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Studies of Fruits and Seeds from the Pleistocene of northeastern Thailand

With 40 figs

Paul J. Grote

Abstract

A remarkable assemblage of plant and animal fossils has recently been discovered in Nakhon Ratchasima province in Northeast Thailand. The fossils were deposited in a fluvial system considered to be Middle Pleistocene in age. Plant remains include fruits, seeds, leaves, wood, tubers, amber, and pollen. The most common fruit type is preserved either as an elliptic endocarp with three or four valves or as a whole fruit with mesocarp and exocarp present and a suprabasal rim above the peduncle. These fruits are proposed as a new species of *Ziziphus* (Rhamnaceae). A second type consists of a globose fruit surrounded by five rather narrow wings and is considered to belong to *Dipterocarpus costatus* (Dipterocarpaceae). A third type is an elliptic endocarp with five elongate ridges and a central cavity apical to the locules. The endocarp dehisces at least partly into five valves. This type is considered to belong to *Melia azedarach* (Meliaceae). A fourth type consists of a fragment of a lenticular endocarp showing affinity to *Dracontomelon dao* (Anacardiaceae). Tubers have also been recovered that are similar to those of *Cyperus* or *Bolboschoenus* (Cyperaceae). Clear resin, which may have come from trees of Dipterocarpaceae or Burseraceae, as well as very well preserved leaves and wood, has also been found. The above specimens suggest the presence of tropical mixed deciduous and dry evergreen forests during the Middle Pleistocene. In addition to plant fossils, a number of vertebrate fossils have also been recovered from the site, including bones, teeth, or other remains of fish, soft-shelled and other turtles, gavials, bovids, deer, *Stegodon*, and a hyena.

Key words: Pleistocene, Thailand, Khok Sung, *Ziziphus*, *Dipterocarpus*, *Melia*, *Dracontomelon*, fossil fruits and seeds

Introduction

Although Thailand, as well as elsewhere in Southeast Asia, possesses a very high level of plant diversity at present, relatively few studies of plant fossils from the Cenozoic have been reported. Several species of plant macrofossils were described from the Oligocene or Miocene of northern Thailand by Endo (1964, 1966) and from the Miocene of western Thailand by Endo & Fujiyama (1966). More recently, silicified wood from northern Thailand was described by Vozenin-Serra et al. (1989). Fossil wood from northeastern Thailand was reported by Prakash (1979) from the Tertiary, by Vozenin-Serra & Privé-Gill (1989) from the Plio-Pleistocene, by Vozenin-Serra & Privé-Gill (2001) from the lower Pleistocene, by Benyasuta (2003) from the Miocene-Pleistocene, and by Wang et al. (2006) from the Miocene to Pleistocene. These fossil woods, however, have not been dated precisely. Vozenin-Serra & Privé-Gill (1994) reported on wood from presumably Middle Pleistocene deposits in Vietnam, and Vozenin-Serra & Privé-Gill (1991a, b) reported on Pleistocene wood from Cambodia. Suwonwimol (2000) described more or less unaltered wood from the Late Pleistocene (back to approximately 30,000 years ago) and Holocene in Kanchanaburi province, western Thailand. However, there have been few reports of fossils of reproductive material (flowers or fruits) or leaves from the late Cenozoic. In March, 2005, a remarkable fossiliferous deposit was discovered near the village of Khok Sung, in Nakhon Ratchasima province, northeastern Thailand, containing many well preserved animal and plant fossils. The plant fossils include wood, tubers, leaves, fruits, seeds, resin, and pollen. Much of the plant material is rather un-

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altered and has not been coalified. In this paper, selected fruits, seeds, tubers, and resin will be described.

Khok Sung site

The Khok Sung fossil site (figs 1–3) is located in an open field near Khok Sung village, in Khok Sung subdistrict, Muang district, Nakhon Ratchasima province, in northeastern Thailand (SUT locality 040). The site is approximately 15 km north of the town of Nakhon Ratchasima near Highway 205 (15° 5' N. lat.; 102° 7' E. long.). The site was discovered at a depth of about five meters in March 2005 while a reservoir was being dug. The succession consists of layers of sand and gravel alternating with layers of clay thought to be part of an ancient fluvial system (DEPARTMENT OF MINERAL RESOURCES 2006). Fruits and seeds, as well as other plant remains, were found in a layer of mud from a floodplain and from overlying channel lag gravelly sand deposits (J. DUANGKRAYOM, pers. comm., April 2007; DUANGKRAYOM 2007). Numerous vertebrate bones, teeth, and antlers were recovered from the site, in addition to the plant remains. The vertebrates include fish, gavials, turtles, soft-shelled turtles, spotted deer, bovids including water buffalo, *Stegodon* (Order Proboscidea), and a hyena. All of the vertebrate species are extant except *Stegodon* (DEPARTMENT OF MINERAL RESOURCES 2006). At present, the site is completely flooded.

The age of the deposits is thought to be older than 40,000 years (from ^{14}C dating) and younger than 780.000 years based on paleomagnetic polarity analysis. An estimated age of 400.000 years was obtained from the assemblage of extinct and extant vertebrate species found at the site (Y. CHAIMANEE, pers. comm., Jan. 2006).

Materials and Methods

Fossil specimens were collected from the Khok Sung deposits both *ex situ* and *in situ*. Some fruits were found in blocks of mud that had been taken to the laboratory. The fossils were preserved in 2:3:5 solution of water:glycerin: 95% ethanol. Selected specimens were placed in 48% HF to remove clay, rinsed repeatedly with water, and air-dried. Recent fruits (wild and cultivated) for comparison were collected from the campus of Suranaree University of Technology, Nakhon Ratchasima, or obtained from herbarium sheets from the Forest Herbarium, Bangkok. Selected recent fruits of *Ziziphus* MILLER and *Melia* LINNAEUS were boiled for several hours in 10% NaOH to allow removal of the exocarp and mesocarp (This treatment was suitable for fruits with hard stony endocarps, but was found to be too harsh for some fruits). Recent and fossil fruits were measured dry, as they became enlarged when placed in liquids. Modern and fossil specimens were photographed with a film or digital camera.

Results

Most of the fruits and seeds were collected *ex situ*, and it is uncertain which of these came from the gravelly sand layer and which came from the mud layer. However, some specimens were collected *in situ* in the mud layer. Approximately 12 types of fruits and seeds were collected totaling 64 fruits plus 7 winged calyces. The most common fruit type is *Ziziphus* with 45 specimens. In addition, 10 tubers, 3 pieces of resin, and numerous pieces of wood were collected. Clay collected for pollen preparation showed a diversity of types (W. RUGMAI, pers. comm., 2006).

Systematics

The systematic arrangement follows that of the ANGIOSPERM PHYLOGENY GROUP (2003).

Poales Small

Cyperaceae JUSSIEU, nom. cons.

cf. *Cyperus* LINNAEUS vel *Bolboschoenus* (ASCHERSON) PALLAH

Specimens: SUT1812 (fig. 4), SUT1820, SUT1821, plus 5 additional specimens.

Description: Tubers with attached roots and rhizomes or stolons. The tubers are obovoidal or ovoidal (10 to 16 mm long; 5 to 10 mm wide). The surfaces of the tubers are abraded with many loose fibers exposed. Several transverse grooves are present on the surface.

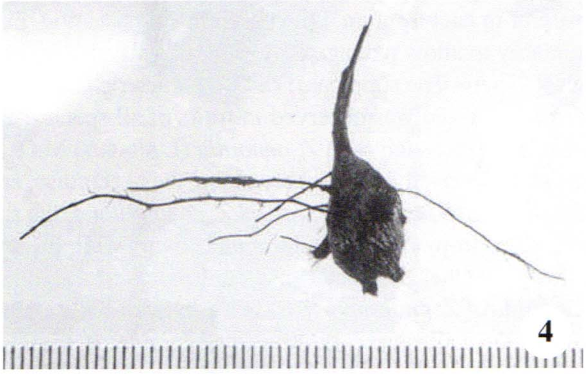
Affinities: The tubers are very similar to those found in some extant species of *Cyperus* (fig. 5), such as *C. rotundus* LINNAEUS, in which they arise from stolons. They are also similar to tubers of extant *Bolboschoenus maritimus* (LINNAEUS) PALLAH, which have elongate rhizomes.

Rosales Perleb

Rhamnaceae JUSSIEU, nom. cons.

Ziziphus MILLER

Ziziphus is a genus of approximately 100 species of deciduous or evergreen shrubs or small to medium sized



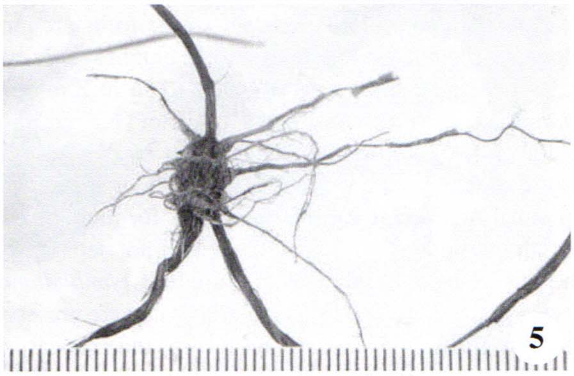


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Fig. 1: Map of mainland Southeast Asia, showing location of Khok Sung fossil site. — Fig. 2: Khok Sung site showing mud layer with pieces of wood. — Fig. 3: Khok Sung site showing layer of mud densely filled with leaves (at rock hammer). — Fig. 4: Fossil tuber of cf. *Cyperus* vel *Bolboschoenus* (Cyperaceae), photographed in water: glycerin:alcohol solution (SUT1821). Scale units = 1 mm. — Fig. 5: Tuber of Recent *Cyperus* sp. (Nakhon Ratchasima). Scale units = 1 mm. — Figs. 6–7: Fossil resin. Scale units = 1 mm. — Fig. 6: Resin attached to wood (SUT1807). — Fig. 7: Two pieces of resin (SUT1830, left, and SUT1831, right).

trees. The distribution is nearly pantropical with the centers of diversity in tropical America and Southeast Asia (MEDAN & SCHIRAREND 2004). Based on morphology and molecular studies the genus can be divided into two clades, an Old World group and a New World group (ISLAM & SIMMONS 2006).

Ziziphus khoksungensis n. sp.

Holotype: SUT1824 (figs. 8, 12);
Paratypes: SUT1800, SUT1801, SUT1813, SUT1822 (fig. 20), SUT1823 (fig. 9), SUT 1824, SUT1826 (fig. 17), SUT1827 (figs. 11, 14 ,19), SUT1828, SUT1829. The holotype and paratypes are stored at the Center for Scientific and Technological Equipment, Suranaree University of Technology, Nakhon Ratchasima.
Type locality: Khok Sung fossil site (SUT locality 040).
Derivation of specific epithet: Refers to the village and subdistrict in which the specimens were found.
Diagnosis: Whole fruits or endocarps similar to those of *Z. cambodiana* Pierre, except that the fruits are more elongate (height greater than width; height:width ratio 1.21–1.43 in *Z. khoksungensis*, 0.85–0.86 in *Z. cambodiana*) and have a thicker suprabasal rim (1.2 mm thick in the *Z. khoksungensis*, ~0.3–0.4 mm in *Z. cambodiana*). Endocarps globose, with three or four locules and an equal number of valves, the valves for most of their length contiguous with each other and not separated at the surface by the septum as they are in *Z. cambodiana*.
Description: The fruits are drupes and are preserved as entire fruits, with exocarp, mesocarp, and endocarp, or as endocarps. The entire fruits are obovoidal or ellipsoidal (length 11.4–19.3 mm, width 8.5–13.6 mm, N=4), with a slightly wrinkled surface. Above the base is a rim, referred to here as a suprabasal rim, with a thickness of approximately 1.2 mm. The basal part of the rim plus the fruit between the rim and the pedicel appear to be derived from the calyx tube or receptacle. The distal part of the rim appears to be part of the pericarp. Between the two layers of the rim are lens-shaped scars from the bases of filaments. One fruit (SUT1824) had a small flap of tissue basal to one of the lenses, presumably derived from a petal. A small knob (approximately 0.2 to 0.4 mm representing the base of the style is present at the apical end of the fruit. The fruits are usually attached to a short section of the pedicel.

The endocarps are globose and exteriorly show three or four valves. Three-valved endocarps are 11.2–13.4 mm long by 9.6–11.9 mm wide (N=2). Four-valved endocarps are 12.2 wide by 12.2 mm wide (N=1). The valves are broadly rounded basally, 2.2 to 4.8 mm from the base of the endocarp, and extend to the apex of the endocarp. The valves are contiguous with each other for most of their lengths, except for one specimen of uncertain affinity in which the valves are separated for most of their lengths by the septa (SUT1825). Of the fruits in which the number of valves could be determined, 23 (82%) have three valves and five (18%) have four valves. In cross-section, the endocarps show three or four locules in agreement with the number of valves. Each locule has one seed. The valves are 3.5 to 4 mm thick (in SUT1822). A septum (0.9 to 1.2 mm thick) separates adjacent locules. A plane of dehiscence is visible between each side of the valve and the septum. In addition, planes of dehiscence can be seen between septa where they join in the center of the endocarp. The endocarp, including the valves, is composed primarily of sclereids. Two or three holes are present in each septum, when seen in cross section, presumably to allow passage of the vascular tissue.
Affinities: The suprabasal rim is characteristic of fruits of *Ziziphus* and was observed in fruits of all species studied. In some, such as in *Z. oenoplia* (LINNAEUS) MILLER, the rim is derived from the calyx tube, the nectar disc, and the ovary wall. In others, such as *Z. cambodiana*, the rim is derived from the calyx tube and the ovary wall. It is not known whether the nectar disc contributes to the rim in the fruits of *Z. khoksungensis*. In a survey of recent fruits of *Ziziphus*, all species observed had endocarps with two valves or no distinctive valves, except for *Z. cambodiana*, which had endocarps with three (4 specimens) or four (11 specimens) valves. PITARD (1912) described the flowers of *Z. hoaensis* Pierre from Vietnam as having three locules, but the fruits were unknown to him.

The fossils share many characters with fruits of *Ziziphus* and are considered to belong to this genus. The fruits are most similar to *Z. cambodiana* in having globose endocarps with three or four valves (figs. 15, 18). However, *Z. cambodiana* fruits (figs. 10, 13) are depressed globose (width greater than height) and have a thin suprabasal rim (~0.3–0.4 mm thick), while the fossil fruits are ellipsoidal with a thicker suprabasal rim.

Figs. 8–21: Fossil and Recent fruits of *Ziziphus* (Rhamnaceae). All scale units = 1 mm. Fruits of *Ziziphus khoksungensis* n. sp. — Figs. 8, 12: Whole fruit, side and basal view (SUT1824, holotype). Arrow indicates suprabasal rim. — Fig. 9: Whole fruit, side view (SUT1823, paratype). Arrow indicates suprabasal rim. — Figs. 11, 14, and 19: Endocarp with three valves, side, basal, and apical view (SUT1827, paratype). — Fig. 17: Endocarp with four valves, basal view (SUT1826, paratype). — Fig. 20: Abraded fruit with three valves and locules, cross section (SUT1822). Arrow indicates plane of dehiscence between valve and septum. V= valve. — Fruits of *Z. cambodiana* PIERRE (Nakhon Ratchasima, Thailand). — Figs. 10, 13: Whole fruit, side and basal view. Arrow indicates suprabasal rim. — Figs. 15–16: Endocarp with three valves, basal and side view. Arrow indicates small knob near apex of valve. — Fig. 18: Endocarp with four valves, basal view. — Fig. 21: Endocarp with four valves and four locules, cross section. Arrow indicates plane of dehiscence between valve and septum.


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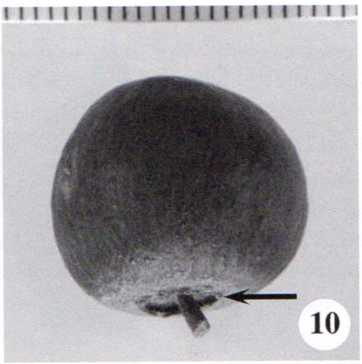
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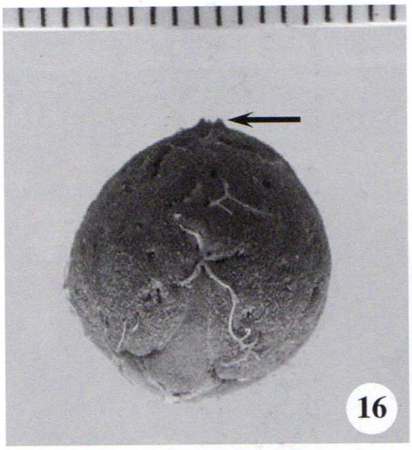
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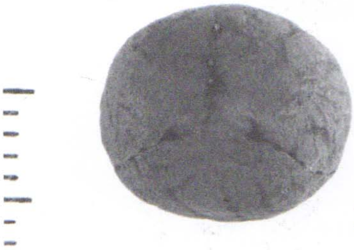
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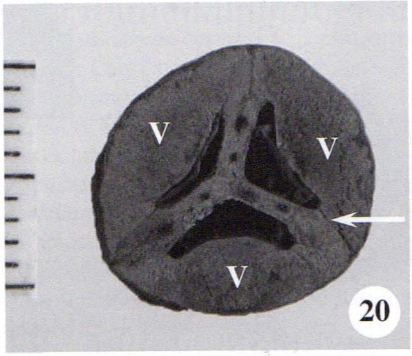

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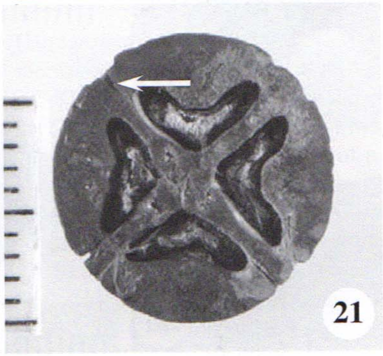
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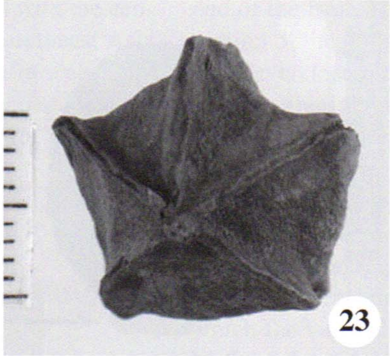
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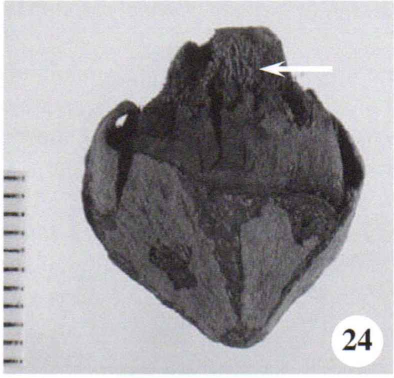
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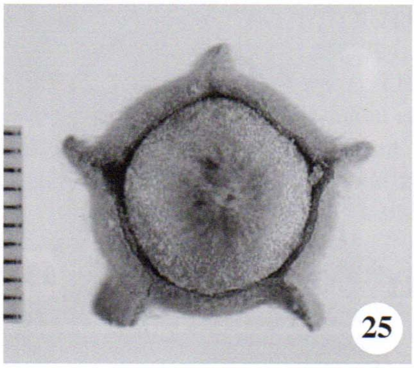
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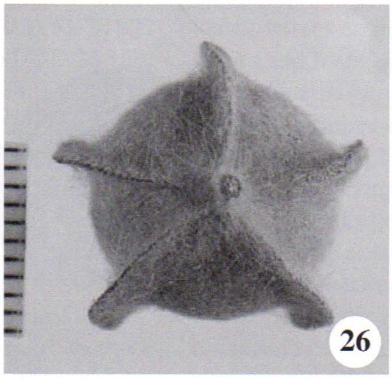
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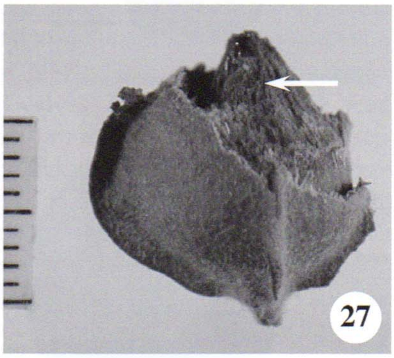
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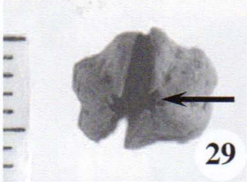
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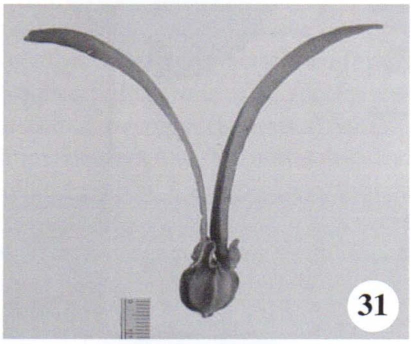
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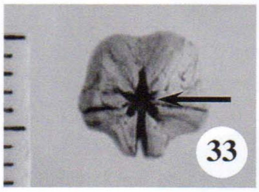
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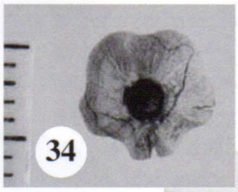
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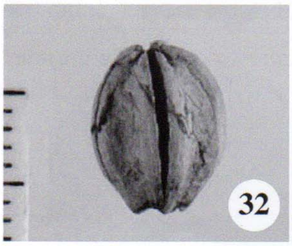
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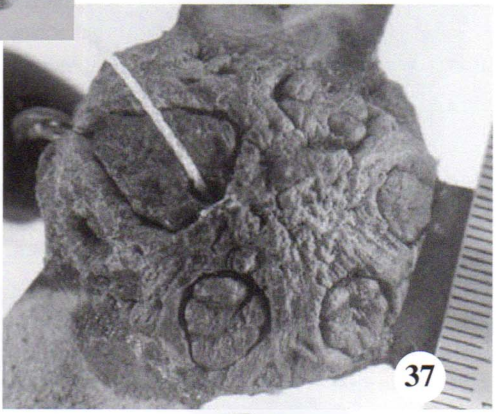
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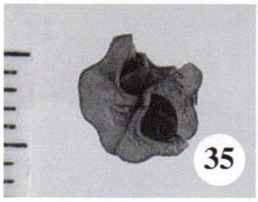
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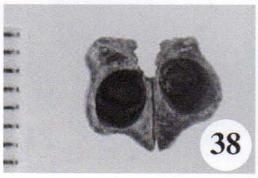
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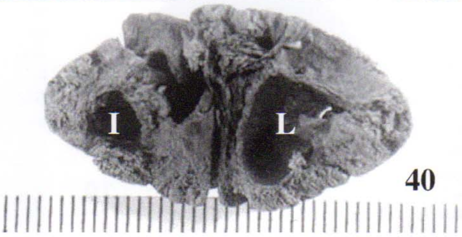

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The valves of the endocarps of *Z. cambodiana* (fig. 16) are not contiguous for approximately half their lengths but are rather separated by the septa, whereas in the fossils the valves are contiguous. One exception is a fossil fruit (SUT1825) in which the valves are separated most of their distances by the septa. This specimen is similar, however, to the other fossils in remaining characters. The exact relationship of this specimen to the other fossils is uncertain. *Z. cambodiana* endocarps have three or four (fig. 21) locules, each with one or two seeds. Near the apex of each valve in *Z. cambodiana* a small knob is present (fig. 16), a character which does not occur in the fossil. Because the fossils, although similar to *Z. cambodiana*, show consistent differences from the extant species, they are proposed to represent a new species, *Ziziphus khoksungensis*.

The fossil record of *Ziziphus* is not extensive, but fossils have been reported from Asia, North America, and Europe. *Ziziphus* fossils have been reported from the Jurassic of China (Zhou 1995) and the Cretaceous of the USA (Graham 1999), but are considered to be unreliable or in need of reinvestigation, respectively. *Ziziphus florissantii* (Lesquereux) MacGinitie was described based on leaves from the Late Eocene Florissant Formation of Colorado, USA, and is considered to be similar to extant plants in Texas and Mexico (Meyer 2003). This species is also known from the Late Oligocene Creede flora of Colorado (Graham 1999). The European record includes *Z. striata* (Ludwig) Mai & Gregor, known from endocarps from the middle Oligocene to upper Miocene of Central Europe and considered to show affinity to *Z. incurva* Roxburgh (Czaja 2003). This species is quite distinctive from *Z. khokhungensis* in having a single locule. *Ziziphus paradisiacus* Heer, known from leaves from the Miocene of Serbia, is thought to have affinity to *Z. sinica* (Utescher & Mosbrugger 2006). *Ziziphus pseudocretacea* Tao was reported from the Late Cretaceous or Early Paleocene Wuyun Formation in northern China (Sun et al. 1995). Specimens referred to *Ziziphus* sp. are known from the Fushun flora of northeastern China, probably middle Eocene in age, and from the Eocene of Turkmenistan (Li & Zheng 1995). *Ziziphus miojujuba* Hu & Chaney, from the Miocene Shanwang flora of eastern China, is based on leaf fossils and was considered by the authors to be similar to the extant *Z. jujuba* Miller, which occurs today in China and Japan (Hu & Chaney 1940). *Ziziphus khoksungensis*, proposed in this paper, shows closest affinity to *Z. cambodiana*, which can be placed in the Old World clade of *Ziziphus*, based on morphology, specifically, the presence of stipular spines (Islam & Simmons 2006). The author of this paper is unaware of any additional reported fossils similar to *Z. khoksungensis* or to the extant *Z. cambodiana*.

Malvales Dumortier

Dipterocarpaceae Blume, nom. cons.

Dipterocarpus C.F. Gaertner

Dipterocarpus is a genus of approximately 70 species of medium to large trees. This genus is found only in Asia, occurring from Sri Lanka to the Philippines, Borneo, and Sumbawa, in tropical evergreen forests and savanna woodlands (Ashton 2002).

Dipterocarpus costatus C.F. Gaertner

Specimens: Two fruits, SUT1817 (figs. 22, 23) and SUT 1818 (fig. 24)

Description: One fruit (SUT 1817) is compressed apically-basally and is 16.4 mm wide and approximately 11 mm high. The second fruit (SUT1818) is compressed laterally and is 16.0 mm wide, approximately 8 mm thick (in compressed dimension), and 17.8 mm high. The fruits were probably more or less globose before compression. The external part of each fruit, derived from the calyx tube, has five elongate wings approximately 1.3 mm wide and 0.4 to 0.5 mm thick. Inside of the calyx tube is the pericarp, which is not fused with the calyx. The pericarp wall is broken in some places exposing fibers within the

Figs. 22–27, 31: Fossil and Recent fruits of *Dipterocarpus costatus* C.F. Gaertner (Dipterocarpaceae). All scale units = 1 mm. — Fossil fruits of *D. costatus*. — Figs. 22–23: Calyx tube and pericarp, missing the calyx wings, apical and basal views (SUT1817). — Fig. 24: Calyx tube and pericarp, missing the calyx wings, side view (SUT1818). Arrow indicates fibers exposed in abraded pericarp. — Recent fruits of *D. costatus* (Chiangmai, Thailand). — Figs. 25–26: Calyx tube and pericarp, calyx wings removes, apical and basal view. — Fig. 27: Calyx tube and pericarp, calyx wings, part of calyx tube, and outer surface of pericarp removed. Arrow indicates inner fibers exposed in pericarp. — Fig. 31: Whole fruit with calyx wings, side view. — Figs. 28–30, 32–35, 38: Fossil and Recent fruits of *Melia azedarach* Linnaeus (Meliaceae). All scale units = 1 mm. — Fossil fruits of *M. azedarach.* — Figs. 28–30: Endocarp, side, apical, and basal views (SUT1802). Arrow indicates apical wedge-shape. — Fig. 35: Endocarp, cross section, showing two developed locules, each with one seed (SUT1819). — Recent fruits of *M. azedarach* (Nakhon Ratchasima, cultivated). — Figs. 32–34: Endocarp, side, apical, and basal views. Arrow indicates apical shape. — Fig. 38: Endocarp, cross section, showing two developed locules, each with one seed. — Figs. 36–37, 39–40: Fossil and Recent fruits of *Dracontomelon dao* (Blanco) Merrill & Rolfe. All scale units = 1 mm. — Fossil fruit of *D. dao.* — Figs. 36, 39–40: Endocarp, apical, side, and inside view (SUT1810). Arrows indicate openings to interlocular cavities. I = interlocular cavity; L = locule. — Recent *D. dao.* — Fig. 37: Endocarp, showing five apical plugs, apical view.

wall. Inside the pericarp is a seed, the seed coat of which has a palisade layer of cells. Yellow resin can be seen inside the seed.

Affinities: The nut-like pericarp within a calyx tube is characteristic of some species of Dipterocarpaceae. In *Dipterocarpus*, the calyx tube is free from the pericarp except near the base, whereas in *Anisoptera*, the tube is fused with the pericarp. In some species of *Vatica*, the calyx is fused into a tube and united to the lower portion of the pericarp (SMITINAND et al. 1980). In the fossil fruits, the calyx tube is not adnate to the pericarp, which is consistent with *Dipterocarpus*. In fruits of *Dipterocarpus*, two calyx lobes are elongated into wings. These wings are not present in the fossil fruits and presumably broke off or were abraded away before deposition. Approximately seventeen species of *Dipterocarpus* occur today in mainland Southeast Asia (SMITINAND et al. 1980). Of these, six species have wings on the fruiting calyx tube. In *D. grandiflorus* (Blanco) BLANCO and *D. alatus* ROXBURGH ex G. DON, the calyx tube and wings are much larger than in the fossils, the tubes being 6 to 8 cm long and 3.5 cm long, respectively. In *D. dyeri* PIERRE and *D. oblongifolius* BLUME, the calyx tubes are more elongate than in the fossil. In *D. intricatus* DYER, the wings are highly folded. The calyx tubes of *D. costatus* C.F. GAERTNER (figs. 25, 26, 31) are globular (15–17 mm high; 14–17 mm wide (N = 5)) with wings approximately 1.2–3 mm wide (N = 5). As the fossils are very similar to recent fruits of *D. costatus*, they are placed into this recent species.

D. costatus ranges today from Bangladesh, to Myanmar, throughout Thailand, to Laos, Cambodia, and Vietnam (SMITINAND et al. 1980).

VOZENIN-SERRA & PRIVÉ-GILL (2001) reported fossil wood of *Dipterocarpoxylon sarapeense* VOZENIN-SERRA & PRIVÉ-GILL from Tachang (Tha Chang) village, Nakhon Ratchasima, with an age attributed to Lower Pliocene. They found the fossil to be close to the extant species *D. turbinatus* C.F. GAERTNER However, the fruits of this species differ from those of *D. costatus* in that the fruiting calyx tube is ellipsoidal and without wings.

At least seven fragments of accrescent calyces were seen among fossil leaves from Khok Sung, each with approximately 8–12 parallel veins. They are different from winged calyces of *Dipterocarpus*, in which there are three main parallel veins (SMITINAND et al. 1980). They are, however, similar to winged calyces of *Shorea* or *Hopea* (Dipterocarpaceae) and are being investigated further.

Sapindales DUMORTIER

Meliaceae JUSSIEU, nom. cons.

Melia LINNAEUS

Melia is a genus of 2–15 species in the paleotropics and subtropics (WILLIS 1973).

Melia azedarach LINNAEUS

Specimens: SUT1802 (figs. 28–30), SUT1816, SUT1819 (fig. 35).

Description: The fruits are ellipsoidal endocarps (fig. 28) 10.0–11.9 mm long by 8.8 mm wide. They are five-angled in cross-section with elongate depressions between the locules (figs. 29, 30, 35). The endocarps dehisce loculicidally from the apex to nearly the base. A conical opening is present at the central base, which continues as a narrow cylindrical opening to the apex of the endocarp. At the apex this narrow opening widens into a rounded opening. Viewed from above (fig. 29), the apical opening appears star-shaped (in non-dehisced endocarps) because each side of the valve wall extends at the apex as a narrow wedge. In the single fruit cross-sectioned, two locules were developed, each with one seed. The locular cavity is round in cross-section and narrowly elliptic from base to apex. An opening extends apically to the apical opening of the endocarp. The seeds are attached apically and fill the locular cavity. The thickness of the valve wall is approximately 1.1–1.6 mm. The endocarp is composed mainly of fibers.

Affinities: The fossil endocarps are very similar to recent endocarps of *Melia azedarach* LINNAEUS (figs. 32–34, 38). One difference is that the valve walls appear to be thicker in the fossil endocarps, being 1.1–1.6 mm (N = 2) thick in the fossils compared with 0.6–0.7 mm (N = 2) in recent endocarps. However, the sample size is very small and little is known of the amount of variation among either the fossil or recent fruits. Therefore, the fossils are tentatively included in the recent species, *M. azedarach*.

Anacardiaceae R. BROWN , nom. cons.

Dracontomelon BLUME

Dracontomelon is a genus of eight species ranging from Southeast Asia to New Guinea, Fiji, and Samoa (GROTE 1989).

Dracontomelon dao (BLANCO) MERRILL & ROLFE

Specimen: SUT 1810 (figs. 36, 39–40)

Description: This fossil type is represented by a fragment of one lens-shaped endocarp. The fragment is 16.0 mm high (probably close to the total height of the endocarp), 28.9 mm long, and 16.0 mm thick. One locule and parts of two more are present. A thick elliptic plug, approximately 3.7 mm thick, covers each locule apically. The one complete locule has a shrunken plug (6.7 by 4.6 mm) within a cavity of 11.8 by 8.6 mm. Interlocular cavities are present inside the endocarp, with two holes open to the exterior along the equator of the endocarp between each locule plus additional openings above and below. The endocarp wall is composed mainly of fibers.

Affinities: This specimen is very similar to endocarps of the recent species *D. dao* (Blanco) Merrill & Rolfe, which is the only species occurring in Thailand today (Chayamarit 1994). In recent endocarps of *D. dao*, five locules are present, some of which have developed seeds (fig. 37). Interlocular cavities alternate with the locules and open externally through two holes at the equator of the endocarp (Grote 1989). As the fossil specimen is similar to fruits of the recent species, it is here included in *D. dao*.

This species today is distributed from east India, the Andaman Islands, and Myanmar, to Thailand, Indochina, south China, and Malesia to New Guinea and the Solomon Islands (Gardner et al. 2000).

Resin

Three pieces of resin were collected. One piece (SUT1807, fig. 6) is approximately cylindrical (20 mm long by 19 mm wide by 11 mm thick) with wood attached to one side, so the resin may have filled a cavity in the wood. The resin is clear and is still fragrant. A second piece (SUT1830, fig. 7) is also roughly cylindrical (15 mm long by 15 mm wide). The third piece (SUT1831, fig. 7) is a fragment 13 mm long. The resin was transparent and more or less colorless when collected and remained so when stored in a water:glycerin:ethanol solution. However, the largest piece became opaque and white at the surface when transferred to water. The wood attached is that of a dicot, but has not been identified to family. However, Dipterocarpaceae is the most important family of resin-producing plants in Southeast Asia, with the resin being called dammar. Prominent resin producing trees include those in the genera *Shorea*, *Hopea*, *Dipterocarpus*, *Vatica*, and *Anisoptera* (Langenheim 2003). Thus, the resin may have been produced by the same species as the fruits, *D. costatus*, or the winged calyces (*Shorea* or *Hopea*). However, resin is also produced copiously by trees of Burseraceae, including some species of *Canarium*, *Dacryodes*, *Santiria*, and *Protium* (Langenheim 2003).

Discussion

The most common fruit or seed type collected was that of *Ziziphus*, accounting for more than half of the fossil diaspores. Although fruits of *Ziziphus* are dispersed by both birds and mammals (Medan & Schirarend 2004), it is thought the fruits had fallen from nearby trees and were washed into the site of deposition because of the large number of fruits of this species. Some of the *Ziziphus* fruits had partly abraded exocarps and mesocarps, however. The tubers, cf. *Cyperus* vel *Bolboschoenus*, might have been washed into the waterway by flooding. The resin may be dammar, derived from plants of Dipterocarpaceae or Burseraceae. Dammar is heavier than water and can be transported in the bedload (Gastaldo & Huc 1992). The fossil fruits collected were of intermediate size. No small (i.e., less than 5 mm across) specimens were collected, even with careful searching through masses of leaves in the mud. Apparently there was a sorting process with deposition of clasts of similar size. Rounded pieces of wood were also collected.

The climate today at the fossil site is seasonal tropical. Santisuk (2006) has classified the modern forests in Thailand into 14 type of evergreen forest and three types of deciduous forest, based predominantly on climatic, edaphic, and biotic factors, as well as elevation. Patches of forest remaining today in Muang district of Nakhon Ratchasima, in which the fossil site is located, are tropical deciduous dipterocarp and mixed deciduous forests. The fossil assemblage may provide some information as to the past vegetation types and climate. *Z. khoksungensis* shows closest affinity to *Z. cambodiana*, which is a scandent large shrub or tree that can be found in mixed deciduous forests. *D. costatus* consists of briefly deciduous trees reaching 40 m in height (Gardner et al. 2000) and occurs in dry evergreen or semi-evergreen forest, according to Santisuk (2006), or also in deciduous dipterocarp forest (Pooma 2003). *M. toosendan* Siebold & Zuccarini (sometimes considered a synonym of *M. azedarach*, e.g., Forest Herbarium (2001)) is a deciduous tree reaching 25 m in height and is common in open areas (Gardner et al. 2000) (mixed deciduous forest according to Santisuk (2006)). *D. dao* is a briefly deciduous tree up to 35 m tall. It is found in evergreen forests by streams (Chayamarit 1994) and is often locally common and often emergent in mature evergreen forests (Gardner et al. 2000). Comparison with extant plants suggests that at the time of deposition there were mixed deciduous and dry evergreen forests in the area. The climate may have been slightly wetter than at present since the forests in the area today are deciduous. Although the time of deposition is considered Pleistocene and likely Middle Pleistocene, it was not determined from the plant assemblage whether the time was a glacial or interglacial period.

The detailed preservation of the fruits and seeds from Khok Sung allows comparisons to be made at the specific level. The fruits of *Z. khoksungensis* are similar to those of the extant *Z. cambodiana*. However, consistent differences were found and a new species is being proposed. It is not known whether *Z. khoksungensis* was a sister species to *Z. cambodiana* and became extinct or whether it was part of an ancestral complex of populations that evolved to the current species. The fossil fruits of *D. costatus* and *D. dao* are quite similar to extant specimens.

However, the sample sizes are very small and analysis of a greater number of specimens may show distinctive differences at the populational or specific level. The fossil fruits of *M. azedarach* differ from the extant specimens in having thicker endocarp walls but the small sample size precludes identifying them as a new species.

Additional analysis of the plant assemblage from Khok Sung along with integration of the results with those of studies of the fauna and geology currently being undertaken by various researchers will allow a better understanding of the communities and environment during the Pleistocene in northeastern Thailand.

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