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Tertiary leaf fossils of *Semecarpus* (Anacardiaceae) from Li Basin, Northern Thailand

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ABSTRACT. Two leaf compressions preserved by pyritization were collected from the lacustrine deposits in Li basin, Northern Thailand which was considered to be Late Oligocene to Early Miocene. Besides features described in previous leaf architectural studies, a detailed study of marginal venation patterns of modern leaves was important in establishing the relationship between the fossil and the living species. After this analysis, they were assigned to *Semecarpus paleocurtisioides*. This fossil finding, together with the pattern of modern distribution, helps to propose a land on the west of Wallace's line as the possible origin of the genus. In addition, these leaf fossils and fossil leaves of the genus *Mangifera* previously described suggest that northern Thailand is an area with a long history of evolution and diversification of the family Anacardiaceae and these two genera.

KEY WORDS: Anacardiaceae, leaf fossil, Li basin, *Semecarpus*, Tertiary, Thailand.

INTRODUCTION

Our increased understanding of the origin, history and biogeography of the present-day distribution pattern of plants is partly contributed by paleobotany. The Anacardiaceae is known to the public as an economically important family for its fruits and seeds such as cashew nut (*Anacardium occidentale* L.), oriental cashew nut (*Semecarpus orientale* L.), mango (*Mangifera indica* L.), and pistachio (*Pistacia vera* L.). The family has received much attention, from paleobotanists, on the aspects mentioned above. The emergence of the family is suggested to extend back to the Cretaceous of Argentina and by the Paleogene they are found in southern England and Oregon (Raven & Axelrod, 1974).

Recently, the poorly understood phytogeographic and phylogenetic relationships of the Anacardiaceae were studied and the results support the idea of a Southeast Asian origin for the family (Martínez-Millán et al., 1999). Two dispersion routes were proposed to link the American taxa and Asian taxa, one via the Northern hemisphere: Southeast Asia – Europe – North America – South America, and the other via the Southern hemisphere: Southeast Asia – Africa – South America – North America (Martínez-Millán et al., 1999). American fossil taxa have received considerable attention concerning their taxonomic affinities, evolution, and phytogeography as documented by various authors (cited in Ramírez & Cevallos-Ferriz, 2002). The Asian taxa, on the other hand, have received less attention. Tertiary Asian anacardiaceous fossils so far reported were mostly from India and Nepal, with some from Japan and China. These tropical anacardiaceous fossils are mostly leaves, although some are wood, fruits, and seeds. Examples of anacardiaceous wood, which show similarity with wood of extant *Gluta* L., were reported by Mehrotra et al. (1999) and by Poole & Davies (2001) from India and Bangladesh, respectively. Konomatsu & Awasthi (1999) described a seed and a leaf impression of *Swintonia butwalensis* Griff. from the Middle-Upper Miocene of Nepal.

Tertiary fossil leaves of the tropical genera including *Bouea* Meisn, *Dracontomelon* Bl., *Gluta* L., *Lannea* A.Rich., *Mangifera* L., *Nothopegia* Bl., *Parishia* Hook.f., *Spondias* L., and *Swintonia* Griff.

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were reported from different ages and different localities of India and Nepal (Awasthi & Prasad, 1990; Awasthi & Srivastava, 1990; Bande & Srivastava, 1990; Bande, 1992; Antal & Awasthi, 1993; Awasthi & Mehrotra, 1995; Arya & Awasthi, 1996; Prasad & Awasthi, 1996; Mehrotra et al., 1998; Konomatsu & Awasthi, 1999). Fossil leaves of *Melanorrhoea* Wall. (= *Gluta*), *Pistacia* L., and *Rhus* Ding Hou were reported from Tertiary localities of China (Hu & Chaney, 1940; Li & Zheng, 1995; Liu & Zheng, 1995). Recently, Sawangchote et al. (2009) described two Tertiary *Mangifera* species including *Mangifera paleoindica* and *M. paleocaloneura*, from Li Basin, northern Thailand. Previous studies of Tertiary leaf fossils of Thailand (Endo, 1964, 1966; Grote, 2000; Grote et al., 2001; Sawangchote et al., 2009) and pollen (Ratanasthien, 1984; Meesuk, 1986; Watanasak, 1988, 1990; Songtham, 2000; Songtham et al., 2000, 2001, 2003), show no fossil species with affinities to *Semecarpus* L.f.. In addition, of all the taxa studied worldwide, no members of this genus have been validly described and reported.

The recent discovery of fossil leaves, potentially those of *Semecarpus*, in Thailand together with an understanding of the phylogenetic relationships of modern species in Thailand and all areas of modern distribution as a whole will be the essence of understanding the origin, the long history of establishment and diversification, and the biogeographical patterns of this genus. The purpose of this study was to taxonomically analyze potential *Semecarpus* leaf fossils from Thailand and to compare them with other recent and fossil leaves of Anacardiaceae and other families with similar leaf features using detailed leaf architecture analysis.

MATERIALS AND METHODS

The fossil material presented here comes from Li Basin located in Li District, Lamphun Province, Northern Thailand, at latitude 17º45′N and longitude 99º00′E. The basin is a smooth depression surrounded by Early and Middle Paleozoic rocks and late Paleozoic and Triassic rocks. The center of the depression is filled up with Quaternary sediments (Ginsburg et al., 1991). The basin is subdivided into 4 subbasins: Banpu, Ban Pa Kha, Ban Nasai, and Mae Long. By using mammalian fossils, the former two subbasins were determined to be Paleogene in age and the latter two are thought to be Neogene (Ginsburg et al., 1991). Ban Pa Kha Subbasin, from which the fossil leaves in this study were collected, covers an area of 8 km^2 and is located in the SE part of the Li Basin (Map. 1). The Tertiary sequence of this subbasin consists of 5 units including an overburden (20–150 m thick), an upper coal seam (10–15 m thick), an interburden layer (10–15 m thick), a lower coal seam (15–20 m thick), and an underburden (more than 30 m thick) (Uttamo, 1998). Fossil leaves, preserved by pyritization, were collected from an interburden layer (clay stone) which lies between upper and lower coal seams (Fig. 1).

Age determination of this basin has varied. From comparison of leaf fossils of Ban Pa Kha to those of Fushun in northeastern China, Endo (1964, 1966) considered this basin to be upper Eocene. However, the finding of *Sequoia langsdorfii* (Brongniart) Heer. from the Upper Eocene to the Pliocene (Mai & Walther, 1978), *Glyptostrobus europaeus* (Brongniart) Ung. during the Miocene of Europe (Kovar-Eder et al., 2001), and *Fagus feroniae* Ung. from the Miocene (Unger, 1847)

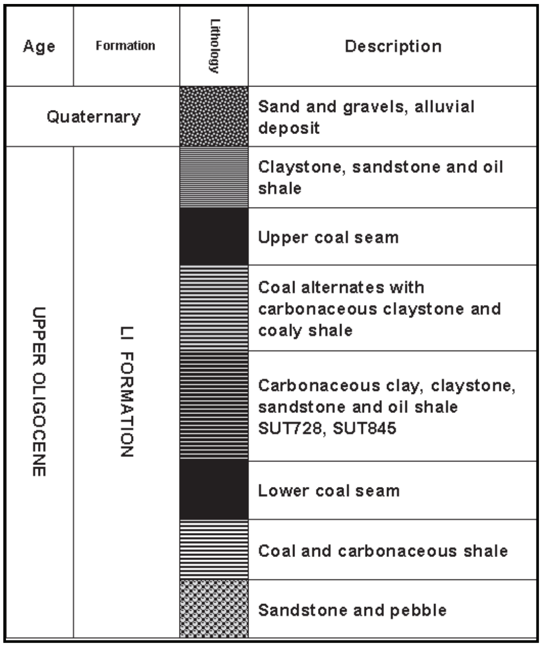
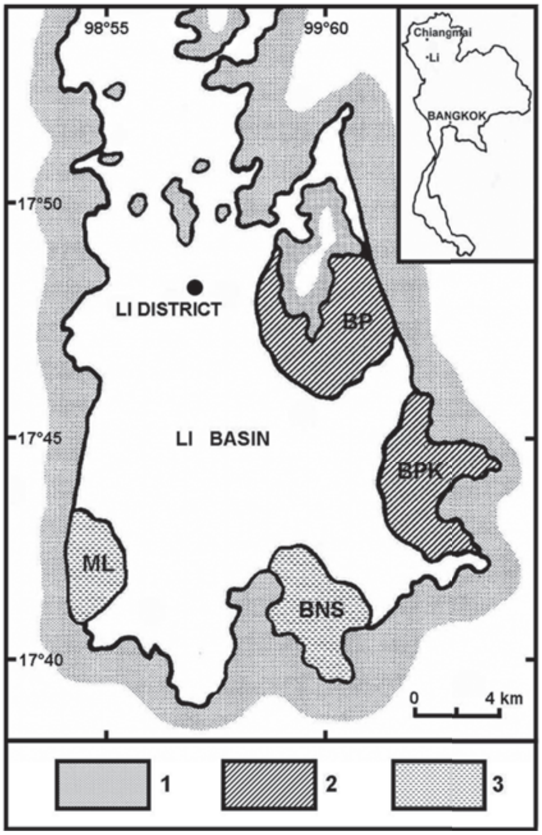


Figure 1. Cenozoic sequence of Ban Pa Kha subbasin. SUT728 and SUT845 were from clay stone of the middle layer which lies between upper and lower coal seam. Thickness of each layer is not to scale (Simplified from Uttamo, 1998).

casts doubt on the age interpretation of Ban Pa Kha by Endo. The age determination of the basin, from various evidences, ranges from Oligocene to Early Miocene. Based upon pollen at Banpu mine, Watanasak (1990) determined the age to be Late Oligocene to Early Miocene. Songtham et al. (2001) used pollen evidence at Ban Pa Kha mine to date this basin back to the Oligocene to Early Miocene. Based on rodent fossils, Na Sai Subbasin of Li Basin was determined to be Middle Miocene (Chaimanee, 1998). The climate under which the Li fossil flora flourished was determined to be warm temperate (Endo, 1964) or temperate (Songtham et al., 2001).

Morphological characters and venation patterns of the fossil leaves were described and compared with those of modern leaves by the application of methods described by Hickey (1973), Hickey & Wolfe (1975), Dilcher (1974), and the Leaf Architecture Working Group (1999). In addition to features of venation in marginal areas as presented in these publications, the terminology and classification of marginal venation patterns (MVP) developed by Sawangchote et al. (2009) were used as supplemental taxonomic tool (see Appendix).



Map 1. Geological map of Li Basin (redrawn and modified from Ginsburg et al., 1991) 1 = Pre-Tertiary rocks. 2 = Paleogene subbasins. 3 = Neogene subbasins. BP, BPK, BNS, and ML = Ban Pu, Ban Pa Kha, Ban Nasai, and Mae Long subbasin respectively.

The taxonomic assignments were made based upon the published literature, study of extant specimens from the Bangkok Forest Herbarium (**BKF**) and the Herbarium of Prince of Songkla University (**PSU**), and collection and observation of wild and cultivated plants. Leaves of all genera and species of Anacardiaceae and leaves of other families with similar leaf features (in the above herbaria and from online virtual herbaria) were examined. Leaves of 35 species with simple leaves from 8 genera (Table 1) of Anacardiaceae were cleared, stained with Safranin, mounted between two glass slides or sheets, and photographed using methods modified from Dilcher (1974). In species where 30 leaf specimens were available, an effort was made to include extremes of size and shape, as well as sun and shade leaves. Only part of larger leaves or leaves of uncommon species were used. In addition, photographs of the whole leaves of these species were taken using oblique lighting to enhance the view of venation patterns as a supplement to the cleared leaves. Cuticular preparations of the fossil leaf materials in order to study stomata and epidermal cells were not successful.

All fossil and living specimens in this study are deposited in the paleobotanical collections, Center for Scientific and Technologic Equipment, Suranaree University of Technology (SUT), Nakhon Ratchasima, Thailand.

RESULTS

Although these two fossils were identified as the same species, the authors prefer to describe and compare them to the living species separately to show detailed leaf analysis. This will aid future comparative study. The complete details of terms and classification of MVP are in Sawangchote et al. (2009). The short descriptions of terms are also presented here in the Appendix.

Systematic description

Division.— Magnoliophyta Cronquist, Takhtajan & W. Zimmermann

Table 1. Thirty five species with simple leaves from 8 genera (Table 1) of Anacardiaceae that were examined in this study.

Species	No. specimens (leaves)	Source of specimens	Occuring in Thailand[a]
Bouea macrophylla Griff.	30	FC[b], BKF[c]	Yes
B. oppositifolia (Roxb.) Meisn.	30	FC, BKF	Yes
Buchanania arborescens (Blume) Blume	30	FC, PSU[d]	Yes
B. lanzen Elm.	30	FC, SUT CLC[e]	Yes
B. sessifolia Blume	30	FC, BKF	Yes
B. siamensis Miq.	30	FC, SUT CLC	Yes
Drimycarpus luridus (Hk.f.) Hou	30	PSU	No
Gluta elegans (Wall.) Hook.f.	30	BKF, PSU	Yes
G. renghas L.	10	BKF	Yes
Mangifera caesia Jack	1	Florida[f]	No
M. caloneura Kurz	4	BKF	Yes
M. camptosperma Pierre	3	BKF	Yes
M. chamaoensis[g]	10	FC, BKF	Yes
M. collina Kosterm.	5	BKF	Yes
M. duperreana Pierre	30	FC, BKF	Yes
M. flava Evrard	30	FC, BKF	Yes
M. foetida Lour	30	FC, BKF	Yes
M. gedebe Miq.	10	BKF	Yes
M. griffithii Hook. f.	7	BKF	Yes
M. indica L.	30	FC	Yes
M. linearifolia (Mukh.) Kosterm.	30	FC, BKF	Yes
M. macrocarpa Bl.	30	FC	Yes
M. microphylla Griff. ex Hook.f.[h]	4	BKF	Yes
M. odorata Griff.	30	FC	Yes
M. pentandra Hook.f.	30	FC, BKF, PSU	Yes
M. quadrifida Jack var. *quadrifida*	4	BKF	Yes
M. sylvatica Roxb.	4	BKF	Yes
Melanochyla angustifolia Hook.f.	6	BKF	No
M. bracteata King	7	BKF	Yes
M. nitida Ridl.	5	BKF	No
Semecarpus sp.	6	PSU	Yes
S. cochinchinensis Engl.	5	BKF	Yes
S. curtisii King	30	FC, BKF	Yes
Swintonia floribunda Griff.	30	FC, PSU	Yes
S. schwenkii (Teijsm. & Binn.) Teijsm. Binn.	30	FC, BKF	Yes

[a] According to Chayamarit (1994)

[b] Field collection

[c] Forest Herbarium, Bangkok

[d] Herbarium of Prince of Songkla University

[e] Clearing leaves collection of Suranaree University of Technology

[f] Modern Leaf Reference Collection of the Paleobotany and Palynology Collections, Florida Museum of Natural History

[g] The epithet "*Chamaoensis*" was written on the herbarium sheet, but it is likely and unpublished name. The leaves are distinctive form leaves of the other species.

[h] A synonym of *M. griffithii* according to Chayamarit (1994)

Order.— Sapindales Dumortier

Family.— Anacardiaceae Lindl.

Genus.— *Semecarpus* L.f.

Species.— *Semecarpus paleocurtisioides* **sp. nov.** Sawangchote, Grote, and Dilcher

Number of specimens.— The material comprises two pyritized well-preserved leaf compressions.

Holotype.— Specimen number SUT845, paleobotanical collection, Center for Scientific and Technologic Equipment, Suranaree University of Technology, Thailand.

Paratype.— Specimen number SUT728, paleobotanical collection, Center for Scientific and Technologic Equipment, Suranaree University of Technology, Thailand.

Diagnosis.— Simple, oblanceolate (SUT845) or intermediate between narrowly oblong and narrowly elliptic (SUT728), approximately 2.2 by 11.7 cm; pinnate eucamptodromous; approximately 25–28 pairs of secondary veins; MVP intermediate between type I and II (SUT728) or intermediate between type II and III (SUT845), approximately 5–7 exmedial loop and/or multiangular shape (ELMAs); intersecondary veins frequent, simple to composite; tertiary veins percurrent/forked, alternate and opposite; quaternary and quinternary veins thick and orthogonal; areoles well developed, oriented, mostly quadrangular and pentagonal, small to medium in size (Figs. 2E–F, I–M; 3G–H, O–R).

Locality.—Li Basin, Ban Pa Kha mine, Li District, Lamphun Province, Northern Thailand, 17°45′N, 99°00′E, locality number 019.

Age.— Late Oligocene to Early Miocene.

Etymology.— The specific epithet refers to the sharing of features between the fossil and the extant *Semecarpus curtisii* King and *Semecarpus* sp.

Description.— SUT845. Leaf simple, symmetrical, oblanceolate; preserved lamina length 8.4 cm (estimated lamina length 11.7 cm), width 2.3 cm; apex missing; base cuneate; margin entire; texture probably coriaceous; petiole 1.0 cm, strongly inflated; venation pinnate, eucamptodromous; primary vein stout, markedly curved at basal 1/3; estimated number of secondary veins 28 pairs, 0.2–0.8 cm apart, mostly subopposite and alternate, thick, angles of divergence mostly moderate to widely acute (50°–76°) and some right angle (80°–88°) at about lower 1/6 in particular, slightly more acute for apical veins than for basal veins and more acute on one side than on the other secondary veins mostly straight most of the distance to margin and bending up sharply to join with the superadjacent secondary veins or some uniformly curved; MVP intermediate between type II and III, approximately 5–7 ELMAs, gradually (Fig. 2I) or rapidly (Fig. 2J) diminishing in size apically, quadrilateral and rectangular; Branching angle of tertiary veins (BATV) widely acute and right angle; intramarginal vein absent; intersecondary veins frequent, strong, simple to composite, proceeding 1/3–4/5 of the distance between midvein and leaf margin; tertiary veins percurrent/forked, predominantly alternate and close, oblique in relation to the midvein; tertiary vein angle of origin mostly right angle-right angle (RR) and acute angle-right angle (AR) (the combination of the angle of tertiary origin on the exmedial (lower) side of the secondary veins and that on the admedial (upper) side of the secondary veins) with predominantly widely acute angle (65°–80°), tertiary vein angle decreasing outward, ; quaternary and quinternary veins thick and orthogonal; highest vein order 7, highest vein order showing excurrent branching 6; marginal ultimate venation fimbriate; well developed areoles, oriented, mostly quadrangular and pentagonal, size small to medium (mostly 0.25–0.35 mm), freely ending veinlets (FEV) mostly simple or branched once, a few twice or three times (most of the higher vein order not observed due to preservation process) (Figs. 2E–F, I–M).

Affinities.— Seven species with oblanceolate leaves, namely *Buchanania sessifolia* Bl., *Drimycarpus luridus* (Hook.f.) Ding Hou, *Mangifera linearifolia* Kosterm., *Melanochyla angustifolia* Hook.f., *Semecarpus cochinchinensis* Engl., *Semecarpus curtisii* King, and *Semecarpus* sp. (all Anacardiaceae), were compared to this fossil leaf (Figs. 2A–D). Oblanceolate leaves rarely occur among *Mangifera* species but are rather common among species of *Melanochyla* and *Semecarpus*. Of fifteen *Mangifera* species described from Malaysia (Kochummen, 1989), oblanceolate leaves are only rarely found in *Mangifera quadrifida* Jack with a lower l/w ratio than this fossil leaf and than *M. linearifolia* in this study. For *Semecarpus* sp., in addition to similarity in leaf shape, the venation patterns are almost the same as in *S. curtisii*. Therefore, these two specimens, based on these features, can possibly be considered the same when comparing them with the fossil. On consideration of leaf shape analysis (reflected mainly by l/w ratio), type of MVP, and number and course of secondary veins, *B. sessifolia*, *D. luridus*, and *S. cochinchinensis* were excluded. The rest of the species have leaves that are more similar in shape (l/w ratio up to 4 or greater) and number of secondary veins to *S. paleocurtisioides*. The course of the secondary veins, that is, mostly straight most of the distance to margin and bending up sharply, seems to be shared equally among *M. angustifolia*, *S. curtisii*, *Semecarpus* sp., and *S. paleocurtisioides* (Figs. 2B–F). *M. angustifolia* and *S. paleocurtisioides* have the same intermediate MVP type II and type III, whereas *S. curtisii* and *M. linearifolia* have type III (Figs. 2G–I). *Semecarpus curtisii* and *Semecarpus* sp. show close affinity to *S. paleocurtisioides* not only because they have overlapping type of MVP but also they exhibit similarity in features of the areoles which are mostly well developed, oriented, predominantly quadrangular to pentagonal, and medium in size. FEV of *S. curtisii* and *Semecarpus* sp. mostly branched 3 times while those of *S. paleocurtisioides* are predominantly simple or branched once or sometimes twice or thrice. This feature of the FEV in *S. paleocurtisioides* may be the result of the process of fossilization in which not all the branches of the FEV were preserved. The reticulation patterns of *S. curtisii* and *Semecarpus* sp. are the most similar to those of *S. paleocurtisioides*. On the contrary, *M. angustifolia* has a similar MVP type to that of *S. paleocurtisioides*, but the former has some different characters of areoles, such as being mostly larger in size (1–2 mm), FEV mostly branched once or simple and curved, some with no veinlets, quinternary veins and FEV mostly thin, and some quaternary veins thin (Fig. 2G). Together, these different characters make reticulation of veins as a whole look clearly looser than those of *M. linearifolia*, *S. curtisii*, *Semecarpus* sp., and *S. paleocurtisioides* (Figs. 2H–I). In addition to the size and density of areoles, the relatively weak and infrequent intersecondary veins of *M. angustifolia* are also a major difference between *S. paleocurtisioides* and *M. angustifolia*. When comparing marginal venation of this fossil leaf and *S. curtisii*, it is evident that they share the features of veinlets that join between the curving-up secondary veins and fimbrial veins at the margin. These veinlets are thick and have a relatively straight course.

Semecarpus paleocurtisioides also shares some similarities in marginal venation with *M. linearifolia* in that they possess overlapping of MVP type III. Moreover, *M. linearifolia* and *S. paleocurtisioides* share the following features: size (lower limit of the size range of *M. linearifolia* is the closest to that of *S. paleocurtisioides*), a lanceolate leaf (Fig. 2A), number and angle of divergence of secondary veins, number and characters of intersecondary veins, and presence of several small intersecondary veins that run parallel to main intersecondary veins. There are some differences of features of secondary veins between the fossil and *M. linearifolia*, however. Apical secondary veins are more acute than basal in *S. paleocurtisioides* but vice versa in *M. linearifolia*, especially those veins at the base which are perpendicular to the primary in *S. paleocurtisioides* but moderately acute in *M. linearifolia*. The angle of divergence being more acute on one side than on the other was more clearly seen in *M. linearifolia* than in *S. paleocurtisioides*, and some are even a right angle in *S. paleocurtisioides*, a character not found in *M. linearifolia*. The secondary veins are mostly uniformly curved in *M. linearifolia* but mostly straight most of the distance to the margin and bending up sharply to join with the superadjacent secondary veins in *S. paleocurtisioides* (*S. paleocurtisioides* shares this character more with *S. curtisii* and *M. angustifolia*). Furthermore, the areoles of *M. linearifolia* are less developed, larger in size on average, and relatively more irregular in shape.

Given these similarities and differences, the genus *Semecarpus* is selected as a living relative over *Mangifera* and *Melanochyla*. Furthermore, the common features between *S. paleocurtisioides* and *S. curtisii* (also *Semecarpus* sp.) are in such a significant degree that the authors propose to name it *Semecarpus paleocurtisioides*.

Description.— SUT728. Leaf simple, symmetrical, shape intermediate between narrowly oblong and narrowly elliptic; preserved lamina length 10.8 cm (estimated lamina length 11.2 cm), width 2.2 cm; apex acuminate; base acute cuneate;

petiole missing; margin entire; texture probably coriaceous; venation pinnate, eucamptodromous; primary vein stout, markedly curved; estimated number of secondary veins 25 pairs, 0.3–0.6 cm apart, opposite, subopposite, and alternate, thick, angle of divergence narrowly to widely acute (35°–71°), those of apical veins more acute than those of basal veins and more acute on one side than on the other, mostly straight most of the distance to margin and bending up sharply near leaf margin, although some uniformly curved; MVP intermediate between type I and II, approximately 5–7 obvious ELMAs, gradually diminishing in size apically, quadrilateral and rectangular; BATV widely acute and right angle; intramarginal vein absent; intersecondary veins frequent, strong, simple to composite, proceeding 1/6–2/3 of the distance between midvein and leaf margin; tertiary veins percurrent/forked, alternate and opposite, close, oblique in relation to the midvein; tertiary vein angles of origin RR, right angle-acute angle (RA), or acute angle-acute angle (AA), with predominantly widely acute angles (70°–80°); tertiary vein angles decreasing outward; quaternary and quinternary veins thick and orthogonal; highest vein order 7, highest vein order showing excurrent branching 6; marginal ultimate venation not completely seen but presumably strongly fimbriate; areoles well developed, oriented, mostly quadrangular and pentagonal, size medium (mostly 0.3–0.5 mm), FEV branched up to 3 times (Figs. 2G–H, O–R).

Affinities.— This fossil leaf also shows a venation pattern that is very similar to that of SUT845. The differences between these two fossil leaves are leaf shape and type of MVP. SUT728 possesses MVP intermediate type I and II, but *S. paleocurtisioides* has MVP intermediate type II and III (Figs. 2I–K, 3O–P). The difference in leaf shape is not as significant in separating these two fossil leaves because leaf shape may be only common variation found among leaves of any individual species (leaves in Fig. 2D and 3F are from the same specimen). Although the type of MVP as examined so far in this study (also in previous study on *Mangifera* fossil leaves by Sawangchote et al. (2009)) is rather constant in the same leaf or in the same species, we think there may be more variation than we have seen in limited specimens of fossil and living species (see Table 1 and discussion in Sawangchote et al. (2009)). These two fossil leaves were, therefore, determined to have the same affinities.

The leaves of five modern species of Anacardiaceae, *Bouea oppositifolia* (Roxb.) Meisn., *Gluta elegans* (Wall.) Hook.f., *Mangifera indica* L., *Semecarpus cochinchinensis* Engl., and *Semecarpus* sp., were compared with this fossil leaf (Figs. 3B–F). In addition, one species of Sapindaceae, *Nephelium lappaceum* L., is shown as an example of a leaf that has a similar leaf shape but a different venation pattern (Figs. 3A, I). Although weak sigmoid-curved primary veins and general leaf shape were shared between these modern leaves and the fossil, some different features are crucial in discrimination of some of these modern leaves from the fossil. The leaf base of *N. lappaceum* is not cuneate as in the fossil, and it is asymmetric. Although it shares a eucamptodromous type of venation, it does not possess intersecondary veins. In addition, tertiary veins are more percurrent/simple and areoles paxillate, quadrangular, with no veinlets or with simple veinlets. *B. oppositifolia* and *G. elegans* have narrowly to widely elliptic leaf, smaller numbers of secondary veins, and less developed areoles. *Semecarpus cochinchinensis* shows less resemblance in leaf shape than the other species, has a venation pattern in common with the fossil, but clearly has a smaller number and different course of secondary veins. *M. indica* and *Semecarpus* sp., when compared with the species mentioned above, share more features. *M. indica*, with leaves having a sigmoid-curved primary vein, could have been considered the closest/nearest living relative (NLR) of this fossil if the base were cuneate, instead of normal acute. To use this character to distinguish *M. indica* from the fossil, hundreds of leaves of *M. indica* were examined, and a long cuneate base, as present in *S. cochinchinensis*, *Semecarpus* sp., and in this fossil, was never observed. Moreover, the range of variation in angle of divergence of secondary veins in most leaves of *M. indica* (51°–61°) is narrower than that of *Semecarpus* sp. (43°–69°) and of the fossil (35°–71°). In spite of the incompleteness of the marginal venation in the fossil, the MVP can be determined to be type I and II (Figs. 3O–P), which is similar to that of *S. cochinchinensis* (type I) and *Semecarpus* sp. (intermediate type I and II). In conclusion, the

Figure abbreviations: BKF = Bangkok Forest Herbarium; MVP = marginal venation pattern; PMArC = partial column of marginal areoles; PSU = Herbarium of Prince of Songkla University; S1 and S2 = secondary vein, secondary vein 1 and secondary vein 2 respectively; (Details for classification and terminology of marginal vein patterns are in Sawangchote et al. (2009) and short description of terms are in appendix).

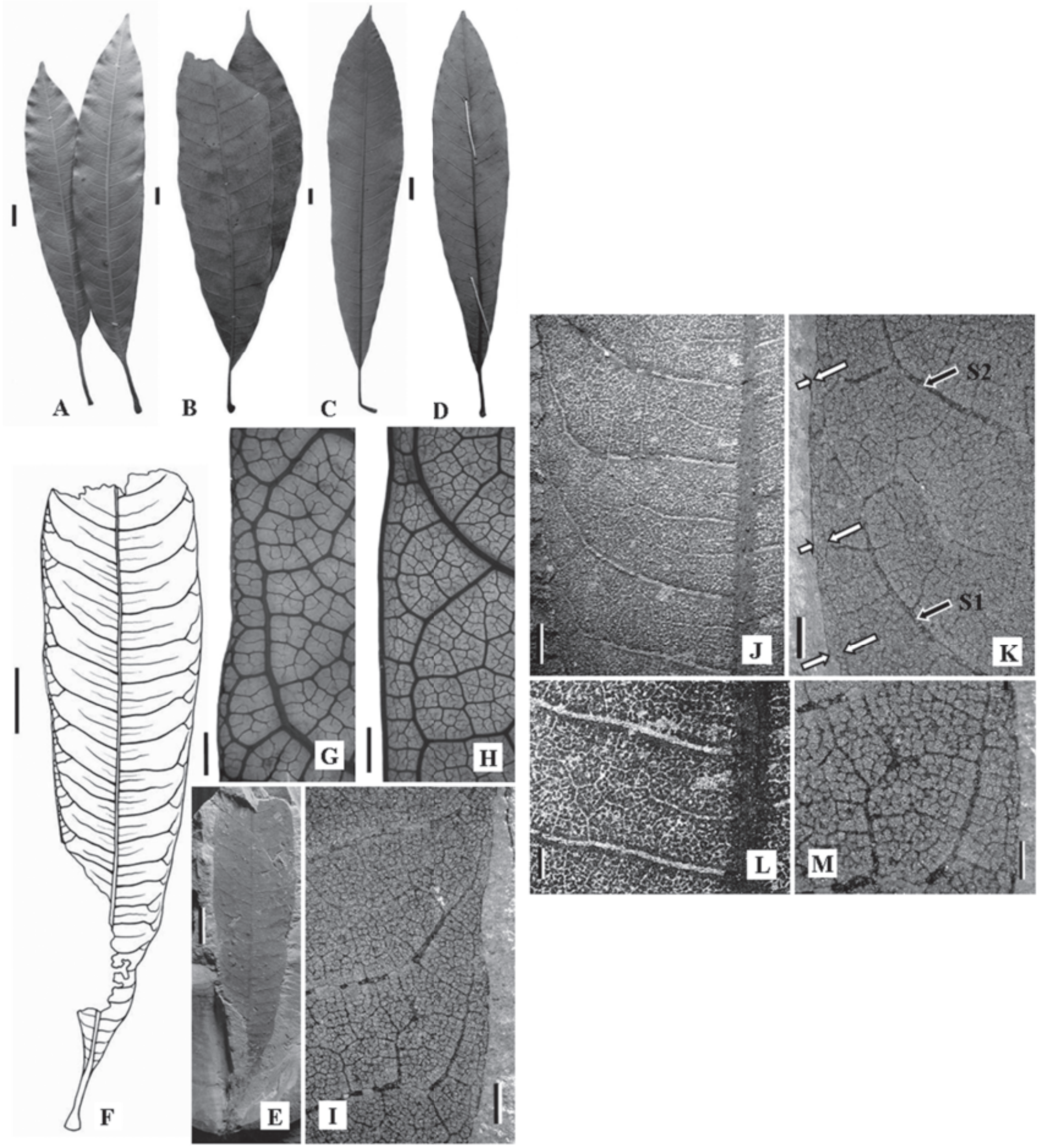


Figure 2. *Semecarpus paleocurtisioides* (SUT845) and possible NLRs. (A–D) leaves of *Mangifera linearifolia* (BKF SN 002938), *Melanochyla angustifolia* (BKF SN 092806), *Semecarpus curtisii* (field-collected), and *Semecarpus* sp. (PSU SN180478), respectively, that are similar to *S. paleomangiferoides* in (E). (F) Line drawing of the fossil. (G–H) Part of the cleared leaf of *Melanochyla angustifolia* and *Semecarpus curtisii*, respectively (*M. linearilfolia* is not shown but *Semecarpus* sp. is shown in Fig. 4F). (I) MVP of the fossil showing gradually diminishing in size of ELMAs. (J) In contrast to MVP shown in (I), ELMAs in this marginal portion of the fossil show relatively rapid diminishing in size of ELMAs (similar to those of *M. linearifolia* in Fig. 3N). (K) Magnified portion of MVP showing PMArC (area between each of two adjacent arrows) that lie along the outer border of ELMAs; the most lower and most upper two arrows are at the level of the first and of the last ELMA of S1 respectively. Note that the last ELMA and the one below it have the outer borders fused with the fimbrial vein at the leaf margin. The last ELMA is located at the same level as the first ELMA of S2. (L) Intersecondary veins and orientation of tertiary veins of the fossil. (M) Magnified portion in (I) showing areoles and MArC that are more clearly seen than in (K). Scale bar = 1 cm in A–F, 2 mm in G–H, J, 1 mm in I, K–L, T, 0.5 mm in M.

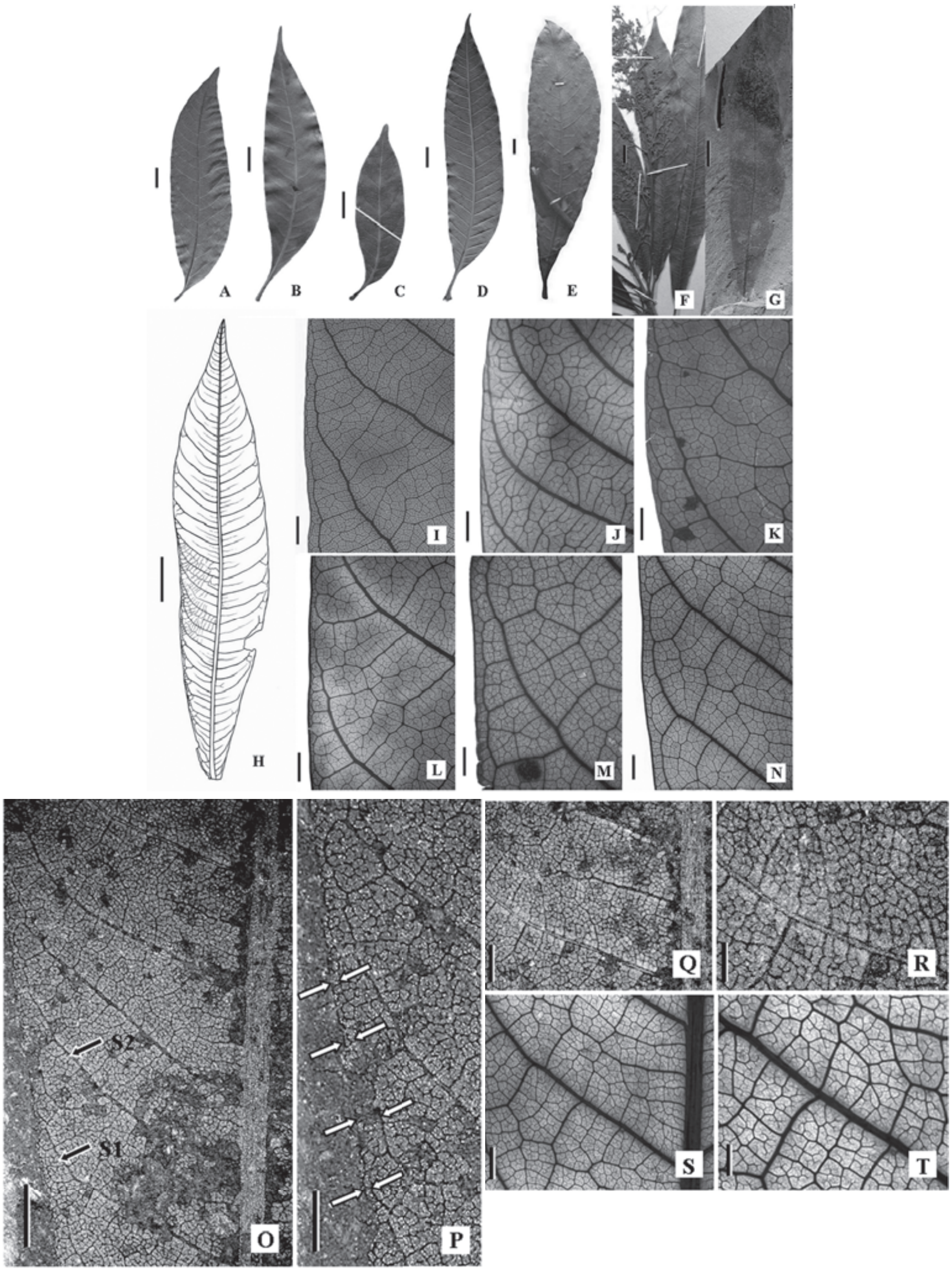


Figure 3. *Semecarpus paleocurtisioides* (SUT728) and its possible NLRs. (A–D), (F) Leaves with slightly sigmoid primary vein of *Nephelium lappaceum* (field-collected), *Bouea oppositifolia* (field-collected), *Gluta elegans* (PSU SN 180438), *Mangifera indica* (field-collected), *Semecarpus cochinchinensis* (BKF SN 118520) and *Semecarpus* sp. (PSU SN180478), respectively, that are more or less similar to *Semecarpus paleosiamensis* shown in (G). (H) Line drawing of the fossil. (E) *Semecarpus cochinchinensis* (BKF SN 118520) was brought into comparison on the basis of similarity of MVP. (I–N) Part of the cleared leaf of each species in (A–F), respectively. (O) MVP of the fossil. (P) Magnified portion in (O) showing MArC (area between heads of two adjacent arrows) that lie along the outer border of ELMAs; most lower two arrows are at the level of the last ELMA of S1 in (O) and the pair of arrows above these are at the level of the first ELMA of S2 in (O). (Q), (S), comparison of intersecondary veins and orientation of tertiary veins of the fossil and *Semecarpus* sp., respectively. (R), (T) Comparison of areoles of the fossil and *Semecarpus* sp., respectively. Scale bar = 1 cm in A–H, 2 mm in I–O, S, 1 mm in P–Q, T, 0.5 mm in R.

fossil leaf shares more features with the genus *Semecarpus* and with *Semecarpus* sp. (which has the same venation pattern with *S. curtisii*) in particular. The name *S. paleocurtisioides* is thus proposed for this fossil as for SUT845.

Despite our intensive examination of the fossil leaves and other simple leaved plants (Table 1) we are aware that a degree of caution about the identity of the fossils must still be exercised as workers have found that whilst leaf architecture of the Anacardiaceae may be useful as a taxonomic tool at generic level it is useful for most genera only at specific level. As the Anacardiaceae has 80 genera we have been unable to compare the majority of the genera with our fossil and as there are a very large number of species with similar leaf morphology in gross terms in other families, all of which we have not examined, it is possible, though we believe unlikely, that the fossil material is not a member of the Anacardiaceae nor of the genus *Semecarpus*.

DISCUSSION

Taxonomy of the genus *Semecarpus* and recent distribution of some species related to the fossils

Semecarpus is a tropical genus and is one of approximately 70 genera (Ding Hou, 1978a; Kochummen, 1989) of the family Anacardiaceae, comprising about 60, 63 or 70 species (Ding Hou, 1978a; Kochummen, 1989; Sosef et al., 1998 respectively) chiefly found in Indo-Malesia. Its complete range spans from India, Ceylon, Burma, Thailand, Indochina, Formosa, through Malesia, to Australia, Micronesia, the Solomon Islands, New Caledonia, and Fiji (Ding Hou, 1978a). According to Smitinand (2001) there are four species in Thailand, *S. albescens* Kurz, *S. cochinchinensis*, *S. curtisii*, and *S. reticulata* Lecomte. *S. albescens* has been reported from the northeastern (Loei Province), the central and the southern part of Thailand (Yala Province) (Smitinand, 2001; Veesommai & Kavduengtain, 2004). However, *S. albescens* is in reality conspecific with *Holigarna kurzii* King. Taxonomically the genus *Semecarpus* can be differentiated from the genus *Holigarna* by the following contrasting characters: unisexual versus polygamous plants, imbricate versus valvate petals, superior versus inferior ovaries, and leaves without versus with appendages at bases of petioles (Chayamarit, 1994). *Semecarpus cochinchinensis* is distributed in deciduous forests particularly on limestone hills throughout the country, *S. curtisii* occurs in both deciduous and evergreen forests of the Peninsular region and *S. reticulata* grows in evergreen forests of the North and the Southwest (Chayamarit, 1994). The distribution range of *Semecarpus curtisii* does not extend to northern Thailand where the fossils were discovered. Also, *Semecarpus* sp. (PSU SN 180478) was collected from Phuket Province. If the fossils are really *S. curtisii*, they indicate that the species has become locally extinct from the North and has more limited range or *S. curtisii* may have been in existence in the North but never been reported. If they are not *S. curtisii*, they indicate two possibilities; the first, it has become globally extinct and has no living counterparts or locally extinct and become restricted in distribution range and may exist somewhere within the modern range of distribution which we cannot thoroughly examine; the second, the living counterpart may have evolved from the fossil species (with variation in venation patterns) and exist somewhere within the modern range of the genus. Ding Hou (1978a) stated that the *Semecarpus* is a very difficult genus in which to study taxonomy due to a high degree of geographically influenced variation in morphology in several species. Therefore, this can be a problem in studying fossils as well. Out of approximately 70 species of the genus *Semecarpus*, a fraction of these members were examined due to lack of cleared leaf database to access. To yield valid interpretation of the history of evolution (i.e. the relationship of the fossils and the living species) intensive data from spatial and temporal study of fossils and living species and others aspects as discussed in the next section are needed.

The origin and migration routes of the genus *Semecarpus*

Hollick (1936) reported two species of *Semecarpus*, *S. alaskana* Hollick and *S. prindlei* Hollick, based on fossil leaves from the Tertiary of Alaska. However, Wolfe (1969) redetermined *S. alaskana* to be *Melanorrhoea* (= *Gluta*) sp. Subsequently, Ding Hou (1978b) concluded that the marginal leaf venation of this fossil species was similar to that of *Semecarpus*, *Melanorrhoea* (= *Gluta*), and *Melanochyla* and that it could hardly be determined to any one genus, if it did belong to Anacardiaceae. The leaf shapes and venation patterns in general of *S. alaskana* are clearly different from those of *S. paleocurtisioides*. The leaf shape of *S. alaskana* is broadly elliptic whereas that of *S. paleocurtisioides* is oblanceolate (l:w ratio approximately 1.35 and 5 respectively). The number of secondary viens is larger in *S. paleocurtisioides* than in *S. alaskana* (25–28 versus 19–20). The spaces between secondary veins of *S. alaskana* is strongly uneven compared wtih those of *S. paleocurtisioides*. Moreover, intersecondary veins in *S. paleocurtisiodes* are very strong but absent in *S. alaskana*. Other features smaller than tertiary veins were not described by Hollick (1936) and are not visible in the picture in his publication. The fossil *Semecarpus* proposed in this paper are thus most likely the first fossil evidence to be recorded within the modern range of the genus.

Discussion of origin and migration routes ideally needs data of various types including the spatial and temporal scales of paleophytogeography, paleogeography, and paleoclimatology, complete taxonomic revision of the genus, phylogenetic study of all the species within the genus, and plant and animal relationships, etc.

The degree of endemism of the *Semecarpus* species might indicate, to some extent, the dispersal paths. From the map of density and endemism of *Semecarpus* species in Ding Hou (1978a), New Guinea is the only island to the east of Wallace's line that has the highest degree of endemism (9 endemic species from 11 species). In contrast, on the west of Wallace's line the degree of endemism seems to be lower. Endemic species are present in the Peninsular Malaysia (2 from 6), Borneo (3 from 7), and the Philippines (6 from 9). Thailand probably possesses no endemic species. However, when indigenous genera and species density of Anacardiaceae were considered, the richest endemic development is in the Peninsular Malaysia and Borneo (Fig. 1 and 2. in Ding Hou, 1978a). This suggests that the origin and/or long history of evolution of the genus *Semecarpus* should be on the west of Wallace's line and migration across the line to the east might have occurred later. Based on the fossil evidence of *S. paleocurtisioides* and the possible dispersal routes discussed above and on two species of the fossil *Mangifera* reported from the same basin (Sawangchote et al. 2009), northern Thailand is one of the areas with long history of evolution and diversification of the family Anacardiaceae and of these two genera. Some biological processes influenced by plate tectonics and climate changes could have shaped the modern distribution pattern. These include speciation, extinction, vanishing, and flourishing (in term of both species number and population size) in the place of origin and the places of new establishment. However, without complete studies on the aspects mentioned at the beginning of this topic, a complete picture of migration cannot be obtained.

Paleovegetation and paleoclimate at the Ban Pa Kha subbasin

The leaf fossils in this study, those from previous studies (Endo, 1964, 1966; Grote, 2000; Grote, 2004; Grote et al., 2001; Grote & Sawangchote, 2003) together with pollen studies (Songtham et al., 2001, 2003) of the Ban Pa Kha subbasin indicated that this assemblage may represent mixed forests of deciduous-evergreen broadleaf angiosperms and conifers of tropical to warm temperate climates. The conifers comprised *Sequoia* Endl., *Glyptostrobus* Endl., *Sciadopitys* Siebold & Zucc., and the form genus *Podocarpoxylon* Gothan (Grote, 2000; Grote & Sawangchote, 2003). The form genus *Podocarpoxylon*, with affinity to Podocarpaceae, identified from charcoalified wood, probably indicate forest fires occurred in the dried lignite-forming swamp (Grote et al., 2001). In addition to the *Semecarpus* (Anacardiaceae) in this study, angiosperm leaves so far identified in preliminary studies belong to the families Annonaceae, Betulaceae, Fagaceae, Lauraceae, Leguminosae, etc. Among these, legumes seem to be the most dominant element of the flora. Fragments of fern fronds also occur (Grote, 2004; Grote & Sawangchote, 2003). About the same epoch, the vegetation cover of the southern Yunnan Province, located close to the north of Thailand, was also tropical and subtropical (Axelrod et al., 1996). Concerning this, Songtham et al. (2003) proposed that an increase of tropical palynological assemblages during the Oligocene to Early or Middle Miocene resulted from changing the position from a temperate latitude to a tropical latitude by the moving southward or southeastward of the Southeast Asian landmass.

CONCLUSIONS

Our evidence suggests that *Semecarpus paleocurtisioides* probably grew in northern Thailand during the Late Oligocene to Early Miocene, and, most likely, our material represents the first fossil evidence to be recorded within the modern range of the genus. From analysis of the modern geographical range of the genus, the fossil suggests that the origin and/or long history of evolution of the genus *Semecarpus* should be on the west of Wallace's line and migration across the line to the east might have occurred later. In addition, *Semecarpus paleocurtisioides* in this study and the previously described *Mangifera paleoindica* and *M. paleocaloneura* suggest that northern Thailand is an area with a long history of evolution and diversification of the family Anacardiaceae in general and these two genera in particular.

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APPENDIX. Terminology of marginal vein patterns (MVP). Full descriptions and classification of MVP are available in Sawangchote et al. (2009).

1. *Marginal venation pattern (MVP)* — The venation pattern of marginal areas of any leaf that comprises repeated sets of two definable areas, namely, 1) exmedial loops and/or multiangular shapes (ELMA), and 2) marginal ultimate venation. In any type of marginal ultimate venation, areoles can be present on the outer borders of ELMAs and will be called marginal areoles (MAr, details mentioned below).

2. *Exmedial loop and/or multiangular shape (ELMA) of secondary veins* — An area of leaf tissue of different shapes formed by two adjacent secondary veins and tertiary veins (cross veins according to Dilcher, 1974) lying between them. These ELMAs are located on the exmedial side of each secondary vein. They may be composed of a single areole to several areoles. Each ELMA is surrounded by four borders: upper, lower, outer and inner. The upper and lower borders are formed by tertiary veins while the outer and inner ones are formed by adjacent secondary veins. Small ELMAs, which comprise a single areole, located at the upper part of the column of ELMAs have the same features as an areole, but are still considered to be ELMAs whenever they have the features mentioned above, especially being located on the exmedial side of a secondary vein.

By this definition, ELMAs can be clearly seen in leaves with pinnate eucamptodromous (Dilcher, 1974) or weakly brochidodromous (Leaf Architecture Working Group, 1999) types of venation.

3. *Number of ELMAs* — Counting starts at the first ELMA formed by the first tertiary vein branching from the exmedial side of the secondary vein without coalescing with the others until the last tertiary vein located at the same level as the tertiary vein forming the first ELMA of the super-adjacent secondary vein. In the case of leaves in which most of the tertiary veins are percurrent/simple, it is rather hard to determine the first ELMA because of the similarity of the tertiary vein presumed to be the lower border of the first ELMA and the others that lie below it. However, the first ELMA can be determined by observing the first notch on the adjacent secondary vein at which the lower and outer borders of this first ELMA meet. By this counting system, there will be sets of ELMAs equal to the number of secondary veins, and these sets of ELMAs can be a useful guideline for comparison of marginal venation patterns.

4. *Branching angle of tertiary veins (BATV)* — The angle measured above the point of branching of tertiary veins from secondary veins, between the admedial side of these tertiary veins and exmedial side of the secondary vein from which they branch. The categories of these angles follow those of the angles of divergence of the secondary veins as described in Dilcher (1974).

5. *Shape of ELMAs* — The shape of ELMAs will be determined, in part, the way the shape of areoles are determined (Dilcher, 1974). In addition, special shapes may occur and the descriptions will be up to the authors' consideration.

6. *Marginal areoles (MArs)* — Areoles located along the outermost areas of the leaf margin or lying next to ELMAs toward the leaf margin. These may be formed by recurved marginal ultimate venation and identified as looped marginal ultimate venation according to Dilcher (1974). When the higher order veins are fused to form a fimbrial vein, these areoles will have this vein as their outermost borders. In some cases, where the ELMAs are rather small, lie close to the margin, and look the same as marginal areoles, they are still identified as ELMAs by holding the rule that these ELMAs are located on the exmedial side of secondary veins.

7. *Column of marginal areoles (MArC)* — This term is used to describe a column of two or more MArs that lie along the outer borders of ELMAs. In some instances, in which ELMAs diminish in size apically and their outer borders lie close to the leaf margin, such mentioned column will be identified as absent. The number of columns may be one or more, and the columns can be complete (CMArC) or partial (PMArC) marginal areole columns.