Palaeogeography, Palaeoclimatology, Palaeoecology 518 (2019) 82–88

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

Age constraints on a Neogene tropical rainforest in China and its relation to the Middle Miocene Climatic Optimum

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ARTICLE INFO

Keywords:
$^{40}Ar/^{39}Ar$ dating
Ecosystems
Paleoclimate
Paleogeography
Amber

ABSTRACT

Tropical rainforests have strongly influenced Earth systems throughout their evolutionary history. Plant taxa found in the Fotan Group of Fujian Province indicate that an Asian tropical rainforest prevailed in southeastern China during the Miocene. Abundant insect-bearing ambers co-occur with diagnostic plant fossils in outcrop. Fotan Group fossils demonstrate that highly diverse tropical ecosystems existed during the early Neogene in southeastern China. This study reports a robust $^{40}Ar/^{39}Ar$ age of 14.7 ± 0.4 Ma for the Fotan fossils. This age constrains interpretations of 1) when tropical rainforest ecosystems developed in China, 2) whether the Fotan flora temporally overlapped with the Asian tropical forest in India, and 3) whether the Middle Miocene Climatic Optimum triggered expansion of tropical rainforests in Asia. A precise age for Fotan units provides important constraints on the biogeographic history of the field area and paleographic models linking Asian and Indian biota.

1. Introduction

Tropical rainforests play an important role in modern ecosystems and the global carbon cycle. The tropics host an estimated two-thirds of flowering plant species (Pimm and Joppa, 2015), with the greatest diversity of these taxa occurring in rainforests. Major proportions of birds, mammals, amphibians, and most arthropod groups also reside in these ecosystems (Corlett, 2014; Williams et al., 2003). Fossil pteridosperms, an extinct seed plant with fern-like leaves, indicate that Earth's first rainforests developed in the late Carboniferous at around 300 Ma (DiMichele et al., 2007). Research indicates that the rise and fall of rainforests in Earth history exerted dynamic influence on the biosphere and atmosphere (e.g., Lawton et al., 1998; Falcon-Lang and Scott, 2000; Bonan, 2008; Sahney et al., 2010; Dunne et al., 2018). For example, a recent study by Dunne et al. (2018) suggested that Carboniferous rainforest collapse led to extinction of some groups of tetrapods, but allowed amniotes, a group which ultimately gave rise to modern mammals, reptiles, and birds, to expand globally. On the other hand, tectonics, ecosystems, and environmental circumstances also strongly influenced the development and diversification of tropical rainforests (e.g., Dettmann, 1989; Johnson and Ellis, 2002; Rust et al., 2010).

Tropical rainforests occur only sparsely in modern-day China but their distribution and diversity is well-documented (Zhu, 2006, 2013). The origin and evolution of tropical rainforests in China however remain unresolved. Based on the discovery of fossil winged fruits belonging to the mega-plant Dipterocarpaceae in the Fotan Group of Fujian Province, southeastern China, Shi and Li (2010) first suggested that Asian tropical rainforests appeared in China during the Miocene. This interpretation was challenged because Dipterocarpaceae were not unique to modern tropical rainforests (Ghazoul, 2011). Additional discoveries of new tropical elements from the Fotan flora provided further evidence for the existence of a Miocene tropical rainforest in southeastern China (Shi et al., 2014a, 2014b; Jacques et al., 2015). For example, Dipterocarpaceae fossils co-occurred with *Artocarpus*, *Boehmeria*, *Macaragna*, *Flacourtia*, *Shorea* and *Calophyllu*, which represent typical tropical flora (Jacques et al., 2015). In addition to plant fossils,

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https://doi.org/10.1016/j.palaeo.2019.01.019
Received 4 October 2018; Received in revised form 11 January 2019; Accepted 11 January 2019

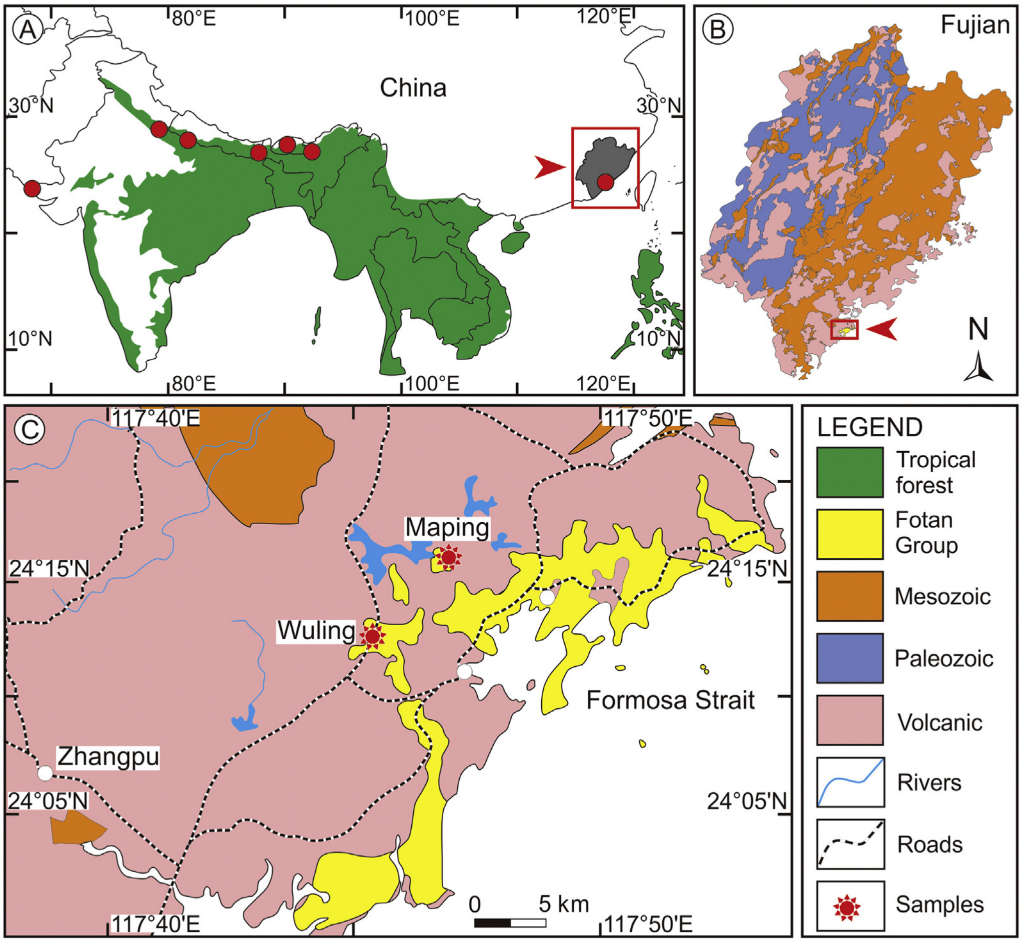

Fig. 1. (A) Distribution map of modern tropical forest (green colour) and Neogene tropical flora sites (red circles). Map revised from Jacques et al. (2015). (B) Geological map of Fujian Province, southeastern China. (C) Geological map showing Fotan Group outcrop distribution and sampling localities in southeastern Fujian. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

recent discoveries have identified more than ten thousand arthropod and plant inclusions in Fotan Group ambers. While none of these specimens have been described in scientific journals, the deposit may represent one of the most fossil-rich amber deposits in the world. Discoveries from SE Fujian represent a highly diverse paleobiotic assemblage. Fotan fossils can help constrain plant evolution and diversification over a critical interval of Earth history.

Determining the age of Fotan fossil horizons can help date the Miocene tropical rainforest in China and constrain its long-term history. This report presents new $^{40}Ar/^{39}Ar$ ages for two basalt samples collected from just above the fossiliferous beds. Our robust age results provide critical geochronological constraints on tropical plant evolution and diversification.

2. Geological background

The Fotan Group was named for the Fotan bed, whose type locality occurs in Fotan, Zhangpu County, Fujian Province, southeastern China. The Fotan Group occurs widely throughout eastern and western Fujian (Fig. 1; Zheng and Wang, 1994; BGMRFP, 1985). Initial studies described the Fotan Group as terrestrial and consisting primarily of three basaltic layers and three sedimentary layers (Zheng and Wang, 1994). A typical stratigraphic section includes basalts, arenaceous conglomerates, sandstone, and mudstone interbedded with lignite and diatomite (Fig. 2; Zheng, 1984, 1987; BGMRFP, 1985; Zheng and Wang, 1994).

The Fotan Group hosts abundant amber and plant fossils containing spores and pollen (Figs. 3, 4; Table 1). The plant fossils are preserved in a light brown diatomite (Fig. 4A), while the amber occurs within coal seams and diatomite that directly underlie the layer hosting plant flora (Fig. 4B–D), both from the second sedimentary layers (Fig. 2). The spore-pollen assemblage consists of two sub-assemblages, the *Quercoidites-Liquidambarpollenites-Dacrydiumidites* assemblage and the *Symplocoipollenites-Liquidambarpollenites* assemblage, which occur in separate sedimentary layers. The fossil assemblages indicate a middle to late Miocene biostratigraphic age for the Fotan Group (Zheng and Wang, 1994). The Fotan Group units have not previously been subjected to geochronologic analysis using radiogenic isotopic methods. Previous paleontological studies have often cited a 14.8 ± 0.6 Ma age reported by Ho et al. (2003) for a nearby locality. This is the only published chronostratigraphic age constraint on the Fotan Group. However, Ho et al. (2003) did not offer detailed description of the sample locality or stratigraphic position for the dated sample and we consider its relationship to the Fotan fossils to be uncertain.

3. Sampling and analysis

We collected two fresh basalt samples from the Fotan Group as it occurs in Zhangpu County, Fujian Province, China. Figs. 1 and 2 show the sampling locality and its stratigraphy. Although previous studies have described basaltic layers in the lower Fotan Group, their exposure near the fossil-bearing outcrop is very poor. We therefore collected samples FT-1 and FT-2 from interbedded volcanics just above the fossil beds.

Sample preparation and analysis were conducted at the AGES

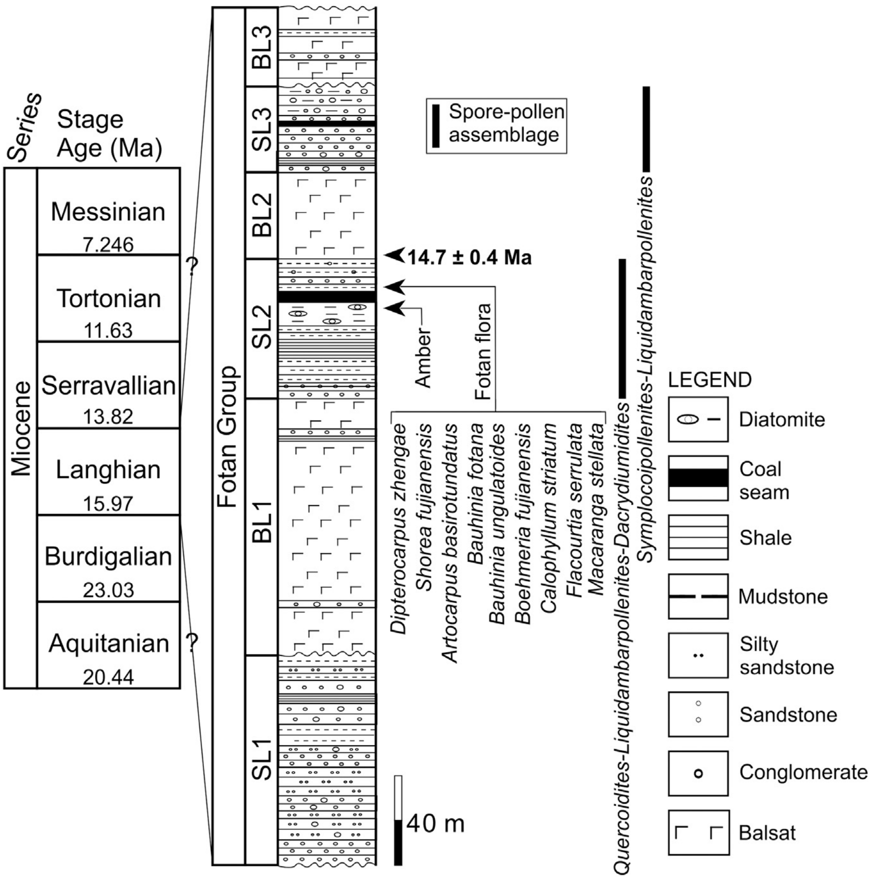

Fig. 2. Stratigraphic section showing biostratigraphy and geochronologic age result (BL, basaltic layers; SL, sedimentary layers).

facility (Argon Geochronology for the Earth Sciences) of Lamont-Doherty Earth Observatory, Columbia University. After crushing, the 180–250 μm size fractions of fresh groundmass from both samples were hand-picked under a binocular microscope and washed ultrasonically in distilled water. Following selection, groundmass fragments along with bracketing standards of Fish Canyon sanidine (dated at 28.201 ± 0.046 Ma; Kuiper et al., 2008) were loaded onto a 1.9 cm diameter by 0.3 cm deep Al disk. Samples and standards were irradiated for 8 h duration at the US Geological Survey TRIGA reactor in Denver, CO, USA. After irradiation, all standards and samples were degassed using an automated CO_2 laser-based extraction system and analyzed with a Micromass VG5400 mass spectrometer at the AGES lab. Analytic procedures followed those described in detail in Chang et al. (2012, 2014). Details of analysis procedures, Ar isotopic data corrected for blanks, mass discrimination, radioactive decay, and J values are provided in the supplement.

4. Results

Incremental heating analysis of FT-1 groundmass yielded a plateau age of 14.5 ± 1.5 Ma (errors reported as 2σ throughout the paper), with MSWD of 0.65 (see Fig. S1 in Supplementary file). The age spectrum for FT-1 shows systematically younger apparent ages at low temperatures, indicating certain degrees of alteration. Data from the step-heating analysis were plotted on an inverse isochron isotope correlation diagram ($^{36}Ar/^{40}Ar$ vs. $^{39}Ar/^{40}Ar$). The isochron age of 15.2 ± 2.0 Ma (MSWD of 1.2) shows good agreement with the plateau age including its error term.

Incremental heating analysis of FT-2 groundmass yielded a well-defined plateau age of 14.7 ± 0.4 Ma with MSWD of 0.28 (Fig. 5A). The isochron age of 14.7 ± 0.4 Ma (MSWD of 0.96) is identical with the plateau age (Fig. 5B). The 302 ± 2 $^{40}Ar/^{36}Ar$ intercept from the inverse isochron diagram resembles atmospheric values (i.e., 295.5 from Neir, 1950 or 298.56 from Lee et al., 2006). Although the age results for both samples are indistinguishable at the 2σ level, we interpret the more precise 14.7 ± 0.4 Ma ages as the upper limit of the depositional age of the Fotan fossils.

5. Discussion

5.1. The origin and evolution of tropical rainforests in China

Tropical rainforests are defined as tall, dense, multi-layered, broad-leaved evergreen forests that form the natural vegetation in tropical areas with a warm climate and a short to non-existent dry season (Grentry, 1992; Whitmore, 1998). Most tropical rainforests occur around the equator. Although tropical rainforests represent the world's most diverse ecosystems, their origins and history remain unclear. Tropical rainforests having similar structure but different flora and fauna relative to those found today have existed since the Cretaceous (e.g., Ziegler et al., 1987; Dettmann, 1989; Davis et al., 2005; Couvreur et al., 2011).

Evidence for the oldest-known Asian tropical rainforest occurs in early Paleogene sedimentary deposits in India (Prasad et al., 2009). Previous studies demonstrated that many current organisms found on the Indian subcontinent relate closely to those found in Africa, Madagascar, and the Seychelles (these islands are a Cretaceous fragment of the India-Madagascar landmass) (Murphy and Collier, 1997; Bijou and Bossuyt, 2003; Noonan and Chippindale, 2006). Fossils and phylogenetic data also suggest that many recent taxa found in southeastern Asia represent basal Indian lineages, indicating migration from the Indian subcontinent, an interpretation sometimes called the "out-of-India"

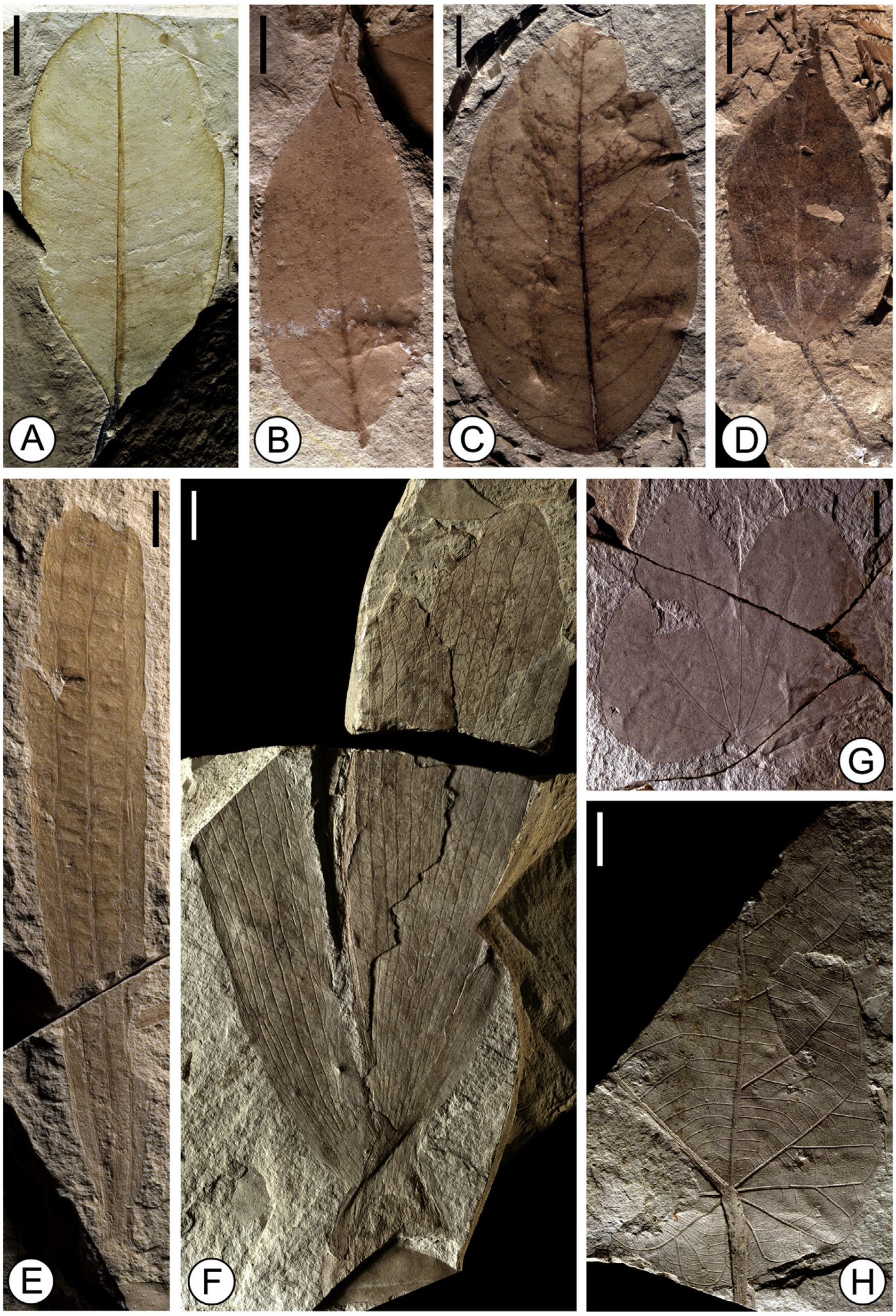

Fig. 3. Well-preserved plant fossils from the Fotan Group: (A) *Calophyllum striatum*, (B) *Flacourtia serrulata*, (C) *Artocarpus basirotundatus*, (D) *Boehmeria fujianensis*, (E) *Dipterocarpus zhengae*, (F) *Shorea fujianensis*, (G) *Bauhinia fotana*, and (H) *Macaranga stellata*. All scale bars = 1 cm.

hypothesis (e.g., Macey et al., 1999; Bossuyt and Milinkovitch, 2001; Gower et al., 2002; Conti et al., 2002; Corlett, 2007; Rust et al., 2010). This hypothesis helps explain many Indian plants and animals now found in Asia, but the timing of this expansion is subject to considerable uncertainty given that India and Asia were not contiguous until sometime between the Cretaceous (~70 Ma) and the Eocene-Oligocene boundary (~35 Ma) (e.g., Yin and Harrison, 2000; Aitchison et al., 2007; Najman et al., 2010; Bouilhol et al., 2013; Hu et al., 2017).

Modern tropical rainforests have only a limited distribution in China (Zhu, 2006, 2013). A true southeastern Asian tropical forest was documented in Xishuangbanna, Yunnan based on recognition of Dipterocarpaceae in this area during the 1970s (Zhu, 2006). The timing and establishment of tropical forest ecosystems in China remained unclear until recently. Based on winged fruit fossils belonging to two genera of the Dipterocarpaceae and fossil resins, Shi and Li (2010) first interpreted the Fotan Group as an Asian tropical rainforest and Dipterocarpaceae fossils as evidence of the out-of-India hypothesis. This hypothesis was challenged because Dipterocarpaceae are not restricted to tropical rainforest ecosystems (Ghazoul, 2011).

Jacques et al. (2015) also interpreted the Fotan fossil assemblages as a classic rainforest. Its fossil assemblage includes eight genera, including *Artocarpus*, *Bauhinia*, *Boehmeria*, *Calophyllum*, *Dipterocarpus*, *Flacourtia*, *Macaranga*, and *Shorea*. Of these, *Dipterocarpus*, *Shorea*, *Flacourtia*, and *Calophyllum* are restricted to tropical regions in China

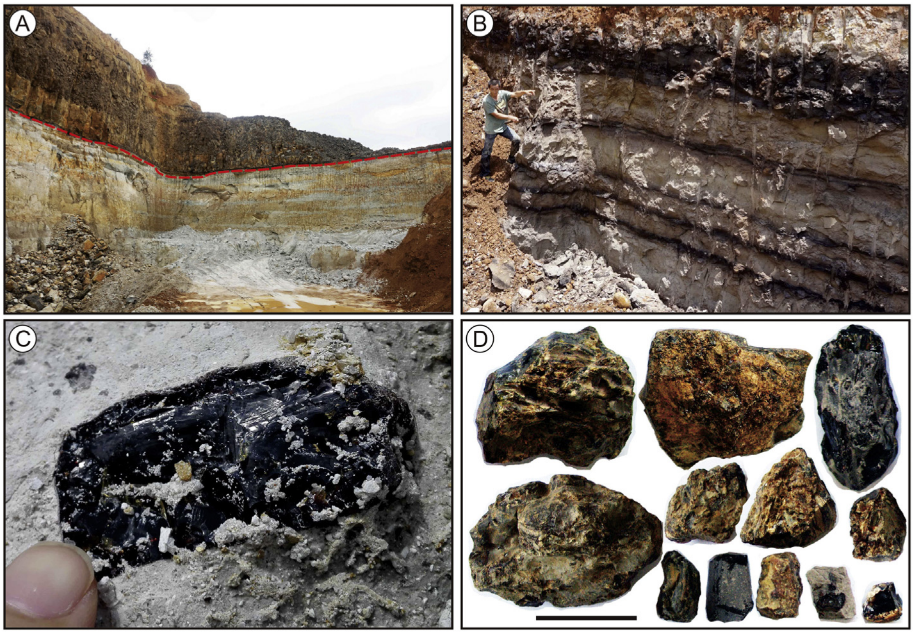

Fig. 4. (A) Photograph showing boundary between basalt and diatomite. (B) Photograph of coal seam and diatomite bearing amber. (C) Photograph of amber lenses in diatomite. (D) Photograph of unpolished amber pieces. Scale bar = 50 mm. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Tropical rainforest flora occurring in the Fotan Froup.

Plant mega-fossils	Reference
Dipterocarpus zhengae	Shi and Li, 2010
Shorea fujianensis	Shi et al., 2014a, 2014b
Artocarpus basirotundatus	Jacques et al., 2015
Bauhinia fotana	Jacques et al., 2015
B. ungulatoides	Lin et al., 2015
Boehmeria fujianensis	Jacques et al., 2015
Calophyllum striatum	Jacques et al., 2015
Flacourtia serrulata	Jacques et al., 2015
Macaranga stellata	Jacques et al., 2015

today. Other genera listed occur mainly in tropical areas, but with some representatives in subtropical regions and a few in temperate regions. Given prevailing tropical interpretation of its fossil plant assemblage, the Fotan flora represent a Miocene rainforest in China. The age reported here for the basalt overlying the Fotan fossil beds dates this tropical rainforest at 14.7 ± 0.4 Ma.

5.2. Plant expansion and the Middle Miocene Climatic Optimum

The modern geographic distribution of Dipterocarpaceae is often cited as evidence of the out-of-India hypothesis (Ashton, 1982; Ashton and Gunatilleke, 1987). A number of Dipterocarpaceae sp. and early Eocene fossil resins derived from Dipterocarpaceae occur in India (Rust et al., 2010; Dutta et al., 2011). Dipterocarpaceae mega-fossils reported from Neogene sedimentary units in India and Nepal (e.g., Prakash et al., 1994; Khan et al., 2011) are absent from the Paleogene of India but appear in the Paleogene of southeastern Asia (Shukla et al., 2013). The older fossil evidence from southeastern Asia led Mehrotra et al. (2005) to question links between Miocene vegetation in China and India. Because these types of plants are typical of Neogene strata in India, the discovery of Dipterocarpaceae in Miocene deposits of China further indicates exchange between Chinese and Indian floras. In addition to Dipterocarpaceae, Jacques et al. (2015) identified several fossils in the Fotan Group, which also occur among Indian fossil flora (Fig. 1A). This overlap supports the interpretation of links between Chinese and Indian palaeofloras. Sharing several components, some of them presumably dominant, the Fotan and Indian palaeofloras clearly demonstrate vegetation exchanges occurred between the Gondwanide India and Laurasia. According to the out-of-India hypothesis, after docking of India, the uniqueness of the Indian flora was diluted by the floristic exchange with Asia. Based on the Fotan palaeoflora, Jacques et al. (2015) suggest that this dilution was already occurring by the Middle Miocene. Their results do not necessarily imply that the out-of-India hypothesis is true, only that Chinese and Indian palaeofloras are linked.

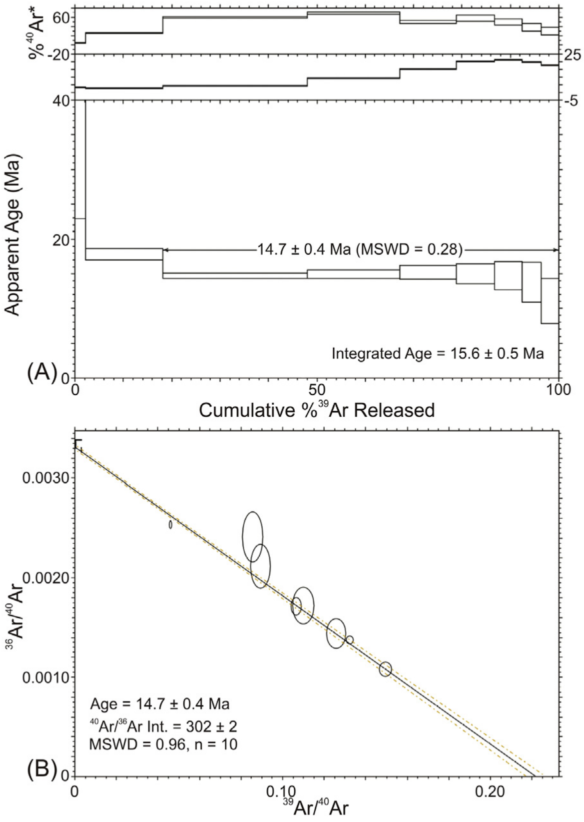

Fig. 5. (A) ^{40}Ar/^{39}Ar apparent age spectra for FT-2 groundmass. (B) inverse isochron plot for FT-2 groundmass.

The Fotan fossil outcrops formed at a geographic position similar to its modern location (i.e., ~24° north latitude, and not far from the coastline) during the Middle Miocene. This area experiences a subtropical monsoon climate and hosts subtropical coniferous broadleaf forests (Wu, 1980). The appearance of tropical rainforests during the Middle Miocene indicates that this area was warmer and more humid than it is at present (Shi and Li, 2010). Several studies have linked this phenomena with the Middle Miocene Climatic Optimum, which occurred at 16.8–14.7 Ma (Shi and Li, 2010; Shi et al., 2014a, 2014b; Jacques et al., 2015). The Middle Miocene Climatic Optimum represents Earth's most recent, natural, prolonged global warming event, and one that is thought to have caused major global ecological shifts (e.g., Flower and Kennett, 1994; Böhme, 2003; Mosbrugger et al., 2005; Maguire, 2015). Oxygen isotopic profiles measured from deep-sea benthic foraminifera in sediment indicate that temperatures were significantly warmer in the deep ocean and at middle to high latitudes (Zachos et al., 2008; Shevenell et al., 2008). Other studies have shown that tropical sea surface temperatures were also higher than current values (You et al., 2009; LaRiviere et al., 2012). Paleobotanical records suggest a significant warming on land at middle to high latitudes, with temperature anomalies ranging from $+10\,^{\circ}\mathrm{C}$ to $+20\,^{\circ}\mathrm{C}$ in central and east Asia, a weak equator-to-pole latitudinal temperature gradient, and very humid conditions without significant seasonal patterns (Bruch et al., 2007, 2011; Utescher et al., 2011). Despite considerable research, specific effects of the Middle Miocene Climatic Optimum on local paleocommunities remains uncertain. Based on the plant fossils, Jacques et al. (2015) suggested that tropical rainforests migrated northwards to the Fujian area of southeastern China. Our new age data for the Fotan fossils further constrains the timing of this expansion as occurring around the time of the Middle Miocene Climatic Optimum.

5.3. Biodiversity hotspot

Ambers containing Miocene biota come from about 14 different deposits found in Europe, Asia, North America, and South America (Martínez-Delclòs et al., 2004; Antoine et al., 2007; Shi et al., 2014a, 2014b). Most of these deposits have not been systematically investigated however and only three, from the Dominican Republic, Mexico, and Peru, include tropical insect fossils (Iturralde-Vinent and MacPhee, 1996; Antoine et al., 2007; Castañeda-Posadas and Cevallos-Ferriz, 2007). The Dominican amber has been well-studied throughout the last century and is interpreted to be 20–15 Ma based on biostratitigraphic and paleogeographic evidence (Iturralde-Vinent and MacPhee, 1996). The Mexican amber deposit, formed west of the Dominican Republic, also hosts abundant inclusions but has not been studied in detail (Solórzano Kraemer, 2007). The Mexican amber is generally interpreted to have a similar history and age as that of the Dominican amber. The recently discovered amber from Peru is considered to originate from an angiosperm tree and hosts a diverse Neotropical biota including arthropods (13 hexapod families and 3 arachnid species) and macrofossil inclusions (Antoine et al., 2007).

In addition to plant fossils, abundant insect-bearing ambers (also referred to as Zhangpu Amber) have been discovered in the Fotan Group. In contrast to the tropical amber deposits described above, the Zhangpu Amber is the only Miocene deposit from Asia, and one formed by members of the Dipterocarpaceae (Shi et al., 2014a, 2014b). More than ten thousand arthropod and plant inclusions have been recently identified from the Zhangpu Amber (personal communication). While none of these discoveries have been described in scientific journals, the deposit may represent one of the most fossiliferous amber deposits in the world and may record considerable biodiversity. Our age indicates that this area of Asia thus represented a biodiversity hotspot at 14.7 Ma.

6. Conclusions

Two basalt samples collected directly above fossil beds in the Fotan Group of Zhangpu County, southeastern China yielded a robust $^{40}\mathrm{Ar}/^{39}\mathrm{Ar}$ age of 14.7 ± 0.4 Ma. Plant mega-fossils and insect-bearing ambers have been recovered and studied from outcrops in this area over the last two decades. This age provides an accurate age constraint for fossils belonging to a Neogene tropical rainforest in China. The Fotan Group plant fossils indicate warm and humid paleoenvironments. The locality currently enjoys a subtropical climate, and previous studies attribute the appearance of tropical rainforests at middle latitudes to the Middle Miocene Climatic Optimum. Our age data provide the chronological constraints on rainforest expansion in Asia. In addition to plants, abundant insects from ambers have been discovered from the same strata, suggesting a diverse ecosystem. The well-constrained age for these insect-bearing ambers will help improve general understanding of middle Miocene ecosystems, including the co-evolutionary history of insects and plants.

Acknowledgments

This research was supported by the RGC General Research Fund (Grant no. 17300217) and the National Natural Science Foundation of China (41772014, 41472010). We thank Professor Thomas Algeo and two anonymous reviewers for their constructive comments.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2019.01.019.

References

Aitchison, J.C., Ali, J.R., Davis, A.M., 2007. When and where did India and Asia collide? J. Geophys. Res. Solid Earth 112, B05423. https://doi.org/10.1029/2006JB004706.

Antoine, R.O., Franceschi, D.D., Flynn, J.J., Nel, A., Baby, P., Benammi, M., Calderón, Y., Espurt, N., Goswami, A., Salas-Gismondi, R., 2007. Amber from western Amazonia reveals Neotropical diversity during the middle Miocene. Proc. Natl. Acad. Sci. U. S. A. 103, 13595–13600. https://doi.org/10.1073/pnas.0605801103.

Ashton, P.S., 1982. Dipterocarpaceae. In: van Steenis, C.G.G.J. (Ed.), Flora Malesiana, Series 1. Spermatophyta, vol. 9. Martnius-Nijhoff Publications, The Hague, The Netherlands, pp. 237–552.

Ashton, P.S., Gunatilleke, C.V.S., 1987. New light on the plant geography of Ceylon. I. Historical plant geography. J. Biogeogr. 14, 249–285. https://doi.org/10.2307/2844895.

Bijou, S.D., Bossuyt, F., 2003. New frog family from India reveals an ancient biogeographical link with the Seychelles. Nature 425, 711–714. https://doi.org/10.1038/nature02019.

Böhme, M., 2003. The Miocene Climatic Optimum: evidence from ectothermic vertebrates of Central Europe. Palaeogeogr. Palaeoclimatol. Palaeoecol. 195, 389–401. https://doi.org/10.1016/S0031-0182(03)00367-5.

Bonan, G., 2008. Forests and climate change: forcing, feedbacks and the climate benefits of forests. Science 320, 1444–1449. https://doi.org/10.1126/science.1155121.

Bossuyt, F., Milinkovitch, M.C., 2001. Amphibians as indicators of Early Tertiary "out-of-India" dispersal of vertebrates. Science 292, 93–95. https://doi.org/10.1126/science.1058875.

Bouilhol, P., Jagoutz, O., Hanchar, J.M., Dudas, F.O., 2013. Dating the India-Eurasia collision through arc magmatic records. Earth Planet. Sci. Lett. 366, 163–175. https://doi.org/10.1016/j.epsl.2013.01.023.

Bruch, A., Uhl, D., Mosbrugger, V., 2007. Miocene climate in Europe — patterns and evolution: a first synthesis of NECLIME. Palaeogeogr. Palaeoclimatol. Palaeoecol. 253, 1–7. https://doi.org/10.1016/j.palaeo.2007.03.030.

Bruch, A., Utescher, V., Mosbrugger, N., 2011. Precipitation patterns in the Miocene of Central Europe and the development of continentality. Palaeogeogr. Palaeoclimatol. Palaeoecol. 304, 202–211. https://doi.org/10.1016/j.palaeo.2010.10.002.

Bureau of Geology, Mineral Resources of Fujian Province (BGMRFP), 1985. Regional Geology of Fujian Province. In: Beijing: Geology Publishing House, (in Chinese).

Castañeda-Posadas, C., Cevallos-Ferriz, S.R.S., 2007. *Swietenia* (Meliaceae) flower in Late Oligocene–Early Miocene amber from Simojovel de Allende, Chiapas, Mexico. Am. J. Bot. 94, 1821–1827. https://doi.org/10.3732/ajb.94.11.1821.

Chang, S., Zhang, H., Hemming, S.R., Mesko, G.T., Fang, Y., 2012. Chronological evidence for extension of the Jehol Biota into Southern China. Palaeogeogr. Palaeoclimatol. Palaeoecol. 344–345, 1–5. https://doi.org/10.1016/j.palaeo.2012.05.014.

Chang, S., Hemming, S.R., Gao, K., Zhou, C., 2014. $^{40}\mathrm{Ar}/^{39}\mathrm{Ar}$ age constraints on cretaceous fossil-bearing formations near the China-North Korea border. Palaeogeogr. Palaeoclimatol. Palaeoecol. 396, 93–98. https://doi.org/10.1016/j.palaeo.2014.01.004.

Conti, E., Eriksson, T., Schönenberger, J., Sytsma, K.J., Baum, D.A., 2002. Early Tertiary out-of-India dispersal of Crypteroniaceae: evidence from phylogeny and molecular dating. Evolution 56, 1931–1942. https://doi.org/10.1554/0014-3820(2002)056[1931:ETOOID]2.0.CO;2.

Corlett, R.T., 2007. What's so special about Asian tropical forests? Curr. Biol. 93, 1551–1557. http://www.jstor.org/stable/24099084.

Corlett, R.T., 2014. The Ecology of Tropical East Asia, 2nd edn. Oxford University Press

(291 pp.).

Couvreur, T.L.P., Forest, F., Baker, W.J., 2011. Origin and global diversification patterns of tropical rain forests: inferences from a complete genus-level phylogeny of palms. BMC Biol. 9, 44. https://doi.org/10.1186/1741-7007-9-44.

Davis, C.C., Webb, C.O., Wurdack, K.J., Jaramillo, C.A., Donoghue, M.J., 2005. Explosive radiation of malpighiales supports a mid-cretaceous origin of modern tropical rain forests. Am. Nat. 165, E36–E65. https://doi.org/10.1086/428296.

Dettmann, M.E., 1989. Antarctica: cretaceous cradle of austral temperate rainforests? Geol. Soc. Spec. Publ. 47, 89–105. https://doi.org/10.1144/GSL.SP.1989.047.01.08.

DiMichele, W.A., Falcon-Lang, H.J., Nelson, W.J., Elrick, S.D., Ames, P.A., 2007. Ecological gradients within a Pennsylvanian mire forest. Geology 35, 415–418. https://doi.org/10.1130/G23472A.1.

Dunne, E., Close, R., Button, D., Brocklehurst, N., Cashmore, D., Lloyd, G., Bulter, R., 2018. Diversity change during the rise of tetrapods and the impact of the "Carboniferous rainforest collapse". Proc. R. Soc. B Biol. Sci. 285 (1872). https://doi.org/10.1098/rspb.2017.2730.

Dutta, S., Tripathi, S.M., Mallick, M., Mathews, R.P., Greenwood, P.F., Rao, M.R., Summons, R.E., 2011. Eocene out-of-India dispersal of Asian dipterocarps. Rev. Palaeobot. Palynol. 166, 63–68. https://doi.org/10.1016/j.revpalbo.2011.05.002.

Falcon-Lang, H., Scott, A.C., 2000. Upland ecology of some Late Carboniferous cordaitalean trees from Nova Scotia and England. Palaeogeogr. Palaeoclimatol. Palaeoecol. 156, 225–242. https://doi.org/10.1016/S0031-0182(99)00142-X.

Flower, B.P., Kennett, J.P., 1994. The middle Miocene climatic transition-East Antarctic ice-sheet development deep-ocean circulation and global carbon cycling. Palaeogeogr. Palaeoclimatol. Palaeoecol. 108, 537–555. https://doi.org/10.1016/0031-0182(94)90251-8.

Ghazoul, J., 2011. The challenge of inferring palaeoclimates from extant plant distributions: an example from Dipterocarpus. Rev. Palaeobot. Palynol. 173, 80–81. https://doi.org/10.1016/j.revpalbo.2011.09.003.

Gower, D.J., Kupfer, A., Oommen, O.V., Himstedt, W., Nussbaum, R.A., Loader, S.P., Presswell, B., Müller, H., Krishna, S.B., Boistel, R., Wilkinson, M., 2002. A molecular phylogeny of ichthyophiid caecilians (Amphibia: Gymnophiona: Ichthyophiidae): out of India or out of South East Asia? Proc. R. Soc. Lond. B 269, 1563–1569. https://doi.org/10.1098/rspb.2002.2050.

Grentry, A., 1992. Tropical forest biodiversity: distributional patterns and their conservational significance. Oikos 63, 19–28. https://doi.org/10.2307/3545512.

Ho, K., Chen, J., Lo, C., Zhao, H., 2003. ^{40}Ar-^{39}Ar dating and geochemical characteristics of late Cenozoic basaltic rocks from the Zhejiang-Fujian region, SE China: eruption ages, magma evolution and petrogenesis. Chem. Geol. 197, 287–318. https://doi.org/10.1016/S0009-2541(02)00399-6.

Hu, X., Garzanti, E., Wang, J., Huang, W., An, W., Webb, A., 2017. The timing of India-Asia collision onset–facts, theories, controversies. Earth-Sci. Rev. 160, 264–299. https://doi.org/10.1016/j.earscirev.2016.07.014.

Iturralde-Vinent, M.A., MacPhee, R.D.E., 1996. Age and paleogeographical origin of Dominican Amber. Science 273, 1850–1852. https://doi.org/10.1126/science.273.5283.1850.

Jacques, F.M.B., Shi, G., Su, T., Zhou, Z., 2015. A tropical forest of the middle Miocene of Fujian (SE China) reveals Sino-Indian biogeographic affinities. Rev. Palaeobot. Palynol. 216, 76–91. https://doi.org/10.1016/j.revpalbo.2015.02.001.

Johnson, K.R., Ellis, B., 2002. A tropical rainforest in Colorado 1.4 million years after the Cretaceous-Tertiary boundary. Science 296, 2379–2383. https://doi.org/10.1126/science.1072102.

Khan, M.A., Ghosh, R., Bera, S., Spicer, R.A., Spicer, T.E.V., 2011. Floral diversity during Plio-Pleistocene Siwalik sedimentation (Kimin Formation) in Arunachal Pradesh, India, and its palaeoclimatic significance. Palaeobiodivers. Palaeoenviron. 91, 237–255. https://doi.org/10.1007/s12549-013-0127-7.

Kuiper, K.L., Deino, A., Hilgen, F.J., Krijgsman, W., Renne, P.R., Wijbrans, J.R., 2008. Synchronizing rock clocks of earth history. Science 320, 500–504. https://doi.org/10.1126/science.1154339.

LaRiviere, J., Ravelo, A., Crimmins, A., Dekens, P., Ford, H., Lyle, M., Wara, M., 2012. Late Miocene decoupling of oceanic warmth and atmospheric carbon dioxide forcing. Nature 486, 97–100. https://doi.org/10.1038/nature11200.

Lawton, J.H., Bignell, D.E., Bolton, B., Bloemers, G.F., Eggleton, P., Hammond, P.M., Hodda, M., Holt, R.D., Larsen, T.B., Mawdsley, N.A., Stork, N.E., Srivastava, D.S., Watt, A.D., 1998. Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. Nature 391, 72–76. https://doi.org/10.1038/34166.

Lee, J., Marti, K., Serveringhaus, J.P., Kawamura, K., Yoo, H., Lee, H., Kim, J., 2006. A redetermination of isotopic abundance of atmospheric Ar. Geochim. Cosmochim. Acta 70, 4507–4512. https://doi.org/10.1016/j.gca.2006.06.1563.

Lin, Y., Wong, W.O., Shi, G., Shen, S., Li, Z., 2015. Bilobate leaves of *Bauhinia* (Leguminosae, Caesalpinioideae, Cercideae) from the middle Miocene of Fujian Province, southeastern China and their biogeographic implications. BMC Evol. Biol. 15, 252. https://doi.org/10.1186/s12862-015-0540-9.

Macey, J.R., Wang, Y., Anajeva, N.B., Larson, A., Papenfuss, T.J., 1999. Vicariant patterns of fragmentation among gekkonid lizards of the genus *Teratoscincus* produced by the Indian collision: a molecular phylogenetic perspective and an area cladogram for Central Asia. Mol. Phylogenet. Evol. 12, 320–332. https://doi.org/10.1006/mpev.1999.0641.

Maguire, K.C., 2015. Dietary niche stability of equids across the mid-Miocene Climatic Optimum in Oregon, USA. Palaeogeogr. Palaeoclimatol. Palaeoecol. 426, 297–307. https://doi.org/10.1016/j.palaeo.2015.03.012.

Martínez-Delclòs, X., Briggs, D.E.G., Peñalver, E., 2004. Taphynomy of insects in carbonates and amber. Palaeogeogr. Palaeoclimatol. Palaeoecol. 203, 19–64. https://doi.org/10.1016/S0031-0182(03)00643-6.

Mehrotra, R.C., Liu, X.Q., Li, C.S., Wang, Y.F., Chauhan, M.S., 2005. Comparison of the Tertiary flora of southwest China and northeast India and its significance in the antiquity of the modern Himalayan flora. Rev. Palaeobot. Palynol. 135, 145–163. https://doi.org/10.1016/j.revpalbo.2005.03.004.

Mosbrugger, V., Utescher, T., Dilcher, D.L., 2005. Cenozoic continental climatic evolution of Central Europe. Proc. Natl. Acad. Sci. U. S. A. 102, 14964–14969. https://doi.org/10.1073/pnas.0505267102.

Murphy, W.J., Collier, G.E., 1997. A molecular phylogeny for aplocheiloid fishes (Atherinomorpha, Cyprinidontiformes): the role of vicariance and the origins of annualism. Mol. Biol. Evol. 14, 790–799. https://doi.org/10.1093/oxfordjournals.molbev.a025819.

Najman, Y., Appel, E., Boudagher-Fadel, M., Bown, P., Carter, A., Garzanti, E., Godin, L., Han, J.T., Liebke, U., Oliver, G., Parrish, R., Vezzoli, G., 2010. Timing of India-Asia collision: geological, biostratigraphic and palaeomagnetic constraints. J. Geophys. Res. Solid Earth 115, B12416. https://doi.org/10.1029/2010JB007673.

Neir, A.O., 1950. A redetermination of the relative abundance of the isotopes of carbon, nitrogen, oxygen, argon and postassium. Phys. Rev. 77, 789–793. https://doi.org/10.1103/PhysRev.77.789.

Noonan, B.P., Chippindale, P.T., 2006. Vicariant origin of Malagasy reptiles supports Late Cretaceous Antarctic land bridge. Am. Nat. 168, 730–741. https://doi.org/10.1086/509052.

Pimm, S.L., Joppa, L.N., 2015. How many plant species are there, where are they, and at what rate are they going extinct? Ann. Mo. Bot. Gard. 100, 170–176. https://doi.org/10.3417/2012018.

Prakash, U., Vaidyanathan, L., Tripathi, P.P., 1994. Plant remains from the Tipam sandstones of northeast India with remarks on the palaeoecology of the region during the Miocene. Palaeontogr. Abt. B 231, 113–146.

Prasad, V., Faroogui, A., Tripathi, S.K.M., Garg, R., Thakur, B., 2009. Evidence of late Palaeocene-early Eocene equatorial rain forest refugia in southern Western Ghats, India. J. Biosci. 34, 777. https://doi.org/10.1007/s12038-009-0062-y.

Rust, J., Singh, H., Rana, R.S., McCAnn, T., Singh, L., Anderson, K., Sarkar, N., Nascimbene, P.C., Stebner, F., Thomas, J.C., Kraemer, M.S., Williams, C.J., Engel, M.S., Sahni, A., Grimaldi, D., 2010. Biogeographic and evolutionary implications of a diverse paleobiota in amber from the early Eocene of India. Proc. Natl. Acad. Sci. U. S. A. 107, 18360–18365. https://doi.org/10.1073/pnas.1007407107.

Sahney, S., Benton, M.J., Falcon-Lang, H.J., 2010. Rainforest collapse triggered Carboniferous tetrapod diversification in Euramerica. Geology 38, 1079–1082. https://doi.org/10.1130/G31182.1.

Shevenell, A., Kennett, J., Lea, D., 2008. Middle Miocene ice sheet dynamics, deep-sea temperatures and carbon cycling: a Southern Ocean perspective. Geochem. Geophys. Geosyst. 9, Q02006. https://doi.org/10.1029/2007GC001736.

Shi, G., Li, H., 2010. A fossil fruit wing of Dipterocarpus from the middle Miocene of Fujian, China and its palaeoclimatic significance. Rev. Palaeobot. Palynol. 162, 599–606. https://doi.org/10.1016/j.revpalbo.2010.08.001.

Shi, G., Dutta, S., Paul, S., Wang, B., Jacques, F.M.B., 2014a. Terpenoid compositions and botanical origins of Late Cretaceous and Miocene amber from China. PLoS One 9, e111303. https://doi.org/10.1371/journal.pone.0111303.

Shi, G., Jacques, F.M.B., Li, H., 2014b. Winged fruits of Shorea (Dipterocarpaceae) from the Miocene of southeast China: evidence for the northward extension of dipterocarps during the Mid-Miocene Climatic Optimum. Rev. Palaeobot. Palynol. 200, 97–107. https://doi.org/10.1016/j.revpalbo.2013.09.003.

Shukla, A., Mehrotra, R.C., Guleria, J.S., 2013. Emergence and extinction of Dipterocarpaceae in western India with reference to climate change: fossil wood evidences. J. Earth Syst. Sci. 122, 1373–1386. https://doi.org/10.1007/s12040-013-0341-8.

Solórzano Kraemer, M.M., 2007. Systematic, palaeoecology and palaeobiogeography of the insect fauna from Mexican amber. Palaeontogr. Abt. A 282, 1–133. https://doi.org/10.1127/pala/282/2007/1.

Utescher, T., Bruch, A., Micheels, A., Mosbrugger, V., Popova, S., 2011. Cenozoic climate gradients in Eurasia? A palaeo-perspective on future climate change? Palaeogeogr. Palaeoclimatol. Palaeoecol. 304, 351–358. https://doi.org/10.1016/j.palaeo.2010.09.031.

Whitmore, T.C., 1998. An Introduction to Tropical Rain Forests. Clarendon Press, Oxford, UK (296 pp.).

Williams, S.E., Bolitho, E.E., Fox, S., 2003. Climate change in Australian tropical rainforests: an impending environmental catastrophe. Proc. R. Soc. B Biol. Sci. 270, 1527. https://doi.org/10.1098/rspb.2003.2464.

Wu, Z.Y., 1980. Vegetation of China. Science Press, Beijing (1375 pp.).

Yin, A., Harrison, T.M., 2000. Geologic evolution of the Himalayan-Tibetan Orogen. Ann. Rev. Earth Planet Sci. 28, 211–280. https://doi.org/10.1146/annurev.earth.28.1.211.

You, Y., Huber, M., Müller, R.D., Poulsen, C.J., Ribbe, B., 2009. Simulation of the Middle Miocene climate Optimum. Geophys. Res. Lett. 36, L04702. https://doi.org/10.1029/2008GL036571.

Zachos, J., Dickens, G., Zeebe, R., 2008. An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. Nature 451, 279–283. https://doi.org/10.1038/nature06588.

Zheng, Y., 1984. Marginipollis (Lecythidaceae) from the upper Tertiary Fotan group in southern Fujian. Acta Palaeontol. Sin. 23, 764–767 (in Chinese with English abstract).

Zheng, Y., 1987. Fossil pollen grains of Podocarpaceae from Upper Tertiary in Fujian. Acta Palaeontol. Sin. 26, 604–615 (in Chinese with English abstract).

Zheng, Y., Wang, W., 1994. Sequence of Miocene Fotan group in SE Fujian and its palynoassemblages. Acta Palaeontol. Sin. 33, 200–216 (in Chinese with English abstract).

Zhu, H., 2006. Forest vegetation of Xishuangbanna, south China. For. Stud. China 8, 1–58.

Zhu, H., 2013. Geographical elements of seed plants suggest the boundary of the tropical zone in China. Palaeogeogr. Palaeoclimatol. Palaeoecol. 386, 16–22. https://doi.org/10.1016/j.palaeo.2013.04.007.

Ziegler, A.M., Raymond, A.L., Gierlowski, T.C., Horrell, M.A., Rowley, D.B., Lottes, A.L., 1987. Coal, climate and terrestrial productivity: the present and early Cretaceous compared. Geol. Soc. Spec. Publ. 32, 25–49. https://doi.org/10.1144/GSL.SP.1987.032.01.04.