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Paleovegetation of a Late Middle Pleistocene Fossil Site in Northeastern Thailand

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ABSTRACT. – Vegetation and environment during the cooler and drier periods of the Pleistocene in mainland Southeast Asia are still a controversial issue and need more evidence. In this study, a late Middle Pleistocene sediment sample from a prominent fossil site in northeastern Thailand was processed for pollen analysis and plant community reconstruction. The sediment layer was interpreted as an ancient river terrace from the late Middle Pleistocene. Pollen investigation revealed plants from various habitats: riparian, evergreen and deciduous forests, and also a high proportion of grasses. The evidence therefore suggests that the ecosystems of the area consisted of gallery forest and open woodland, where the gallery forest persisted along the ancient river and the landscape farther from the river appeared to be open woodland in which *Quercus* dominated.

KEYWORDS: palynology, late Middle Pleistocene, gallery forest, open woodland, Northeastern Thailand

INTRODUCTION

The Khok Sung sand pit in Nakhon Ratchasima Province, Northeastern Thailand has become the richest vertebrate Pleistocene fossil site of Thailand since thousands of important fossil specimens were discovered in 2005. Well preserved vertebrate fossils have been identified, including fish, gavials (*Gavialis* cf. *bengawanicus*) (Martin et al., 2012), tortoises (*Batangur* cf. *trivittata*, *Heosemys annandalii*, *Heosemys* cf. *grandis*, and *Malayemys* sp.), soft-shelled turtles (*Chitra* sp. and cf. *Amyda* sp.) (Claude et al., 2011), *Crocodylus* cf. *siamensis*, *Python* sp., *Varanus* sp. (Suraprasit et al., 2016), and 15 species in 13 genera of mammalian fauna, including a primate (*Macaca* sp.), a canid (*Cuon* sp.), a hyaenid (*Crocuta crocuta ultima*), proboscideans (*Stegodon* cf. *orientalis*, *Elephas* sp.), rhinocerotids (*Rhinoceros sondaicus*, *R. unicornis*), a suid (*Sus barbatus*), cervids (*Axis axis*, *Panolia eldii*, *Rusa unicolor*), and bovids (*Bos sauveli*, *B. gaurus*, *Bubalus arnee*, *Capricornis sumatrensis*) (Suraprasit et al., 2015, 2016). An abundance of plant fossils, such as fruits (Rhamnaceae, Dipterocarpaceae, Meliaceae, and Anacardiaceae), tubers (Cyperaceae), wood, seeds, leaves and resin were also found (Grote, 2007).

Various studies have attempted to reconstruct the vegetation history of the Southeast Asia region. During the Neogene (ca. 20 million years BP), the evidence showed that seasonal and everwet rain forests were present, extending from Indochina to Borneo (Muller, 1972; Morley and Flenley, 1987; Morley, 2012). During the Middle -Late Miocene, the areas occupied by the tropical rain forest reached as far north as southern China and southern Japan (Song et al., 1984; Tsuda et al., 1984, Jacques et al., 2014) and westward to northern India (Mathur, 1984). In Thailand, pollen evidence also reveals changes to a warmer and wetter climate during the Early or Middle Miocene transition (Songtham et al., 2003, 2005) and the existence of the seasonal (monsoon) tropical climates since the Late Palaeogene in northern Thailand (Malaikanok et al., 2023). During the Middle - Late Miocene the climate was not stable, with oscillations between tropical woodlands and grasslands in the North and widespread grasslands in the Northeast (Sepulchre et al., 2010).

During the Pleistocene, there is evidence of expansion of dry, cooler climates and seasonality in Thailand, Malaysia, and west Java (Morley and Flenley, 1987; van der Kaars, 1991; van der Kaars and Dam, 1995; Zheng and Lei, 1999; Morley, 2000; Penny, 2001; Meijaard, 2003; White et al., 2004; Tougard and Montuire, 2006; Louys and Meijaard, 2010; Yang and Grote, 2017). According to Heaney (1991), the rapid expansion of open savanna at that time, perhaps forming a 'savanna corridor' from Indochina to Java, allowed migration of 'savanna' plants and animals across the areas. Mammal fossils and isotope evidence from cave in Krabi (Suraprasit et al., 2019) also suggest savanna corridor in peninsular Thailand during the Pleistocene. However, this savanna corridor suggestion has been argued to be unlikely because there is no botanical evidence of a continuous seasonal climate corridor from north to south of Sundaland (Morley, 2012). The model studies to reconstruct climate and past vegetation reveal the widespread extent of rainforests that even covered a larger area than at present during the Last Glacial Maximum (Cannon et al., 2009). The sustainability of

dipterocarp rainforests in Sundaland during the Last Glacial Maximum is also supported by the climatic niches model (Raes et al., 2014). The rainforests had probably contracted or migrated further south because of the drier climate during the Pleistocene. However, they still persisted in several areas, such as west Sumatra, northwest Borneo, the Malacca Straits, and around Palawan (Morley, 2000; Meijaard, 2003; Cannon, 2009).

In Thailand, because of a lack of sufficient information covering the long time period involved, the ecosystem reconstruction during the glacial times remains debatable. It is still inconclusive how strong and extended the dry and seasonal climates were, or how persistent the rainforest areas were, throughout the time. At the prominent fossil site of Khok Sung, vertebrate fossils, most importantly the spotted hyena (*Crocuta crocuta ultima*), suggest open canopy habitats, such as semi desert, savanna, open woodland, or dense dry woodland (Suraprasit et al., 2015, 2016). This is in contrast with the presence of some degree of wet environment of the tropical mixed deciduous and dry evergreen forests as suggested by fruit and seed fossils, where many leaf and wood fossils were associated in the same layer of the same site (Grote, 2007). In this report, we analyze a pollen assemblage retrieved from the same layer with that of vertebrate, fruit and seed fossils from the ancient Mun River terrace at Khok Sung fossil site to reconstruct plant communities and environment of the late Middle Pleistocene.

Study area

The Khok Sung fossil site is situated near Khok Sung Village of Mueang District, Nakhon Ratchasima Province, at latitude 15°06'18" N, longitude 102°06'08" E, altitude 173 m a.m.s.l., approximately 15 km to the north of the city of Nakhon Ratchasima, along the highway No. 205. The site is located on the Khorat Plateau, which is situated in the central part of mainland Southeast Asia (Fig. 1: A). The area was an ancient river terrace of former floodplain deposition (Duangkrayom et al., 2014).

A sediment sample was collected for pollen analysis at a depth of approximately 5 meters, where remains of leaves, seeds and vertebrate fossils were abundant (Fig. 1: B, C). It is the same sedimentary unit from which the *Crocuta crocuta ultima* (Suraprasit et al., 2015), other mammalian and reptilian specimens (Suraprasit et al., 2016), and plant macrofossils (Grote, 2007) were retrieved and studied. Chaimanee et al. (2005) assigned these sediment layers to be sedimentary unit F, which is characterized by well-sorted dark-gray, subround to round, coarse-grained sands and matrix-supported gravels. The sedimentary unit is interbedded by some layers of silty mud lenses at its upper part. The presence of *Crocuta crocuta ultima* and the combined Uranium Series - Electron Spin Resonance (US-ESR) dating indicated the age of the deposit as the late Middle Pleistocene. The direct dating of tooth fossils by combined US-ESR techniques provides two possible ages of 130 ± 29 ka and 217 ± 36 ka (Duval et al., 2019).

The present climate of the fossil site is seasonal tropical. Sparse patches of deciduous dipterocarp and mixed deciduous plant communities are distributed around the site today. Dense and spacious forests exist south from the site, around 60 km, at the southwestern boundary of the Khorat Plateau, where two national parks, Khao Yai National Park and Thap Lan National Park, are located. This forest area is mountainous, ranging from 250-1,351 m a.m.s.l., with 5 categories of vegetation type, deciduous dipterocarp forest, dry mixed deciduous forest, seasonal rain forest, hill evergreen forest, and grassland and secondary growth (Santisuk, 2012).

MATERIALS AND METHODS

The 20 g of dark gray clay sediment sample were processed for palynological analyses by using various chemical treatments, including HCl for $CaCO_3$ removal, HF for siliceous matter removal, and acetolysis mixture for cellulose removal (Erdtman, 1960; Paudayal, 2002). No staining was necessary since the pollen grains became yellow upon treatment. The palynomorphs were identified, counted, and photographed with a light microscope (Zeiss: Axio Lab. A1) with a magnification of 400x. A scanning electron microscope (SEM) (Carl Zeiss: AURIGA) was also used for detailed morphological observation. After taking photographs of a selected pollen grain under the light microscope, the same pollen grain was moved from the glycerine slide using a specially adapted needle with a human hair glued at the tip (Zetter, 1989; Ferguson et al., 2007) and placed on a SEM stub. The specimen was then coated with gold, investigated, and photographed with the scanning electron microscope. The identifications were made by comparison with reference collections and illustrations in the literature, according to the morphological characteristics: position and number of apertures, shape, size and exine sculpture. The terminology to describe pollen grains follows Punt et al. (2007) and Halbritter et al. (2018). The pollen percentage calculations are based on the counting of 509 grains of pollen and spores.

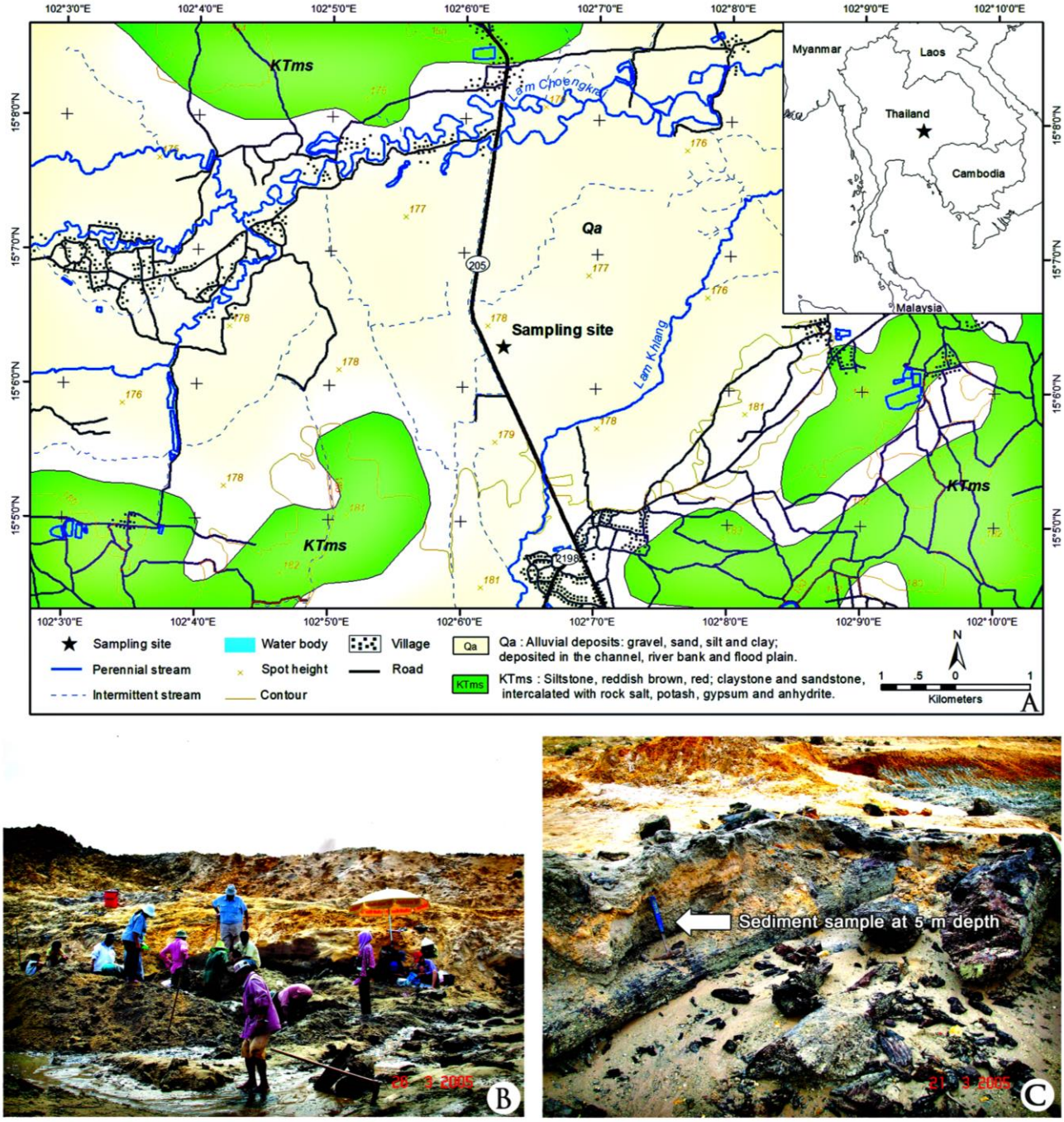

FIGURE 1. (A) Map of the study site at Khok Sung locality, (B, C) photographs showing the study site during the excavation in March, 2005, (C) arrowing show position of the sedimentary layer at 5 m-depth. (Map produced by Tharaphong Phetprayoon, photographs by Jaroon Duangkrayom)

RESULTS AND DISCUSSION

Late Middle Pleistocene Palynoflora

Palynomorphs in this study were identified mostly to the genus or family levels. They are in 18 families with 10 genera of angiosperms as follows: Acanthaceae (*Justicia*); Anacardiaceae, Aquifoliaceae (*Ilex*), Arecaceae, Asteraceae, Bignoniaceae, Chenopodiaceae, Cyperaceae, Dipterocarpaceae (*Hopea/ Shorea*), Ebenaceae (*Diospyros*), Euphorbiaceae (*Croton, Homonoia, Mallotus*), Fabaceae (*Albizia*), Fagaceae (*Quercus, Quercus* section *Cyclobalanopsis)*, Malvaceae, Poaceae, Rosaceae, Ulmaceae (*Ulmus*), Urticaceae *(Urtica*), and one family with one genus of conifers, Pinaceae (*Pinus*). There are various types of pteridophyte spores, including Selaginellaceae. Based on a count of 509 pollen grains, the percentages of palynomorph types are presented in Fig. 2, and microphotographs of selected palynomorph types are shown in Fig. 3 and 4. Morphology of pollen and their ecological characteristics are discussed below.

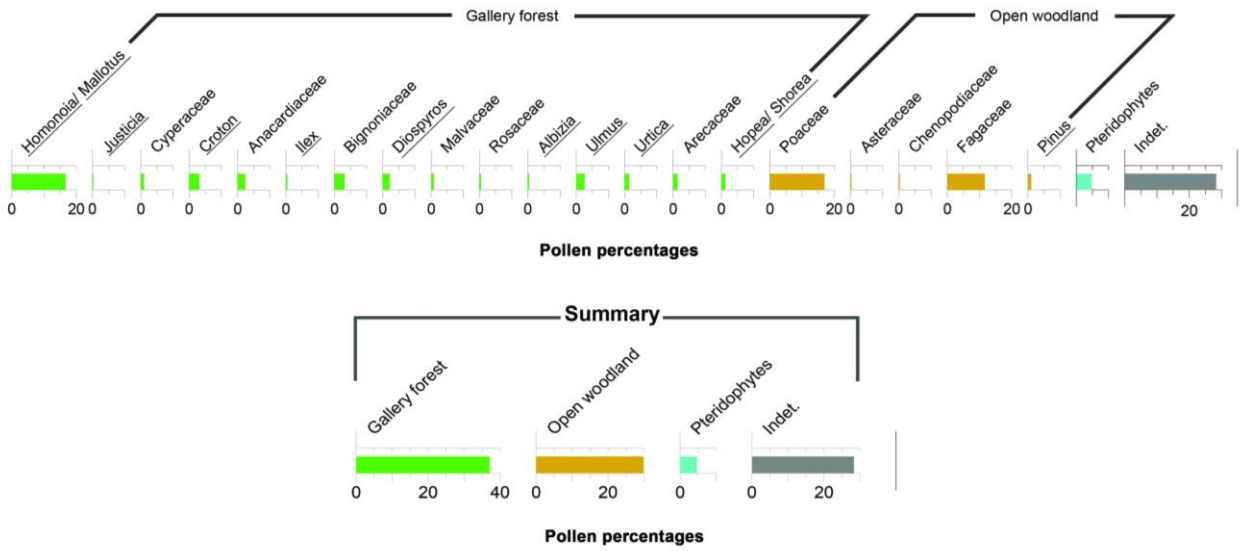

FIGURE 2. Percentages of pollen types associated in the pollen assemblage.

Three genera of pollen from the family Euphorbiaceae, *Homonoia*, *Mallotus* and *Croton*, were present in the sample. *Mallotus* and *Homonoia* together were the most abundant comprising 16.7%, while *Croton* was 3.1 % of the total pollen.

Mallotus is a large paleotropical genus, comprising 150 species ranging from Africa and Madagascar through South and Southeast Asia and Malesia to Australia and the West Pacific. In Thailand, there are 39 species of *Mallotus* (van Welzen and Chayamarit, 2007). *Mallotus* species are shrubs to trees and have been found growing in many different habitats, including various types of evergreen, deciduous, and bamboo forest. They often grow in disturbed areas, including areas damaged by fire or human activity, and some are pioneer species (van Welzen and Chayamarit, 2007; Sierra et al., 2007). Parent plants of *Homonoia* are also shrubs to small trees. They are rheophytes, which can be found as groups on river banks. There are 2 species of this genus in Asia, with one restricted to Central India, and another, *Homonoia riparia*, widespread from India to China and Taiwan, from Malesia to New Guinea, and the only species found today in Thailand (van Welzen and Chayamarit, 2007).

Homonoia/*Mallotus* pollen is circular in polar view, 20-27 µm wide, with tricolporate apertures, colpi 7.5-8.0 µm long. Pollen of these two genera is very similar when observed under the light microscope so they were lumped together in pollen counting. However, there are minor differences in sculpture patterns observed under the scanning electron microscope (SEM) between *Mallotus* (Fig. 3: 1-3*)* and *Homonoia* (Fig. 3: 4-6). *Homonoia* sculpture is uniformly nanoechinate with dense and random arrangement, whereas that of *Mallotus* is uniformly perforate-nanoechinate with random arrangement (Nowicke and Takahashi, 2002). There are also similarities between *Mallotus* and *Macaranga* pollen morphology. *Macaranga* was excluded by the smaller size of the pollen grains. In addition, the pollen sculpture under SEM of *Macaranga* is more loosely (micro/nano) echinate and perforate than that of *Mallotus* (Takahashi et al., 2002; Lee et al., 2010).

Croton pollen was represented by 3.1% of the total palynomorphs. Pollen is spheroidal, inaperturate with a croton-pattern sculpture (Fig.3: 7-9). *Croton* spp. are trees, shrubs or herbs, sometimes climbers. It is a large genus with 800 or more species distributed mostly pantropically, with the center of diversity in tropical America. There are slightly fewer than 100 species in Asia, with 31 species found in Thailand. *Croton* species have wide ecological ranges. They can grow in evergreen and deciduous forests, on stream banks, in peat swamps, dry deciduous oak forests, the understory of dry deciduous forests, dry and savanna-like dipterocarp forests, open grasses or high grass savannas (Chayamarit and van Welzen, 2005).

Cyperaceae pollen was represented by 1.0% of the total. Pollen of Cyperaceae is prolate, 20-30 µm in length, with 1-6 elongate or spheroid apertures. Its exine sculpture is nanoechinate and perforate with areolae and microechini at the aperture membrane as observed under SEM (Fig.3: 10-12). The parent plants are annual or perennial, rhizomatous to stoloniferous herbs. There are 277 species found in Thailand (Phonsena, 2017), which mostly grow in wet places, swamps, or along river banks (Simpson and Koyama, 1998).

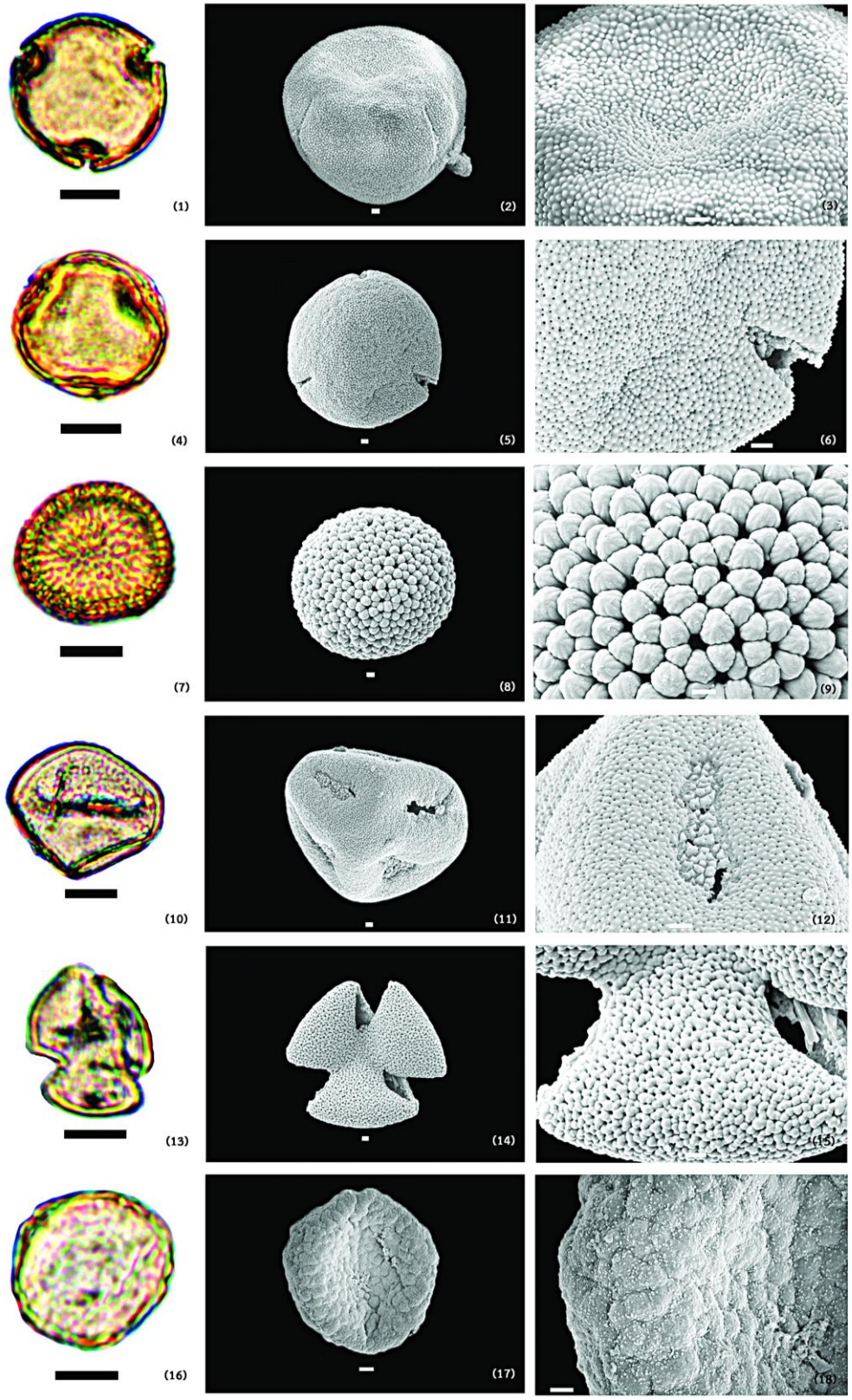

FIGURE 3. Some pollen types present in the Khok Sung sediment sample. Light microscope (1, 4, 7, 10, 13 and 16) and scanning electron microscope (2, 3, 5, 6, 8, 9, 11, 12, 14, 15, 17 and 18) microphotographs. (1-3) *Mallotus* sp.; (4-6) *Homonoia* sp.; (7-9) *Croton* sp.; (10-12) Cyperaceae; (13-15) *Hopea*/*Shore*a sp.; (16-18) *Ulmus* sp. Scale bars: 10 μm (1, 4, 7, 10, 13 and 16); 2 μm (17); 1μm (2, 3, 5, 6, 8, 9, 11, 12, 14, 15, and 18).

Hopea/*Shorea* pollen in Dipterocarpaceae was represented by 1.2% of the total. The pollen is circular in polar view, with tricolpate apertures having long and narrow colpi. The exine sculpture under SEM is

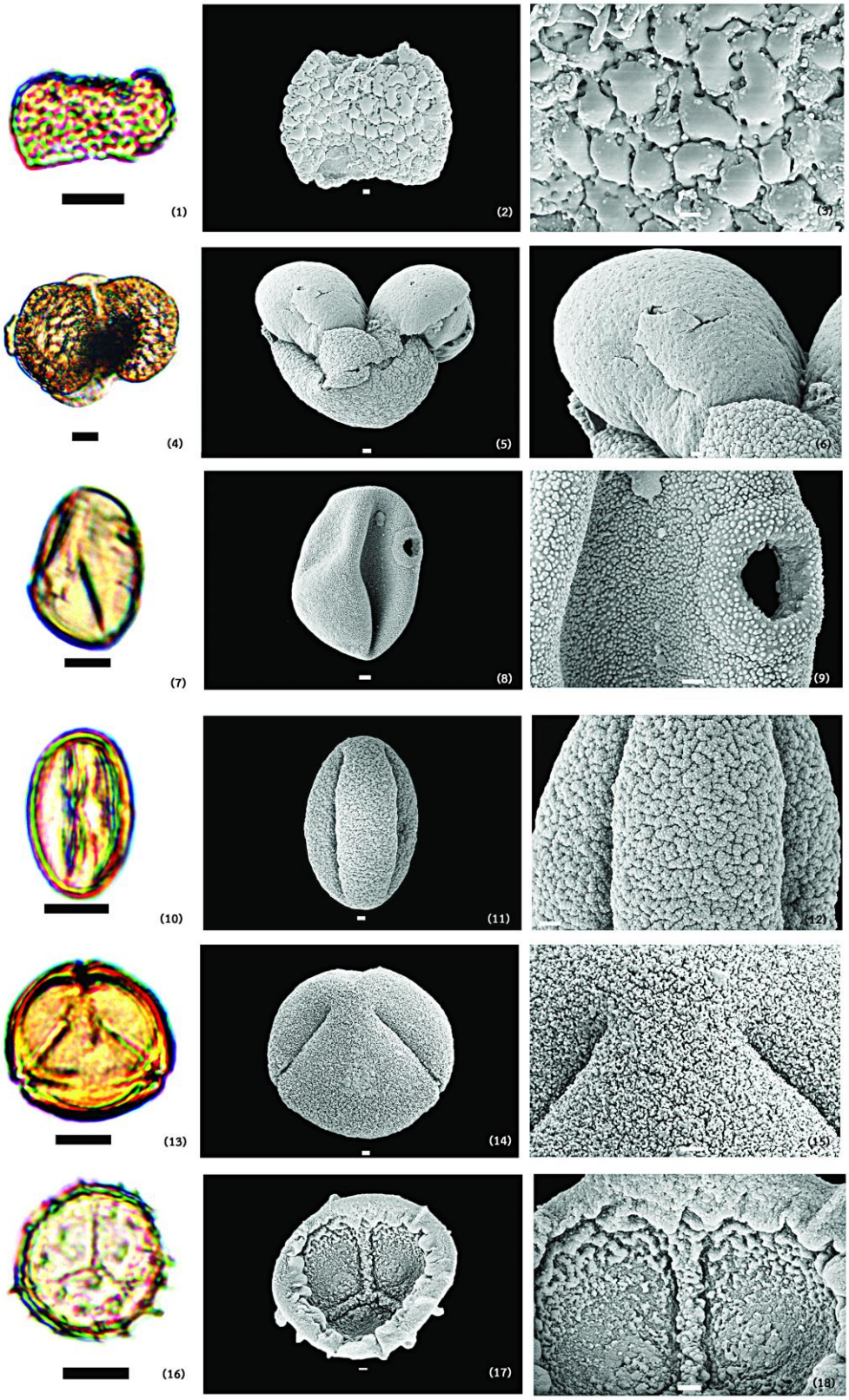

FIGURE 4. Some pollen and spore types present in the Khok Sung sediment sample. Light microscope (1, 4, 7, 10, 13 and 16) and scanning electron microscope (2, 3, 5, 6, 8, 9, 11, 12, 14, 15, 17 and 18) microphotographs. (1-3) Arecaceae; (4-6) *Pinus* sp.; (7-9) Poaceae; (10-12) *Quercus* section *Cyclobalanopsis* sp.; (13-15) *Quercus* sp.; (16-18) Selaginellaceae. Scale bars: 10 μm (1, 4, 7, 10, 13 and 16); 2 μm (5); 1μm (2, 3, 6, 8, 9, 11, 12, 14, 15, 17 and 18).

microreticulate to perforate-rugulate with transverse arrangement on the surface of muri/rugulae (Fig. 3: 13-15). Dipterocarpaceae are mostly restricted to Asia where *Hopea/Shorea* grow in tropical rainforest and

dry evergreen forest, with some species occurring in deciduous dipterocarp, pine deciduous dipterocarp or pine-oak deciduous dipterocarp forests (Pooma et al., 2017).

Ulmus (Ulmaceae) pollen was represented by 2.6% of the total. The pollen is spheroidal, with 5-porate apertures, and verrucate to rugulate with microgranulate sculpture under SEM (Fig. 3: 16-18). Only one species of this genus, *Ulmus lanceifolia*, occurs in Thailand today, found in evergreen forests or by streams in mixed deciduous forest or scrub jungle (Phuphathanaphong, 2015).

In addition, pollen of Arecaceae (1.4%), disulcate and areolate under SEM (Fig. 4: 1-3), *Justicia* in Acanthaceae (0.2%), Anacardiaceae (2.4%), *Ilex* in Aquifoliaceae (0.4%), Bignoniaceae (3.1%), *Diospyros* in Ebenaceae (2.2%), *Albizia* in Fabaceae (0.4%), Malvaceae (0.8%), Rosaceae (0.4%) and *Urtica* in Urticaceae (1.4%) were found in the assemblage (Fig. 2). Those pollen taxa could be produced by parent plants that are commonly found in various types of evergreen and deciduous forests.

The bisaccate pollen of *Pinus* (Pinaceae) (Fig. 4: 4-6) was represented by 1.0% of the total. There are 2 indigenous species of *Pinus* in Thailand today, *P. kesiya* and *P. latteri* (sometimes included with *P. merkusii* (Businský, 2014)), which grow naturally in various areas of lower montane and occasionally lowland forests, including pine-deciduous dipterocarp forest, pine-oak-savanna and lower montane pine-oak forest in the west, north and northeast. Of the 2 species in Thailand, *P. latteri* occurs at lower altitudes, most commonly below 1,000 m. a.m.s.l., but is found as scattered stands in southwestern Thailand at 70-250 m. *P. kesiya* is generally found at higher altitudes, from 1,000 - 1,500 m a.m.s.l. *P. latteri* is more tolerant to high temperatures than *P. kesiya* (Santisuk, 1997; Werner, 1997). *Pinus* is a wind pollinated tree. Pollen grains with two wings or air bladders are produced in large amounts and can be dispersed very far from their parent plants (Williams, 2010). Therefore, the low percentage of *Pinus* pollen may suggest a less significant contribution to local vegetation of the site.

Poaceae was represented by 16.9% of the total palynomorphs. Pollen is spheroidal, ulcerate with annulate and areolate with microechinate under SEM. (Fig. 4: 7-9). Although Poaceae have been used as an indicator of openness and a strong signal of savanna vegetation or grassland (Bush, 2002), actually they can live in a wide range of environments including the temporary wet conditions of marsh and ponds, as well as in poor nutrient soil (Guimarães et al., 2017).

Quercus in Fagaceae was represented by 11.6% of the total palynomorphs. The pollen has a prolate shape and tricolporate apertures (Fig. 4: 10-15). The characteristics of microrugulate with nanoechinate suprasculpture under SEM of pollen in Fig. 4 (10-12) suggest *Quercus* section *Cyclobalanopsis* (Malaikanok et al., 2023). Presence of various pollen types of *Quercus* indicates the diversity of *Quercus* growing in deciduous or evergreen forests (Liu et al., 2007). The genus *Quercus* is anemophilous, so the pollen may not be from the immediate vicinity of the site of deposition. Today, there are 29 species, 1 subspecies and 1 variety of *Quercus* indigenous to Thailand (Menitsky, 2005; Phengklai, 2008).

The unique spheroidal shape with pantoporate aperture pollen (> 6 apertures) of Chenopodiaceae was represented by 0.2% of the total palynomorphs. This pollen type shares similarities with *Liquidambar* pollen in Altingiaceae family. However, *Liquidambar* can be excluded by the thinner exine membrane and a smaller number of apertures (Willis, 2018). Plants in Chenopodiaceae family commonly tolerate dry and saline soil.

Asteraceae was represented by 0.2% of the total palynomorphs. Plants in the Asteraceae are mostly annual or perennial herbs or subshrubs to shrubs. They are commonly found in open to semi-open habitats rather than dense forest. Moreover, Asteraceae very rarely grow in truly aquatic environments (Koyama et al., 2016).

Some pteridophyte spore types, including the trilete spore of Selaginellaceae (Fig. 4: 16-18), were also found at 4.7%. The indeterminable palynomorphs (28.3%) are mostly well-preserved grains of unknown affinity. This high percentage problem needs further investigation in future studies. However, this can arise in Cenozoic palynoflora studies from Southeast Asia with the high diversity of flora and still insufficient pollen databank.

Late Middle Pleistocene Ecosystems

Thailand is located on the Southeast Asian mainland and is influenced by seasonally reversing summer and winter monsoon winds. The Pleistocene epoch is widely recognized as a time of alternating cool, dry environments and warm, wet environments caused by various factors. The continental glaciation in high latitudes also influenced Southeast Asia giving rise to lowered sea level, cooler temperatures, lowered evaporation and humidity content of the monsoon winds, and decreased precipitation. The above factors intensified the influence of the monsoon winds on the area, resulting in climate and vegetation changes during the Pleistocene (Morley, 2012).

Pollen found in the sediment from the late Middle Pleistocene from the Khok Sung site suggests at least 2 main ecosystems based on their parent plant ecology,

i.e., open woodland at the regional scale and gallery forest at the local scale.

Open woodland

This ecosystem refers to forests consisting of trees, shrubs and grasses where tree canopies do not continuously cover the forest floor (Grainger, 1990). The relatively high proportion (16.9%) of grass pollen (Poaceae) associated with a few percentages of Asteraceae and Chenopodiaceae pollen in this study suggests rather open environments. However, the high proportion (11.6%) of *Quercus* and the occurrence of *Pinus* (1%) evidently shows the coexistence of wooded habitats. *Quercus* (Fagaceae) has been found growing widely in the temperate-subtropical zone and also at high altitudes in the tropics. However, some species are also present at low altitude (0–800 m. a.m.s.l) in the tropics, such as *Quercus aliena, Q. brandisiana, Q. kerrii, Q. kingiana,* and *Q. mespilifolia*. In present day Thailand, members of *Quercus* are the dominant plants in montane forests, with the understory covered by grasses, such as lower montane oak forest, which can change to lower montane pine-oak forest upon disturbance (Gardner et al., 2000; Santisuk, 2012). The presence of *Quercus* with very rare *Pinus* in this study indicates differences in pollen records when compared with assemblages from Nong Pa Kho in northeastern (Penny, 1999) and Phayao in northwestern Thailand (Penny and Kealhofer, 2005) during the Last Glacial Maximum, which showed high percentages of *Pinus* along with *Quercus* pollen and suggested the presence of tropical pine forest at that time.

Since broadleaved plants in Anacardiaceae, Bignoniaceae, Malvaceae, Rosaceae, *Diospyros* in Ebenaceae, *Albizia* in Fabaceae, *Urtica* in Urticaceae, Dipterocarpaceae, and Arecaceae (altogether 16%) could naturally grow in both evergreen and deciduous forests, they could also be present as scattered trees and shrubs associated with lowland to montane habitats together with grasses and herbaceous understory.

Poaceae pollen could come from local floodplain habitats, but in this case more likely indicate regional open woodlands. This could be comparable to percentages of Poaceae pollen from the Late Miocene of Nakhon Ratchasima, which ranged from 20 to 74% (local palynomorphs excluded) and were indicators of widespread grasslands in the area (Sepulchre et al., 2010). In this study, if autochthonous pollen (Cyperaceae, *Homonoia*/*Mallotus*, pteridophytes) from the gallery forest were not calculated, Poaceae pollen would be approximately 22%. The presence of a relatively high percentage of grasses, associated with some *Quercus* and low percentages of various broadleaf trees could be characteristics of a grassy wooded environment consisting of an open canopy of *Quercus* mixed with some other broadleaf trees and sparse *Pinus* trees with a grassy understory. This could therefore be designated as an open woodland rather than a closed canopy forest. The grassy wooded environment may be regionally widespread with the pollen transported and precipitated at the site.

This open woodland ecosystem interpretation coincides with similar suggestions from various studies in Southeast Asia. Palynological evidence suggests that dry ecosystems such as savannas may have extended from Myanmar to Java during the Middle Pleistocene (less than 0.78 Ma) (Louys and Meijaard, 2010). In addition, montane seasonal forests may have expanded their range in Southeast Asia at that time (Heaney, 1991; Morley, 2000). Moreover, the increased seasonality, reduced rainfall, colder temperature and increased grassland were detected in Bandung basin, west Java, Indonesia, at 80 – 10 ka (van der Kaars and Dam, 1995). Data from the Lombok Ridge site (Indonesia) also indicated drier climates with increased grassland during the intervals of 300 – 244, 190 – 130, and 38 – 12 ka (van der Kaars, 1991). The Middle Pleistocene at Subang airport, near Kuala Lumpur, Peninsular Malaysia, was suggested to be a drier, grass-*Pinus* savanna system (Morley, 2000). The interpretation in the present paper is similar to the interpretation from a pollen assemblage (sample 16A) from the Middle Pleistocene (172,739 ±22,400 BP) of the nearby locality at Tha Chang sand pit beside the ancient Mun River channel in Nakhon Ratchasima Province (Yang and Grote, 2017). These authors suggested the presence of temperate savanna with scattered trees and bushes characterized by a cool and dry climate. Moreover, the suggestion in the present paper is also consistent with the evidence from *Crocuta crocuta ultima* and other vertebrate fossils recovered from the same sediment layer of the same study site, which suggests an open canopy environment (Suraprasit et al., 2015). Likewise, the $\delta\ ^{13}C$ values of tooth enamel carbonate of various mammals from the same sediment layer at Khok Sung show a diversity of diets ranging from C_3 to mixed C_3/C_4 to C_4 plants suggesting that the wildlife habitats ranged from closed forests to open grasslands. C_4 grasses were considered to be a major component during the late Middle Pleistocene (Suraprasit et al., 2018).

Gallery forest

A gallery forest is characterized by the long and narrow strips of forest associated with rivers or creeks in riparian habitats. The boundary of the forest is usually abrupt because the surrounding area conditions do not support forest (Veneklaas et al., 2005). At the local scale, the pollen vegetation components indicate gallery forest with associated riparian and channel

habitats. The *Homonoia/Mallotus* pollen from Euphorbiaceae was the most dominant pollen in the sample. There is only one species, *Homonoia riparia*, found today in Thailand as a rheophytic shrub, that is, growing in streams with fast moving water currents. Finding of the tetrad form, 4 grains attached together, of pollen in *Homonoia/Mallotus* type indicates the likely possibility of short distance transportation because there was insufficient force to separate the grains. The greater weight of 4 attached grains also makes long distance dispersal less likely. This suggests a parent plant habitat near the depositional site. The occurrence of Cyperaceae pollen in this study is consistent with the discovery of tubers with attached roots and rhizomes or stolons of *Cyperus* or *Bolboschoenus maritimus* in the same sediment layer of this study site by Grote (2007), which indicated wetland or moist environments. The presence of pteridophyte spores also supports interpretation of areas with high humidity. These pollen and spore vegetation components confirm evidence of the ancient stream occurring in the late Middle Pleistocene at the Khok Sung site. This agrees with the sedimentary study of the site in Duangkrayom et al. (2014) that suggested this site as an ancient Mun River terrace from the former floodplain deposition.

Although pollen of Anacardiaceae, Arecaceae, Bignoniaceae, *Croton* in Euphorbiaceae, Malvaceae, Rosaceae, *Diospyros* in Ebenaceae, *Albizia* in Fabaceae, and *Urtica* in Urticaceae (totaling 19%) could suggest various habitats in both evergreen and deciduous forests, they are more common in tropical evergreen forest. Notably, most recent members of *Hopea* and *Shorea* in Thailand are specific to evergreen forest. Four species of *Hopea* and 11 species of *Shorea* are predominantly found in tropical evergreen rain forest, whereas 2 species of *Hopea* and 2 species of *Shorea* are dominant in seasonal rain forest, semi evergreen forest or dry evergreen forest. *Shorea siamensis* and *S. obtusa* are dominant in deciduous dipterocarp forest (Santisuk, 2012). Presence of a low percentage of *Hopea*/*Shorea* pollen may be the result of the entomophilous pollination strategy of this family. Importantly, some fruit specimens of *Dipterocarpus costatus* were discovered by Grote (2007) from the same sediment layer. The well-preserved fruits of *D. costatus* are indicative of habitation close to the deposition site. This is strong evidence indicating the establishment of tropical evergreen forest along the ancient river as a gallery forest. This forest might be composed of plant components which currently are in moist, seasonal, semi, or dry evergreen forests and probably mixed with some plant components from deciduous forest adjacent to the open woodland with decreased moisture. Studies in Central America show that it is possible for patched or fragmented small gallery forests to exist in the midst of a regional dry environment. Those small gallery forests have low tree density but retain a relatively high diversity of tropical rainforest tree species even in an area smaller than 1 ha or a narrow strip of trees 5 meters wide along 2 sides of a creek (Pitcher and Kellman, 2002).

Even though the Pleistocene epoch is widely recognized as a time of cyclical glaciation at high latitudes, during which it was difficult for tropical rainforest to survive, large rivers that flowed through dry areas probably provided moisture and enabled tropical rainforests to persist adjacent to the surrounding dry environment. Thus, the surviving closed canopy forest habitats could appear during the dry and cool episodes (Cannon, 2009; Morley, 2012).

CONCLUSION

Palynological data analyzed in this study suggest that ecosystems during the late Middle Pleistocene in the ancient Mun River terrace at Khok Sung site are generally open woodland along with the persistence of tropical evergreen plant communities appearing as gallery forest. The wet environment forest surviving by supplementary moisture from streams might exist along the sides of the ancient Mun River, as evidenced by the presence of plants from riverine and evergreen habitats. Far from the ancient river, the landscape is suggested to be open woodland characterized by an open canopy of scattered trees and shrubs, dominated by *Quercus* and accompanied by other broadleaf plant species, with an understory mainly occupied by grasses.

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