

## AN INTRODUCTION TO THE SANTALACEAE R. BR. OF THAILAND

JILL MACKLIN\* & JOHN PARNELL\*

**ABSTRACT.** This paper presents an introduction to the Santalaceae, a family of hemiparasitic plants, in Thailand. It outlines the characteristics which unite the family in S.E. Asia and provides some detail on those characters which can be used to distinguish the genera in Thailand. A key to the genera is provided, which employs a combination of vegetative and reproductive characters. The paper is concluded with a short discussion on the distribution of the genera within Thailand, which includes reference to their ecology and habitats.

### INTRODUCTION

The family Santalaceae is contained within the Order Santalales. The five families which represent this group are united on the basis that they exhibit at least some degree of hemi-parasitism. The Santalaceae, with 540 species in 34 genera, (Mabberley, 1997) holds a relatively advanced position within the Order and is thought to be closely related to the Viscaceae. Recent molecular evidence suggests that the family is paraphyletic with respect to the Eremolepidaceae (Nickrent, 1999), a small South American family of branch parasites. Although the Santalaceae has a cosmopolitan distribution, it probably originated on the Gondwanic landmass, because its representation in the northern hemisphere is limited to a small number of species (Barlow, 1983).

The family derives its name from the Sanskrit word *shandal* which was attributed to the Sandalwood tree (*Santalum album* L.), a native of Eastern Java and the Timor Islands (Uphof, 1959). It is thought that this species has been cultivated throughout S.E. Asia since pre Christian times, ca. 2000 years ago. The wood has a high commercial value and is used in the perfumery and pharmaceutical industries (Lewington, 1990).

The species exhibit a variety of growth forms from small trees, shrubs and climbers to inconspicuous herbs. The basic characteristics which unite the family are the flowers that are small, actinomorphic and usually fairly inconspicuous. The perianth is commonly pale green or yellow in colour and is undifferentiated into calyx and corolla. The tepals number from three to six and may be valvate or lightly imbricate, inserted in a single whorl on a fleshy receptacle. The stamens are equal in number and opposite each tepal. There is usually a tuft of glandular hairs behind each anther, which emanates from the tepal base. The nectarial disc, which lines the receptacle,

---

\*Department of Botany, Trinity College, Dublin 2, Ireland.

may be brightly coloured and produces copious amounts of nectar; this is one of the most distinctive features of the Santalaceous flower. The fruit is a 1-seeded nut or drupe, the fleshy parts being provided by the receptacle, fused bracts or petiole.

In S.E. Asia the Santalaceae is fairly well represented by 51 species in nine genera. There have been no recent revisions of the Santalaceae for the region. The last major work involving the S.E. Asian species was the tribal revision of Anthoboleae by Stauffer which covered Australian species (Stauffer, 1959). Stauffer also investigated the classifications within the family and established tribe Amphorogyneae, which includes all of the branch parasitic genera of S.E. Asia (Stauffer, 1969). The latest revisions of the family for the countries surrounding Thailand were completed at the beginning of the 20th century for Indochina and the Malay Peninsula (Lecomte, 1915; Ridley, 1924). However, the classification systems which were utilised are out of date and many of the descriptions are vague and inadequate.

Under the current system the family is segregated into four tribes based on the morphology and position of the ovary, fruit structure and growth habit (Pilger, 1935; Stauffer, 1969). The tribal classification is not always clear-cut and this, together with recent molecular evidence, suggests the need for an entire familial revision. As a full revision of the family is beyond the scope of current work the traditional tribal groupings have been adhered to. In S.E. Asia (including Thailand, Laos, Cambodia, Vietnam and the countries which make up the phytogeographical region of Malesia) all of the tribes are represented. Two of these, Anthoboleae and Thesieae, are represented by single species, which are elements of larger genera with much wider distributions and are simply limited expansions of the Australian and African groups respectively. There are just three genera of the tribe Osyrideae present in the region: *Osyris* L., *Santalum* L. and *Scleropyrum* Arn. Of those *Scleropyrum* is the only genus restricted to S.E. Asia.

There is one monophyletic group within S.E. Asia. This group, contained within the tribe Amphorogyneae, represents the majority of the species in the region. In total 43 species in four genera are contained within this group. All of the species are lianas or dendro-parasites. The word dendro-parasite is here used to describe species with the same growth habit as the mistletoes of the Loranthaceae and Viscaceae. S.E. Asia is home to the only group of Santalean dendro-parasites. Initially these genera were contained within a single genus *Henslowia* Blume (1850). However, in the mid-20th century, *Henslowia* was split into four segregate genera: *Dendromyza* Danser, *Cladomyza* Danser, *Dufrenoya* Chatin and *Dendrotrophe* Miq. by Danser based on fruit morphology (Danser, 1940). Danser considered that the fruits were sufficiently dissimilar to warrant the division. He also reasoned that if he did not separate the species, he would have to include the leafless hyperparasitic genus *Phacellaria* Benth. within *Henslowia*, because the fruits of *Phacellaria* are identical to some of the other dendro-parasitic species. Controversy has existed over the validity of the segregation of the *Henslowia*-complex and some of the generic boundaries will be changed under the current revision.

Like their close relatives, the Viscaceae, the Santalean dendro-parasites have developed novel methods of dispersal and seedling establishment. In the fruits of the Viscaceae the mesocarp consists of a viscous substance, which enables the seed to adhere

to a host plant to ensure establishment of a young seedling. In species of Santalaceae with a similar growth habit a different method of establishment has evolved, which achieves the same result. In the fruits of these species the mesocarp consists of an indument of sericeous or membranous strands attached to, and often wrapped around, the endocarp. When wet the mesocarp is slippery so that the seed may slip down branches and find a suitable position on a host plant (Kuijt, 1969). As it dries, however, the mesocarp becomes sticky thus enabling the seed to become anchored to the surface of the branch.

Under one quarter of the S.E. Asian species of Santalaceae and over two thirds of genera are found in Thailand. The seven genera recorded in the country represent a relatively heterogeneous assemblage of just 13 species. The fact that there are few species in relation to the number of genera may be related to the connection of Thailand to the rest of Asia. Some genera have just a single representative with broader distributions in Asia and Africa. Although *Santalum* is not native to Thailand, *Santalum album* L. is a cultivated and economically important species and has, therefore, been included in the list of species for Thailand.

### CHARACTERS OF TAXONOMIC IMPORTANCE

Within the S.E. Asian taxa there are several disparate groups and the characteristics which have been used to define them are often variable. In terms of generic boundaries in Thailand at least five of the genera are easily identifiable and can be simply distinguished using a combination of vegetative and floral characteristics (Table 1). However, the genera within tribe Amphorogyneae, are not so easily distinguishable and many of the characteristics used elsewhere in the Santalaceae are not applicable to the species in this group. These characters are used rather in infra-generic classification.

#### Habit

The growth habit of the species is variable and their ecology can be of significant importance at the tribal and to a certain extent generic level. Tribe Osyrideae contains the arborescent and shrubby genera, whilst tribe Thesieae is represented by one small herbaceous species. In Thailand tribe Amphorogyneae contains three genera which are all climbing or branch parasites. Within this group the genus *Dendrotrophe* contains species, which are very variable in their growth habit and at least one of the species can be terrestrial, climbing or dendro-parasitic. The other two genera, *Dufrenoya* and *Phacellaria*, are very closely related and may be united into a single genus. Both genera are aerial parasites with shrubby and climbing growth forms and display a degree of host specificity. *Phacellaria* may also possess the capability for some endophytic growth and has been observed to emerge through lenticels along the branches of a host plant.

#### Stems and branches

Branching is dichotomous although, characteristically amongst the aerial parasites, several branches may arise from a single thickened node. Within the majority of the species the juvenile branches are constricted and bracteate at the base and the nodes appear

articulated or jointed, although this articulation is usually confined to the Amphorogyneae. A typical feature of all the genera is the flattening of juvenile branches towards the apex. This may provide a wider area for photosynthetic activity, particularly as many of the species are only sparsely leafy. These flattened stems are usually longitudinally grooved. Older branches can be distinctly different to the young growth. They are generally terete, smooth or with longitudinal fissures which are usually a different colour to the outer bark. *Scleropyrum* is the only genus whose trunk and branches are armed with spines which may be several centimetres long and are a distinctive characteristic of the genus.

### Leaves

The leaves are generally spirally arranged or may be alternate and rarely opposite. They are usually fleshy, always with entire margins, elliptical to orbicular and may be mucronate at the apex. In *Thesium* the leaves are reduced to phylloclades, whilst in tribe Osyrideae the leaves are generally larger with pinnate venation. In tribe Amphorogyneae there is considerable variation in leaf size. Some species have leaves of similar size to *Scleropyrum* and *Santalum*, whilst for the majority of the species they are much smaller and in extreme cases, bract-like. In the leafless genus *Phacellaria*, photosynthetic activity is carried out by the stems and minute bracts. Within the rest of the Amphorogyneae leaf venation is curvipalmate with 3–11 primary veins. In some species the leaf is greatly thickened and the veins can become obscured. However, 3–5 primary veins are usual.

The presence of an indument on the leaves or stems is generally of little diagnostic value as all of the Santalaceae are primarily glabrous. In Thailand the genus *Scleropyrum* has an indument of simple trichomes on its leaves, inflorescences and young stems. Previously, the density of this indument has been used to delimit the species within this genus. However, on careful examination, the quantity of indument appears to be continuously variable throughout the species. In *Phacellaria* the species generally have a dense, hirsute indument on the young shoots, which may be caducous, so that the older branches appear papillate.

### Inflorescence structure

Inflorescences are spirally or alternately arranged at leafless nodes or in leaf axils and may be cauliflorous. In general, inflorescence structure is highly variable at the generic level. The most common type of inflorescence construction is a raceme (*Dendrotrophe*, *Scleropyrum*) or spike. The raceme may be erect or pendulous with a distinct catkin-like appearance (*Scleropyrum*). The basic racemose scheme varies to form umbellate (*Dufrenoya*) or sessile (*Phacellaria*) structures. The inflorescence is reduced to a single flower in the female inflorescence of *Dufrenoya* and *Dendrotrophe*. Within the umbellate inflorescence the individual flower may be pedicellate or sessile and within the sessile inflorescences of *Phacellaria* the flowers may be sunken into the stem. The situation can become more complicated in species of *Dufrenoya*, where the individual umbels are spirally arranged on a leafless side shoot forming a compound umbellate raceme. Tribe Amphorogyneae shows the most variability within the racemose scheme and will be discussed in greater detail in a future paper.

The other genera, *Santalum* and *Osyris*, exhibit a different inflorescence construction as the branching pattern within these genera is cymose i.e. with no central rachis. The branching pattern within *Osyris* is a compact version of that found in *Santalum*.

### Bracts

Bracts are confined to the inflorescence and the bases of young shoots. They are usually deltoid or ovate in shape, lanceolate in *Osyris*. The outer surface of the bracts is usually glabrous, tomentose in *Scleropyrum* and densely hirsute in *Phacellaria*. Bracts are generally fleshy but may be membranous in *Dendrotrophe*, or papyraceous in some species of *Dufrenoya*, where they are a partially diagnostic character. Bract margins are entire with the exception of *Dufrenoya*, where they are ciliate to a greater or lesser degree. The bracts of the female inflorescence of *Dendrotrophe*, *Dufrenoya*, and *Phacellaria* form an involucre under the flower, which may be persistent after flowering, although they are usually caducous in species of *Dendrotrophe*. In *Phacellaria* the bracts are generally persistent but occasionally withering.

### Floral characteristics

Flowers may be hermaphrodite or dioecious, with staminodes or pistillodes in the female or male flower which can be quite substantial. The perianth is undifferentiated and each perianth segment within the flower is termed a tepal. There are three to six tepals and the arrangement of the androecium and gynoecium is stable. The individual tepals are usually sepal-like and are green or pale yellow. In the majority of species the perianth and nectary change colour after flowering and become dark red or purple. The tepals are attached to the receptacle, which is concave or flat on the male plants and elongated in the hermaphrodite and female flowers. There is usually a group of glandular hairs behind each stamen, which is absent in *Phacellaria* and occasionally in species of *Dufrenoya*.

The anthers have two thecae, each of which is bilocular. The shape of the anthers and their mode of dehiscence has previously been used to group genera or species (Pilger, 1935) as follows:

Anthers 4 - locular, locules distinctly parallel, dehiscence longitudinal: *Santalum*, *Osyris*, *Scleropyrum*

Anthers 4 - locular, locules divergent, dehiscence transversal: *Dufrenoya*, *Dendrotrophe*, *Phacellaria*

However the situation is more variable than originally believed. In *Santalum*, *Osyris*, and *Scleropyrum* the anthers are parallel. In *Scleropyrum* the thecae are separated at the top of the filament and in *Osyris* the locules are unequal in size.

Within tribe Amphorogyneae the shape and mode of dehiscence of the anthers is generally characteristic, and can be used to group species within genera as well as in conjunction with other characters in the diagnosis of species. Within this group the anther locules may be equal or unequal in size in a single plane or with anterior and posterior locules. The locules may also be placed horizontally or longitudinally to the filament. Anther dehiscence is transversal or longitudinal.

### Pollen morphology

Within the Santalaceae the pollen structure is highly variable and can be a diagnostic feature. In the species from Thailand pollen grain size and sculpturing patterns of the ectexine or outer surface of the pollen grain can be useful diagnostic characters at the generic level and, occasionally, at the species level. Within tribe Osyrideae (*Santalum*, *Scleropyrum*, *Osyris*) the pollen grains are generally large, between 19–24  $\mu\text{m}$  in polar length. The exine sculpturing is microperforate or rugulate in *Scleropyrum* and perforate in species of *Osyris*. *Santalum* is unique in that the pollen grains of *S. album* are verrucate (wart-like) in the region of the intercolpium. Typically the genera in tribe Amphorogyneae (*Dendrotrophe*, *Dufrenoya*, *Phacellaria*) have smaller pollen grains, 11–16  $\mu\text{m}$  in polar length. Exine ornamentation is highly variable within this tribe as a whole, but is most useful at the specific rather than the generic level. In Thailand, the species of *Dendrotrophe* and *Phacellaria* have either rugulate or microperforate pollen grains. However, in *Dufrenoya* the pollen can be either rugulate or echinate. There are also differences in polar length between the species, which can be used in combination with sculpturing patterns to differentiate between the species. Pollen morphology within the dendroparasitic species will be discussed in greater detail in a future paper.

### Ovary position and topography

The position of the ovary is very variable within the family as a whole but stable at the tribal level. It is inferior in tribes Amphorogyneae and Thesieae, semi-inferior in tribe Osyrideae and superior in tribe Anthoboleae. The shape and position of the placenta can also be an important taxonomic character. Within tribe Amphorogyneae the ovary is 4–6-locular. Placentation is free central, the placenta is slightly convex and may extend into the base of the style; the placental column is straight and may be broad or narrow. In tribe Osyrideae the morphology of the ovary is variable at the generic level. The ovary is 3–5-locular and the apex of the placenta may extend into the base of the stylar canal. In *Scleropyrum* the ovary is 3-locular, the placental lobes are long and convoluted, curling under the placenta; the placental column is long and convoluted. In *Thesium* the ovary is 4-locular, the placenta is short and the placental column is long and tortuous. In both *Osyris* and *Santalum* the placental column is very short, the placenta is convex, 3-locular and almost sessile in *Osyris*, sagittate and 4-lobed in *Santalum*.

### Fruit morphology

The fruit is an indehiscent nut or drupe, usually crowned by a persistent perigone. In *Santalum* and *Osyris* the fruits are globose and almost identical. The main difference between the two is in fruit size and there are also slight differences in the endocarp. The fruits of *Scleropyrum* are pyriform and its species show variation in endocarp surface. *Thesium* is the only genus in this area where the fruit is a nut and the main attractant for dispersal may be an eliasome on the pedicel. The greatest diversification in fruit morphology exists in the Amphorogyneae, where fruit characteristics are used to delimit the genera. The differences in the morphology of the fruits of these genera will be discussed in a future paper.

## KEY TO THE GENERA

- 1. Herb to 50 cm. Leaves reduced to cladodes **Thesium**
- 1. Tree, shrub, liana or dendroparasite
  - 2. Small tree, 7–10 m high
    - 3. Trunk usually armed with spines, 1–3 cm in length. Leaves alternate. Inflorescence pendulous, tomentose. Fruit pyriform **Scleropyrum**
    - 3. Trunk unarmed. Leaves opposite. Inflorescence glabrous, erect. Fruit globose **Santalum**
  - 2. Shrub 1–2 m high, liana or dendroparasite
    - 4. Liana or shrub with pendulous branches or straggling growth habit
      - 5. Leaf venation pinnate. Male inflorescences cymose. Fruits globose; endocarp smooth **Osyris**
      - 5. Leaf venation curvi-palmate with 3–5 primary veins. Inflorescences racemose. Fruits globose, elliptical; endocarp rugulate, tuberculate **Dendrotrophe**
    - 4. Dendroparasite, with climbing or shrubby growth habit
      - 6. Leafless hemiparasite on Loranthaceae and Viscaceae. Inflorescences sessile, covering entire surface of the branches **Phacellaria**
      - 6. Shrubby or climbing dendroparasite usually found in association with Fagaceae. Male inflorescences umbellate **Dufrenoya**

## DISTRIBUTION PATTERNS

Within Thailand the genera exhibit distinctive distribution patterns, which follow ecological and climatic boundaries. Several of the species are restricted to the northern montane regions of the country, whilst others are found only in southern areas below the Isthmus of Kra, which is the traditional phytogeographical boundary between the Malesian and Thai floras (van Steenis, 1950). Only *Scleropyrum pentandrum* (Dennst.) Mabb. has a widespread distribution in Thailand and is found in a variety of habitats, such as open areas, forest clearings and stream margins, suggesting an affinity with disturbed habitats. *Scleropyrum* has a very broad distribution from Southern China and India to New Guinea and is represented in Thailand by just two species. *Scleropyrum pentandrum* is the most widespread species in the genus and occurs over its entire geographical range (Map 3).

The genera restricted to the northern regions of Thailand are *Osyris*, *Thesium*, *Dufrenoya* and *Phacellaria*. Both *Osyris* and *Thesium* are each represented by a single species which are elements of the African flora that has extended in to the northern part of S.E. Asia. These genera are found above 1000 m in open grassy places and *Osyris*, at least, is usually found in association with bamboo, which again indicates a preference for disturbed places (Map 2). Climatic conditions may be responsible for the distribution patterns of these species as above this altitude there is high precipitation and a degree of unseasonality, in contrast to lower lying areas which have a distinctive monsoonal climate.

The other genus found in the northern areas of Thailand is *Dufrenoya*, which is represented by four species, one of which, *D. robusta* Stauffer, is endemic to Thailand. All species of this genus are dendroparasitic and are always found in association with Fagaceae genera such as *Castanopsis*, *Lithocarpus*, and *Quercus*. These three genera, together with *Pinus*, form the distinctive vegetation type often referred to as hill evergreen or temperate evergreen forest. They are found at elevations above 1000 m and resemble (at least superficially) temperate forests (Rundel and Boonpragob, 1995).

This type of forest is most widespread in the montane, northern regions of Thailand, particularly Chiang Mai and Loei provinces. *Dufrenoya* contains 12 species with a distribution from southern India and China to western Borneo. The fact that the Thai species follow the same distribution pattern as the hill evergreen forests, and are not found in southern Thailand, indicates that they are intimately associated with this habitat. In Thailand they form a fairly homogeneous group of species except for *D. robusta* which shows greater similarities to the southern Chinese and Indochinese species. *Phacellaria* may also be placed within this group, because it essentially occupies the same habitat as *Dufrenoya*. Species of this genus are highly evolved in terms of parasitism, being leafless and exhibiting a degree of endoparasitic growth. They are also hyperparasites on species of Loranthaceae and Viscaceae. *Phacellaria* is extremely close to *Dufrenoya* in terms of fruit structure and it may be that the generic boundaries will be modified (Map 1).

In peninsular Thailand there are relatively few species of Santalaceae. Apart from the two species of *Scleropyrum* there is just one other genus represented here. This probably reflects the different climatic conditions in this region, which approach those of Indochina and western Malesia. *Dendrotrophe* is perhaps the most widespread Santalaceous genus in S.E. Asia, occurring from southern China to Australia. The species in this genus also exhibit a variety of growth habits, from small shrubs to climbers and dendro-parasites. In Thailand there are two species, which are always terrestrial but often climbing. In Indochina and Malesia these species are occasionally recorded as aerial parasites and this may be correct or they may be secondarily branch-parasites. In Thailand *Dendrotrophe* is restricted to southern provinces, at lower elevations than *Dufrenoya* and *Phacellaria* and characteristically occupies areas from sea level to approximately 150 m (Map 4). *D. buxifolia* (Blume) Miq. is recorded in areas with waterlogged soil and in Thailand is found at the edges of peat swamps. *Dufrenoya varians* is the most widespread species of the genus. In Thailand it occupies similar habitats to *Scleropyrum* i.e. disturbed vegetation or forest margins. However, it has a more restricted distribution than *S. pentandrum*, which again may be due to a combination of climate and terrain.

## CONCLUSIONS

The species of Santalaceae in Thailand occupy a large number of habitats and exhibit a wide variety of life forms. The family is not always easily identifiable due to reduction in reproductive characters and the inconspicuous nature of the flowers. However, once the family has been identified the genera are easily distinguished using a combination of vegetative and reproductive characteristics. Growth habit is a distinctive generic characteristic and is also particularly useful at the tribal level. The species are generally associated with particular habitats and in particular the dendroparasitic genera *Dufrenoya* and *Phacellaria* are found in association with specific plant communities. There is a general distinction between the species are found in the north and south of the country. There are a greater number of species in the north of Thailand and several of these are representatives of wider Asian distributions. In the south the species are generally confined to lower elevations and show a greater affinity with the Indochinese

and western Malesian species. The distribution patterns may be a reflection of environment and elevation. However, there are many areas which are undercollected and, therefore, the current patterns may not reflect true distributions.

The number of collections of *Dufrenoya* and *Phacellaria* are quite low in Thailand. Both of these genera are dendroparasites and the low number of records is probably a reflection of their growth habit. It is a common feature of plant collecting in S.E. Asia in general that it has concentrated on the tree species as they are the generally better known elements of the flora and are relatively easy to access. In contrast, species in the canopy are often inaccessible and consequently overlooked. As collections increase and new areas are explored it is probable that more species will be discovered. In particular the mountainous regions along the Myanmar and Laos borders should yield new records and possibly new species.

### ACKNOWLEDGEMENTS

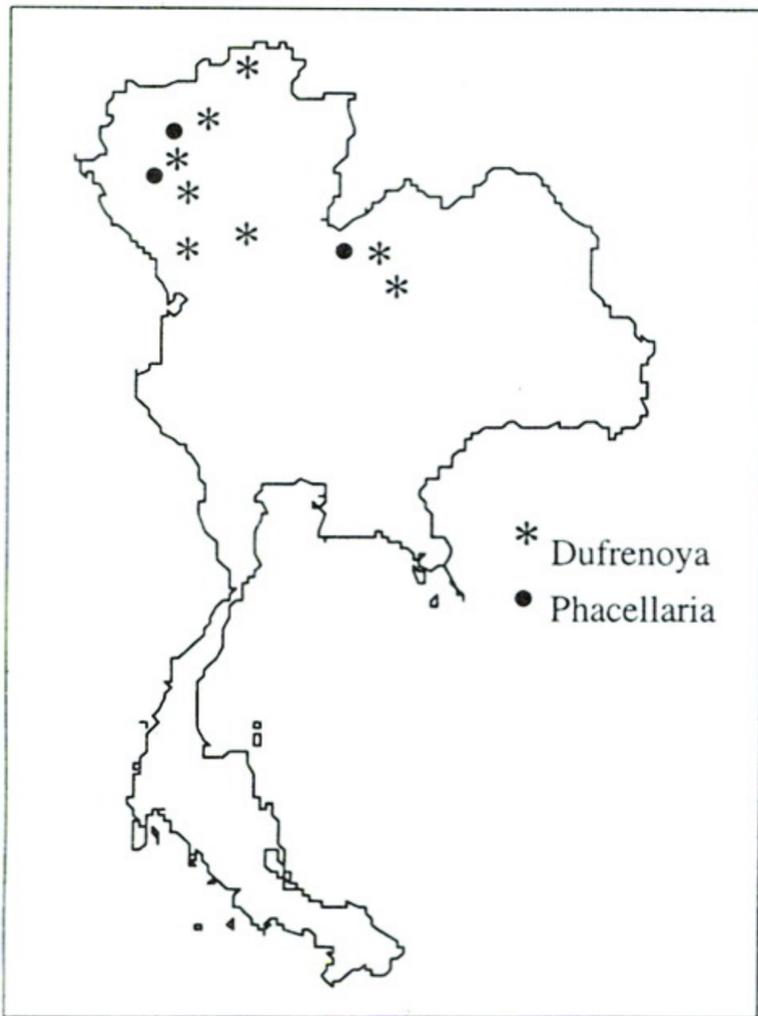
We would sincerely like to thank David Simpson for all of his help and encouragement in the preparation this manuscript. Sincere thanks also to Marcella Campbell, Conor Meade and Pam Opie for (amongst many other things) their helpful suggestions, patience and encouragement over the last few years.

**Table 1.** Comparison of generic characteristics of Santalaceae in Thailand

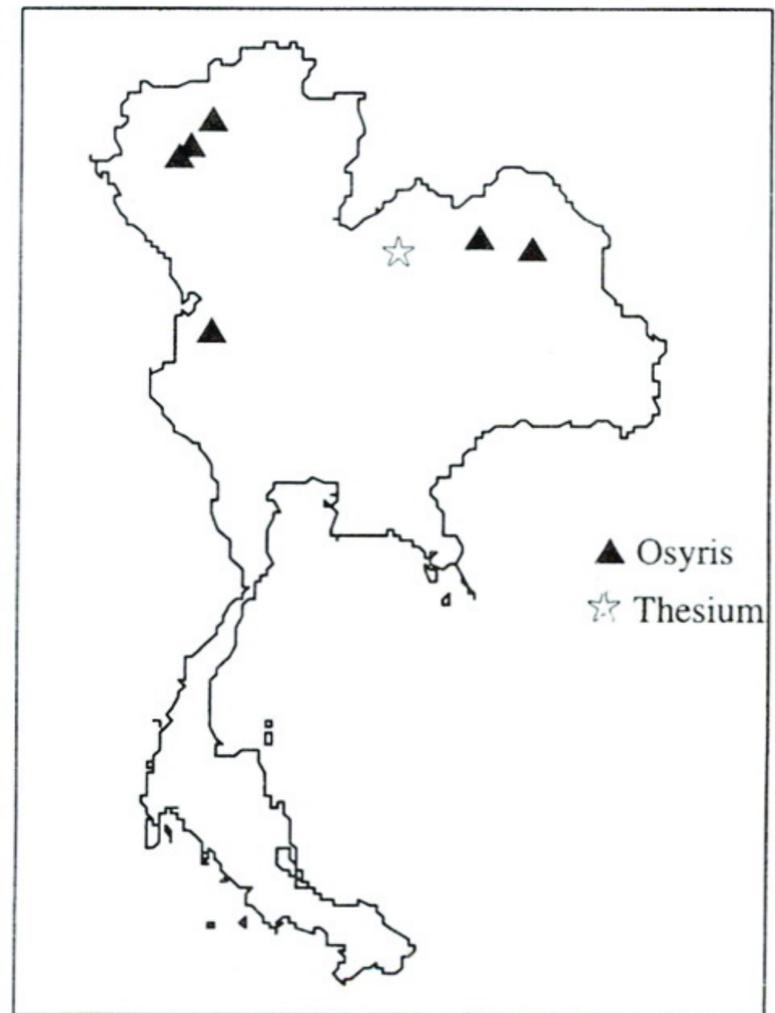
Genus	Habit	Inflorescence branching	Sexual dimorphism	Anther dehiscence	Ovary locule number	Fruit shape	Mesocarp
<i>Santalum</i>	Tree	Cymose	Hermaphrodite	Longitudinal	Four	Globose	Carnosus
<i>Scleropyrum</i>	Tree	Racemose (Catkin)	Dioecious	Longitudinal	Three	Pyriform	Carnosus
<i>Osyris</i>	Shrub	Cymose	Dioecious	Longitudinal	Three	Globose	Carnosus
<i>Dendrotrophe</i>	Shrub/climber	Racemose	Hermaphrodite	Transversal	Four / Five	Globose / Elliptical	Carnosus
<i>Dufrenoya</i>	Dendroparasite	Umbellate	Dioecious	Longitudinal/ Transversal	Five / Six	Oblong / Ovoidal	Membranous
<i>Phacellaria</i>	Dendroparasite	Sessile	Monoecious / Dioecious	Transversal	Four / Six	Oblong	Carnosus
<i>Thesium</i>	Herb	1-flowered	Hermaphrodite	Longitudinal	Three	Globose	Absent

## REFERENCES

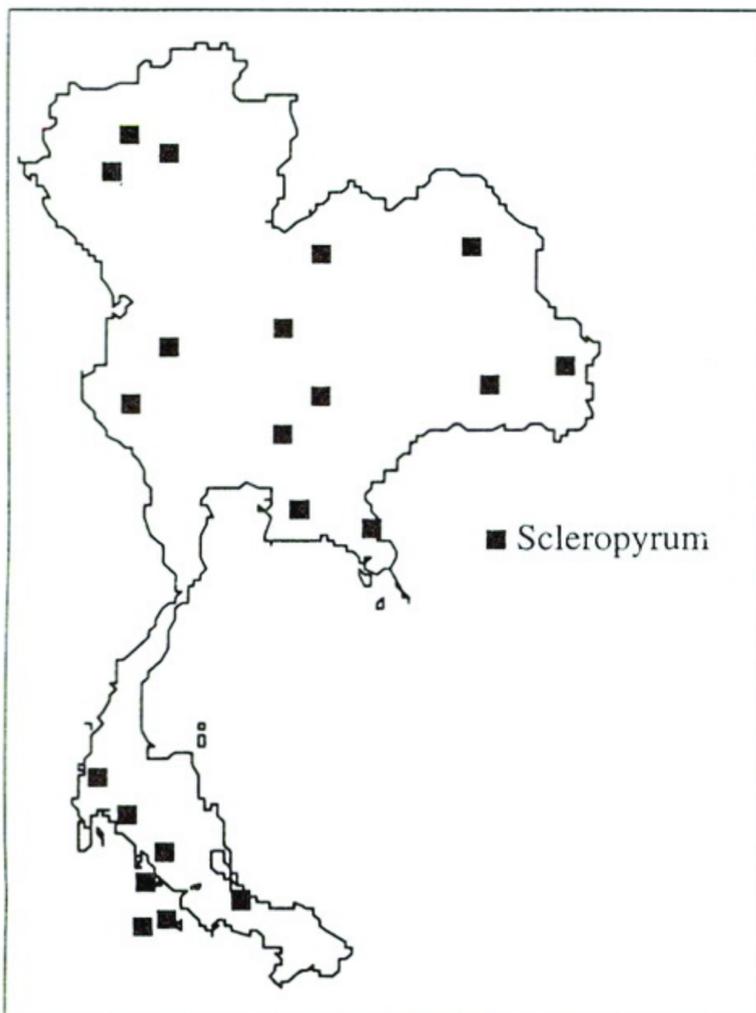
- Barlow, B. 1983. Biogeography of Loranthaceae and Viscaceae. In: Calder, D.M. (ed.), *The biology of mistletoes*. Academic Press, Australia.
- Blume, C.L. 1850. Santalaceae. *Mus. Bot. Lugd.-Bat.* 1: 242–244.
- Danser, B.H. 1940. On some genera of Santalaceae Osyrideae from the Malay Archipelago. *Nova Guinea, New Ser.* 4: 133–150.
- Kuijt, J. 1969. *The biology of parasitic flowering plants*. University of California Press, Berkeley.
- Lecomte, H. 1915. Santalaceae. In: Lecomte, H. (ed.), *Flore Générale de l'Indo-Chine* 5: 211–221. Masson et Cie, Paris.
- Lewington, A. 1990. *Plants for people*. Natural History Museum, London.
- Mabberley, D.J. 1997. *The plant book*, 2nd. ed. Cambridge University Press, Cambridge.
- Nickrent, D. 1999. *The Parasitic Plant Connection*. Internet: <http://www.science.siu.edu/parasitic-plants/index.html>.
- Pilger, R. 1935. Santalaceae. In: Engler A. & Prantl, H.A.V. (eds), *Die Natürlichen Pflanzen Familien*. 2nd ed., 16b: 52–91.
- Ridley, H.N. 1924. *Flora of the Malay Peninsula* 3: 166–171. Reeve & Co. Ltd., London.
- Rundel, P.W. & Boonpragob, K. 1995. Dry forest ecosystems of Thailand. In: Bullock, S., Mooney, H. & Medina, E. (eds), *Seasonally dry tropical forest*. Cambridge University Press, Cambridge.
- Stauffer, H.U. 1959. Santalales-Studien IV. Revisio Anthobolearum. *Mitt. Bot. Mus. Univ. Zurich* 213: 1–160.
- Stauffer, H.U. 1969. Amphorogyneae, eine neue Tribus der Santalaceae. *Vierteljahrsschr. Naturforsch. Gesellsch. Zurich* 114: 49–76.
- Steenis, C.G.G.J. van. 1950. The delimitation of Malaysia and its main plant geographical divisions. In: van Steenis, C.G.G.J. (ed.), *Flora Malesiana* 1: 70–75.
- Uphof, J.C.T. 1959. *Dictionary of Economic Plants*. Engelmann (J. Cramer), New York.



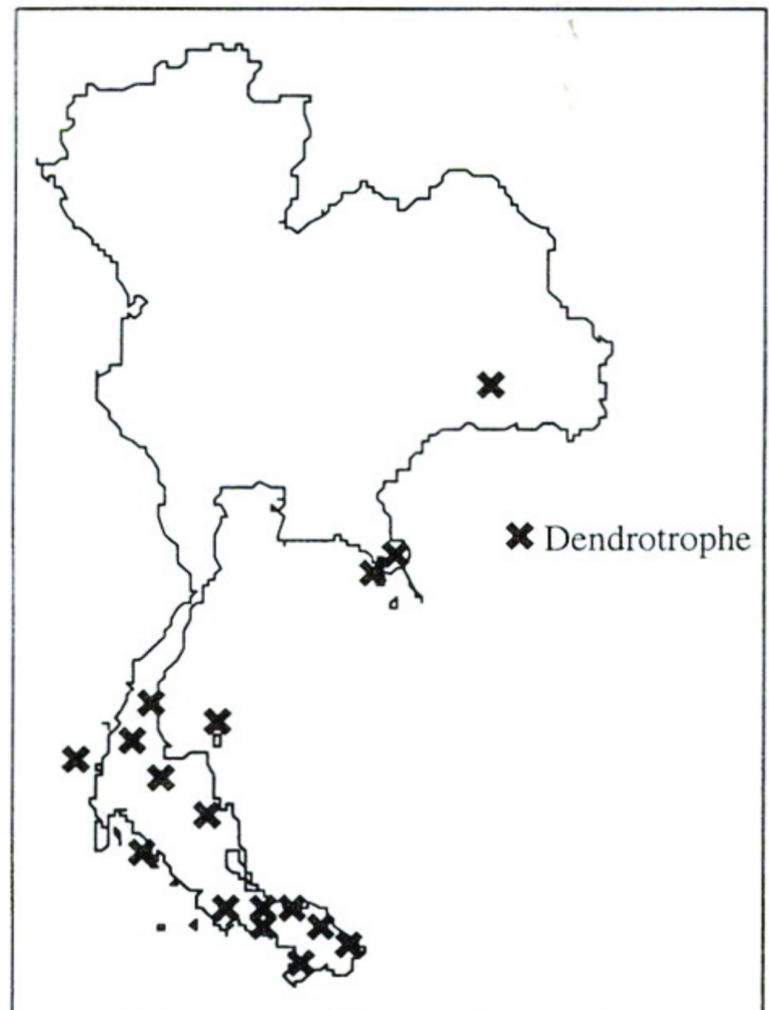
Map 1. Distribution of *Dufrenoya* and *Phacellaria* in Thailand, both are restricted to northern montane regions.



Map 2. Distribution of *Osyris* and *Thesium* in Thailand. These genera occur above 1000 m in open, grassy habitats.



Map 3. Distribution of the genus *Scleropyrum* in Thailand, which is widespread throughout the country from sea level to 1000 m



Map 4. Distribution of the genus *Dendrotrophe* in Thailand, found between sea level and 150 m in disturbed areas or at the edges of peat swamps.