An account of the Santalaceae of Thailand

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ABSTRACT. The Santalaceae is a relatively small family of hemiparasites with a sub-cosmopolitan distribution whose species are most commonly found in semi-arid areas. In Thailand, the family is represented by 13 species in seven genera. Ecologically, species are generally associated with disturbed conditions and secondary vegetation. The majority of the species in Thailand belong to the tribe Amphorogynae. This tribe contains a unique group of aerial parasites which have some morphological and ecological similarities to the Visaceae. Many of the species in this group display a degree of host specificity and generally inhabit montane regions, where they are usually parasitic on species associated with higher elevations such as Quercus, Lithocarpus (Fagaceae) and Vaccinium (Ericaceae). All of the species in Thailand are fully described herein with accompanying identification keys.

INTRODUCTION

Santalaceae, or the sandalwood family, contains herbs, shrubs, small trees and climbers. Southeast Asia is home to a unique group of branch-parasitic Santalaceae. The main characteristic which distinguishes the family is a hemiparasitic growth habit. However, the extent to which santalaceous species are facultative (not always requiring a host plant) or obligate (always requiring a host) hemiparasites is not known (Kuijt 1969, Nickrent & Starr 1994).

In general flowers are small and inconspicuous, odourless or with a faint scent and borne in dense inflorescences of various kinds. Plants are dioecious or hermaphrodite, radially symmetrical with 3–6 undifferentiated perianth lobes (tepals) inserted in a single whorl. Despite the presence of hermaphrodite flowers, the family is thought to be strictly outbreeding. In Santalum album L. the bisexual flowers are homogamous (anthers and stigma receptive at the same time) but studies have shown that some kind of self-incompatibility mechanism exists which ensures that self-fertilisation is prevented (Sindhuveerendra & Sujatha 1989, Bhaskar 1992). Stamens numbers equal the number of perianth segments and stamens are placed one opposite each tepal. The nectarial disc, which lines the receptacle of the flower, produces copious amounts of nectar which is the main attractant for visiting pollinators. A tuft of hairs, which is usually present behind each anther emanating from the tepal base, is known to produce a viscous oily fluid that

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may act as a secondary attractant. The ovary is unilocular, and variable in position with 1–6 ovules, only one of which develops into a seed. The fruit is a nut or drupe, which can be brightly coloured, and seed dispersal is facilitated by animal vectors, frugivorous birds being the most common dispersal agents (Herrera 1988).

DISTRIBUTIONS AND AFFINITIES

The most recent classifications of Mabberley (1997), Heywood (1997) and Stauffer (1969) recognise three to four tribes of Santalaceae: Amphorogynae, Santaleae, Anthocholeae and Thesieae with between 400–540 species in 30–32 genera. The family has a subcosmopolitan distribution in tropical and temperate regions with a concentration in arid and semi arid areas. Almost one third of the species (126) and over half the number of genera (16) are located in Southeast Asia and Australia. The rest are scattered across the continents of America, Africa and, to a lesser extent, Europe. More than half of the species are contained within the genus Thesium which has its centre of diversity in South Africa. There are eight monotypic genera in the family but five of them are restricted to North or South America (Brummitt 1992). Southeast Asia is home to 48 species of Santalaceae in nine genera. In terms of species numbers the Thai Santalaceae are depauperate, with just 13 species in total. The number of genera is large in comparison, with seven genera, and reflects southern European and Asian as well as Indo-Malesian influences.

None of the genera are restricted to Thailand; indeed a number do not have a strict affinity with the region and are represented by a single species at the limit of their generic range. Table 1 enumerates the species in Thailand and their geographic distributions. Santalum L. which contains ca. 25 species worldwide is represented in Southeast Asia by a single small tree, S. album, which is native to Java and Timor, but is widely cultivated in Thailand and India for its valuable, fragrant timber and essential oil (Lewington 1992). The mainly African genus Thesium L. is represented by a single herbaceous species, T. psilotoides Hance, which is distributed in southern China, Laos and northern Thailand. Ozyris L., which consists of two species, has a single representative, O. lanceolata Hochst. & Steud., which has a widespread distribution from southern Europe to northern Thailand. Species of the Southeast Asian genus Scleropyrum Arn. are small trees characterised by amentiferous inflorescences and pyriform fruits. The genus contains four species, two of which are found in Thailand. One of these species is very widespread from southern China to New Guinea.

The other three genera Phacellaria Benth., Dufrenoya Chatin and Dendrotrophe Miq. are part of a closely related group of climbing or branch parasites which are confined to Southeast Asia. Dendrotrophe contains just four species and occurs from southern China to northern Australia making it the most widespread Santalaceous genus in Southeast Asia. It has two representatives in Thailand but due to the effect of climatic influence they do not occur above the peninsular region and in Cambodia and Vietnam are found only in areas which have climatic affinities with the Malay Peninsula. The genus is therefore confined to regions where there is a degree of unseasonality and high precipitation. Dufrenoya is restricted to west of Wallace’s line and has its greatest species diversity in northern Vietnam. This genus contains 11 species, which are confined to montane regions.
above 1000 m. There are four species in Thailand which are restricted to the north of the Khorat Plateau. Species are generally parasitic on temperate taxa such as Fagaceae and occasionally Myrtaceae and Juglandaceae and may be tracking the distribution of those species in Southeast Asia. In contrast to Dendrotrophe, which is found in warm tropical, aseasonal climates, species of Dufrenoyia are restricted to cooler montane climatic conditions. Like Dufrenoyia, species of Phacellaria are confined to montane regions and indeed the geographic distribution of Phacellaria follows that of Dufrenoyia but with a more restricted range. Phacellaria species are, however, more host specific, being hyperparasites on Loranthaceae and occasionally Dufrenoyia. There are four species of Phacellaria, two of which are found in Thailand.

**TAXONOMIC HISTORY**

In his Prodromus Brown (1810) described a new family, Santalaceae from Eleagni of Jussieu (1789) (Table 2). The characters which he used to circumscribe the family were: alternate leaves without stipules; an undifferentiated perianth with valvate aestivation; stamens equal to and opposite the perianth lobes and an unilocular ovary with pendulous ovules. Brown’s description was comprehensive and contains most of the essential elements of the Santalaceae as known today. However, the parasitic nature of the family and the variable position of the ovary were not recognised by him.

In 1850 Blume separated and described the Southeast Asian genus Henslowia which had previously been included in Viscum of the Loranthaceae. The delimitation and placement of Henslowia (now Dendrotrophe Miq.) in the Santalaceae meant that for the first time aerial parasitic species were included in the family. Blume described eight species of Henslowia which was later reduced to six by Miquel (1856) who realised that the genus name was a homonym of Henslowia Wall. (1832). Miquel renamed Henslowia Blume as Dendrotrophe and the species he described are now recognised to include elements of the genera Dendromyza and Dendrotrophe.

Alphonse de Candolle (1857) treated 208 species in 18 genera of Santalaceae, producing the first comprehensive account of the family. Of the 208 species, 104 belonged to the genus Thesium and to the present day this genus contains more than half of the number of species in the family. De Candolle split the family into three tribes, Buckleyaeae, Santaleae and Anthoboleae, and two subtribes Thesieae and Santaleae, based on the distribution of the sexes, the aestivation of the tepals and most importantly the position and topography of the ovary. Of the tribes which he described, the Anthoboleae remains unchanged to the present day. His tribe Santaleae was the largest and contained elements of all the other currently recognised tribes.

In his treatment of the Santalaceae Bentham (1883) described four tribes, of which tribe Anthoboleae corresponded to that of de Candolle whilst two others, Osyrieae and Thesieae, contained elements of the Santalaceae. The name Osyrieae has been used extensively in taxonomic literature but it is now a recognised synonym of Santalaceae as described by De Candolle (Hewson & George 1984, Heywood 1997). The last tribe, Grubbieae, was accepted as anomalous within the Santalaceae but placed with it based on the fact that the species contained in it were parasitic. Bentham also described a new
genus, *Phacellaria* (an aerial hyperparasite from Southeast Asia), and expanded the definition of the Santalaceae (Bentham 1883) to include *Myzodendron* which is now accepted as the monogeneric family *Mysodendraceae*. The characters which Bentham used to delimit the first three tribes are still used today in the suprageneric classification of the family. They consist of three main characters: the position of the ovary, the presence or absence of a nectarial disc and fruit type.

Focusing on the Southeast Asian species, Danser completed a revision of *Phacellaria* in 1939, describing in great detail the inflorescence morphology of the species; he then turned his attention to the other aerial parasitic species. In 1940 he recognised the complexity of the construction of the fruits of *Henslowia* from observations which he had made and possibly from illustrations and descriptions given in isolation from other authors. He split the genus *Henslowia* into four separate genera (*Dendromyza, Cladomyza, Hylomyza, Dendrotrophe*) based on fruit morphology. The delimitation of the genera was based on the structure of the mesocarp and the shape and internal construction of the endocarp. Of the genera described, it was subsequently discovered that *Hylomyza* was a synonym of *Dufrenoya* which had been described by Chatin in 1860.

In 1969 Stauffer separated and described the tribe *Amphorogynaeae* which had previously been included in the *Osyrideae* which includes all of the stem parasitic genera (including *Dendrotrophe, Dufrenoya* and *Phacellaria*) and most of the genera from Australia, which are not members of the *Anthoboleae* (Stauffer 1969). The characters used to delimit the tribe are clustered inflorescences, small flowers, an inferior ovary and the retention of the perianth on the fruit. Some of the other characters which were included in the tribal description such as the presence of a nectarial disc, the presence of glandular hairs in the flowers and the fact that the fruit is a fleshy drupe are also characteristics which can be applied to other tribes.

**SPECIES CONCEPT**

Often one of the greatest challenges in a systematic study is choosing the most appropriate units to call species (Mayr 1982). It is a necessary process, however, as in recognising species we attempt to comprehend evolutionary relationships and to provide a framework on which the diversity of the natural world can hang (Claridge *et al.* 1997).

The Linnean idea of a species as based on morphological similarity is the foundation for the Taxonomic Species Concept (TSC) and indeed the majority of the 250,000 or so flowering plant species which have been so far named, are based on morphological characteristics (Gornall 1997). The basis of the taxonomic (or morphological) species is the ultimate requirement that species must be easily identifiable and the characters, which are used to define them, are the most accessible. Species are therefore described based on their overall similarity and individual members of a species are more similar to each other than to members of other species (Judd *et al.* 1999).

A species has been compared to a giant jigsaw puzzle where the upper surface is the taxonomic species and the parts that are used to fit it together are reproductive isolating mechanisms, genetic drift and natural selection: the processes which maintain
the species integrity (Gornall 1997). This analogy eloquently demonstrates the complex nature of species as morphologically distinct units held together by reproductive and genetic forces.

It is important to consider all forms of evidence when formulating species concepts within a particular group and to accept that species in practical terms are open to repeatable testing as new data or methods of analysis become available. The basis of what constitutes a species can also vary from one group of plant to another (Gornall 1997, Judd et al. 1999), a condition that is acceptable under the Composite Species approach (Kornet 1993).

Returning to the practical requirement that species should be readily identifiable, the Taxonomic Species Concept has been taken as the basic unit of the species in this study, with additional information obtained via ecological observations and phylogenetic investigations. Primarily morphological characteristics have been studied but palynological and molecular information has been used to confirm and investigate species identities and relationships.

**DIAGNOSTIC CHARACTERISTICS**

A previous paper (Macklin & Parnell 2000) detailed characteristics of taxonomic importance which can assist in the delimitation of genera and species. This paper will therefore summarise those findings. Table 3 also describes the characteristics which can be used to distinguish the genera in Thailand.

**Growth habit** is variable at the tribal level. Tribe Santaleae contains larger shrubby or arborescent genera (Scleropyrum, Santalum, Osyris). Tribe Amphorogyneae generally consists of those genera which have a climbing and dendroparasitic habit (Dendrotrophe, Dufrenoya, Phacellaria) and one genus, Phacellaria, is capable of endophytic growth. Tribe Thesieae, which has a single representative in Thailand (Thesium), contains herbaceous species.

**Leaves** are spiral, alternate or, rarely, opposite. They are generally fleshy and all have an entire leaf margin. In tribe Santaleae leaf venation is pinnate, whilst in Amphorogyneae venation is palmate with the exception of Phacellaria where leaves are very reduced, bract-like and usually withering. In Thesieae leaves are also bract-like but in this case they are persistent and quite conspicuous.

**Inflorescence** structure is a valuable diagnostic characteristic at the generic and, occasionally, species level. It should generally only be considered for male reproductive structures as female inflorescences are often 1-flowered. In Thesium, however, the inflorescence is always 1-flowered and the flower hermaphrodite. Generally, the basic inflorescence structure is racemose. The raceme may be erect (Dendrotrophe varians) or a pendulous catkin (Scleropyrum). This basic scheme can be compressed and therefore umbellate in Dufrenoya or sessile and sunken (Phacellaria). The other genera, Santalum and Osyris, have cymose inflorescences and the branching pattern found in their inflorescence of Osyris is a compact version of that in Santalum.
**Flowers** may be hermaphrodite or unisexual, with staminodes or the rudiment of a style present in the female or male flower, either of which can be quite substantial. In Thailand species are generally dioecious, except *Theesium, Santalum* and *Dendrotrophe buxifolia* (Blume) Miq. which have hermaphrodite flowers. Anther dehiscence is longitudinal in *Santalum, Osyris, Scleropyrum* and *Theesium* and transverse in *Dendrotrophe, Phacellaria* and the majority of *Dufrenoya* species. In this latter genus the mode of dehiscence of the anthers and the presence or absence of glandular hairs behind the stamens can be used to group species.

**Ovary** position is stable at the tribal level. It is semi-inferior in *Santaleae* and inferior in *Amphorogyneae* and *The sieae*. In *Amphorogyneae* placenta is free central, the placenta is convex with 4–6 short in-curving lobes and the placental column is long and straight (*Dendrotrophe, Dufrenoya*) or very short (*Phacellaria*). In *Santaleae* the placenta is saggitate (*Santalum*) or convex (*Scleropyrum, Osyris*). It is 3–4-lobed and the lobes may be long and convoluted (*Scleropyrum*) or short (*Santalum, Osyris*). The placental column is short (*Osyris, Santalum*) or contorted (*Scleropyrum*). In *Theesium* the placental column is similar to *Scleropyrum* but the lobes of the placenta are short.

**Fruits** are dry and indehiscent nuts in *Theesium*, but fleshy drupes in *Santalum, Scleropyrum, Osyris* and *Dendrotrophe*. In *Dufrenoya* and *Phacellaria* the mesocarp consists of membranous strands which are short and randomly oriented or long and wrap around the endocarp. The fruits of *Osyris, Santalum* and *Scleropyrum* are unilocular but in *Dendrotrophe* and *Dufrenoya* fruits are chambered at the apex and the base. Furthermore, there are transverse chambers in the fruits of *Dendrotrophe*. In *Phacellaria* only apical chambers are present in the fruits.

**GLOSSARY**

*Specialised terms*

**Dendrophasite** Woody plant which is parasitic on the branches of trees or shrubs; attaching by means of a primary haustorium and occasionally secondary haustoria (synonymous with mistletoe). This term was first used by Macklin & Parnell (2000) as an alternative to mistletoe, which is usually associated with the Loranthaceae, and the more cumbersome term branch parasite. It can also be used as an adjective *i.e.* dendrophasitic.

**Endophytic** A portion of a plant that grows within another plant, in this case the haustorium, which extends into the host tissue; shoots then emerge on different parts of the host plant. This term is used exclusively in association with the genus *Phacellaria*.

**Fungiform** Mushroom-like. Cylindrical with rounded convex, overhanging extremities.

**Glandular hair** Long, unicellular hair which exudes a viscous, oily fluid. In Santalaceae these hairs are found emanating from the inner surface of the tepal base behind the stamens. Glandular hairs are often a striking feature of the santalaceous flower and are particularly distinctive in the genera *Santalum* and *Scleropyrum*.

**Haustorium** A specialised root structure which physically connects the parasite to its host.
and through which it obtains chemical substances. It is a primary haustorium if the radicle apex is directly transformed into a haustorium and a secondary haustorium if formed from tissue other than the radicle apex such as aerial roots on stems. In Thailand all species of Santalaceae have primary haustoria. Secondary haustoria are found on species of *Dendromyza*, a genus which is generally confined to eastern Malesia.

**Hemiparasite** A parasitic plant which lives on and derives water and nutrients from its host but possesses chlorophyll and therefore retains photosynthetic activity. All species of Santalaceae are hemiparasites. Some species, however, may be yellowish in colour indicating some change in chlorophyll composition.

**Hyperparasite** A parasitic plant which is attached to another parasite. This characteristic is again associated with the genus *Phacellaria* which may be parasitic on species of Loranthaceae, or less frequently, *Dufrenoya*.

**Perigone** A perianth which is undifferentiated into a calyx and corolla (Stearn 1996). In the santalaceous flower the perigone is usually inconspicuous in colour, usually green or yellowish. In some cases, however, the nectary may be brightly coloured and appear corolla-like.

**Leaf venation**

**Co-arcuate** Joined together in a bow-like pattern.

**Compound rectipinnate** A single primary vein with the secondary veins arranged along its length at regular intervals, the secondary veins branch and run into the leaf margin. This type of venation is found in *Santalum* (Melville 1976).

**Curvipalmate** Primary veins radiating from a node which may be basal or supra basal, the veins converge at a node which is usually at the apex of the leaf. This kind of venation is found in the genera *Dendrotrophe* and *Dufrenoya* (Melville 1976).

**Curvipinnate** Similar to compound rectipinnate but the secondary veins curve gradually towards the margin of the leaf not supplying it directly. This type of venation is associated with *Osyris* species (Melville 1976).

**Multi-arcuate** Similar to compound rectipinnate but the secondary veins are connected by arching loops from some distance from each other and a series of smaller loops form a zone between the secondaries and the leaf margin. This, more complex, venation type is found in *Scleropyrum* species (Melville 1976).

**TAXONOMIC TREATMENT**

To avoid confusion between the genera *Dendrotrophe* and *Dufrenoya*, the abbreviation *Dr* before a species epithet refers to *Dendrotrophe* while *Df* refers to *Dufrenoya*. The species are generally dioecious and therefore an effort has been made to incorporate characteristics of both male and female reproductive characteristics in the keys. If difficulty is encountered remember that the genera *Scleropyrum*, *Santalum* and *Osyris* are all trees or large shrubs and *Thesium* is herbaceous. *Dufrenoya* and *Phacellaria*
are dendroparasites confined to the north of Thailand and *Dendrotrope* is a climber or scrambling shrub in southern Thailand. Within the former group, species of *Phacellaria* all have leaves which are reduced to scales, whilst species of *Dufrenoya* all have an obvious leaf blade. Species descriptions are based on original observations from herbarium material. In the account three measurements have been made from the leaves: length, width at the mid-point and width at the base. The leaf widths are indicated between brackets just after the leaf length. As measurements have been made from dried specimens they may differ slightly from fresh material.

**SANTALACEAE**


Hemiparasitic small trees, shrubs, climbers, dendroparasites attaching to host by means of a primary haustorium, stems and leaves often suffused yellow. *Leaves* large or bract-like, margins entire, stipules absent. *Inflorescences* terminal and axil, subtended by a single bract which covers the juvenile inflorescence, bract caducous or persistent. *Flowers* small, inconspicuous, radially symmetrical; perianth undifferentiated into calyx and corolla, tepals 3–6 in a single whorl, separate or united into a shallow hypanthium; stamens equal in number and opposite each tepal, adnate to the tepal base; anthers bilocular, locules bilobed, dehiscence extrorse; style simple, stigma 3–5-lobed, occasionally entire; nectarial disc present or absent, where present, covering the surface of the receptacle and the base of the style, 3–6-lobed, lobes short or long, alternating with the tepals. *Ovary* basifixed, placenta central, placentation free central, placentae more or less convex, 3–6-lobed, lobes short or long and tortuous, placental column long or short, straight or contorted; ovules pendulous from tips of placental lobes, integuments absent, 1 ovule developing per fruit. *Fruit* a drupe or nut; exocarp thin, mesocarp thin, fleshy, membranous or sericeus, endocarp hard or splitting easily. *Seed* 1, fleshy or woody, entire or lobed, testa absent, endosperm copious.

400 species, cosmopolitan in distribution but mainly southern hemisphere, with the greatest concentration in arid and semi-arid tropics. Thirteen species in Thailand.

Note.—Based on molecular evidence the family is thought to be paraphyletic. *Thesium* and some of the South American species form a separate group from the Southeast Asian species and the Eremitolepidaceae, a small family of dendroparasites from South America (Niekren 2001). In several species the flowers change colour with age from yellowish green to dark red or brown which may act to make pollinated flowers invisible or unattractive to prospective pollinators (Endress 1994). The nectarial disc is one of the most striking features of the santalaceous flower, it lines the entire surface of the receptacle and produces copious amounts of nectar: in *Santalum* the lobes are prolonged and brightly coloured and have been interpreted as corolla lobes on several occasions (Jussieu 1789).
In several species, there are glandular hairs behind the stamens producing a viscous, oily fluid, which is secreted onto the anthers. It may serve to attract pollinators and has been implicated in pollen maturation and germination (Paliwal 1956, Bhaskar 1992).

In this account tribes and genera appear in order as follows:

1. Tribe AMPHOROGYNEAE
   1. Dendrotrophe, 2. Dufrenoya, 3. Phacellaria
2. Tribe SANTALEAE
3. Tribe THESIEAE
   1. Thesium

KEY TO THE GENERA

1. Small trees
   Shrubs, climbers, dendroparasites, herbs
2. Plants hairless; leaves opposite, inflorescences cymose, flowers hermaphrodite
   Plants sparsely or densely hairy; leaves alternate; inflorescence a catkin; flowers unisexual
3. Herbs; fruit nut-like
   Shrubs, climbers, dendroparasites; fruit a drupe
4. Shrub with pendant branches; leaf venation pinnate; male inflorescences cymose
   Scandent shrubs, climbers, dendroparasites; leaf venation palmate or leaves reduced to scales;
   male inflorescences paniculate, racemose, umbellate or forming sessile clusters
5. Stems hisurate or papillosae; leaves bract-like; hyperparasite on Loranthaceae and Dufrenoya
   Stems hairless; leaves not bract-like; not hyperparasitic
6. Male inflorescences, paniculate, racemose; fruits spherical, elliptic, mesocarp fleshy, endocarp
tuberculate
   Male inflorescences umbellate; fruits, obovoid, oblong, mesocarp membranous, endocarp smooth

TRIBE AMPHOROGYNEAE


Shrubs, climbers, dendroparasites, leaves spiral, often scale-like, caducous, venation curvipalmate. Inflorescences racemose, umbellate, clustered or reduced to a single flower, female inflorescences always 1-flowered. Flowers small, yellow, green or occasionally red; hermaphrodite or dioecious; anther locules isomeric or more commonly unequal in size; style short, stigma 5-lobed; nectary present, fleshy, shortly 4–6-lobed. Ovary inferior, placenta 4–6-lobed, lobes rounded, short, curling underneath and in towards the placental column, placental column slender, short or long. Fruit a drupe; exocarp smooth, coriaceous, perianth persistent, mesocarp fleshy, membranous; endocarp chambered. Seed lobed.

Note.— Genera restricted to Southeast Asia and Australia, containing many dendroparasitic species and exhibiting the most variation within the family in terms of fruit and pollen morphology. 3 genera (Dendrotrophe, Dufrenoya, Phacellaria) in Thailand. Dendrotrophe is generally found south of the Isthmus of Kra, while Phacellaria and Dufrenoya are distributed in the north and northeast of the country.
1. DENDROTROPE


Hairless terrestrial shrub, climber or dendroparasite, often with twining stems; bark smooth or with longitudinal fissures. Leaves variable in size but usually quite large, fleshy, primary veins 3–5–7. Plants dioecious, or flowers hermaphrodite, solitary or 1–3 together, flowers yellow or green. Male inflorescences racemose, peduncles bracteate, bracts crowded at the apex and base to form an involucre, caducous. Male flower buds globose, receptacle flat, tepals 5, deltoid, ovate, valvate, glandular hairs present or absent; anthers basifixed, bilocular, locules bilobed, lobes unequal in size, posterior broader and longer than the anterior, dehiscence transverse; nectary fleshy, flat or concave, lobed; style rudiment slender, capit ate; ovary present, semi inferior, straight, abortive. Hermaphrodite inflorescences paniculate, bracteate. Hermaphrodite flowers with enlarged receptacle; style short, stigma 5-lobed, fleshy, papillate. Female inflorescences 1-flowered, shortly pedunculate, subtended by a series of involucral bracts. Female flowers with staminodes which are well developed but lack pollen; style and stigma as in hermaphrodite flower. Ovary 0.3–0.4 by 0.6 mm, placenta convex, 4–6-lobed, placental column long, straight. Fruit red or black, globose, elliptic, perianth persistent, eecr; exocarp thin, smooth or rugulose; mesocarp thin, fleshy; endocarp hard, globose or elliptic, tubercul ace, apex shortly apiculate, internally 4–6-chambered at the apex and the base, each chamber may be further lobed, 5–10-lobed for the rest, transverse chambers present. Seed rudimate, reminiscent of Juglans. Embryo situated in the centre of the endocarp.

Four species from Southern China to Australia. Two species in Thailand.

Ecology.—On poor sandy, loamy soil in kerangas forests and coastal areas; waterlogged, peaty soil in forests at the edge of peat swamps. In Quercus/Larix or Eugenia (/ Syzygium) forests in montane regions and in disturbed areas in secondary vegetation, up to 3000 m.

Note.—Name derived from dendron meaning tree-like and trophe, to nourish, referring to the parasitic habit. Contains one very widespread and variable species, D.t varians (Blume) Miq., which occurs across the geographical range of the genus and three others with narrower distributions; one species is found in western Southeast Asia as far as Borneo and two others are endemic to New Guinea. The genus is characterised by a twining or prostrate growth habit, paniculate or racemose inflorescences and a tuberculace endocarp with transverse chambers. Occasionally, species may be sparsely leafy or leafless. Dendrotrophe was originally described by Miquel to replace Henslowia of Blume.
KEY TO THE SPECIES

Primary veins obscure, 2–3; inflorescences paniculate, flowers hermaphrodite
Primary veins usually obvious 3–5; male inflorescences racemose, flowers dioecious


Erect or prostrate shrub. Juvenile stems flattened and twisted, surfaces powdery, older branches terete, very occasionally completely flattened; bark smooth, slightly pustulate. Leaves sparse, occasionally caducous, yellowish green, fleshy. 13–45 (8–9: 2–3) mm, primary veins 2–3, inconspicuous; petiole short angular, decurrent. Inflorescences prolific, in clusters of more than 10 together, on mature and juvenile branches, often on raised scars, paniculate, 5–10-flowered, rachis 4–8 by 0.5–0.8 mm, subtended at the base by an involucre of 5, imbricate bracts, also bracteate along its length, bracts deltoid, 0.5–0.6 by 0.4–0.6 mm, margins villose; axial flowers pedunculate, peduncle bracteate along its length and subtended at the base by an involucre of bracts, eventually flower buds developing in the axils of the bracts, this pattern often repeating several times. Flowers hermaphrodite, yellowish green, buds obconical, sessile or very shortly pedicellate, pedicel 0.5 mm in length; receptacle short, broad, 1–1.5 by 1.5 mm; tepals 5–6, valvate, deltoid, 0.8–1 by 0.8–1, glandular hairs absent; filaments broad, 0.1–0.2 by 0.2 mm, anthers 0.3 by 0.3 mm; style short, as broad as long, 0.2–0.3 by 0.2–0.3 mm; nectary lobed, very shallowly concave, punctate, ridged, the ridges running into the nectarial lobes. Fruit ripening black, small, spherical, 3–3.5 by 2.5–3.5 mm, very shortly pedicellate, pedicel 0.3–0.5 by 0.5 mm; exocarp smooth, endocarp globose, 2–2.5 by 2.5 mm, tuberculate, 5–armed, with star-shaped scar at the apex which may be prolonged to the base, apex depressed, apiculate.

Thailand.—SOUTH-EASTERN: Trat [Koh Chang island, Koh Mai See, Geesink 6655 (BKF, K)]; Koh Boi Noi, Hansen 12432 (BKF, L)]; PENINSULAR: Chumphon [Langsuan, Kerr 1889 (L)]; Krabi [Ko Pu, Kerr 18946 (L)]; Phang-nga, 8°25’N, 98°30’ E, Geesink 5259 (BKF)]; Narathiwat [Ban Sai, Niyomdham 1734 (K)]; Rangae, Sangkhachand 53357 (BKF); Tak Bai, Chanthy 1151 (BKF)]; Satun [Adang, Kerr 14106 (K)]; Tola Satul, Kerr 13854]; Songkhla [Kampeng Pet, Kerr 15916 (L)]; Hat Yai, Condon 26 (AAU); Ton Nga Chang reserve, Hat Yai, Maxwell 84/505 (A, BKF); Ko Khlong, Hat Yai, 100°20’ E, 7°00’ N, Larsen 42184 (AAU); Ko Khlong hill, Hat Yai, Maxwell 84/183 (A, BKF)]; Surat Thani [Ko Phangan, 9°55’N, 100°20’ E, Geesink 7788 (BKF)]; Katuli, Put 4177 (L); Ko Phangan, Put 750 (L); Trang, Larsen 44004 (AAU)].
Distribution.—Vietnam, Philippines, Malay Peninsula, Borneo, Sumatra.

Ecology.—Up to 300 m, found mainly in Melaleuca forests at the edge of peat swamps in Peninsular Thailand and also in disturbed areas of primary evergreen forest. In Malaysia and Borneo confined to white, sandy soil in heath forest and coastal areas.

Note.—Name derived from the small elliptic leaves. Characterised by small fleshy leaves and hermaphrodite flowers, this species has a variety of growth forms from a scrambling shrub and climber to occasional dendroparasite. It is sometimes leafless, particularly in collections from the Malay Peninsula and Sumatra. There are also some collections from Peninsular Thailand where the stems are completely flattened, which may be due to a viral infection. *Dendrotrophe huifolia* is vegetatively similar to *Dt varians* and the distributions of the two species overlap. Where the species co-occur *Dt huifolia* may be distinguished by generally lanceolate leaves, smaller globose fruits and a paniculate inflorescence with hermaphrodite flowers.


Climber, occasional dendroparasite. *Juvenile stems* smooth, slightly striated, angular, older stems terete; bark rough with transverse fissures. *Leaves* fleshy, thin or papyraceous, elliptic, obovate, orbicular, 13–75 by (6.5–50 : 2–12) mm, primary veins 3–5; petiole long, narrow, decurrent. *Inflorescences* dioecious, 1–8 clustered together on juvenile branches. *Male inflorescences* racemose, 7–8-flowered, rachis 1–10 by 0.2–1 mm, an involucre of imbricate bracts at the apex and the base, sparsely bracteate along its length, bracts membranous, deltoid, ovate, 0.5–1 by 0.3–0.8 mm, caducous except at the base; 4–5 flowers crowded at the apex and 2–3 inserted spirally along the rachis. *Male flower* buds globose, pedicellate, pedicel 0.8–2 by 0.5–0.8 mm, tepals 4–5, imbricate at the base, ovate, 0.8–1.3 by 0.5–1 mm, apiculate on the inner surface at the apex, glandular hairs present; filaments broading towards the base, 0.2–0.5 by 0.1–0.3 mm, anthers 0.2–0.4 by 0.2–0.4 mm; nectary slightly concave, smooth, angular; style rudiment 0.3–0.7 by 0.1–0.2 mm. *Female inflorescences* fewer in number, 1-flowered, pedunculate, peduncle shorter, 2–6 by 0.8–1.4 mm. *Flower* buds obconical, sessile or shortly pedicellate, pedicel 0.5–2 by 0.5 mm; tepals 5, deltoid, 0.8–1.7 by 0.7–1.3 mm, receptacle 2.5 by 1 mm, decurrent with the pedicel; stamina present, large, similar to stamens in male flower; nectary convex, unlobed, smooth or slightly pubescent; style short 0.2–0.5 by 0.3–0.4 mm. *Fruit* red or black, elliptic or obovoid, 4–14 by 3–11 mm; exocarp coriaceous, endocarp globose, elliptic, 5–12 by 4–8 mm, smooth, rugulate, 5–6-armed, with star-shaped scar radiating from the apex, apex apiculate.

Thailand.—SOUTH-EASTERN: Chumphon [Langsuan, *Put* 1672 (L); Na Sak, Langsuan, *Kerr* 11853 (A, L); Na Sak, Langsuan, *Kerr* 11887 (L)]. PENINSULAR: Nakhon Si Thammarat [Ta Samet, *Kerr* 14277 (K)]; Narathiwat [Bang Nara river, Tak Bai, *Niyomdham* 1454 (AAU, L); Ban Ko Sawat, *Kerr* 18116 (K); Sangkhachand 29950 (K); Larsen 33105 (BFK)]; Ranong [Ko Chang, *Kerr* 16586 (K); Santitsuk s.n. (BFK)]; Satun [Thung Wa, *Niyomdham* 1285 (K, L)]; Songkhla [Khlong Ngae, Hat Yai, *Maxwell* 85/60 (BFK, A, L); Ko Hong hill, Hat Yai, *Maxwell* 85/113 (A, BKF); *Maxwell* 85/35 (A); Kuan Meed, south of Hat Yai, *Congdon* 39 (A); Hat Yai, *Kerr* 14758 (L)]; Surat Thani [Geesink 7750 (AAU, BKF, L, P); Geesink 7776 (BFK)]; Koh Phangan, Geesink 7788 (AAU);
Haniff 3896 (K); Put 789 (L); Surin, Kerr 8262 (K); Trat [Kao Kuap, Put 3030 (K); Put 3039 (L); Kerr 17750 (K); Kerr 17873 (L); Yala, Put 3667 (L); Krabi, Kerr 18949 (L).

Distribution.—Southern China to Australia.

Ecology.—On poor sandy, loamy soil in kerangas forest and coastal areas; in swamp forest and in montane regions in Fabaceae, Quercus/Larix or Eugenia s.l. forests; in upper montane mossy forests, up to 2500 m. In Thailand it occurs predominantly in disturbed areas in secondary vegetation.

Note.—Name derived from the fact that this species exhibits a variety of leaf shape. This, together with the considerable variation that exists in fruit morphology, has led to the description of extreme forms as new species; hence the extensive synonymy. Like D. buxifolia, D. variae exhibits a variety of growth forms from erect to prostrate shrub, to dendroparasite but it is generally climbing. Characterised by dioecious flowers and a racemose male inflorescence. In Thailand and western Malesia the distribution of D. variae overlaps with D. buxifolia but it is normally found at higher elevations and in drier habitats. It can be easily distinguished by its unisexual flowers and usually larger leaves and fruits.

2. DUFRENOY


Hairless dendroparasitic shrubs; bark smooth, pustulate or with longitudinal fissures. Leaves varying in size but usually large, upper surfaces smooth, shining, lower surfaces dull, granular, primary veins 3–11. Inflorescences dioecious, solitary or 1–3 together, flowers yellow or green. Male inflorescences umbellate, 6-flowered, pedunculate; pedunules bracteate, bracts crowded at the apex and base to form an involucre, persistent; flowers developing in the axils of the upper bracts, the central flower not subtended by a bract and developing first. Male flower buds globose, fungiform, receptacle flat, tepals 5–6, valvate, shortly apiculate at the tip on the inner surface, glandular hairs usually present; anthers bilocular, locules bilobed, lobes isomerous or unequal in size with the posterior larger than the anterior, dehiscence transverse or longitudinal; nectary fleshy, flat or slightly concave, smooth and scarcely 5-lobed, apiculate in the centre. Female inflorescences 1-flowered, pedunculate. Female flowers green or yellow, tepal apiculate on the inner surface at the apex: style short, stigma papilllose; nectary flat or convex, unlobed. Ovary 0.2–0.4 by 0.5–0.6 mm, placenta convex, 5–6-lobed, placental column long, straight. Fruit green or red, elliptic, obovoid, perianth persistent, erect or flat; exocarp thin, smooth; mesocarp consisting of membranous strands which are attached to the endocarp and wrap around it, finally lying against the inner surface of the exocarp; endocarp hard or splitting easily, ovoid, oblong or obovoid, apex obtuse or acuminate, base rounded; internally 5–7-chambered at the apex and the base, 5–7-lobed for the rest. Seed with separate lobes at the
apex and the base, lobed for the rest. Embryo located near the apex of the endocarp between the apical lobes.

Eleven species from India and China to western Borneo. Four species in Thailand.

Ecology.— Restricted to mountainous regions in mostly open areas in sub-montane and hill evergreen forests in Fagaceae/Pinus and Fagaceae/Larix associations, above 1000 m. Parasitic on Quercus and Lithocarpus (Fagaceae) and Eugenia (Myrtaceae).

Note.— Name derived from the French geologist Pierre Dufrenoy. The majority of the species are restricted to continental Southeast Asia with only a small number in Java, Sumatra and Borneo. In Thailand species occur to the north of the Khorat Plateau. The genus is characterised by an aerial, shrubby growth habit, quite large leaves, umbellate male inflorescences and a membranous mesocarp. A number of species have been described from very sparse collections which may mean that they are very rare or that they have been overlooked due to the difficulty in collecting specimens from the tree canopy. The inconspicuous nature of the foliage and flowers may also be a contributing factor.

The species are all morphologically similar and show a large degree of uniformity in inflorescence and floral structure. There are often insect galls in the male flowers which causes the receptacle to become enlarged and may confuse identification. In Thailand the vernacular name Ka Fak is applied to two species, in Nepal another species is called Aijeru. Both of these names are synonymous with mistletoe and may refer to the growth habit and the mode of fruit dispersal. In Thailand the name Mai Teen Nok has also been used which literally means plant from the feet of a bird. Birds are obviously the main dispersal agents, the exocarp is removed during digestion and when excreted the seeds become sticky as the mesocarp dries, ensuring secure establishment of the young plant.

**KEY TO THE SPECIES**

1. Stems pustulate
   Stems smooth, rough, striated, fissured

2. Male flowers with glandular hairs and anther locules unequal; staminodes present in female flower, stigma lobed
   Male flowers with glandular hairs absent and anther locules isomerous; staminodes absent in female flower, stigma entire

3. Bark faintly corrugated with short elliptic, transverse fissures; primary veins 9–11, almost parallel; male flowers pendulous
   Bark smooth or with longitudinal fissures; primary veins obscure or 3–9, not parallel; male flowers not pendulous

2. *D. platyphylla*  
3. *D. robusta*  
1. *D. colletii*  
4. *D. sessilis*


Erect shrub. **Juvenile stems** furrowed, angular, bracteate at the base, older branches terete, bark faintly corrugated with short transverse, elliptic fissures, arranged in rows. **Leaves** spatulate, 70–95 (25–350 : 10–20) mm, margins crisp, weakly undulate, primary
veins 9–11, raised on both surfaces, secondary venation sparse, arising at acute angles and parallel to the primary veins, percurrent with supra-secondaries and rarely with opposite veins; petiole long, slender, 9–10 by 2.5–3 mm. Male inflorescences on all branches, solitary or 2–3 together, pedunculate, peduncles long, angular, 2.5–4 by 0.8 mm, with 3 rings of imbricate bracts at the base of the peduncle, upper involucre extending up to one-third the length of the rachis, apical involucre imbricate; bracts ovate, margins ciliate, 1.2 by 1 mm. Male flower buds green, fungiform, pendulous, pedicellate, pedicel long, slender, 1.5–2 by 0.4 mm; tepals 5, valvate, 1–1.5 by 1.1 mm, glandular hairs present; filaments white, short, dilated at the base, 0.3–0.4 by 0.1 mm, anthers pale yellow, basifixed, locules unequal in size, anterior lobes shorter and broader than the posterior, dehiscence transverse; nectary concave, weakly pustulate. Female flower buds turbinate, yellow, tepals 5–6, elongate-deltoid, 1–1.2 by 1 mm, staminodes present; filaments 0.3 by 0.1 mm, anthers 0.2 by 0.4 mm; style short, broad, 0.2 by 0.3 mm, stigma 5-lobed, lobes reflexed. Fruit yellowish green to reddish brown, oblong, 4.5–5.5 by 3.5–4.5 mm, persistent perigone erect; exocarp smooth, thick; mesocarp long, membranous, wrapping around the endocarp; endocarp splitting easily, oblong, slightly obovate, 3.5–4 by 2–2.5 mm, 5-grooved, apex apiculate.

Thailand.—NORTHERN: Chiang Mai [Doi Chiang Dao, Bunchuai 128 (BKF); Doi Inthanon, Garrett 1119 (E, L, TCD); Garrett 847 (BM, K, L); Coolidge & Carpenter 63 (A); Doi Inthanon, Mae Pau, 18 40N 98 25E, van Beusekom 2372 (AAU, BKF, CBG, L); Mae Soi ridge, Maxwell 91/243 (GH); Maxwell 91/404 (GH); Mae Taeng, Santisuk 1469 (A); Mae Sanam, Smitinand & Seidenfaden 47642 (K); Phrae, ridge between Phrae and Uttaradit, van Beusekom 4830 (BKF, L); Doi Khun Tan, 18 58N 98 10E, Hansen & Smitinand 12862 (BKF); Hansen & Smitinand 12873 (K); Hansen & Larsen 10871 (K, L); Doi Chong, 19 25N 98 18E, Hansen & Smitinand 12632 (AAU, BKF, E); Doi Suthep, Sorensen et al. 2869 (BKF); Put 3795 (BM, K); Petchaboon, Nam Nao forest, Smitinand 583 (BKF, K)].

Distribution.—Myanmar.

Ecology.—Mostly in open areas of hill evergreen forests in Fagaceae/Pinus and Fagaceae/Larix associations, 1500–1700 m. Parasitic on Quercus and Lithocarpus (Fagaceae).

Vernacular.—Ka-fak kha-dam (mistletoe with black leg).

Note.—The name is derived from the collector and author of Flora Simiensis, Collett, who collected in Myanmar from 1887–88. It is characterised by its large spatulate, multi-nerved leaves and large male flowers. It is similar to Df sessilis and Df platyphylla, but distinguished by larger, spatulate leaves and larger, pendulous male flowers. The vernacular name in Thailand refers to the dendroparasitic growth habit and the dark brown-black stems.


Erect and pendulous shrub, branches all of almost the same length, often 3–4 from a single node. *Juvenile stems* terete, pubescent, flattening towards the apex, slightly keeled, bracteate at the base, older wood distinctly different, pale in colour with longitudinal fissures which are raised and covered in a smooth waxy deposit. *Leaves* coriaceous, elliptic, ovate, obovate, 40–75 (25–55 : 5–18) mm, primary veins 5–7, raised on the upper surface, secondary veins fine, arising at ca. right angles, opposite secondaries percurrent; petiole long, slender, angular, 8–10 by 1.5 mm. *Male inflorescences* solitary or in groups of 3–4, on juvenile stems and on short shoots arising from the older stems, pedunculate; peduncles angular, 2–3.5 by 0.5–0.7 mm, 2–3 involucres of bracts at the base, a single quincuncially arranged involucre at the apex; bracts broadly ovate, minutely ciliate, 0.8–1 by 0.8–0.9 mm. *Male flower* buds yellowish green, globose, subsessile, tepals 5–6, lanceolate, 1.4–1.5 by 1 mm, weakly apiculate on the inner surface near the tip, glandular hairs present; filaments short, slightly dilated at the base, 0.2–0.3 by 0.1–0.2 mm, anthers basifixed, 0.2–0.3 by 0.4–0.5 mm, lobes unequal in size, anterior shorter and broader than the posterior, dehiscence transverse; nectary 5–6-lobed, flat. *Female inflorescences* sessile or shortly pedunculate. *Female flower* buds green, distinctly turbinate, tepals 5–6, ellagolate-ovate, apex acuminate, 1 by 0.6 mm, staminodes present; filaments 0.2 by 0.2 mm, anthers 0.3 by 0.4 mm; style short, broad, 0.3 by 0.3 mm, stigma 3–5-lobed. *Fruit* pale green ripening purple, globose or slightly obovoid, 3.8–5 by 3–4 mm, persistent perigone flattened; exocarp quite thick, loose; mesocarp short membranous, randomly oriented, apical ‘tails’ present, filiform, lying against the inner surface of the exocarp; endocarp hard, globose or slightly obovoid, distinctly 4–6-lobed, rounded at the apex, apiculate at the base.

**Thailand.**— NORTHERN: Chiang Mai [Doi Suthep, south side above Puping palace, Maxwell 91/298 (GH); Doi Suthep, Nanakorn 91023 (AAU, BKF, GH)].

NORTH-EASTERN: Loei [Phu Kradueng, Smitinand 2116 (GH, L)].

**Distribution.**— India, Myanmar.

**Ecology.**— Open areas in slightly disturbed evergreen forests, 1500–2500 m. Parasitic on *Quercus, Castanopsis* (Fagaceae), *Dipterocarpus* (Dipterocarpaceae).

**Note.**— Name derived from the large, broadly elliptic leaves. Characterised by pubescent juvenile stems which are distinctly different from the older branches. The only member of this genus to have apical ‘tails’ attached to the endocarp. These ‘tails’ are long filamentous strands which are attached to the apex of the endocarp and lie along the inner surface of the exocarp and which may assist in anchoring the juvenile plant to a host tree. *Df platyphylla* is similar to *Df sessilis* but distinguished by its pale striated bark, pubescent juvenile stems, longer pedunculate male inflorescences, distinctly turbinate female flower buds and apical ‘tails’ on the endocarp.

Pendant shrub, often with 3–4 branches arising from a single node. *Juvenile stems* flattened, striate, bracteate at the base, older branches distinctly different from juvenile stems, bark punctate with raised, elliptic fissures which become pronounced and finally very rough, nodes swollen, with raised bract-scars. *Leaves* coriaceous, narrowly to broadly obovate, 30–50 (25–30 : 6–8) mm, primary veins 5–7, raised on the upper surface, secondary venation obscure; petiole short, broad, angular, 4–5 by 2 mm. *Male inflorescences* confined to older wood, occasionally spirally arranged on shorter, leafless side branches arising from older stems, 3–7 together, pedunculate; peduncles 2–3 by 0.7–0.8 mm, a single involucre of bracts at the apex and the base, bracts 0.7 by 0.7 mm, reflexed, involuted, margins entire or serrated. *Male flower* buds subsessile, green, globose, flattened at the apex; tepals 5, narrowly deltoid, 1.5 by 1 mm, glandular hairs absent; filaments long, narrow 0.5 by 0.2 mm, anthers large, dorsifixed, 0.5 by 0.5 mm, lobes isomerous, dehiscence longitudinal; nectary 5-lobed, convex, pubescent. *Female inflorescences* fewer together and usually shorter pedunculate, peduncle 0.3–0.5 by 0.8 mm. *Female flower* buds turbinate; tepals 5, narrowly deltoid, ovate, 1 by 0.8 mm, staminodes absent; stigma sessile, fleshy, entire, weakly papillate; nectary flat, angular, fleshy. *Fruit* immature, persistent perianth erect; exocarp smooth, mesocarp and endocarp not clearly defined as yet but endocarp clearly 4–5-chambered at the apex and the base.

Thailand.—NORTH-EASTERN: Loei [Phu Luang, Koyama et al. 31633 (A, BKF); Niyomdham & Tidal 446 (AAU, BFK, P); Smitinand 70389 (BKf); Hoet That, Muong Khu, Ogawa 21651 (KYO)].

Distribution.—Myanmar.

Ecology.—Hill evergreen forest, 1000–1500 m. Parasitic on *Quercus* (Fagaceae).

Note.—Name derived from thick older branches which are distinctly different from juvenile stems. This species is known from just three locations in Thailand and one in Myanmar. Characterised by very rough, fissured bark, leaves which are generally confined to the tips of the branches, longitudinally dehiscing anthers and a large entire stigma. Differs from other species of *Dufrenoya* found in Thailand in its longitudinally dehiscing anthers and entire stigma.


Erect or pendulous shrub, branches twining, much interwoven. *Juvenile stems* slightly flattened and nodes keeled, older branches smooth or with shallow elliptic, vertical fissures, pale in colour. *Leaves* coriaceous, elliptic to broadly obovate, 35–85 (28–50 : 8–15) mm, primary veins 5–9, raised on the upper surface, secondary veins fine, some diverging acutely, prolonged from the base and joining with upper secondaries, others
shorter and diverging at right angles, recurved and occasionally joining with opposite
veins; petiole 5–7 by 1–1.5 mm. Male inflorescences confined to juvenile wood, solitary
or 2–3 together on shorter side branches, pedunculate; peduncles 1.5–2 by 0.5–0.6 mm,
bracteate, 2 involucres of imbricate bracts at the base and 1 at the apex; bracts broadly
ovate, 0.7–1 by 0.6–0.8 mm, margins ciliate. Male flower buds yellowish-green, globose,
subsessile or shortly pedicellate, pedicel 0.6 by 0.6 mm; tepals 4–5, elongate-deltoid, 1–1.2
by 0.6 mm, glandular hairs present; stamens subsessile, filaments dilated at the base, 0.2–0.3
by 0.2 mm, anthers dorsifixed, lobes unequal in size, posterior much larger than the
anterior, 0.2 by 0.4 mm, dehiscence transverse; nectary 4–5-lobed, flat, fleshy. Female
inflorescences sessile or pedunculate, peduncles 0.2–1 by 0.8 mm. Female flower buds
yellowish, oboconical; tepals 5–6, deltoid, 1 by 1 mm; staminodes present, quite large,
filaments 0.2 by 0.1 mm, anthers 0.2 by 0.4 mm; style short, angular 0.3 by 0.3 mm,
stigma 5-lobed, lobes reflexed, smooth. Fruit yellowish-green, oblong or ovoid, 4.5 by
3.5–4 mm, persistent perianth erect; exocarp quite thick, smooth; mesocarp long,
membranous, wrapping around the endocarp; endocarp splitting easily, ovoid, 2.5 by
1 mm, shallowly 5–6-grooved.

Thailand.— NORTHERN: Chiang Mai [Doi Suthep, Kerr 1768 (K); Kerr 3240 (BM,
K); Larsen & Hansen 892 (BFK); Maxwell 92/249 (GH); Niyomdhun & Kubat 1351
(AAU, BKF, E); Sorensen et al. 6615 (A, Z); Mae Taeng, Santisuk 1049 (BFK); Sukkri
13 (BFK); north Chiang Mai, Pangbok hill, Smitinand 8717 (K); Doi Pui, 19 N 98 30 E,
Nootboom 670 (BFK); Lampang, Doi Khun Tan, Mae Tha district, Phengklai & Koyama
39106 (A); Northern Pong Pho, near Doi Chiang Dao, Larsen & Santisuk 2867 (BFK, E)];
Chiang Rai [Mae Suai, bunchu & Nimanong 1407 (BFK, L)]; NORTH-EASTERN: Loei
[Phu Krading, Kerr 20059 (BM); Smitinand 2105 (BFK); Smitinand 2205 (BFK);
Smitinand 2533 (BFK, BK); Sorensen et al. 6272 (E, SING); Abbe & Smitinand 9429
(A, BKF, L)].

Distribution.— Laos, Vietnam.

Ecology.— Hill evergreen and open grassy forests with Quercus and Castanopsis,
1500–2500 m. Parasitic on Lithocarpus, Quercus, Castanopsis (Fagaceae), Englehardtia
(Juglandaceae).

Vernacular.— Ka fak, mai tin nok (Thailand) (mistletoe, sticking to the feet of birds).

Uses.— Ingested to prevent food poisoning.

Note.— Name derived from the sessile female flowers. Characterised by interwoven
branches, broadly elliptic, obovate leaves and sessile to subsessile female inflorescences.
Taxonomically close to Df/ platyphylla, distinguishable by its smooth juvenile shoots
and weakly fissured bark, the fruit also lacks apical ‘tails’ on the endocarp.

3. PHACELLARIA

Benth., Gen. Pl. 3: 229. 1883; Hook. f., Fl. Brit. Ind. 5: 235. 1886; Pilger in Engl. & Harms,
1940.
Erect dendra parasitic shrubs, with some endophytic growth, stems originating in bundles from the branches of the host plant through lenticels, seldom branching, never climbing, hairless or with a hirsute indument, juvenile stems always at least papillose. Leaves reduced to scales. Inflorescences dioecious or monoeious, profuse, occasionally overtopping each other, sessile or sunken, arranged along the branches in spiral bands or rounded groups, flowers yellow or green. Male inflorescences 1–6-flowered, subtended by 1–2 involucres of bracts, bracts persistent or withering. Male flower buds globose, receptacle flat, tepals 4–6, deltoid, valvate, apiculate on the inner surface at the tip, glandular hairs absent; anthers cream, dorsiﬁxed, 0.2 by 0.5 mm, bilocular, locules bilobed, lobes isomerous, divergent, dehiscence transverse; style rudiment long, slender, capitate; nectary fleshy, 4–5-lobed. Female inflorescences 1-flowered, sessile. Female flowers with or without staminodes; style short, stigma 4–5-lobed. Ovary 0.2–0.3 by 0.3–0.4 mm, placenta convex, sessile, 4–6-lobed, lobes short. Fruit green, oblong, ovoid, perianth persistent, erect; exocarp smooth, thick; mesocarp consisting of membranous or sericeous strands which are attached to the endocarp and wrap around it, finally lying against the inner surface of the exocarp; endocarp splitting easily, oblong or obovoid, apex obtuse or acuminate, base rounded; internally 5–7-chambered at the apex, 5–7-lobed for the rest. Seed with separate lobes at the apex. Embryo located near the apex of the endocarp between the apical lobes.

Four species from Southern China to the Malay Peninsula. Two species in Thailand.

Ecology.—Hill evergreen forest, ridge forest and open forest of Pinus khasya and Dipterocarpus tuberculatus, above 1000 m. Hyperparasite on species of Scirrula, Macrosolen, Taxillus and Loranthus (Loranthaceae); Viscum (Viscaceae); Dufrenoya (Santalaceae).

Note.—Name refers to the fasciculate nature of the stems and possibly to the origin of the stems from the lenticels of the host plant. The majority of species are described from very few collections which, like Dufrenoya, indicates they are either rare or overlooked. This problem may be particularly acute in Phacellaria where stems are slender and almost leafless and fruits and flowers are inconspicuous. The species are all closely related and distinguished on the basis of inflorescence structure and growth habit. They are also hyperparasites (parasitic on other parasitic plants). Phacellaria is the only genus in the family where endophytic growth has been observed. It follows closely the distribution of Dufrenoya but with a more contracted geographic range and both genera occupy similar habitats. Phacellaria fruits are also dispersed in a similar manner to Dufrenoya and parallel evolution may have resulted in a similar fruit type in genera that in other respects are different.

**KEY TO THE SPECIES**

Juvenile branches covered in a dense, villous tomentum; inflorescence 1-flowered, bracts not withering

1. P. compressa

Juvenile branches entirely papillose or weakly hirsute; inflorescence 5–6-flowered, bracts withering

2. P. rigidula

Branches light green, slender, tortuous, slightly flattened and ridged, covered in a dense, villous tomentum, short side shoots arranged spirally, curving upwards. Juvenile stems 1 mm in diam., thickening to 2–2.5 mm at maturity and becoming papillose. Plants dioecious. Inflorescences 1-flowered, initially crowded at the tips of shoots, later separating into oblong groups along the ridges of the stems, flowers sunken, subtended by an involucre of persistent, minute, completely villous–hairy bracts. Male flower buds light green, covered in the same tomentum as the stems, later becoming papillose, tepals 4–5, 0.7–1 by 0.7–1 mm, slightly contracted at the base; filaments dilated at the base, 0.3 by 0.1 mm; nectary, green, fragrant, flat. Female flower buds green, turbinate, tepals 4–5, 0.4 by 0.6 mm, thick, receptacle 0.5 by 0.5 mm; staminodes absent or occasionally 1–2; stigma subsessile, 4-lobed, lobes rounded; nectary flat, angular. Fruit oblong, 5–6 by 3 mm; mesocarp short, sericeous, abundant at the apex of the endocarp extending 0.5 mm beyond it; endocarp oblong or slightly ovoid, 4 by 2.5 mm, distinctly 4–6-lobed, apiculate at the base.

Thailand. — NORTHERN: Chiang Mai [Doi Saket, Santisuk 10603 (BFK); Dan Sai, Kao Keo, Kerr 5796, (BM, L); Mae Soi ridge, Maxwell 91-242 (GH)].

Distribution. — Southern China, southern India, Myanmar, Vietnam.

Ecology. — Primary evergreen and mixed evergreen forest 800–1200 m. Hyperparasite on Viscum (Viscaceae) Loranthus, Macrosolen (Loranthaceae) and Dufrenoya (Santalaceae).

Note. — Name derived from the slightly flattened juvenile stems. The most widespread species of Phacellaria, characterised by densely villous-hairy juvenile stems, thickened mature shoots and oblong flower groups. Closely allied to P. rigidula but distinguished by branched stems, 1-flowered male inflorescences subtended by minute bracts and a sericeous rather than membranous mesocarp.


Branches slender, tortuous, terete, not at all branching, entirely papillose or weakly hirsute. Juvenile stems faintly striate and ridged, less than 1 mm in diam., thickening to 1.5–2 mm. Inflorescences monoecious, male and female flowers on separate shoots, initially crowded at tips of the branches, later separating into distinct spiral band along stems, initially 1-flowered, subtended by an involucre of 3–5 small bracts; bracts elongate, ovate, papillose on the outer surface and along the margins, flowers developing in the axils of the bracts. Inflorescence finally 5–6-flowered, globose. Male flowers green, hairless, tepals 5–6, elongate-deltoid, 1 by 0.5 mm; filaments dilated at the base, 0.2 by 0.1 mm; nectary slightly angular, apiculate in the centre. Female flower buds turbinate, receptacle 0.8 by 0.5 mm; tepals 5, deltoid, 0.5 by 0.5 mm, inflexed at the tips; staminodes absent; stigma subsessile, 4-lobed, lobes rounded, weakly papillose; nectary flat, lobed, lobes rounded. Fruit yellowish, oblong, ovoid, 6–7 by 3.5–4 mm; mesocarp long, membranous; endocarp oblong, ovoid, 5–6-lobed.

Thailand.—NORTHERN: Chiang Mai [Ob (Bo) Luang, road to Omkoi, Beusekom & Phengkhai 2546 (AAU, BKF, E, KYO, L)].

Distribution.—Southern China and India.

Ecology.—Secondary and dry dipterocarp forest, 500–2500 m. Parasitic on Loranthus and Scurrula (Loranthaceae).

Note.—Name derived from the ridged stems. Characterised by slender, weakly hirsute juvenile stems. Taxonomically similar to P. compressa, differentiated from it by monoecious, multi-flowered inflorescences which are subtended by a distinct involucre of bracts and a long, silky mesocarp.

TRIBE SANTALEAE


Trees or shrubs, leaves alternate or spiral, usually relatively large, persistent. Inflorescences racemose, cymose, multi-flowered. Flowers relatively large, yellow, green or white often changing colour with maturity, hermaphrodite or dioecious; glandular hairs present; stamens flexed into the centre of the flower at anthesis, anther bilocular, locules bilobed, dehiscence longitudinal, incomplete at the base; style long, slender or broad, stigma 3–5-lobed, lobes elongate; nectary present, fleshy, lobed, lobes short or prolonged between the perianth segments. Ovary semi-inferior, placenta large, 3–5-lobed, placental column long or short, contorted or straight. Fruit a drupe, perianth persistent or caducous, exocarp thin, mesocarp fleshy, thin, endocarp unilocular, hard, smooth or punctate. Seed
entire; embryo located at the centre of the endocarp.

Note.—Distribution cosmopolitan but generally southern hemisphere, containing mainly shrubby and tree species. Several monotypic genera in South America. Variable in terms of ovary construction. Fruit construction varying at generic level only.

4. OSYRIS


Hairless shrub, branches pendulous, bark smooth or faintly striate. Leaves spiral, rounded, elliptic, lanceolate, fleshy, glaucous; venation curvippinate, secondary veins 6–7, curving outwards, not connecting at the margins. Inflorescences dioecious, pedunculate, subtended by a single lanceolate bract which is usually caducous; peduncle long and slender, angular, dilated at the apex. Male inflorescences in leaf axils, cymose, 8–10-flowered, each flower subtended by a single lanceolate bract. Male flowers pedicellate, tepals valvate, 3–4, outspread, glandular hairs present; anther lobes unequal in size, posterior smaller than the anterior; nectary flat, lobed, apiculate in the centre. Female inflorescences 1-flowered, pedunculate, peduncle slightly shorter than the male. Female flowers pedicellate, receptacle enlarged and elongated, staminodes present; style long, angular, stigma 3-lobed. Ovary inferior, sub-sessile, 0.3 by 0.3 mm, placenta shallowly convex, 3-lobed, lobes rounded, short, curling under the placenta, placental column short, broad. Fruit ripening red, orange or black, globose, perianth caducous, leaving a faint circular scar, nectary and style may be persistent; exocarp smooth; endocarp thin, completely smooth, globose, slightly obovate. Seed fleshy.

Two species from southern Europe to Africa, India, Myanmar and Vietnam. One species in Thailand.

Ecology.—In disturbed and exposed, dry areas on limestone, above 1000 m. Associated with bamboo.

Note.—Name derived from the goddess Osiris. Southeast Asia is the most southerly distribution of this genus which is most common in Africa. It is characterised by shrubby growth, pendulous branches and flowers which change colour with maturity, in a similar way to Santalum album, from yellow or green to dark red or brown. The volatile oil obtained from the wood is sometimes used as an inferior substitute for Santalum album.


Shrub, creeping when young by means of stolons. Juvenile stems angular, flattened, keeled at nodes, smooth and slightly ridged, bracteate at the base, giving a jointed appearance, older branches terete, bark with shallow longitudinal fissures. Leaves 22–44 (11–28 : 7–12) mm, apex acuminate, tip mucronate, base attenuate, primary vein raised on the upper and lower surfaces, leaves sometimes covered in a powdery bloom. Male inflorescences in leaf axils, peduncles angular, 6–10 by 0.5 mm, flowers crowded at the apex of the peduncle, many caducous, only 4–5 reaching maturity; each flower subtended by a single tortuous, lanceolate bract, the bract 1 by 0.2 mm; flowers grouped in triads with 1 central and 2 lateral flowers, the central flower reaching maturity first. Male flowers green, pedicel ca. 1 mm long, tapering towards the base; tepals fleshy, broadly ovate, 1–2 by 1.2–1.5 mm, leaf-like with one central veinlet, apiculate at the tip on the inner surface, margins slightly involuted, papilllose; filaments slightly dilated at the base, 0.4 by 0.1 mm, anthers 0.2 by 0.3 mm. Female inflorescences with peduncle 3–4 mm long. Female flowers subtended by an involucre of 3 tortuous, lanceolate, valvate bracts, which reach at least halfway up the flower, resembling a calyx; tepals broadly ovate, 1–2 by 1.2–1.5 mm, shortly apiculate on the inner surface, papilllose along the inner margin; style 0.5 by 0.3 mm, stigma lobes fleshy, pointed, smooth; nectary flat or slightly concave. Fruit ripening orange or red, 5–6 by 5–5.5 mm.

Thailand.— NORTHERN: Chiang Mai [Doi Chiang Dao, Put 4483 (AAU, E); Smitinand 7246 (BKF); Geesink et al. 8134 (AAU); Bunchuai 1308 (BKF); Bunchuai 1335 (BKF); Sorenson et al. 4191 (BKF); Sleumer 4746 (SING); Hansen & Smitinand 12635 (AAU, E); Doi Inthanon Ivatsuki & Fukuhira 3666 (BKF); Garrett 823 (BKF, E, K); Koyama et al. 15627 (AAU); Smitinand & Anderson 25887 (E, KYO); Kerr 6121 (K); Kerr 6614 (K); Tak [Umphang district, Mae Rim & Samoeng border, Sudee & Pooma 834 (BKF, TCD)].

Distribution.— Southern Europe and Africa to China, India, Vietnam.

Ecology.— Often associated with bamboo, in exposed areas on limestone, 1000–2000 m.

Uses.— Has been traditionally used as a tea substitute in the foothills of the Himalayas, which led to the mistaken belief, that the true tea plant, Camellia sinensis, was native to this region.

Note.— Name derived from the lanceolate leaves. Characterised by a shrubby, pendulous growth habit, lanceolate leaves and typically trimerous, unisexual flowers. This species is similar to Santalum album, but distinguished by its smaller, inconspicuous, unisexual flowers and shorter nectarial lobes.
5. SANTALUM


Small hairless tree to 6 m; bark smooth or rough, brown or dark grey. Leaves opposite, alternate, large, elliptic, thin, venation compound rectipinnate, secondary veins 5–6, inter-secondaries relatively thick, acutely angled to the primary vein. Inflorescences 9–15-flowered, branching cymose, flowers grouped into triads on terminal branches. Flowers hermaphrodite, pedicellate; tepals cream, white, 4–5, reflexed, fused into a deep hypanthium, glandular hairs profuse; anthers dorsifixed, separated by a relatively thick connective, diverging near the apex, posterior lobes slightly shorter than the anterior; nectary bright red, lobes short or long and protruding between the perianth segments; style long, slender, stigma 2–4-lobed, lobes erect. Ovary semi-inferior, the apex of the placenta protruding into the base of the style, 1.3–1.5 mm long, placenta sagittate, 3–4-lobed, lobes very short, not curling in towards the placental column, column short, broad. Fruit pedicellate, red or black, globose, perianth caducous, leaving a circular raised scar at the apex of the fruit, style and nectary sometimes persistent; endocarp smooth with a tri–radiate scar running from the apex to the base. Seed fleshy.

Twenty-five species from Java to the Pacific Islands. One species, traditionally cultivated in Southeast Asia, in Thailand.

Ecology.— In coastal areas, behind beaches, on rocky, free draining soil in lowland forests, secondary woodland and savannah, up to 300 m.

Note.— Name derived from the Sanskrit, shandal, the meaning of which is unknown. Characterised by relatively large flowers with petaloid perianth segments and a large, brightly coloured nectary. The flowers change colour from white or cream to dark red or brown with maturity. This may be a way of discouraging pollinators from visiting the flowers after fertilisation, so increasing efficiency in pollinator/flower interaction. It is thought that *Santalum* species rely on a host plant only in the early stages of development and that they are not host specific. In India, however, *Senna siamea* is used as a host in cultivation. The wood is a source of sandalwood oil which is widely used in perfumery and traditional medicine. The active constituent is santalol which has cooling and expectorant properties. Some species are now rare or extinct due to the over exploitation of their timber, e.g. *S. freycinetianum* is known to have become extinct in the Hawaiian islands around 1916 and *S. spicatum* is rare in Australia due to over-exploitation. *S. album*, which is cultivated in Southeast Asia, is currently the most commercially valuable species, containing the highest concentrations and the best quality sandalwood oil.

Juvenile stems smooth, angular, bracteate at the base, appearing jointed, older branches terete, bark rough, cracked, with narrow horizontal fissures. Leaves opposite or subopposite, coriaceous, brittle, elliptic, ovate, 50–70 (22–31: 7–11) mm, apex acute, shortly acuminate, base obtuse, attenuate, margin undulate, primary vein raised on both surfaces, tertiary veins variable in direction but generally at right angles to the secondary veins, seldom anastomosing, branching twice dichotomously, vein endings free; petiole slender, 8–9 by 1.1–1.2 mm, upper surface involuted, lower surface angular. Inflorescences terminal and axillary, cauliflorous and on young shoots, pedunculate, peduncle slender, 10–13 by 0.6–0.7 mm, tortuous, angular, sulcate, each flower on a very short stalk, 0.3–0.5 mm long. Flower scented, creamy white turning red and purple, buds turbinate, shortly pedicellate, pedicel slender, angular, 1–1.5 by 0.5 mm, receptacle 1–1.5 by 2 mm; tepals large, narrowly deltoid, 3–3.5 by 1–1.5 mm, reflexed; filaments narrow, 1.4–1.5 by 0.3 mm, weakly dilated at the base; style angular, extending beyond the hypanthium, 2.5–2.7 by 0.3 mm, broadening towards the base, stigma 3-lobed, weakly papillate; nectary concave, deeply 5-lobed, lobes tongue-shaped, up to 1 mm long, protruding between the perianth segments. Fruit 8–10 by 8–9 mm, exocarp smooth, endocarp globose, 7.5–8.5 by 7.5–8.5 mm.

Thailand.—CENTRAL: Saraburi [Phu Khae Botanic Garden, Smitinand 89/48 (BKF); Santisuk 6874 (BKF)].

Distribution.—Native from Java to the Timor Islands. Cultivated in India.

Ecology.—In secondary woodland and savannah, 30–100 m. Also cultivated at roadsides or beside villages.

Note.—Name derived from the white flowers and pale, scented wood. Widely cultivated in India for its fragrant, valuable timber but not native to this region. S. album is the only species of this genus in Southeast Asia, the rest of the species are found in Australia and the Pacific islands. Characterised by relatively large flowers, with petal-like perianth segments which are fused into a hypanthium-like structure and a large, distinctive, brightly coloured nectary. Allied to Osyris lanceolata but distinguishable by the larger, hermaphrodite, more showy flowers.
Linnaeus (1753) cited Breynius (Prodromus fasciculi rariorum plantarum 1: t5 (1680)) and Bauhin (Pin. 392). Jarvis (pers. comm.) suggests that the latter probably leads to a wood sample in Herb Burser XXII:20 at UPS. Sa’ad (1983) in Taeckholmia, Add. Ser. 2: 16 indicated Linn 161.1 as type, but this sheet lacks a Species Plantarum number, is not original material for that name and has been determined by J.E. Smith (in sched.) as Memexylon capillatum (Jarvis, pers. comm.). Following Jarvis’s suggestion we have therefore lectotypified herein the Breynius plate. However, as the detail on the Breynius’ s plate is insufficient (it shows just the vegetative structure of this species); we have also been designated an epitype here to avoid confusion with other species.

6. SCLEOUPYRUM


Small trees, 4–6 m tall, occasionally with spines on the trunk, branches weakly or densely pubescent, nodes thickened and raised, covered with bract and inflorescence scars, scars 10 mm in diam., suberous; bark white or brown, smooth. Leaves large, hairless or ± tomentose beneath; venation multi-arcuate, veins raised on the lower surface, secondary veins 3–10, basal veins placed opposite each other, others arranged alternately, forming a co-arcuate inframarginal vein and breaking up into a series of small arching loops, forming a zone between the inframarginal vein and the leaf margin. Inflorescences cauliflorous and in leaf axils, greater than 15 mm long, dioecious, catkins, solitary or 2–3 together, densely pubescent with a long wiry indument; each flower subtended by a single persistent bract. Male inflorescences many-flowered (up to 100 per inflorescence), rachis slender, ridged, flowers placed along the ridges. Male flowers green or pale yellow, buds initially globose, later broadly campanulate, sessile, shortly pedicellate, receptacle flat to deeply concave; tepals 4–5, valvate or lightly imbricate at the base, sparsely hairy, outspreading and reflexed forming a shallow hypanthere, glandular hairs profuse; anthers basifixed, separated by a narrow connective, anther lobes unequal in size, the posterior longer and broader than the anterior; nectary fleshy, concave, 4–6-lobed, lobes smooth; rudimentary style short, slender, capitulate; ovary present, superior, slender, sagittate, abortive. Female inflorescences fewer flowered than the male, rachis broader, flowers larger. Female flowers subsessile, pedicel extending considerably at fruiting, receptacle enlarged, elongated; staminodes present, curving under the stigma; style large, broad, taking up the centre of the flower, stigma large, peltate; nectary fleshy, flat or convex. Ovary semi-inferior, placenta convex, apex protruding into the base of the style, 3-lobed, lobes long, contorted, curving in and under the main body of the placenta, ovules placed at the tips of the lobes, placental column long, twisted and coiled in the ovarian cavity so that the lobes of the placenta rest on top of it. Fruits large, green or yellow, pyriform, perianth persistent, erect, pedicel decurrent with the base of the fruit; exocarp thin, smooth, waxy; endocarp thick, globose, with a circular depression at the apex. Seed woody.
Four species from southern China and India to New Guinea. Two species in Thailand.

Ecology.—Generally associated with disturbed habitats, up to 1500 m. Locally common on limestone and sandy soil, in lowland hillside forest, in the undergrowth of Castanopsis/Quercus forest and in Eurya (Theaceae)-dominated secondary forest. Common by streams in open areas of evergreen forests, dry evergreen forests, lowland Dipterocarp forests, also coastal areas from vegetation behind beaches.

Note.—Name derived from Sclero- meaning hard and pyrus meaning pear, name refers to the pear-shaped fruit and the hard endocarp. Characterised by pyriform fruits, catkins and hairy stems and inflorescences. Contains one very widespread species, which occurs across the range of the genus, and three with narrower distributions. The species are all morphologically similar but can be distinguished on the size and aestivation of the male flowers and the shape of the fruits, which are poisonous.

**KEY TO THE SPECIES**

Spines absent, stems and leaves hairless or weakly hairy; tepals valvate; filaments 0.3–0.5 mm long 1. S. maingayi
Spines present; stems and leaves hairy; tepals weakly imbricate; filaments 0.7–1 mm long 2. S. pentandrum


*Juvenile stems* terete, smooth, shining, initially sparsely hairy then hairless and occasionally pubescent; bark smooth with a glossy sheen and narrow longitudinal fissures, becoming occluded, spines absent. *Leaves* narrowly to broadly ovate, 140–270 (80–100 : 25–40) mm, base obtuse, apex shortly acuminate, upper surface shining, both surfaces sparsely hairy or hairless; secondary veins 3–4, tertiary veins relatively thick, almost perpendicular, percurrent with opposite veins, where anastomosing forked and giving rise to 4th order venation, vein endings not free, connecting and forming an orthogonal reticulate pattern; petiole 5–6 by 2 mm. *Male inflorescences* cauliflorous and probably also on young wood; bracts lanceolate, ovate, 1–1.2 by 0.2 mm. *Male flowers* yellow, fragrant, shortly pedicellate, pedicel 0.7–1 by 0.4–0.5 mm; tepals valvate, ovate, 1.7–2.2 by 1.5 mm, tips recurved and shortly apiculate; filaments short, broad, 0.3–0.5 by 0.3–0.5 mm, anthers twice as broad as long, 0.3–0.4 by 0.7–1 mm; style rudiment short, thick, 0.3–0.5 by 0.3–0.5 mm, stigma indistinctly lobed. *Female flower* unknown. *Fruit* yellow, 20–35 by 20–30 mm, pedicellate, pedicel extending to 15 mm; endocarp surface entirely weakly punctate.

Thailand.—**PENINSULAR**: Satun [Rawi Island, Congdon 1003 (A); Ko Adang, Kerr 14116 (K); Ban Tin, Kerr 5012 (L)]; Trang [Kaw Libong, Kerr 19061 (L); Khao Chong, Phusomsaeng & Smithinand 180 (L)].

Distribution.—Malay Peninsula, Sumatra, Java, Borneo.

Ecology.—Open areas in primary evergreen forest, 100–1400 m.
Note.—Name derived from the collector of the type specimen, A. C. Maingay, a doctor and magistrate who collected in the Malay Peninsula from 1862–68. Characterised by the absence of spines on the trunk; large, almost hairless leaves; small, fragrant male flowers and large yellow fruits. This species, similar to *S. pentandrum*, differs in its large ovate, hairless leaves, smaller male flowers with valvate tepals, and shorter filaments. The species is newly recorded here for Thailand.


*Juvenile stems* striate, covered in a light waxy sheen, slightly flattened, becoming terete, initially densely pubescent becoming hairless; bark smooth, grey, waxy; spines present, solitary or several together emerging above leafless nodes, initially narrow, 0.7 mm long, pubescent, a series of small bracts concentrated at the base but also arranged spirally along its length, quickly becoming covered in a waxy deposit, thickening and lengthening with maturity. *Leaves* narrowly to broadly elliptic, ovate, 100–180 (35–58 : 15–25) mm, base attenuate, apex acute, shortly acuminate, upper surface shining, pubescent along mid-vein, under surface sparsely or densely hairy; secondary veins 4–9, tertiary veins fine, almost perpendicular to the secondary veins, opposite territories perpendicular, course straight or veins forked when anastomosing, higher order venation indistinct or absent; petiole 6–10 by 2 mm. *Male inflorescences* cauliflorous; bracts ovate-lanceolate, 1.3–1.5 by 0.3–0.5 mm, apex acuminate, base rounded. *Male flowers* smelling unpleasant, yellow, greenish-yellow, subserial or pedicellate, pedicel 0.5–1.5 by 0.3 mm; tepals weakly imbricate at the base, ovate, 2–3 by 1.3–1.6 mm, tips recurved but not apiculate; filaments long, narrow, 0.7–1 by 0.2–0.4 mm, anthers 0.4–0.5 by 0.6–0.8 mm; style rudiment slender, 0.4–0.9 by 0.2–0.4 mm. *Female flowers* sessile, obconical in bud, densely pubescent; receptacle 2.5 mm long; tepals imbricate, 2–2.5 by 1–1.5 mm, ovate, apiculate on the inner surface at the apex; style short, broad, 0.5–0.6 by 0.4 mm, not extending above the rim of the nectarial disc, stigma large, peltate, 3-lobed, lobes recurved, margins uneven with two shorter and one longer section. *Fruits* green, turning
yellow, poisonous, 18–33 by 13–26 mm, pedicel extending to 17 mm; endocarp surface perforate or sulcate, particularly near the apex.

Thailand.—NORTHERN: Chiang Mai [Maxwell 88/354 (AAU, L); Maxwell 88/225 (L); Maxwell 88/533 (A); Ban Ta Fang, Vidal 5336 (P); Mc Tsung, Kerr 16 (K); Ban Sun, Doi Saket, Kerr 1026 (K, TCD); Doi Suthep, Kerr 1701 (AAU, K); Kerr 1711 (K, TCD); Larsen & Hansen 6882 (BKF); Native Collector 410 (A); Smitinand 3307 (BKF); Sukkri 2 (BKF); Sorenson et al. 3415 (BKF); Sorenson, Larsen & Hansen 6894 (BKF); Suvarnakoses 68 (BK); Doi Inthanon, Worawot 3 (BKF)]. NORTHEASTERN: Udon Thani [van Beusekom & Santisuk 2912 (AAU, BKF, L); Phu Phan, Suvarnakoses & Smitinand 2037 (L); Smitinand 11295 (E, K, L); Phu Phan National park, 17 03N, 103 58E, trail north of park headquarters, Suddee et al. 1007 (BKF, TCD); Phetchbun, Sangkadand 3080 (L)]; Loei [Phu Kradung, Suwatabandhn 75 (BKF, K)]. EASTERN: Si Sa Ket [East Si Sa Ket, Suvarnakoses 1502 (BKF, L)]; Nakhon Ratchasima [Hui Taleng, Put 2212 (K)]; SOUTH-EASTERN: Trat [Kao Saming, Kerr 9428 (L)]; Prachin Buri [Koyama et al. 33012 (A, L); Tapaya, Put 39 (BKF)]; Rayong [Ban Phe, Niyomdhon & Kubat 1306 (AAU, E, L); Phengklai 4009 (A)]. SOUTH-WESTERN: Kanchanaburi [Phengkrai 362 (BKF, B, L)]. PENINSULAR: Satun [Smitinand 7320 (AAU); Tarutao, Smitinand 387 (A); Smitinand 2685 (BK); Tarutao, Hansen Smitinand 12497 (K); Tarutao national park, northeast from Adang HQ, Congdon 387 (AAU); east side of Koh Tarutao, 6 30N, 99 45E, Geesink & Hattink 7320 (L)]; Phangnga [Phu Muang, Hansen 11162 (E, K)]; Krabi [Sakeo, Kerr 9791 (K)]; Ranong [Kampang, Kerr 16865 (K); Kuan San, Kerr 20184 (K)]; Satal, Kao Keo range, Kerr 14567 (E, L, TCD); Songkhla [Hat Yai, Dton Nga Chang reserve, Maxwell 85/290 (A, AAU, E); Maxwell 85/336 (BKF, L); Ubol, Pho Sai, Pong Ta Wang, Santisuk 6685 (BKF); Tat Noi, Smitinand 10239 (L); Smitinand 85/290 (A, L)]. Chon Buri [southeast Chon Buri, Sangkhachon 618 (BKF, L)]; Rayong [12°37' N, 101°10' E, Smitinand et al. 6039 (L); Suwatabandhn 7824 (L)].

Distribution.—India to Irian Jaya.

Ecology.—Up to 1000 m, generally associated with disturbed habitats on sandy soil. Common by streams in open areas of evergreen forests, dry evergreen forests, lowland dipterocarp forests. Also collected in coastal areas from vegetation behind beaches.

Vernacular.—Mo sa lo, Kaa nam (Thailand) (spiny); Lo lok keo (Cambodia).

Note.—Name derived from the pendulous inflorescences. In Rheede's Hortus Malabaricus (1688) Tirri refers to the racemose inflorescence and itticanni means parasite. Flowers may have a slightly foetid smell and the fruits are poisonous. Characterised by spines on the trunk and young branches, pubescent leaves and quite large pyriform fruit. Scleropyrum ridleyi was separated from S. pentandrum on the basis of it having a greater number of secondary veins and hairier leaves. In reality, however, the degree of hairiness of the stems and leaves is continuously variable and the number of primary veins is dependent on leaf size. In Borneo the flowers and fruits are slightly larger than elsewhere. There are, however, no discrete characteristics which can be used to separate them from individuals in Thailand and the Malay Peninsula. The two varieties var. mekongense and var. siamensis were separated based on mainly vegetative characteristics: var. siamensis was supposedly distinguished by its leaves which are velvety on the under surface, whereas var. mekongense was said to have almost hairless leaves.
However, the degree of hairiness of the leaves is not a good taxonomic character as it varies continuously within the species, and therefore the varieties cannot be maintained based on this feature. In addition, var. mekongense is said to have subsessile flowers. This characteristic seems to vary continuously, however, within S. pentandrum and all states from from subsessile to distinctly pedicellate flowers may be found. Scleropyrum pentandrum may be confused with S. maingayi but can be distinguished by its larger flowers with imbricate aestivation, longer filaments and larger anthers in the male flower. It is also usually found at lower elevations in areas more prone to disturbance.

TRIBE THESIEAE


Hairless herbs, small shrubs, leaves alternate, spiral, large or reduced to phylloclades. Inflorescences reduced to a single flower, solitary. Flowers yellow or green, hermaphrodite, glandular hairs present, profuse; anther locules isomerous; style short or absent, stigma capitate, 3–5-lobed; nectary absent or thin, membranous, extralocular nectaries occasionally present. Ovary inferior, placenta 3–4-lobed, lobes long, contorted, placental column short, slender. Fruit nut-like, exocarp thin, mesocarp very thin, dry. Seed entire, eliasomes sometimes present.

Note.—Cosmopolitan distribution but mostly confined to Africa. Species distinctive in terms of solitary inflorescences and dry fruits.

7. THESIUM


Slender, hairless herbs, erect or prostrate, branches angular, sulcate. Leaves small, often bract-like, decurrent, crowded near shoot apices. Inflorescences sessile or pedunculate. Flowers hermaphrodite, receptacle slender, elongate; tepals valvate, sometimes united into a short hypanthium; anthers bilocular, locules bilobed, dehiscence longitudinal; stigma capitate, smooth. Ovary relatively large, placenta, convex, 3-lobed, lobes long, slender, curling around the short placental column. Fruit globose, nut-like, sessile or shortly pedicellate, perianth persistent, erect; exocarp ribbed; endocarp globose, apex apiculate, outer surface sulcate, rugulate.

Ca. 325 species worldwide, this genus has a cosmopolitan distribution, is concentrated in Africa, and has not been the subject of any recent revision. One species in Thailand.

Ecology.—In grassland, above 1000 m.
Note.— Name derived from Theseus of Greek mythology. Characterised by herbaceous, often prostrate growth, small, scale-like leaves and a nut-like drupe.


Herb, stems long, angular, sulcate, side shoots concentrated at shoot apices, spirally inserted. *Leaves* bract-like. *Juvenile shoots* bracteate at the apex, bracts crowded, spirally inserted, 1–1.5 by 0.6 mm, elongate-deltoid, outer surface covered in a smooth waxy deposit, older stems sparsely bracteate with occasional side shoots arising from bract axils. *Inflorescences* terminal, subtended by an involucre of quinuncially arranged bracts; bracts ovate, lanceolate, 1.5–2 by 0.7 mm, apex acuminate, outer surfaces convex, inner surface flat. *Flowers* with receptacle 1 by 0.8–1 mm; tepals deltoid 0.5–0.6 by 0.5 mm, fleshy, outer surface convex, inner surface flat with a distinctive lip or edge at the margin; filaments slender, tortuous, 0.3 by 0.1 mm, anthers dorsifixed, 0.4 by 0.3 mm; nectary membranous, concave, smooth, 5-lobed; stigma sessile. *Fruit* 4–4.5 by 3–3.5 mm, sessile or shortly pedicellate, pedicel decurrent, exocarp thin, rugulate with 10 longitudinal, raised bands running from the apex to the base of the fruit, mesocarp absent, endocarp 2.5–3 by 3–3.5 mm.

Thailand.— NORTH-EASTERN: Loei [Phu Kradung, *Poona* 67 (BKF); *Smitinand* 437 (BKF); *Smitinand* 1116 (BKF); *Smitinand* 5872 (BKF); *Hance* 7570 (BKF)].

Distribution.— Laos.

Ecology.— Between in open areas in marshy grassland and grassy areas of *Quercus/ Pinus* forests, 1200–1300 m.

Note.— Name derived from the smooth, hairless stems. The only representative of this genus in Thailand. Characterised by herbaceous growth form, angular stems and bract-like leaves.

**ACKNOWLEDGEMENTS**

We would sincerely like to thank the Curators of A, AAU, B, BK, BKF, BM, BO, K, L, P, U, SING and Z for the loan of herbarium material. We are grateful to the Trinity College Foundation, Trust and Graduate Studies offices who funded visits to several European herbaria. The following individuals are particularly thanked for their help in various ways: Marcella Campbell, Trevor Hodkinson, Charlie Jarvis, Conor Meade, David Simpson and Somran Suddee.

**REFERENCES**

der Naturforschenden Gesellschaft in Zürich 114: 49–76.

NON-THAI SPECIMENS EXAMINED

Dendrotrophe buxifolia (Blume) Miq.
CHINA: Hong Kong, Happy Valley, Bodinier 124 (L).
VIETNAM: Bhudec, Pierre 1409 (E, GH).
CAMBODIA: Cheko, Koh Kong province, Kira et al. 387 (KYO).
MALAY PENINSULA: Kingdom Ward 37469 (K); Ridley s.n. (K); Sargent 27 (A); Went
s.n. (BO); Johor [Shah 2920 (SING); Corner & Henderson 36616 (SING, P)]; Kelantan
[path to Gunong Rabong, Shah 2485 (SING)]; Pahang [Maxwell 80-25 (L); Corner 29917
(BO); Bukit Kroh forest reserve, Burkill 2615 (L); north of Dunggun, Poore 741 (K);
Pangkor island, Telok Gedong, Burkill 292 (L, SING)]; Penang [Penor (George Town),
Corner 29917 (BO); Balgooy 2200 (L); Batoe district, si Boeoea 3615 (A); Labochean,
si Boeoea 3364 (A)]; Terengganu [Burkill 4614 (L, SING)].
SARAWAK: Bako National Park [Telok Asam, Purseglove 5561 (L, SING); Purseglove
4920 (L, SING); Telok Tajor, Chai 18009 (L); northeast of Kuching; Jacobs 5508 (L);
Kuching, Sleumer 4677 (L); Litang, path below Bukit Tambi, Ashton 17969 (L, SING);
Bukit Pantu, Ibrahim 183 (SING)]; Chew 1411 (A, L, SING); Mt Santubong, Castro 9992
(A); summit of Santubong, Dunselman 169 (L); Lambirs hills, Dan Bin & Bakar 3019 (L);
Dayang 50406 (L); Polak 253 (BO). SABAII: Sipitang [Beaman 8407 (A, L); Madani &
Amin 86230 (L, SING)]; Mt Kinabalu, path to Ranau, Carr 26951 (SING); Hallier 1490
(L); Karimata island, Meijer 37869 (L); Karimata island, Poelau Seroetoe, Mondi 186
(L, U).
BRUNEI: Belait [near Labi road, Nangkat 23 (A)]; Tutong [Pasir Puteh, 4°42’ N, 114°31’
E, Boyce 227 (L)].
PHILIPPINES: Palawan [Lapu lapu river, Edano 115 (A, SING)].
SUMATRA: west coast, Tiku, north of Pariaman sand dunes, Meijer 7593 (L); si Boeoea
3623 (A);
BANGKA: Teysmann s.n. (U); Teysmann 3460 (P, U); Bunneymiejer 1473 (BO, L);
Bunneymiejer 1621 (L); Burger 25 (L); Huitema 39 (L); Kostermans & Anita 1353 (L, P).

Dendrotrophe varians (Blume) Miq.
CHINA: Hainan [Changjiang, Chow 78375 (E); Yacheng, How & Chun 70121 (E); Yeung
Lam Shan, near Yeung Lam village, Sai-hsien district, Lau 6145 (E); Mt Chim Fung, near
Fong Ngau Po village, Kan-en district Lau 5435 (E); Lau 20199 (L); Lingshi, Lei 374 (P);
Henry 8527 (P); Liang 66469 (P); How 73951 (P); Mo San Leng, Chun 44326 (L);
Kwangtung [Luo-fu Shan, Tung 5756 (L); Gaozhou, Guangdong, Yip 382 (L); Kwangtung
border. Tsang 22338 (P); Schindler 437 (P)]; Hong Kong [Ma On, Hu & But 20103 (L);
Wright 400 (K); Shan, Wright 12 (P)]. LAOS: Harmand (P).
VIETNAM: Bac Phan [Sia Wong Mo Shan, Lung Wan village, Dam-ha, Tsang 30073 (A, E, K); Santay, Hung Hoe, Petelot 6170 (A); Fan Si Pan, Petelot 6179 (A); Bac Phan, Vinh Yen, Petelot 2.563 (A); Fan Si Pan, Petelot 2.561 (A); Fan Si Pan, Petelot 6185 (A); Petelot 5703 (A) Bac Phan, Balansa 1565 (P); Bac Phan, Balansa 2320 (P)]; Chai 39734 (K); Vinh Yen [road to Tom Dao, Petelot 2563 (A); Eberhardt 3824 (P); Clemens (A); Pierre 1409 (A); Poilane 7132 (L)]; Huc [Squires 100 (A, E, K); Bien Hoa, Thorel 647 (K, E); Nam Phan, Langbian, Chevalier 40.447 (P); Trung Phan, Da Nang, Clemens 3420 (K); Pierre 326 (P); Nam Phan, Nha trang, Chevalier 3800 (P); Nam Phan, Muller 1111 (P); Nam Phan, Poilane 27661 (P); Nam Phan, Kontum, Poilane 32.771 (P, TCD); Kontum, Poilane 32822 (P); Kontum, Eberhardt 2608 (P); Thorel 9770 (P); Nam Phan, Haut Donai, Poilane 21945 (P); Nam Phan, Langbian, Chevalier 30819 (P); Kontum, Poilane 32149 (P); Nam Phan, Poilane 30928 (P); Nam Phan, Poilane 3499 (P)].
CAMBODIA: Kampot, Mt Bokor Smitinand & Abbé 24672 (L); Pierre 1410 (P).
PHILIPPINES: Palawan [Mt Victoria, Trident mine, Dransfield 1260 (L); Mt Victoria, Trident mine, Dransfield 1255 (L); Pulot, Massin river, 12km north of Brook point, Ridsdale 1039 (L); forest north of Tagburos, 17 km north of Puerto Princessa, Ridsdale 1111 (L); Narra, Mt Victoria, Ridsdale 1739 (L); Victoria range, Soejarso & Madulid 6168 (A, L); Mt Victoria, Sulit 12326 (A, L); Mt Sorogson, Ebalo 429 (A, SING); Lapu Lapu, Iwahig, Edano 115 (A); Mt Victoria, Edano 14242 (L); Brook point, Elmer 12752 (BO, L, U)].
MALAY PENINSULA: Kedah [Curtis 2593 (SING); Gunong Jerai forest reserve, Chevallier 98112 (L); Gunong Jerai, Burkill 3317 (L, SING); Whitmore 12651 (K); Gunong Jerai, Lo 86 (A)]; Kelantan [Shah 2483 (SING); Malvius s.n. (SING); Malvius 773 (SING); Ridley 359 (SING); Burkill 3220 (SING); Holttum s.n. (SING); Hur & Kiah 7804 (SING); Kiah 31858 (BO, L, SING); Kampong Gobek, Kerilla estate, Tamangkan, Shah & Kadim 557 (BO, L); Gunong Rabong, Soepadmo 1077 (BO); Gunong Thana, Soepadmo 974 (L)]; Pahang [Frasers hill, Kochummen 11470 (L); Government hill, Maingay 1315 (L); Fraser hill, Sinclair 39039 (BO, L, P, SING); Fraser hill, Kochummen 16255 (L); Fraser hill, Stone 9369 (L); Fraser hill, Pine Tree Hill, Whitmore 15179 (L, SING); Cameron highlands, Balgooy 2684 (CANB, L); Bukit Kroh forest reserve, Burkill 2614 (L); Cameron highlands, Gunong Jasar 4 29N 101 22E, Chew 943 (SING, L); Gunong Tapis, Cockburn 10996 (L); Ayer Hitam dam reserve, Hardial & Samsuri 223 (L); Gunong Benom game reserve, Ulu Krau, Ismail 97808 (L); Gunong Tahan, Ng 20946 (L); Maxwell 80-24 (BKF, L); path to Sungai Teku, Shah 1469 (A, L, SING); Genting highlands, Stone 11052 (L); northwest Pahang, Bukit Chergar, Whitmore 20029 (A); Haniff & Nur 7892 (SING); Holttum 20721 (SING); Ridley 89 (SING); Ridley 1239 (SING); Robinson 5484 (SING); Samsuri 930 (SING); Shah 2727 (SING); Gunong Tapis, Kuantan, Symington & Kiah 28842 (SING); Sibu, Ridley 13 (SING); Kota Tinggi, Maxwell 78/226 (L); Bukit Lawi, Awa 50867 (L)]; Penang [Hardial 689 (SING); Penang hill, Maxwell 82-208 (L, SING); Shimizu 13183 (KYO)]; Perlis [Bukit Ketri, Henderson 22939 (SING)]; Ridley 14933 (SING); Selangor [Gunong Tapis, Cockburn 11032 (L); Terengganu [Moyses & Kiah 31067 (L, SING); Liew 366 (L); Nur 11286 (BO)].
SINGAPORE: Sungei Peropak, Jurong road Sinclair 39243 (L); Jurong road, Sinclair s.n. (P).
SARAWAK: Lambir hills, Miri district, Anderson 3044 (L); Anderson 9835 (L); Mt Santubong, Chew 1392 (A, L); Chew 1411 (A); Bukit Dutil, Tinjar, Dyg et al. 46864 (K);
Santubong, Haron 21443 (L); Gunong Gaharu, 1st division, Ilias Azahari 35679 (L); Bako National Park [Telok Asam, Purseglove 5623 (L); Purseglove 5624 (L, SING); Telok Asam, Purseglove 5626 (L); Litang path, Sleumer 4676 (L); Pulau lakei, 30 km northeast of Kuching, Jacobs 5503 (CANB, L); Jacobs 5508 (CANB, K, L); Telok Asam, Chai & Wright 29915 (L); Othman 37157 (L); Pulau lakei, Jawa 36623 (K); Gunong Besi, Paie 46090 (L); Bukit Regu, Paul et al. 37399 (L)]; Kuching, Brunig 10332 (L); Dalat, Wiridimanta 870 (BO, L); Gunong Majar, Tebakang, Y. Othma 46284 (L); Gunong Mulu, path from Melinau Paku, Anderson 4570 (L); Baram, Gunong Api, Anderson 4742 (BO); Gunong Api, Ulu Melinau, Tutoh, Baram district, Anderson 30936 (L); Awa & Lee 50867 (L); Barem district, Chai 35925 (L); Bukit Salong, Hose Mt, Melinau, Chai 37238 (L); Gunong Buda, Gunong Mulu national park, Chai 39096 (L); Pulau Lakei, Purseglove 5032 (L, SING); Limbang, Amin & Haya 102259 (L, SING).

SABAH: Sipitang [ Talib 50602 (L); Merintaman forest reserve, Saikeh 72302 (L); Bukit Sebuboh, 8 km southwest of Sipitang, Beaman 8726 (A, L); 5 02N 115 32E, Beaman 8407 (K, L); Beaufort, 1.5 km south of Weston, Beaman 9431 (A); Mt Kinabalu [Crocker range, 5 50N 116 20E Beaman 6947 (A, L); Olombon basin, Clemens 34416 (A, L); Tenom, Clemens 28620 (A, L); Clemens 29322 (A, L); upper Penibukan, west ridge, Clemens 50332 (A, L); Clemens 9577 (A); Penibukan, Clemens s.n. (A); Clemens 31501 (L); Tenom, Clemens 29398 (L); near boundary pole 76, Meijer 57544 (L); Bembangan river, Chew 4634 (L); Carr 26951 (SING)]; Kepayan, Dewol & Talib 80417 (L); Mandahan forest reserve, Dewol & Karim 78036 (L); Pontianak, Kp. Mandor, Mondi 283 (L, SING, U); Banjara forest district, Pingkun 10152 (BO, L); Temburong, summit of Bukit Patoi, Smythies & Wood-Ashton 17143 (L); Sandakan [Leila, Meijer 48279 (L); Leila, Stevens 345 (L); Segantor river, Wood 3656 (L)]; Mandahan, Papar, Husin 86192 (L); Kimanis, Talib & Haya 80533 (L); Kimanis forest reserve, Ampuria 41423 (L); Membakut, Bidin 80556 (K, L).

BRUNEI: Tutong [Bukit Pasir Puteh, Ashton 285 (L); Ashton 5021 (L); Barakas, Ashton 946 (L); Marundi, Ashton 5574 (L); Ashton 970 (L); west Tutong district, near Telambang bridge, Jacobs 5671 (CANB, L)]; Temburong [north ridge of Bukit Retak, Wong 768 (A)]; KALIMANTAN: west Koetai, Endert 2011 (L); South Kalimantan, Giesen 160 (L); South Kalimantan, Giesen 161 (L); Hallier 318 (P); Hallier 1451 (L); Hallier 2351 (L); Koyama & Terao 31633 (A); East Kalimantan, north of Samarinda, Kuswata 1174 (L); Kalimantan, Tengah, Sidyasa 223 (E, SING); East Kalimantan, Samboja, Ambri & Arifin 126 (L).

SUMATRA: Palembang, de Raadt 93 (L); Palembang, de Raadt 95 (L); south-southwest of Gunong Leuser National park, Belintang village, 2 43N 97 54E, de Wilde 20704 (L); Lintong, Dolok SangoeI, Huitema 76 (L); Huitema 77 (L); Lorzing 7983 (BO); Halaban, Maradjo 397 (L); Mt Sago near Payakumbuh, Meijer 5377a (L); Mt Sago near Payakumbuh, Meijer 7369 (L); Taram, east of Payakumbuh, sandstone region of River Tyampo, Meijer 7072 (L); south of Mt Sago, 0 22S 100 40E, Nagamasu 3814 (L); west coast, near Tiku, Meijer 7336 (L); Tiku sand dunes, west coast, Meijer 7340 (L); Soengi Kanan, si Boeoa 4186 (A); Langgapayung, si Boeoa 3465 (A, L); Soengi Kanan, Loboehan Batoe, si Boeoa 3999 (A); Rantau Parapat, Bila, si Boeoa 2220 (A); Soengi Kanan, Loboehan Batoe, si Boeoa 4186 (A); Sibolga, Blume 628 (L); Malili, Langea, Kjellberg 2078 (BO); Sibolga, Reinwardt 628 (L, U); Bangka [Teysmann 3509 (U); Teysmann 3323 (L, U); Teysmann s.n. (U); Teysmann 7560 (L, P); Teysmann s.n. (U); Huitema 14 (L); Teysmann 3509 (U); Huitema 76 (L); Kostermans 1553 (L)].
MOLUCCAS: Halmahera, southern peninsula, *De Haan* 651 (BO, L); Obi island, W Jikodolong, *de Vogel* 4344 (CANB, L); Morotai, Gunong Pare, *Kostermans* 1312 (L).

PAPUA NEW GUINEA: Markham point, near Lae, *Henty* 13684 (A, L); Morobe district, Markham point, *Stauffer & Henty* 5546 (A, CANB).

AUSTRALIA: Queensland, Mt Edith Lamb, *Smith* 3752 (L).

**Dufrenoya colletti** (Gamble) Stauffer

MYANMAR: Shan hills, *Collett* 772 (K); Mt Victoria, *Cooper* 5910a (E).

**Dufrenoya platyphylla** (Spreng.) Stauffer

INDIA: Assam, Hmuntha hills, *Koelz* 27552 (L); Assam, Hmuntha hills *Koelz* 27607 (L);

Karong, Manipur, *Koelz* 26626 A (L); Assam, Hmuntha, Lushai hills, *Thakur Rup Chand* 4462 (L); Sikkim, North district, north of Gangtok 27 24N, 88 36E, *Long et al.* 939 (E);

Sikkim, *Gamble* 27937 (K); Nepal, Pasgam, *Stainton et al.* 5927 (Z). MYANMAR: Tista valley, *Haines* 2017 (E); Yetagoni, *Dickinson* 7303 (E); Yetagoni, *Dickinson* 7307 (L);

*Dickinson* 7430 (L); Kyautsit, Chaung, Chin hills, *Dickinson* 8573 (L); Mindat, west central Myanmar, *Kingdom Ward* 21820 (BM, Z).

**Dufrenoya robusta** Stauffer

MYANMAR: *Kurz* 381 (K).

**Dufrenoya sessilis** (Crab) Stauffer

INDIA: Assam, near Nokrek, Garo hills, *Thakur Rup Chand* 2771 (L); Manipur, Myang Khong, *Watt* 6041 (E). LAOS: between Nam Ma Oun and Nam Long, Haut Mekhong province, *Poilane* 26319 (L, P); *Poilane* 20376 (P, Z). VIETNAM: Sai Wong Mo Shan, Bac Phan, *Tsang* 30272 (A, E, K); Kontum, northwest slopes of Ngoc Linh, *Averyanov et al.* 157 (P); Tran, *Chevalier* 1053 (P); Da Nang [Trung Phan, *Poilane* 7994 (P); Trung Phan, *Poilane* 13411 (P); Trung Phan, *Poilane* 29068 (P); *Poilane* 30928 (P)]; Nam Phan, Nui Dai Ding near Dak, *Poilane* 32822 (P); Nam Phan, north of Kontum on summit of Ngoe Pong, *Poilane* 32149 (P); near Da Lat, *Poilane* 32567 (P); Nam Phan, near Thu Dau Mot, *Chevalier* 20403 (P).

**Phacellaria compressa** Benth.

INDIA: Assam, Khasia hills, *Thakur Rup Chand* 5287 (L).


MYANMAR: Taungsi crags, Southern Shan States, *Robertson* 2110 (K); Shan hills, *Collett* 331 (K).

VIETNAM: Kontum, *Averyanov* 834 (P); Da Lat, *Evrard* 934 (L, P); Braian, Haut Donai, *Poilane* 22512 (P); Braian, *Poilane* 24714 (L, P); Nam Phan, Dran, Langbian, *Boden Kloss* s.n. (BM); Nam Phan, Langbian, Dalat, *Chevalier* 30755 (L, P); Nam Phan, Langbian, *Chevalier* 30791 (P).

**Phacellaria rigidula** Benth.

CHINA: Yangbajain, west side of Diancang, Shan montain range, 25°43' N, 100°02' E, *Bartholomew et al.* 207 (E); Yunnan, *Henry* 11085 (K).
**Osyris lanceolata** Hochst. & Steud. ex. A.D.C.
INDIA: Nepal, Bagmati zone, Lalitpur district, Nicolson 2232 (BO).
CHINA: Peiping, Hsien Lan ling, Tsai 56195 (P); west China, Wilson 4443 (P); Yunnan, Simeon (P).
LAOS: Tranminh [near Xiengkhouchang, Melville 37.11 (P); Poilane 2201 (P); Muong Soni, Poilane 20096 (P); Muong Soui, Poilane 20023 (P, Z).
VIETNAM: Bac Phan [Ke Dua, Bon 5006 (P); Luang Xa mountain, Bon 3346 (P)]; Nam Phan [Langbian, Da Lat, Chevalier 30708 (P); Balansa 1010 (P); Poilane 32470 (P); Pierre 3077 (P)]. AFRICA: East Africa, Schliessen 4606 (Z); Burundi, Lewalle 2476 (Z).
EUROPE: Portugal [Lagos, Algarve, Daveau s.n. (Z); Lagos, Algarve, Kramer 8785 (Z).

**Santalum album** L.
INDIA: Royle s.n. (TCD); Mysore [Hassan district, Nicolson 232 (E); Nalur Agumbe, Sundara Raghavan 69577 (K); Gandhi 2106 (K)]; Pondicherry, Perrotet s.n. (K); Madras [Gamble 10762 (K); Wight 2496 (K); Matthew et al. 19326 (K)]; Tamilnadu [Ridsdale 47 (K), Courtallum, van der Maesen 3441 (K); van der Maesen 3520 (K)]; Hatties 2136 (K), Dehra Dun.
BHUTAN: Samchi district, 26°54’ N, 89°06’ E, Grierson & Long 3511 (E).
PHILIPPINES: Luzon [Laguna province, Makiling national park, Sult 7028 (A)].
JAVA: Zollinger 2804 (A); East Java, Groenhart 92 (U); Paserooean, Malang, Altona s.n. (BO). TIMOR: Kapan, Soe, Darnaed 649 (K).
PAPUA NEW GUINEA: Central district, Port Moresby, north end Palli Palla hills, 8°10’ S., 146°17’ E, Zieck 36143 (CANB); Rigo sub district, Zieck 36121 (BO).

**Scleropyrum maingayi** Hook.f.
MALAY PENINSULA: Langkawi, north Kedah, Chan 6849 (SING).
SUMATRA: Ketambe, Lau Asis valley, Gunong Setan, de Wilde & de Wilde Duyfjes 14387 (K).
SARAWAK: Lambir hills, Ashton 16764 (BO, L).
JAVA: Koeders 10045 (BO).

**Scleropyrum pentandrum** (Dennst.) Mabb.
INDIA: Madras, Bourdillon 517 (K).
SRI LANKA: Walker 48 (E); Lawson s.n. (K); Ratna Hura district, Huber 546 (E);
CHINA: Hainan [Po ting, How 73290 (P); Fleury 32036 (P); Changjiang district, Ue lung ling, Lau 1346 (P); Changjiang district, Lau 3086 (P); Tan district, I Kap Shan, Lau 1188 (P); Telegraph, Poilane 13472 (P); How 73290 (P)].
MYANMAR: Mandalay, English 46 (K).
LAOS: Sa Phan Menk, Vidal 1466 (P); Luangprabang, Spire 743 (P); Pierre 5040 (P); Se Moun, Harmand 247 (P); Savannakhet, Poilane 11921 (A, P).
VIETNAM: Bac Phan [Chapa, Petelot 3.785 (P); Chapa, Petelot 3.765 (P); Sai Wong Mo Shan, Tsang 30317 (A, BO, E, P); Sai Wong Mo Shan, Tsang 30021 (A, E)]; Phu Looke, Pierre 1427 (P); Nam Phan, Bienhoa, Fleury 32036 (P).
CAMBODIA: Pierre 856 (P); Chevalier 176 (P).
MALAY PENINSULA: Penang [Curtis 3082 (SING)]; Negeri Sembilan [Pasoh reserve, 2°58’ N, 102°19’ E, Rogstad 528 (A)]; Selangor [Kepong Panti 1683 (A); Kepong ridge,
Kochummen 23009 (L)); Kedah [Kiah 35071 (SING); Gunong Baling, Kiah 35374 (SING);
Kelantan [Henderson 22652 (A, SING); Gunong Musang, Whitmore 4011 (A)]; Terengganu
[Pulau Redang, Liew 285 (A)]; Pahang [Henderson 22278 (BO); Lesong, Kamarudin 28381
(A)]; Johor [Corner 29348 (BO); Forbes 3227 (L)].
SUMATRA: Upper Riauw, Soepadmo 217 (A); Palembang, Teysmann 3833 (BO); Bukit
Batu, south Sumatra, Djunaedi 1636 (K, L); central Sumatra, Taluk region, Meijer 33 (L).
SARAWAK: Ulu Medamit, George 43059 (K); Permantang, south of Kwajan, Alston 13327
(A); Long Dam, Ulu Dapoi, 4th division, Suib 23467 (SING); Belaga, Othman et al. 43533
(K).
SABAH: Elmer 21735 (A); Mt Nunkok, Clemens 32836 (A); Pa Sia on Sarawak border,
4°20' N, 115°39' E, de Vogel 8551 (L); west coast, Crocker range, 5°29' N, 116°01' E, de
Vogel 8061 (L); above Thamis, Carr 27848 (SING); Kampung Nalumad, Ranau, Sigin et
al. 112265 (K); Mt Kinabalu, Clemens 32836 (A).
BRUNEI: Temburong, Bukit Belalong, Wong 1468 (A); Bukit Belalong, 42°09' N, 115°11'
E, Dransfield 7140 (K).
WEST PAPUA: Boridi, Carr 14812 (CANB); Vogelkop peninsula, Aifat river valley, van
Ryen & Sleumer 7248 (L).

Thesium psilotoides Hance
LAOS: Phu Luoc, Pierre 5506 (P).
Table 1. Geographic distributions of Santalaceae in Thailand. Many of the species do not have strict affinities with Thailand and represent part of much broader distributions.
Af=Africa; Au=Australia; B=Myanmar; Bo=Borneo; C=China; Ca=Cambodia; E=Europe; I=India; J=Java; L=Laos; Mol=Moluccas; MP=Malay Peninsula; NG=New Guinea; P=Philippines; S=Sumatra; Si=Singapore; Su=Sulawesi; T=Thailand; Ti=Timor; V=Vietnam

<table>
<thead>
<tr>
<th>GENUS</th>
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<tr>
<td>Dendrotrophe</td>
<td><em>Dendrotrophe buxifolia</em> (Blume) Miq.</td>
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<td><em>Dendrotrophe varians</em> (Blume) Miq.</td>
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<td>Dufrenoya</td>
<td><em>Dufrenoya colletii</em> (Gamble) Stauffer</td>
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<td><em>Dufrenoya platyphylla</em> (Spreng.) Stauffer</td>
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<td>Scleropyrum</td>
<td><em>Scleropyrum pentandrum</em> (Dennst.) Mabb.</td>
<td>B, Bo, C, Ca, I, L, MP, NG, S, T, V</td>
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<td>Thesium</td>
<td><em>Thesium psilotoides</em> Hance</td>
<td>L, T</td>
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*Cultivated*
Table 2. Taxonomic history of the Southeast Asian genera of Santalaceae. Generic circumscription has remained fairly constant except within the aerial parasites (Henslowia). This group has been divided into several genera (Dendrotrophe, Dendromyza, Dufrenoya, Phacellaria) and is now contained within the tribe Amphorogyneae.

<table>
<thead>
<tr>
<th>Brown 1810</th>
<th>Blume 1850</th>
<th>Miquel 1856</th>
<th>A.D.C. 1857</th>
<th>Benth. 1883</th>
<th>Danser 1940</th>
<th>Stauffer 1969</th>
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F = Family; O = Order; T = Tribe