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Tibet, the Himalaya, Asian monsoons and biodiversity – In what ways are they related?

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ABSTRACT

Prevailing dogma asserts that the uplift of Tibet, the onset of the Asian monsoon system and high biodiversity in southern Asia are linked, and that all occurred after 23 million years ago in the Neogene. Here, spanning the last 60 million years of Earth history, the geological, climatological and palaeontological evidence for this linkage is reviewed. The principal conclusions are that: 1) A proto-Tibetan highland existed well before the Neogene and that an Andean type topography with surface elevations of at least 4.5 km existed at the start of the Eocene, before final closure of the Tethys Ocean that separated India from Eurasia. 2) The Himalaya were formed not at the start of the India–Eurasia collision, but after much of Tibet had achieved its present elevation. The Himalaya built against a pre-existing proto-Tibetan highland and only projected above the average height of the plateau after approximately 15 Ma. 3) Monsoon climates have existed across southern Asia for the whole of the Cenozoic, and probably for a lot longer, but that they were of the kind generated by seasonal migrations of the Inter-tropical Convergence Zone. 4) The projection of the High Himalaya above the Tibetan Plateau at about 15 Ma coincides with the development of the modern South Asia Monsoon. 5) The East Asia monsoon became established in its present form about the same time as a consequence of topographic changes in northern Tibet and elsewhere in Asia, the loss of moisture sources in the Asian interior and the development of a strong winter Siberian high as global temperatures declined. 6) New radiometric dates of palaeontological finds point to southern Asia's high biodiversity originating in the Paleogene, not the Neogene.

1. Introduction

Southern Asia hosts several of Earth's most important biodiversity hotspots (Myers et al., 2000). These include the Indo-Burma (which spans the Himalaya and Hengduan Mountains, Myanmar, Thailand, Vietnam, Laos and southwestern China), the Western Ghats and Sri Lanka, and South Central China hotspots (Fig. 1). Three things characterize these areas of high biodiversity and endemism: 1) they occupy low (>35°N) latitudes, 2) they are in areas that include complex and often considerable topographic relief, 3) they all experience Asian monsoon climates.

To understand the evolution of these unique diverse biotas we need to look back in time and consider their geological, climatological and biological context. The biodiversity we see around us today (but are rapidly destroying) is an expression of the dynamic interplay between topography, climate and life processes that operate over geological as well as biological timescales and is just flicker in the history of life; only a transient ripple in the river of gene flow through time.

The aim of this paper, first given as a plenary keynote talk at the 2017 Association for Tropical Biology and Conservation conference, March 25–28th, Xishuangbanna Tropical Botanical Garden, Yunnan, China, is to review and examine current evidence for topographic, climatic and palaeontological change across southern Asia for the last 60 million years in order to address the following questions:

i) Paying particular attention to major features such as Tibet and the Himalaya, how and when did the regional topography evolve?

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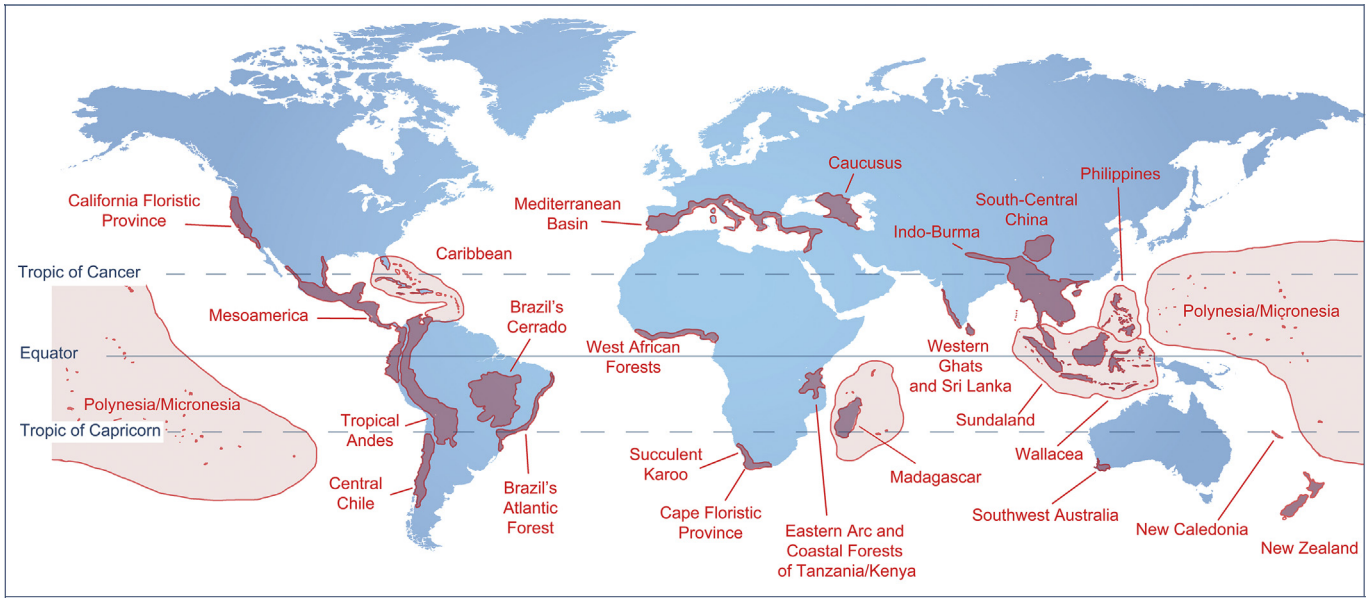

Fig. 1. Map of the world showing areas of exceptional biodiversity 'hotspots' based on Myers et al. (2000).

ii) How and when did the Asian monsoon systems develop, and were the origins of the modern monsoon systems concurrent with the uplift of Tibet and/or the Himalaya?
iii) How old are the Asian biodiversity 'hotspots', and how do they relate to the development of the Asian monsoon systems?

First, however, it is useful to examine, briefly and simply, the links between topography, climate heterogeneity in space and time, and biodiversity.

1.1. What is so special about low-latitude mountainous regions that might contribute to high biodiversity and endemism?

Many, but not all, of the world's areas of high biodiversity and endemism occur in places that encompass mountainous regions. In addition to the areas considered in this work there are, for example, the Tropical Andes and Central Chile, the Caucasus, the Sierra Nevada and Coast Ranges of the California Floristic province and New Zealand (Fig. 1). In all these regions complex topographies juxtapose, at the sub-kilometre scale, profoundly different local climates as a function of aspect and altitude, and inevitably in mountainous landscapes, complex geology. Geology, slope and climate heterogeneity give rise to a patchwork of soil types. Arising from this small-scale granular environmental mosaic is close-proximity niche diversity.

This close-proximity niche diversity is also accompanied in many areas of high biodiversity by seasonally varying climates. Returning to Myers et al. (2000) (Fig. 1) one might cite the winter-wet summer-dry climates of the Mediterranean Basin, The California Floristic Province, or Central Chile hotspots, while seasonal migrations of the thermal equator and the associated Inter-tropical Convergence Zone (ITCZ) bring summer-wet, winter-dry monsoonal regimes to the tropics in all but an ever-wet zone centred on the Equator. Across southern Asia biodiversity hotspots fall under the influence of seasonally wet and dry regimes driven either by seasonal migrations of the ITCZ (ITCZ monsoon climates) or seasonal ITCZ migrations modified by land-sea thermal contrast and topography (modified monsoon climates) (Spicer et al., 2016). Plants and animals across southern Asia have to be adapted to strong seasonal variations in rainfall, and on an annual basis tolerate water saturated soils and atmosphere for several months and extreme drought for several months. These extremes in water availability are often accompanied by marked variations in temperature and more complex climate metrics that have profound influences on photosynthesis, such as vapour pressure deficit (the difference between saturated vapour pressure and actual vapour pressure VPD) (Singh, 2010).

Global biodiversity hotspots are not confined to mountainous regions and seasonal climates. Many regions of high biodiversity identified by Myers et al. (2000) occur on islands. Examples here include the Caribbean, Polynesia and Micronesia, Madagascar, New Zealand and across southern Asia there is Sri Lanka and the islands making up Sundaland, Wallacea and the Philippines (Fig. 1). In these areas various degrees of isolation operating over varying timescales play a role in speciation (e.g. Cowie and Holland, 2008; Darwin, 1860; Emerson, 2008; Presgraves and Glor, 2010; Whittaker et al., 2008). Mountainous regions host many so called 'sky islands' (e.g. Dodge, 1943; McLaughlin, 1994) where similar isolating mechanisms, and refugia, operate.

So far I have concentrated on the spatial component of niche diversity, but time is also an important ingredient in speciation. With time comes climate change. Superimposed on seemingly stochastic inter-annual fluctuations in weather, climate (meteorological variables averaged over 30 years or more) changes also occur over thousands of years (kyrs) due to repeated changes in the shape of Earth's orbit around the Sun, changes in the angle of inclination of Earth's rotational axis with respect to the orbital plane, or procession of that axis. These so-called Milankovitch–Croll cycles (Croll, 1875; Milankovic, 1998) are highly predictable and have also operated throughout much of Earth history (Hays et al., 1976).

This millennial scale cyclicity is also superimposed on longer-term (millions of years) climate variations (e.g. Frakes et al., 1992; Zachos et al., 2001) due to changes in atmospheric composition, positions of the continents etc. In mountainous regions both short- and long-term climate variability generates a 'speciation pump': repeated up and down slope niche migration results in vagility-dependent repeated isolation and re-mixing of gene pools.

Mountainous regimes such as those across much of southern Asia therefore combine all the main properties of global

biodiversity hotspots: seasonal climate variation pre-adapts organisms to tolerate climate extremes and close proximity niche diversity is accompanied by repeated episodes of genetic isolation in 'sky islands' during warm climate phases, followed by downslope migration to mingle and hybridize in the lowlands during cool climate phases. The combination of complex topography and varying climates turns areas such as southern Asia into 'biodiversity factories'.

1.2. Monsoons and biodiversity

A long favoured model for monsoon and biodiversity evolution is based on the concept that Tibet acts as a driver of the Asian monsoon system and any change in the surface height or extent of Tibet will affect monsoon intensity and, in turn, biotic evolution. This model consists of three elements: 1) the Tibetan plateau is exclusively the result of the Indo-Eurasian collision, 2) that Asian monsoon circulation was created by a Neogene (younger than 23 myrs) uplift of the plateau resulting from that collision, and that 3) these changes had a major impact of the evolution of the Asian biota and, in particular, widespread Miocene speciation. This is a common concept that has become a self-sustaining explanation for Miocene phylogenetic differentiation across large parts of Asia. As shown by Renner (2016), this concept is flawed. A major problem with this concept is that geological evidence shows that both an elevated Tibet and the Asian monsoon system predate the Miocene and even the onset of the India–Asia collision.

2. The elevation history of Tibet

The Himalaya are often shown to be the first expression of the collision between India and Eurasia (e.g. Favre et al., 2015). The exact date of the onset of this collision is uncertain, but in their extensive review Wang et al. (2014) give a date of 55 Ma ± 10 Ma, close to the beginning of the Eocene. At 45–35 Ma Favre et al. (2015), drawing on the work of Li and Fang (1999), Mulch and Chamberlain (2006) and Rowley and Currie (2006), among others, show an elevated Himalaya and by 25 Ma an elevated southern Tibet. Subsequently the Tibetan Plateau is supposed to have risen to its present mean surface elevation of ~5 km a.m.s.l., progressively developing in a northeasterly direction such that by 15 Ma all but the northeastern part of the plateau was elevated to close to its present height.

This model of plateau uplift is, however, contradicted by a large body of evidence brought together in the review of Wang et al. (2014). The model synthesised in Wang et al. (2014) envisages an elevated proto-Tibetan upland before the arrival of India (Fig. 2). In some respects this model reprises the idea, developed around 30 years ago, that some parts Tibet were at an elevation of at least 3 km between 45 and 30 Ma (Burg and Chen, 1984; Dewey et al., 1989; England and Searle, 1986; Murphy et al., 1997). However this pre-collision elevated Tibet idea subsequently lost favour, subsumed by a more stepwise SW–NE model of plateau evolution (e.g. Mulch and Chamberlain, 2006; Rowley and Currie, 2006; Tapponnier et al., 2001), or the assumption that the Tibetan Plateau behaved more or less as a single entity that rose as one block in the late Miocene around 10–8 Ma (England and Houseman, 1989; Harrison et al., 1992; Molnar et al., 1993; Platt and England, 1994). The timing of this late Miocene rise was linked to an observed intensification of the South Asian monsoon at this time (An et al., 2001; Derry and France Lanord, 1996; Kroon et al., 1991). This supposed rapid uplift was inferred from a geophysical model that envisaged thermal removal of the relatively cold, and therefore dense, thickened lithosphere beneath Tibet arising from the India–Eurasia collision. As this cold dense Tibetan 'ballast' fell away Tibet would correspondingly float upwards. One consequence of such a recent rapid uplift to near present surface elevation would have been the onset of gravitational collapse of the plateau that, given the on-going northward compression derived from the continued northward movement of India, would be constrained to occur in an East–West direction. However, it has been clear for some time that E–W extension was occurring before 10 Ma (Coleman and Hodges, 1995), and evidence for the onset of this extension is in the formation of N–S trending dykes and normal faulting, which in south central Tibet have been dated not at 10 Ma, but ~18.3 ± 2.7 Ma (Williams et al., 2001) and some N–S trending faults and dykes are even as old as Eocene (~47–38 Ma) (Lan et al., 2007; Yang et al., 2008; Wang et al., 2010).

The concept of a rapid recent uplift of Tibet at 10–8 Ma was also compromised severely by the finding that an area of south central Tibet known as the Namling-Oiyug Basin, which sits near the southern margin of a tectonic block known as the Lhasa Terrane (Fig. 3), was already near its present elevation at 15 Ma in the mid Miocene (Currie et al., 2005; Spicer et al., 2003) (Fig. 4). Subsequently a wealth of evidence has confirmed these high elevations (Currie et al., 2016; Khan et al., 2014) and shown that numerous parts of Tibet, including both the Lhasa Terrane and its immediate northern neighbour the Qiangtang Terrane, have been high (>4.5 km) since at least 45 Ma (Xu et al., 2013; works reviewed in Ding et al., 2014; Wang et al., 2014).

The existence of an old Paleogene (66–23 Ma) proto-Tibetan upland is supported by an expanding body of palaeoaltimetric data derived primarily from isotopic studies. Put simply, the principle behind isotope-based estimates of surface elevation is based on a Rayleigh distillation model in which heavy isotopes preferentially rain out of parcels of air as those parcels are forced to rise on encountering a mountain front. In the case of oxygen isotopes the heavy isotope ^{18}O rains out more than the lighter ^{16}O, so parcels of rising air are progressively depleted in ^{18}O but enriched with ^{16}O. The result of this fractionation is that on the windward side of a mountain the higher the elevation at which precipitation occurs the greater the proportion of the light isotope of oxygen (^{16}O) that is contained in meteoric water (rain and snow) (e.g. Currie et al., 2005; Garzione et al., 2000; Rowley et al., 2001). Any isotopes preserved in sediments that accurately reflect meteoric water can therefore be used to estimate palaeo-elevation. There are of course many caveats and assumptions associated with this technique, but the principle seems to work well when there is a single mountain range with moist air consistently delivered to the windward side. This ideal situation applies to the Himalaya, which receive summer moist air from the Indian Ocean. However, this simple distillation model breaks down on the leeward side over an extensive highland, such as the Tibetan Plateau. Here multiple evaporation (from plateau lakes, vegetation, soils etc.) and precipitation cycles increasingly favour moisture in clouds (and precipitation) enriched with the light ^{16}O isotope, which can lead to overly high surface elevation estimates. A more complete review of isotope palaeoaltimetry is given in Mulch (2016), and Mulch includes a comment on the necessity of factoring in isotopic fractionation due to transpiration as well as evaporation. To do that successfully, a detailed understanding of the palaeovegetation is required.

It follows then that when using isotopic palaeoaltimeters the palaeo-surface elevation of the proto-Tibetan highland may be exaggerated in the highland interior. However, at locations close to the southern margin of Tibet, where the simple distillation model does apply, Eocene surface heights of the ancient Gangdese Mountains (part of the southern Lhasa Terrane) have been estimated at ~4.5 km (Ding et al., 2014) (Fig. 2).

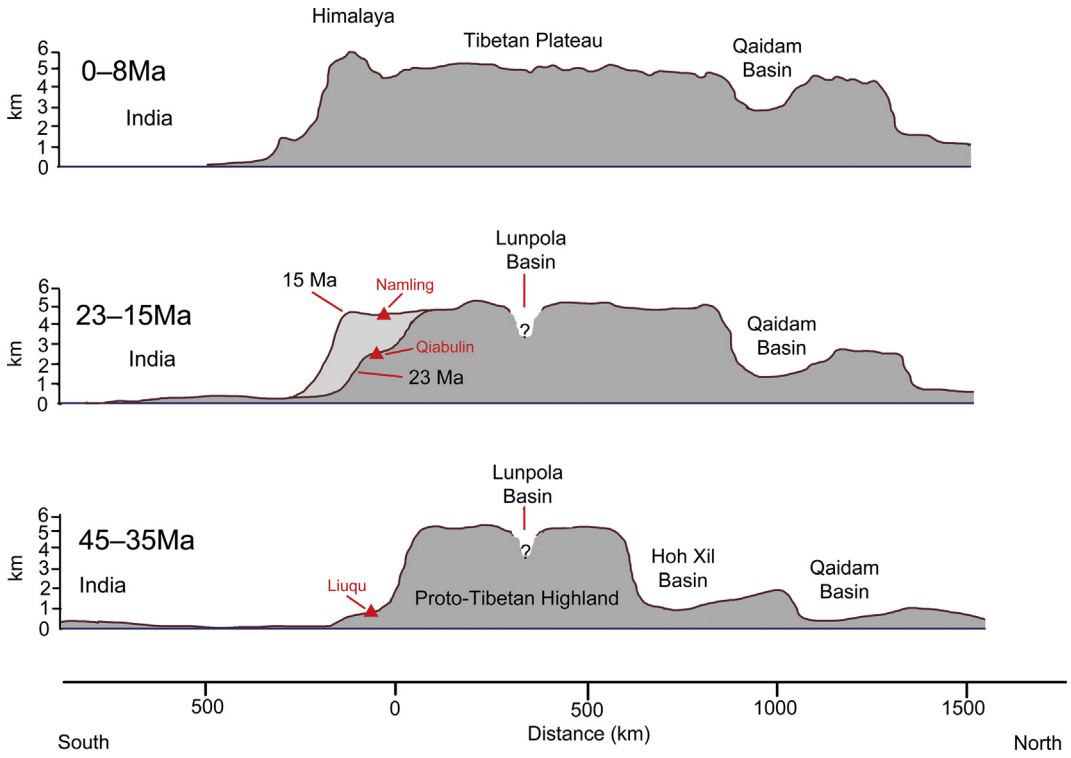

Fig. 2. South–North transect from India to the Qaidam basin, China, showing likely surface elevations at three time slices: 45–35 Ma, 23–15 Ma and 8 Ma to present based on Ding et al. (2017, 2014), Wang et al. (2014).

Additional evidence that a Paleogene proto-Tibetan highland existed comes from palaeomagnetism. The ancient latitudinal position of a rock body can be determined from the direction of preserved ancient magnetism. Using this technique Tong et al. (2017) have shown that the Lhasa Terrane moved from 7.5 ± 8.5°N at 64–60 Ma to 13.7 ± 7.3°N at 55 Ma, and then to 16.5 ± 5.7°N at 53 Ma. This demonstrates considerable crustal shortening prior to 53 Ma (possibly as much as 1600 km) that must have been associated with mountain building. Subsequently an additional ~1300 ± 410 km of shortening seems to have been accommodated by southeastward extrusion of the Qiangtang Terrane, apparently beginning in the early Oligocene, and impacting on the development of what we now call the Hengduan Mountains.

The central area of the present day Tibetan Plateau is remarkably flat (Fielding et al., 1994; Liu-Zheng et al., 2008) and large parts of it appear not to have undergone any compressional deformation since the early Miocene (Wang et al., 2014; Wu et al.,

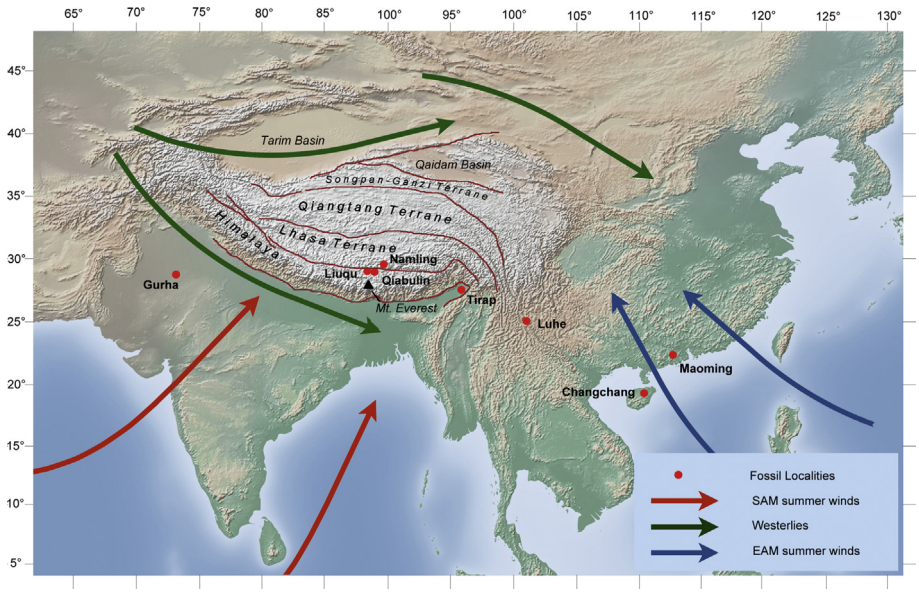

Fig. 3. Map of southern Asia showing the major tectonic terranes and features referred to in the text, the positions of key fossil localities referred to in the text, and the directions of major wind patterns associated with the South Asia Monsoon and East Asia Monsoon in summer and winter Westerlies.

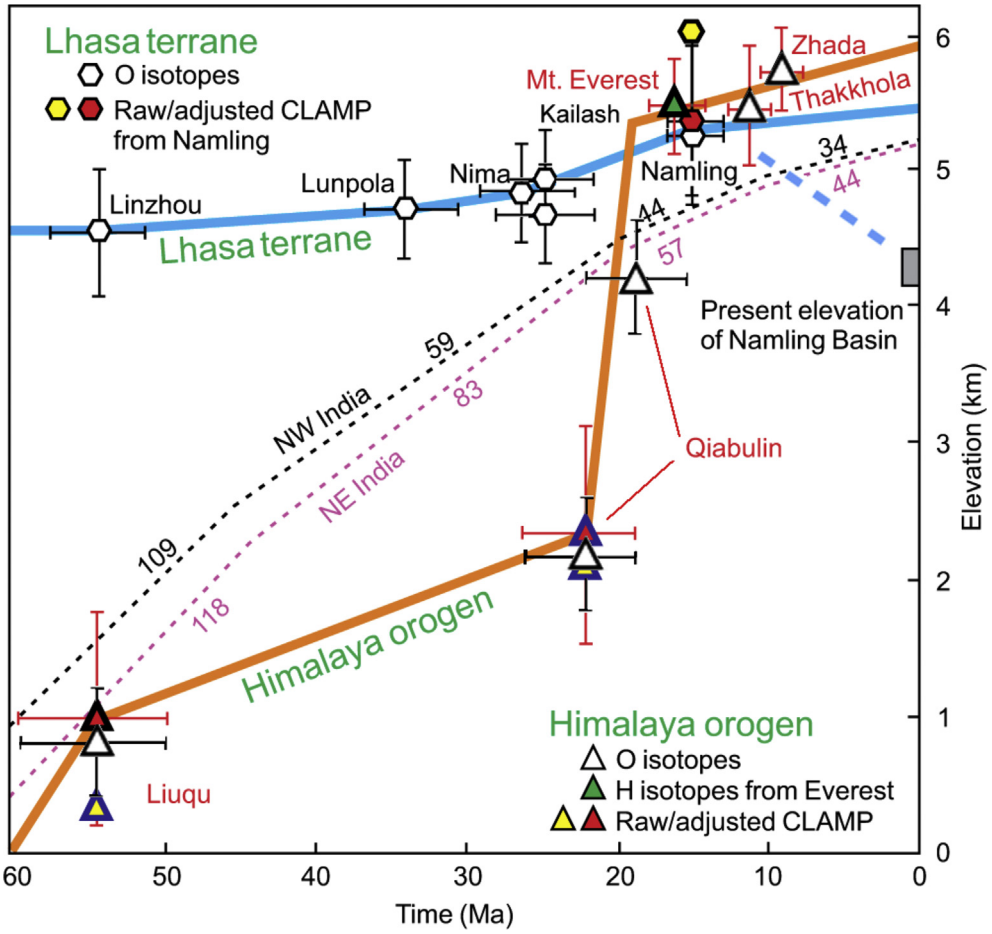

Fig. 4. Graph showing elevation changes over time for the Lhasa Terrane and the Himalaya region based on isotopic and foliar physiognomic proxies modified from Ding et al. (2017). India/Asia convergence rates are from Molnar and Stock (2009).

2008). However, it is unlikely that the Paleogene proto-Tibetan highland was a plateau like it is today because it was the product of Mesozoic accretion of the Qiangtang and Lhasa terranes. This accretion was followed by subduction of oceanic crust eventually giving rise to folding, faulting and uplifting of Cretaceous marine sediments as well as folding and thrusting of older rocks of the accreted Lhasa and Qiangtang terranes (Fig. 3). The Paleogene proto-Tibetan highland was likely to have consisted of at least two major east–west oriented mountain ranges separated by a string of basins. Estimates of the elevation of the floors of major basins such as the Lunpola Basin (Polissar et al., 2009; Rowley and Currie, 2006) are far from definitive because of proxy limitations (e.g. repeated evaporation/precipitation isotopic fractionation or lack of precise palaeontological altimeters) (Fig. 2). Floral and faunal remains from the Lunpola Basin suggest palaeosurface surface elevations perhaps some 2 km lower than the published isotopic analyses (Deng et al., 2011; Sun et al., 2014). However, what we can be certain of is that in the Paleogene, before the closure of the Tethys Ocean and the onset of collision of Indian continental crust, the part of Asia that we today call the Tibetan Plateau was not a vast plain at sea level, but displayed considerable topographic relief, perhaps somewhat like the Andes today (Ding et al., 2014) with deep valleys between mountain ranges. Like the modern Andes this proto-Tibetan highland, made up of the Lhasa and Qiangtang terranes (Fig. 3), would have hosted extremely high biodiversity, arising from the mechanisms outlined in Section 1.1.

3. The rise of the Himalaya

A notable feature of the Wang et al. (2014) model of Tibetan evolution is that until very recently in geological terms (within the last 15 million years) a high Himalayan mountain front was missing (Fig. 2). Elevation estimates based on isotopic methods all show present elevations either being attained within the last 15 Ma (Garzione et al., 2000; Rowley et al., 2001; Saylor et al., 2009) or a major feature of the Himalaya such as Mt. Everest (otherwise known as Qomolangma or Sagarmāthā) had achieved ~5 km at 15 Ma (Gébelin et al., 2013) and subsequently continued to rise another ~3 km. These measurements, showing the Himalaya were the most recent component of the Tibet-Himalaya edifice (HTE) to be elevated, are in stark contrast to earlier models that suggest the Himalaya were the first element of the HTE to be uplifted.

Quantifying the uplift of the Himalaya is quite challenging because overall any mountain system is an erosional environment in which evidence of past conditions is constantly being destroyed. However using plant fossils and isotopic data in preserved pockets of sediment along the southern edge of the Tibetan Plateau (Ding et al., 2017) (Fig. 3) show that the Himalaya began to rise against the Gangdese mountain front along the southern part of the Lhasa Terrane soon after the last Tethyan ocean sediments were deposited at ~58 Ma. By ~56 Ma this proto-Himalaya had achieved, at least in what is now the central Himalaya, an elevation of ~1 km (Ding et al., 2017). By earliest Miocene time this part of the proto-Himalaya had risen to 2.3 ± 0.9 km, and by 19 Ma basin floors were

at ~4 km (Fig. 4). Isotopic analyses from Mount Everest indicate an elevation of ~5 km at 15 Ma (Gébelin et al., 2013), similar to that of the Namling-Oiyug basin just to the North on the Lhasa Terrane (Currie et al., 2016; Khan et al., 2014). Ding et al. (2017) argue that their relatively localised data reflect a more general uplift along most of the Himalayan chain because the timing of their uplift coincides with a general slowing down of the northward movement of India (Molnar and Stock, 2009) as it encountered increasingly significant resistance (Fig. 4). Following a very rapid rise in early Miocene time the Himalaya began to project significantly above what is now the average elevation of the plateau (5 km) from 15 Ma onwards (Figs. 2 and 4).

4. The role of the Himalaya in shaping monsoon characteristics

This post-15 Ma elevation of the Himalayan front above the mean plateau height is important because it is only in the last 15 Ma that the Himalaya would have formed a significant barrier to airflow, both northwards and southwards, and this barrier effect is fundamental to determining the characteristics of the South Asia Monsoon (SAM) (Boos and Kuang, 2010; Molnar et al., 2010). At 15 Ma the Namling-Oiyug Basin supported a cool temperate broadleaved woodland surrounding a large lake (Khan et al., 2014; Spicer et al., 2003), which in itself indicates far wetter conditions in southern Tibet at that time than exist at present. After the development of the high Himalaya from 15 Ma onwards this part of the plateau experienced marked drying, particularly in the wet (summer) season (Ding et al., 2017). This would have occurred when northward moving wet air from the Indian Ocean became obstructed by the high Himalaya (Molnar et al., 2010). In contrast, there is no evidence of any significant change in the precipitation regime experienced in the lowlands immediately south of the mountains (in the Himalayan Foreland Basin) (Ding et al., 2017), although the precision of wet season rainfall estimates is poor because in wet regimes leaf architecture (upon which these estimates were based) is poorly constrained by precipitation (see http://clamp.ibcas.ac.cn for details). There is some evidence of an intensification of rainfall seasonality in the eastern Himalaya since the mid Miocene, especially in the dryness of the dry season, reflected in a transition from evergreen to semi-evergreen tropical forests in that area (Khan et al., 2017).

In a climate modelling exercise Boos and Kuang (2010) noted that today's SAM conditions were considerably weakened when both the Himalaya and the Tibetan Plateau were flattened to sea level, but modern SAM characteristics were retained when only the Himalaya were left in place. This suggests that the Himalaya have a major role in determining the primary characteristics of the monsoon circulation over South Asia. In addition (Molnar et al., 2010) argued that the idea that the Tibetan Plateau operated as a kind of 'hotplate in the sky' (Flohn, 1968; Yanai and Wu, 2006), heating up to form a summer low pressure area that draws in moist air from the Indian Ocean across India, must be false because the observed area of maximum heating is not over the plateau at all, but south of the Himalaya over north-western India and Pakistan. They argued instead for the Himalaya acting as a barrier to winds from the north that would otherwise cool and ventilate the northwestern parts of the subcontinent during the summer. So, it seems it is the presence of the Himalaya, not the Tibetan Plateau, which allows an intense hot low-pressure cell to develop and drive the SAM system.

If Boos and Kuang (2010) and Molnar et al. (2010) are correct then we would expect to find the an intensification of the SAM system after 15 Ma when the Himalaya rose to form their present barrier to both northward and southward air flows. However, this leaves the question: did the SAM system exist before the Himalaya developed their modern elevations? If not, did any kind of monsoon exist? To answer these questions first it is necessary to be clear about what is meant by the term 'monsoon' and how we can characterise monsoons in the deep past.

5. Monsoons – what are they?

There is a great deal of confusion in the scientific literature as to what constitutes a monsoon. Technically no more than a seasonal reversal of wind direction (Ramage, 1971), monsoons are often associated with marked seasonal variations in precipitation. Although palaeo-wind strengths and direction can sometimes be recovered from the geological record, particularly in sediments laid down in ancient arid environments (see overview in Parrish, 1998), winds are often impossible to determine routinely from the geological record. For this reason some measure of the ratio between wet season and dry season precipitation has become a preferred proxy for palaeoclimate studies aimed at understanding the history of monsoon climates (e.g. Jacques et al., 2014; Quan et al., 2011; Shukla et al., 2014a; West et al., 2015). However, there are two problems with this approach: 1) meteorological definitions of monsoons are far more complex that just wet/dry seasonal precipitation ratios, particularly as marked wet/dry ratios can occur in non-monsoonal climates, and 2) geological evidence for wet/dry seasonal precipitation ratios are invariably preserved in sediments that accumulate on the floors of sedimentary basins, exactly where water also accumulates. This ponding of moisture buffers and biases the precipitation proxies, whether they be palaeontological (e.g. Jacques et al., 2014; Quan et al., 2011; Shukla et al., 2014a; West et al., 2015) or sedimentological (e.g. Liu and Ding, 1998; Mack et al., 1993; Retallack, 1990; Sonnenfeld and Perthuisot, 1989).

5.1. Monsoon definitions and detection from the geological record

Recognising the need for consistent definitions of what constitutes a monsoon for meteorological purposes Wang and Fan (1999), Wang and Ho (2002) and Zhang and Wang (2008) used a combination of rainfall amounts, the timing of the onset and cessation of the rainy season as well as atmospheric pressure to distinguish monsoons from other climates characterised by marked wet and dry seasons. Examples of non-monsoonal rainfall seasonality include those around the Mediterranean Sea, in California and Chile. Fig. 5a reflects the belt of global monsoons recognised by Zhang and Wang (2008). They all lie at low latitudes, which reflects their origins in the seasonal migrations of the ITCZ. In an ocean-covered world there would be a continuous northern and southern monsoon belt each side of a central equatorial wet zone. In the real world these belts are broken up by a combination of land/sea contrasts produced by the presence, position and size of landmasses, ocean bathymetry and currents, as well as complex elevated topographies such as the mountains of southern Asia, which redirect airflow. Of all the monsoon areas that across Asia is the most complex. The Asia monsoon system is divisible into a SAM, an East Asia Monsoon (EAM, although some authorities question if it really is a distinct monsoon system (Molnar et al., 2010)) a Western Northern Pacific Monsoon (WNPM) and a Transitional Area (TA) (Wang and Ho, 2002) (Fig. 5b). The WNPM is mirrored, approximately, by the Indonesia–Australia Monsoon (I-AM), which occurs south of the Equator. Both the WNPM and the I-AM are expressions of the climate arising from the seasonal migrations of the ITCZ virtually unmodified by topography.

There is increasing evidence that because ITCZ seasonal migrations are an inevitable consequence of Earth's obliquity, ITCZ

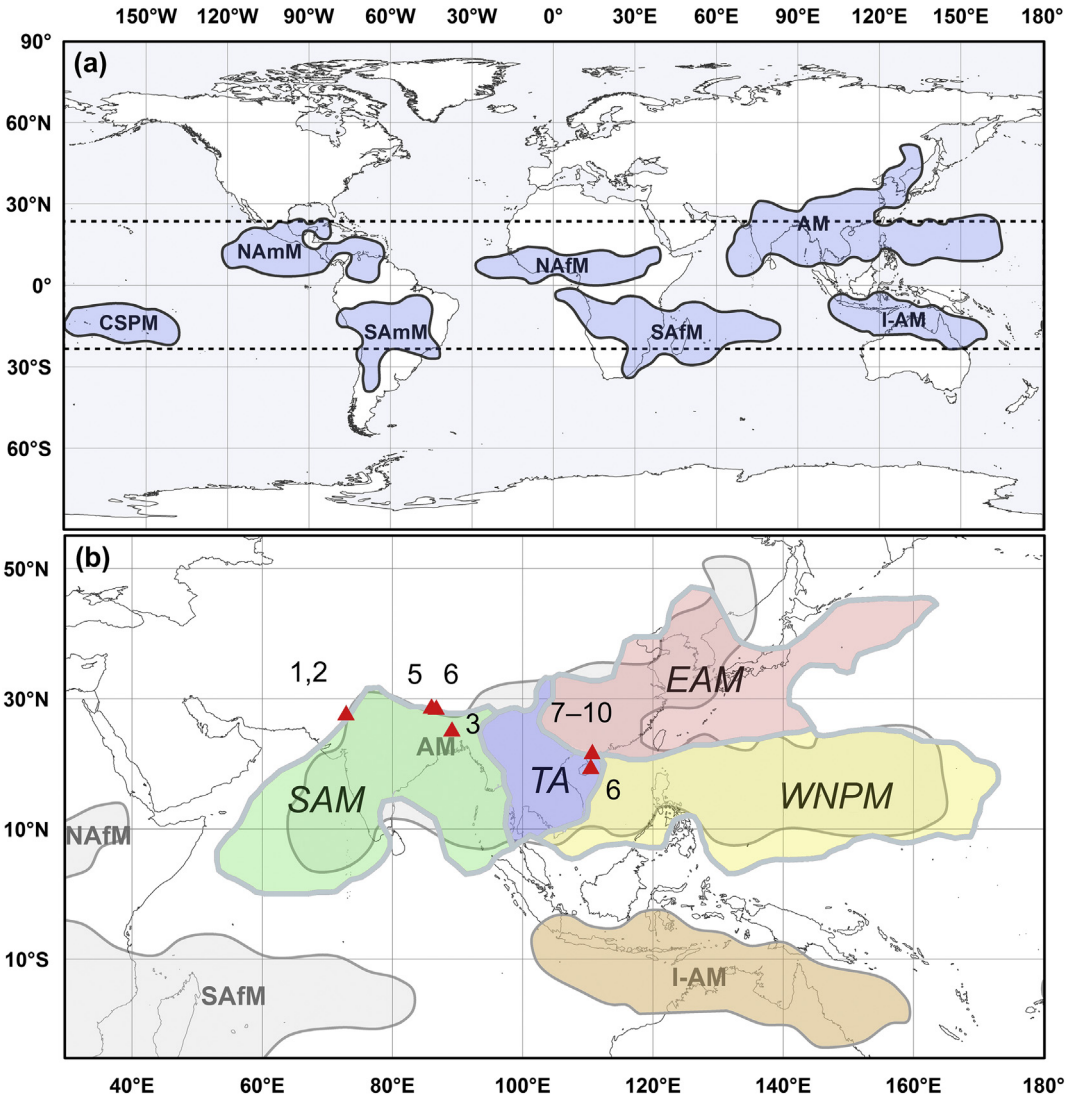

Fig. 5. a) Map showing the positions and aerial extent of monsoons as defined by the meteorological parameters of Zhang and Wang (2008). CPSM – Central Pacific Summer Monsoon, NAmM – North America Monsoon, SAmM – South America Monsoon, NAfM – North Africa Monsoon, SAfM – South Africa Monsoon; AM – Asia Monsoon, I-AM – Indonesia–Australia Monsoon. b) Map of southern Asia showing the influenced by the South Asia Monsoon (SAM), the East Asia Monsoon (EAM), the Transitional Area of interaction of the SAM and EAM, The Western Northern Pacific Monsoon (WNPM), and the Indonesia–Australia Monsoon (I-AM). Monsoon boundaries based on meteorological parameters of Wang and Ho (2002). Fossil sites (red filled triangles): 1 – Gurha 72, 2 – Gurha 32, 3 – Tirap, 4 – Liuqu, 5 – Qiabulin, 6 – Changchang, 7 – Youganwo, 8 – Huangniuling Lower, 9 – Huangniuling Upper, 10 – Shangcun.

generated monsoon climates should have been present at low latitudes throughout Earth's history, but modified to greater or lesser extents over time by changing palaeogeography. This is stark contrast to the idea that the Asian monsoon system is a Neogene phenomenon (e.g. An et al., 2001; Guo et al., 2008), related to Tibetan uplift (Liu and Dong, 2013).

The latitudinal range of ITCZ migrations, and the characteristics of Hadley circulation that generates the ITCZ, are not static over time but depend in part on the Equator-to-pole temperature gradient. In the past (such as in the Eocene) these gradients have been much shallower than at present (e.g. Greenwood and Wing, 1995). This gives rise to a change in the Hadley circulation (Hasegawa et al., 2012) and a change in the spatial distribution of precipitation generated by the ITCZ. Late Cenozoic cooling (steepening of the Equator-to-pole thermal gradient) and ice sheet formation, both at the poles and over high mountains, affects atmospheric circulation including that of the monsoons (e.g. Liu et al., 1998) and recent kilo-year variations in monsoon characteristics could well be influenced by fluctuations in ice volumes (Ding et al., 1995). Despite thermal gradient affects on ITCZ characteristics modelling shows that in an Eocene world with, or without an elevated Tibet, southern Asia would have experienced a pronounced monsoonal climate (Huber and Goldner, 2012).

If theory and modelling are correct the following questions arise: is there evidence of such old monsoons and if there is, what kind of monsoon are they? Clues to answering these questions can be found in the findings of Shukla et al. (2014) and Licht et al. (2014). Both works included data interpreted in terms of wet/dry ratios although Licht et al. (2014) provided some information on prevailing wind directions and incorporated climate modelling. While these works support the presence of monsoon systems they do not indicate whether the monsoons concerned were those of the simple and inevitable ITCZ type, or were those with strong geographic and topographic modification typical of today's SAM.

5.2. Monsoon 'fingerprinting' using leaf form

To operate efficiently leaves of perennial woody plants have to be adapted to their immediate environment, especially atmospheric conditions, and leaves of evergreen taxa (common at low latitudes) that are exposed to monsoon climates have to be particularly well adapted to the seasonal extremes they experience across all climate variables (both thermal and hydrological). These adaptations give rise to unique monsoon 'fingerprints' encoded in leaf architecture. On a global scale climate controls leaf form more powerfully than phylogeny (Yang et al., 2015). Plant taxa able to survive at a given location under a given climate either are 1) selected because they inherently have the appropriate leaf architectures to function most efficiently in those situations, or 2) are capable of easily moderating leaf form to suite local conditions (i.e. natural selection has given rise to a genome capable of generating highly plastic phenotypes), or 3) both these scenarios. It is no surprise then that monsoon climates select for distinctive woody dicot leaf trait spectra (Jacques et al., 2011; Spicer et al., 2016).

By using fossil leaf trait spectra Spicer et al. (2017) positioned early Eocene to early Miocene fossil leaf assemblages from across India and South China in a multidimensional physiognomic space defined by modern global woody dicot leaf form (Fig. 6). They were able to demonstrate that all the fossils from southern Asia showed leaf trait spectra typical of those exposed to monsoon climates, but more specifically they showed that Paleogene leaf architectures were most similar to those seen today in areas exposed to the I-AM, but not the SAM. None clearly displayed SAM type adaptations although a few, notably the Eocene and Oligocene Indian samples (Gura and Tirap respectively) and an Eocene Tibet sample (Liuqu), plotted close to the modern SAM physiognomic space (Fig. 6), the boundaries of which are necessarily gradational.

The fossil assemblages from the early Eocene of India (the Gurha Mine assemblages reported by Shukla et al. (2014) (Fig. 3), are particularly interesting in that they were close to the Equator ($<10^{\circ}$) when they were being formed. If the Eocene ITCZ behaved similarly to the ITCZ of today in both migration range and Hadley cell circulation, then we should expect that the Gurha mine area would have been within, or very near to, the Equatorial ever-wet zone. However, both sedimentological and leaf architectural evidence indicated pronounced seasonal variations in rainfall (Shukla et al., 2014). It is not possible to come to definitive conclusions regarding the width of the Equatorial ever-wet zone (conceivably it may not even existed if the latitudinal migrations of the ITCZ were large enough) because of uncertainties in the palaeomagnetic positioning of India (Molnar and Stock, 2009), but any taxa on the Indian raft must have been exposed to strong seasonal variations in precipitation as India approached the Equator, and again as it moved into the northern Hemisphere. This 'monsoon filter' would have pre-selected taxa on the Indian 'raft' for the climate regime that now predominates across southern Asia. Moreover, seasonal reversals in air flow associated just with the ITCZ migrations would have facilitated genetic interchange by air and sea prior to a land bridge being established during the early phase of collision (Spicer et al., 2017).

The lack of a distinctive SAM type leaf trait spectrum in the low altitude (~1 km) early Eocene Liuqu flora, southern Tibet, suggests that the proto-Tibetan highland did not enhance the prevailing ITCZ monsoon system to any great extent. Situated on the central southern slopes of the proto-Tibetan highland the Liuqu site is analogous to areas of the modern Gangetic Plain or Siwaliks today, which experience a strong SAM. The nearby Qiabulin site, recording earliest Miocene climate (Ding et al., 2014), also does not display a strong SAM signature, possibly in part because the higher elevation was associated with elevation-induced rainfall even in the dry season. In the middle (13 Ma) and late Miocene to Pleistocene, however, near sea-level leaf assemblages from the eastern Siwaliks show monsoon signatures and vegetation not dissimilar to those existing there today (Khan et al., 2014). This shows that the modern SAM is a middle Miocene and later phenomenon.

The onset of the SAM and EAM are often linked (e.g. An et al., 2001), but in terms of their climatological characteristics they are distinctly different (Molnar et al., 2010) and are unlikely to be driven by the same mechanisms. Not having a significant mountain range, like the Himalaya, to the north of China means that seasonal temperature and pressure variations in Central Asia influence strongly seasonal reversals in air parcel trajectories over China. These influences would be stronger in a cool world (such as the present) when the Asian continental interior cools down dramatically in winter forming a strong Siberian High pressure area. Today moist summer winds from a warm ocean to the south, combined with cold dry air from an intense Siberian High flooding into northern and western China in the winter, generates an EAM characterized by a marked summer wet/winter dry oscillation in wind direction and moisture, accompanied by significant temperature differences. In a warmer than present Paleogene Central Asia winter temperatures are likely to have been higher and winter high-pressure systems less intense. Without the very cold dry winter air-flow southwards from Central Asia, the EAM in the Paleogene would not have existed in its current form.

Could a Paleogene proto-Tibetan highland have influenced the climate over that part of Asia that today experiences the EAM? The proto-Tibetan highland, with elevations approaching 5 km and made up of the Lhasa and Qiangtang terranes, would certainly have influenced the passage of eastward air-flow (Westerlies) much as Tibet does today. However, perhaps more importantly, north of the proto-Tibetan highland large depositional basins existed. There were the Hoh Xil and Qaidam basins (Figs. 2 and 3), which possibly at some point were connected (Yin et al., 2008), and which received sediment from the Qiangtang block via northward-flowing rivers (Liu and Wang, 2001). Beginning at ~52 Ma and ending at 13.5 Ma, the Hoh Xil Basin accumulated >5000 m of sediments making up the Fenghuaoshan, Yaxicuo and Wudaoliang groups. The characteristics of the sediments indicate fluvial, lacustrine and playa depositional environments. In other words these northern basins were full of water and not the arid regions they are today. Before the Miocene the Hoh Xil basin was seemingly at low elevation ($\geq$2 km (Cyr et al., 2005), but subsequently, based on isotopic studies, rose to ~4 km in the Miocene (Polissar et al., 2009) (Fig. 2). For the reasons given above this elevation may be an overestimate, but there can be no doubt that Miocene sediments (23.5–13.5 Ma) within the Hoh Xil Basin point to it supporting a vast lake system (Wu et al., 2008). Winter Westerlies (Fig. 3) would have supplied humid air from these lakes to large parts of China, so wet/dry season precipitation was far less pronounced than in the modern EAM.

Based on leaf form there is no evidence of an identifiable EAM in the Eocene (Spicer et al., 2016), but other palaeobotanical data suggests that as early as ~40 Ma the start of the EAM may have been underway (Quan et al., 2011). However, if this was the case, the strength of the EAM was insufficient to re-organise the major climatic zones in China until 17 Ma later (Guo et al., 2008). The re-organisation, exemplified by the loss of an arid belt spanning central China to a broad arid zone across northwestern China, did not happen until the start of the Miocene (Sun and Wang, 2005).

A Neogene (early Miocene) intensification of the EAM, supported by palaeobotanical data (Sun and Wang, 2005), finds of Miocene loess (e.g. Guo et al., 2002) and carbon isotope studies (Jia et al., 2003), suggests that, as with the SAM, the presence of a proto-Tibetan highland did not by itself bring into being the Asian

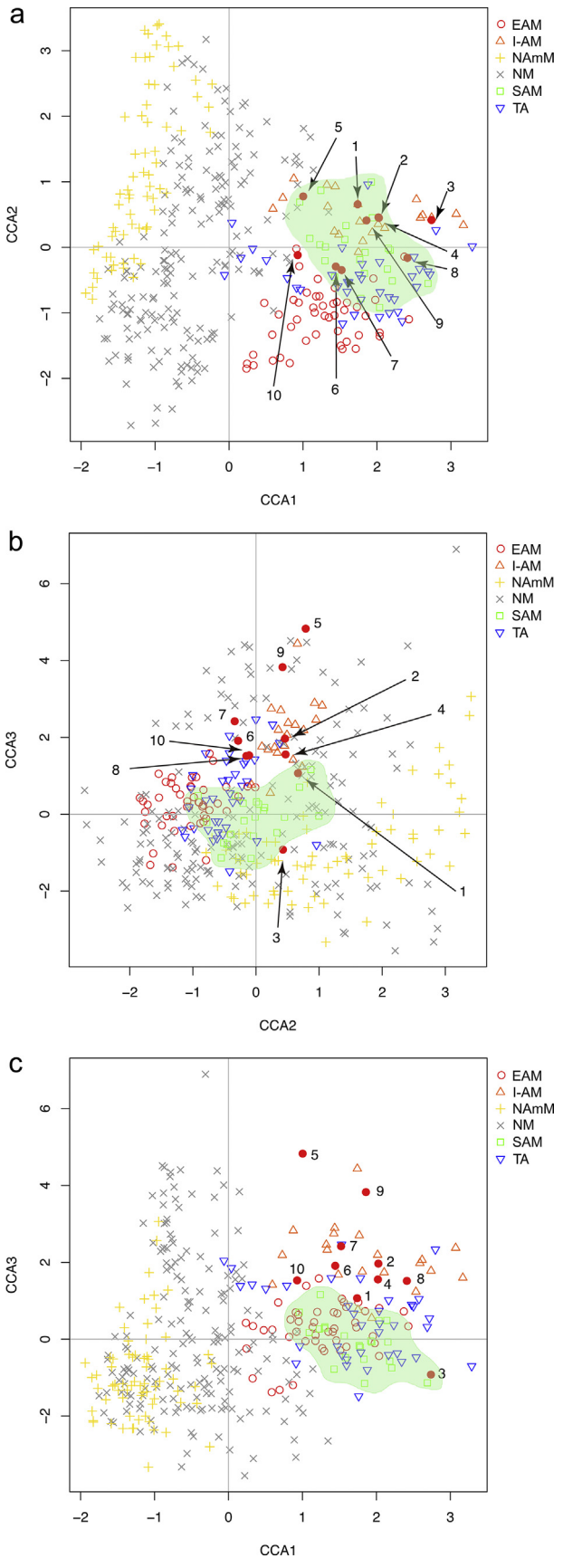

Fig. 6. CLAMP-based multidimensional plot of woody dicot leaf form. Modern vegetation sites positioned grouped by their occurrence in the monsoon areas of Wang and Ho (2002) and Zhang and Wang (2008) (Fig. 5): EAM – East Asia Monsoon, I-AM – Indonesia–Australia Monsoon, NAmM – North America Monsoon, NM – No Monsoon, SAM – South Asia Monsoon, TA – Transitional Area. Fossil sites are shown as filled numbered 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. Sites 7–10 are all from the Maoming Basin and are in stratigraphic order range from middle Eocene to late Eocene (7–9) and late early Oligocene (10). When CCA axes 1–3 are taken together all fossil sites plot in the area occupied by the modern Asia monsoon system so clearly the fossil leaf forms showed adaptations to monsoon conditions. No fossil assemblages sit within the area occupied by the modern SAM (green shading), while most are within the modern I-AM and TA.

monsoon system as we know it today. That both the SAM and the EAM appear to be largely Neogene only phenomena requires predominantly Neogene driving mechanisms. Clearly the rise of the Himalaya is a likely cause of the development of the SAM through redirection of airflow, and this could also have contributed to reorganization of atmospheric circulation to form the EAM. However, other factors may also be at play.

If the isotope-derived elevations are correct the rise of large parts of the northern Tibetan Plateau took place after 23 Ma (Wang et al., 2014) (Fig. 2). This, and the subsequent loss of large moisture sources north of the developing plateau, may also have influenced the formation of the EAM. On at least four occasions during the Cretaceous and Paleogene shallow marine sediments periodically connected the Tarim Basin (Fig. 3) (Bosboom et al., 2014) to the Mediterranean Tethys, however there is some evidence in the form of foraminiferal remains and isotopic signatures that in the early Miocene the Tarim Basin was connected to open marine conditions to the west and at sea level (Kent-Corson et al., 2009; Ritts et al., 2008). It was only in the middle Miocene that the Tarim Basin finally became isolated and elevated above sea level cutting off a major moisture supply to the Asian interior. It is also at this time that lake deposition in the Hoh Xil Basin seems to cease.

In the Eocene southern China appears to have had only a weak monsoon presence compared to today (Spicer et al., 2016; Herman et al., 2017), but precipitation seasonality increased over time such that by the late early Oligocene an I-AM type monsoon climate was beginning to be established (Herman et al., 2017). Today this part of China (specifically the Maoming Basin, Guangdong Province) (Fig. 3) is located in the Transitional Area of Wang and Ho (2002) (Fig. 5) and experiences the influence of both the SAM and EAM. With the lack of both the SAM and EAM in the Paleogene it is not possible to attribute the cause of the trend towards monsoon conditions recorded in the Maoming fossil leaf architectures, but it is possible that future Earth system modelling might help resolve this.

6. The origins of the modern exceptional biodiversity across southern Asia

It is clear from theoretical considerations, climate modelling and observation that southern Asia must have been exposed to ITCZ monsoon climates since at least the early Eocene (and probably long before), and that monsoon climates predominated across the region even in the absence of an elevated Tibetan Plateau or Himalaya. However, we have also seen that there is an abundance of evidence to suggest there was a proto-Tibetan highland in Eocene time, but that this did not, by itself, generate modern SAM or EAM type monsoon systems. Such a highland would, however, have hosted considerable biodiversity (see Section 1.1) by virtue of its low latitude position and complex topographic relief. Because the high Himalaya were yet to form this highland would, as fossil evidence suggests (Ding et al., 2017; Khan et al., 2014), have had a wetter climate than the Tibetan Plateau does today.

In her critical review Renner (2016), notes that numerous Asian molecular phylogenies are linked to a supposed Miocene uplift of

the Tibetan Plateau. However, as evidenced above, large parts of Tibet were already high in the Paleogene and must have already supported high biodiversity long before the Miocene. What we do see in Miocene time is a modification of the prevailing ITCZ type monsoon systems towards the modern SAM conditions coincident with the high Himalaya projecting above 5 km at around 15 Ma. If the Miocene nodal ages seen in the molecular phylogenies are real and not an artifact of circular reasoning, then it is possible that the rise of the Himalaya not Tibet, and the subsequent development of the SAM, had major impacts on species diversification across southern Asia.

6.1. The need for accurate dating of fossil assemblages

Molecular phylogenies are often constrained using fossil data (Renner, 2016) and it is not just the molecular phylogenies that have been linked to the Miocene. Many fossil floras across the 200 or so fossiliferous Cenozoic basins of Yunnan have been regarded as being Miocene because they appear modern: they contain a large number of modern genera. Almost all these fossiliferous basins lack radiometric dates, the exceptions being the Pliocene Tengchong deposits reported by Li et al. (2000) and the Eocene Jianchuan Basin (Gourbet et al., 2017). Correlation between the vast majority of basins has been made on the basis of their contained fossil fauna and flora, particularly the pollen floras. Many of the basins contain a modern-looking palynoflora and so have been assigned Miocene or younger ages (Province of Yunnan Bureau of Mining and Geology, 1990). Inevitably this sets up a circular pattern of reasoning that re-enforces the Miocene as being a critical period for Asian biodiversity evolution.

Recently, however, pristine volcanic ashes were discovered in one such basin, the Lühe Basin of central Yunnan, that had been regarded as late Miocene in age, containing as it does a diverse pollen, leaf and wood flora (Ma et al., 2005; Xu et al., 2008; Yi et al., 2003; Zhang et al., 2007) of modern appearance. U/Pb dating of well preserved zircons in the ashes yielded youngest ages of 33 ± 1 Ma making the fossiliferous beds early Oligocene, some 20 million years older than previously thought (Linnemann et al., in press). This shows that in this basin at least, a modern type of vegetation existed long before the Miocene. Although other basins rich in plant and animal fossils have yet to be similarly dated, it is likely that a modernization of the flora in this part of southern Asia was a Paleogene phenomenon unconnected with the onset of the SAM but rooted, nevertheless, in a monsoon climate regime similar to that of today's I-AM. It is possible that this modernization took place, as elsewhere in the world, across the Eocene–Oligocene transition (Prothero, 1994) or more likely earlier, but further work using accurately dated deposits is needed to explore this.

Another consequence of the revised age for the Lühe basin is that isotope palaeoelevation estimates that used a Miocene isotopic lapse rate and sea level comparator (Hoke et al., 2014; Li et al., 2015) will be erroneous, leading to a revised understanding of landscape evolution in Yunnan. This error is not restricted to the Lühe Basin but also applies to the Jianchuan Basin, also in Yunnan, close to the Tibetan Plateau. Long regarded as accumulating sediment from the Eocene to as recently as the Pliocene, radiometric dating has shown that the uppermost part of the Jianchuan basin-fill, previously considered to be of Pliocene age, dates from 35.4 ± 0.9 Ma and so is late Eocene (Gourbet et al., 2017). Consequently the isotope-derived palaeoelevations of the Jianchuan Basin of Li et al. (2015) of 2.6 + 0.8/−1.1 km in the Miocene and Hoke et al. (2014) of 3.3±1 km in the late Eocene can no longer be regarded as plausible. Correcting for age-related changes in isotope lapse rates, temperatures, trajectories and palaeogeographic positioning etc. Gourbet et al. (2017) have recalculated the late Eocene elevation of the Jianchuan Basin to be 1.2 ± 1.2 km. Clearly the application of quantitative dating methods to the numerous Cenozoic sedimentary basins of Yunnan and across southern Asia will, in the coming years, completely transform our current ideas of landscape evolution (including mountain building, river courses, climate and biota) in the region. This has profound implications for understanding the antiquity of the Indo-Burma biodiversity hotspot as well as monsoon evolution.

6.2. Quaternary whiteout?

The preceding review has focused on tectonic timescales over which significant mountain building can take place. However, it is worth remembering that shorter timescale events can also have significant impact upon biodiversity and migration of biotas. In respect of Tibet perhaps most important of these in the last 1 million years has been glaciation. If estimates of the extent of late Pleistocene glaciation are correct then Tibetan Plateau was covered in 2.4 million km^2 of ice (Kuhle, 1998), which must have either led to extinction or driven many taxa off the plateau and downslope to potentially hybridize with, or compromise, biota in the surrounding regions. Certainly parts of northwestern Yunnan show signs of recent glacial activity in terms of well developed 'U' shaped valleys down to elevations of ~2 km, but the extent to which Quaternary Tibetan ice cover overwrote the history of more deep rooted biodiversity origins across the region remains to be investigated.

7. Summary and conclusions

To return to the questions posed at the beginning of this review:

i) Paying particular attention to major features such as Tibet and the Himalaya, how and when did the regional topography evolve?

   Elevated terrain over the area we call Tibet existed well before the Miocene and in fact an Andean type topography with surface elevations of at least 4.5 km existed at the start of the Eocene before final closure of the Tethys Ocean that separated India from Eurasia. The Himalaya were formed not at the start of the India–Eurasia collision but after much of Tibet had achieved its present elevation. The Himalaya built against a pre-existing proto-Tibetan highland and only projected above the average height of the plateau at around 15 Ma.

ii) How and when did the Asian monsoon systems arise, and are the current monsoon systems connected with the height of Tibet and or the Himalaya?

   Paleogene monsoons of the type seen in today's Indonesia–Australia region existed in the Paleogene and were simply an expression of the seasonal migrations of the ITCZ. Climate modelling demonstrates that such monsoons would have existed even in the absence of significant topography over Tibet. This suggests that a proto-Tibetan highland had only a minor influence, if any, in shaping monsoon systems over Asia in the Eocene. The South Asia Monsoon appears to have arisen after the mid Miocene, probably in response to the presence of a high (>5 km) Himalaya, acting as a barrier to north–south airflow.

   The East Asia Monsoon also appears to be a Neogene phenomenon, arising in the Early Miocene (~22 Ma), and may be associated with cooling over central Asia as global temperatures declined, the rise of large parts of northern Tibet and possibly other parts of Asia deflecting air-flow,

and the loss of large water bodies in the Tarim, Hoh Xil and Qaidam Basins.

iii) How old are the Asian biodiversity 'hotspots' and how do they relate to development of the Asian monsoon systems?

Newly discovered and dated volcanic ash beds in the Lühe Basin, previously regarded as late Miocene, show that the modernization of the flora in this region took place by the earliest Oligocene and not the Miocene as previously assumed. This demonstrates a Paleogene origin of the modern rich biota of the region. The southern Asia biodiversity is therefore deep rooted in an orographically complex region under a monsoonal climate dating back at least 50 Ma.

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