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The Cenozoic leaf morphotypes and palaeoclimate interpretation from the Doi Ton Formation, Mae Sot District, Tak Province, western Thailand

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ABSTRACT

The Cenozoic palaeovegetation and palaeoclimate of Doi Ton, western Thailand, megaflora are reconstructed based on physiognomic climate analysis, including Leaf Margin Analysis (LMA), Leaf Area Analysis (LAA), Leaf Size Index (LSI), Climate Leaf Analysis Multivariate Program (CLAMP), and systematic descriptions of each leaf morphotype. The leaf fossils were divided into 23 dicotyledonous leaf morphotypes and two unknown leaf morphotypes. The mean annual temperature results from LMA indicate 32.3 ± 1.17°C and CLAMP shows 21.2°C. CLAMP also provides temperature data of a warm month mean temperature (WMMT) of 27.4°C and a CMMT of 14.2°C, which is similar to the present climate. The mean annual precipitation is estimated by LAA to be ~ 125 cm. CLAMP suggests precipitation in the 11 months of growing period was 154.9 cm with the three wettest months having precipitation of 73 cm, widely contrasting with 15.5 cm for the three driest months. The precipitation shows the signal of the monsoon effect. The temperature, precipitation, and LSI mirrored the vegetation of the contemporary Doi Ton area which is a semi-evergreen forest in the tropical zone. The palaeoclimatic parameters of Doi Ton are in good agreement with those of south China and northwest India from the Eocene period and the present-day Mae Sot area. Moreover, the Doi Ton flora also closely matches the humid sub-tropical modern vegetation of south China. Palaeoclimate and vegetation analysis support an Eocene age estimate for the Doi Ton Formation however further independent age estimates are required to test this working hypothesis.

KEYWORDS: Cenozoic, Doi Ton Formation, leaf morphotypes, Palaeoclimate, western Thailand.

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INTRODUCTION

The fossil site, Doi Ton, is located in Mae Sot Basin, 30 km north of Mae Sot district, Tak province, western Thailand and close to the frontier between Thailand and Myanmar (Fig. 1A–1B). Doi Ton is a small hill, which rose in the middle of the Mae Sot Cenozoic Basin (Fig. 2A). The leaf fossils were collected from outcrops and in-situ float rocks around Doi Ton temple (16°54′17.12″N, 98°35′56.82″E). These leaf fossils are imprinted in sandstone layers and associated with branch, tree bark, bivalve, and gastropod fossils. The stratigraphy, lithology, and palaeontology of Doi Ton, consistent and comparable with the Mae Ramat Formation of the Mae Sot Group (Fig. 3) (Ampaiwan *et al.*, 2003), imply that age of Doi range lies between the late Mesozoic to the early Miocene. Nevertheless, many papers indicate that this formation should be a part of Cenozoic formation. Because the exact geological age of Doi Ton Formation is still unknown, this study used leaf physiognomy and palaeoclimate estimates to try to constrain the age of the formation further as a starting point.

The adaptation of plants is clearly mirrored in leaf anatomy, which is strongly related to temperature and precipitation. Intact leaves are mostly transported short distances from the source area, so they can be excellent proxies to indicate the local land environment (Maxbauer *et al.*, 2013). For more than a century, botanists have studied the relationship between leaf characters and climatic conditions and have attempted to construct various techniques to estimate past temperatures and precipitation. Large entire margined leaves are more common in wet tropical forests with decreasing latitude, whereas

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leaves of temperate vegetation tend to be smaller with a toothed margin and/or lobes (Bailey & Sinnot, 1916; Wolfe, 1993; Burnham *et al*., 2001; Kowalski & Dilcher, 2003; Royer *et al*., 2005); moreover, large leaf areas show a positive correlation with increased precipitation (Givnish, 1984; Wilf *et al.*, 1998). Thus, these relationships can be used to reconstruct climatic conditions, an approach known broadly as the leaf physiognomic method (Greenwood, 2005; Green, 2006; Peppe *et al.*, 2018).

In Thailand, there have been a few studies of plant fossils in Tertiary basins, but these are mainly studies of pollen, wood or fruits for taxonomic research, and few are leaf studies (Grote, 2005). Leaf fossils in Thailand are mostly found in Cenozoic terrestrial sediments (Grote, 2005; Sawangchote, 2006; Sawangchote *et al.*, 2010). In this study, we describe and diagnose leaf fossils to estimate climate parameters by using physiognomic method including Leaf Margin Analysis (LMA), Leaf Area Analysis (LAA), Leaf Size Index (LSI) and Climate Leaf Analysis Multivariate Program (CLAMP) (Webb, 1968; Wolf, 1979; Wing & Greenwood, 1993; Wilf *et al.*, 1998; Yang *et al.*, 2011; Peppe *et al.*, 2018). This study presents a new study of a poorly known fossil flora thereby reassembling the past vegetation within Doi Ton. The comparison of modern and past vegetation can provide significant insights into the evolution and relationships of these flora assemblages.

Geological Setting

Doi Ton is located in the Mae Sot Basin, western Thailand. This basin is typically a deposit of Tertiary sediments of Mae Sot Group along the half-graben basin (Morley & Racey, 2011). This basin had been open since the Eocene to the deposition of the fluvial-lacustrine sediments of the Mae Ramat Formation (Charusiri & Pum-Im, 2009). At that time, the basin was widely opened to deposition of lacustrine sediments of the Mae Pa Formation, which have the potential of developing into oil shale. The uppermost formation is the Mae Sot Formation, which was deposited in lacustrine to fluvial environments (Thanomsap, 1983; Thanomsap & Sitahirun, 1992). Tantiwanit *et al.* (1986) established the Doi Ton Formation for the Doi Ton area, which mainly consists of conglomerate, gravelly sandstone, sandstone, and siltstone and plant fossils were preserved in white sandstone. From the lithology, the Doi Ton Formation should be equivalent to Mae Ramat Formation in early Cenozoic.

Stratigraphy

Doi Ton, a hill reaching 300 m elevation, has several outcrops found near the top at ca 300 m (Fig. 2B). The measured stratigraphic sections range from 160 to 480 cm in length. These sections are mainly composed of sandstone with minor conglomerate and siltstone with highly weathered and red and whitish grey fresh colour. The lower part is made

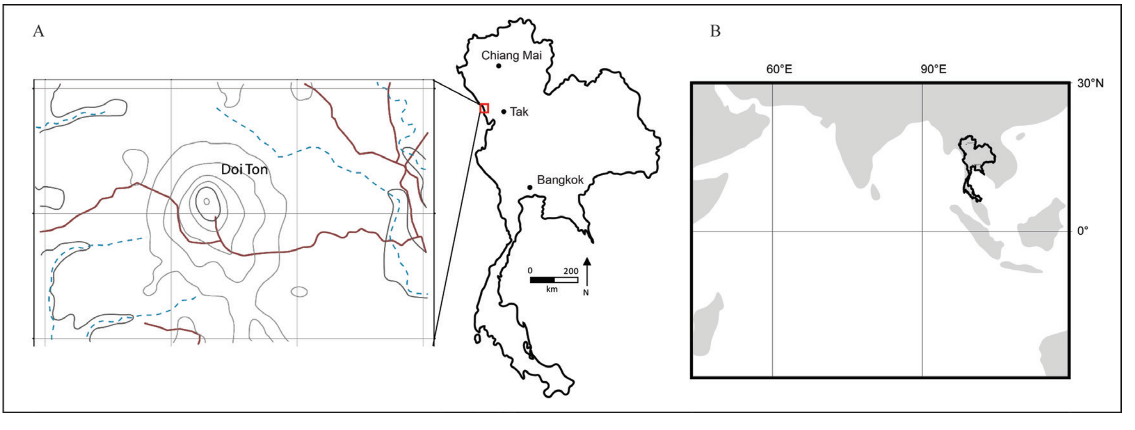

Figure 1. A. Geographic location of fossil in Doi Ton, Mae Sot, Tak, western Thailand. B. Thailand located in SE Asia.

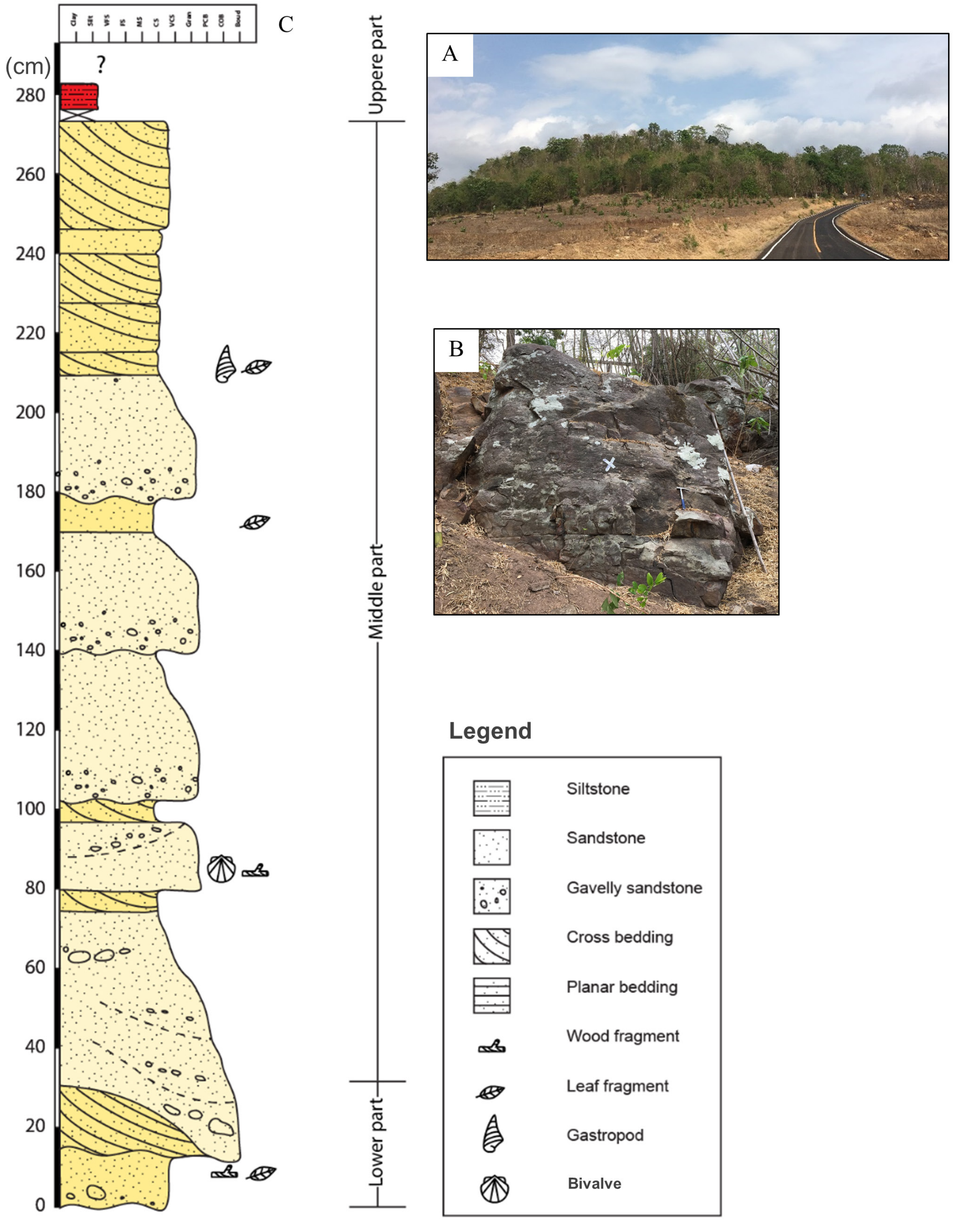

Figure 2. A. The small hill of Doi Ton rose in the middle Mae Sot Basin with surrounded by the undulating plain. B. The outcrop section on the top of Doi Ton. C. Stratigraphic section of Doi Ton exposed at fossil leaf position.

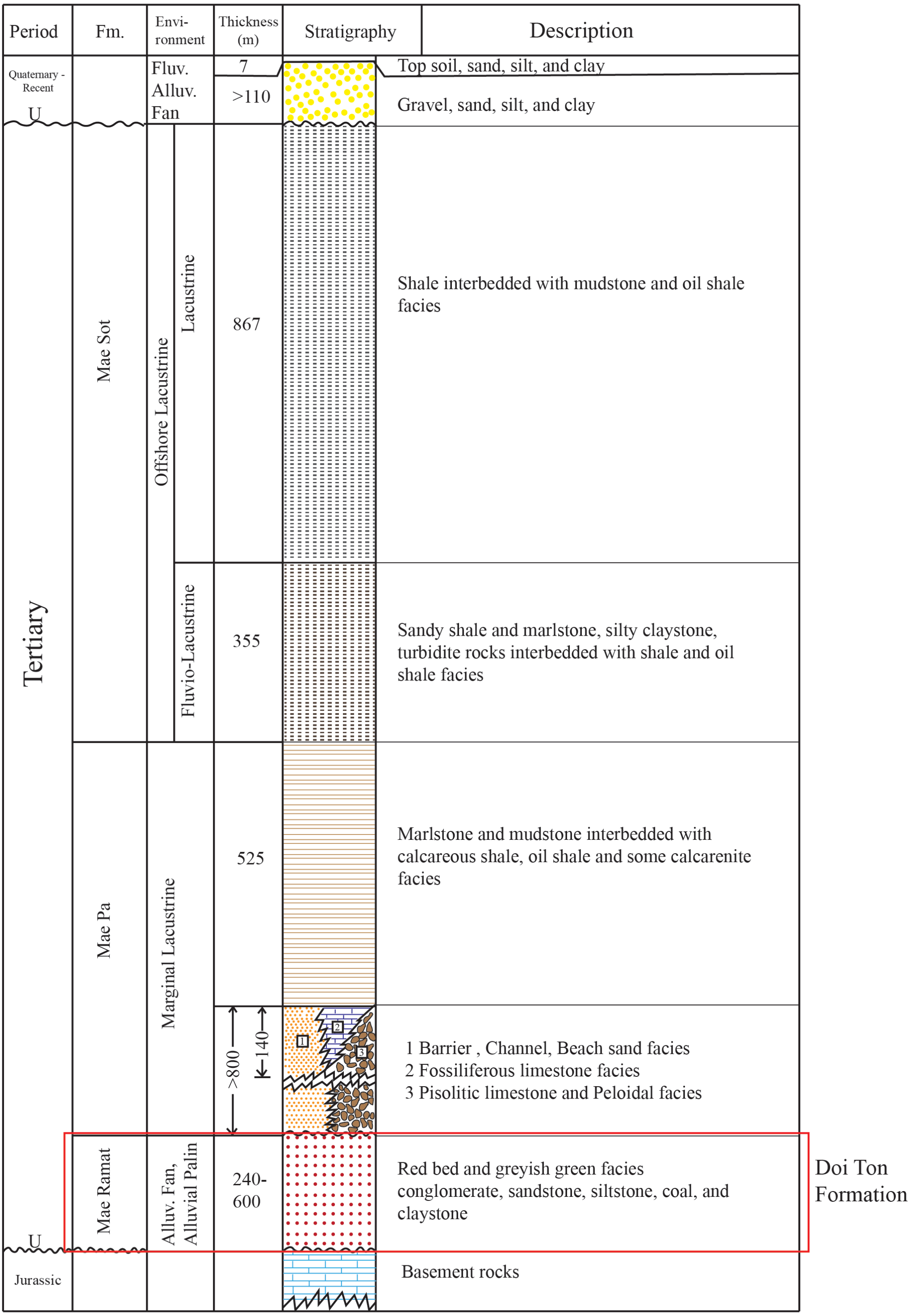

Figure 3. Stratigraphy of the Mae Sot Group, Mae Sot's Tertiary basin. The Doi Ton Formation is equivalent to the Mae Ramat Formation.

up of thin to medium bedded sandstone to siltstone couplets. The cycles demonstrate slightly fining upward from sand to silt size. Each cycle is capped by a rippled sand layer. The plant fragments are found in the sandstone layers. In the middle part, the lithologic sequence begins with a granule conglomerate, followed by thin to medium bedded, coarse to fine grained sandstone, and topped by fine grained sandstone with ripple marks. The conglomerate shows erosive base of channels deposit in the lower part and was deposited with tree trunks. Most of the plant remains (leaves, tree barks, and branches), and a few gastropods and bivalves, were found together in the sandstone layers in this part. The primary sedimentary structures, ripple marks, and bottom structures, indicate the NW palaeocurrent direction. The uppermost part mainly includes siltstone in reddish weathered colour and greyish black fresh colour (Fig. 2C).

MATERIALS & METHODS

Materials

The leaf fossils were collected from sandstone outcrops and in-situ float rocks around Doi Ton Temple, Doi Ton Formation. All specimens in this study collected by the authors are housed at the Department of Geological Sciences, Chiang Mai University, and those collected by the Ban Nam Dib Primary School's director are housed at the school. The sample ordering in this study was started by the "DT" to represent Doi Ton (and followed by the direction alphabet N, W, E, or S if collected from floated rock) and "BD" to represent samples collected and exhibited at Ban Nam Dib school. For example, the sample number DT-W18 indicates that this leaf that was collected from the west side of Doi Ton.

Methods

Morphological study. The leaf fossils specimens were photographed with a digital camera, then they were grouped into morphotypes according to their leaf architecture. The morphotype is proposed to classify leaves based on leaf morphology which is not a formal taxonomic identification. Morphotype groups are not directly related to particular species of plants but are often equivalent to biological species (Leaf Architecture Working Group, 1999). The systematic description and terminology of the dicotyledonous leaf-architecture characters follow Dilcher (1974), Leaf Architecture Working Group (1999), Ellis *et al.* (2009), Hickey (1973) and Singh (2010). The size of each leaf was measured and compared with the Raunkiaer (1934) and Webb (1959) leaf size classifications.

Physiognomic method for climate reconstructions. The physiognomic methodology rests on the physical character of leaves and their established correlations with climatic parameters to resolve palaeoclimate conditions. Because the plant adapts their foliar features, e. g. size, shape, margin, to survive under the land climatic conditions. Palaeobotanists use these concepts of modern leaves to calibrate the climate with the fossil leaves. The causal mechanisms underlying the relationships between leaf physiognomic characters and climate parameters remain an active area of research (Little *et al.*, 2010; Edwards *et al.*, 2016).

Leaf Margin Analysis (LMA): Temperature or mean annual temperature (MAT) is significantly correlated with the proportion of entire (smooth) leaf margin vs toothed margin of flowering dicot plants in a collection or assemblage of leaves from at least 20 different species (Peppe *et al.*, 2018). From this relationship, the MAT was estimated by used the LMA analysis of a fossil leaf assemblage. To decrease uncertainty of this method, the fossil flora must contain more than 20 different morphological types of leaf fossil (Wolfe, 1971).

In this study, we choose the linear regression equation of Su *et al.* (2010) who combined the LMA data of China's humid forest. This equation better fits with our data (in linear line) than the others equation based on the LMA equations (Peppe *et al.*, 2018).

$$MAT = 27.6P + 5.884 \qquad (1)$$

where MAT is average annual temperature estimated using LMA and P is defined as:

$$P = \frac{\mathrm{r}}{\mathrm{n}}$$

where n is the number of all morphotypes, and r is the number of entire margined leaf morphotypes.

Leaf Area Analysis (LAA): This analysis uses the modern correlation of leaf area and precipitation (Givnish, 1984; Webb, 1968; Wilf *et al.*, 1998; Jacobs, 1999; Peppe *et al.*, 2018). This model uses the average natural log of leaf area in each morphotype that can be used to estimate the mean annual precipitation (MAP), which is called "Leaf Area Analysis" or LAA (Wilf *et al.*, 1998; Peppe *et al.*, 2018). The leaf area can be measured by the indirect method by assigning the leaf to a size class of the Raunkiaer-Webb leaf size scale (Leaf Architecture Working Group, 1999).

We follow the linear regression models of Peppe *et al.*, 2011 (Eq.2), who studied leaves from North and South America, Japan, and Oceania. This equation better fits with our data than the other models. Moreover, we did not use the model from China as for LMA since there has been no study about LAA modelling from the China region before (Peppe *et al.*, 2018).

$$\ln MAP = 0.283(MlnA) + 2.92 \qquad (2)$$

where *MlnA* is a mean natural log (ln) of morphotype's area (Peppe *et al.*, 2018). This value can be calculated by entering the natural log value in each size class of Raunkier-Webb (Webb, 1959) of each leaf morphotype. Then, calculating the average of the mean natural log in each leaf morphotype (if the morphotype has a various size of leaf). The mean natural log's leaf area value for each category is leptophyll: 2.12, nanophyll: 4.32, microphyll: 6.51, notophyll: 8.01, and mesophyll: 9.11. The *MlnA* was calculated the average of mean natural log of the entire flora to put in the Peppe *et al.*, (2011)'s equation. This method has an uncertainty for the estimate of precipitation based on this equation. The standard error for LAA is 0.572. Moreover, almost of leaf fossils in this study are broken, so the estimate can be an underestimate or an overestimate of the precipitation.

Leaf Size Index (LSI): Each leaf fossil was assigned to a size class of Raunkiaer-Webb (Leaf Architecture Working Group, 1999). The size of leaves also provides important data of forest type, which is related to climate estimation. The ratio of small leaf classes and large leaf classes (Raunkiaer, 1934; Webb, 1959) with the percentage of smoothed leaf margin (Webb, 1959; Webb, 1968) were compared with the rain forest plant in Australia of Webb (1968). Moreover, the proportion of small and large leaf sizes has the potential to be compared with equatorial Africa flora that have been measured by Jacobs (1999). The result of LSI is compared with the modern vegetation in each area of the world.

Climate Leaf Analyses Multivariate Program (CLAMP): This method is based on the combination of LMA and LAA with 31 leaf features for climate interpretation. The 31 features are associated with margin style, size (CLAMP' leaf size classification scheme), length to width ratio, lobbing, and shape: base, apex, and whole shape. Each leaf character was scored for calculation in the spreadsheet and analysed using a multidimensional tool (canonical correspondence analysis, CCA) (Wolfe, 1995; Kovach & Spicer, 1995; Spicer *et al.*, 2004; Spicer *et al.*, 2009). In this study the PhysgAsia2's flora data set and HiResGridMetAsia2's meteorological data were used for analysing. The best prediction of CLAMP was produced by more than 20 morphological species. The leaf character scores in this study were analysed by the online version of the CLAMP website (http://clamp.ibcas.ac.cn/CLAMP_Run_Analysis.html).

MORPHOTYPE CATALOGUE

The morphological study of 55 leaf fossils was classified using similar leaf characters and grouped into 25 morphotypes of 23 dicotyledonous leaves and two unknown leaves. The first sample in the material name means the reference material present in Fig. 4.

Dicotyledonous leaves morphotypes

Morphotype A.

Material: DT-0241 (Fig. 4A)

Description: Leaf moderately to poorly preserved. Lamina oblong to narrowly oblong with medial symmetry, laminar size-mesophyll, 14.50 cm long, 5.54 cm wide; length to width ratio 2.6:1. Margin entire. Apex and base unknown. Midvein stout, markedly curved approximately 2° from a straight line. Primary venation pinnate. Basal and agrophic veins not preserved. Secondary veins faint, opposite, arising from midvein at a moderately acute angle (50°–62°), running straight toward the margin. Higher-order veins not preserved.

Morphotype B.

Material: DT-D5 (Fig. 4B)

Description Leaf poorly preserved. Lamina ovate to narrowly ovate; laminar size-microphyll, 3.56 cm long, 2.13 cm wide; length to width ratio 1.7:1. Medial and basal symmetry unknown. Margin entire. Apex and base poorly preserved. Midvein stout, straight, unbranched. Venation pinnate. Basal and agrophic veins not shown. Secondary and higher-order veins not preserved.

Morphotype C.

Material: DT-SR6 (Fig. 4F)

Description: Leaf moderately to well preserved. Lamina obovate to narrowly obovate; laminar size-notophyll, 7.69 cm, 3.85 cm wide; length to width ratio 2:1. Medial and basal symmetry unknown. Margin entire. Apex acuminate, base missing. Midvein weak, curved markedly to the right about 6° from a straight line. Primary venation pinnate. Basal and agrophic veins not shown. Secondary veins opposite arising from midvein at a narrowly acute angle (26°–44°), running uniformly curved toward the apex. Venation eucamptodromous. Higher-order veins not preserved.

Morphotype E.

Material: DT-W33, DT-BD2, DT-BD7, DT-0192 and DT-2.4 (Fig. 4G)

Description: Leaf moderately well preserved. Lamina elliptic to narrowly elliptic; laminar size-notophyll to microphyll, 7.05–10.30 cm long, 2.78–3.60 cm wide; length to width ration 2.4–3:1. Medial and basal symmetry. Margin entire. Apex acute; base rounded with acute angle. Midvein moderately to weak sized from base to apex, markedly curved to the right approximately 7° from a straight line. Primary venation pinnate. Basal and agrophic veins not preserved. Secondary venation preserved only on one side of leaf, arising from midvein at a narrowly acute angle (38°–43°), running uniformly curved to the margin. Venation craspedodromous. Higher-order veins not preserved.

Morphotype F.

Material: DT-5.4, DT-BD2, DT-BD3.2 and DT-N5 (Fig. 4D)

Description: Leaf moderately well preserved. Lamina elliptic to narrowly elliptic; laminar size-microphyll, 4.1–4.67 cm long, 1–1.53 cm wide; length to width ratio 2.7–3.7:1. Medial and basal symmetry. Margin entire. Apex acute; base narrowly cuneate. Midvein weak, straight, unbranched. Primary venation pinnate. Basal and agrophic veins not shown. Secondary and higher venation not preserved.

Morphotype H.

Material: DT-D1, DT-SR4, DT-W11, DT-N2 and DT-E1 (Fig. 4E)

Description: Leaf moderately well preserved. Lamina ovate to narrowly ovate; laminar size-microphyll to mesophyll; 7.76–12.11 cm long, 4.19–6.98 cm wide; length to width ratio: 1.5–2.5:1. Medial and basal symmetry. Margin entire. Apex unknown; base rounded with obtuse angle. Midvein stout, straight, unbranched. Primary venation pinnate. Basal and agrophic veins not shown. Secondary veins subopposite arising from midvein at a moderately acute angle (45°–47°) and running uniformly curved toward the apex. Venation eucamptodromous. Interior secondary vein space uniform. Higher-order veins not preserved.

Morphotype I.

Material: DT-SR4, DT-D1, DT-W11, DT-N2 and DT-E1(Fig. 4H)

Description: Leaf moderately well preserved. Lamina oblong; laminar size-microphyll, 5.3 cm long, 2.3 cm wide; length to width ratio 2.3:1. Medial symmetry, basal symmetry unknown Margin entire. Apex acute; base unknown. Midvein weak, straight, unbranched. Primary venation pinnate. Basal and agrophic veins not shown. Secondary veins faint, arising from midvein at a narrowly acute angle (30°–41°) and abruptly curved toward the apex. Venation eucamptodromous. Interior secondary vein space uniform. Higher-order veins not preserved.

Morphotype J.

Material: DT-D6, DT-8.1 and DT-SR7 (Fig. 4I)

Description: Leaf moderately well preserved. Blade attachment marginal with petiole. Lamina elliptic; laminar size-notophyll, 3.02–13.02 cm long, 1.19–5.36 cm wide; length to width ratio 2.4–3.6:1. Medial and basal symmetry. Margin entire. Apex acute; base narrowly acute. Midvein weak, straight, unbranched. Primary venation pinnate. Basal and agrophic veins not shown. Secondary veins only preserved on one half side of leaf, arising from midvein at a narrowly acute angle (20°–25°) and running uniformly curved toward apex. Venation weakly brochidodromous. Interior secondary vein space uniform. Higher-order veins not preserved.

Morphotype K.

Material: DT-7.1 and DT-10.1 (Fig. 4J)

Description: Leaf moderately well preserved. Lamina oblong to linear, laminar size-nanophyll, 1.97–2.34 cm long, 0.23–1.26 cm wide; length to width ratio 1.9-8.8:1. Medial asymmetry, basal symmetry. Margin entire. Apex unknown; base rounded with an acute angle. Midvein weak, straight, unbranched. Primary venation pinnate. Basal and agrophic veins not shown. Secondary veins faintly preserved, alternate arising from midvein at a moderately acute angle (47°–48°), running abruptly curved toward the apex. Venation eucamptodromous. Higher-order veins not preserved.

Morphotype O.

Material: DT-5.1 (Fig. 4R)

Description: Leaf poorly preserved. Lamina oblong to lanceolate; laminar size-microphyll, 10.25 cm long, 2.46 cm wide, length to width ratio 4.2:1. Medial symmetry. Margin entire. Apex acuminate with an acute angle; base unknown. Midvein weak, straight, unbranched. Primary venation; faintly preserved, pinnate. Basal and agrophic veins not shown. Secondary veins and higher-order veins not preserved.

Morphotype P.

Material: DT-3.2 (Fig. 4S)

Description: Leaf moderately well preserved. Lamina ovate to lanceolate, laminar size-microphyll, 5.61 cm long, 1.72 cm wide; length to width ratio 3.3:1. Medial and basal symmetry unknown. Margin entire. Apex unknown; base narrowly cuneate. Midvein massive, markedly curved to the right about 6° from a straight line. Primary venation pinnate. Basal and agrophic veins not shown. Secondary veins alternate arising from midvein at a moderately acute angle (46°–63°), running straight toward the apex. Venation eucamptodromous. Interior secondary vein space uniform. Higher-order veins not preserved.

Morphotype R.

Material: DT-9.7, DT-D3 and DT-W4 (Fig. 4M)

Description: Leaf moderately to well preserved. Lamina obovate to narrowly obovate, laminar size-microphyll to notophyll, 3.31–7.03 cm long, 1.98–3.12 cm wide; length to width ratio 1.7–2.1:1. Medial and basal symmetry. Margin entire. Apex emarginate, broadly obtuse, base narrowly cuneate. Midvein massive, markedly curved to the left about 8° from a straight line. Primary venation pinnate. Basal and agrophic veins not shown. Secondary veins subopposite, arising from midvein at a narrowly acute angle (46°–50°), running uniformly curved toward the apex. Venation eucamptodromous. Interior secondary vein space increasing toward base. Higher-order veins not preserved.

Morphotype S.

Material: DT-D9 (Fig. 4N)

Description: Leaf moderately well preserved. Lamina elliptic; laminar size-microphyll, 4.13 cm long, 2.53 cm wide; length to width ratio 1.6:1. Medial and basal symmetry unknown. Margin entire. Apex and base unknown. Midvein stout, straight, unbranched. Primary venation pinnate. Basal and agrophic veins not shown. Secondary veins opposite to subopposite arising from midvein at a narrowly acute angle (45°–56°), running uniformly curved toward the apex. Venation eucamptodromous. Interior secondary vein space uniform. Higher-order veins not preserved.

Morphotype T.

Material: DT-BD1 (Fig. 4O)

Description: Leaf moderately well preserved. Lamina obovate to narrowly obovate; laminar size-microphyll, 4.2 cm long, 2.1 cm wide; length to width ratio 2:1. Medial symmetry, basal symmetry unknown. Margin entire. Apex and base unknown. Midvein weak, straight, unbranched. Primary venation pinnate. Basal and agrophic veins not shown. Secondary veins alternate, arising from midvein at a narrowly acute angle (40°–47°), running abruptly curved toward the apex. Interior secondary vein space uniform. Higher-order veins are not preserved.

Morphotype U.

Material: DT-5.5, DT-7.3 (Fig. 4P)

Description: Leaf moderately well preserved. Lamina oblong to lorate; laminar size-nanophyll to microphyll, 1.75–7.97 cm long, 0.25–1.99 cm wide, length to width ratio 4–7:1. Medial and basal symmetry. Margin entire. Apex acuminate, acute angle; base unknown. Midvein weak, markedly curved to the left about 4o from a straight line. Primary venation pinnate. Basal and agrophic veins not shown. Secondary and higher-order veins not preserved.

Morphotype V.

Material: DT-3.1 (Fig. 4Q)

Description: Leaf moderately well preserved. Lamina elliptic, laminar size-notophyll, 6.22 cm long, 3.28 cm wide; length to width ratio 1.9:1. Medial symmetry, basal asymmetry. Margin entire. Apex and base unknown. Midvein stout, markedly curved to the right about 6° from a straight line. Primary venation pinnate. Basal and agrophic veins not shown. Secondary veins opposite, arising from midvein at moderately acute angle (46°–56°), running uniformly curved toward the apex. Venation eucamptodromous. Interior secondary vein space uniform. Higher-order veins not preserved.

Morphotype: W.

Material: DT-5.2 (Fig. 4L)

Description: Leaf moderately to well preserved. Lamina cordiform; laminar size-microphyll, 7 cm long, 5.1 cm wide; length to width ratio 1.4:1. Medial symmetry; basal symmetry unknown. Margin entire. Apex acuminate, acute angle; base cordate. Midvein faintly preserved, moderate size, straight, unbranched. Primary venation pinnate. Basal and agrophic veins not shown. Secondary veins random, arising from midvein at a moderately acute angle (51°–62°), running uniformly curved toward the apex. Venation eucamptodromous. Interior secondary vein space uniform. Higher-order veins not preserved.

Morphotype X.

Material: DT-5.2 (Fig. 4T)

Description: Leaf moderately to well preserved. Lamina obovate to narrowly obovate; laminar size-notophyll, 6.1 cm long, 3.3 cm wide; length to width ratio 1.9:1. Medial and basal symmetry. Margin entire. Apex round with obtuse angle; base narrowly cuneate. Midvein weak, straight, unbranched. Primary venation pinnate. Basal and agrophic veins not shown. Secondary veins random arising from midvein at a moderately acute angle (42°–52°), running uniformly curved toward the apex. Venation eucamptodromous. Interior secondary vein space uniform. Higher-order veins not preserved.

Morphotype Y.

Material: DT-SR1, DT-9.8 (Fig. 4U)

Description: Leaf moderately well preserved. Lamina preserved in some parts (other parts cannot be identified); laminar size-microphyll to mesophyll, 3.5–12.54 cm long, 2.25–7.23 cm wide; length to width ratio 1.7:1. Medial and basal symmetry unknown. Margin, apex, and base unknown. Midvein weak, curved slightly toward the apex. Primary venation actinodromous, at least four veins arising from the base. Secondary veins faintly preserved, arising at a narrowly acute angle (25°–37°), running uniformly curved toward the apex. Tertiary veins opposite percurrent, slightly arched.

Morphotype Z.

Material: DT-5.2 (Fig. 4V)

Description: Leaf moderately well preserved. Lamina ovate to narrowly ovate; laminar size-microphyll, 3.71 cm long, 2.1 cm wide; length to width ratio 1.9:1. Medial symmetry unknown, basal symmetry. Margin entire. Bass broadly cuneate. Midvein weak, markedly curved to the right about 9° from a straight line. Primary venation faintly preserved, pinnate. Basal and agrophic veins not shown. Secondary veins faintly preserved, subopposite arising from midvein at a narrowly acute angle (40°–43°), running uniformly curved toward the apex. Venation eucamptodromous. Higher-order veins not preserved.

Morphotype AA.

Material: DT-D7 (Fig. 4W)

Description: Leaf moderately well preserved. Lamina elliptic to narrowly elliptic, laminar size-microphyll, 5.93 cm long, 1.93 cm wide; length to width ratio 3:1. Medial and basal symmetry unknown. Margin entire. Apex round, acute angle. Midvein weak, markedly curved to the right about 6o. Primary venation pinnate. Basal and agrophic veins not shown. Secondary veins alternate arising from midvein at a moderately acute angle (55°–56°), running uniformly curved toward the apex. Interior secondary vein space uniform. Higher-order veins not preserved.

Morphotype AB.

Material: DT-4.4 (Fig. 4X)

Description: Leaf moderately well preserved. Lamina oblong, laminar size-microphyll, 5.74 cm long, 2.4 cm wide; length to width ratio 2.4:1. Medial and basal symmetry unknown. Margin toothed, crenate. Apex and base unknown. Midvein stout, straight, unbranched. Primary venation pinnate. Basal and agrophic veins not shown. Secondary veins alternate; arising from midvein at a narrowly acute angle (35°–37°), running uniformly curved toward the margin. Venation craspedodromous. Tertiary vein not opposite reticulate.

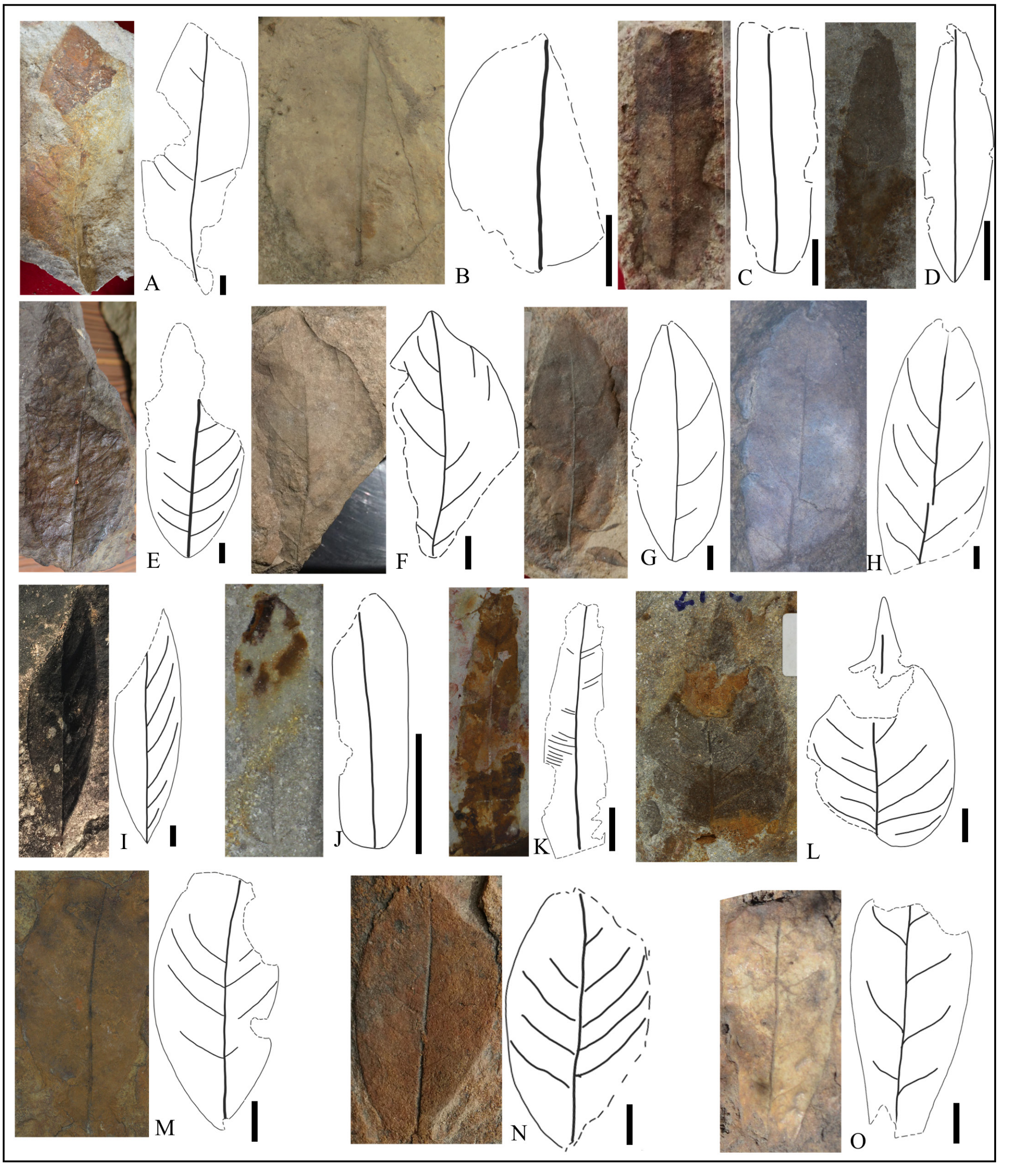

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Figure 4. A. Morphotype A; B. Morphotype B; C. Morphotype D; D. Morphotype F; E. Morphotype H; F. Morphotype C; G. Morphotype E; H. Morphotype I; I. Morphotype J; J. Morphotype K; K. Morphotype M; L. Morphotype W; M. Morphotype R; N. Morphotype; O. Morphotype T. P. Morphotype U; Q. Morphotype V; R. Morphotype O; S. Morphotype P; T. Morphotype X; U. Morphotype Y; V. Morphotype Z; W. Morphotype AA; X. Morphotype AB; Y. Morphotype AC. All drawn by Kobkul Keiwsanuan. (scale bar = 1 cm).

Morphotype AC.

Material: DT-W8, DT-4.1 (Fig. 4Y)

Description: Leaf moderately well preserved. Lamina preserved in some parts (other parts cannot be identified); laminar size-microphyll to mesophyll, 3.42–8.86 cm long, 4.57–9.97 cm wide; length to width ratio 0.7–0.9:1. Medial and basal symmetry unknown. Margin, apex, and base unknown. Midvein stout, straight, unbranched. Primary venation pinnate. Basal and agrophic veins not shown. Secondary veins alternate, arising from midvein at a moderately acute angle (48°–56°), running uniformly curved toward the apex. Tertiary veins opposite, percurrent.

Unknown leaves morphotypes

Morphotype D.

Material: DT-W16, DT-W18, DT-2.3, DT-SR2, DT-D11, DT-2.6 and DT-5.3 (Fig. 4C)

Description: Leaf moderately well to poorly preserved. Lamina oblong to linear; laminar size-microphyll, 3.33–7.60 cm long, 1.38–2.53 cm wide, length to width ratio 2.5–3.4:1. Medial and basal symmetry. Margin entire. Apex unknown, base rounded, acute angle. Midvein massive, straight, unbranched. Primary venation pinnate. Basal and agrophic veins not shown. Secondary veins faintly preserved, subopposite arising from midvein at a

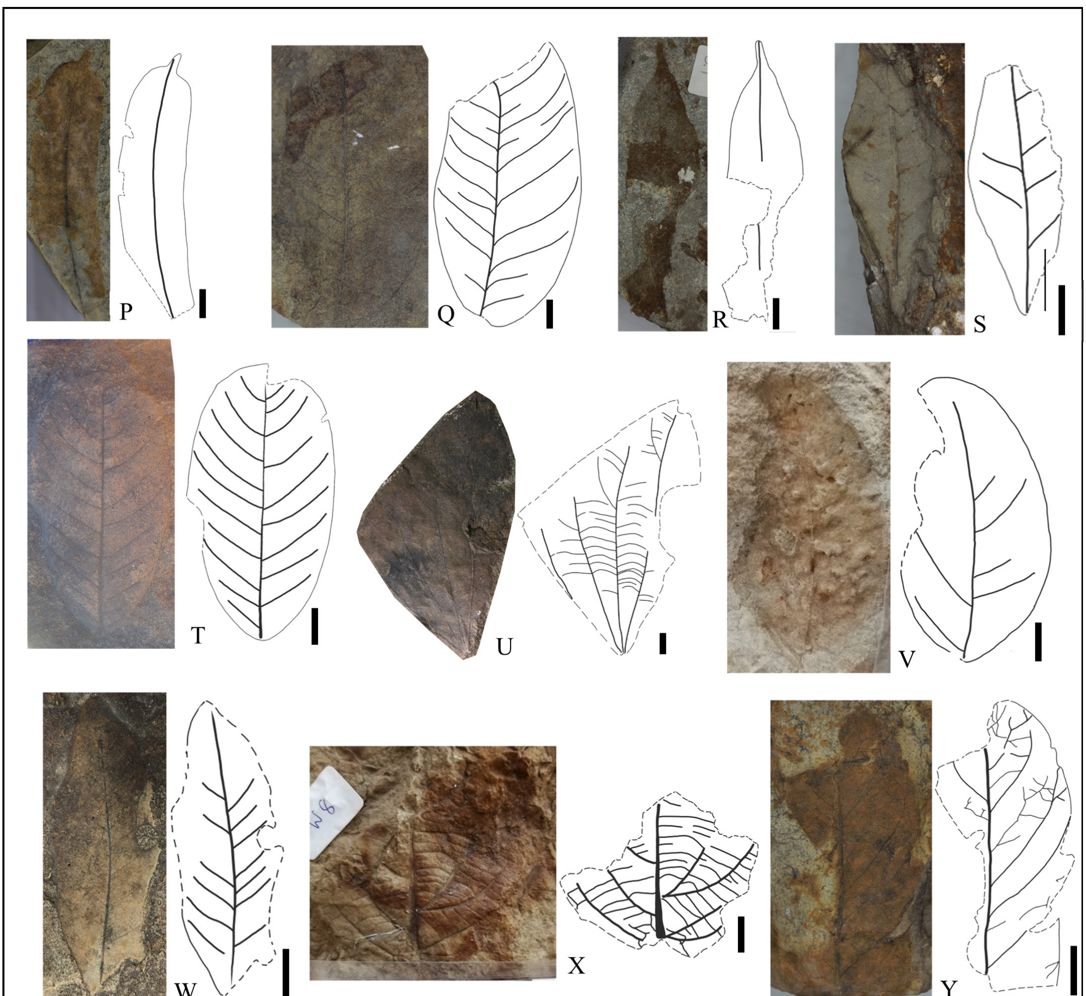

Figure 4. (Continued from preceding page).

widely acute angle (60°–76°), running the straight toward margin. Higher-order veins not preserved.

Morphotype M.

Material: DT-9.3 and DT-N13.1 (Fig. 4K)

Description: Leaf moderately well to poorly preserved. Lamina ovate to lanceolate; laminar size-microphyll, 5.29–7.05 cm long, 1.31–1.48 cm wide; length to width ratio 3.6–5.4:1. Medial and basal symmetry. Margin entire. Apex and base rounded, both with acute angle. Midvein weak, markedly curved to the left about 4° from a straight line. Primary venation pinnate. Basal and agrophic veins not shown. Secondary veins faintly preserved, arising from midvein at a moderately acute angle (70°–79°), running straight toward the margin. Interior secondary vein space uniform. Higher-order veins not preserved.

PALAEOCLIMATE RESULTS

Leaf Margin Analysis (LMA)

Doi Ton leaves contain a higher proportion of leaves with entire margins than toothed margins. Only one morphotype from the 23-dicot leaf morphotypes, or 4%, have toothed margins (Table 1). Following LMA this result is a high MAT estimate for the Doi Ton leaf assemblages (Wolfe, 1979; Wing & Greenwood, 1993; Wilf, 1997; Peppe *et al.*, 2018). MAT is 32.3°C ±1.17 from equation 1 (binomial sampling error (Miller *et al.*, 2006)).

Leaf Area Analysis (LAA)

Dicotyledonous leaf fossils of Doi Ton were compared in size with the leaf size class of Raunkier-Webb (Webb, 1959) and the natural log of each leaf size was used to calculate the MAP (Table 1). According to the univariate regression model of natural log of leaf area and natural log of MAP of Wilf *et al.*, 1998; Peppe *et al.*, 2018, these models provide the MAP estimates of Doi Ton leaf assemblages. This study used the model of Peppe *et al.* (2011) and shows a MAP of 125 cm/yr (error of this equation -57 to +105 cm, calculated by sampling error of this equation: error = [MAP-($e^{(\ln(MAP)-0.61)}$]

Leaf Size Index (LSI)

Forty-two leaf sizes of dicotyledonous leaf (size category) were classified into five classes of Raunkiaer's (1934) and Webb's (1959) leaf size classification scheme for Doi Ton. Small leaf classes are more abundant than large leaf classes: 60% are microphyll (25 samples); 7% nanophyll (three samples) and 2% leptophyll (one sample). There are two classes of large leaves comprising of 12% mesophyll (five samples) and 19% notophyll (eight samples).

Climate Leaf Analyses Multivariate Program (CLAMP)

Multiple variable quantitative leaf physiognomy analyses of Doi Ton were made using CLAMP with the calibration of the Asian flora and climatic dataset to estimate palaeoclimate of Doi Ton leaf assemblages. The 23 leaf morphotypes were scored and analysed following CLAMP protocols. CLAMP CCA axis 1 and axis 3 biplot displays the position of the Doi Ton assemblages (red filled circle) close to the modern calibration site from East Asia and northern America (Fig. 5A to 5C). For Fig. 5, data plotted on the CCA axis 1 and axis 2, indicates that the Doi Ton is positioned among East Asia, North America, and the Caribbean modern sample localities and climates. The CCA plot between axis 2 and axis 3 shows the Doi Ton in close proximity to the site of East Asia and northern America, which is similar to CCA axis 1 and 3 plotting. Regression modelling was applied for estimating mean annual temperature (Fig. 5D), mean temperature of the three warmest and three coldest months (Fig. 5E to 5F), and precipitation of the three-wettest and three-driest months (Fig. 5G to 5H); uncertainty of the analysis is ± 2 S.D. as shown as vertical error bars from the yellow filled circles. CLAMP analysis suggests that the Doi Ton's temperatures and precipitation fall in the humid regime. The calculated temperatures of Doi Ton include MAT 21.2°C, WMMT 27.4°C, and CMMT 14.2°C. The precipitation was estimated as high. The precipitation during the growing period is 154.9 cm in 11 months. The mean precipitation during the growing months is 13.4 cm. The precipitation of the three wettest months is 73 cm, which contrasts widely 15.5 cm for the three driest months.

DISCUSSION

The relationship between leaf characters and inhabited climatic conditions is a powerful tool for palaeoclimate reconstruction. Most of the leaf fossils

Table 1. Scores of Doi Ton leaf fossil of LMA and LAA methods.

Doi Ton Flora			leaf size class (Manual of leaf architecture)				
Morphotype	%	number of specimens scored	nanophyll	microphyll	notophyll	mesophyll	MLnA
A		1				9.11	9.11
B		1		6.51			6.51
C		1			8.01		8.01
E		5		6.51	8.01		7.26
F		3		6.51			6.51
H		5		6.51	8.01	9.11	7.88
I		1		6.51			6.51
J		3	4.32		8.01		6.17
K		2	4.32				4.32
O		1		6.51			6.51
P		1		6.51			6.51
R		3	4.32	6.51			5.42
S		1		6.51			6.51
T		1		6.51			6.51
U		2			8.01		8.01
V		1		6.51			6.51
W		1		6.51			6.51
X		1		6.51		9.11	7.81
Y		2		6.51			6.51
Z		1		6.51			6.51
AA		1		6.51			6.51
AB		1		6.51			6.51
AC		2		6.51			6.51
			0.1	0.6	0.2	0.1	6.7

in Doi Ton are entire margined. Ninety six percent of fossil morphotypes observed possess entire margins while 4% of leaf morphotypes show a toothed margin. This ratio is indicative a higher mean annual temperature (Bailey & Sinnott, 1916; Wolfe, 1979; Wing & Greenwood, 1993; Royer *et al.*, 2005; Su *et al.*, 2010; Steart *et al.*, 2010). The range of temperatures suggests the vegetation is as in a tropical zone, such as a tropical dry forest (Murphy & Lugo, 1986). But only a single leaf in the Doi Ton leaf morphotypes has a toothed margin is a small sample size and can introduce uncertainty into the estimation of mean annual temperature. There are different calibrations based on modern vegetation in other parts of the world. For example, the Australian LMA is more appropriate for a Thailand fossil flora, as like Australia, Thailand does not experience freezing in winter and many of the samples in the Australian calibration are tropical sites (MAT 18°C–25°C) with many of these showing seasonally dry climates (Wolfe, 1979), as seen in the monsoonal forests of Thailand. One should be cautious with using the error for LMA, as original modern calibration for all modern samples has a variance of 2°C simply from the natural year to year variation seen in meteorological/weather station data, the error from the fossils cannot be smaller than 2°C. (Royer *et al.*, 2005; Su *et al.*, 2010).

Leaf size is valuable for estimating climatic conditions. Larger leaves are enriched in the mesic environment compared to the dry environment (Webb, 1968; Dilcher, 1974; Dolph & Dilcher, 1980a, b; Givnish, 1984). Following Webb (1968), who studied the leaf size and margin types of the rain forest plants in Australia for subdividing the forest types, for Doi Ton, there are 34% of the large leaf class (e.g., 13% mesophyll; 21% notophyll), 66% microphyll (small leaf class) and 96% with entire margins. The leaf size ratio and margin type agree well with data of the semi-evergreen vine thicket (SEVT) sub-formation of the rain forest. This interpretation can be used for reconstructing the palaeoforest that was a source of Doi Ton leaf fossils, which is also similar to the present day South East Asian forest type. The palaeoforest of Doi Ton had an abundance of microphyll and smaller leaf sizes. The canopy level was uneven at 4.5–9 m, with mixed evergreen, semi-evergreen and deciduous emergent to 9–18 m. This forest was in the subtropical rain forest region with lowland and lower montane forests. Moreover, the proportion of leaf sizes was used to estimate the rainfall in tropical Africa by Jacobs (1999). The study of Jacobs found that the ratio of the large leaves (notophyll + mesophyll + macrophyll)

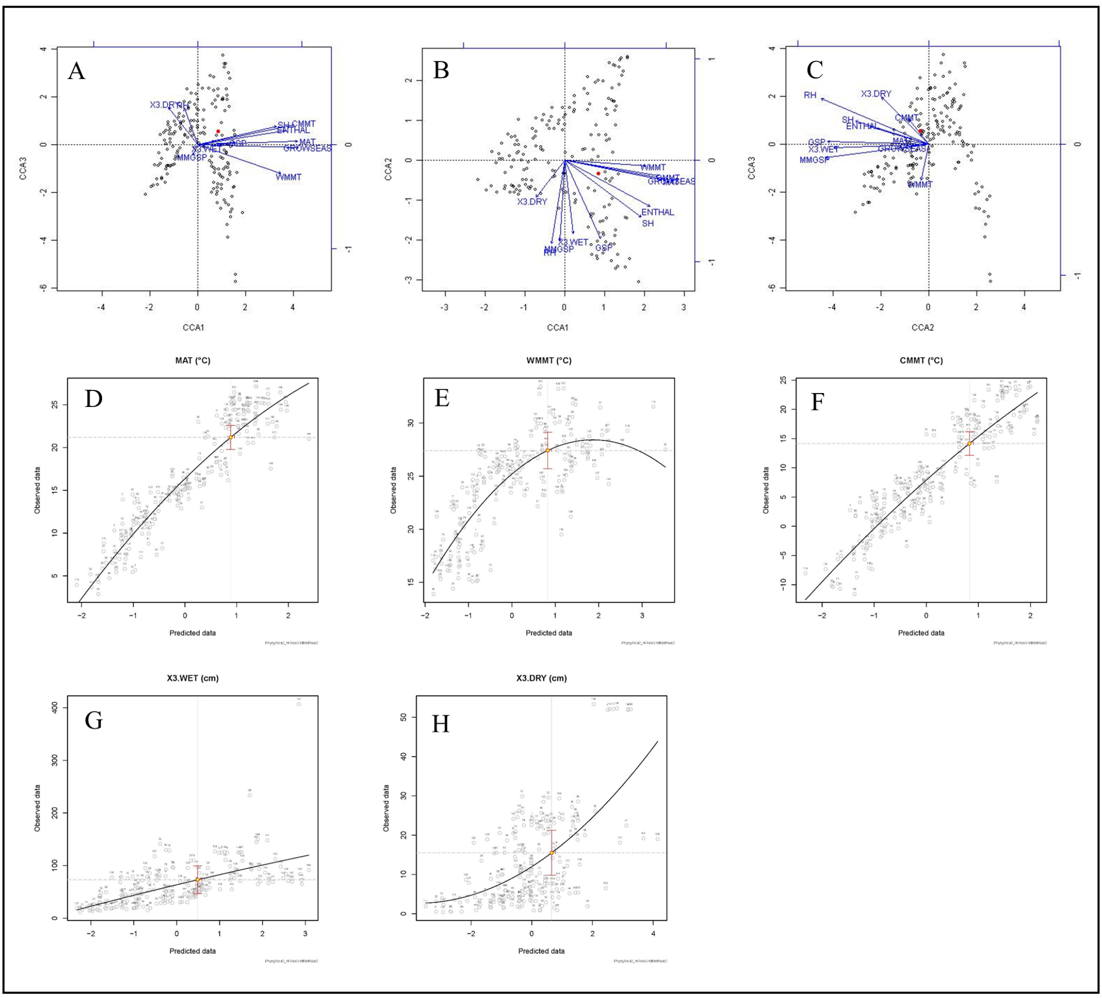

Figure 5. CCA plots showing the relationship between the leaf fossil morphology and modern vegetation A. Axes 1 vs 3 B. Axes 1 vs 2 C. Axes 2 vs 3 D. Regression model for mean annual temperature E. Regression model for warmest month mean temperature F. Regression model for coldest month mean temperature G. Regression model for precipitation on three-wettest month H. Regression model for precipitation on three-driest month.

vs small leaves (leptophyll + nanophyll + microphyll) was positively correlated to mean annual precipitation, that can use to interpret the palaeoenvironment of Doi Ton area. There are 31% larger leaves and 69% smaller leaves, indicating a relatively dry environment. The proportion is similar to the deciduous forest of the study sites of Africa, such as the Arabuko-Sokoke Natural Reserve deciduous forest in Kenya and the Lengwe deciduous forest in Malawi.

The forest types from LMA and LSI are very close to the present vegetation widely distributed in the Mae Sot area. Nevertheless, the large number of small leaves are of concern, because large leaves are easily broken while being transported to the deposition site. Moreover, the smaller leaves and their characters are also associated with the condition of temperature (e.g., altitude or latitude), soil character (moisture, draining, nutrient) and lightness and spaces of the forest (Jacobs, 1999; Royer *et al.*, 2005; Greenwood, 2007).

Mean annual temperature and mean annual precipitation of the Doi Ton site can be used to construct the vegetation based on the Whittaker biomes classification scheme (Whittaker, 1975). Palaeoforest is matched with the seasonal tropical rain forest known as semi-evergreen forest, tropical mixed or moist deciduous forest by the data of CLAMP. The LMA and LAA analyses provide the plot slightly outside seasonal tropical rain forest's modern biomes (Fig. 6).

The wide range of precipitation of CLAMP can be the evidence of a period of aridity during the summer months. That means that the palaeoflora indicates a different distribution of precipitation throughout the year. However, the dryness data has never been supported by other leaf quantifiable analyses.

Comparing the MAT and MAP data of Doi Ton leaf assemblages with the present-day (Thai Meteorological Department, 2010), over 30 years

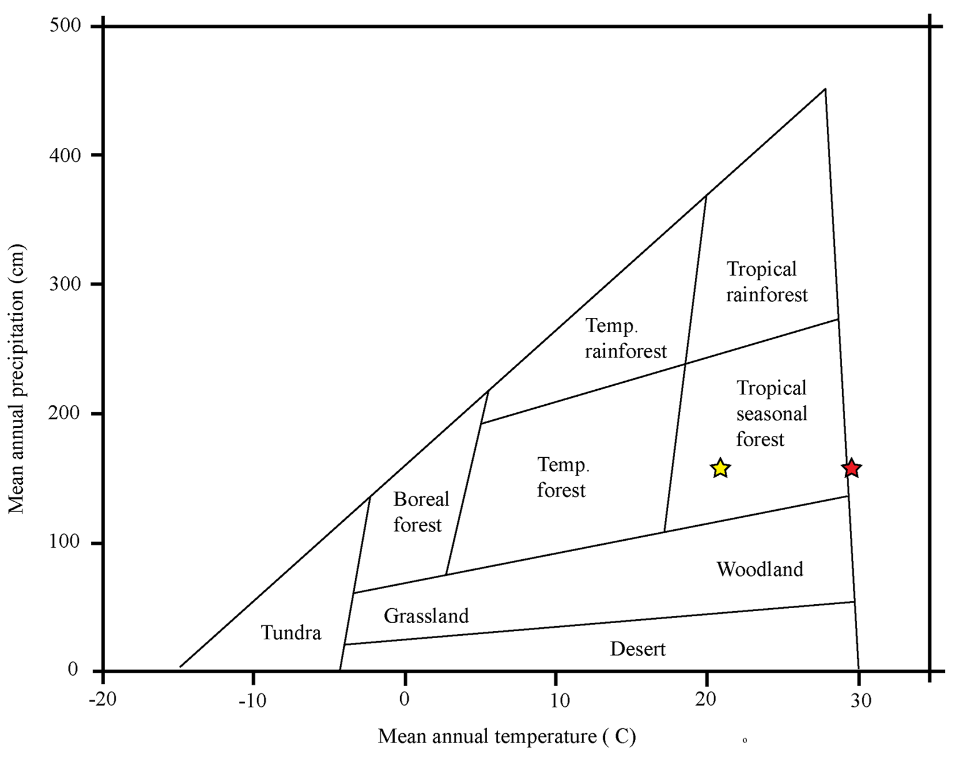

Figure 6. Climatic distribution of Doi Ton site. Red star is represented MAT from LMA and MAP from LAA. Yellow star is represented MAT and MAP from CLAMP. The biomes followed Wittaker (1975).

the mean annual temperature and mean annual precipitation are similar. The MAT from LMA indicates that temperatures were hotter than the present-day, in the range of 32.3°C ± 1.2 from the fossil data and 26.15°C nowadays. On the other hand, the CLAMP indicates MAT as 21.2°C. The MAT from CLAMP suggests that the climate was cooler than nowadays but the WMMT is close to MAT of Mae Sot today, which may be the effect of CLAMP uncertainty. The MAT derived from LMA (32.3 ± 1.17°C) and CLAMP (21.2°C) are obviously different and not close in value to each other. But, nevertheless, similar values occur in hot and tropical climatic conditions today including those existing at Mae Sot currently. Also, the precipitation, the fossil data and present-day are in very good agreement. The precipitation from the fossil data, which is derived by LAA and CLAMP, is in range of ~ 1,250 mm/yr – ~ 1,549 mm/11 months, and the present day is 1,230.9 mm/yr. This means the climate of the LAA is more similar with the present day than the CLAMP result.

Results from CLAMP can be underestimated values when compared with the single variable model because some characters for scoring are ambiguous (Wilf, 1997; Green, 2006) and not clearly related to climate parameters. According to Wilf, 1997; Kowalski & Dilcher, 2003; Royer, 2012; and West *et al.*, 2015, who studied the palaeoclimate by LMA, LAA, and CLAMP, MAT of CLAMP was no more precise than LMA, while precipitation is overestimated as compared with LAA. LAA and LMA analyses may both be affected by taphonomic conditions that can make a high uncertainty for estimation. Moreover, all methods use dicot plants to interpret palaeoclimate and disregarded other plant types. The study of other taxa of plants may increase the accuracy of the reconstructions.

The quantitative palaeoclimate of CLAMP results from Doi Ton were compared with the CLAMP results of Cenozoic leaf floras from the adjacent areas (China and India) because the vegetation will show a similar character when controlled by the same climate zone.

Previous study of plant fossils and palaeoclimate since the Cretaceous to Palaeocene (Wolfe & Upchurch, 1987; Spicer & Corfield, 1992; Pirrie & Marshall, 1990; Wolfe, 1990; Wilf *et al.*, 2003) do not conform together with Doi Ton climate and vegetation. Most plants in the Cretaceous to Palaeocene were deciduous and located in the cool temperate regions with a 5°C to 13°C mean annual temperature. Moreover, sedimentary rock data from the southern hemisphere suggest the palaeotemperature varied between 10°C to 20°C (Wolfe & Upchurch, 1987; Spicer & Corfield, 1992; Pirrie & Marshall, 1990).

The climate from leaf fossils of Doi Ton (MAT = 21.2°C, GSP = 154.9 cm) suggests the climate parameters maybe similar to the palaeoclimate based on Eocene data from south China; Changchang (MAT = 21.5°C, GSP = 201.35 cm) and Youganwo (middle Eocene) (MAT = 20.2°C, GSP = 233.4 cm), Huangniuling (late Eocene) (MAT = 22.35°C, GSP = 236.45 cm), and northwest India; Gurha (early Eocene) (MAT = 25.2°C, GSP = 181.5 cm) (Table 2) (Fig. 7) (Spicer *et al.*, 2016), more than the other site with leaf fossils from early Oligocene to early Pleistocene.

The geographic location of western Thailand and south China have little changed since the late Cretaceous (Spicer *et al.*, 2014). The early Eocene climate of India was probably hotter and rainier than Doi Ton and south China because the palaeolatitude of the Indian plate was situated in southern and nearer the equator than today. After that, during the middle Eocene, the Indian plate moved northward from the southern pole (Metcalfe, 2017) and was situated at the same latitude as Doi Ton (including western Thailand) and south China (Fig. 8). Thus, the palaeoclimate correlation between northwest India, western Thailand, and south China is easy to compare and more reliable because the palaeolocation is similar. During the early Eocene, the Doi Ton climate parameters do not match with the India's climate. Doi Ton shows a lower MAT, drier than India, because at this time India was at a lower latitude, nearer to the equator, which resulted in high temperature and precipitation.

The MAT of Doi Ton disagrees with the middle Eocene of India. Doi Ton was as cold as south China, but colder than India. WMMT of Doi Ton is similar to both south China and India, but CMMT is closer to that of India than south China, which was hotter than south China. These comparisons are the only aspect of climate parameters that cannot be accurately dated to the geologic age (ideally estimated)

Table 2. CLAMP climate reconstruction for Asia Eocene to Pleistocene fossil assemblages and Doi Ton.

Sites	Age	MAT (°C)	WMAT (°C)	CMAT (°C)	LGS (months)	GSP (cm)	MMGSP (cm)	3-WET (cm)	3-DRY (cm)	3W/3D	RH (%)	References
Arunachal Pradesh Upper Siwalik	ePle	25.4	28.1	20.9	12.6	189.9	15.9	101.6	9.0	11.3	82.4	Khan *et al.*, 2014
Arunachal Pradesh Middle Siwalik	Pli	23.7	28.1	16.9	12.1	198.1	17.9	99.4	13.8	7.2	78.8	Khan *et al.*, 2014
Arunachal Pradesh Lower Siwalik	mM	25.3	27.8	21.3	12.5	174.1	14.0	96.2	7.3	13.2	81.2	Khan *et al.*, 2014
Darjeeling Lower Siwalik	mM	25.4	28.4	17.9	13.0	242.3	24.5	111.7	28.9	3.9	81.0	Khan *et al.*, 2014
Tirap (India)	lO	26.1	27.9	20.7	13.7	246.0	20.6	138.1	6.7	20.6	76.6	Srivastava *et al.*, 2012
Shangcun Flora (souther china)	eO	23.1	28.2	12.0	12.3	225.0	23.4	103.7	20.0	5.2	70.8	Herman *et al.*, 2017
Huangniuling Upper (souther china)	lE	24.0	28.4	15.0	12.0	240.1	25.3	114.3	26.9	4.2	80.1	Spicer *et al* ., 2014
Huangniuling Lower (souther china)	lE	20.7	28.4	8.9	11.4	232.8	25.3	104.6	32.7	3.2	75.0	Spicer *et al* ., 2014
Changchang 1 (souther china)	mE	21.6	28.4	11.2	11.7	200.7	19.5	87.7	21.2	4.1	68.4	Spicer *et al* ., 2014
Changchang 2 (souther china)	mE	21.3	28.4	10.8	11.5	202.0	19.7	88.0	22.6	3.9	69.0	Spicer *et al* ., 2014
Youganwo (souther china)	mE	20.2	28.4	7.9	11.3	233.4	25.7	103.7	34.9	3.0	74.4	Spicer *et al* ., 2014
Gurha 39 m (India)	eE	26.4	28.2	19.0	12.0	183.8	15.8	98.4	8.3	11.9	78.6	Shukla *et al* ., 2014
Gurha 72 m (India)	eE	23.9	27.2	18.2	12.0	179.2	15.3	93.8	10.6	8.8	78.0	Shukla *et al* ., 2014
Doi Ton		21.2	27.4	14.2	11.1	154.9	13.4	73.0	15.5	4.7	70.6	This study

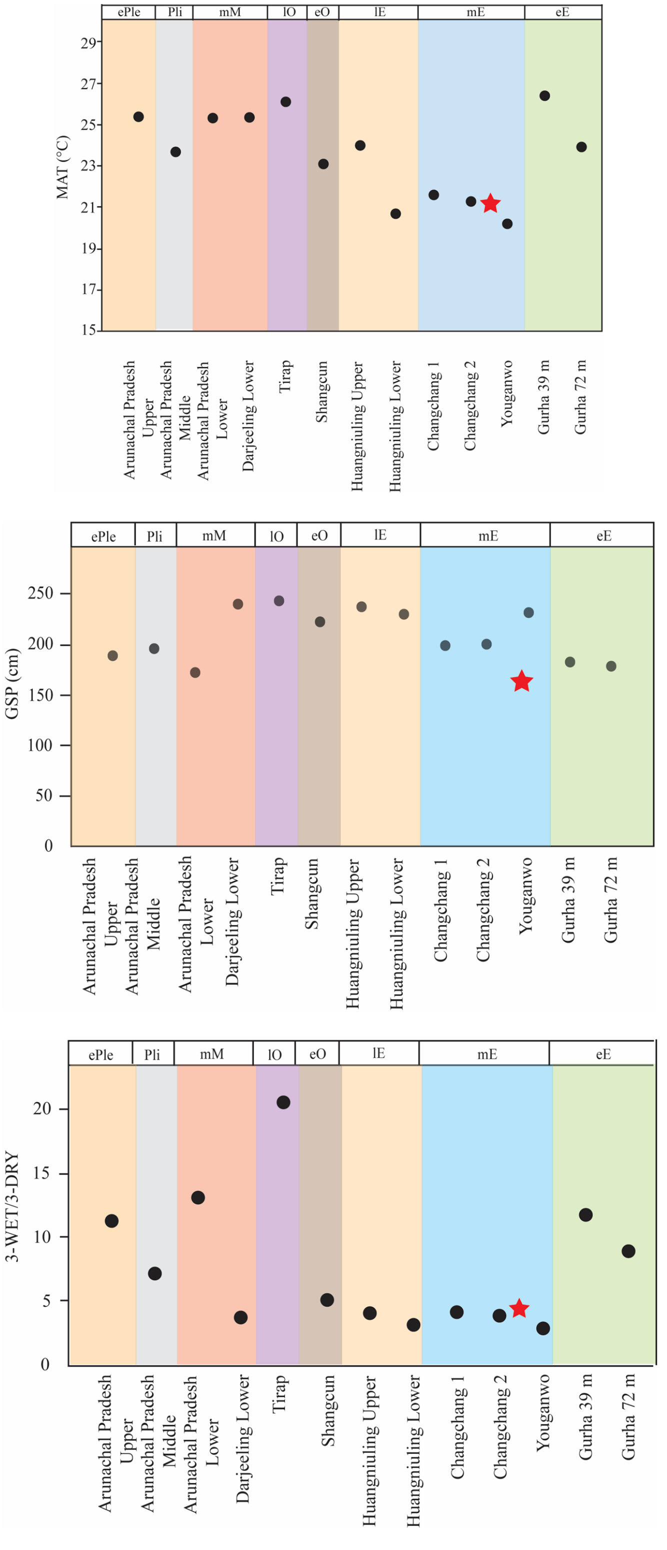

Figure 7. The CLAMP comparison of Cenozoic leaf fossils from north India, south China, and Doi Ton (red star). A. MAT comparation B. GSP comparison C. The ratio of precipitation on three-wettest month and three-driest month.

which can only be estimated independently using biostratigraphy or some chronostratigraphic method. Moreover, the fewer data of climate from leaf fossils in Thailand and neighbouring areas can be make it difficult to propose an exact age. The palaeoclimate interpretation of this work can, perhaps, shed light on the climate from Doi Ton leaf fossils allowing comparison with adjacent areas.

Moreover, Doi Ton's CLAMP data also show the Doi Ton assemblages lie close to the humid subtropical climate of present-day vegetation from southwest China (Mengla and Pingbian, Yunnan) and southeast China (Zhaoqing, Guangdong) (CLAMP website), which show a humid subtropical climate.

The difference of precipitation between wet and dry seasons of Doi Ton suggests the plants are slightly affected by monsoon phenomenon, but not to a large extent. That means Doi Ton's monsoon mirrored highly precipitation throughout the year or wetter dry period. This result can be used as a proxy to indicate the monsoon character at that time. The monsoon of SE Asia is caused by the strength of the humid wind in the summer period more than the

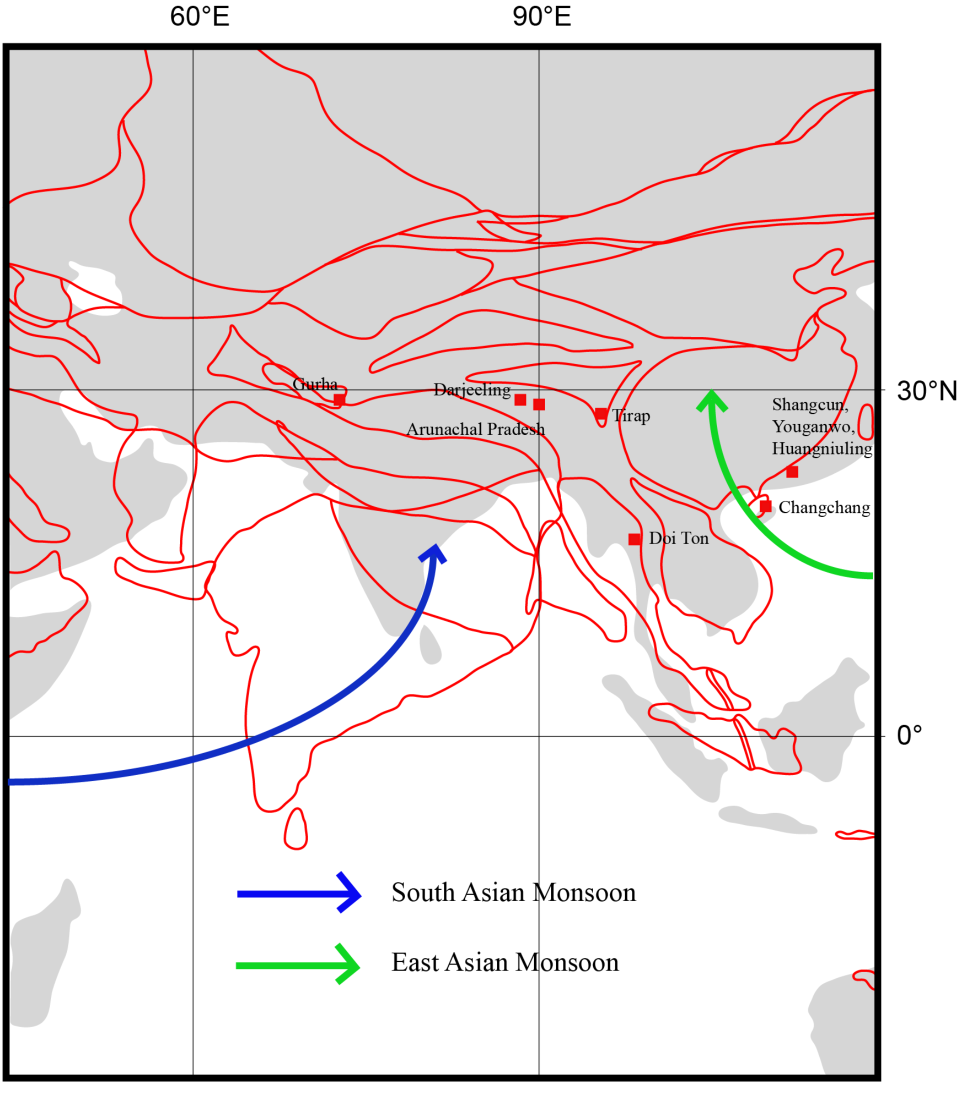

Figure 8. The palaeolatitude and palaeogeographic map showing of Doi Ton, India, and south China landmass at 40 Ma. (red line) with present-day (grey area) and the monsoon direction (modified from Plate Tectonic Reconstruction Service, 2011).

strength of dry wind in winter period. Doi Ton leaf fossils indicate that the monsoon at that time was weak. This suggestion conforms to that of Huber & Goldner (2012), who show weak effects by the monsoon in SE Asia during Eocene. This is caused by the lack effect of humid wind in the East Asian Monsoon during the summer period.

Leaf traits are significantly more strongly related to mean annual temperature than mean annual precipitation (Moles *et al.*, 2014). So, the result of precipitation of Doi Ton leaf assemblages may not be of precise value. Leaf characters and leaf diversity of Doi Ton were directly affected by pre- and post-deposition processes (i.e., transportation, sorting, deposition pattern, and decay by organism or diagenesis). In fluvial environment, leaves are considered as parautochthonous, which are derived from near the location of the living plant (Gastaldo *et al.*, 1996; Greenwood, 2005; Kunzmann & Walther, 2007; Su *et al.*, 2010). The preservation of the flora can be an indicator of the volume of leaf character information that has been lost along the process. Leaves falling from the forest into the stream or lacustrine must originate within 50 m of the water if the leaf materials are to be transported in high quantity. Moreover, the increasing intensity of leaf fragment and clustering of leaves suggest fluvial deposit (Gastaldo *et al.*, 1996). This means the plant growing along river or bank environments has a high chance of being deposited during a period of flooding more than plants in another environment. This suggests that the Doi Ton leaves were possibly deposited in fluvial environments.

Most of fossil leaf reports come from the Li Basin, north Thailand (Grote, 2005; Sawangchote *et al.*, 2010). In addition, the Tertiary basins of north Thailand include Mae Moh Basin, Na Hong Basin, Mae Lamao Basin, and Chiang Muan Basin present the temperate vegetation in Oligocene - early Miocene and tropical vegetation in early-middle Miocene (Songtham *et al.*, 2003). Temperate elements suggest that the north Thailand climate during the Oligocene - early Miocene was cooler than the present-day (Grote, 2005). The comparison of leaf fossils between Li Basin and Doi Ton is clearly different in terms of leaf characters, especially the margin character. Doi Ton leaves have a smaller proportion of toothed leaves than Li leaves, which implies that Doi Ton was hotter than Li. Vegetation types of Doi Ton and Li are similar; however, the details of climate are different. This evidence is supported by the 55 leaves morphotypes from Nong Ya Plong coal mine, western Thailand, which is the late Oligocene to early Miocene as Li Basin. Those leaves from Nong Ya Plong contain a high proportion of toothed leaves (Sawangchote, 2006). Additionally, palynological analysis from Li and Nong Ya Plong indicates the vegetation was a mix with temperate and warm species (Watanasak, 1988; Grote, 2005). That means the Doi Ton vegetation differs from the late Oligocene to early Miocene in both climatic factors and vegetation type. Vegetation of Doi Ton, Li, and Nong Ya Plong differ suggesting that they grew at different time periods. Moreover, Endo & Fujiyama (1995) examined the Miocene leaves from the oil shale in the uppermost part of the Mae Sot Group. These leaves were identified as *Bauhinia* sp., *Podogonium Knorrii* Heer, and *Apocynophyllum* sp. in the Miocene, which cannot compare with the Doi Ton leaf assemblage at all.

Furthermore, Doi Ton climate and vegetation also conform to the Krabi Basin. This interpretation of Krabi Basin was based on palynological study (Watanasak, 1990) and mammal fauna study (Benammi *et al.*, 2001). The vegetation and climate of Krabi Basin, late Eocene, is a tropical forest, hot and humid like the present-day. On the other hand, Doi Ton is not similar to the middle Pleistocene vegetation of northeast Thailand that comprised mixed evergreen-deciduous forest (Grote, 2006) or its climate is drier than Doi Ton.

CONCLUSION

The Doi Ton fossil flora consists of 23 angiosperm morphotypes and two unknown morphotypes. Doi Ton fossil floras present a new point of view of palaeoclimate parameters of western Thailand, which is like the present-day. Sedimentology and palaeobotanical evidence are illustrative of a seasonal tropical environment and vegetation in a warm climate with weak monsoon conditions. This indicates the semi-evergreen forest was a major constituent of Doi Ton palaeoecology. The comparison of the Cenozoic climate data from adjacent areas indicated that Doi Ton is similar climatically to south China and northwest India in the Eocene period. Moreover, the Doi Ton fossil flora is also similar to modern vegetation of humid climatic areas of south China. Likewise, the results should be critically considered and discussed in terms of taphonomic effects, taxonomic and climatological localization, e.g., some species are tolerant in a wide range of environmental conditions. Further work with a larger flora database or collection and accurate taxonomy are needed to confirm the palaeoclimate interpretation. Furthermore, independent assessment of the age of the Doi Ton formation is now needed to test our assessment based on flora and climate that this formation was likely Eocene in age.

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