

Mid-Tertiary paleoenvironments in Thailand: pollen evidence

P. Sepulchre^{1,2}, D. Jolly^{*,†}, S. Ducrocq³, Y. Chaimanee⁴, J.-J. Jaeger³, and A. Raillard²

¹Laboratoire des Sciences du Climat et de l'Environnement/Institut Pierre Simon Laplace, UMR 8212 CEA/CNRS/UVSQ, Orme des Merisiers, bât. 709, 91191 Gif-sur-Yvette cedex, France

²Laboratory of Paleoenvironments, ISE-M, UMR 5554, Case 61, Université Montpellier II, 34095 Montpellier Cedex 05, France

³Institut International de Paléoprimatologie, Paléontologie Humaine: Evolution et Paléoenvironnements, UMR 6046 CNRS, Université de Poitiers, 40 avenue du Recteur Pineau, 86022 Poitiers, France

⁴Paleontology Section, Department of Mineral Resources, Rama VI Road, Bangkok 10400 Thailand

*formerly at: Laboratory of Paleoenvironments, ISE-M, UMR 5554, Case 61, Université Montpellier II, 34095 Montpellier Cedex 05, France

†deceased

Received: 9 January 2009 – Published in Clim. Past Discuss.: 27 February 2009

Revised: 9 June 2010 – Accepted: 8 July 2010 – Published: 23 July 2010

Abstract. Only few well-dated records document the evolution of Southeast Asian paleoenvironments during the Cenozoic. Here we analyse continental pollen assemblages from Late Oligocene and Miocene fossil sites of Thailand. In agreement with previous studies, palynoflora from the Oligocene suggests warm temperate forested habitats at 24–26 Ma, whereas Middle Miocene assemblages are made of thermophilous taxa. This change can be linked to the major climate reorganization that brought warmer and wetter conditions over Southeast Asia around 22 Ma. This study also provides the first submillennial records from the Middle Miocene of Thailand. Thirteen samples of lignite layers from the sivaladapid-bearing Mae Moh site, dated between 13.3 and 13.1 Ma, and six samples from the hominoid-bearing Chiang Muan deposit, dated between 12.4 and 12.2 Ma, document oscillations between tropical woodlands and grasslands in northern Thailand. These pollen records likely reflect climate variations linked to insolation variations. Late Miocene palynological assemblages from Khorat, northeastern Thailand, document fluvio-lacustrine paleoenvironments alternatively covered by thermophilous trees and grasslands. These records show that both sivaladapids and early hominoids from Thailand have evolved in tropical environments with high variability in the vegetation cover.

1 Introduction

Paleontological surveys in Miocene sites of Thailand have yielded several fossil primates. Two species of the hominoid genus *Khoratpithecus*, considered as a sister-group of the extant orang-utan, have been described: *Khoratpithecus chiangmuanensis* from the Middle Miocene (13.5–10 million-years, hereafter Ma) and *Khoratpithecus piriya* (Chaimanee et al., 2006), from the Late Miocene (9–7 Ma). These primate bearing sites are critical because they provide new insights on the Asian hominoid radiation and paleobiogeographical history, as well as the environmental conditions they lived in. Preliminary analyses of associated pollen assemblages suggested a mosaic of tropical freshwater swamps and a forest flora dominated by the genus *Syzygium*, reminiscent of the extant African habitat that characterizes the White Nile headwaters (Chaimanee et al., 2003).

During the Miocene, global cooling leads to an “icehouse world” (a world with glacial/interglacial cycles, as opposed to a greenhouse world). This period is marked by a “climatic optimum” occurring at 16.5–15 Ma (Zachos et al., 2008), followed by a decrease in temperatures between 15 and 9 Ma, contemporaneous with the establishment of the East Antarctic Ice sheet (Zachos et al., 2001a). Flora has recorded this climate change as shown by pollen data from the Middle and Late Miocene of the Siwaliks (Central Nepal). The uplift of the Himalayas and its possible link with monsoon intensification may have played a role in the replacement of



Correspondence to: P. Sepulchre
(pierre.sepulchre@lscce.ipsl.fr)

subtropical and temperate forests by grassland (Hoorn et al., 2000). Numerous palynological studies have been carried out by petroleum companies in this part of the world, but were not published until Morley (2000) made some of them available. In Thailand, previous studies have focused on Cenozoic basins, describing the general traits of palynoflora from Oligocene and Miocene sediments (Watanasak, 1988, 1990).

This paper has two aims. First we describe new palynological data from Cenozoic basins of Thailand that have yielded accurately dated mammal fossils. The analysis of Neogene palynofloras provides new constraints on paleoenvironments in which early hominoids evolved. Records from Mae Moh and Chiang Muan basins, northern Thailand, well dated by magnetostratigraphy, gives the opportunity to discuss sub-millional paleoenvironmental variations during the Miocene, contemporaneous with the evolution of sivaladapids and hominoids. Second, we discuss the plausible climate mechanisms that have induced vegetation changes in SE Asia during the Late Cenozoic through the use of an Oligocene record and by comparing previous studies with our data.

2 Regional environmental setting

2.1 Physiographic areas and climate

Ogawa et al. (1961) divided Thailand into four physiographic areas:

- 1) the North Western Highlands (Fig. 1) are a mountainous region and the southern extension of the Myanmar (Burma) Shan Highlands. Several parallel ridges extend southward and four important rivers run between the valleys within narrow alluvial plains. Rainfall has a strong seasonal cycle over the North Western Highlands. Maximum precipitation occurs between May and September, during the monsoon season, with rates ranging from 4.5 to 7 mm/day (New et al., 2002);
- 2) the Khorat Plateau forms the northeastern part of the country. Its northern and eastern sides drain to the Mae Kong River. The southern and western borders are marked by the presence of flattopped peaks (up to 1600 m a.s.l.). The seasonal rainfall cycle is very similar to that of the North Western Highlands, with a higher peak in September (9 mm/day) and a totally dry season between November and February (Fig. 1);
- 3) southward is the Central Plain which includes vast deltas and alluvial plains formed by the rivers coming from north and south. This region is regularly flooded during the rainy season;
- 4) the peninsular region, which extends from the Gulf of Thailand as a long belt, is characterized by mountains

stretching southward with an altitude up to 1800 m a.s.l. Rainfall distribution depends on topography that faces the dominant monsoon winds. Following the seasons, these winds are from the north-east (dry monsoon) or the south-west (wet monsoon). Northeastern winds bring less than 50 mm of rainfall to Thailand during January, while southwestern winds bring up to 400 mm of rainfall during July, depending on the location. The rainy season is longer here than in the northern parts of the country, and rainfall rates are higher throughout the year.

2.2 Regional vegetation

The question of vegetation classification in Thailand has been subject to many debates between botanists and ecologists for at least 40 years. In 1957, the Royal Forest Department of Thailand (Ogawa et al., 1961) recognized 6 main types of forest vegetation and only one type of grassland (savanna), whereas modern authors (Maxwell and Elliott, 2001) defined only three vegetation types, each of them subdivided into sub-types (Fig. 1). The North Western Highlands are covered essentially by “Mixed Deciduous Forest”, with Teak (*Tectona grandis*; very important for the local economy), as well as many other tropical deciduous trees such as the genera *Xylia*, *Dalbergia*, *Acacia*, *Nauclea*. By contrast, the Khorat Plateau is dominated by deciduous dipterocarp forests, although they have been strongly reduced due to human activities, as shown by the cropland cover (Fig. 1). Among the natural indigenous taxa, species such as *Shorea obtusa*, *Dipterocarpus tuberculatus*, and *Dipterocarpus obtusifolius* tend to form monospecific stands. The Peninsular and the Central Plain regions are covered by the so-called “Tropical Evergreen Forest”, including both needle-leaved and broadleaved.

2.3 Geological settings and stratigraphic control

The Cenozoic fossiliferous localities of Thailand discussed here (Table 1) are situated in three main areas:

- (1) Nong Ya Plong coal mine (13°9′ N, 99°40′ E) is located in Phetchaburi Province, 100 km south-west of Bangkok at the northern end of the peninsular region. Fossil mammals have been discovered in a black claystone bed situated under a 30-m lignite bed. This fauna suggests a Late Oligocene age, between 26 and 24 Ma (Marivaux et al., 2004, 2006). The pollen sample discussed here comes from the mammals layer.
- (2) Northern deposits: the basins of Mae Moh (18°19′ N, 99°41′ E) and Chiang Muan (18°56′ N, 100°14′ E) are located in the northwestern part of the country, in a rift zone that crosses Myanmar and Laos and ends in the Gulf of Thailand (Malaysian and Indonesian Rifts). This NW-SE system extends over more than 2000 km

Table 1. Age, lithology, and present-day environmental characteristics of the four sites studied.

	Nong Ya Plong	Mae Moh	Chiang Muan	Khorat
Age	26–24 Ma	13.3–13.1 Ma	12.4–12.2 Ma	9–6 Ma
Sediment type	Claystone/lignite	Lignite	Lignite	Clay lenses in sand
Present-day vegetation	Tropical Evergreen Forest	Mixed Deciduous Forest + Seasonal dry evergreen	Deciduous dipterocarps Forest /cropland	
Present-day climate	Dry during boreal winter, Wet during boreal summer (monsoonal). Max rainfall ranges from 7 to 9 mm/day.			

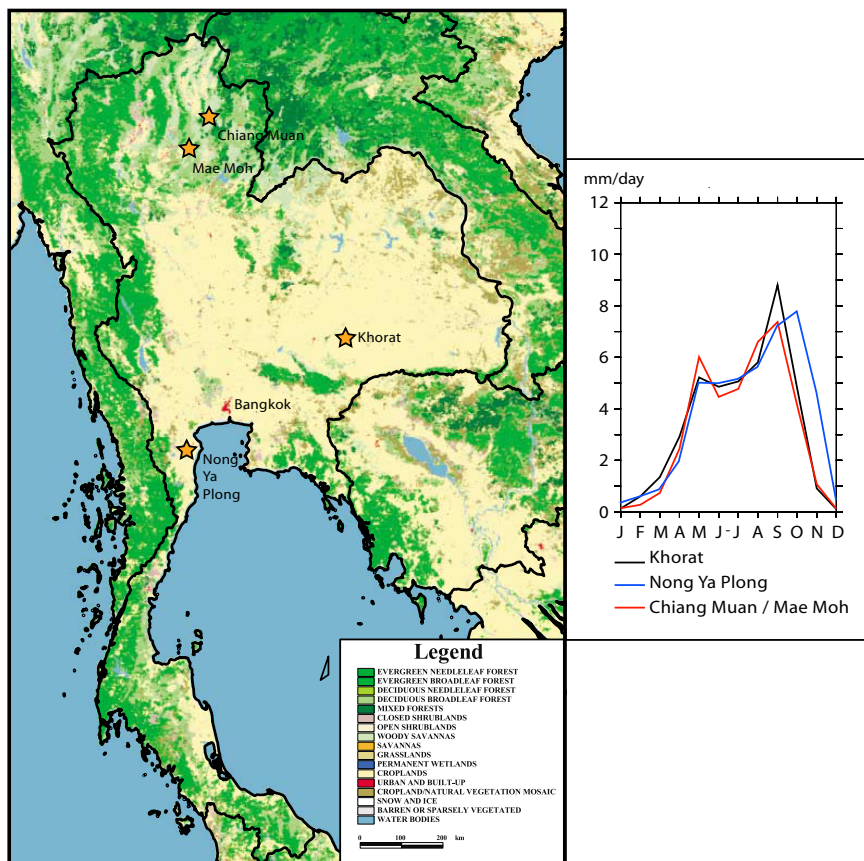


Fig. 1. Map of Thailand indicating the present-day land cover and vegetation types. Modified after Parnell et al. (2003). Plots indicate rainfall seasonal cycle for the three areas of interest. Data from the Climate Research Unit, averaged between 1961 and 1990 (New et al., 2002). Units are mm/day.

and is delimited by two faults zones: the Sagaing Fault Zone to the west and the Red River Fault Zone to the east (Morley, 2002). These faults result from the India-Asia collision. During the early Miocene, this tectonic extrusion mechanism was responsible for the creation of the basins depicted here. The Mae Moh and Chiang Muan Basins have a similar three-step sedimentation scheme. When they began to fill, the subsidence of the basins was weak and fluvial and fluviolacustrine sediments were deposited. Then subsidence started to

increase. Lignite and claystone sediments, originating from swamps or little lakes, were progressively laid in the basins. Finally, subsidence slowly decreased and the basins filled with fluvial sediments with a deltaic regime. The Mae Moh Basin (Lampang Province) contains the largest coal deposit in Thailand (16.5 km long and 9 km wide). The stratigraphy was divided into three formations (Corsiri and Crouch, 1985) (see also Morley et al., 2001): the Huai King Formation (fluvial and alluvial sandstones, up to 320 m thick), the

Na Khaem Formation (lignite interbedded with lacustrine claystones and mudstones, ca. 420 m thick), and the Huai Luang Formation (red-brown and grey claystones and mudstones, up to 400 m thick). Biostratigraphic studies suggested that the Mae Moh sequence extends from the Middle Miocene to the beginning of the Late Miocene (Ginsburg et al., 1988; Tassy et al., 1992; Ducrocq et al., 1994; Peigné et al., 2006). Magnetostratigraphy has provided more precise dating: the Na Khaem sequence has been correlated to the geomagnetic polarity time scale (GPTS), and situated between the C5ABn and C5An chrons, between 13.5 and 12.2 Ma (Bennami et al., 2002; Coster et al., 2010). Pollen samples from Mae Moh come from the Q lignite layers in which remains of a sivaladapid primate have been discovered (Chaimanee et al., 2008). These layers are correlated with the chron C5Aar dated from 13.3 to 13.1 Ma (Fig. 2).

Chiang Muan Basin (Ban Sa locality) is located northeast of Mae Moh Basin and is much smaller (1 km long and 300 m wide). Sediments from the Miocene consist of sandstones, mudstones and thin lignite beds. The lower, middle and upper lignite seams of Chiang Muan Basin yielded remains of the hominoid *Khoratpithecus chiangmuanensis* (Chaimanee et al., 2003; Kunitatsu et al., 2005). Associated large fossil mammals in the Ban Sa locality gave an age between 10.8 and 14 Ma. Paleomagnetic data of the Chiang Muan section revealed a reversed polarity zone between two normal events, indicating four possible estimated ages between 13.5 and 10 Ma (Benammi et al., 2004). A recent study have unravelled possible ages by using correlation of ash layers that are present simultaneously at Mae Moh and Chiang Muan sites (Coster et al., 2010). This correlation provided an age between 12.4 and 12.2 Ma for the Upper Lignite Member (including middle and upper lignite seams) that delivered pollen samples analysed here (Fig. 2).

(3) Northeastern deposits: Khorat (15°01' N, 102°16' E)

Samples were collected in a paleo-river deposit which was exploited as a sand quarry (Somsak sandpit). The stratigraphy of the sandpit is difficult to constrain, because of numerous crossovers between sediment layers. Chaimanee et al. (2006) have described two sand units for the Somsak sandpit. The upper sand unit consists of “*yellowish sand, silt and gravel with cross-bedding structures*” that indicate fluvial deposition. The lower sand unit “*consists of grey organic-rich sand and gravel, with some clay lenses intercalated. Intense cross-bedding indicates fluvial regime with intermittent swamp deposits*”. Five pollen samples analysed here come from the lower sand unit: three of them were collected from a sandy clay layer that yielded fossil mammal remains and two samples were obtained

from the overlying dark organic clays. The large mammal fauna of Somsak sandpit (*Alicornops complanatum*, *Brachypotherium perimense*, *Deinotherium indicum*) is reminiscent of those from the Dhok Pathan Formation in the Siwaliks (Pakistan, ca. 8 Ma) and from the Shansi Red Claystones (China, ca. 7 Ma), and suggests the pollen assemblage is Late Miocene in age (9–6.5 Ma).

3 Methods

3.1 Field and laboratory

The samples were collected by the ISEM paleoenvironment team at the four sites following the same technique, i.e. carefully scraping the beds in order to prevent present-day pollen contamination and immediately isolating the samples in sterile plastic bags. Our study includes 25 samples (see supplemental information). Mae Moh and Chiang Muan samples come from lignite deposits, whereas Nong Ya Plong and Khorat samples come from organic-rich claystones. The Chiang Muan site includes 4 samples partly published in (Chaimanee et al., 2003) and 2 unpublished samples. The samples were submitted to a four-step chemical treatment. First, caustic potash (KOH 10%) was used to remove humic acids and plant matter. The samples were filtered through a 180 µm mesh and centrifugated several times (Faegri et al., 1989). Then, the residues were treated with Hydrofluoric Acid (HF) to remove mineral elements. Finally, acetolysis was performed to get rid of possible remaining plant fragments, and a final centrifugation with glycerine water was carried out before mounting samples on microscope slides.

3.2 Pollen identification and countings

Pollen grains were observed under a light microscope at ×600 magnification. Pollen recovery was poor, ranging from 37 (Mae Moh) to 1195 (Chiang Muan) grains counted per sample, the average being ca. 416. Modern (Linnaean) family and genus names were used for the identified taxa (Germeraad et al., 1968). The fossil palynomorphs were directly compared to palynological references (Bonnefille and Rioulet, 1980; Huang, 1972). A published SE Asia Flora (Jensen, 2001) and the ISEM palynological reference collection (48 000 slides of angiosperms, 2400 gymnosperms, 2000 pteridophytes) were used as well to identify palynomorphs. The state of preservation of palynomorphs was very poor: 15% were so strongly corroded that it was impossible to describe them. The poor state of preservation of the pollen grains might be explained by oxidation during fossilization (Hoorn et al., 2000). *Indeterminable* grains (corroded, indescribable grains) were distinguished from *unidentified* (i.e. unknown) grains, which have been described but not referred to any taxon.

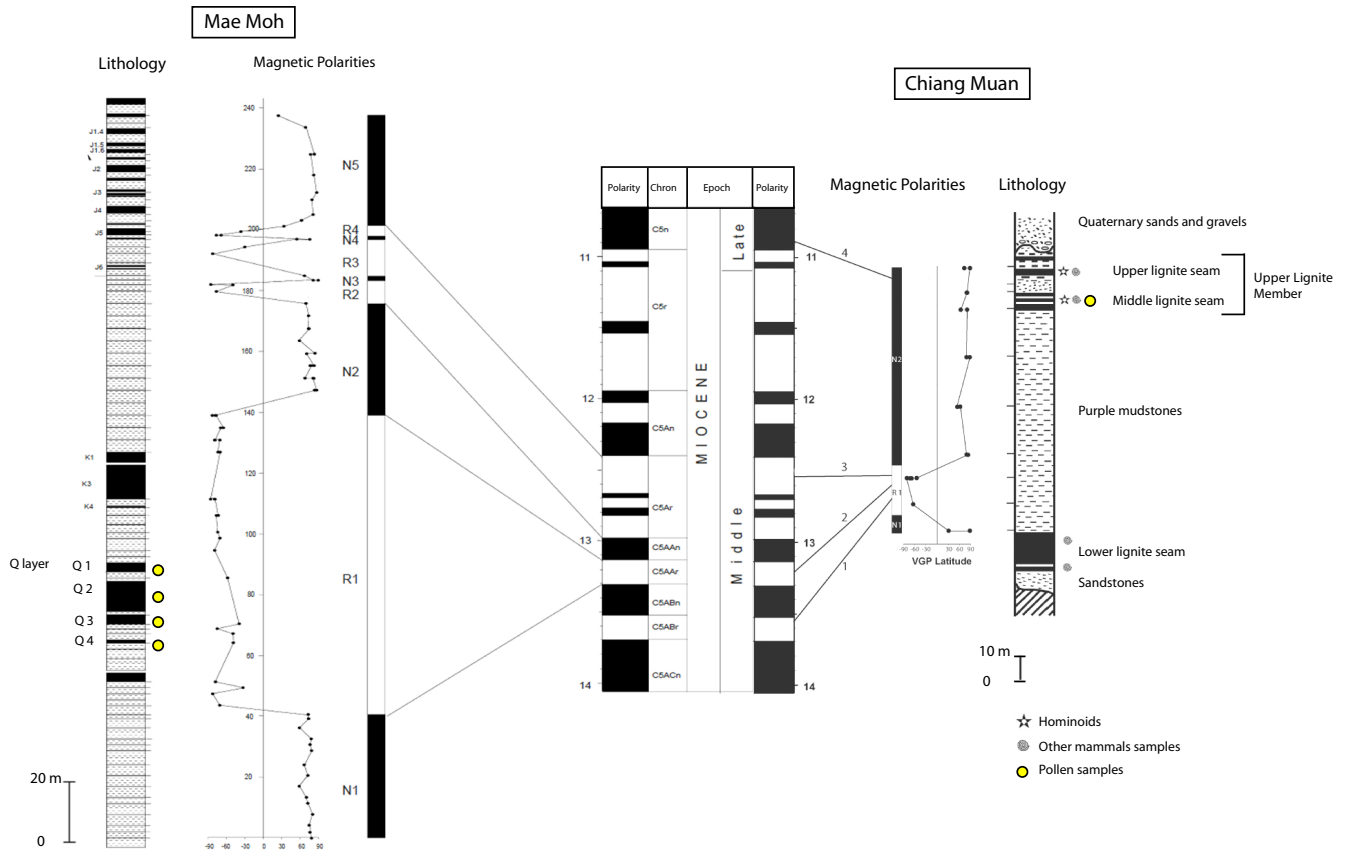


Fig. 2. Lithological information, magnetostratigraphy and stratigraphic control of Mae Moh and Chiang Muan pollen samples (after Bennami et al., 2002, 2004).

3.3 Construction of pollen diagrams

Taxa have been grouped according to their ecological affinities (Fig. 2). Groups were chosen using online databases (Watson and Dallwitz, 2006) and specialized literature on India (Blasco, 1971), East-Asia (Hooker, 1875), and Thailand (Ogawa et al., 1961; Kuchler and Sawyer, 1967; Maxwell and Elliott, 2001).

Cyperaceae are riparian wetland plants that very likely represent vegetation from the vicinity of the deposition site. Pteridophytes are usually considered local as well, extending from several meters to a few hundreds of meters around the deposition sites. This hypothesis is supported by the low position of gametophytes on most extant fern species, which prevents spores from being transported by wind. However, several authors consider that spores can be transported by water flooding (Maley and Brenac, 1998; Anshari et al., 2004). High percentages of spores could indicate a high volume of water invading the basin, and varying pteridophytes percentages can be interpreted as indicating a varying hydrology of the deposition zone (Maloney, 1999). Cyperaceae, pteridophytes and aquatic taxa are considered local vegetation, corresponding to the ferns and the aquatic plants living

in the vicinity of the deposition site. A diagram excluding this local signal and corroded pollen grains was constructed (Fig. 3). In the following section, the term “regional signal” refers to the sum of pollen grains excluding the local signal and corroded grains. Unknown pollen grains were not excluded from the pollen sum to avoid artificially high percentages of identified taxa.

4 Palynological results

4.1 Nong Ya Plong (1 sample)

A total of 313 pollen grains have been counted, but 31% were indeterminable. 13 taxa are present in the sample which is dominated by pteridophytes (monoete spores, 41% of total count). The regional signal is dominated by *Alnus* (37%) associated with *Pinus* (13%) and *Castanea* (3%). The association of *Alnus*, *Pinus* and *Castanea* denotes a mesothermic signal and makes the Nong Ya Plong record very distinct from the other sites analysed in this paper. The only extant species of *Alnus* in Thailand is *Alnus nepalensis*, a deciduous tree that grows in moist and cool areas (mean annual

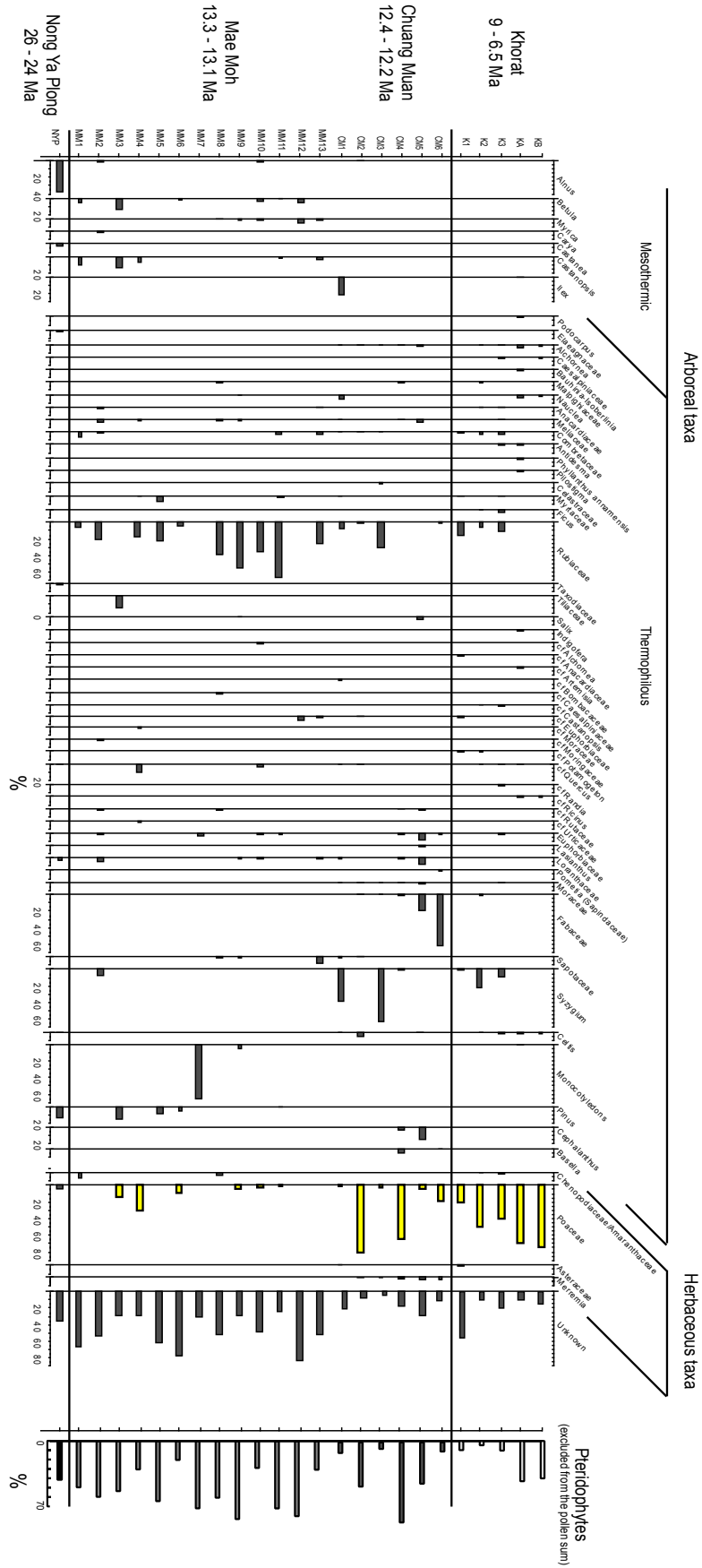


Fig. 3. Synthesis of the pollen record for the 4 sites discussed in the text. Taxa with percentages lower than 1% have been omitted for clarity. The local vegetation signal, including pteridophytes and Cyperaceae, has not been included in the total sum for the main diagram.

temperature range: 13–26 °C, annual rainfall from 500 to 2500 mm, with a dry season up to 6 months long) (Neil, 1990). The extant species *Pinus kesiya* is widespread in Thailand and can be mixed with temperate taxa such as *Quercus* or with Dipterocarpaceae, and is confined to a montane habitat (700–1650 m a.s.l.) (Werner, 1997). This species is also found in pure stands in monsoonal regions with a strong seasonal precipitation cycle and annual precipitation ranging from 1400 to 1600 mm. Furthermore our record contains pollen grains from Loranthaceae (3%) and Poaceae (5%). Extant Loranthaceae contains 700–950 species of usually hemi-parasitic plants, mostly found in tropical and subtropical regions (eFlorae, 2008). Poaceae could come from local monocotyledon aquatic vegetation but more likely indicate regional open woodlands, savanna or grasslands (Bonnefille et al., 2004). Their percentage in the Nong Ya Plong record is weak, suggesting arboreal-dominated environments. This interpretation is consistent with the associated fossil fauna that includes dermopterans (flying lemurs), whose extant species are dependent on forested habitats.

Only one sample from this site barely captures the paleoenvironmental signal of the basin, but previous palynological assemblages from the Oligocene of Thailand provide information to assess the relevance of our sample. Assemblages from the Upper Oligocene to Mid Miocene of Nong Ya Plong have yielded pollen grains such as *Alnipollenites verus* (*Alnus*-like), *Caryapollenites simplex* (*Carya*-like), *Faguspollenites* sp. (*Fagus*-like), which “have affinities with modern pollen of temperate regions” (Watanasak, 1990). Other pollen records from the Oligocene of northern Thailand (Li Basin) also suggest a warm temperate vegetation (Songtham et al., 2003, 2005). These data compare well with our sample and gives credits to the presence of a temperate vegetation between 26 and 24 Ma in Thailand.

4.2 Mae Moh (13 samples)

A total of 3342 grains were counted. The state of preservation was very poor since 31% were undeterminable. The percentage of unknown pollen grains is also very high, ranging from 9% to 86% of the total regional signal. High percentage of unidentified is problematic and will need to be assessed in future studies. However it is typical of Cenozoic palynoflora from SE Asia (e.g. see Songtham et al. (2005) where identified pollen grains represent no more than 30% of the total tropical assemblages). Pteridophytes are omnipresent (between ca. 20% and 80%). Once local signals are excluded, the Rubiaceae spectrum mostly dominates (up to 66%), although this group is not represented in all levels. Even if they are distributed over several bioclimatic conditions, extant Rubiaceae are mainly found in the lower montane forests of north-western Thailand (*Psychotria*, *Lasianthus*, *Nauclea*, *Mycetia*, *Tarenna*), associated with mesothermic taxa like *Castanopsis* and *Cryptocarya* (Kanzaki et al., 2004). Mesothermic elements are present

in 10 out of the 13 levels analysed. Their percentage is rather low, except for one particular level (MM3) in which *Castanopsis*, *Betula*, *Pinus* and Tiliaceae are the only arboreal taxa observed. Thermophilous trees are very rare or absent. *Syzygium* is absent except in one level (8%). These diagrams might represent a midaltitude forest including tropical taxa.

4.3 Chiang Muan (6 samples)

A total of 4877 pollen grains (360 grains in the smallest sample and 1195 in the largest one) have been counted. The pollen spectra are characterized by relatively high taxonomic diversity (between 12 and 24 taxa) suggesting a better pollen preservation (confirmed by less than 6% of indeterminable pollen grains). The low percentage of unidentified pollen (<30%) leads us to consider that these spectra are a significant representation of the vegetation of the Ban Sa Basin. Chiang Muan pollen count is very heterogeneous. The local swamp flora (pteridophytes, Cyperaceae) ranges between 10 and 85%. Once this local signal is excluded, Chiang Muan records can be classified into three types. CM1 and CM3 are dominated by *Syzygium* and Rubiaceae, with small percentages of Poaceae (1 and 3%, respectively). CM2 and CM4 are dominated by Poaceae (81 and 65%, respectively) and clearly suggest regional environments dominated by grasslands including some thermophilous trees (*Alchornea*) and dryland taxa (Combretaceae, *Celtis*).

CM5 and CM6 spectra are also characterized by the presence of Poaceae (4 and 19%, respectively), here associated with Fabaceae (19 and 61%, respectively) and *Merremia* (3 and 4%, respectively). CM5 is distinct with the presence of *Cephalanthus*. Extant *Cephalanthus* correspond to small trees or shrubs, while extant *Merremia* are mostly herbs and shrubs. The Chiang Muan water pond might have been colonized several times by *Syzygium*. The main extant species of this genus in Africa are known to colonize borders of rivers in quasi-monospecific populations (Letouzey, 1968). However, *Syzygium*, with eighty-four known species, is today the most diversified genus of Myrtaceae in Thailand (Parnell et al., 2003), and it occurs in a wide range of types of vegetation, from dry evergreen to deciduous Dipterocarps forest (Sookchaloem, 2004).

4.4 Khorat (5 samples)

A total of 1881 pollen grains were counted, among which 11% were indeterminable. Four levels contained well-preserved material (93.2%) but the level K1 had 33% corroded pollen grains. The pteridophytes signal is variable (between 4 and 43%). Extra-local counts are clearly dominated by Poaceae (ranging from 20 to 74%), clearly suggesting widespread grasslands at the regional scale. Thermophilous (*Syzygium*, *Alchornea*) and dryland elements (*Celtis*, Combretaceae) complete the record. Differences in the pollen counts allow two groups to be distinguished: KA and KB

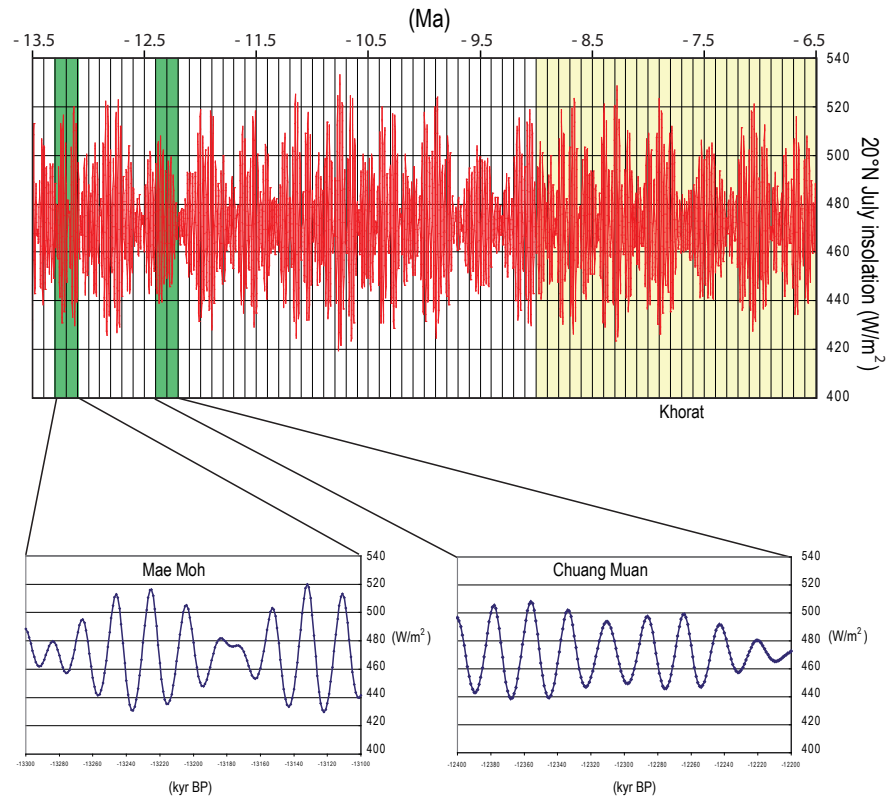


Fig. 4. Northern Hemisphere summer insolation computed at 20° N, between 13.5 and 6.5 Ma, from La2004 numerical solutions (Laskar et al., 2004). Bottom panel indicates values over the Mae Moh and Chiang Muan record timespans. Color-bars indicate estimated time range of the Miocene records.

samples are very similar in composition, being dominated by Poaceae with a weak signal corresponding to thermophilous trees. These levels are also characterized by the presence of aquatic taxa, especially Cyperaceae. Levels K1, K2, and K3 contain very few spores but high percentages of Rubiaceae associated with Poaceae. *Syzygium* is also present, ranging from 1 to 22%. Although former studies (Watanasak, 1989) have described the presence of Dipterocarpaceae in Thailand since the early Miocene, no palynomorphs corresponding to this family have been found in our samples. This may be linked to the entomophilous pollination strategy of this family, as well as the poor preservation of this kind of pollen grain.

Vegetation variability, as well as the distinction of two groups of clays, depicts a differential sedimentation linked to changes in river bed position through time. When the river ran over the deposition area, sandy clays were deposited. During drier periods, sedimentation was slower, and organic matter accumulated in several ponds to produce black clays. The surroundings were colonized by heliophilous and aquatic plants such as pteridophytes, Poaceae and Cyperaceae. The presence of *Syzygium* may be related to the existence of a gallery forest dominated by this genus and including other tropical taxa such as *Alchornea*, *Nauclea*,

Caesalpinaceae, Combretaceae and Malpighiaceae. These changes in hydrology and vegetation cover were likely linked to rainfall variability and suggest climatic variability during the Middle to the Late Miocene.

5 Discussion

5.1 Climatic and environmental changes between the Oligocene and the Miocene

The pollen record discussed in this paper shows a clear difference between Oligocene mesothermic elements (*Alnus*, *Castanea*) and Miocene thermophilous elements. The Oligocene record presented here is well constrained in time (between 26 and 24 Ma) but lacks supplemental samples to definitely state that regional vegetation is represented. However it compares well with previous studies depicting warm temperate paleoenvironments in Thailand between the Late Oligocene and early Miocene (Songtham et al., 2003, 2005). Further information come from leaf fossils of the genus *Mangifera* (Anacardiaceae) recorded in Late Oligocene-early Miocene sandstones and claystones of the Li basin (Sawangchote et al., 2009). Together with palynological data, these remains suggest various mixed forested environments. A review of

Cenozoic pollen records from the Sunda region also shows that the Oligocene is considered to be cooler and drier than the mid-Miocene in SE Asia (Morley, 1998). A major climatic change occurring through the early Miocene was invoked to explain the great northward extension of rain forests. This Oligocene-Miocene climatic transition is also documented in loess sequences, fossil leaves and pollen records from China that show that the transition from a mainly zonal to a monsoon climate system occurred in the latest Oligocene in East Asia (Sun and Wang, 2005; Wang et al., 2005; Guo et al., 2008). The difference between Oligocene and Miocene pollen assemblages very likely documents these large-scale changes in temperature and rainfall, but mechanisms to explain such a transition are still debated. A shift in the position of SE Asia to lower latitudes during the Oligo-Miocene interval was evoked (Songtham et al., 2003), but the latitudinal extent of Thailand displacement is not very well constrained (Briais et al., 1993; Hall, 2002) and its consequences on large-scale rainfall and temperatures remain to be quantified. Climatic changes in SE Asia between 25 and 10 Ma were related to the Tibetan Plateau uplift, as well as the Paratethys sea shrinkage (Ramstein et al., 1997). Latest modelling studies showed that the uplift of the Tibetan Plateau progressively increased the amount of precipitation in East Asia and that the Paratethys retreat intensified the summer monsoon (Zhongshi et al., 2007). These two tectonics factors could explain the environmental transition observed in the palynological record between the Oligocene and the Miocene, although the timing of the Tibetan Plateau uplift is still debated (Rowley and Currie, 2006). Further modelling experiments are still needed to focus on SE Asia and to bring quantifications of climate change in this region at the Oligo-Miocene transition. Zachos et al. (2001b) also documented a major glaciation event at 23 Ma, likely linked to a rare orbital configuration allowing lower seasonality in temperatures and subsequent ice-sheet expansion in Antarctica. This global signal might have an impact on climate in the tropics, and should be considered in future studies.

5.2 Paleoenvironmental and climatic variability during the Miocene

Magnetostratigraphy provides accurate chronology for Mae Moh and Chiang Muan deposits (documenting 200 000-year interval, between 13.3 and 13.1 Ma for Mae Moh, between 12.4 and 12.2 Ma for Chiang Muan). These rather short intervals allow considering these two pollen records as a sub-millional picture of variability of SE Asian environments during the Middle Miocene.

Mae Moh diagram depicts a background of mesothermic elements that are absent from Chiang Muan and Khorat records. This record is also characterized by the abundance of Rubiaceae and arboreal taxa, as well as weak percentages of *Syzygium* and Poaceae, while Chiang Muan and Khorat show the opposite for these three taxa (Fig. 3). Mae

Moh signal represents a forested environment with a mixed vegetation including deciduous, evergreen and needle-leaved trees. The persistence of pteridophytes indicates wet conditions, whereas mesothermic elements very likely correspond to a regional mid-altitude forest signal. Although the high percentage of unknown and corroded pollen grains causes problems in fully describing these paleoenvironments, the SE Asian paleoclimatic context gives some clues. As stated earlier, the Middle Miocene is a period of warm and moist climate conditions over a large part of SE Asia, during which extension of rain forests is well documented (Morley, 1998). Mae Moh record very likely depicts a warm tropical forest, similar to paleoenvironments described in the adjacent Sunda region, but surrounded by a mid-altitude deciduous forest. The variability of the Mae Moh record, with a level dominated by monocotyledons (likely *Palmae*) and two levels dominated by Poaceae associated with mesothermic elements (*Castanopsis*, *Betula*), shows that vegetation cover and climate were far from stable between 13.3 and 13.1 Ma. Within these 200 000 years, insolation variations driven by orbital cycles are the main climate forcing factors. By changing temperature seasonal cycles, as well as land-ocean thermal contrasts, insolation variations have a huge impact on atmospheric dynamics (latitudinal position of trade winds and Intertropical Convergence Zone -ITCZ), and monsoon geographic extent. Insolation quantities can be computed for the Neogene by using numerical solutions (Laskar et al., 2004). Following the orbital cycles, summer insolation at 20° N has a strong variability, ranging from ca. 425 to ca. 535 W/m² over the 13.5–6.5 Ma interval (Fig. 3). Within each 200 000-year interval of Mae Moh and Chiang Muan records, insolation amplitudes are either comparable or larger than the ones computed for the Pleistocene-Holocene interval, a period during which large changes in SE Asian monsoon activity have been recorded (White et al., 2004). Such variations induce strong changes in rainfall patterns over Thailand and very likely explain the variability depicted in Mae Moh and Chiang Muan pollen assemblages.

The dominance of Poaceae in some levels of Chiang Muan record could be interpreted as a trend towards expansion of grasslands, but this analysis is still hypothetical, as this signal does not concern every level of Chiang Muan, and no climatic mechanism for aridification at 12.4–12.2 Ma has been evidenced so far. Chaimanee et al. (2003) have suggested that the presence of *Syzygium* during the Miocene might indicate a connection with floras from eastern Africa. Songtham et al. (2004) challenged this hypothesis, arguing that *Syzygium* originated from SE Asia or Oceania. Sytsma et al. (2004) and Wilson et al. (2005) suggested that *Syzygium* belonged to a clade clearly separated from other Myrtaceae, but the question of the timing of African colonization and possible Miocene connections with Asia remains unresolved. *Syzygium*-like pollen grains have been found recently in the Turkana basin (Kenya, eastern Africa) and dated from about 25 Ma (Vincens et al., 2006), suggesting that this genus

was present earlier in East Africa, giving more credit to the hypothesis proposed by Chaimanee et al. (2003). Records described here provide evidence of expansion and decline of *Syzygium* in the Miocene flora of Thailand, and these new data should be considered in future discussions. The existence of a paleoenvironmental corridor between SE Asia and eastern Africa during the Middle Miocene is still a matter of debate and will have to be tested with climate and vegetation models in the future. In this respect, gathering new data concerning paleogeography and long-term evolution of vegetation is pivotal, as modelling studies have shown that tectonics trigger atmospheric dynamics and aridification episodes in the tropics (Sepulchre et al., 2006).

The repeated occurrences of Poaceae-dominated levels at Khorat mark a clear difference between environments of Middle and Late Miocene, with a transition from woodlands to grassland-dominated landscapes. These results can be related to a long-term climatic change that occurred between 8.5 and 6 Ma that led to a major environmental change with C4 savannas replacing C3 forests and woodlands (Cerling et al., 1994). Stable isotopes measurements made on mammalian faunas from the Miocene confirmed that this change occurred at South Asian continental scales (Badgley et al., 2008). Our record cannot decipher C₃ and C₄ vegetations, but clearly stands for an opening of landscapes during the late Miocene.

6 Conclusions

SE Asian paleoenvironments varied drastically during the late Cenozoic. Differences between Oligocene and Miocene palynofloras suggest that the climate reorganisation that led to warmer and wetter conditions in China and Sunda also impacted SE Asia.

Data presented in this paper suggest that vegetation variability occurred at different timescales within the Miocene. Although the timing of this variability needs further investigation, pollen assemblages show that climate was far from stable during the Middle to Late Miocene in Thailand. The Mae Moh record depicts 200 000 years of vegetation dynamics between 13.3 and 13.1 Ma, with basin hydrology variations very likely driven by changes in insolation. This variability is also documented in Chiang Muan records that show oscillations between tropical woodlands and grasslands. These grasslands are widespread in the Khorat record (although associated with a local arboreal flora), thereby documenting the climate trend towards development of savannas in SE Asia. The potential consequences of this paleoenvironmental variability on primates and mammals evolution will have to be accounted for and quantified in future studies. As far as the Oligo-Miocene transition is concerned, it appears that both tectonics and orbital forcing have interplayed to change the Asian climate drastically. However, we still need to unravel and quantify through time the respective

roles of Tibetan uplift, Paratethys shrinkage, and orbital forcing (as well as the interactions between these three forcing factors) on climate and paleoenvironments. The challenge is similar concerning the Middle and Late Miocene climate variability, as mechanisms driving the transitions from woodlands to grasslands in Asia are still unexplained. Modelling studies have demonstrated that aridification episodes, previously thought to be due to global climate changes, could be related to rapid mountain building that influence atmospheric dynamics, moisture transport and rainfall patterns (Hay et al., 2002; Liu and Yin, 2002; Sepulchre et al., 2006). More research is needed to reconstruct the evolution of Tibetan Plateau paleoaltitude through time and to quantify its impact during the Miocene. Obtaining more data concerning paleogeography and environmental evolution during the Late Cenozoic is crucial. It will help constraining future modelling studies, documenting the environmental context in which mammals have evolved, and understanding the interactions between tectonics, climate and biosphere during the last 25 Ma.

Supplementary material related to this article is available online at:

<http://www.clim-past.net/6/461/2010/cp-6-461-2010-supplement.zip>

Acknowledgements. Professor Dominique Jolly actively participated in the fieldwork and the shaping of this manuscript. This paper is dedicated to his memory.

Authors are very grateful to Danielle Duzer for her valuable help in preparing the samples, counting and identifying pollen grains. We also thank Raymonde Bonnefille for giving comments on the manuscript. This work has been supported by the Department of Mineral Resources, Bangkok, C.N.R.S.-T.R.F. (Cenozoic Biodiversity Program), C.N.R.S. Eclipse II Program, and the University of Poitiers. We thank EGAT (Electricity Generating Authority of Thailand) for providing scientific assistance, cored samples information and access to the mine and Mana Rugbumrung for fieldwork assistance. We are also very grateful to Jean-Pierre Cazet for his help in processing the pollen diagrams.

Edited by: D.-D. Rousseau



The publication of this article is financed by CNRS-INSU.

References

- Anshari, G., Kershaw, P., Van Der Kaars, S., and Jacobsen, G.: Environmental change and peatland forest dynamics in the Lake Sentarum area, West Kalimantan, Indonesia, *J. Quaternary Sci.*, 19, 637–655, 2004.
- Badgley, C., Barry, J., Morgan, M., Nelson, S., Behrensmeyer, A., Cerling, T., and Pilbeam, D.: Ecological changes in Miocene mammalian record show impact of prolonged climatic forcing, *P. Natl. Acad. Sci. USA*, 105, 12145–12149, 2008.
- Benammi, M., Chaimanee, Y., Urrutia-Fucugauchi, J., and Jaeger, J. J.: Magnetostratigraphic Study of the Continental Sedimentary Sequence of the Chiang Muan Basin, Northern Thailand: Implications for the Age of the First Miocene Hominoids from Thailand, *Int. Geol. Rev.*, 46, 646–654, 2004.
- Bennami, M., Urrutia-Fucugauchi, J., Alva-Valdivia, L. M., Chaimanee, Y., Triamwichanon, S., and Jaeger, J.-J.: Magnetostratigraphy of the Middle Miocene continental sedimentary sequences of the Mae Moh Basin in northern Thailand: evidence for counterclockwise block rotation, *Earth. Planet. Sci. Lett.*, 204, 373–383, 2002.
- Blasco, F.: Montagnes du sud de l'Inde: Forêts, savanes, écologie, in: *Travaux de la Section Scientifique et Technique, Institut Français de Pondichéry, Pondicherry*, 349–389, 1971.
- Bonnefille, R. and Riollet, G.: *Pollens des savanes d'Afrique orientale*, Editions du Centre National de la Recherche Scientifique, Paris, 256 pp., 1980.
- Bonnefille, R., Potts, R., Chalief, F., Jolly, D., and Peyron O.: High-resolution vegetation and climate change associated with Pliocene *Australopithecus afarensis*, *P. Natl. Acad. Sci. USA*, 101, 12125–12129, 2004.
- Briais, A., Patriat, P., and Tapponnier, P.: Updated interpretation of magnetic anomalies and seafloor spreading stages in the South China Sea- Implications for the Tertiary tectonics of Southeast Asia, *J. Geophys. Res. Solid Earth*, 98, 6299–6328, 1993.
- Cerling, T. E., Quade, J., and Wang, Y.: Expansion and Emergence of C4 Plants, *Nature*, 371, 112–112, 1994.
- Chaimanee, Y., Jolly, D., Bennami, M., Tafforeau, P., Duzer, D., Moussa, I., and Jaeger, J. J.: A Middle Miocene hominoid from Thailand and orangutan origins, *Nature*, 422, 61–65, 2003.
- Chaimanee, Y., Yamee, C., Tian, P., Khaowiset, K., Marandat, B., Tafforeau, P., Nemoz, C., and Jaeger, J. J.: *Khoratpithecus piriya*, a Late Miocene hominoid of Thailand, *Amer. J. Phys. Anthropol.*, 131, 311–323, 2006.
- Chaimanee, Y., Yamee, C., Tian, P., Chavasseau, O., and Jaeger, J. J.: First middle Miocene sivaladapid primate from Thailand, *J. Hum. Evol.*, 54, 434–443, 2008.
- Corsiri, R. and Crouch, A.: Mae Moh coal deposit: Electricity Generating Authority of Thailand, Report of Thailand Australia Lignite Mine Development Project, 1, 448, 1985.
- Coster, P., Benammi, M., Chaimanee, Y., Yamee, C., Chavasseau, O., Emonet, E., and Jaeger, J.: A complete magnetic-polarity stratigraphy of the Miocene continental deposits of Mae Moh Basin, northern Thailand, and a reassessment of the age of hominoid-bearing localities in northern Thailand, *Geol. Soc. Am. Bull.*, 122, 1180–1191, 2010.
- Ducrocq, S., Chaimanee, Y., Suteethorn, V., and Jaeger, J. J.: Ages and paleoenvironment of Miocene mammalian faunas from Thailand, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 108, 149–163, 1994.
- eFloras: Flora of China, Missouri Botanical Garden, St. Louis, MO & Harvard University Herbaria, Cambridge, MA, available online at: <http://www.efloras.org> (last access: May 2009), 2008.
- Fægri, K., Iversen, J., Kaland, P. E., and Krzywinski, K.: *Textbook of Pollen Analysis*, IV ed., John Wiley and Sons Ltd., Chichester, England, 328 pp., 1989.
- Germeraad, J. H., Hopping, A., and Muller, J.: Palynology of tertiary sediments from tropical areas, *Rev. Palaeobot. Palynol.*, 6, 189–348, 1968.
- Ginsburg, L., Mein, P., and Thomas, H.: The Miocene of Thailand: Recent contribution to vertebrate paleontology and stratigraphy, The paleoenvironment of East Asia from the mid-Tertiary: Hong-Kong, University of Hong Kong, Centre of Asian Studies, Occasional Papers and Monographs, 77, 897–907, 1988.
- Guo, Z. T., Sun, B., Zhang, Z. S., Peng, S. Z., Xiao, G. Q., Ge, J. Y., Hao, Q. Z., Qiao, Y. S., Liang, M. Y., Liu, J. F., Yin, Q. Z., and Wei, J. J.: A major reorganization of Asian climate by the early Miocene, *Clim. Past*, 4, 153–174, doi:10.5194/cp-4-153-2008, 2008.
- Hall, R.: Cenozoic geological and plate tectonic evolution of SE Asia and the SW Pacific: computer-based reconstructions, model and animations, *J. Asian. Earth. Sci.*, 20, 353–431, 2002.
- Hay, W. W., Soeding, E., DeConto, R. M., and Wold, C. N.: The Late Cenozoic uplift - climate change paradox, *Int. J. Earth. Sci.*, 91, 746–774, 2002.
- Hooker, J. D.: *The Flora of British India*, L. Reeve & Co Ltd, Covent Garden, 1875.
- Hoorn, C., Ohja, T., and Quade, J.: Palynological evidence for vegetation development and climatic change in the Sub-Himalayan Zone (Neogene, Central Nepal), *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 163, 133–161, 2000.
- Huang, T.-C.: *Pollen Flora of Taiwan*, edited by: Press, N. T. U. B. D., Ching-Hwa Press co., Ltd., 297 pp., 1972.
- Jensen, M.: *Trees and Fruits of Southeast Asia*, 2 ed., Orchid Guides, Orchid Press, Bangkok, 234 pp., 2001.
- Kanzaki, M., Hara, M., Yamakura, T., Ohkubo, M., Tamura, M., Sri-Ngernyuang, K., Sahunalu, P., Teejuntuk, T., and Bunyavejchewin, S.: Doi Inthanon Forest Dynamics Plot, Thailand, Tropical Forest Diversity and Dynamism: Findings from a Large-Scale Network Forest Dynamics Plots (Ed. EC Losos, and EG Leigh), The University of Chicago Press, Chicago, Illinois, USA, 474–481, 2004.
- Kuchler, A. W. and Sawyer, J. O.: A study of the vegetation near Chiang Mai, Thailand, *Trans. Kansas Acad. Sci.*, 70, 281–347, 1967.
- Kunimatsu, Y., Ratanasthien, B., Nakaya, H., Saegusa, H., and Nagaoka, S.: Hominoid fossils discovered from Chiang Muan, northern Thailand: The first step towards understanding hominoid evolution in Neogene Southeast Asia, *Anthropol. Sci.*, 113, 85–93, 2005.
- Laskar, J., Robutel, P., Joutel, F., Gastineau, M., Correia, A. C. M., and Levrard, B.: A long-term numerical solution for the insolation quantities of the Earth, *Astron. Astrophys.*, 428, 261–285, 2004.
- Letouzey, R.: *Etude phytogéographique du Cameroun*, Lechevalier Paris, 1968.
- Liu, X. and Yin, Z. Y.: Sensitivity of East Asian monsoon climate to the uplift of the Tibetan Plateau, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 183, 223–245, 2002.

- Maley, J. and Brenac, P.: Vegetation dynamics, palaeoenvironments and climatic changes in the forests of western Cameroon during the last 28 000 years BP, *Rev. Palaeobot. Palynol.*, 99, 157–187, 1998.
- Maloney, B.: A 10 600 year pollen record from Nong Thale Song Hong, Trang Province, south Thailand, *Bulletin of the Indo-Pacific Prehistory Association*, 18, 129–137, 1999.
- Marivaux, L., Chaimanee, Y., Yamee, C., Srisuk, P., and Jaeger, J. J.: Discovery of *Fallomus ladakhensis* Nanda & Sahni, 1998 (Mammalia, Rodentia, Diatomyidae) in the lignites of Nong Ya Plong (Phetchaburi Province, Thailand): systematic, biochronological and paleoenvironmental implications, *Geodiversitas*, 26, 493–507, 2004.
- Marivaux, L., Bocat, L., Chaimanee, Y., Jaeger, J. J., Marandat, B., Srisuk, P., Tafforeau, P., Yamee, C., and Welcomme, J. L.: Cynocephalid dermopterans from the Palaeogene of South Asia (Thailand, Myanmar and Pakistan): systematic, evolutionary and palaeobiogeographic implications, *Zool. Scr.*, 35, 395–420, 2006.
- Maxwell, J. F. and Elliott, S.: Vegetation and Vascular Flora of Doi Sutep-Pui National Park, Northern Thailand, *Thai. Stud. Biodivers.*, 5, 45–46, 2001.
- Morley, C. K., Woganan, N., Sankumarn, N., Hoon, T. B., Alief, A., and Simmons, M.: Late Oligocene–Recent stress evolution in rift basins of northern and central Thailand: implications for escape tectonics, *Tectonophysics*, 334, 115–150, 2001.
- Morley, C. K.: A tectonic model for the tertiary evolution of strike-slip faults and rift basins in SE Asia, *Tectonophysics*, 347, 189–215, 2002.
- Morley, R.: Palynological evidence for Tertiary plant dispersals in the SE Asian region in relation to plate tectonics and climate, in: *Biogeography and geological evolution of SE Asia*, edited by: Halloway, R. H. J. D., Backhuys, Leiden, 211–234, 1998.
- Morley, R. J.: *Origin and Evolution of Tropical Rain Forests*, John Wiley and Sons Ltd., Chichester, England, 362 pp., 2000.
- Neil, P. E.: *Alnus nepalensis* – a multipurpose tree for the tropical highlands, in: *Nepal-United Kingdom Forestry Research Project - NFT Highlights*, Department of Forestry and Plant Research, Kathmandu, Nepal, 1990.
- New, M., Lister, D., Hulme, M., and Makin, I.: A high-resolution data set of surface climate over global land areas, *Clim. Res.*, 21, 1–25, 2002.
- Ogawa, H., Yoda, K., and Kira, T.: A preliminary survey on the vegetation of Thailand, *Nature and Life in Southeast Asia*, 1, 21–157, 1961.
- Parnell, J. A. N., Simpson, D. A., Moat, J., Kirkup, D. W., Chantaranonthai, P., Boyce, P. C., Bygrave, P., Dransfield, S., Jebb, M. H. P., and Macklin, J.: Plant collecting spread and densities: their potential impact on biogeographical studies in Thailand, *J. Biogeogr.*, 30, 193–209, 2003.
- Peigné, S., Chaimanee, Y., Yamee, C., Tian, P., and Jaeger, J. J.: A new amphicyonid (Mammalia, Carnivora, Amphicyonidae) from the late middle Miocene of northern Thailand and a review of the amphicyonine record in Asia, *J. Asian. Earth Sci.*, 26, 519–532, 2006.
- Ramstein, G., Fluteau, F., Besse, J., and Joussaume, S.: Effect of orogeny, plate motion and land sea distribution on Eurasian climate change over the past 30 million years, *Nature*, 386, 788–795, 1997.
- Rowley, D. and Currie, B.: Palaeo-altimetry of the late Eocene to Miocene Lunpola basin, central Tibet, *Nature*, 439, 677–681, 2006.
- Sawangchote, P., Grote, P., and Dilcher, D.: Tertiary leaf fossils of *Mangifera* (Anacardiaceae) from Li Basin, Thailand as examples of the utility of leaf marginal venation characters, *Am. J. Bot.*, 96, 2048–2061, 2009.
- Sepulchre, P., Ramstein, G., Fluteau, F., Schuster, M., Tiercelin, J. J., and Brunet, M.: Tectonic uplift and Eastern Africa aridification, *Science*, 313, 1419–1423, 2006.
- Songtham, W., Ratanasthien, B., Mildenhall, D. C., Singharajwarapan, S., and Kandharosa, W.: Oligocene-Miocene climatic changes in northern Thailand resulting from extrusion tectonics of Southeast Asian landmass, *Science Asia*, 29, 221–233, 2003.
- Songtham, W., Ratanasthien, B., Watanasak, M., Mildenhall, D., Singharajwarapan, S., and Kandharosa, W.: Tertiary basin evolution in northern Thailand: a palynological point of view, *Nat. Hist. Bull. Siam Soc.*, 53, 17–32, 2005.
- Sookchaloem, D.: Outline of the forest flora in Northeastern Thailand, *Proceedings of the 42nd Kasetsart University Annual Conference*, Kasetsart, Thailand, 3–6 February 2004, 40–47, 2004.
- Sun, X. and Wang, P.: How old is the Asian monsoon system?—Palaeobotanical records from China, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 222, 181–222, 2005.
- Sytsma, K. J., Litt, A., Zjhra, M. L., Chris Pires, J., Nepokroeff, M., Conti, E., Walker, J., and Wilson, P. G.: Clades, Clocks, and Continents: Historical and Biogeographical Analysis of Myrtaceae, Vochysiaceae, and Relatives in the Southern Hemisphere, *Int. J. Plant Sci.*, 165, 85–105, 2004.
- Tassy, P., Anupandhanant, P., Ginsburg, L., Mein, P., Ratanasthien, B., and Sutteethorn, V.: A new *Stegolophodon* (Proboscidea, Mammalia) from the early Miocene of northern Thailand, *Geobios*, 25, 511–523, 1992.
- Vincens, A., Tiercelin, J. J., and Buchet, G.: New Oligocene–early Miocene microflora from the southwestern Turkana Basin. Palaeoenvironmental implications in the northern Kenya Rift, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 239, 470–486, 2006.
- Wang, P., Clemens, S., Beaufort, L., Braconnot, P., Ganssen, G., Jian, Z., Kershaw, P., and Sarntheim, M.: Evolution and variability of the Asian monsoon system: state of the art and outstanding issues, *Quaternary Sci. Rev.*, 24, 595–629, 2005.
- Watanasak, M.: Palaeoecological reconstruction of Nong Ya Plong Tertiary Basin (Central Thailand), *Journal of ecology (Thailand)*, 15, 51–70, 1988.
- Watanasak, M.: Palynological Zonation of Mid-Tertiary Intermontane Basins in Northern Thailand, *International Symposium on Intermontane Basins: Geology and Resources*, Thailand, 216–225, 1989.
- Watanasak, M.: Mid Tertiary palynostratigraphy of Thailand, *J. Southe. Asian Earth*, 4, 203–218, 1990.
- Watson, L. and Dallwitz, M. J.: The families of flowering plants: descriptions, illustrations, identification, and information retrieval, available online at: <http://delta-intkey.com>, (last access: December 2006), 1992.
- Werner, W.: Pines and other conifers in Thailand – a Quaternary relic?, *J. Quaternary Sci.*, 12, 451–454, 1997.
- White, J. C., Penny, D., Kealhofer, L., and Maloney, B.: Vegetation changes from the late Pleistocene through the Holocene from three areas of archaeological significance in Thailand, *Quater-*

- nary Int., 113, 111–132, 2004.
- Wilson, P. G., O'Brien, M. M., Heslewood, M. M., and Quinn, C. J.: Relationships within Myrtaceae sensu lato based on a matK phylogeny, *Plant Syst. Evol.*, 251, 3–19, 2005.
- Zachos, J., Pagani, M., Sloan, L., Thomas, E., and Billups, K.: Trends, Rhythms, and Aberrations in Global Climate 65 Ma to Present, *Science*, 292, 686–693, 2001a.
- Zachos, J., Shackleton, N., Revenaugh, J., Palike, H., and Flower, B.: Climate response to orbital forcing across the Oligocene-Miocene boundary, *Science*, 292, 274–278, 2001b.
- Zachos, J., Dickens, G., and Zeebe, R.: An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics, *Nature*, 451, 279–283, 2008.
- Zhongshi, Z., Wang, H., Guo, Z., and Jiang, D.: What triggers the transition of palaeoenvironmental patterns in China, the Tibetan Plateau uplift or the Paratethys Sea retreat ?, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 245, 317–331, 2007.