



รายงานการวิจัย

การใช้สถาปัตยกรรมและกายวิภาคของใบในการศึกษาความหลากหลายของพืช  
ในยุคเทอร์เชียรีและปัจจุบันของประเทศไทย  
(Use of Leaf Architecture and Anatomy in the Study of Plant  
Diversity in the Tertiary and Recent of Thailand)

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การใช้สสารที่ดัดและกายวิภาคของใบในการศึกษาความหลากหลายของพืช  
ในอุทยานเข็ชรีและปัจจุบันของประเทศไทย

เนื่องจากซากดึกดำบรรพ์ของพืชสามารถให้ข้อมูลถึงลักษณะพืชพรรณ ภูมิอากาศ รวมทั้งสภาพแวดล้อมในอดีตได้ จึงได้เกิดการศึกษาซากดึกดำบรรพ์ขนาดใหญ่ของพืชจากเหมืองลิกไนต์ในแอ่งลี้ อำเภอลี้ จังหวัดลำพูน ซึ่งตั้งอยู่ในภาคเหนือของประเทศไทย โดยคาดว่าเป็นชั้นหินที่มีอายุอยู่ในระหว่างช่วงต้นของยุคโอลิโกซีน จนถึงช่วงปลายของยุคไมโอซีน ตัวอย่างซากดึกดำบรรพ์พืชที่เก็บรวบรวมได้ส่วนใหญ่เป็นซากใบไม้ จึงใช้วิธีนำมาศึกษาเปรียบเทียบกับใบไม้ของพืชในยุคปัจจุบัน โดยเตรียมตัวอย่างที่เห็นเส้นใบ (cleared leaf specimens) ของใบพืชยุคปัจจุบันจากหอพรรณไม้จำนวน 253 ตัวอย่าง อันประกอบด้วยพืชจาก 77 วงศ์, 146 สกุล, 157 ชนิด โดยได้ศึกษาทิวติงของซากใบไม้ภายใต้กล้องจุลทรรศน์ และกล้องจุลทรรศน์อิเล็กตรอนแบบส่องกราด แต่พบว่าไม่สามารถมองเห็นการจัดเรียงตัวของเซลล์คุม (guard cells) และ เซลล์ผิว (epidermal cells) ได้อย่างชัดเจน อย่างไรก็ตาม ยังสามารถใช้ลักษณะรูปร่างใบ, รูปแบบของพินที่ขอบใบ รวมทั้งลักษณะเส้นใบ มาใช้ในการศึกษาเปรียบเทียบได้ โดยสามารถอธิบายลักษณะพืช ต่อไปนี้ คือ *Cyclosorus* sp. ในวงศ์ Thelypteridaceae, พืชในวงศ์ Hamamelidaceae ซึ่งไม่สามารถจำแนกได้ถึงระดับสกุล, รวมทั้งลักษณะใบพืช 4 ชนิด ซึ่งมีความสัมพันธ์กับพืชสกุล *Quercus* และ *Castanopsis* ในวงศ์ Fagaceae, *Alnus* sp. และ สกุล cf. *Betula* หรือ *Carpinus* ในวงศ์ Betulaceae ทั้งนี้ ข้อมูลจากตัวอย่างซากดึกดำบรรพ์พืชข้างต้นรวมทั้งจากตัวอย่างอื่นๆ สามารถบอกได้ว่าภูมิอากาศในภาคเหนือของประเทศไทย ในระหว่างต้นยุคไมโอซีน หรือปลายยุคโอลิโกซีน มีความหนาวเย็นกว่าปัจจุบัน ซึ่งอาจจะเป็นแบบเขตกึ่งร้อน โดยปรากฏป่าทั้ง 2 แบบ คือ ป่าไม้ผลัดใบและป่าผลัดใบ หรือเป็นแถบผสมผสานระหว่างป่าไม้ผลัดใบและป่าผลัดใบ

## Use of Leaf Architecture and Anatomy in the Study of Plant Diversity in the Tertiary and Recent of Thailand

Because plant fossils can provide information on past vegetation types, climates, and environments, a study of plant macrofossils from lignite mines in the Li Basin, Amphoc Li, Lamphun, Northern Thailand, was undertaken. The deposits are thought to be early Miocene or late Oligocene in age. The fossils collected are predominantly leaf compressions, so comparison with leaves of Recent plants were made. Cleared leaves were prepared from 253 herbarium specimens, comprising 77 families, 146 genera, and 157 species. Cuticles of fossil leaves were prepared as both microscope slide mounts and SEM samples; the arrangement of guard cells and other epidermal cells were poorly discernible, however. Leaf shape and patterns of teeth and venation were used for comparison, therefore. Leaves of the following taxa were described: *Cyclosorus* sp. (Thelypteridaceae); indeterminate genus (Hamamelidaceae); four species of leaves with affinities to *Quercus* and *Castanopsis* (Fagaceae); *Alnus* sp. (Betulaceae); and cf. *Betula* or *Carpinus* (Betulaceae). These fossils plus other specimens suggest that the climate in Northern Thailand during the early Miocene or late Oligocene was cooler than at present, being perhaps subtropical. Both evergreen and deciduous forests or mixed evergreen-deciduous forests were present.

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## Chapter 1

### Introduction

Thailand, like most tropical and other countries, has experienced much destruction of forests in recent years. Because of this forest loss, many species of plants and animals face extinction. It is thus important and urgent that studies be made of the living things found in Thailand, *i.e.*, biodiversity studies. The flora as observed in Thailand today is a result of many events occurring in the past, including migrations, extinctions, and speciation. Study of fossils in addition to study of modern plants may thus help shed light on changes in the flora of Thailand over geologic time and how plants respond to changes in the environment. Tertiary age flowering plants have been reported from Tertiary basins in Northern Thailand (Chiangmai, Lampang, Lamphun, Phayao, and Tak provinces), in Southern Thailand (Krabi province, Songtham and Watanasak, 1999), and in Central Thailand (Phetchburi province, Watanasak, 1999a), as well as from deposits in Northeastern Thailand. Most of the fossils have been found as isolated organs, including wood, leaves, fruits, and pollen.

When taxonomic studies are made of Recent plants, many plant parts, including flowers, fruits, leaves, wood, and pollen, are available for study. Additionally, when using a key to identify plants, characteristics of flowers, leaves, sometimes fruits, and the plant's habit and size need to be known. However, when conducting taxonomic or other studies of plant fossils, most commonly only isolated organs are available. In any particular fossil deposit, one may encounter more than one plant part, such as leaves, pollen, wood, fruit, and rarely flowers, but it is generally not known which plant parts are from the same species. This is true when studying fossil leaves, such as those found in the Tertiary basins in Northern Thailand.

Many paleobotanical studies have been done worldwide using fossil leaves. However, some authors relied predominantly on the overall shape of the leaf to identify the specimens. Later researchers (Dilcher, 1971; Hickey, 1973) discovered that this method of identification led to frequent misidentifications: 60% of the taxa of Berry (1916, 1930) that were restudied had to be reassigned to a different genus or even different family (Dilcher, 1971). In order to conduct proper taxonomic studies, leaf architecture and cuticular studies need to be undertaken. Leaf architecture refers to the "placement and form of those elements constituting the outward expression of leaf structure, including venation pattern, marginal configuration, leaf shape, and gland position"



(Hickey, 1973). Cuticular analysis refers to the use of cuticle in identifying the arrangement and shape of epidermal cells of a plant, including guard cells and subsidiary cells, as well as structural features of the cuticle itself.

### Fossils described from Thailand

Very little taxonomic work has been done on plant macrofossils from the Tertiary of Thailand. Endo (1964, 1966) described several plant fossils from the Li Basin, Li District, Lamphun Province, in Northern Thailand (presumably from Ban Pa Kha mine, pers. comm., C. Chonglakmani), as follows:

#### Conifers

*Glyptostrobus europaeus* (Brongn.) Heer (= *G. europaea* (Brongn.) Unger), cones and stem  
*Sequoia langsdorffii* (Brongniart) Heer (= *Sequoia abietina* (Brongn. in Cuvier) Knobloch),

leaves, cone

*Taxodiumthaiensis* Endo, cone

#### Angiosperms

*Ficus cowightiana* Endo, leaves

*Alnus thaiensis* Endo, catkins

*Alnus thaiensis* Endo?, leaves possibly allied to *A. thaiensis*

*Carpinus* (?) sp., leaf fragments

*Fagus feroniae* Ung., leaves

*Quercus* cf. *lanceaefolia* Roxb., leaves

*Quercus protoglauca* Endo, leaves

*Salix* ? sp., leaves

*Sparganium thaiensis* Endo, fruits, leaves.

Additionally, Yabe (2002) has reported fruits of *Acer* from Ban Pa Kha mine.

Macrofossils, considered to be Miocene, have also been described from the Mac Sot Basin, Tak Province, western Thailand (Endo and Fujiyama, 1966):

*Bauhinia* sp., leaf

*Podogonium Knorrrii* Heer (= *Podocarpium podocarpum* (A. Braun) Herendeen), leaves

(See Herendeen, 1992)

*Apocynophyllum* sp., leaves.

Some reports on fossil wood from the Tertiary of Thailand have also been published. Vozenin-Serra *et al.* (1989) described silicified wood of five dicotyledonous species from Pong Basin (Phayao), Northwest Thailand, considered to be Miocene in age. Silicified wood has also been reported and described from the Tertiary of Northeastern Thailand: Chaiyaphum (Prakash, 1979) and Nakhon Ratchasima (Vozenin-Serra and Privé-Gill, 1989, 2001).

There have also been several studies of pollen from the Tertiary of Thailand. Of special interest related to this research are the studies of Watanasak (1988b) and Songtham *et al.* (2001). Watanasak's study included pollen from Banpu 1 mine, Li Basin, and Songtham *et al.* (2001) presented a study of pollen from Ban Pa Kha mine, Li Basin.

### Localities

Li Basin is a Tertiary basin in Li District, Lamphun Province, in Northern Thailand. This basin consists of 4 sub-basins, Banpu and Ban Pa Kha in the eastern part of the basin, Na Sai in the southern part, and Mac Long, in the southwestern part (Songtham *et al.*, 2001). The specimens used in this study were collected from Ban Pa Kha, Banpu 1, and Banpu 3 coal mines. Ban Pa Kha coal mine is in the Ban Pa Kha sub-basin, and is operated by the Lanna Resources Public Co., Ltd. Banpu 1 and 3 coal mines have been operated by Banpu Public Company, Ltd.; Banpu 1 mine is in the Banpu sub-basin, while Banpu 3 mine is in the Ban Pa Kha sub-basin.

Based on pollen assemblages, Watanasak (1988b) suggested an age of Late Oligocene for the main coal seam of Pan Bu 1 mine, while Songtham *et al.* (2001) suggested an age of Oligocene to Early Miocene for the Ban Pa Kha sub-basin. Endo (1964, 1966) noticed a similarity between the Li flora and the flora of Fushun, northeastern China, which he considered to be upper Eocene in age. He consequently stated that the age of the Li Basin must be Paleogene in age. However, the species found in both Li Basin and the Fushun coal field have also been found in younger deposits. *Sequoia langsdorfii* (= *Sequoia abietina*) is known from the Upper Eocene to the Pliocene (Mai and Walther, 1978), *Glyptostrobus europaea* is abundant in some deposits during the Miocene of Europe (Kovar-Eder *et al.* (2001), and *Fagus feroniae* has been reported from the Miocene (Unger, 1847).

## Chapter 2

### Material and Methods

#### Collection of fossil specimens

Leaf and other fossil remains were collected at the following sites:

Ban Pa Ka lignite mine, Amphoe Li, Lamphun

Banpu 1 lignite mine, Amphoe Li, Lamphun

Banpu 3 lignite mine, Amphoe Li, Lamphun

The fossils are stored at the Center for Scientific and Technological Equipment (CSTE), Suranaree University of Technology, Nakhon Ratchasima.

#### Collection of Recent leaf specimens

Voucher plant specimens were collected in the field to use for comparison with fossil leaves. Since the climate at the time of deposition of at least some of the fossils was non-tropical (temperate or subtropical), specimens were collected from both tropical and temperate regions. Temperate specimens were collected in Hebei and Liaoning provinces, China (August, 2000), New Mexico, USA (August, 2001), Alachua County, Florida, USA (warm temperate forest and campus of University of Florida; July, 2002), Cedarburg Bog, Wisconsin, USA (August, 2002), and temperate forest near Vienna, Austria (August, 2003). In Thailand, specimens were collected from many localities including Phu Hin Rong Kla National Park, Phitsanulok, Phu Luang Wildlife Sanctuary, Loei, Queen Sirikit Botanic Garden, Chiangmai, and the campus of Suranaree University of Technology, Nakhon Ratchasima.

Additional herbarium specimens were studied at the Forest Herbarium (BKF), Bangkok, and the National Herbarium of China (PEP), Beijing, China.

#### Dégagement of fossil leaves

Dégagement refers to the technique of removing sediment surrounding a fossil plant by using a needle and hammer or needle alone (Fairon-Demaret *et al*, 1999). Some of the fossil leaf compressions in this study were partly exposed and partly buried in clay. A three-angle dental tool was used to remove the overlying clay (e.g., see Figure 7).

### **Preparation of leaf cuticles (microscope slides)**

Fossil leaf cuticle was prepared by a modification of Dilcher (1974). Broken pieces of compressed leaf fossils were lifted with a piece of tracing paper and placed into a polypropylene depression dish; for one specimen, part of a leaf attached to clay was separated by a razor blade. The pieces of leaf were kept in one depression, with the solutions being changed using pipets. Next, Schulze's solution (one part saturated  $\text{KClO}_3$ ; two parts concentrated  $\text{HNO}_3$ ) was added into the depression. Schulze's solution was sometimes replaced with fresh solution, and left for 4 hours to more than 2 days. Next, the specimens were rinsed several times with distilled water, then brought through an ethanol series (50%, 75%, 95%), before staining with 1% safranin O in 95% ethanol. The stain was replaced with absolute ethanol, then 50%:50% ethanol and toluene, and then toluene. The specimens were then placed on a microscope slide by sucking with a pipet.

As only one piece of cuticle showed signs of the epidermal cells, slides of modern leaf cuticle for comparison were not prepared.

### **SEM cuticle preparation**

Fragments of compressed leaf specimens were scraped onto SEM stubs covered with double-sided sticky tape or a piece of the fossil leaf attached to clay was removed by razor blade and placed onto the stub. For modern leaves, two rectangular pieces of each leaf were cut with a razor blade and placed onto an SEM stub covered with double-sided tape, with the adaxial and abaxial surfaces facing upwards, respectively. The cuts were made along the leaf margin approximately halfway between the apex and base of the leaf lamina. The specimens were coated with gold and observed with a JEOL JSM-6400 scanning electron microscope at 10 kV. Some specimens were photographed with Fuji film. For the fossil leaves, the arrangement of epidermal cells could not be clearly observed, so SEM studies were not continued.

### **Clearing modern leaves**

For a study of leaf venation, modern leaves were cleared using a modification of Dilcher (1974). Leaves were placed in 10% NaOH solution in polypropylene dishes. The solution was heated (but not to boiling) for several minutes; then the leaves were left in the NaOH solution for up to several days. The leaves were then treated with 50% strength commercial bleach ( $\text{NaClO}_2$ ). The leaves were washed with distilled water, then brought through an ethanol series to 95%

ethanol. Next, the leaves were stained with safranin O in 95% ethanol. The staining solution was removed and replaced with absolute ethanol. This was replaced with 1:1 ethanol: toluene, then toluene (using a fume hood). Next, the leaves were mounted between two sheets of glass with Permout, a synthetic resin.

### **Photography and illustrations**

Fossil and modern specimens were photographed with a Nikon FM2 SLR camera with a 50 mm lens using color print film or with a Nikon Coolpix950 digital camera.

Illustrations were made using a drawing tube with a Nikon SMZ800 stereomicroscope.

### **Description of leaf architecture**

In describing the architecture of fossil and modern leaves, the terminology of Hickey (1973) and Dilcher (1974) was used. Dilcher (1974) also presented terminology used in describing fossil and modern cuticle.

### **Comparison with Recent leaves**

For comparison of the fossil leaf specimens with Recent leaves, both cleared leaves and leaves on herbarium sheets were studied. In addition, illustrations (photographs and drawings) of both Recent and fossil leaves from printed books and from the Internet were studied. Useful books include Gardner *et al.* (2000) for trees of Northern Thailand, Preston (1976), Heywood (1978), Mitchell (1987), Coombes (1992), Klucking (1995), and Rushforth (2000). Books and theses concentrating on specific families include Jones (1984) on fossil and Recent Fagaceae, Manchester (1987) on fossil and Recent Juglandaceae, and Budantsev (1994) on fossil and Recent Leitneriaceae, Myricaceae, and Juglandaceae. Cutler and Gregory (1998) provide useful information about leaf anatomy.

## Chapter 3

### Results

#### Cleared leaves

Cleared leaves were prepared from 253 herbarium specimens, comprising 77 families, 146 genera, and 157 species, plus additional unidentified genera and families. The cleared leaf specimens are housed at the Center for Scientific and Technological Equipment (CSTE), Suranaree University of Technology, Nakhon Ratchasima. Each of the cleared leaves is associated with a voucher herbarium sheet stored in the herbarium at the CSTE, Suranaree University of Technology. Additional specimens of plants have been collected and stored in the herbarium but have not been cleared.

Actinidiaceae	<i>Saurauia leprosa</i> Korth.
Alismataceae	<i>Echinodorus cordifolius</i> (L.) Griseb.
Annonaceae	<i>Polyalthia</i> sp.
Apocynaceae	<i>Aganonerion polymorphum</i> Pierre ex Spire
Apocynaceae	<i>Alstonia scholaris</i> (L.) R.Br.
Apocynaceae	<i>Beaumontia</i> sp.
Apocynaceae	<i>Carissa spinarum</i> L.
Apocynaceae	<i>Ichnocarpus frutescens</i> (L.) W.T. Aiton
Apocynaceae	<i>Wrightia</i> sp.
Araceae	<i>Pseudodracontium</i> sp.
Asclepiadaceae	<i>Cryptostegia grandiflora</i> R.Br.
Asteraceae	<i>Ageratum conyzoides</i> L.?
Asteraceae	<i>Lagascea mollis</i> Cav.
Asteraceae	<i>Tithonia diversifolia</i> (Hemsl.) A. Gray
Asteraceae	<i>Vernonia squarrosa</i> D. Don (Less.)
Auracariaceae	<i>Araucaria excelsa</i> R. Br.
Begoniaceae	<i>Begonia</i> sp.
Betulaceae	<i>Corylus sieboldiana</i> Bl.
Bignoniaceae	<i>Fernandoa adenophylla</i> (Wall. ex G. Don) Steenis

Bonnetiaceae	<i>Ploiarium alternifolium</i> (Vahl) Melchior
Cactaceae	<i>Pereskia bleo</i> (Kunth) DC.
Capparaceae	<i>Capparis echinocarpa</i> Pierre ex Gagnep.
Capparaceae	<i>Capparis flavicans</i> Kurz
Capparaceae	<i>Maerua siamensis</i> (Kurz) Pax
Celastraceae	<i>Cassine glauca</i> (Rottb.) Kuntze
Celastraceae	<i>Celastrus paniculatus</i> Willd.
Celastraceae	<i>Euonymus</i> sp.
Clusiaceae	<i>Cratoxylum</i> sp.
Combretaceae	<i>Getonia floribunda</i> (Roxb.) Lam.
Combretaceae	<i>Terminalia chebula</i> Retz.
Combretaceae	<i>Terminalia glaucifolia</i> Craib
Connaraceae	<i>Ellipanthus tomentosus</i> Kurz
Convolvulaceae	<i>Jacquemontia paniculata</i> (Burm. f.) Hallier f.
Cucurbitaceae	<i>Solena amplexicaulis</i> (Lam.) Gandhi
Cupressaceae	<i>Cunninghamia lanceolata</i> (Lamb.) Hook.
Dilleniaceae	<i>Dillenia</i> sp.
Dilleniaceae	<i>Tetracera</i> sp.
Dioscoreaceae	<i>Dioscorea</i> sp.
Dipterocarpaceae	<i>Shorea roxburghii</i> G. Don.
Ebenaceae	<i>Diospyros castanea</i> Fletcher
Ebenaceae	<i>Diospyros ehretoides</i> Wall. ex G. Don
Ebenaceae	<i>Diospyros rhodocalyx</i> Kurz
Ehretiaceae	<i>Ehretia</i> sp.
Elaeagnaceae	<i>Hippophae</i> sp.?
Elaeocarpaceae	<i>Elaeocarpus hygrophilus</i> Kurz
Elaeocarpaceae	<i>Elaeocarpus robustus</i> Roxb.
Erythroxylaceae	<i>Erythroxylum</i> sp.
Euphorbiaceae	<i>Antidesma</i> sp.
Euphorbiaceae	<i>Aporosa villosa</i> (Wall. ex Lindl.) Baill.
Euphorbiaceae	<i>Baliospermum</i> sp.

Euphorbiaceae	<i>Bridelia ovata</i> Decne.
Euphorbiaceae	<i>Cladogynos orientalis</i> Zipp. ex Span.
Euphorbiaceae	<i>Croton sublyratus</i> Kurz.
Euphorbiaceae	<i>Excoecaria cochinchinensis</i> Lour.
Euphorbiaceae	<i>Macaranga</i> sp.
Euphorbiaceae	<i>Sauropus</i> sp.
Euphorbiaceae	<i>Suregada multiflorum</i> (A. Juss.) Baill.
Euphorbiaceae	<i>Trigonostemon</i> sp.
Fabaceae	<i>Acacia auriculaeformis</i> A. Cunn. ex Benth.
Fabaceae	<i>Afgekia sericea</i> Craib
Fabaceae	<i>Afzelia xylocarpa</i> (Kurz) Craib
Fabaceae	<i>Albizia</i> sp.
Fabaceae	<i>Bauhinia pulla</i> Craib
Fabaceae	<i>Bauhinia viridescens</i> Desv.
Fabaceae	<i>Christia obcordata</i> (Poir.) Bakh. f.
Fabaceae	<i>Clitoria macrophylla</i> Wall.
Fabaceae	<i>Dalbergia nigrescens</i> Kurz
Fabaceae	<i>Derris scandens</i> (Roxb.) Benth.
Fabaceae	<i>Desmodium</i> sp.
Fabaceae	<i>Dialium cochinchinense</i> Pierre
Fabaceae	<i>Erythrophleum succirubrum</i> Gagnep.
Fabaceae	<i>Millettia</i> sp.
Fabaceae	<i>Phyllodium pulchellum</i> (L.) Desv.
Fabaceae	<i>Saraca declinata</i> (Jack) Miq.
Fabaceae	<i>Tephrosia purpurea</i> (L.) Pers.
Fabaceae	<i>Uraria lagopodioides</i> (L.) Desv. ex DC.
Fabaceae	<i>Zornia diphylla</i> (L.) Pers.
Fagaceae	<i>Castanopsis acuminatissima</i> (Bl.) A. DC.
Fagaceae	<i>Lithocapus falconeri</i> (Kurz) Rehder
Fagaceae	<i>Quercus kerrii</i> Craib
Flacourtiaceae	<i>Casearia grewiifolia</i> Vent.



Flacourtiaceae	<i>Flacourtia indica</i> (Burm. f.) Merr.
Flacourtiaceae	<i>Flacourtia rukam</i> Zoll. & Moritz
Gnetaceae	<i>Gnetum</i> sp.
Hamamelidaceae	<i>Altingia excelsa</i> Noronha
Hernandiaceae	<i>Illigera</i> sp.
Irvingiaceae	<i>Irvingia malayana</i> Oliv. ex A.W. Benn.
Lamiaceae	<i>Callicarpa</i> sp.
Lamiaceae	<i>Gmelina elliptica</i> J.E. Smith
Lamiaceae	<i>Hymenopyramis</i> sp.
Lamiaceae	<i>Vitex</i> sp.
Lauraceae	<i>Litsea glutinosa</i> (Lour.) C.B. Rob.
Lecythidaceae	<i>Gustavia gracillima</i> Miers
Loranthaceae	<i>Dendrophthoe pentandra</i> (L.) Miq.
Loranthaceae	<i>Scurulla</i> sp.
Lythraceae	<i>Lagerstroemia speciosa</i> (L.) Pers.
Magnoliaceae	<i>Magnolia coco</i> (Lour.) DC.
Magnoliaceae	<i>Michelia alba</i> DC.
Magnoliaceae	<i>Michelia champaca</i> L.
Magnoliaceae	<i>Michelia figo</i> (Lour.) Spreng.
Malpighiaceae	<i>Tristellateia australasiae</i> A. Rich.
Malvaceae	<i>Gossypium</i> sp.
Malvaceae	<i>Urena lobata</i> L.
Meliaceae	<i>Aglaia odorata</i> Lour.
Meliaceae	<i>Melia azedarach</i> L.
Menispermaceae	<i>Pachygone</i> cf. <i>dasycarpa</i> Kurz
Moraceae	<i>Artocarpus lakucha</i> Roxb.
Moraceae	<i>Ficus retusa</i> L.
Moraceae	<i>Maclura</i> sp.
Moraceae	<i>Morus</i> sp.
Myrsiniaceae	<i>Ardisia</i> sp.
Myrtaceae	<i>Eucalyptus camuldulensis</i> Dehnh.

Ochnaceae	<i>Ochna integerrima</i> (Jour.) Merr.
Oleaceae	<i>Olax scandens</i> Roxb.
Oleaceae	<i>Fraxinus</i> sp.
Onagraceae	<i>Ludwigia hyssopifolia</i> (G. Don) Exell
Opiliaceae	<i>Cansjera rheedei</i> J.F. Gmel.
Opiliaceae	<i>Urobotrya siamensis</i> Hiepko
Passifloraceae	<i>Passiflora foetida</i> L.
Piperaceae	<i>Piper betel</i> L.
Podocarpaceae	<i>Nageia wallichiana</i> (C. Presl) Kuntze
Podocarpaceae	<i>Podocarpus neriifolius</i> D. Don
Podocarpaceae	<i>Podocarpus polystachyus</i> R.Br. ex Endl.
Rhamnaceae	<i>Gouania</i> sp.
Rhamnaceae	<i>Zizyphus cambodiana</i> Pierre
Rhizophoraceae	<i>Carallia brachiata</i> (Lour.) Merr.
Rosaceae	<i>Crataegus</i> sp.
Rubiaceae	<i>Mitragyna</i> sp.
Rubiaceae	<i>Prismatomeris</i> sp.
Rubiaceae	<i>Rothmannia wittii</i> (Craib) Bremek.
Rubiaceae	<i>Uncaria</i> sp.
Rutaceae	<i>Clausena</i> sp.
Rutaceae	<i>Phellodendron amurense</i> Rupr.
Rutaceae	<i>Toddalia asiatica</i> (L.) Lam.
Sapindaceae	<i>Lepisanthes rubiginosa</i> (Roxb.) Leenh.
Sapotaceae	<i>Mimusops elengi</i> L.
Simaroubaceae	<i>Ailanthus</i> sp.
Simaroubaceae	<i>Eurycoma longifolia</i> Jack
Smilacaceae	<i>Smilax inversa</i> T. Koyama
Solanaceae	<i>Cestrum nocturnum</i> L.
Staphyleaceae	<i>Turpinia</i> sp.
Sterculiaceae	<i>Helicteres angustifolia</i> L.
Sterculiaceae	<i>Helicteres lanceolata</i> A. DC.

Sterculiaceae	<i>Waltheria indica</i> L.
Theaceae	<i>Anneslea fragrans</i> Wall.
Theaceae	<i>Eurya nitida</i> Korth.
Tiliaceae	<i>Corchorus aestuans</i> L.
Tiliaceae	<i>Grewia eriocarpa</i> Juss.
Tiliaceae	<i>Microcos tomentosa</i> Sm.
Tiliaceae	<i>Schoutenia</i> sp.
Tiliaceae	<i>Tilia chinensis</i> Maxim.
Tiliaceae	<i>Triumfetta rhomboidea</i> Jacq.
Turneraceae	<i>Turnera ulmifolia</i> L.
Ulmaceae	<i>Ulmus parvifolia</i> Jacq.
Verbenaceae	<i>Sphenodesme</i> sp.
Viscaceae	<i>Viscum</i> sp.
Vitaceae	<i>Cayratia trifolia</i> (L.) Domin

### Fossil specimens

Division Pteridophyta

Family Thelypteridaceae Ching

*Cyclosorus* sp.

(Figures 1, 2, 4, 5)

**DESCRIPTION:** Pinnae or fragments of pinnae preserved as compressions or impressions. The pinnae are lobed on either side with the sinus reaching approximately one third to almost one half of the way to the main vein (costa) of the pinna. The largest pinna fragment has at least nine lobes per side and is 3.3 cm in length. The pinna is fed by one primary vein (costa), with secondary veins, one per lobe (pinnule), arranged pinnately. There appears to be a groove adaxial to the primary vein. Tertiary veins are arranged pinnately on the secondary vein, extending to (or at least close to) the margin. The tertiary veins are not forked. The veins reaching the margin distal to the sinus are free, not forming areoles. The lower veins anastomose forming an excurrent vein which extends from the basalmost tertiary veins to the sinus, forming quadrangular areoles (a venation type known as goniopteroid (Kramer, 1990a)). The basalmost tertiary vein on the lower side of the

secondary vein may arise from the primary vein of the pinna rather than from the secondary vein, this type of venation being called catadromous (Kramer, 1990a).

SPECIMENS: SUT 1608 (Figures 1, 2), SUT 1609 (Figures 3, 4), SUT 1610

LOCALITY: Banpu 1 mine, Li District, Lamphun Province (SUT locality 031)

AFFINITIES: Fragments of pinnae are common in Banpu 1 deposits. Extant ferns with goniopteroid venation can be found in the family Thelypteridaceae (see Smith, 1990; Figure 3) and in the subfamily Athyrioideae of Dryopteridaceae (Kramer, 1990b). Smith (1990) conservatively divides the family Thelypteridaceae into five genera. Species with goniopteroid venation comprise part of the genus *Cyclosorus*. In the *Flora of Thailand*, Tagawa and Iwatsuki (1988a) place species with goniopteroid venation in *Thelypteris* and *Meniscium*, whereas, in Smith (1990), these species of *Thelypteris* and the genus *Meniscium* are included in the genus *Cyclosorus*. In Athyrioideae (= family Athyriaceae in the *Flora of Thailand* (Tagawa and Iwatsuki, 1988b)), ferns with goniopteroid venation occur in *Athyrium cunningianum* (= *Anisocampium cunningianum* in Tagawa and Iwatsuki, 1988b) and in some species of *Diplazium*. However, venation of *Athyrium cunningianum* appears to be isodromous or anadromous, rather than catadromous as in the fossil (from fig. 47.7 in Tagawa and Iwatsuki, 1988b). *Diplazium* consists of 400 (or probably fewer) species of fern found mostly in warmer climates and only locally in temperate regions (Kramer, 1990b). In *Diplazium*, the majority of the species have free veins, with a minority having a goniopteroid or another type of venation pattern. The veins are either simple or forked and tertiary level veins are arranged either anadromously or catadromously. More investigation of this genus is necessary to see if the combination of characters of the fossil, i.e., goniopteroid and catadromous venation, simple veins, and lobes reaching about one third of the way to the primary vein or costa, could allow placement in the genus *Diplazium*. Until such further study can be carried out, however, the fossil is here tentatively placed in the genus *Cyclosorus* of Thelypteridaceae. This genus consists of twenty subgenera and approximately 670 species of which most are tropical and subtropical, although some species are temperate. Figure 3 shows a leaf of *Cyclosorus* sp. (*Thelypteris* in Tagawa and Iwatsuki (1988a)). No fertile material is known for the fossil.

Division Magnoliophyta  
 Order Saxifragales Dumortier  
 Family Hamamelidaceae R. Br.

Genus?

(Figures 6, 7)

DESCRIPTION: Compressed leaf, widely elliptic, slightly asymmetric; apex acuminate; base approximately rounded; length 3.7 cm (plus small broken tip), width 2.2 cm; margin serrate-dentate, teeth with apex pointed or narrowly rounded, toward apex of leaf very acute; more basal teeth obtuse to very obtuse; venation pinnate, craspedodromous; primary vein thick, slightly zigzag; secondary veins alternate, 6 per side of leaf, diverging from primary vein at approximately 50°, curving apically, reaching and entering teeth.

SPECIMEN: SUT 1120 (Figures 6, 7)

LOCALITY: Banpu 1 mine, Li District, Lamphun Province (SUT locality 026)

AFFINITIES: The shape and venation pattern of this specimen are similar to those of some species of *Hamamelis* and *Fothergilla* in the Hamamelidaceae, especially *H. mollis* Oliver (Figure 8), which is native to central China (Rushforth, 2000). However, *H. mollis* is more asymmetric than the fossil. *Hamamelis* consists of six species in Eastern Asia and Eastern North America. *Fothergilla* comprises four species in the Atlantic region of North America (Willis, 1973). Today there are five genera and six species of Hamamelidaceae recorded from Thailand (Phengklai, 2001), but the fossil is not similar to any of these.

Order Fagales Engler  
 Family Fagaceae Dumortier  
 cf. *Quercus* or *Castanopsis* sp. 1

(Figures 9-12)

DESCRIPTION: Leaves elliptic or narrowly elliptic?, with acuminate apex; width to at least 4.1 cm; margins serrate with teeth present on approximately the apical half of the leaf, but not the basal half; teeth with tip rounded to nearly pointed; apical edge of tooth concave or straight; sinus rounded; basal edge convex; venation pinnate, semicraspedodromous; secondary veins arising from the primary vein at an angle of approximately 50-75° and curving apically; near margin the secondary vein branching, one branch entering a tooth medially, the other branch heading apically

and branching again two or three times, with each branch joining the superadjacent secondary, resulting in two or more tertiary arches exmedial to secondary arch.

SPECIMENS: SUT 966 (Figures 9, 10), SUT 903 (Figure 11), SUT 904, SUT 906, SUT 907, SUT 1000 (Figure 12)

LOCALITY: Banpu 3 mine, Li District, Lamphun Province (SUT locality 021)

AFFINITIES: This species is known from several leaf fragments, none of which has a complete base. The restriction of teeth to the apical half of the leaf and the venation pattern are characteristic of some species of *Quercus* and *Castanopsis* in the Fagaceae, such as *Quercus kerrii* Craib (Figures 13, 14) and *Castanopsis acuminatissima* (Blume) A. DC. (Figures 15, 16), both species of which can be found in mountainous areas in Thailand. In *C. acuminatissima*, the venation pattern is clearly craspedodromous, with the secondary vein ending in a tooth. However, in *Q. kerrii*, the venation pattern is borderline craspedodromous-semicraspedodromous, with the secondary vein branching near the margin, with one branch entering a tooth and the other heading apically. The branch entering the tooth is slightly thicker than the other branch. This suggests that the fossil may be more closely related to *Q. kerrii* than to *C. acuminatissima*, although further study of additional modern leaves is necessary. In addition, leaves of some species of *Lithocarpus* show similarities to the fossil leaves.

Extant *Quercus* comprises 531 species in North America to western tropical South America, temperate and subtropical Eurasia, and North Africa (Willis, 1973; Govaerts and Frodin, 1998). *Quercus kerrii* is placed in the subgenus *Cyclobalanopsis*, which is raised to the rank of genus, in the *Flora of China* (Huang *et al.*, 1999). *Cyclobalanopsis* comprises about 150 species

mainly in tropical and subtropical Asia. *Quercus kerrii* itself occurs in southern China (Guanxi, Guizhou, Hainan, and Yunnan), northern Thailand, and Vietnam (Huang *et al.*, 1999).

*Castanopsis* is also large genus with 134 species in tropical and subtropical Asia and Malesia. *Lithocarpus* consists of 325 species all found in Asia and Malesia except one species which occurs in western North America (Govaerts and Frodin, 1998). In Thailand, there are at least 31 species of *Quercus*, 26 species of *Castanopsis*, and 42 species of *Lithocarpus* (Forest Herbarium, 2001). In order to get a clearer picture of the affinities of the fossil specimens, better preserved specimens and a more thorough study of the extant species are required.

cf. *Quercus* or *Castanopsis* sp. 2

(Figures 17-18)

DESCRIPTION: Leaves narrowly to very narrowly elliptic; apex tapering acute or acuminate; base acute; petiole thick; margin serrate with teeth present on approximately the apical half of the leaf, but not the basal half; one nearly complete leaf (SUT 900) 16.3 cm in length (plus missing apex), approximately 2.9 cm in width; teeth with tip round; apical edge straight or convex; basal half convex; sinus rounded, acute to very obtuse; venation pinnate, more or less craspedodromous; primary vein thick basally, becoming thinner apically; secondary veins arising from the primary vein at a low angle (approximately 30 to 50°), and curving slightly apically; secondary veins in apical part of leaf branch near the margin, one branch reaching a tooth, the other branch heading toward superadjacent secondary vein.

SPECIMENS: SUT 900 (Figure 17), SUT 901 (Figure 18), SUT 994

LOCALITY: Banpu 3 mine, Li District, Lamphun Province (SUT locality 021)

AFFINITIES: This taxon includes a nearly complete specimen (SUT 900), a specimen with a nearly complete apex but missing base (SUT 994), and one with a missing apex and base (SUT 901). These specimens show affinity to Fagaceae, especially some species of *Quercus* and *Castanopsis*. They differ from sp. 1 above in being narrowly to very narrowly acute and in having a low angle of divergence of the secondary veins (approximately 30 to 50°, as compared with 50-75° in sp. 1). The secondary veins appear to be craspedodromous as compared with semicraspedodromy in sp. 1, but this difference is equivocal as the secondary veins are not clearly visible near the margins. The teeth of this taxon have a straight to convex apical edge, whereas in sp. 1 the apical edge is concave to straight. Leaf shape and even presence or absence of teeth can be quite variable within species in the Fagaceae. For example, the extinct species *Eotrigonobalanus furcinervis* (Rossmässler) Walther and Kvaček includes leaves that are lanceolate to ovate, entire margined to serrate, and craspedodromous to camptodromous in Abbildung (Illustration) 1 of Walther and Zetter (1993). Finding additional specimens may allow a better understanding of the range of variation within each species.

cf. *Quercus* or *Castanopsis* sp. 3

(Figure 19)

DESCRIPTION: Leaf with acuminate apex; margin serrate, with teeth closely spaced; teeth with tip rounded to subpointed; apical edge of tooth straight or concave; basal edge convex; venation not clear.

SPECIMEN: SUT 1339 (Figure 19)

LOCALITY: Banpu 3 mine, Li District, Lamphun Province (SUT locality 021)

AFFINITIES: One specimen, missing basal half of leaf. This specimen is similar SUT 996 (sp. 1) but has more closely spaced teeth and the leaf widens somewhat more abruptly below the apex. More specimens are needed to determine if these are constant species-specific differences.

cf. *Quercus* or *Castanopsis* sp. 4

(Figure 20)

DESCRIPTION: Leaf elliptic; apex and base unknown; width 5.1 cm; margin serrate (the basal approximately one third of leaf appears to lack teeth); teeth large, the tip rounded to subpointed; the apical edge of the teeth straight or concave or S-shaped, with the base concave and the distal region convex; the basal edge more or less convex; the sinus rounded to angular; venation pinnate, appearing to be craspedodromous; the secondary veins arise from the primary at an angle of approximately 55- 70° and curve apically.

SPECIMEN: SUT 1001 (Figure 20)

LOCALITY: Banpu 3 mine, Li District, Lamphun Province (SUT locality 021)

AFFINITIES: Known from one specimen missing the apex and base. This species shows affinities to *Quercus* and *Castanopsis* (Fagaceae). This specimen is similar to sp. 1, but has larger teeth. More specimens are needed to indicate whether the differences shown are species-specific.

Family Betulaceae Gray

*Alnus* sp.

(Figures 21-23)

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 teeth fed by the first branch of a secondary vein being larger than the other 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, semicraspedodromous, 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; 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 supramedially 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 arc 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.

SPECIMENS: SUT 1003 (Figures 21, 22), SUT 1607 (Figure 23)

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)

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, or cucumptodromous 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. The pattern of veins and teeth of the fossil species is similar to that of the modern species *A. fernandicoburgii* Schneid. (Figure 25) and *A. cremastogyne* Burk. (Figure 26). 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*.

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 to two extant species in China, *A. cremastogyne* and *A. fernandi-coburgii*.

#### Genus?

(Figure 27, 28)

DESCRIPTION: Compressed leaf, with most of the right margin and the apex missing; elliptic, slightly asymmetric (length = 7.7 cm plus missing tip; width = approximately 2.9 cm.); apex apparently acuminate; base rounded; petiole thick; margins serrate, 5 or 6 teeth per secondary vein; tooth exmedial to secondary vein generally the largest, with 4 or 5 teeth basal to it, one or two of which may be smaller secondary teeth on basal flank of the larger tooth; teeth with acute or obtuse apex; apical side straight or convex; basal side straight or convex; venation pinnate, craspedodromous(?); secondary veins straight or curving slightly apically, disappearing before reaching margin; at least 17 on left side of leaf (apical veins not clear); angle of divergence from primary vein 75-80°; basal veins curving slightly apically, with more apical veins having greater curves.

SPECIMEN: SUT 582 (Figures 27, 28)

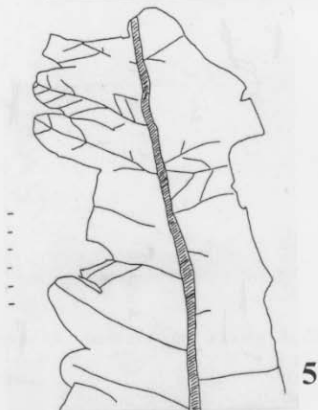
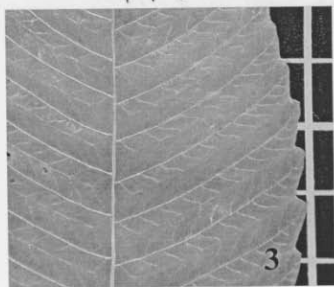
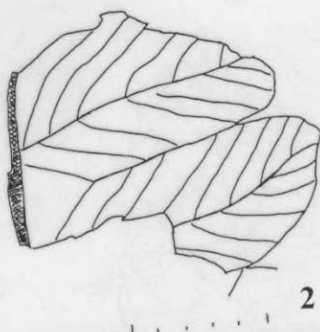
LOCALITY: Ban Pa Kha mine, Li District, Lamphun Province (SUT locality 019)

AFFINITIES: The pattern of teeth with larger teeth separated by several smaller teeth can be found in genera of the Betulaceae (*Betula*, *Carpinus*, *Ostrya*, some species of *Alnus*). The elliptic slightly asymmetrical shape of the fossil is similar to *Betula alnoides* Buc. Ham. ex G. Don (Figure 29), an extant species occurring in mountainous areas of Thailand. However, the angle of divergence of the secondary veins is smaller in the extant species than in the fossil. Also similar to the fossil is *Carpinus viminea* Wall. ex Lindl. (Figure 30), extant in mountainous regions of Thailand, though the extant species also has a small angle of divergence of the secondary veins. Although a precise comparison cannot be made with extant genera because of the lack of visible higher order veins in the fossil, the specimen appears to have affinity to *Betula* or *Carpinus*.

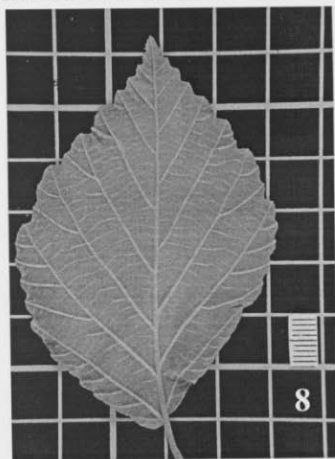
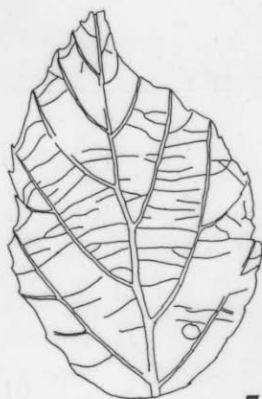
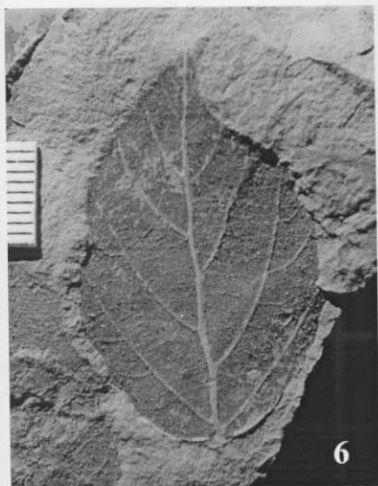
	<i>Alnus</i> sp. (SUT 1003)	<i>A. ferdandi-</i> <i>coburgii</i>	<i>A.</i> <i>cremastogyne</i>	<i>A. nepalensis</i>	<i>A.</i> <i>newberryi</i> <sup>1</sup>	<i>Betula</i> <i>alnoides</i>
Secondary vein	Semicraspedo- dromous	Semicraspedo- dromous	Semicraspedo- dromous	Semicraspedo- dromous	Craspedo- dromous	Craspedo- dromous
Vein to sinus	+	+	+	- or +	-(rarely +)	-
Intersecondary veins	+	+	+	+	-	-
Tertiary veins	Percurrent	Percurrent	Percurrent	Percurrent	Percurrent	Percurrent
Teeth	Two sizes	Equal size	Equal size	Equal size	Two sizes	Two sizes
Tooth apex	Rounded	Rounded	Rounded	Rounded	Rounded	Acuminate

<sup>1</sup>Meyer and Manchester, 1997

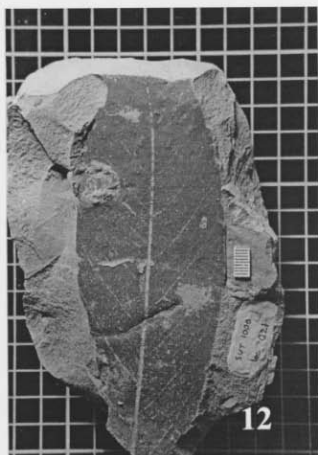
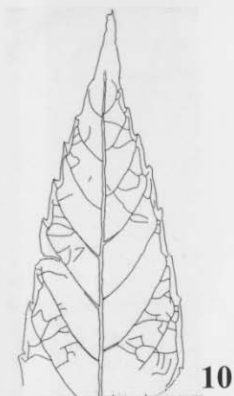
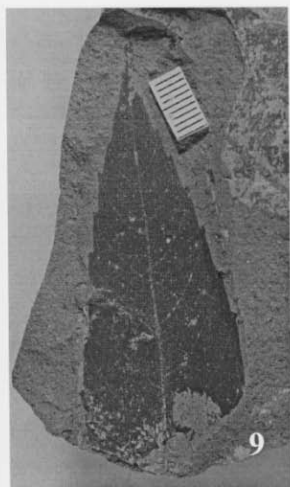
Table 1. Comparison of some leaf characteristics of the fossil *Alnus* sp. and other species in Betulaceae.



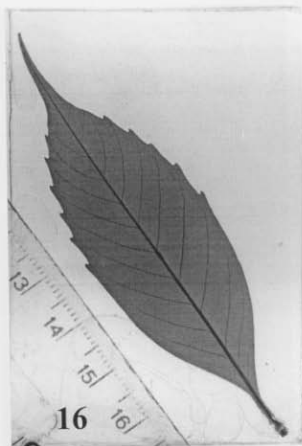
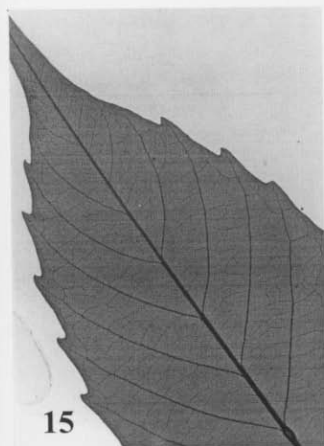
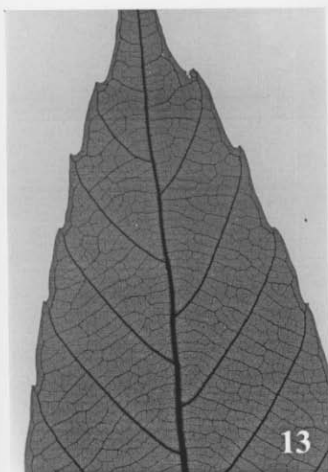
Figs. 1-5. 1. *Cyclosorus* sp. (SUT 1608), Thelypteridaceae. 2. Same as 1., line drawing. 3. Recent *Cyclosorus* sp. (*Thelypteris* sp.), Thelypteridaceae, Khao Yai National Park, Thailand. 4. *Cyclosorus* sp. (SUT 1609), Thelypteridaceae. 5. Same as 4., line drawing, after removal of some overlying matrix.



Figs. 6-8. 6. Genus? (SUT 1122), Hamamelidaceae. 7. Same as 6., line drawing. 8. *Hamamelis mollis* Oliver, Hamamelidaceae, cultivated, Austria.

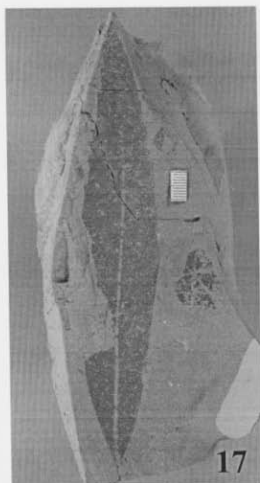


Figs. 9-12. 9. cf. *Quercus* or *Castanopsis* sp. 1 (SUT 966), Fagaceae. 10. Same as 9., line drawing. 11. cf. *Quercus* or *Castanopsis* sp. 1 (SUT 903). 12. cf. *Quercus* or *Castanopsis* sp. 1 (SUT 1000).



Figs. 13-16. 13. and 14. Cleared leaf of *Quercus kerrii* Craib, Fagaceae, Phu Hin Rong Kla, Phitsanulok, Northern Thailand. 15. and 16. Cleared leaf of *Castanopsis acuminatissima* (Blume) A. DC., Fagaceae, Phu Hin Rong Kla, Phitsanulok, Northern Thailand.

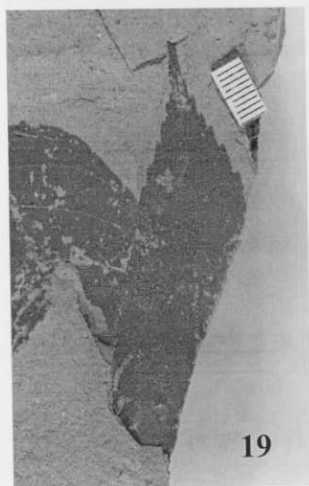




17



18

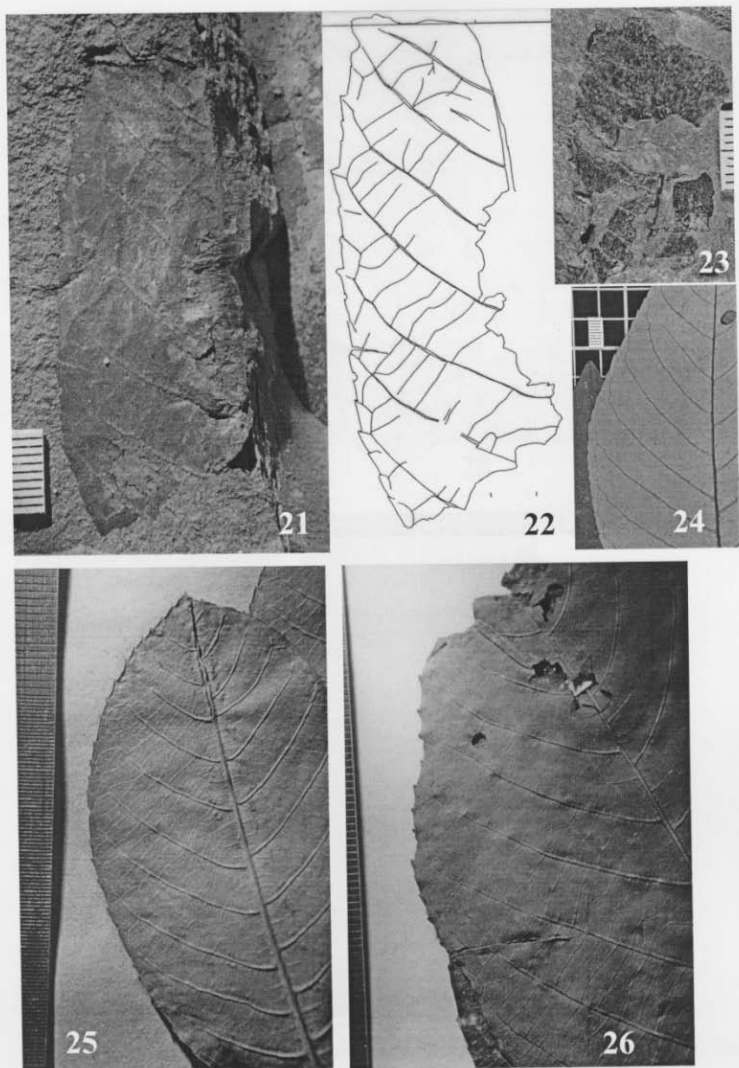


19

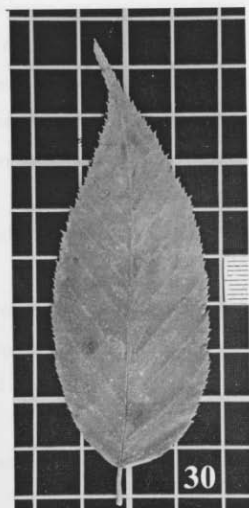
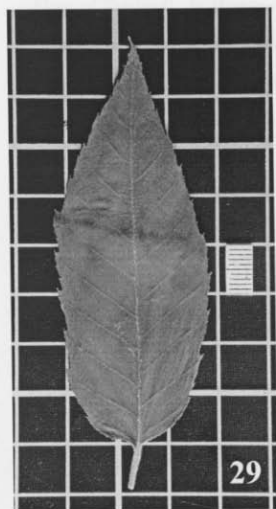
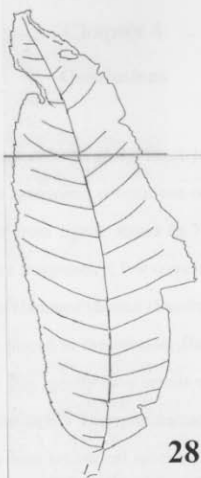
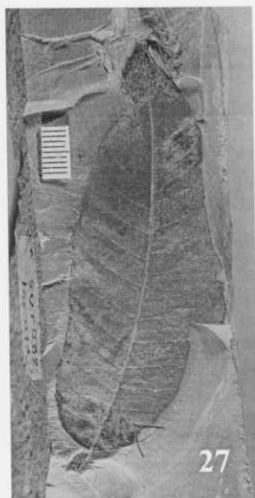


20

Figs. 17-20. 17. cf. *Quercus* or *Castanopsis* sp. 2 (SUT 900), Fagaceae. 18. cf. *Quercus* or *Castanopsis* sp. 2 (SUT 901). 19. cf. *Quercus* or *Castanopsis* sp. 3 (SUT 1339). 20. cf. *Quercus* or *Castanopsis* sp. 4 (SUT 1001).



Figs. 21-26. 21. *Alnus* sp. (SUT 1003), Betulaceae. 22. Same as 21., line drawing. 23. *Alnus* sp. (SUT 1607). 24. *Alnus nepalensis* D. Don, Phu Luang, Loei, Northeastern Thailand. 25. *A. fernandi-coburgii* Schneid., China. 26. *A. cremastogyne* Burk., Sichuan, China.



Figs. 27-30. 27. Genus ? (SUT 582), Betulaceae. 28. Same as 27., line drawing. 29. *Betula alnoides* Buc. Ham. ex G. Don., Betulaceae, Phu Luang, Loei, Northeastern Thailand. 30. *Carpinus viminea* Wall. ex Lindl., Betulaceae, Phu Luang, Loei.

## Chapter 4

### Conclusions

Although attempts to use cuticle to study fossil leaves from the Tertiary of Northern Thailand were unsuccessful, some taxonomic conclusions could be made using leaf architecture. Many leaves have been collected from lignite mines in Tertiary basins in Northern Thailand, although many of the specimens are fragmentary; few complete leaves have been collected. In this project, specimens with affinity to Hamamelidaceae (Saxifragales) and Fagaceae and Betulaceae (Fagales) (all three families were placed in the subclass Hamamelidae by Cronquist, 1981) were chosen for detailed study because they mostly have serrate margins and are rather common in the collections. In addition, ferns in the family Thelypteridaceae were studied. The ferns were placed in the genus *Cyclosorus*, of which there are several species extant in Thailand (as *Thelypteris* in the *Flora of Thailand*). In Hamamelidaceae, one species was studied that showed possible affinity to *Hamamelis*. This specimen was not similar to any living member of the family in Thailand. In Fagaceae, four species were tentatively delineated which showed affinities to *Quercus* and *Castanopsis*. Both of these genera are extant in Thailand. In Betulaceae, one species of *Alnus* was described based on leaf remains with some similarities to the extant Thai species, *A. nepalensis*, but seemingly with greater affinity to the extant Chinese species *A. fernandi-coburgii* and *A. cremastogyne*. An additional leaf appears related to *Betula* or *Carpinus*, both genera extant in Thailand.

Additional leaf fossils from the lignite mines of Northern Thailand have been studied by Prakart Sawangchote using comparison of leaf architecture of Recent leaves and fossil leaves (Sawangchote, 2003; unpublished data).

#### Reconstructing past climates and forest types

There are several ways of using fossils for reconstructing past climates. One method is to look at the physiognomy, or shape, of the fossil leaves and correlate it to climatic parameters. In this approach, identification of the fossil taxa is not necessary. A second method is the Nearest Living Relative (NLR) approach. In this method, the assumption is made that the physiological tolerances of the fossil plants were not much different from the tolerances of the most closely related plants living today. A third method is the coexistence approach (Mosbrugger and Utescher,

1997). In this method the same assumptions are made as in the NLR approach. Climatic parameters of the NLRs, such as mean annual temperature (MAT) and mean annual precipitation (MAP), are first determined. The overlap of these parameters for all NLRs is used to derive the inferred climatic parameters of the site at the time of deposition.

A physiognomic approach was carried out by Yabe (2002) using two plant megafossil assemblages from Northern Thailand, namely, from Mae Lai Basin and from Ban Pa Kha subbasin of Li Basin. Using 30 species of dicotyledonous leaves from Ban Pa Kha subbasin, Yabe looked at 31 characters including those related to presence, shape, and arrangement of teeth along the margin, shape and size of the leaf, and shape of leaf apex and base. These characters correlated with the following climatic parameters: mean annual temperature of 17.6°C, cold month mean temperature of 7.5°C, warm month mean temperature of 27.8°C, and growing season precipitation of 324.5 cm. These climatic characters are consistent with a notophyllous broad-leaved evergreen forest, which would be subtropical or warm temperate (Morley, 2000).

Below are listed fossil taxa from deposits in the Li Basin considered to be early Miocene or late Oligocene in age along with the nearest living relative and the climate and habit of the NLR:

Fossil taxa	Organ <sup>1</sup>	Nearest living relative	Climate (of NLR) <sup>2</sup>	Habit (of NLR)
<b>Ferns</b>				
<i>Cyclosorus</i> sp. (Thelypteridaceae)	l	<i>Cyclosorus</i>	Mostly tropical and subtropical; some temperate	
<b>Conifers</b>				
<i>Sequoia</i> sp. (Cupressaceae s.l.)	t, l, c, s	<i>Sequoia sempervirens</i>	Temperate	Evergreen
<i>Glyptostrobus</i> cf. <i>europaea</i> (Cupressaceae s.l.)	t	<i>Glyptostrobus pensilis</i>	Subtropical to tropical	Deciduous or semievergreen
<i>Taiwania</i> sp.? (Cupressaceae ?)	t, c	<i>Taiwania cryptomerioides</i>		
<i>Podocarpoxylon</i> sp. 1, 2 (Podocarpaceae)	cw	Podocarpaceae	Mostly tropical and subtropical	Evergreen
<i>Sciadopitys</i> sp. (Sciadopityaceae)	t, l	<i>Sciadopitys verticillata</i>	Cool temperate	Evergreen
<b>Angiosperms</b>				
<i>Oxymitra</i> cf. <i>affinis</i> (Annonaceae)	l	<i>Oxymitra affinis</i>	Tropical	
<i>Phyllanthus</i> sp. (Euphorbiaceae)	l	<i>Phyllanthus</i>	Tropical to	

			temperate	
cf. <i>Mesua</i> (Clusiaceae)	1	<i>Mesua</i>	All tropical?	Evergreen (Thai species)
<i>Albizia</i> sp. (Fabaceae, Mimosoideae)	1	<i>Albizia</i>	Warm temperate? to tropical	Evergreen (Thai species)
<i>Archidendron</i> (Fabaceae, Mimosoideae)	1	<i>Archidendron</i>	Tropical	Evergreen (SE Asian spp.)
<i>Bauhinia</i> (Fabaceae, Caesalpinioideae)	1	<i>Bauhinia</i>	Warm	Evergreen or sometimes deciduous
<i>Caesalpinia</i> (Fabaceae, Caesalpinioideae)	1	<i>Caesalpinia</i>	Tropical to subtropical	Evergreen (Thai species)
<i>Antheroporum</i> sp. (Fabaceae, Faboideae)	1	<i>Antheroporum</i>	Tropical	
cf. <i>Quercus</i> or <i>Castanopsis</i> sp. 1 (Fagaceae)	1	<i>Quercus</i> subgenus <i>Cyclobalanopsis</i>	Mainly subtropical and tropical	Evergreen
<i>Alnus</i> sp. (Betulaceae)	1	<i>Alnus</i>	Temperate to tropical or subtropical	Deciduous
<i>Mangifera</i> spp. 1, 2, and 3 (Anacardiaceae)	1	<i>Mangifera</i>	Subtropical to tropical	Evergreen
<i>Semecarpus</i> spp. 1 and 2 (Anacardiaceae)	1	<i>Semecarpus</i>	Tropical	Evergreen ( <i>S. cochinchinensis</i> )
<i>Canarium</i> sp. (Burseraceae)	1	<i>Canarium</i>	Tropical	Deciduous

<sup>1</sup>Abbreviations: c, cone; cw, charcoalified wood; l, leaf or leaflet; s, seed; t, twig

<sup>2</sup>Information from the following sources: Willis (1973), Larsen *et al.* (1984), Nielsen (1985), Farjon (1998), Page (1990), Fu *et al.* (1999), Huang *et al.* (1999), Li and Skvortsov (1999), Gardner *et al.* (2000), and Sawangchote (2003).

In the above list, we can see that some NLRs are tropical, such as *Archidendron*, *Antheroporum*, *Semecarpus*, and *Canarium*. Others are tropical to subtropical, such as *Glyptostrobus pensilis* and *Caesalpinia*. *Phyllanthus* and *Cyclosorus* range from tropical to temperate, and *Sequoia sempervirens* and *Sciadopitys verticillata* are temperate plants. The range of climates of the NLRs makes it difficult to determine the climate in Northern Thailand during the

early Miocene or late Oligocene. However, the climate was probably cooler than the tropical climate found today and was possibly subtropical with some temperate elements and tropical elements near the southern and northern edges of their ranges, respectively. Furthermore, the presence of some deciduous species suggests that the climate was seasonal, with an annual drier or cooler period.

The third approach for inferring past climates, the coexistence approach, could not be carried out in this study because the climatic parameters of most of the NLRs are unknown.

Forests may have included swamp forests with *Glyptostrobus* and more upland forests with *Sequoia*. The forests may have contained both evergreen and deciduous trees, with some trees reaching a great height and size. A very large coalified tree stump with a diameter greater than one meter and appearing to have been preserved *in situ* was observed at Banpu 1 lignite mine, Lamphun. This specimen shows affinity to Cupressaceae. The NLRs *Sequoia sempervirens* and *Taiwania cryptomerioides*, both in Cupressaceae, can reach heights of 110 and 75 meters, respectively (Fu *et al.* 1999).

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## **Curriculum Vitae**

Paul J. Grote was born in Ohio, USA, on 26 November, 1954. He graduated with a B.S. from Xavier University, USA, in 1977, majoring in Biology. Next he received a M.S. degree from the University of Cincinnati, USA, in 1979, majoring in Biological Sciences, and a Ph.D. degree from Indiana University, USA, in 1989, with a major in Biology and a minor in Geology. He has taught at Dhurakijpundit University from 1990-1991, at Rangsit University, 1991, and at Mahidol University, from 1991-1995. He is currently a lecturer, since 1995, in the School of Biology, Institute of Science, Suranaree University of Technology, Nakhon Ratchasima 30000. He has engaged in research on the systematics of Tephritid flies and on Tertiary plant fossils. He can be contacted at [paul@ccs.sut.ac.th](mailto:paul@ccs.sut.ac.th).