



รายงานวิจัย

การใช้หลักฐานจากบรรพชีวินเพื่อศึกษาการเปลี่ยนแปลงด้าน
ภูมิศาสตร์โบราณคดีและโบราณคดีสิ่งแวดล้อม
ของประเทศไทยในสมัยไมโอซีน
(Paleobiogeographic and paleoenvironmental changes in
Thailand since the Miocene: evidence from plant fossils)

ได้รับทุนอุดหนุนการวิจัยจาก
มหาวิทยาลัยเทคโนโลยีสุรนารี

ผลงานวิจัยเป็นความรับผิดชอบของหัวหน้าโครงการวิจัยแต่เพียงผู้เดียว



รายงานวิจัย

การใช้หลักฐานจากบรรพชีวินเพื่อศึกษาการเปลี่ยนแปลงด้าน
ภูมิศาสตร์โบราณคดีและโบราณคดีสิ่งแวดล้อม
ของประเทศไทยในสมัยไมโอซีน
(Paleobiogeographic and paleoenvironmental changes in
Thailand since the Miocene: evidence from plant fossils)

คณะผู้วิจัย

หัวหน้าโครงการวิจัย

Dr. Paul J. Grote

สาขาวิชาชีววิทยา สำนักวิชาวิทยาศาสตร์ มหาวิทยาลัยเทคโนโลยีสุรนารี

ได้รับทุนอุดหนุนการวิจัยจากมหาวิทยาลัยเทคโนโลยีสุรนารี ปีงบประมาณ พ.ศ. 2544-2545

ผลงานวิจัยเป็นความรับผิดชอบของหัวหน้าโครงการวิจัยแต่เพียงผู้เดียว

กันยายน 2558

Acknowledgements

Thanks to Pramook Benyasuta, Prakart Sawangchote, Wipanu Rugmai, Nareerat Boonchai, and other students and research assistants for assistance in the field. Special thanks to Paladej Srisuk for permission to study fossils from Srisuk's House Museum, Petchaburi. Assistance on using the SEM was provided by Sangphet Ngonchaiyaphum. Thanks to an anonymous reviewer for helpful suggestions. Financial support for research was provided by Suranaree University of Technology.



บทคัดย่อ

งานวิจัยนี้ใช้ซากบรรพชีวินพืชในประเทศไทยเพื่อศึกษาการเปลี่ยนแปลงด้านชีวภูมิศาสตร์และภูมิอากาศในยุคเทอร์เชียรี โดยเก็บตัวอย่างบรรพชีวินพืชจากแอ่งในจังหวัดลำพูนและลำปางซึ่งมีอายุในยุคไมโอซีนตอนต้นหรือโอลิโกซีนตอนปลาย นอกจากนี้ได้เก็บตัวอย่างเพิ่มเติมจากชั้นตะกอนในจังหวัดเพชรบุรี ภาคกลางของประเทศไทย ซึ่งมีอายุในยุคไมโอซีนตอนต้นหรือโอลิโกซีนตอนปลายเช่นกัน ในการศึกษาชั้นได้มุ่งเน้นที่ซากบรรพชีวินพืชกลุ่มสนและพืชดอกในสกุล *Alnus* ซึ่งเป็นกลุ่มที่มีการพบฟอสซิลที่สมบูรณ์ทั่วโลก ซากบรรพชีวินขนาดใหญ่ของพืชกลุ่มสนที่พบ ได้แก่ กิ่งและใบของสกุล *Sciadopitys* และสกุล *Glyptostrobus* กิ่ง ใบ และโคนของสกุล *Sequoia* และสกุล *Taiwania* รวมทั้ง ใบ โคน 2 ชั้น และเมล็ดมีปีก 1 ชั้น ของสกุล *Pinus* ซากบรรพชีวินใบของสกุล *Alnus* จากลำพูนแสดงให้เห็นถึงลักษณะที่ใกล้เคียงกับพืชปัจจุบัน คือ *Alnus japonica* โดยปัจจุบันนี้สกุล *Sciadopitys* *Taiwania* *Glyptostrobus* และ *Alnus japonica* พบอยู่ในเขตอบอุ่นหรือกึ่งเขตร้อนของเอเชีย ขณะที่สกุล *Sequoia* ปัจจุบันจำกัดเขตอาศัยอยู่เพียงในเขตอบอุ่นทางตะวันตกเฉียงเหนือของทวีปอเมริกาเท่านั้น หลักฐานซากบรรพชีวินพืชประกอบกับละอองเรณูในงานวิจัยอื่นชี้ว่าภาคเหนือและภาคกลางของประเทศไทยในยุคไมโอซีนตอนต้นมีความหนาวเย็นกว่าปัจจุบัน และภูมิอากาศได้กลายเป็นแบบร้อนชื้นในช่วงยุคไมโอซีนตอนกลาง



Abstract

Plant fossils from Thailand were used in an attempt to study paleobiogeographical and paleoclimatic changes during the Tertiary. Fossils were collected from basins in Lamphun and Lampang, thought to be early Miocene or late Oligocene in age. Additional specimens were collected from deposits in Phetchaburi, central Thailand, also considered to be early Miocene or late Oligocene. This study focused on conifers and the angiosperm genus *Alnus*, which have very good fossil records worldwide. Macrofossils of conifers included twigs and needles of *Sciadopitys* and *Glyptostrobus*. Twigs, needles, and cones were collected from *Sequoia* and *Taiwania*, and needles, two cones, and a seed wing were collected from *Pinus*. Leaves of *Alnus* from Lamphun showed affinity to the extant genus *Alnus japonica*. *Sciadopitys*, *Taiwania*, *Glyptostrobus*, and *Alnus japonica* are all extant in temperate or subtropical regions in Asia, whereas *Sequoia* today is restricted to temperate western North America. The evidence from the fossils, along with evidence from pollen provided by other researchers, suggests that northern and central Thailand were cooler during the early Miocene and that the climate became tropical during the middle Miocene.

Table of Contents

	Page
Acknowledgements	i
บทคัดย่อ	ii
Abstract	iii
Table of contents	iv
Tables	v
Figures	vi
Chapter 1 Introduction	1
Chapter 2 Materials and methods	5
Chapter 3 Results	8
3.1 Systematics	8
3.1.1 Pinaceae Adanson	8
3.1.2 Podocarpaceae Endl. nom. cons.	15
3.1.3 Sciadopityaceae Luerssen	15
3.1.4 Cupressaceae Gray nom. cons.	16
3.1.5 Betulaceae Gray (Fagales)	18
3.2 Character evolutions of <i>Alnus</i>	21
Chapter 4 Discussion and Conclusions	23
References	32
Curriculum vitae	53

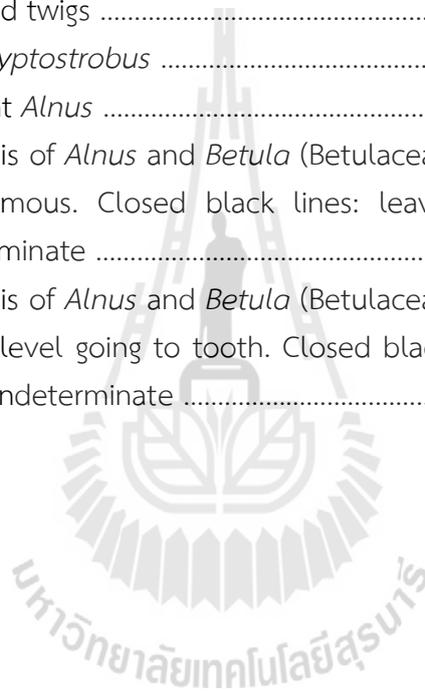
Tables

Table 3.1. Leaf and seed characters of extant <i>Pinus</i> species occurring in southeast and eastern Asia (Gernandt et al., 2005; Eckenwalder, 2009)	10
Table 4.1. Species of conifers in mainland Southeast Asia	26
Table 4.2. Fossil record of conifers in mainland Southeast Asia	26



Figures

Figure 1. Fossil sites	40
Figure 2. Seed cones and seeds of <i>Pinus</i>	41
Figure 3. Needles of <i>Pinus</i>	42
Figure 4. Fusainized wood	43
Figure 5. <i>Sciadopitys</i> sp. from Ban Pa Kha	44
Figure 6. <i>Sciadopitys</i>	45
Figure 7. <i>Sciadopitys</i> anatomy	46
Figure 8. <i>Sciadopitys verticillata</i> , in natural habitat, Japan, except C, cultivated	47
Figure 9. <i>Sequoia</i> cones and twigs	48
Figure 10. <i>Taiwania</i> and <i>Glyptostrobus</i>	49
Figure 11. Fossil and Recent <i>Alnus</i>	50
Figure 12. Character analysis of <i>Alnus</i> and <i>Betula</i> (Betulaceae), using parsimony. Open lines: leaves craspedodromous. Closed black lines: leaves not craspedodromous. Partly closed lines: indeterminate	51
Figure 13. Character analysis of <i>Alnus</i> and <i>Betula</i> (Betulaceae), using parsimony. Open lines: Secondary or lower level going to tooth. Closed black lines: Veins not going to tooth. Partly closed lines: indeterminate	52



Chapter I

Introduction

The present flora as well as fauna of Thailand are a result of both present ecological factors and historical events of the geologic past. The species found today are those ecologically adapted to current environments, both biotic and abiotic. However, the species composition in any area such as Thailand is also the historical end result of speciation locally or elsewhere and patterns of emigration, immigration, and extinction. As climatic and other environmental factors changed, some species were able to change their distribution to more suitable habitats or to survive in restricted refugia. Other species, unable to adapt to environmental changes or to migrate, became extinct. Study of the distribution of species in the past is expected to shed light on the current distribution of species. Furthermore, an understanding of the changes in plant communities resulting from environmental changes over geologic time may help indicate changes that may occur in species composition due to the environmental changes caused by the activities of humans.

A series of Tertiary basins are exposed in Thailand from Chiang Mai south to Krabi (Buffetaut et al., 1989; Watanasak, 1990). Past environments in these basins included swamps and lakes at various times, depending on the water level in the basins. Plant remains from swamps are sometimes preserved as lignite deposits, in which carbonized wood can be found. Lake deposits also contain plant remains, including leaves, gymnosperm cones, and pollen. These basins, at least in the North of Thailand, are thought to be Miocene in age (C. Chonglakmani, personal communication). In addition to these basins in northern and southern Thailand, extensive deposits of permineralized wood occur in Northeast Thailand in Nakhon Ratchasima and other provinces. Permineralized wood is common in some areas in unconsolidated sand and conglomerate sediments and considered to be Miocene, Pliocene, or Pleistocene in age (C. Chonglakmani, personal communication). Collection and analysis of fossils in northern and northeastern Thailand will provide knowledge of past floras in Thailand and can help answer questions as to what extent plants can survive in the face of environmental change.

Although much paleobotanical research has been carried out in India (many articles in the journal *The Palaeobotanist*, published in India), and in China (e.g. Li, 1995; Sun et al., 1998), limited research has been carried out on plant fossils in Thailand. Palynological studies on Tertiary deposits in Thailand include

the work of Watanasak (1988a, b, 1990), Getahun and Ratanasthien (1993), and Ratanasthien (1989). Additional palynological work was undertaken by Songtham and colleagues (Songtham et al., 2003, 2005). The only studies of fossil leaves are those of Endo (1964, 1966) on deposits from the Li Basin, Lampun, and Endo and Fujiyama (1966), on leaves from Tak. Petrified wood has been studied from northern Thailand, at Pong Basin, Phayao (Vozenin-Serra et al., 1989), and in northeast Thailand (Prakash, 1979; Vozenin-Serra and Privé-Gill, 1989). Petrified wood has also been studied in the nearby countries of Burma (Bande and Prakash, 1986; Chowdhury and Tandon, 1964); Vietnam (Bande and Prakash, 1986; Serra, 1981; Vozenin-Serra and Privé-Gill, 1994); and Cambodia (Bande and Prakash, 1986; Vozenin-Serra and Privé-Gill, 1991a, b).

Quite a bit of research has been done in Thailand on vertebrate fossils, mostly by members of the Thai-French Vertebrate Paleontology Project. For example, vertebrate fossils, including fishes, reptiles, birds, and mammals - insectivores, primates, bats, rodents, mastodons, deer, and rhinoceros-like mammals - from the Li Basin, have been collected and studied (Buffetaut et al., 1989; Ginsburg, 1989; Ginsburg et al., 1991; Ducrocq et al., 1993a,b). Perhaps the most detailed published work is a study of Plio-Pleistocene rodents in Thailand by Chaimanee (1998).

Many researchers have been interested in biogeographical relationships between Eurasia and North America, such as the detailed review by Manchester (1999, and references cited therein). By analyzing the fossil records of Tertiary plants from Asian, European, and North American countries, patterns of migration of plants among these Northern Hemisphere continents can be seen. However, most of the analyses have dealt mainly with records from temperate countries, as very little paleobotanical data is available from tropical countries, especially countries in Southeast Asia (India is an exception, with extensive literature on paleobotany). Results obtained from the research proposed here is expected to make a contribution to the study of plant evolution and migration throughout the Northern Hemisphere.

Both pollen and animal fossils have been used to deduce information about past environments in Thailand. Watanasak (1988b) used pollen to determine that temperate forests were present in central Thailand during the Mid-Tertiary. Based on mammalian faunas during the Middle Miocene, Ducrocq et al. (1993a) suggested the presence of small areas of forest probably mixed with grassland occurring in a wet environment with a presumed monsoonal climate. Chaimanee (1998) used data on fossil rodents to indicate both biogeographic and

environmental changes during the Pliocene and Pleistocene. Researchers overseas have used foliar physiognomy (size and shape patterns of leaves) (Christophel and Greenwood, 1989; Wiemann et al., 1998; Wilf, 1997; Wilf et al., 1998; Wing, 1997; Wing and Greenwood, 1993; Wolf, 1978, 1993) and stomatal density of leaves (McElwain and Chaloner, 1996; Van Der Burgh, 1993), as well as presence or absence of particular taxa, to provide evidence on past environments and climates. An international project, NECLIME (Neogene Climate Evolution in Eurasia), has been collecting and sharing data on fossil occurrences contributed by researchers around the world with the goal of determining changes in climate during the Neogene in Eurasia.

Researchers at Suranaree University of Technology have begun investigations of past floras and climates in Thailand. Research by the author, Chongpan Chonglakmani, and Pramook Benyasuta (funded by BRT grant 141020, *Changes in plant diversity over geologic time during the Cenozoic era in Thailand*, Paul J. Grote, principal investigator) concentrated on changes in plant diversity during the Cenozoic era. Collections have been made at lignite mines in the Li Basin, Amphoe Li, Lamphun (Miocene age), a lignite mine at Amphoe Chiang Muan, Phayao (Miocene), and at Ban Mak lignite mine in Krabi (Tertiary age). Leaves, some with intact cuticle, gymnosperm cones, seeds, coalified wood, and permineralized wood, has been collected from the Li Basin. Leaves, fruits, and permineralized wood has been collected from Ban Mak mine in Krabi. Additionally, a large quantity of silicified wood has been collected from Nakhon Ratchasima, Chaiyaphum, and Khon Kaen (Miocene, Pliocene, or Pleistocene) and from Kalasin and Mukdahan (late Jurassic?). Work has begun in identifying the Northeastern silicified wood as well as some leaves and cones from the lignite mines. Of interest are needles and cones of *Sequoia* found in the Li Basin; this genus is presently restricted to temperate coastal mountains in the western U.S., and the fossil may indicate a formerly more temperate climate in northern Thailand. Another conifer found in Li Basin is *Sciadopitys*, which today is only found in central and southern Japan. Additional families represented by leaves in the Li Basin appear to include Fagaceae and Betulaceae; a species of fern has also been collected.

Research into leaf architecture of fossil and modern leaves has been in progress (Use of leaf architecture and anatomy in the study of plant diversity in the Tertiary and Recent of Thailand, research grant funded by SUT, Paul J. Grote, Principal Investigator, October, 1999,- September, 2000). Preparation and clearing of fossil leaves from the Li Basin has begun.

The research proposed here will continue the work begun in the research on leaf architecture. However, fruits, seeds, and cones, as well as leaves will be studied in an attempt to look at past floras. An emphasis will be placed on biogeographic changes: the species identified as fossils in the Miocene will be compared with plants living today in Thailand. They will also be compared with plant species found in nearby countries, including China and Japan, both during past epochs and in the present. A second emphasis will be deducing past environments, especially changes in temperature and moisture, by analysis of plant species present as well as by physiognomic characters.



Chapter 2

Materials and methods

Field trips were made to the following areas in Thailand:

- 1) Lampang Mine, Mae Than Subbasin, Lampang, 27 November to 2 December 2002, possibly Miocene or Oligocene in age.
- 2) Nong Ya Plong, Phetchaburi, central Thailand, from 8-11 December 2004, Miocene or Oligocene
- 3) Lamphun, Chiangmai, and Samut Songkhram, 21 to 18 April 2005. Banpu 1 mine, thought to be Oligocene to Early Miocene

Additional fossils from the paleobotany collection Center for Scientific and Technological Equipment, Suranaree University of Technology, were used in the investigation. Several specimens were borrowed from the Srisuk's House Museum, Phetchaburi (Figure 1F)

Several trips were made to the Forest Herbarium (BKF), Bangkok, to study living plant specimens.

Fossil localities

Mae Than Sub-basin (Figure 1C)

Mae Than Sub-basin is one of a series of basins extending from northern Thailand to the Malay Peninsula. The ages of the basins in Thailand range from Late Eocene for the Krabi Basin in southern Thailand (Bennami et al. 2001) to Middle Miocene in the north (Songtham et al., 2005). Mae Than Basin is situated in Lampang province, northern Thailand, southwest of Mae Than village, Ban Bom subdistrict, Mae Tha district, approximately 55 km south of the provincial town of Lampang (Muenlek 1992). Mae Than basin is a small intermontane basin 10-12 km long and 4-5 km wide trending northeast to southwest. This basin is thought to be a graben or half graben structure, which developed during the Oligocene/Miocene with periods of fluvial, lagoonal, and again fluvial activity (Muenlek 1992). This basin is considered by the Department of Mineral Resources (2001) to be one of six sub-basins of the Lampang Basin in Lampang province. The major layers of the sub-basin are the underburden, lower main coal seam, the interburden, the upper coal seam, and the overburden. Dicotyledonous leaves, conifer twigs, and coalified wood were collected from the underburden. Coalified wood was collected from the interburden, while dicotyledonous leaves were collected from the overburden. In addition, a thin layer (several inches thick) composed of coal and compressed ash and larger pieces of charcoal was observed in the interburden. Samples of this layer were collected for study.

The age of the charcoal layer is uncertain. The plant assemblage in the underburden contained twig of *Sequoia* sp. similar to twigs found in a level of deposits of Banpu sub-basin of Li Basin, Lamphun province considered to be early Miocene or late Oligocene based on palynomorphs (Songtham et al. 2003, 2005). Therefore, the age of the charcoal is thought to be from this age or a younger age (up to middle Miocene).

Nong Ya Plong (Figures 1D, E)

These deposits are thought to be late Oligocene in age based on the fossil mammal assemblage (Chaimanee et al., 2007) and also late Oligocene based on palynomorphs (Watanasak, 1988b).

Ban Pu 1 mine, Li Basin, Lamphun (Figure 1B)

These deposits are thought to be early Miocene or late Oligocene based on studies of pollen (Songtham et al., 2003, 2005).

Ban Pa Kha mine, Ban Pa Kha Sub-basin of the Li Basin, Li District, Lamphun (Figure 1A)

These deposits are thought to be early Miocene or late Oligocene based on studies of pollen (Songtham et al., 2003, 2005).

Preparing specimens for SEM

Ten pieces of charcoalified wood were removed from this layer, mostly by using a cleaned razor blade and forceps to slice and break loose fragments from larger pieces of charcoalified wood. The pieces were placed on a brass stub and held in place with silver cement, then coated with gold for 4 or 6 minutes with a JFC-1100E Ion Sputtering Device. The specimens were studied using a JEOL JSM-6400 scanning electron microscope at 15 or 20 kV or a JEOL JSM-5800LV scanning electron microscope at 10 kV. Small pieces of modern wood were cut with a razor blade and prepared in the same manner for viewing with SEM. The fossil specimens are housed at the Center for Scientific and Technological Equipment, Suranaree University of Technology.

Herbarium specimens

Herbarium specimens were observed and photographed at the following herbaria: Beijing (PE), Forest Herbarium, Bangkok (BKF), and the herbarium of Suranaree University of Technology, Nakhon Ratchasima, Thailand. Additional information was obtained from literature and from online. Character analysis using parsimony was

performed using Mesquite (Maddison and Maddison, 2009). The leaf architecture terminology of Hickey (1973, 1979[used?]) and Dilcher (1974) was used.



Chapter 3

Results

3.1. Systematics

The systematics of the following fossils is described below. The sequence of the families follows that of Stevens (2001 onwards).

3.1.1 Pinaceae Adanson

Pinus sp. 1

Specimen: disarticulated wing of seed, compression (SUT631; Figure 2B)

Description: a disarticulated wing of a seed, lacking the seed itself. Length 25.5 mm including two claws; 16.8 not including claws (length not including broken distal tip), and width 6.3 mm. Slightly tapering from proximal to distal end; medial edge nearly straight; lateral edge slightly concave with slight projection approximately 6 mm distal to seed; the distal edge truncate (probably broken). Two claw-like appendages, which presumably extended to the medial and lateral sides of the seed. Many parallel nearly straight or slightly wavy ridges on the surface.

Locality: Ban Pa Kha mine, Li district, Lamphun (locality 019)

Affinities and biogeography: The genus *Pinus* currently comprises 97 species found in much of North America, Europe, and Asia, and northernmost Africa. Only 1 species, *P. merkusii*, reaches the Southern Hemisphere, with a population in Sumatra (Indonesia) at 2°S latitude. In North America, the genus reaches as far south as Guatemala (Eckenwalder, 2009).

Pinus has been traditionally divided into 2 groups: the hardwood pines with hard wood and double vascular strands in the needles, and the softwood pines with soft wood and a single vascular strand in the needles. The former species are placed in subgenus *Pinus* (or subgenus *Diploxylon* Rehder), and the latter in the subgenus *Stobus* J. Lemmon (or subgenus *Haploxylon* Rehder) (Eckenwalder, 2009). These two subgenera have been variously further divided into sections and subsections. A recent classification was proposed by Gernandt et al. (2005) based on molecular studies of DNA. They divided subgenus *Pinus* into sections *Pinus*, with two subsections, and section *Trifolieae*, with three subsections. The genus *Stobus* was divided into section *Parrya*, with three subsections, section *Quinquefoliae*, with two subsection (Gernandt et al., (2005). Table 3 lists the extant species of *Pinus* occurring in southeastern and eastern Asia. These species are restricted to section *Pinus* of subgenus *Pinus* and section *Quinquefoliae* of subgenus *Stobus*. The two species native to Thailand, *P. kesiya* and *P. merkusii* are in the section *Pinus*. Species in the other sections occur in western Asia, Europe, northern Africa, and North America (Eckenwalder, 2009).

Fossil extinct *Pinus* species have been reported from southwestern China. *Pinus prekesiya* Xing, Liu, and Zhou is known from two seed cones from the upper Miocene of central Yunnan province (Xing et al., 2010). Two species based on seed cones were obtained from upper Miocene deposits in Zhejiang province, eastern China: *P. prekesiya* and a new species, *P. preyunnanensis* X.H. Xu and B.M. Sun (Xu et al, 2015). A fossil cone and needles from an upper Miocene deposit in southeastern Yunnan were placed in the extant species *Pinus massoniana* Lambert (Zhang et al., 2015).

Of the approximately 111 extant species of *Pinus* worldwide (or 97 according to Eckenwalder, 2009), most have seeds with wings, while some species have seeds with rudimentary wings or no wings (Lanner, 1999). All the wings are distal to the actual seed. The tissue of the wing is actually derived from the seed scale (Farjon and Styles, 1997). Seeds are either adnate where the wing remains attached to the seed and articulate seeds where the wing eventually detaches from the seed. Wingless seeds are adnate seeds with a vestigial amount of wing tissue on the seed or articulate seeds where the wing tissue remains attached to the seed scale (Farjon and Styles, 1997).

Table 3.1 lists the extant species of *Pinus* in southeastern and eastern Asia. Of eight species in the section *Pinus*, subgenus *Pinus*, eight species, including *P. kesiya* and *P. merkusii* (Figure 2C), which are native to Thailand, have articulated seeds as in the fossil. Of 14 species in section *Quinquefoliae*, 4 have articulate seeds. Of these, *P. bungeana* has small seed wings, 2-5 mm long, while *P. gerardiana* has articulate wings that often remain attached to the seed scale of the cone.

The fossil seed wing is more likely to be a species from subgenus *Pinus*, although species of subgenus *Stobus* cannot be ruled out. The shape and size of the wing is similar to that of wings of *P. merkusii*, which is extant in northern Thailand, so the fossil may have affinity to that species.

The fossil seed wing was collected from a lacustrine deposit between the lower and upper main coal seams (swamp deposits) from the Ban Pa Kha subbasin. The age is considered to be early Miocene or late Oligocene. Both extinct and extant species of conifers have been reported from the upper Miocene of China. The fossil seed wing could either be from a surviving species or an extinct species.

Table 3.1. Leaf and seed characters of extant *Pinus* species occurring in southeast and eastern Asia (Gernandt et al., 2005; Eckenwalder, 2009)

<i>Pinus</i> L.	Distribution	Altitude (m)	Needles per fascicle	Type of seed
<i>Pinus subgenus Pinus</i>				
sect. <i>Pinus</i>				
<i>P. densata</i> M.T. Masters	Southwestern China	(1,100-2,600-3,500 (-4,200))	2 (3)	Articulate
<i>P. densiflora</i> P. Siebold and Zuccharini	Japan (except Hokkaido), Korea, China (south to Jiangsu), north to far eastern Russia	(0-100-900 (-1,400))	2	Adnate
<i>P. kesiya</i> Royle ex G. Gordon	Southeast Asia, from eastern India and southwest China to Myanmar, northern Thailand, Laos, to southern Vietnam; Philippines	(300-700-2,000 (-2,700))	2	Articulate (wing 12-16 (-20) mm)
<i>P. luchuensis</i> H. Mayr	Japan (Ryukyu Islands)	0-300 (-700)	2	Adnate
<i>P. massoniana</i> A. Lambert	China (Sichuan to Yunnan to Hainan and Taiwan), northern Vietnam (perhaps introduced)	0-1,500 (-2,000)	2 (3)	Articulate
<i>P. merkusii</i> Jungh. and de Vriese	Southeast Asia (Myanmar, southern China (Guangxi, Guangdong, and Hainan), Laos, Vietnam, Thailand, northern Sumatra (Malaysia), and Philippines	(50-250-1,500 (-2,000))	2	Articulate (wing 17-25 mm)

Table 3.1. (Continued)

<i>P. roxburghii</i> C. Sargent	Himalaya (Pakistan to Arunachal Pradesh (India))	(450-600-1,500 (-2,300))	3	Clasping (should be adnate)
<i>P. sylvestris</i> L.	Eurasia (Scotland, Norway, and Spain east to Russia (to Pacific Ocean))	0-2,100 (-2,600)	2 (3)	Articulate
<i>P. tabuliformis</i> Carrière	Central China (Qinghai and Sichuan to Shandong and Jilin), Korea	(50-1,000-2,500 (-3,000))	2 (3)	Articulate
<i>P. taiwanensis</i> Hayata	China (Taiwan, Henan, Guizhou, Guangxi)	600-750-3,000 (-3,400)	2	Adnate
<i>P. thunbergii</i> Parlatores	Southern Korea, Japan	0-300 (-1,000)	2 (3)	Articulate
<i>P. yunnanensis</i> Franchet	Southwestern China (Tibet, Yunnan, Guizhou, and Guangxi)	(400-600-2,600 (-3,400))	(2) 3	Articulate
sect. <i>Trifoliae</i> Duhamel				
<i>Pinus</i> subgenus <i>Strobis</i>				
sect. <i>Parrya</i>				
sect. <i>Quinquefoliae</i>				
<i>P. armandii</i> Franchet	Japan; central and southern China	(100-1,000-2,500 (-3,000))	5 (-7)	Wingless or short adnate wing
<i>P. bhutanica</i> A. Grierson, D. Long, and C. Page	Bhutan, northern India, and Tibet, China	1,750-2,400	5	Adnate wing
<i>P. bungeana</i> Zuccarini ex Endlicher	Central China (Shanxu to Gansu to Sichuan and Hubei)	(500-1,000-1,800 (-2,800))	3	Articulate (wing 2-5 mm)

Table 3.1. (Continued)

<i>Pinus dalatensis</i> de Ferré	Central Vietnam	1,500-2,000	5	Wings 15-20 mm
<i>P. gerardiana</i> N. Wallich ex D. Don	Western Himalaya (Afghanistan to Kashmir and Himachal Pradesh (India))	(1,800-) 2,000 – 3,000 (3,350)	3	Wings articulate and often stuck to seed scale
<i>P. koraiensis</i> P. Siebold and Zuccharini	Far eastern Russia, northeastern China, Korea, and Japan (Honshus)	(200-) 600-2,000 (-2,500)	5	Unwinged
<i>P. krempfii</i> Lecomte	Central Vietnam	1,200-2,000	2 (up to 7 mm wide)	Articulate
<i>P. kwangtungensis</i> W.Y. Chun ex Tsiang (syn. <i>P. parviflora</i> P. Siebold and Zuccarina var. <i>kwantungensis</i> (W.Y. Chun ex Tsiang) Eckenwalder	Southeastern China (Guizhou to Guangdong to Hainan), northern Vietnam	?	(2, 3) 5	Adnate
<i>P. parviflora</i> P. Siebold and Zuccarini (excluding <i>P. kwantungensis</i> and <i>P. wangii</i>)	Taiwan, northern to southern Japan, and Korea	(60-) 300-2,000 (-2,500)	5	Adnate
<i>P. pumila</i> (P. Pallas) E. Regel	Northeastern Asia (Eastern Russia, northern Mongolia, northeastern China, Korea, and northern and central Japan)	(0-) 500-2,500 (-3,200)	5	Unwinged
<i>P. sibirica</i> Du Tour	Russia, Kazakhstan, northern and northeastern China, and Mongolia	(100-) 800-2,000 (-2,400)	5	Wingless

Table 3.1 (Continued)

<i>P. squamata</i> X.W. Li and Ji R. Hsüeh	Northeastern Yunnan	2,200-2,500	(4) 5	Articulate
<i>P. wallichiana</i> A.B. Jackson	Himalaya (Afghanistan to Tibet and Yunnan (China)	(1,600-) 2,000-3,000 (-3,900)	5	Adnate
<i>P. wangii</i> Hu and W.C. Cheng (syn. <i>P. parviflora</i> P. Siebold and Zuccarin var. <i>wangii</i> (Hu and Cheng) Eckenwalder	Southern Yunnan (China) and possibly central Vietnam	?	5	Adnate

Pinus sp. 2

Specimens: 5-needle clusters, compressions (SHM-SN 114, 115, 116, 117 (Figure 3B), 118 (Figure 3A), 119, 120, 121, 286 (Figure 3C)

Description: Fascicles of 5 needles. The leaf scales appear absent. Some fascicles are still attached to a short shoot. The longest needle is 10.5 cm long, with the tip missing. Needles 0.6 mm wide.

Locality: Nong Ya Plong, Petchburi

Affinities and biogeography: Adult plants of the genus *Pinus* have both long shoots and short shoots. The long shoots have small scale leaves. Short shoots occur in the axil of a scale leaf. The short short shoot consists of (1) 2-5 (-8) needle-like leaves in a whorl. These needles are surrounded at the base by scale leaf or cataphylls (Eckenwalder, 2009). The number of needles per fascicle in *Pinus* trees is fairly consistent. Most species have 2, 3, or 5 needles per fascicle. One species, *P. monophylla*, has a single needle per fascicle. A few other species can vary from 2 - 5, 3 - 5, or 4 - 5 needles. Four other species have 5, or frequently 6, or up to 8 needles per fascicle (Richardson and Rundel, 1999). Today there are two native species of *Pinus* in Thailand, *P. merkusii* Jungh. and De Vriese and *P. khesiya* Royle ex G. Gordon (Phengklai, 1972a).

Table 3 lists the extant species of *Pinus* from southeastern and eastern Asia. Almost all species in the subgenus *Pinus* have cataphylls that remain attached to the fascicle of needle until the needles are shed (Figure 3E). Almost species of the subgenus *Strobos* have fascicles with cataphylls that are shed before loss of the needles (Figure 3D) (Eckenwalder, 2009). The fossils presented here have 5 needles that appear to be attached to the short shoot and lack cataphylls. This would indicate that the needles are from a species in subgenus *Strobos*. Needles of this subgenus

have 1 vascular strand. However, attempts to determine the number vascular strands in the fossil needles was unsuccessful. Of the extant species of subgenus *Pinus* in southeastern and eastern Asia, all have fascicles of 2 or 3 needles, and none have 5 needles. Of extant species of the subgenus *Strobus* in the same region, 11 or 14 species have 5 needles per fascicle.

It is concluded that the fossil needles belong to a species in subgenus *Strobus* of *Pinus*. This would exclude the two extant species of *Pinus* in Thailand, the 2-needle *P. merkusii* and the 3-needle *P. kesiya*. However, there are extant 5-needle pines in Vietnam and southwestern China. *Pinus dalatensis* de Ferré is restricted to central Vietnam at an altitude of 1,500 to 2,000 m. *Pinus kwangtungensis* W.Y. Chun ex Tsiang occurs in northern Vietnam and southern China, including Hainan. The rare species *P. squamata* X.W. Li and Ji R. Hsüeh occurs in northeastern Yunnan at altitudes of 2,200 to 2,500 m. *Pinus wangii* Hu and W.C. Cheng is found in southern Yunnan and possibly central Vietnam (Eckenwalder, 2009). All of these regions are presumably cooler today than Petchaburi province. Therefore, this would suggest that the climate at the time of deposition was somewhat cooler than today.

Pinus sp. 3

Specimens: Seed cone impression (SHM-SN7; Figure 2A)

Description: Unopened cone of 8.2 cm long and 3.0 cm. wide. The apophysis or external face of the seed scale is diamond-shaped with a centrally located diamond-shaped umbo. The umbo represents the external face of the seed cone in the first year of growth. The umbo appears to be concave with no prickle or point.

Locality: Nong Ya Plong, Petchaburi

Affinities and biogeography: The cone has the characteristics of cones of the genus *Pinus*. Seed cones of other genera in Pinaceae or in Cupressaceae do not have diamond-shaped apophyses. The fossil cone is similar to that of several species of *Pinus*, but in particular shares several characters with cones of *Pinus merkusii* (Figure 2D): the size and relative proportions of the cone, large diamond-shaped apophyses, and a concave umbo. The cones of the other extant Thai species, *P. kesiya* has a pointed projection in the umbo.

The fossil may have affinity with *P. merkusii* with extends from Myanmar, southern China (Guangxi, Guangdong, and Hainan), Laos, Vietnam, Thailand, northern Sumatra (Malaysia), to the Philippines. However, the degree of preservation of the fossil does not allow confirmation of this proposed affinity.

Pinus sp. 4

Specimens: Seed cone compression (SHM-SN 106; Figure 2E)

Description: The distal part of a seed cone, 9.5 cm long (with the basal half missing), 6.5 cm long; long, distal pointing seed scales.

Locality: Nong Ya Plong, Petchaburi

Affinities: The fossil cone appears to be a cone of *Pinus* with elongate distal pointing seed scales. However, affinities to any extant species of *Pinus* are unclear.

3.1.2 Podocarpaceae Endl. nom. cons.

Podocarpoxyton Gothan

Podocarpoxyton sp.

Specimens: SUT1333 (Figure 4A, B, C), SUT1846, SUT1959.

Description: Fragments of charcoalified (fusainized) wood. Details of the wood will be described in a detailed report on fossils from the Mae Than Sub-basin, Lampang (Grote, unpublished data).

Affinities: The fossil wood seems to share the most characters with wood of the extant family Podocarpaceae. However, because of incomplete knowledge of the fossil and also insufficient study of species of this family, the fossils have not been placed in any extant genus. A search was thus made for a form genus that could accommodate these fossils. The charcoalified wood in this study generally shows the characters of *Podocarpoxyton* and is thus placed in this morphogenus.

The fossil wood in this study differs from the fusainized wood *Podocarpoxyton dacryoides* Cui from the early Cretaceous Huolinhe Formation, Inner Mongolia, China (Cui, 1995), in that the fossil has cross-field pits with narrower pit chambers.

3.1.3 Sciadopityaceae Lueresen

Sciadopitya sp.

Locality: Ban Pa Kha mine, Li district, Lamphun (SUT locality 002); in shale in the interburden

Specimens: A conifer stem with needles (SUT571; Figure 5B, and 571'; Figure 5A, C, 6A); 2 needles (SUT 264; Figure 5D)

Description: The exposed part of the stem is approximately 2.4 cm long and 0.18 cm wide with a spiral arrangement of leaf scars, apparently from scale leaves. At the distal end of the stem is a whorl or pseudo-whorl of at least 11 elongate needles up to 6 cm long (the apices of all needles missing). Fragments of prepared cuticle showed stomates aligned in rows, with each stomate surrounded by approximately 6 subsidiary cells (Figures 7A, B). Other epidermal cells near the stomates are rectangular or irregularly shaped. Lateral to the stomatal region are longer rectangular cells.

Affinity and biogeography: From the arrangement of the needles and apparent scale leaves, these fossils can be placed in the genus *Sciadopitys* Sieb. and Zucc. of *Sciadopityaceae* (Figures 6B, C). This family at present consists of only one species, *Sciadopitys verticillata* (Thunb.) Sieb. and Zucc. (the umbrella pine), which is endemic to temperate regions in Japan (Figures 8A, B, C, D, E). However, the fossils differ from the modern species in having subsidiary cells lacking papillae (Figures 7C, D, E, F). The fossils also differ from *S.* sp. from the Miocene of Japan (Uemura, 1986) and *S. tertiara* Menzel emend. Wld., Kilpp., and Ber. from the middle Miocene of Germany (Jähnichen, 1969), both of which have subsidiary cells with papillae.

3.1.4 Cupressaceae Gray nom. cons.

Sequoia sp.

Specimens: Twigs with needles (Figures 9B, D) and isolated needles. Seed cones (Figure A).

Localities: Banpu 1 mine, Li district, Lamphun; Mae Than subbasin (Lampang basin), Mae Tha district, Lampang; Ban Pa Kha mine, Li district, Lamphun.

Description: Twigs with spirally arranged needles. The needles are either short and round distally or elongate and pointed. Seed cones consisting of spirally arranged seed scales with lens-shaped external faces. Note: a more detailed description of this fossil species will be presented in a report on Mae Than fossils (Grote, unpublished data).

Affinity and biogeography: The presence of spirally arranged needles of two sizes plus seed cones with spirally arranged seed cones indicates affinity to plants of the genus *Sequoia*. The genus presently consists of one extant species, *Sequoia sempervirens* (D. Don) Endl. (Figure 9C), growing in California and Oregon, in western North America. The extant species occurs in slopes and valleys that are often covered with fog (Eckenwalder, 2009). Although the current distribution is restricted, fossils of *Sequoia* have been found in many locations in North American and Eurasia from the Tertiary and Cretaceous (Eckenwalder, 2009).

Taiwania?

Specimen: SUT817' (Figure 10A)

Locality: Ban Pa Kha (locality SUT019)

Description: One pyritized compression. A stem appearing to have spirally arranged leaves and a terminal cone.

Affinities and biogeography: The specimen appears to be a conifer with a terminal cone. In gross appearance it is similar to *Taiwania* (Cupressaceae) (Figure 10B). At present, *Taiwania* consists of one extant species (*T. cryptomerioides*), occurring in

disjunct regions in southwestern China, Taiwan, northern Myanmar, and northern Vietnam. It is found altitudes of (1,750-) 1,800 to 2,600 (-2,900) m (Eckenwalder, 2009).

Glyptostrobus sp.

Specimens: Partly pyritized, partly coalified twigs (SUT554; SUT586) (Figure 10C)

Locality: Ban Pa Kha Sub-basin, Li Basin, Li District, Lamphun (Locality 019);

Description: Twigs up to 4 cm in length with spirally arranged needles. Needles up to 7.5 mm long, appear to be laterally flattened, curving outward distally.

Affinities and biogeography: although not well preserved, the needles appear to be flattend laterally. Laterally flattened needles are found in extant *Glyptostrobus pensilis* (Figure 10D) and in the larger juvenile needles of sterile twigs of *Taiwania cryptomerioides*. Needles of *Cryptomeria* are awl-shaped (Page, 1991). The thin needles of the fossils appear most similar to needles of *Glyptostobus*. *Glyptostrobus* consists of one extant species, *G. pensilis*, occurring in subtropical or tropical regions in southern China and in Vietnam and found in swamp and other wet environments. The altitudinal range is 0 to 700 (-1,000) m (Eckenwalder, 2009). The oldest know fossils are from Paleocene deposits in Alaska. Fossils are widespread in the Tertiary of North America and Eurasia (Eckenwalder, 2009)

Taxodioxyton Hartig

Taxodioxyton sp.

Specimens: Charcoalified wood (SUT1330 (lost, Figure 4C), SUT1848, SUT1849, SUT1850)

Localities: Mae Than Sub-basin of the Lampang Basin, Lampang.

Description: Fragments of charcoalified (fusainized) wood. Details of the wood will be described in a detailed report on fossils from the Mae Than Sub-basin, Lampang (Grote, unpublished data).

Affinities: *Taxodioxyton* has been used for fossil wood similar to that of Taxodiaceae and the genera *Cupressus*, *Juniperus*, *Libocedrus*, and *Thuja* in Cupressaceae s.s (Stewart & Rothwell 1993). The fossils studied here show affinity to *Glyptostrobus* and *Sequoia*. However, since several of the genera in the traditional Taxodiaceae have only one extant species, it is difficult to determine the degree of variation that might occur within one genus. Gerards et al. (2007) experimentally charcoalified modern conifer wood and found that changes occurred in the shape of bordered pits in the cross-fields. In wood with piceoid or taxodioid cross-field pits, the pit aperture appeared to be wider because the width of the aperture pit increased more than the width of the pit border. However, for cupressoid pits the pit border increased slightly more than the pit aperture. A possible source that could lead to misidentification of

wood is that piceoid pits in charcoalfied wood have similar dimensions to taxodioid pits in fresh wood. Characters in addition to the shape of cross field pits need to be evaluated when identifying fossil charcoalfied wood.

3.1.5 Betulaceae Gray (Fagales)

Alnus sp. (Description and affinities from Grote, 2005)

Specimens: 2 compressed leaf specimens (SUT 1003; Figures 11A, B, C; SUT 1607).
Infructescence with four cones from Ban Pa Kha Sub-basin (Figure 11C).

Locality: Banpu 3 mine, Li District, Lamphun Province (SUT locality 021) (SUT 1003);
Ban Pa Kha mine, Li District, Lamphun Province (SUT locality 002) (SUT 1607)

Description: Compressed leaf fragments, lacking the base and apex; widest part of lamina (SUT 1003) appears to be basal to midpoint, so leaf possibly narrowly ovate (2:1) or lanceolate (3:1); margin serrate, with 3 or 4 teeth per secondary vein, the secondary teeth (fed by the secondary vein or the first branch of a secondary vein) larger than the intersecondary teeth; teeth with acute apex, the tip rounded, the apical edge straight, and the basal edge approximately straight or slightly concave; sinus of teeth angular, acute or approximately 90°; venation pinnate, mixed craspedodromous, the primary vein approximately straight; secondary veins much thicker than the tertiaries, originating at an angle of 50-60°, the angle of divergence seeming to be greater as one looks more basally; the secondary vein curving slightly apically and dichotomizing not far from the leaf margin, one branch heading toward a tooth, the other branch extending apically roughly parallel to the margin (when this branch is thicker, the secondary vein considered to be eucamptodromous); this vein dichotomizing again, with one branch heading toward a tooth and the other branch connecting to a superadjacent secondary, at an approximately right angle or acute angle; the branch heading to the tooth may also have a vein branching apically which again branches, one vein heading toward a tooth and the other joining the superadjacent secondary; veins entering teeth medially or supramedi ally or possibly going to sinus of tooth; an intersecondary vein appearing to be present; tertiary veins percurrent, usually simple, unbranched, straight or forming a single S-shaped curve convex basally and concave apically, joining secondary veins at approximately right angles; some tertiaries are recurved, joining the primary vein; quaternary veins appearing to be reticulate and joining with tertiaries at approximately right angles; highest order of venation not seen.

Affinities: Leaves with a pattern of several smaller teeth occurring between larger teeth fed by secondary veins can be found in species of *Alnus*, *Betula*, *Carpinus*, and *Ostrya* in the Betulaceae (Mitchell, 1987; Coombes, 1992; personal observation). While the secondary veins are craspedodromous in *Betula*, *Carpinus*, and *Ostrya*, they can be

craspedodromous, semicraspedodromous, eucamptodromous, or brochidodromous in *Alnus* (Schneider, 1994; personal observation); intersecondaries can also occur in leaves of *Alnus*.

The genus *Alnus* comprises 35 extant species in Northern temperate regions extending south to Assam and Indochina and in the Andes (Willis, 1973). One species, *Alnus nepalensis* D. Don (Figure 24), is found in Thailand and is only known from Phu Luang, Loei Province, in the Northeast. The pattern of veins and teeth of the fossil species is most similar to that of the modern species *A. japonica*. The fossils differ, however, in having \pm two sizes of teeth, the teeth fed by the vein branching directly from the secondary vein being larger than the other teeth. The teeth in the two modern species, by contrast, are approximately equal in size. Secondly, veins in the fossils appear to either enter the tooth medially or supramedially or go to the sinus. In both modern species, the vein reaches the sinus with a branch then entering the tooth. The fossils also show affinity to *A. nepalensis*, but not as closely as to the above two species. In both the fossil species and *A. nepalensis* (Figure 24), intersecondaries are present and the tertiaries are percurrent. In *A. nepalensis*, veins generally reach the sinus of a tooth and continue supramedially into the tooth, whereas in the fossils, the nerves appear to either enter the tooth medially or supramedially or go to the sinus. In leaves of *Betula*, *Carpinus*, *Corylus*, and *Ostrya*, and some species of *Alnus* observed, secondary veins entered the teeth medially.

Alnus fernandi-coburgii can be found today in Guizhou, Southwest Sichuan, and Yunnan, China. *A. cremastogyne* occurs today in Southeast Gansu, North Guizhou, South Shaanxi, Sichuan, and Zhejiang, China (Li and Skvortsov, 1999). *A. nepalensis* lives today in India, Nepal, Sikkim, Bhutan, southern and southwestern China, Bangladesh, Myanmar, Thailand (Loei), and northern Vietnam (Li and Skvortsov, 1999; personal observation).

Compared with other reported fossil leaves, the pattern of veins and teeth of the fossil species studied here appears to be closest to that of the extinct species *Alnus newberryi* Meyer and Manchester (1997; their figures 1-4, plate 27; figures 1-3, plate 28) known from the Oligocene of Oregon, U.S.A. *Alnus newberryi* leaves are elliptic to narrowly elliptic to slightly ovate. The margins are serrate with 0-4 usually smaller teeth between those fed by a secondary vein; the tertiaries are percurrent, often with the outermost percurrent having an angular bend and another tertiary arising from the bend and extending to the margin. This pattern is similar to that of the fossil species described here, except that in our fossils the bent vein is thicker than that of *A. newberryi*. Excurrent veins are present in *A. newberryi* leaves as well as in the extant *A. japonica*, but not in our fossil.

Endo (1964) described a fossil species of *Alnus*, *A. thaiensis* Endo, based on catkins, from the Li Basin, Lamphun. He mentioned that the scales are similar to those of the extant species, *A. hirsuta* Rupr. and *A. incana* Willd.. However, leaves of both of these species differ from the fossil leaves reported here. *A. hirsuta* has ovate leaves with lobed margins; *A. incana* has ovate or elliptic leaves with craspedodromous secondary veins. Endo (1966) describes leaves of *A. thaiensis* Endo? from the Li Basin, Lamphun. It is difficult to compare the photo of the leaf fragment with our fossils, but it seems to differ because Endo describes the leaves as being craspedodromous.

Leaflets of *Juglans nigra* L. (Juglandaceae) show a semicraspedodromous pattern similar to that of the fossils, but the teeth differ in being somewhat irregular in size, but not with larger teeth fed by a secondary vein. I have not seen the pattern of larger and smaller teeth in Juglandaceae, although this character is commonly seen in Betulaceae.

It is concluded that these fossil leaf fragments belong to the genus *Alnus*, being close *A. japonica*. *Alnus japonica* is found in temperate eastern Asia (Murai, 1964; Li and Skvortsov, 1999).

An infructescence with four cones shows similarity to cones of *A. japonica* (Figure 1E) as well as to cones of other species of *Alnus*. Because the cones are not physically connected to the leaves, it is not confirmed that they are conspecific with the fossil leaves.

Taxonomy and biogeography of *Alnus*:

Based on a study ITS region of nuclear DNA, *Alnus* is shown to be monophyletic (Chen and Li, 2004). The genus is considered to be a sister group to the other 5 genera in Betulaceae (Li et al., 2004) or as sister to *Betula*, with this pair of genera being sister to the other genera in the family (Chen and Li, 2004). Morphologically, Chen and Li (2004) and previous authors separated species of *Alnus* into those having sessile or subsessile winter buds and long and short branches with those having stalked winter buds and lacking short branches. Chen and Li included the former taxon in the subgenus *Alnobetula* and divided the latter group into 2 subgenera, *Clethropsis* and *Alnus*. *Alnus nepalensis*, the only species found in Thailand, although considered by other other authors to be in the subgenus *Clethropsis*, is embedded in the subgenus *Alnus* in a study of the ITS region of nuclear DNA (Chen and Li (2004). Looking at the biogeography of extant species, the site of origin of the genus is unclear. Of 9 species of *Alnobetula* listed, 5 can be found in eastern Asia; however, another species occurs in western North America, 2 species occur in both eastern and western North America, and 1 species occurs in southern Europe (Chen and Li., 2004). Of the 3 species of *Clethropsis*, 2 occur in eastern Asia

and 1 in eastern North America. Of 22 species listed of subgenus *Alnus*, 9 occur in eastern Asia, while others are found in Europe, the Mediterranean region, eastern and western North America and Central and South America. *Alnus acuminata* from South America and *A. jorullensis* from Central and South America appear most closely related to 2 species from western North America, so may have their origin from that region (Chen and Li, 2004). Migration between Eurasia may have been across the Bering land bridge, although another possible route is the North Atlantic land bridge between Europe and North America (Chen and Li, 2004).

Alnus japonica, the extant species thought to be closest to the fossil species presented here, is restricted to Asia, occurring in Japan (Honshu, Shikoku, Kyushu, and Hokkaido and Ryukyu islands), North Korea, Far East Russia, and China (Anhui, Hebei, Jiangsu, Jilin, Liaoning, Shandong, and Taiwan). The trees are found in temperate forests, along stream banks and on roadsides, at an elevation of 800 to 1,500 m (Murai, 1964; Li and Skvortsov, 1999). If the fossil species of *Alnus* from Lamphun had a physiological tolerance similar to that of extant *A. japonica*, then the paleoclimate of the area may have been temperate or at least cooler than at present.

3.2 Character evolutions of *Alnus*

Since fossil leaves are usually found as isolated organs, Recent leaves and cones were surveyed to search for taxonomically important characters to allow placement of fossil leaves within subgenera or smaller subtaxa of *Alnus*. Cones were available from an insufficient number of species, so characters of cones were not used for character analysis. Peltate glands and acarodomatia were found in leaves of most or all modern species, but were not observed in fossil specimens. Leaf shape and size were variable within a species. Two characters easily observed in fossils were the venation pattern of the secondary veins and whether the secondary or lowest level vein to extend to the margin entered a tooth directly or reached the sinus before branching to the tooth. Semicraspedodromy was observed in some species of the subgenera *Alnus* and *Clethroopsis*, but not in *Alnobetula*. Brochidodromy was observed in *A. formosana*, and eucamptodromy occurred in basal secondary veins of *A. jorullensis* and *A. nitida*.

Character evolution analysis using parsimony (Maddison and Maddison, 2009) was conducted using a cladogram modified from that of Chen and Li (2004) who used sequences of nuclear ribosomal DNA ITS regions. The first character investigated was venation pattern: craspedromy versus loss of craspedromy (brochidodromy or semicraspedodromy (Figure 12). The most parsimonious reconstruction had six steps, including the change in *Betula nana*, with craspedodromy being plesiomorphic. This analysis suggests that craspedodromy is plesiomorphic in the genus *Alnus* with

evolution of non-craspedodromy in the clade that includes the subgenera *Alnus* and *Clethropsis*. The changes in the clade that includes *A. japonica*, *A. serrulata*, and *A. matsumurae* are equivocal. The synapomorphy may have been non-craspedodromy, with regain of craspedromy in two species. Alternatively, the basal condition may have been craspedodromy with a change to non-craspedodromy in *A. japonica*. Likewise, the character state is equivocal in a clade of 14 species of the subgenus *Alnus*. Non-craspedromy may have been basal in the clade, with gaining of craspedromy in two subclades of 2 and 9 species, respectively. Alternatively, the basal condition of the clade may have been craspedromy with a change to non-craspedodromy in the 2 species *A. acuminata* and *A. jorullensis*.

The second character investigated was whether the secondary veins (or higher order veins if the leaves are not craspedodromous) went directly to the teeth or reached the sinus before branching to the teeth (Figure 13). The most parsimonious reconstruction had 5 steps with veins going directly to the teeth being the plesiomorphic character state. This analysis suggests that teeth going to the teeth is plesiomorphic for *Alnus*. However, the basal character state for the clade that includes the subgenera *Alnus* and *Clethropsis* is equivocal. The basal character state may have been veins going to the sinus with reversal to teeth going to the teeth either 3 or 4 times. Alternatively, the basal character may have been veins to teeth with independent evolution to teeth to the sinus 3 times (or possibly a fourth time in the case of *A. japonica*).

Chapter 4

Discussion and Conclusions

Conifers in mainland Southeast Asia today (Table 4.1)

Conifers today in Thailand comprise 11 species:

Podocarpaceae

Dacrycarpus imbricatus (Blume) de Laub.

Dacrydium elatum (Roxb.) Wall.

Podocarpus neriifolius D. Don

P. pilgeri Foxw.

P. polystachyus R. Br.

Nageia motleyi (Parl.) de Laub.

N. wallichiana (Presl.) Kuntze

Cupressaceae

Calocedrus macrolepis Kurz

Cephalotaxaceae

Cephalotaxus mannii Hook. f.

Pinaceae

Pinus merkusii Junghuhn and de Vriese

P. kesiya Royle

Conifers in Viet Nam (Nguyen and Thomas, 2004)

Cephalotaxaceae

Cephalotaxus mannii Hooker f.

Cupressaceae

Calocedrus macrolepis Kurz

Cunninghamia konishii Hayata

Cupressus funebris Endl.

Fokienia hodgsonii A. Henry and H. Thomas

Glyptostobus pensilis (Staunton) K. Koch

Taiwania cryptomerioides Hayata

Xanthocyparis vietnamensis Farjon and T.H. Nguyễn (or *Cupressus vietnamensis* (Farjon and T.H. Nguyễn) Silba (Eckenwalder, 2009)

Pinaceae

Abies delavayi Franchet ssp *fansipanensis* (Q.P. Xiang) Rushforth

(called *A. delavayi* var. *nukiangensis* in Flora of Cambodia, Laos, and Vietnam)

Keteleeria evelynana Masters

Keteleeria davidiana (M. Bertrand) Beissner

Pinus delatensis de Ferre
P. kesiya
P. kwangtungensis Chen (5-needles)
P. krempfii Lecomte (2-needle)
P. merkusii
P. wangii Hu and Cheng (5-needle)
Pseudotsuga sinensis Dode
Tsuga chinensis (Franchet) Pritzel ex Diels
 Podocarpaceae
Dacrycarpus imbricatus (Blume) de Laub.
Dacrydium elatum (Roxb.) Wall.
Nageia fleuryi (Hickle) de Laub.
Nageia wallichiana (Presl.) Kuntze
Podocarpus nerifolius D. Don
P. pilgeri Foxworthy
 Taxaceae
Amentotaxus argotaenia (Hance) Pilger
A. yunnanensis H.L. Li
A. poilanei (de Ferre and Rouane) D.K. Ferguson
A. hatuyenensis H.T. Hiep
Taxus chinensis Pilger
T. wallichiana Zucc.

Laos (Thomas et al., 2007)

Cephalotaxaceae

Cephalotaxus mannii Hook.f.

Cupressaceae

Calocedrus macrolepis

Cunninghamia konishii

Fokienia hodginsii

Pinaceae

Keteleeria evelyniana

Pinus dalatensis

Pinus kesiya

Pinus kwantungensis (likely to occur)

Pinus merkusii

Podocarpus nerifolius

Podocarpaceae



Dacrydium elatum
Dacrycarpus imbricatus
Nageia wallichiana
Nageia fleuryi (Hickel) de Laub.
Podocarpus pilger Foxw.

Taxaceae

Amentotaxus argotaenia (Hance) Pilg.
Amentotaxus yunnanensis H.L.Li
Taxus chinensis (likely to occur)

Cambodia (Thomas et al., 2007)

Pinaceae

Pinus kesiya (new)

Pinus merkusii

Podocarpaceae

Dacrydium elatum

Dacrycarpus imbricatus

Nageia wallichiana

Podocarpus nerifolius

Podocarpus pilgeri

Malaysia (pensinular)

Araucariaceae

Agathis dammara (Lamb.) Rich and A. Rich

Podocarpaceae

Dacrycarpus imbricatus (Eckenwalder, 2009)

Dacrydium beccarii Parlatores

D. comosum Corner

D. elatum

D. medium de Laubenfels

D. xanthandrum Pilger

Falcatifolium falciform (Parlatores) de Laubenfels

Nageia motleyi (Parlatores) de Laubenfels

N. wallichiana?

Podocarpus deflexus N. Ridley

P. nerifolius

P. polystachyus?

P. ridleyi (Wasscher) N. Gray



P. rumphii Blume

P. teysmannii Miquel

Table 4.1. Species of conifers in mainland Southeast Asia

	Thailand	Vietnam	Cambodia	Laos	Malaysia (mainland)	Total
Cupressaceae	1	7		3	-	7
Pinaceae	2	11	2	4	-	11
Podocarpaceae	7	6	5	6	15	18
Araucariaceae	-	-	-	-	1	1
Taxaceae	-	6	-	2	-	6
Cephalo- taxaceae	1	1	-	1	-	1
Total	11	31	7	16	16	44

Table 4.2. Fossil record of conifers in mainland Southeast Asia.

Fossils	Age	Organ	Locality	Reference
Araucariaceae				
<i>Araucarioxylon</i> sp.	Pliocene- Pleistocene	silicified wood	Nakhon Ratchasima	Vozenin-Serra and Privé-Gill, 1989
<i>Araucarioxylon traumaticum</i>	?	Wood	Cambodia	Vozenin-Serra and Privé-Gill, 1989
<i>Araucarioxylon</i> sp.	Tertiary	Wood	Vietnam	Vozenin-Serra and Privé-Gill, 1989
<i>Araucariacites australis</i>	Eocene	Pollen	Viet Nam	Tanh and Khuc, 2003
Cephalotaxaceae				
Cupressaceae				
<i>Glyptostrobus</i> sp.	Miocene- Oligocene	Twigs	Mae Than, Lampang	

Table 4.2 (Continued)

<i>Sequoia</i> sp.	Miocene- Oligocene	Twigs, cones	Banpu 1, Li Basin, Lamphun; Mae Than, Lampang	
<i>Taiwania?</i>		Twigs, cones		
<i>Inaperturopollenites dubius</i>	Late Oligocene	Pollen	Nong Ya Plong, Petchburi	Watanasak, 1988b
Pinaceae				
<i>Pinus</i> sp.	Pliocene	pollen	Viet Nam	Tanh and Khuc, 2003
<i>Pinus</i> sp.3		Cone	Nong Ya Plong, Petchburi	
<i>Pinus</i> sp. 4		Cone	Nong Ya Plong, Petchburi	
<i>Pinus</i> sp. 2		Needles	Nong Ya Plong, Petchburi	
<i>Pinus</i> sp. 1	Miocene- Oligocene	seed wing	Bang Pa Kha, Li Basin, Lampang	
<i>Pinuspollenites</i> sp.	Late Oligocene	Pollen	Nong Ya Plong, Petchburi	Watanasak, 1988b
<i>Piceapollenites alatus</i>	Late Oligocene	Pollen	Nong Ya Plong, Petchburi	Watanasak, 1988b
<i>Piceapollenites</i> sp.	Late Eocene	Pollen	Krabi Basin, Krabi	Songtham and Watanasak, 1999
<i>Piceapollenites</i> sp.	Late Eocene	Pollen	Krabi Basin, Krabi	Songtham and Watanasak, 1999
<i>Tsugapollenites igniculus</i>	Late Oligocene	Pollen	Nong Ya Plong, Petchburi	Watanasak, 1988b
Podocarpaceae				
<i>Podocarpus imbricatus</i>	Pliocene	pollen	Viet Nam	Tanh and Khuc, 2003

Table 4.2 (Continued)

<i>Dacrydium</i> sp.	Pliocene	pollen	Viet Nam	Tanh and Khuc, 2003
<i>Podocarpoxyton</i> sp.	Miocene-Oligocene	charcoalified wood	Mae Than, Lampang	
<i>Podocarpidites ellipticus</i>	Late Oligocene	Pollen	Nong Ya Plong, Petchburi	Watanasak, 1988b
<i>Podocarpidites ellipticus</i>	Late Eocene	Pollen	Krabi Basin, Krabi	Songtham and Watanasak, 1999
Sciadopityaceae				
<i>Sciadopitys</i> sp.	Oligocene-Miocene	Leaves	Ban Pa Kha, Li Basin, Lamphun	

Conifers may have been more common in the past than at present in Thailand. Today Cupressaceae is represented by the single species, *Calocedrus macrolepis* Kurz, known from Phu Luang in Loei province (Phengklai, 1972b). However, during the Oligocene or early Miocene of northern Thailand, this family consisted of *Sequoia*, *Glyptostrobus*, and possibly *Taiwania*. The family Sciadopityaceae is today represented by only one species, *Sciadopitys verticillata*, found in temperate regions of Japan (Eckenwalder, 2009), but was once much more widespread including occurring in northern Thailand. Pinaceae also had more species during the Oligocene or early Miocene in northern Thailand and central Thailand. From macrofossils, *Pinus* is known from the disarticulated wing of a seed, from needles, and from seed cones. The 5-needle fossil pines (*Pinus* sp. 2) known from Phetchaburi in central Thailand may be related to extant *Pinus* species found farther north, such as from Vietnam or southern China. The genera *Picea* and *Tsuga* are evidenced by pollen.

Morley (1998) concluded that angiosperms did not originate in Southeast Asia as had proposed by Takhtajan and others, but rather they dispersed in this region from West Gondwana. From the Cretaceous period onward angiosperms and other plants migrated into Southeast Asia by various routes. Plants from Africa rafted to the region on the Indian plate, which collided with Asia during the middle Eocene (Morley, 1998). Some plants, such as the conifer *Dacrydium* (Podocarpaceae) appear in the Sunda region during the Eocene and are thought to have arrived by long distance dispersal rather than rafting on India. The oldest record of *Dacrydium* is from the Santonian or Coniacian, a time later than the separation of India from Gondwana. The main

collision between the Sunda and Australian plates is thought to have occurred during the middle Miocene. During and after this time, some plants are thought to have migrated westward to the Sunda region from Australasia. For example, the mangrove plant *Campostemon* (Bombaceae), which currently is found in New Guinea and rarely in Borneo, appeared during the middle Miocene (approximately 14 Ma) in Borneo and later in the Malay basin (approx. 10 or 9.5 Ma) (Morley, 1998). Another migration route is along mountainous areas that have connected Southeast Asian plants with Laurasian elements (up to 60 degrees N latitude) during the Cretaceous and Tertiary periods (Morley, 1998).

The fossil record of conifers from the Cenozoic of the Southeast Asian mainland, although limited, can provide information on the biogeography of conifers during this era. Continental tectonic movements and orogenies have enabled several dispersal pathways during the Cenozoic. Montane connections with higher latitudes (up to 60 degrees N latitude) in Asia have allowed northward and southward dispersal of Laurasian montane plants during the late Cretaceous and Tertiary. Collision of the Indian plate with Asia in the middle Eocene permitted dispersal of plants to Southeast Asia. Collision of the Australian plate with Asia is thought to have allowed dispersal of plants during the middle Miocene (Morley, 1998). Fossils of Cupressaceae s.l. (*Sequoia*, *Glyptostrobus*, and *Taiwania*?) are known from macrofossils of northern Thailand and were likely dispersed via Laurasian montane connections. These connections may also account for the presence of *Pinus* and *Picea* (Pinaceae) in the late Eocene of southern Thailand (Songtham and Watanasak, 1999; Bennammi et al., 2001) and *Pinus*, *Picea*, and *Tsuga* (Pinaceae) and *Sciadopitys* (Sciadopityaceae) in the late Oligocene or early Miocene of northern Thailand (Watanasak, 1988a; Grote and Sawangchote, 2003). Most of these elements disappeared by the middle or late Miocene from deposits in northern Thailand. Of the above genera, *Glyptostrobus*, *Taiwania*, *Pinus*, and *Tsuga* still occur in Southeast Asia. For Podocarpaceae, pollen with affinity to *Podocarpus* and *Dacrydium* is known from late Oligocene or Miocene deposits of Thailand and to *Dacrydium* from the late Miocene and Pliocene of Vietnam. *Podocarpus*, a Gondwanan element, may have dispersed via the Indian plate. However, *Dacrydium* may have arrived from long distance dispersal from Australia. The oldest record of *Dacrydium* is from the Santonian or Coniacian in the upper Cretaceous, a time later than the separation of India from Gondwana (Morley, 1998), so *Dacrydium* was unlikely to have rafted from Gondwana on the Indian plate. *Dacrycarpus* (Podocarpaceae) is thought to have reached Southeast Asia later after collision of the Australian plate. Pollen of *Dacrycarpus* was recovered from the Plio-Pleistocene of Borneo and the Pliocene of Vietnam. All three of these podocarpaceous genera are extant in Southeast Asia. Wood with possible affinity to

Araucariaceae has been reported from the Jurassic of Vietnam (*Araucarioxylon colaniae*, Thanh and Khuc, 2003) and the Cretaceous (and possibly Jurassic) of Thailand (*Agathoxylon saravensis*, Philippe et al., 2004). The few records of this family from the Cenozoic include possible pollen from the Eocene of Vietnam (Thanh and Khuc, 2003) and silicified wood from the Plio-Pleistocene of Northeastern Thailand (*Araucarioxylon* sp., Vozenin-Serra and Privé-Gill, 1989) and Pleistocene of Cambodia (at least some of which is likely reworked from the Mesozoic). Philippe et al. (2004) mention that some silicified wood specimens of *Agathoxylon saravensis* from Jurassic?-Cretaceous deposits of Northeastern Thailand are similar to the fossil of *Araucarioxylon* sp. from the Plio-Pleistocene of Northeastern Thailand (Vozenin-Serra and Privé-Gill, 1989) and suggest that the specimen from the younger deposit may be reworked. It is equivocal whether plants of this family survived in Southeast Asia since the Mesozoic (Kunzmann, 2007) or whether they were reintroduced from the Australian plate since the middle Miocene. The family Araucariaceae in the Southeast Asian mainland today consists of the single species *Agathis dammara* (Lamb.) Rich. and *A. Rich.* in Malaysia (Farjon, 1998). The conifers in Southeast Asia today reflect the long history of migrations, extinctions, and speciation within the families.

Both the fossil leaves of *Alnus* from early Miocene or late Oligocene deposits in northern Thailand show similarity to the extant species *A. japonica*. Modern *A. japonica* is found in temperate environments.

The fossils of conifers as well as *Alnus* can provide evidence for past climates in Thailand. However, some taxa such as *Sequoia* are not precise in indication climates. Today *Sequoia* occurs as a single species, *S. sempervirens*, in temperate forests often shrouded by fog in western California and Oregon. However, fossils of the genus have been widely found during the Tertiary, and extending back to the Cretaceous, in North America, Europe, and Asia. Extinct species may have had physiological requirements different from the relict *S. sempervirens*, which has a much restricted range. Today, *Picea* and *Tsuga* are found in temperate regions. Most of the *Pinus* species in Asia occur in temperate or subtropical regions and are usually found at higher altitudes. *Glyptostrobus pensilis* occurs in subtropical swamps. The occurrence of fossils from the early Miocene or late Oligocene with affinities to the above taxa suggest that the climate at the time of deposition was cooler than at present, perhaps temperate or subtropical. The fossil *Alnus*, being similar to extant *A. japonica* also suggests a cooler climate. Macrofossils can better indicate the local paleoclimate, as pollen may have moved long distance from cooler mountains before being deposited. However, even with pollen, deposits from the middle Miocene show an absence of temperate conifers (Songtham et al., 2003, 2005). The conifers and *Alnus* thus suggest a cooler period during the late Oligocene or early Miocene and

then a change to a warmer, tropical climate by the middle Miocene. Plant species unable to tolerate the warmer climate migrated northward or became extinct.



References

- Bande, M.B., and U. Prakash. 1986. The Tertiary flora of Southeast Asia with remarks on its palaeoenvironment and phytogeography of the Indo-malayan region. *Review of Palaeobotany and Palynology* 49: 203-233.
- Barefoot, A.C. & F.W. Hankins. 1982. Identification of modern and Tertiary woods. Clarendon Press, Oxford.
- Bennami, Mouloud, Yaowalak Chaimanee, Jean-Jaques Jaeger, Varavudh Suteethorn, and Stéphan Ducrocq. 2001. Eocene Krabi basin (southern Thailand): paleontology and magnetostratigraphy. *Geological Society of America Bulletin* 113(2): 265-273.
- Bennami, Mouloud, Yaowalak Chaimanee, Jean-Jaques Jaeger, Varavudh Suteethorn, and Stéphan Ducrocq. 2001. Eocene Krabi basin (southern Thailand): paleontology and magnetostratigraphy. *Geological Society of America Bulletin* 113(2): 265--273.
- Buffetaut, Eric, Rucha Helmcke-Ingavat, Jean-Jacques Jaeger, Yaowalak Jongkanjanasontorn, Varavudh Suteethorn, and Haiyan Tong. 1989. Fossil vertebrates and the age of the intermontane basins of Thailand. *International Symposium on Intermontane Basins: Geology & Resources*, Chiang Mai, Thailand, 30 January-2 February, 1989 (edited by Thanasuthipitak, T., and P. Ounchanum), pp. 187-195. Chiang Mai University, Department of Geological Sciences, Chiang Mai, Thailand.
- Chaimanee, Yaowalak. 1998. Plio-Pleistocene rodents of Thailand. *Thai Studies in Biodiversity No. 3*: 1-303.
- Chaimanee, Yaowalak, Chotima Yamee, Pannipa Tian, and Jean-Jacques Jaeger. 2007. Diversity of Cenozoic mammals in Thailand: Paleoenvironment and age updated. In *Geothai'07. International conference on Geology of Thailand: Towards sustainable development and sufficiency economy*. Pages 73-79.
- Chen, Zhiduan, and Jianhua Li. 2004. Phylogenetics and biogeography of *Alnus* (Betulaceae) inferred from sequences of nuclear ribosomal DNA ITS region. *International Journal of Plant Sciences* 165 (2):325-335.
- Chowdhury, K.A., and K.N. Tandon. 1964. A fossil wood of *Terminalia tomentosa* W. & A. from the Tertiary of Burma. *Annals of Botany, N.S.*, (111): 446-451.
- Christophel, David C., and David R. Greenwood. 1989. Changes in climate and vegetation in Australia during the Tertiary. *Review of Palaeobotany and Palynology* 58: 95-109.

- Cui, Jin-Zhong. 2005. Studies on the fusinized-wood fossils of Podocarpaceae from Huolinhe Coalfield, Inner Mongolia, China. *Acta Botanica Sinica* 37: 636-640.
- Department of Mineral Resources. 2001. Geology of Thailand: In Honor of His Majesty the King on the Occasion of the Sixth Twelve Year Cycle on 5 December 1999. Department of Mineral Resources, Bangkok.
- Dilcher, David L. 1974. Approaches to the identification of angiosperm leaf remains. *Botanical Review* 40: 1- 157.
- Ducrocq, S., Y. Chaimanee, V. Suteethorn, and J.-J. Jaeger. 1993a. Biochronology and paleoenvironment of Miocene mammalian faunas from Thailand. *International Symposium on Biostratigraphy of Mainland Southeast Asia: Facies and Paleontology*, 31 January-5 February, 1993 (edited by Thanasuthipitak, T.), p. 452. Chiang Mai University, Department of Geological Sciences, Chiang Mai, Thailand. (Abstract)
- Ducrocq, S., Y. Chaimanee, V. Suteethorn, and J.-J. Jaeger. 1993b. The oldest mammal fauna from Thailand: implications on paleogeography and biostratigraphy of Southeast Asia. *International Symposium on Biostratigraphy of Mainland Southeast Asia: Facies and Paleontology*, 31- January-5 February, 1993 (edited by Thanasuthipitak, T.), p. 453. Chiang Mai University, Department of Geological Sciences, Chiang Mai, Thailand. (Abstract)
- Eckenwalder, James E. 2009. *Conifers of the world: the complete reference*. Timber Press, Portland, Oregon.
- Eckert, Andrew J., and Benjamin D. Hall. 2006. Phylogeny, historical biogeography, and patterns of diversification for *Pinus* (Pinaceae): Phylogenetic tests of fossil-based hypotheses. *Molecular phylogenetics and evolution* 40: 166-182.
- Endo, Seido. 1964. Some older Tertiary plants from Northern Thailand. *Geology and Palaeontology of Southeastern Asia*. Vol. 1:113- 117, Plate X.
- Endo, Seido. 1966. A supplementary note on the Palaeogene Li Flora in North Thailand. *Geology and Palaeontology of Southeast Asia*. Vol. 3:165- 169, Plates XXVIII- XXX.
- Endo, Seido, and Ienori Fujiyama. 1966. Some Late Mesozoic and Late Tertiary plants and a fossil insect from Thailand. *Geology and Palaeontology of Southeastern Asia*. Vol. 2:301- 307, Plate VIII.
- Farjon, Aljos. 1998. *World Checklist and Bibliography of Conifers*. Royal Botanic Gardens, Kew, Great Britain.
- Farjon, Aljos, and Brian T. Styles. 1997. *Pinus* (Pinaceae). *Flora Neotropica. Monograph* 75. New York Botanical Garden, New York. [Check]
- Gerards, T., F. Damblon, B. Wauthoz, and P. Gerienne. 2007. Comparison of cross-field pitting in fresh, dried and charcoalfied softwoods. *IAWA Journal* 28: 49-60.

- Gernandt, et al. 2005. Phylogeny and classification of *Pinus*. *Taxon* 54:29-42.
- Getahun, Belay, and Benjavun Ratanasthien. 1993. *Botryococcus* algae in oil source rocks, Fang Basin, northern Thailand. *Proceedings of the International Symposium on Biostratigraphy of Mainland Southeast Asia: Facies and Paleontology*, 31- January-5 February, 1993 (edited by Thanasuthipitak, T.), pp. 337-346. Chiang Mai University, Department of Geological Sciences, Chiang Mai, Thailand.
- Ginsburg, Leonard. 1989. The fossil mammals of Pong (Payao) and the age of some intermontane basins of Northern Thailand. *International Symposium on Intermontane Basins: Geology & Resources*, Chiang Mai, Thailand, 30 January-2 February, 1989 (edited by Thanasuthipitak, T., and P. Ounchanum), pp. 196-204. Chiang Mai University, Department of Geological Sciences, Chiang Mai, Thailand.
- Ginsburg, Leonard, Pierre Mein, and Pascal Tassy. 1991. The Miocene mammals of Li Basin, Changwat Lamphun, Thailand. *Proceedings of the Annual Technical Meeting 1989 and IGCP-246* (edited by Ounchanum, P., and B. Ratanasthien), pp. 101-109. Chiang Mai University, Department of Geological Sciences, Chiang Mai, Thailand.
- Grote, Paul J. 2005. Use of leaf architecture and anatomy in the study of plant diversity in the Tertiary and Recent of Thailand. Unpublished final report, Suranaree University of Technology.
- Grote, Paul J., and Prakart Sawangchote. 2003. Investigations of plant macrofossils from the Tertiary of Northern Thailand. *Maharakham University Journal* 22 Special Issue: 100
- Heinz, Immo. 2004. Systematische Erfassung und Dokumentation der mickroanatomischen Merkmale der Nadelhölzer aus der Klasse der Pinatae. Dr. rer. Nat. dissertation, Technischen Universität München, Munich, Germany.
- Hickey, Leo J. 1973. Classification of the architecture of dicotyledonous leaves. *American Journal of Botany* 60:17-33.
- Hickey, L. J. 1979. A revised classification of the architecture of dicotyledonous leaves. *In* C. R. Metcalf and L. L. Chalk [eds.], *Anatomy of the dicotyledons*. Second Edition. Volume I, pages 25-39. Clarendon Press, Oxford, UK.
- IAWA Committee. 2004. IAWA list of microscopic features for softwood identification by an IAWA Committee. H.G. Richter, D. Grosser, I. Heinz, P.E. Gassonn (editors). *IAWA Journal* 25: 1-70.
- Jähnichen, Hellmut. 1969. Revision zu Originalen strukturbietender Blätter aus der Lausitzer und Niederrheinischen Braunkohle. *Geologie* 18: 77-111.
- Kunzman, Lutz. 2007. Araucariaceae (Pinaceae): Aspects in palaeobiogeography and palaeobiodiversity in the Mesozoic. *Zoologischer Anzeiger* 246: 255-277.

- Kurmann, Marie H. 1997. Pollen morphology. In Aljos Farjon and Brian T. Styles. *Pinus* (Pinaceae). *Flora Neotropica. Monograph 75*, pages 36-38. New York Botanical Garden, New York.
- Lanner, Ronald M. 1999. Seed dispersal in *Pinus*. In David M. Richardson (ed), *Ecology and biogeography of Pinus*, pages 281-295. Cambridge University Press, Cambridge.
- Li, Peiqiong and Alexei K. Skvortsov. 1999. Betulaceae. In Wu Sheng-yi and Peter H. Raven [eds.], *Flora of China. Cycadaceae through Fagaceae*. 4, 54-61. Science Press, Beijing, China.
- Li, Rui-Qi, Zhi-Duan Chen, An-Ming Lu, Douglas E. Soltis, Pamela S. Soltis, and Paul S. Manos. 2004. Phylogenetic relationships in Fagales based on DNA sequences from three genomes. *International Journal of Plant Sciences* 165 (2):311-324.
- Li, Xingxue (Editor-in chief). 1995. *Fossil floras of China through the geological ages (English edition)*. Guangzhou, China, Guangdong Science and Technology Press
- Maddison, W.P. & D.R. Maddison. 2009. Mesquite: A modular system for evolutionary analysis. Version 2.72. <http://mesquiteproject.org>
- Manchester, Steven R. 1999. Biogeographical relationships of North American Tertiary floras. *Annals of the Missouri Botanical Garden* 86: 472-522.
- McElwain, Jennifer C., and William G. Chaloner. 1996. The fossil cuticle as a skeletal record of environmental change. *Palaeos* 11: 376-388.
- McNeill, J., F. R. Barrie, H. M. Burdet, V. Demoulin, D. L. Hawksworth, K. Marhold, D. H. Nicolson, J. Prado, P. C. Silva, J. E. Skog, J. H. Wiersema, and N.J. Turland (eds.). 2006. International Code of Botanical Nomenclature (Vienna Code). *Regnum Vegetabile* 146. A.R.G. Gantner Verlag KG, Lichtenstein. (online <http://ibot.sav.sk/icbn/main.htm>)
- Morley, Robert J. 1998. Palynological evidence for Tertiary plant dispersals in the SE Asian region in relation to plate tectonics and climate. In Robert Hall and Jeremy D. Holloway (eds.) *Biogeography and geological evolution of SE Asia*, pages 211-234.
- Muenlek, S. 1992. Coal geology of Mae Than basin Amphoe Mae Tha, Lampang. In: C. Piancharoen (ed.), *Supplementary volume of proceedings of a national conference on geologic resources of Thailand: potential for future development: 112—121*. Department of Mineral Resources, Bangkok.
- Murai, S. 1964. Phytotaxonomical and geobotanical studies on gen. *Alnus* in Japan. III. Taxonomy of whole world species and distribution of each sect. *Bulletin of the Government Forest Experiment Station* 171: 1-107 [Japanese, with English résumé]

- Nguyễn, Đức Tô Luu, and Philip Ian Thomas. 2004. *Conifers of Vietnam*. Darwin Initiative, Hanoi.
- Page, C.N.. 1991. Taxodiaceae. Pages 353-361, in Kubitzki, K. 1990. The Families and Genera of Vascular Plants. Volume I. Pteridophytes and Gymnosperm. Kramer, K.U., and P.S. Green (eds.). Narosa Publishing House, New Delhi.
- Phengklai, C. 1972a. Pinaceae. *Flora of Thailand Vol. 2 (Part 2)*: 193-194.
- Phengklai, C. 1972b. Cupressaceae. *Flora of Thailand Vol. 2 (Part 2)*: 196.
- Philippe, Marc, Varavudh Suteethorn, Petra Lutat, Eric Buffetaut, Lionel Cavin, Gilles Cuny, and Georges Barale. 2004. Stratigraphical and palaeobiogeographical significance of fossil wood from the Mesozoic Khorat Group of Thailand. *Geol. Mag.* 319-328.
- Philippe, Marc, and Marion K. Bamford. 2008. A key to morphogenera used for Mesozoic conifer-like woods. *Review of Palaeobotany and Palynology* 148: 184-207.
- Prakash, U. 1979. Fossil dicotyledonous woods from the Tertiary of Thailand. *Palaeobotanist* 26(1):50-62.
- Ratanasthien, Benjavun. 1989. Depositional environment of Mae Lamao Basin as indicated by palynology and coal petrography. *International Symposium on Intermontane Basins: Geology & Resources*, Chiang Mai, Thailand, 30 January-2 February, 1989 (edited by Thanasuthipitak, T., and P. Ounchanum), pp. 205-215. Chiang Mai University, Department of Geological Sciences, Chiang Mai, Thailand.
- Richardson, David M. and Philip W. Rundel. 1999. Ecology and biogeography of *Pinus*: and introduction. In David M. Richardson (ed), *Ecology and biogeography of Pinus*, pages 3-46. Cambridge University Press, Cambridge.
- Serra, C. 1981. Les structures ligneuses Néogène du Plateau de Linch (Sud-Vietnam). *Palaeontographica Abteilung B. Palaeophytologie* 177: 136-161. (Cited in M.B. Bande and U. Prakash. 1986. The Tertiary flora of Southeast Asia with remarks on its palaeoenvironment and phytogeography of the Indo-malayan region. *Review of Palaeobotany and Palynology* 49: 203-233.
- Songtham, Wickanet, and Manas Watanasak. 1999. Palynology, age, and paleoenvironment of Krabi Basin, southern Thailand. In B. Ratanasthien and S.L. Reib [eds.] *Proceedings of the International Symposium on Shallow Tethys (ST) 5*, 426-439. Chiang Mai University, Chiang Mai, Thailand.
- Songtham, Wickanet, Benjavun Ratanasthien, Dallas C. Mildenhall, Sampan Singharajwarapan, and Wittaya Kandharosa. 2003. Oligocene-Miocene climatic changes in northern Thailand resulting from extrusion tectonics of Southeast Asian landmass. *ScienceAsia* 29: 221-233.

- Songtham, Wickanet, Benjavun Ratanasthien, Manas Watanasak, Dallas C. Mildenhall, Sampan Singharajwarapan, and Wittaya Kandharosa. 2005. Tertiary basin evolution in northern Thailand: a palynological point of view. *Natural History Bulletin of the Siam Society* 53(1): 17-32.
- Stevens, P. F. (2001 onwards). Angiosperm Phylogeny Website. Version 9, June 2008 [and more or less continuously updated since]. <http://www.mobot.org/MOBOT/research/APweb/>
- Stewart, Wilson N., & Gar W. Rothwell. 1993. Paleobotany and the evolution of plants. Second edition. Cambridge University Press, Cambridge.
- Sun, Ge, David L. Dilcher, Shaoling Zheng, and Zhekun Zhou. 1998. In search of the first flower: a Jurassic angiosperm, *Archaeofructus*, from Northeast China. *Science* 282: 1692-1695.
- Thanh, Tong-Dzuy, and Vu Khuc. 2003. Paleontological researches in Vietnam – Achievement and contribution. *Maharakham University Journal* 22 Special Issue: 3-31.
- Thomas, P., Khamphone Sengdala, Vichith Lamxay, and Eanghourt Khou. 2007. New records of conifers in Cambodia and Laos. *Edinburgh Journal of Botany* 64: 37-44.
- Uemura, Kazuhiko. 1986. A note on Tertiary *Sciadopitys* (Coniferopsida) from Japan. *Bull. Natn. Sci. Mus., Tokyo, Ser. C* 12 (2): 53-59.
- Van der Burgh, Johan, Henk Visscher, David L. Dilcher, and Wolfram M. Kürschner. 1993. Paleoatmospheric signatures in Neogene fossil leaves. *Science* 260:1788-1790.
- Vidakovic, Mirko (translated by Maja Soljan). 1991. Conifers, morphology and variation. Graficki zavod Hrvatske, Zagreb.
- Vozenin-Serra, C. and C. Privé-Gille. 1989. Plio-Pleistocene woods from Saropee, Khorat Plateau, Eastern Thailand. *Review of Palaeobotany and Palynology* 60: 225-254. [In Fr.]
- Vozenin-Serra, C. and C. Privé-Gille. 1991a. The Mekong Pleistocene alluvial terraces (Cambodia): Homoxylous silicified woods found between Stung-Treng and Snoul. *Review of Palaeobotany and Palynology* 67: 115-132 [In Fr.] (abstract seen)
- Vozenin-Serra, C. and C. Privé-Gille. 1991b. The Mekong Pleistocene alluvial terraces (Cambodia): Heteroxylous silicified woods found between Stung-Treng and Snoul. *Review of Palaeobotany and Palynology* 68: 87-118. [In Fr.] (abstract seen)
- Vozenin-Serra, C. and C. Privé-Gille. 1994. Pleistocene woods from Binh Thang, Vietnam. *Palaeontographica Abteilung B. Palaeophytologie* 232: 175-195. [In Fr.] (abstract seen)

- Vozenin-Serra, C., C. Privé-Gill, and L. Ginsburg. 1989. Bois Miocenes du gisement de Pong, Nord-ouest de la Thaïlande. *Review of Palaeobotany and Palynology* 58: 335-355.
- Watanasak, Manas. 1988a. Mid-Tertiary Palynology of Onshore and Offshore Thailand. Unpublished Ph.D. thesis, University of Adelaide, Adelaide.
- Watanasak, Manas. 1988b. Palaeoecological reconstruction of Nong Ya Plang Tertiary Basin (Central Thailand). *Journal of Ecology (Thailand)* 15(7):61-70.
- Watanasak, Manas. 1990. Mid Tertiary palynostratigraphy of Thailand. *Journal of Southeast Asian Earth Science* 4: 203-218.
- Wiemann, Michael, Steven R. Manchester, David L. Dilcher, Luis Felipe Hinojosa, and Elisabeth A. Wheeler. 1998. Estimation of temperature and precipitation from morphological characters of dicotyledonous leaves. *American Journal of Botany* 85: 1796-1802.
- Wilf, Peter. 1997. When are leaves good thermometers? A new case for Leaf Margin Analysis. *Paleobiology* 23: 373-390.
- Wilf, Peter, Scott L. Wing, David R. Greenwood, and Cathy L. Greenwood. 1998. Using fossil leaves as paleoprecipitation indicators: an Eocene example. *Geology* 26 (3):203-206.
- Wing, Scott L. 1997. Global warming and plant species richness: A case study of the Paleocene/Eocene boundary. Pages 163-185 in Marjorie L. Reake-Kudla, Don E. Wilson, and Edward O. Wilson, eds. *Biodiversity II: Understanding and Protecting our Biological Resources*. Washington, D.C., Joseph Henry Press.
- Wing, Scott L., and David R. Greenwood. 1993. Fossils and fossil climate: the case for equable continental interiors in the Eocene. *Philosophical Transactions of the Royal Society of London B* 341: 243-252.
- Wolfe, Jack A. 1978. A paleobotanical interpretation of Tertiary climates in the Northern Hemisphere. *American Scientist* 66:694-703.
- Wolfe, Jack A. 1993. A method of obtaining climatic parameters from leaf assemblages. *U.S. Geological Survey Bulletin* 2040: 1-71.
- Xing, Yaowu, Yu-Sheng (Christopher) Liu, Tao Su, Frédéric M.B. Jacques, and Zhekun Zhou. 2010. *Pinus prekesiya* sp. nov. from the upper Miocene of Yunnan, southwestern China and its biogeographical implication. *Review of Palaeobotany and Palynology* 160:1-9.
- Xu, Xiao-Hui, Zi-Xi Wang, Guo-Lin Yang, Jin Wang, Yi Yang Fu-Jun Ma, Qiu-Jun Wang, Rui-Yun Li, and Bai-Nian Sun. 2015. Two *Pinus* species from the upper Miocene in Zhejiang, China and their palaeobiogeographic significance. *Review of Palaeobotany and Palynology* 215:68-75.

Zhang, Jian-Wei, Ashalata D’Rozario, Jonathan M. Adams, Xiao-Qing Liang, Frédéric M.B. Jacques, Tao Su, and Zhe-Kun Zhou. 2015. The occurrence of *Pinus massoniana* Lambert (Pinaceae) from the upper Miocene of Yunnan, SW China and its implications from paleogeography and paleoclimate. *Review of Palaeobotany and Palynology* 57:57-67.

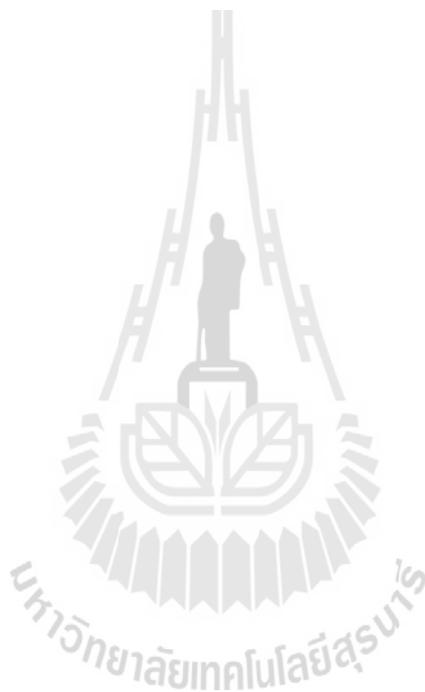




Figure 1. Fossil sites. A. Ban Pa Kha mine, Li District, Lamphun. B. Banpu 1 mine, Li District, Lamphun. C. Mae Than Sub-basin, Lampang Basin, Lampang. D. Nong Ya Plong Basin, Petchaburi, abandoned mine. E. Nong Ya Plong Basin, Petchaburi, *ex situ* fossils. F. Srisuk's House Museum, Khao Yoi District, Petchaburi.

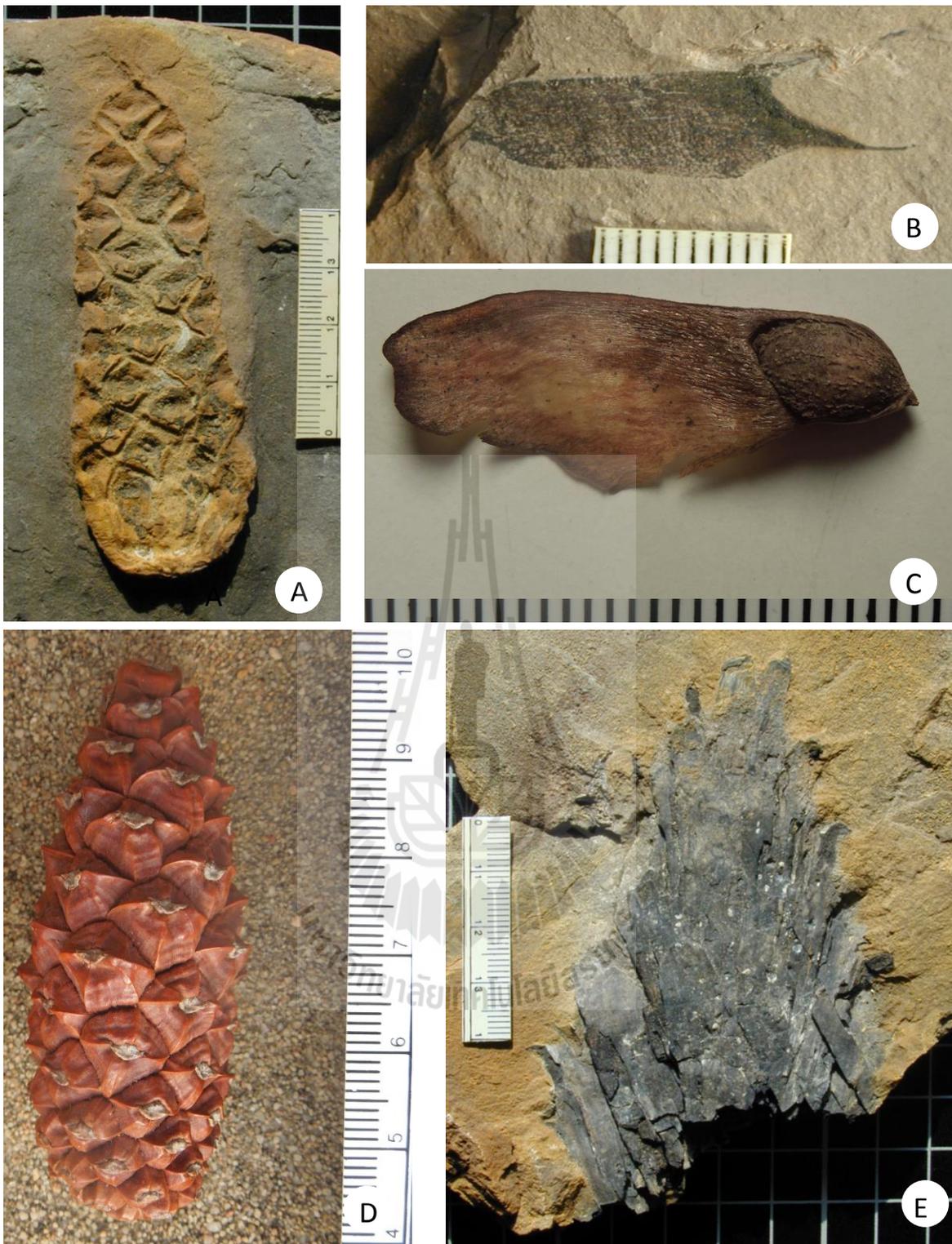


Figure 2. Seed cones and seeds of *Pinus*. A. Compression of seed cone from Nong Ya Plong. B. Detached seed wing from Ban Pa Kha. C. Seed with wing of *P. merkusii*. D. Unopened seed cone of *P. merkusii*. E. Compression of seed cone from Nong Ya Plong.

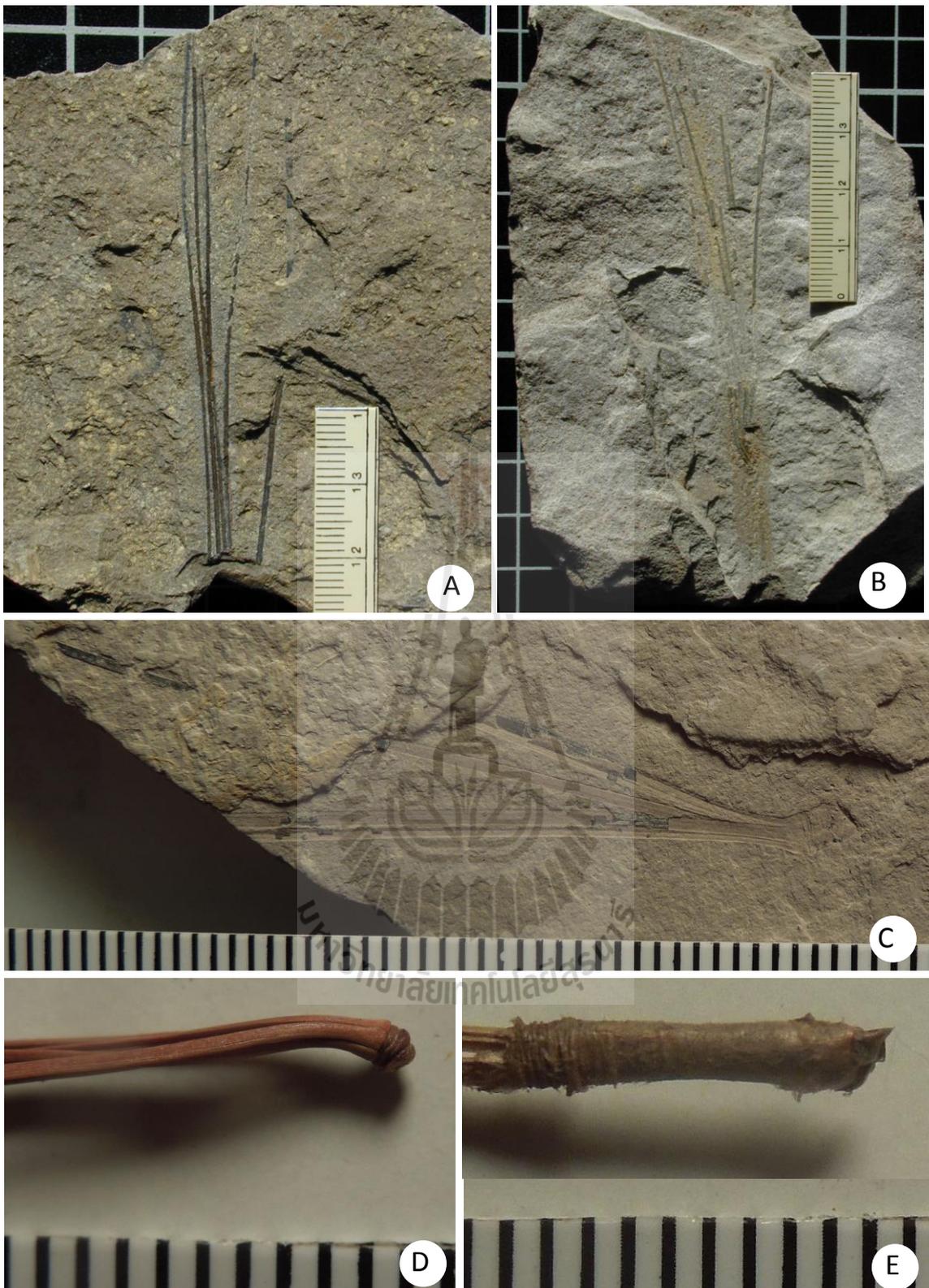


Figure 3. Needles of *Pinus*. A, B, C. Needles from Nong Ya Plong. D. Needles of *P.strobus*. E. Needles of *P. merkusii*.

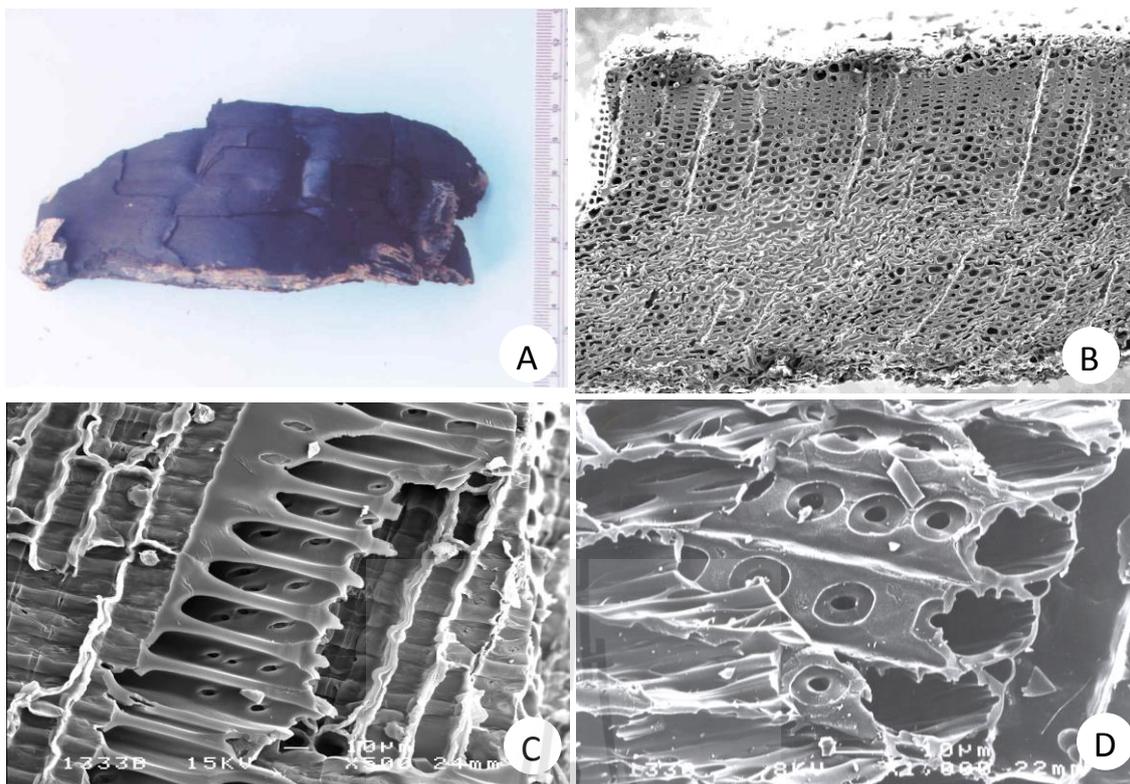


Figure 4. Fusainized wood. A. Fusainized wood of *Podocarpoxyylon*. B. Transverse section of *Podocarpoxyylon* (SEM). C. Radial section of *Podocarpoxyylon* (SEM). D. Radial section of *Taxodioxyylon* (SEM).



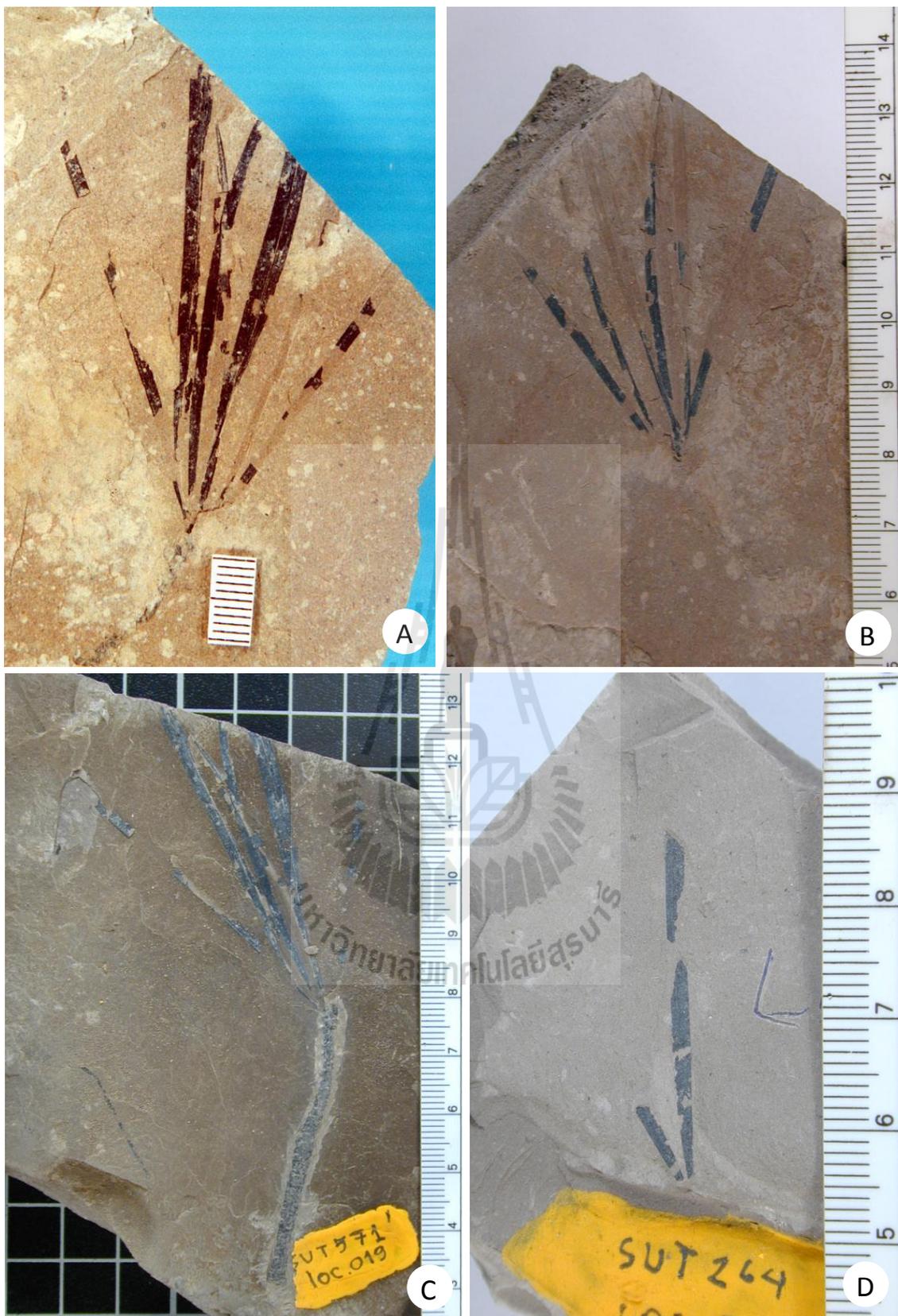


Figure 5. *Sciadopitys* sp. from Ban Pa Kha. A, B. Part and counter-part. C. Same as A, after degausing. D. Two needles.

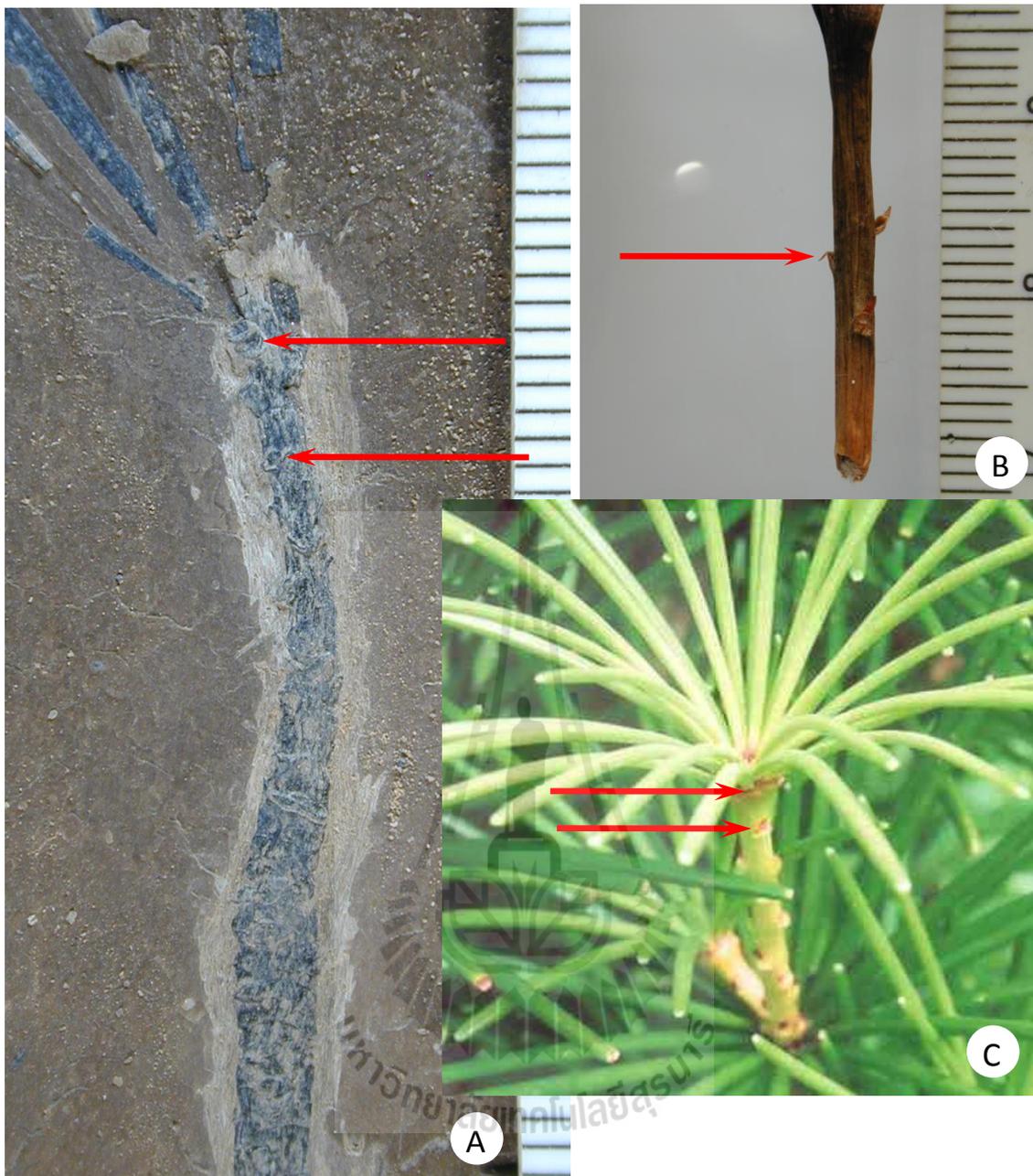


Figure 6. *Sciadopitys*. A. *Sciadopitys* from Ban Pa Kha. B, C. *Sciadopitys verticillata*. Arrows indicate scale leaves.

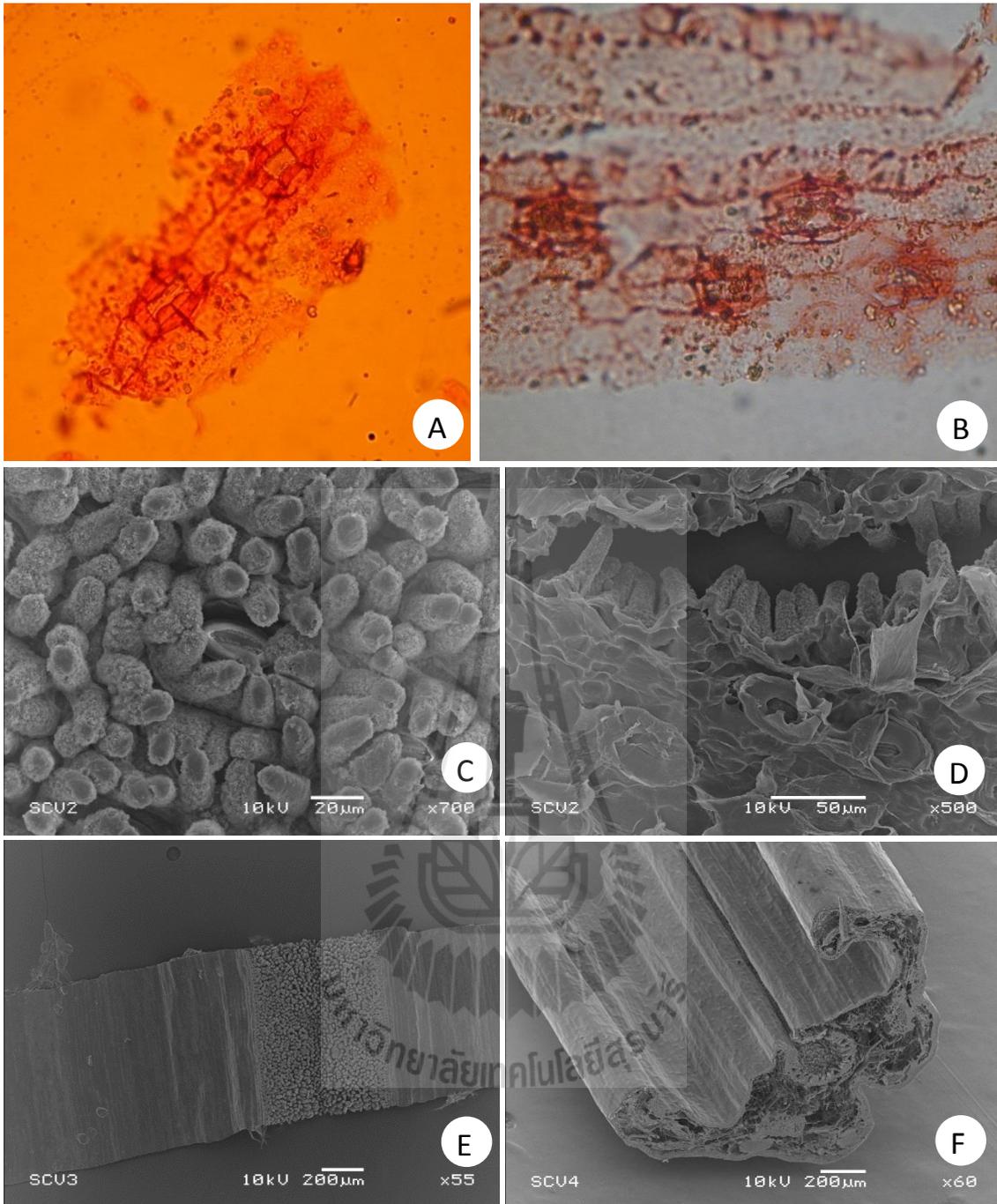


Figure 7. *Sciadopitys* anatomy. A, B. *Sciadopitys* sp. from Ban Pa Kha, cuticles showing stomates. C, D, E, F. *Sciadopitys verticillata*. C. Outer view of stomatal area showing papillae and one stomata. D. Inner view of stomatal area showing stomates. E. Outer view of needle, abaxial surface. Section of needle showing concave stomatal area.



Figure 8. *Sciadopitys verticillata*, in natural habitat, Japan, except C, cultivated. A. Tree on edge of cliff. B. Tree on edge of cliff. C. Branch of cultivated tree. D. Branch with seed cone. E. Seedling.



Figure 9. *Sequoia* cones and twigs. A, B, D. Ban Pu 1 Sub-basin, Li Basin, Lamphun province, Northern Thailand, age late Oligocene or early Miocene. A. Seed cone. B. Twig. C. *Sequoia sempervirens* with seed cones and a pollen cone. D. Twig.



Figure 10. *Taiwania* and *Glyptostrobus*. A. *Taiwania?*, Ban Pa Kha. B. *Taiwania cryptomerioides*. C. *Glyptostrobus* sp., Ban Pa Kha. D. *Glyptostrobus pensilis*

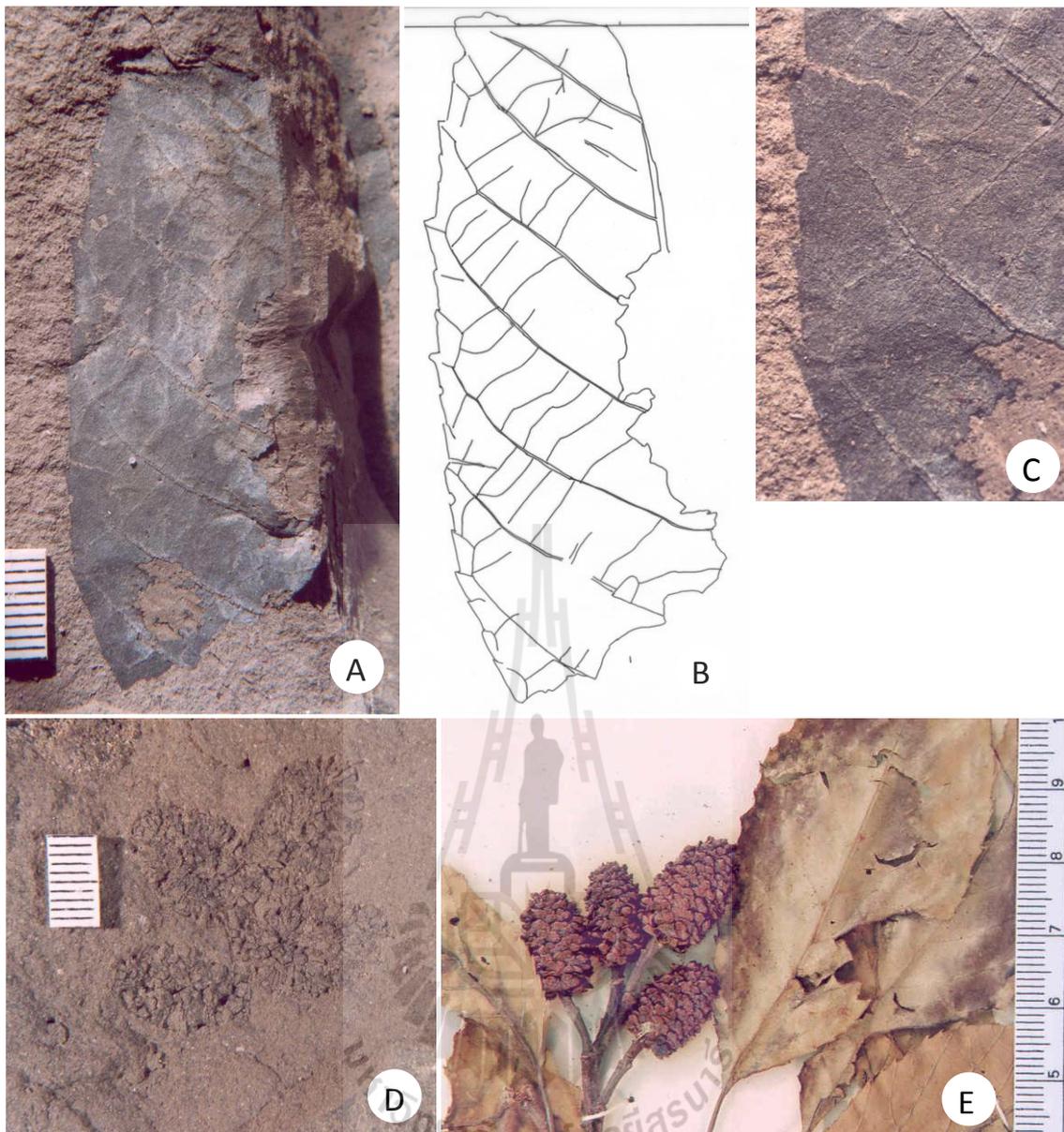


Figure 11. Fossil and Recent *Alnus*. A. Leaf compression of *Alnus* from Ban Pa Kha, Li District, Lamphun. D. Cones of *Alnus* from Ban Pa Kha, Li District, Lamphun. E. Leaves of *A. japonica*.

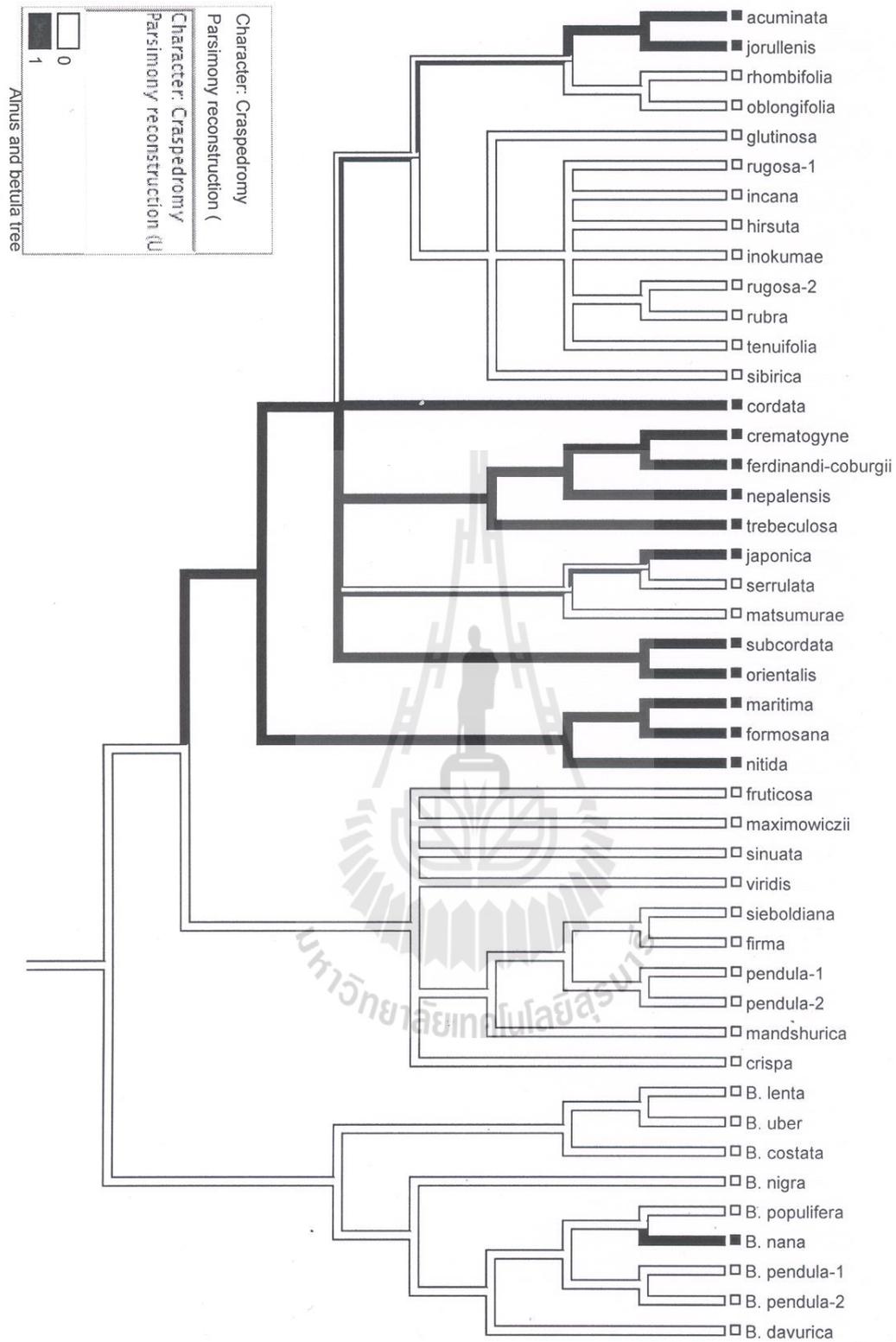


Figure 12. Character analysis of *Alnus* and *Betula* (Betulaceae), using parsimony. Open lines: leaves craspedodromous. Closed black lines: leaves not craspedodromous. Partly closed lines: indeterminate.

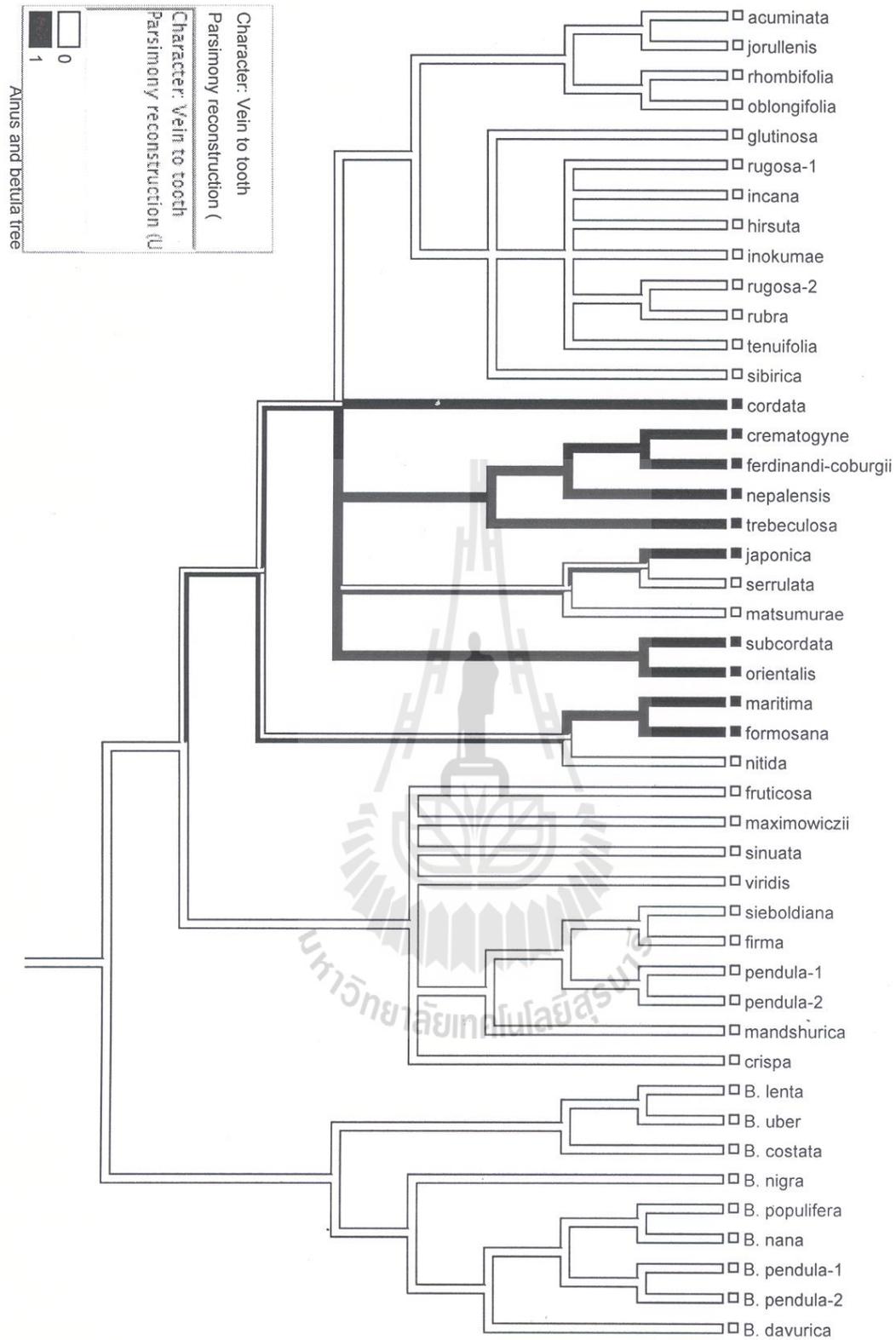


Figure 13. Character analysis of *Alnus* and *Betula* (Betulaceae), using parsimony. Open lines: Secondary or lower level going to tooth. Closed black lines: Veins not going to tooth. Partly closed lines: indeterminate.

Curriculum vitae

Dr. Paul J. Grote, Lecturer
School of Biology, Institute of Science
Suranaree University of Technology

Degrees:

Degree	Field	Date	Institute/Country
Ph.D.	Biology	1989	Indiana University, Indiana, USA
M.S.	Biological Sciences	1979	University of Cincinnati, Ohio, USA
B.S.	Biology	1977	Xavier University, Ohio, USA

Work Experience:

Period	Position	Institution/Firm
1995-Present	Lecturer	Biology, Suranaree University of Technology, Nakhon Ratchasima
1991-1995	Lecturer	Biology, Mahidol University, Bangkok
1991	Lecturer	English, Rangsit University, Pathum Thani
1990-1991	Lecturer	English, Dhurakijpundit University, Bangkok
1982-1989	Associate Instructor	Biology, Indiana University, Indiana, USA
1979-1981	Research Assistant	University of Cincinnati Medical Center, Ohio, USA
1977-1978	Teaching Assistant	Department of Biological Sciences, University of Cincinnati, USA

Current Professional Interests:

- Systematics and evolution of flowering plants and conifers, paleobotany

Member:

-Botanical Society of America
-The Botanical Society (Thailand)

Recent Papers:

1. Chooapan, T., and P.J. Grote. 2014, *Pseuderanthemum pubescens* sp. nov. (Acanthaceae) from Thailand. *Nordic Journal of Botany* 32: 806-810. (Impact factor: 0.844, 2014)

2. Kham, Mahasin Ali, Robert A. Spicer, Subir Bera, Ruby Ghosh, Jian Yang, Teresa E.V. Spicer, Shuang-xing Guo, Tao Su, Frédéric Jacques, and Paul J. Grote. 2014. Miocene to Pleistocene floras and climate of the Eastern Himalayan Siwaliks, and new palaeoelevation estimates for the Namling–Oiyug Basin, Tibet. *Global and Planetary Change* 113: 1–10 (Impact factor: 2.766, 2014)
3. Boonchai, Nareerat, Sun Ge, and Paul J. Grote. 2012. Cenozoic petrified woods from Suranaree area of Nakhon Ratchasima, northeastern Thailand and their implication on paleoenvironment. *Global Geology* 31: 1-8. [Chinese, with English abstract]
4. Sawangchote, P., P.J. Grote, and D.L. Dilcher. 2010. Tertiary leaf fossils of *Semecarpus* (Anacardiaceae) from Li Basin, Northern Thailand. *Thai Forest Bulletin (Botany)* 38: 8-22. (Thai Journal Impact Factor: 0.079, 2010)
5. Sawangchote, Prakart, Paul J. Grote, and David L. Dilcher. 2009. Tertiary leaf fossils of *Mangifera* (Anacardiaceae) from Li Basin, Thailand as examples of the utility of leaf marginal venation characters. *American Journal of Botany* 96: 2048-2061. (Impact factor: 2.684, 2009)
6. Boonchai, Nareerat, Paul J. Grote, and Pratueng Jintasakul. 2009. Paleontological parks and museums and prominent fossil sites in Thailand and their importance in the conservation of fossils. In: Lipps, J.H. and Granier, B.R.C. *Paleoparks – The protection and conservation of fossil sites worldwide. Carnets de Géologie/ Notebooks on Geology*, Brest, Book 2009/03/ Chapter 07, pages 75-95. (Impact factor: 0.719, 2012)
7. Chitnarin, Anisong, Sylvie Crasquin, Chongpan Chonglakmani, Jean Broutin, Paul Joseph Grote, and Nathawut Thanee. 2008. Middle Permian ostracods from Tak Fa Limestone, Phetchabun Province, Central Thailand. *Geobios* 41: 341-353. (Impact factor: 1.089, 2008)
8. Rugmai, Wipanu, Paul J. Grote, Chongpan Chonglakmani, Reinhard Zetter, and David K. Ferguson. 2008. A Late Pleistocene palynoflora from the coastal area of Songkhla Lake, southern Thailand. *ScienceAsia* 34:137-145.
9. Grote, Paul J. 2007. Studies of fruits and seeds from the Pleistocene of northeastern Thailand. *Courier Forschungsinstitut Senckenberg* 258: 171-181.
10. Wang, Yongdong, Zhang Wu, Zheng Shaolin, Pratueng Jintasakul, Paul J. Grote, and Nareerat Boonchai. 2006. Recent advances in the study of Mesozoic-Cenozoic petrified wood from Thailand. *Progress in Natural Science* 16(5): 501-506.