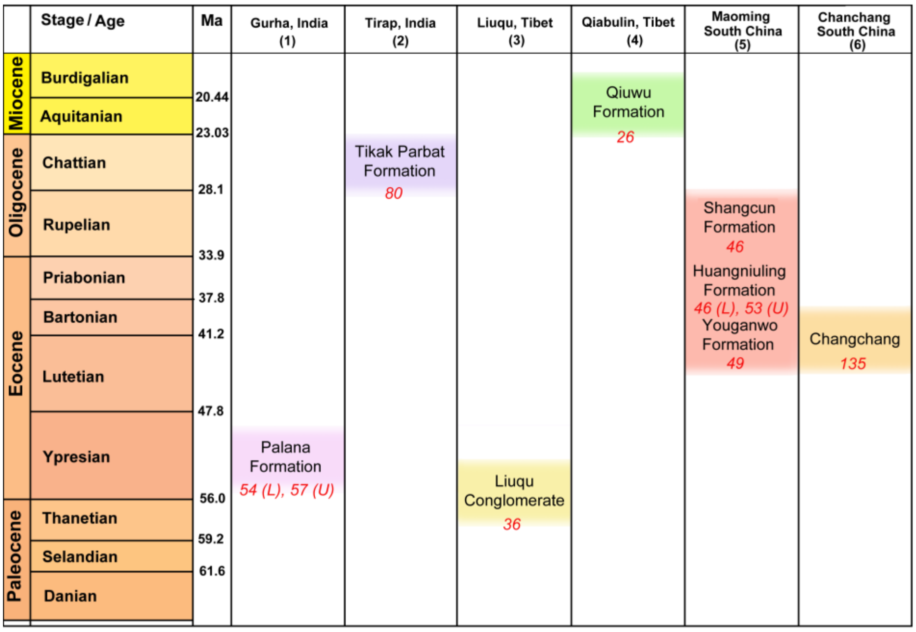
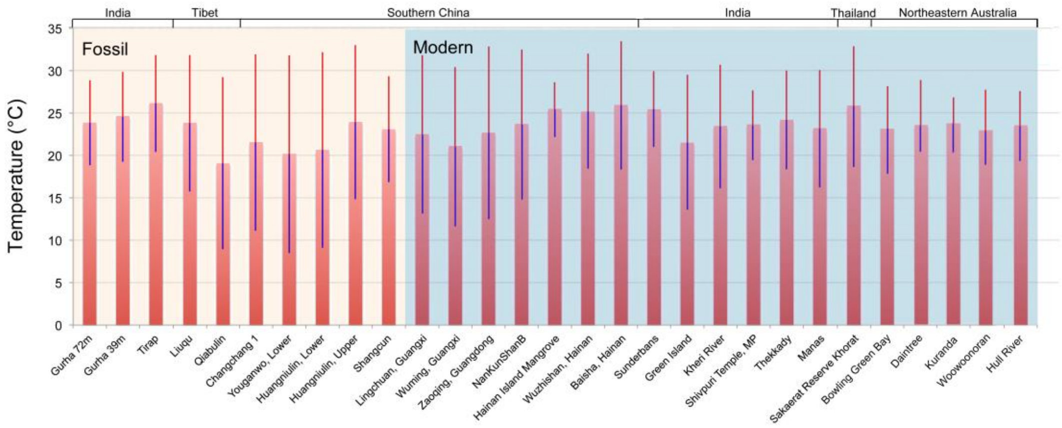

Stage / Age
Ma
Gurha, India (1)
Tirap, India (2)
Liuqu, Tibet (3)
Qiabulin, Tibet (4)
Maoming South China (5)
Chanchang South China (6)
Miocene
Burdigalian
Aquitanian
Oligocene
Chattian
Rupelian
Eocene
Priabonian
Bartonian
Lutetian
Ypresian
Paleocene
Thanetian
Selandian
Danian
20.44
23.03
28.1
33.9
37.8
41.2
47.8
56.0
59.2
61.6
Palana Formation
54 (L), 57 (U)
Tikak Parbat Formation
80
Liuqu Conglomerate
36
Qiuwu Formation
26
Shangcun Formation
46
Huangniuling Formation
46 (L), 53 (U)
Youganwo Formation
49
Changchang
135

Fig. 2



India
Tibet
Southern China
India
Thailand
Northeastern Australia
Fossil
Modern
Temperature (°C)
0
5
10
15
20
25
30
35
Gurha 72m
Gurha 39m
Tirap
Liuqu
Qiabulin
Changchang 1
Youganwo, Lower
Huangniulin, Lower
Huangniulin, Upper
Shangcun
Lingchuan, Guangxi
Wuming, Guangxi
Zaoqing, Guangdong
NanKunShanB
Hainan Island Mangrove
Wuzhishan, Hainan
Baisha, Hainan
Sunderbans
Green Island
Kheri River
Shivpuri Temple, MP
Thekkady
Manas
Sakaerat Reserve Khorat
Bowling Green Bay
Daintree
Kuranda
Woowoonoran
Hull River

Fig. 3

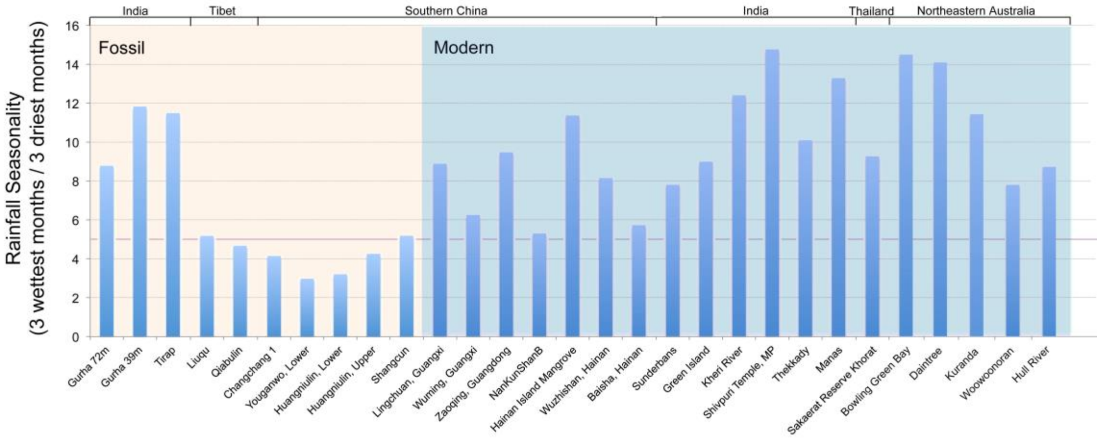

India
Tibet
Southern China
India
Thailand
Northeastern Australia
Fossil
Modern
Rainfall Seasonality
(3 wettest months / 3 driest months)
0
2
4
6
8
10
12
14
16
Gurha 72m
Gurha 39m
Tirap
Liuqu
Qiabulin
Changchang 1
Youganwo, Lower
Huangniulin, Lower
Huangniulin, Upper
Shangcun
Lingchuan, Guangxi
Wuming, Guangxi
Zaoqing, Guangdong
NanKunShanB
Hainan Island Mangrove
Wuzhishan, Hainan
Baisha, Hainan
Sunderbans
Green Island
Kheri River
Shivpuri Temple, MP
Thekkady
Manas
Sakaerat Reserve Khorat
Bowling Green Bay
Daintree
Kuranda
Woowoonoran
Hull River

Fig. 4

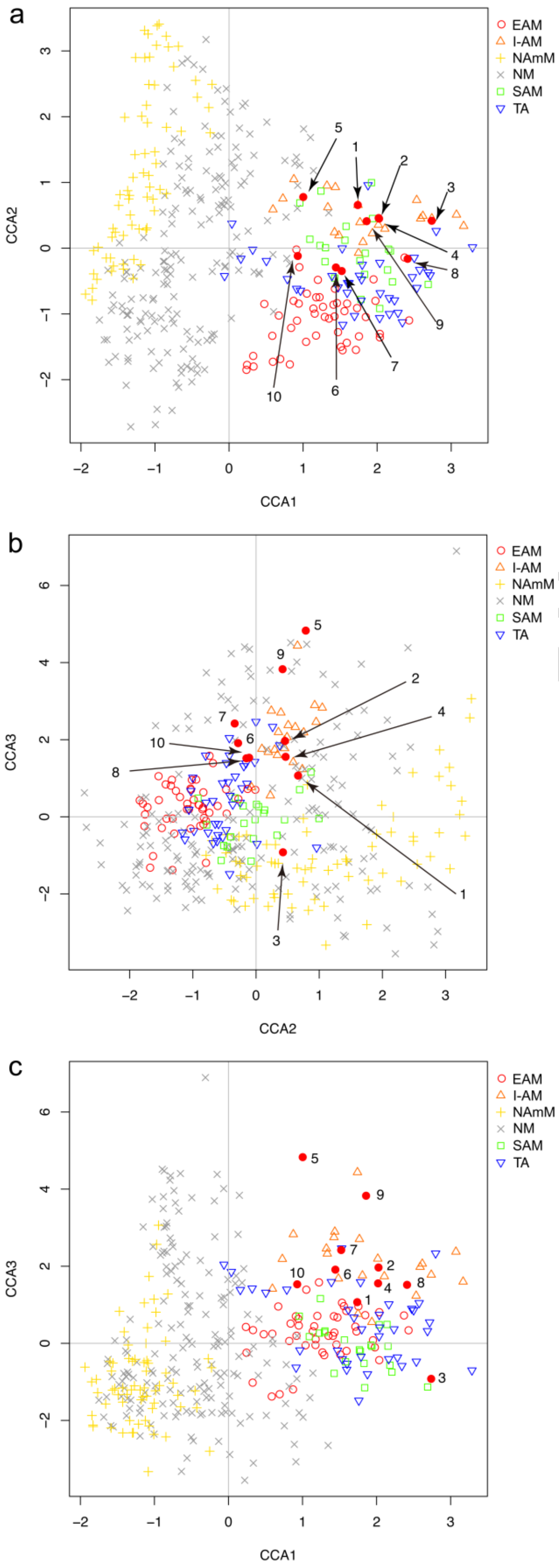
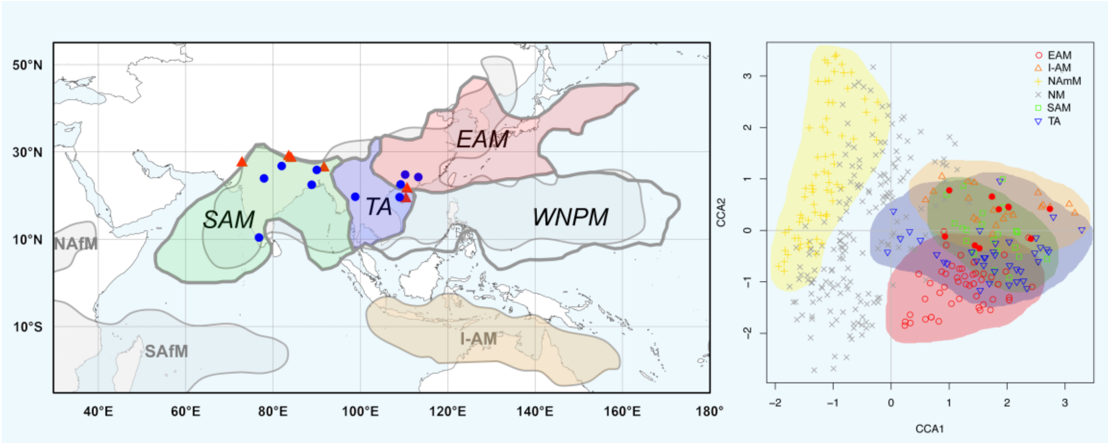


Fig. 5



Graphical abstract

Highlights

- Paleogene leaves from India, Tibet and South China reveal ITCZ-driven monsoons
- There is no evidence of Paleogene monsoon modification by a proto Tibetan plateau
- Gondwanan taxa on the Indian raft were likely filtered by monsoon conditions