

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 Amphorogyneae. This tribe contains a unique group of aerial parasites which have some morphological and ecological similarities to the Viscaceae. 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 (Sindhueverendra & Sujatha 1989, Bhaskar 1992). Stamen 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: *Amphorogyneae*, *Santaleae*, *Anthoboleae* 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. *Osyris* 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 Santalacean 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 *Dufrenoya* are restricted to cooler montane climatic conditions. Like *Dufrenoya*, species of *Phacellaria* are confined to montane regions and indeed the geographic distribution of *Phacellaria* follows that of *Dufrenoya* but with a more restricted range. *Phacellaria* species are, however, more host specific, being hyperparasites on Loranthaceae and occasionally *Dufrenoya*. 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, *Buckleyeae*, *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, *Osyrideae* and *Thesieae*, contained elements of the *Santaleae*. The name *Osyrideae* has been used extensively in taxonomic literature but it is now a recognised synonym of *Santaleae* 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 Misodendraceae. 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 *Amphorogyneae* 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 the 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 *Thesium*, *Santalum* and *Dendrotrophe buxifolia* (Blume) Miq. which have hermaphrodite flowers. Anther dehiscence is longitudinal in *Santalum*, *Osyris*, *Scleropyrum* and *Thesium* 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 *Thesieae*. In *Amphorogyneae* placentation is free central, the placenta is convex with 4–6 short in-curling 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 *Thesium* the placental column is similar to *Scleropyrum* but the lobes of the placenta are short.

Fruits are dry and indehiscent nuts in *Thesium*, 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

Dendroparasite 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.* dendroparasitic.

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*.

Haustrorium 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 at 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 *Dt* 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 *Dendrotrophe* 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

R.Br., Prodr.: 350. 1810; Miq., Fl. Ind. Bat.: 775. 1856; A.DC., Prodr. 14: 619. 1857; Benth., Gen. Pl.: 217. 1883; Hook.f., Fl. Brit. Ind. 5: 228. 1886; Kanjilal, Fl. Assam 4: 128. 1940; Backer, Fl. Java 2: 76. 1965; Gamble, J. As. Soc. Beng. 75: 269. 1912; Stauffer, Vierteljahrsschr. Naturf. Ges. Zürich: 49. 1969; Grierson & Long, Fl. Bhutan 1.1: 140. 1983; Heywood, Flowering Plants of the World: 170. 1993; Mabb., The Plant Book: 636. 1997; Philcox in Dassan. & Clayton, Rev. Fl. Ceylon: 198. 1999.

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 axial, 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, placentation free central, placenta 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 sericeous, 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 Eremolepidaceae, a small family of dendroparasites from South America (Nickrent 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:

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| 1. Tribe <i>AMPHOROGYNEAE</i> | 1. <i>Dendrotrophe</i> , 2. <i>Dufrenoya</i> , 3. <i>Phacellaria</i> |
| 2. Tribe <i>SANTALEAE</i> | 1. <i>Osyris</i> , 2. <i>Santalum</i> , 3. <i>Scleropyrum</i> |
| 3. Tribe <i>THESIEAE</i> | 1. <i>Thesium</i> |

KEY TO THE GENERA

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|--|------------------------|
| 1. Small trees | (2) |
| Shrubs, climbers, dendroparasites, herbs | (3) |
| 2. Plants hairless; leaves opposite, inflorescences cymose, flowers hermaphrodite | 5. Santalum |
| Plants sparsely or densely hairy; leaves alternate; inflorescence a catkin; flowers unisexual | 6. Scleropyrum |
| 3. Herbs; fruit nut-like | 7. Thesium |
| Shrubs, climbers, dendroparasites; fruit a drupe | (4) |
| 4. Shrub with pendant branches; leaf venation pinnate; male inflorescences cymose | 4. Osyris |
| Scandent shrubs, climbers, dendroparasites; leaf venation palmate or leaves reduced to scales; male inflorescences paniculate, racemose, umbellate or forming sessile clusters | (5) |
| 5. Stems hirsute or papillose; leaves bract-like; hyperparasite on Loranthaceae and <i>Dufrenoya</i> | 3. Phacellaria |
| Stems hairless; leaves not bract-like; not hyperparasitic | (6) |
| 6. Male inflorescences, paniculate, racemose; fruits spherical, elliptic, mesocarp fleshy, endocarp tuberculate | 1. Dendrotrophe |
| Male inflorescences umbellate; fruits, obovoid, oblong, mesocarp membranous, endocarp smooth | 2. Dufrenoya |

TRIBE AMPHOROGYNEAE

Stauffer, Vierteljahrsschr. Naturf. Ges. Zürich 114: 49. 1969; Hewson & George, Fl. Australia 22: 43. 1984.

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 isomerous 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. DENDROTROPHE

Miq., Fl. Ind. Bat. 1.1: 779. 1856; Danser, Nova Guinea N.S. 4: 146. 1940; Stauffer, Vierteljahrsschr. Naturf. Ges. Zürich 114: 53. 1969; Hewson & George, Fl. Australia 22: 59. 1984.— *Henslowia* Blume, Mus. Lugd. Bat. 1: 243. 1850 pro parte, non Wall., Pl. As. Rar.: 14 t.221. 1832; A.DC., Prodr. 14: 630. 1857; Benth., Gen. Pl. 3: 228. 1883; Hook.f., Fl. Brit. Ind. 5: 232. 1886, as *Henslowia*; Gamble, J. As. Soc. Beng. 75: 269. 1912; Pilger in Engl. & Harms, Nat. Pflanzenfam. 16b: 71. 1935; Kanjilal, Fl. Assam 4: 129. 1940.

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, capitate; 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 involucre 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, erect; exocarp thin, smooth or rugulose; mesocarp thin, fleshy; endocarp hard, globose or elliptic, tuberculate, 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 ruminant, 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, *Dt 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 tuberculate 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

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|--|-------------------------------|
| Primary veins obscure, 2–3; inflorescences paniculate, flowers hermaphrodite | 1. <i>D. buxifolia</i> |
| Primary veins usually obvious 3–5; male inflorescences racemose, flowers dioecious | 2. <i>D. varians</i> |

1. *Dendrotrophe buxifolia* (Blume) Miq., Fl. Ind. Bat. 1.1: 781. 1856; Miq., Sumatra Seine Pflanzenweit: 342. 1862; Danser, Nova Guinea N.S. 4: 147. 1940; Stauffer, Vierteljahrsschr. Naturf. Ges. Zürich 114: 54. 1969; C.Y.Wu & D.D.Tao, Fl. Yunnan. 4: 293. 1986; Tam, Fl. Reipubl. Pop. Sin.: 72. 1988; P.H.Hô, Càyco Vietnam 2.1: 154. 1992.— *Henslowia buxifolia* Blume, Mus. Lugd. Bat. 1: 244. 1850; A.DC., Prodr. 14: 631. 1857; Hook.f., Fl. Brit. Ind. 5: 234. 1886; Ridl., Fl. Sing.: 133. 1900; Boerl., Handl. Fl. Ned. Ind.: 181. 1900; Gamble, J. As. Soc. Beng. 75: 274. 1912; Lecomte, Bull. Mus. Nat. Hist. [Paris]: 405. 1914; Lecomte, Fl. Gen. I.-C. 5: 217. 1915. Type: Sine loc. *Korthals* s.n. (holotype P!).— *Osyris rotundata* Griff., Notulae: 742. 1854. Type not located.

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, *Chanby* 1151 (BKF)]; Satun [Adang, *Kerr* 14106 (K); Tola Satul, *Kerr* 13854]; Songkhla [Kampeng Pet, *Kerr* 15916 (L); Hat Yai, *Congdon* 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°30' 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 buxifolia* is vegetatively similar to *Dt varians* and the distributions of the two species overlap. Where the species co-occur *Dt buxifolia* may be distinguished by generally lanceolate leaves, smaller globose fruits and a paniculate inflorescence with hermaphrodite flowers.

2. *Dendrotrophe varians* (Blume) Miq., Fl. Ind. Bat. 1.1: 781. 1856; Danser, Nova Guinea N.S. 4: 147. 1940; Stauffer, Vierteljahrsschr. Naturf. Ges. Zürich 114: 56. 1969.— *Henslowia varians* Blume, Mus. Lugd. Bat. 1: 244. 1850; Hook.f., Fl. Brit. Ind. 5: 233. 1886; Gamble, J. As. Soc. Beng. 75: 271. 1912. Type: Borneo, *Korthals* s.n. (holotype L!).— *Henslowia cassiaefolia* Blume, Mus. Lugd. Bat. 1: 244. 1850.— *Dendrotrophe cassiaefolia* (Blume) Miq., Fl. Ind. Bat. 1.1: 781. 1856. Type: Borneo, *Korthals* s.n. (holotype L!).— *Henslowia spicata* Blume, Mus. Lugd. Bat. 1: 244. 1850.— *Dendrotrophe spicata* (Blume) Miq., Fl. Ind. Bat. 1.1: 781. 1856. Type: Borneo, *Korthals* s.n. (holotype L!).— *Henslowia retusa* Blume, Mus. Lugd. Bat. 1: 213. 1850. Type: Java, *Korthals* s.n. (holotype P!).— *Henslowia umbellata* Blume, Mus. Lugd. Bat. 1: 243. 1850.— *Dendrotrophe umbellata* (Blume) Miq., Fl. Ind. Bat. 1, 1: 779. 1855; P.C. Tam, Fl. Reipubl. Pop. Sin.: 72 t.18. 1988; P.H.Hô, Câyno Vietnam 2.1: 155. 1992. Type: not located.— *Henslowia frutescens* Champ., Hook. J. Bot. 5: 194. 1853; Lecomte, Fl. Gen. I.-C. 5: 219. 1915.— *Dendrotrophe frutescens* (Champ.) Danser, Nova Guinea N.S. 4: 148. 1940. Type: China, Hong Kong, *Champion* s.n. (holotype K!).— *Henslowia lobbiana* A.DC., Prodr. 14: 631. 1857; Hook.f., Fl. Brit. Ind. 5: 233. 1886, as *ùHenslowia lobbianaû*.— *Dendrotrophe lobbiana* (A.DC.) Miq., Fl. Ind. Bat. 1.1: 1096. 1858; Danser, Nova Guinea N.S. 4: 148. 1940. Type: Java, *Lobb* 334 (isotype TCD!).— *Henslowia philippinensis* A.DC., Prodr. 14: 631. 1857.— *Dendrotrophe philippinensis* (A.DC.) Miq., Fl. Ind. Bat.: 1096. 1858. Type: Malay Peninsula, *Cuming* 2253 (isotype TCD!).— *Henslowia erythrocarpa* Kurz, J. Bot. 13: 329. 1879. Sine loc., *Korthals* s.n. (holotype L!).— *Henslowia sessiliflora* Hems., J. Linn. Soc. 26: 409. 1891. Type: Kwangtung, *Playfair* s.n. (holotype K!).— *Henslowia ridleyi* Gamble, Kew Bull.: 201. 1912.— *Dendrotrophe ridleyi* (Gamble) Danser, Nova Guinea N.S. 4: 148. 1940. Type: Malay Peninsula, *Ridley* 15560 (holotype K!).— *Henslowia wrayi* King ex Gamble, J. As. Soc. Beng. 75: 201. 1912.— *Dendrotrophe wrayi* (King ex Gamble) Danser, Nova Guinea N.S. 4: 140. 1940; Tam, Fl. Reipubl. Pop. Sin.: 73 t.18. 1988; P.H.Hô, Câyno Vietnam 2.1: 154. 1992. Type: Malay Peninsula, *King* 10834 (holotype K!).— *Henslowia umbellata* var. *longifolia* Lecomte, Bull. Mus. Nat. Hist. [Paris]: 405. 1914. Type: Cambodia, *Pierre* 1267 (holotype P!).— *Henslowia umbellata* var. *harmandii* Lecomte, l.c.: 405. 1914. Type: Cambodia, *Harmand* 220 (holotype P!).— *Henslowia tonkinensis* Lecomte, l.c.: 406. 1914; Lecomte, Fl. Gen. I.-C. 5: 218. 1915.

Type: Vietnam (Tonkin), *Bon* 5117 (holotype P!).— *Henslowia umbellata* sensu Lecomte, Fl. Gen. I.-C. 5: 218. 1915, non Blume.— *Henslowia palawanensis* Elmer, Leaflet. Philipp. Bot. 5: 1834. 1913. Type: Palawan *Elmer* 12752 (holotype U!).— *Exocarpos amboinensis* Merr., Philipp. J. Sci. Bot. 11: 267. 1916. Type: Moluccas, Ambon, *Robinson* 1810 (holotype L!).— *Henslowia minor* Ridl., J. Fed. Mal. St. 7: 50. 1916.— *Dendrotrophe minor* (Ridl.) Danser, Nova Guinea N.S. 4: 148. 1940. Type: Malay Peninsula, *Ridley* s.n. (holotype K!).— *Henslowia schlechteri* Pilger, Bot. Jahrb. 59: 127. 1924. Type: Papua New Guinea, *Schlechter* 19385 (isotype L!).— *Dendrotrophe palawanensis* (Elmer) Danser, Nova Guinea N.S. 4: 148. 1940. Type: Philippines, Palawan, *Elmer* 12752 (holotype U!).— *Henslowia queenslandiae* Smith, Queensl. Nat.: 62. 1951. Type: Australia, *Smith* 3394 (isotype Z!).— *Dendrotrophe varians* var. *multinervis* Stauffer, Vierteljahrsschr. Naturf. Ges. Zürich: 59. 1969, **syn. nov.** Type: Malay Peninsula, *Wray* 278 (holotype K!).— *Dendrotrophe varians* var. *minor* Stauffer, l.c.: 58. 1969, **syn. nov.** Type: not located.— *Henslowia frutescens* var. *subquinquenervia* P.C. Tam, Bull. Bot. Res.: 70. 1981, nom. illegit.— *Dendrotrophe punctata* C.Y. Wu ex D.D. Tao, Fl. Yunnan. 4: 290. 1986, **syn. nov.** Type: China, *Wu* 03707 (holotype KUN!).

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 3–5–7; 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 broadening 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; staminodes present, large, similar to stamens in male flower; nectary concave, unlobed, smooth or slightly pustulate; 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 (BKF)]; Ranong [Ko Chang, *Kerr* 16586 (K); *Santisuk* s.n. (BKF)]; Satun [Thung Wa, *Niyomdham* 1285 (K, L)]; Songkhla [Khlong Ngae, Hat Yai, *Maxwell* 85/60 (BKF, A, L); Ko Hong hill, Hat Yai, *Maxwell* 85/113 (A, BKF); *Maxwell* 84/35 (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 (BKF); 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 Fagaceae, *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 *Dt buxifolia*, *Dt varians* 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 *Dt varians* overlaps with *Dt 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. DUFRENOYA

Chatin, Comptes Rendus Acad. Paris 51: 657. 1860; Stauffer, Vierteljahrsschr. Naturf. Ges. Zürich 114: 66. 1969; Grierson & Long, Fl. Bhutan 1.1: 142. 1983.— *Henslowia* A.DC., Prodr. 14: 630. 1857, pro parte; Benth., Gen. Pl. 3: 228. 1883; Hook.f., Fl. Brit. Ind. 5: 232. 1886; Pilger in Engl. & Harms, Nat. Pflanzenfam. 16b: 71. 1935.— *Hylomyza* Danser, Nova Guinea N.S. 4: 141. 1940; Backer, Fl. Java 2: 77. 1965.

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; peduncles 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 papillose; 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 Ainjeru. 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 (2)
 Stems smooth, rough, striated, fissured (3)
2. Male flowers with glandular hairs and anther locules unequal; staminodes present in female flower, stigma lobed **2. *D. platyphylla***
 Male flowers with glandular hairs absent and anther locules isomerous; staminodes absent in female flower, stigma entire **3. *D. robusta***
3. Bark faintly corrugated with short elliptic, transverse fissures; primary veins 9–11, almost parallel; male flowers pendulous **1. *D. collettii***
 Bark smooth or with longitudinal fissures; primary veins obscure or 3–9, not parallel; male flowers not pendulous **4. *D. sessilis***

1. *Dufrenoya collettii* (Gamble) Stauffer, Vierteljahrsschr. Naturf. Ges. Zürich 114: 69. 1969.— *Henslowia collettii* Gamble, Kew Bull. 1913: 47. 1913. Type: Myanmar, *Robertson* 326 (holotype K!).— *Henslowia heterantha* Wall. ex DC., var. *coriacea* Kurz, Fl. Burm. 2: 328. 1877. Type: Myanmar, *Kurz* 371 (isotype K!)

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 obovoid, 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 Utaradit, *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 Simlensis*, 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.

2. *Dufrenoya platyphylla* (Spreng.) Stauffer, Vierteljahrsschr. Naturf. Ges. Zürich 114: 70. 1969; Grierson & Long, Fl. Bhutan 1.1: 143. 1983.—*Viscum platyphyllum* Spreng., Linn. Syst. Vegetab. XIV. 1824, Curae Poster.: 47. 1827; DC., Prodr. 4: 279. 1830.—*Hylomyza platyphylla* (Spreng.) Danser, Nova Guinea N.S. 4: 145. 1940. Type: not lo-

cated.— *Viscum latifolium* Buch.-Ham. ex D.Don, Prodr. Fl. Nepal.: 142. 1825. Type: not located.— *Viscum heteranthum* Wall. ex DC., Prodr. 4: 279. 1830.— *Henslowia heterantha* (Wall. ex DC.) Hook.f. ex A.DC., Prodr. 14: 632. 1857; Kanjilal, Fl. Assam 4: 130. 1940.— *Dufrenoya heterantha* (Wall. ex DC.) Chatin, Comptes Rendus Acad. Paris 51: 657. 1860.— *Dendrotrophe heterantha* (Wall. ex DC.) A.N.Henry & B.Roy, Bull. Bot. Survey India 10: 274. 1969, **syn. nov.** Type: India, *Wallich* 488 (holotype K!; isotypes P!, TCD!)

Erect and pendulous shrub, branches all of almost the same length, often 3–4 from a single node. *Juvenile stems* terete, pustulate, 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 involucre 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, elongate-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 pustulate 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, pustulate juvenile stems, longer pedunculate male inflorescences, distinctly turbinate female flower buds and apical ‘tails’ on the endocarp.

3. *Dufrenoya robusta* Stauffer, Vierteljahrsschr. Naturf. Ges. Zürich 114: 69. 1969. Type: Thailand, Kanchanaburi, Kao Ri Yai, *Kerr* 10393 (holotype BM!; isotypes K!, L!).

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 pustulate 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, pustulate. *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 & Vidal* 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.

4. *Dufrenoya sessilis* (Craib) Stauffer, Vierteljahrsschr. Naturf. Ges. Zürich 114: 69. 1969.— *Henslowia heterantha* var. *sessiliflora* Hook.f., Fl. Brit. Ind. 5: 233. 1886. Type: India, *Hooker* s.n. (holotype K!).— *Henslowia sessilis* Craib, Kew Bull. 1911: 455. 1911. Type: Thailand, Chiang Mai, Doi Suthep, *Kerr* 1768 (holotype K!; isotypes BM!, TCD!).— *Henslowia shanensis* Gamble, Kew Bull. 1913: 48. 1913. Type: Myanmar, *Robertson* 295 (holotype K!).

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 involucre 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, obconical; 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 (BKF); *Maxwell* 92/249 (GH); *Niyomdham & Kubat* 1351 (AAU, BKF, E); *Sorensen et al.* 6615 (A, Z); Mae Taeng, *Santisuk* 1049 (BKF); *Sukkri* 13 (BKF); north Chiang Mai, Pangboh hill, *Smitinand* 8717 (K); Doi Pui, 19 N 98 30 E, *Nooteboom* 670 (BKF); Lampang, Doi Khun Tan, Mae Tha district, *Phengklai & Koyama* 39106 (A); Northern Pong Pho, near Doi Chiang Dao, *Larsen & Santisuk* 2867 (BKF, E)]; Chiang Rai [Mae Suai, *Bunchuai & Nimanong* 1407 (BKF, L)]; NORTH-EASTERN: Loei [Phu Kradung, *Kerr* 20059 (BM); *Smitinand* 2105 (BKF); *Smitinand* 2205 (BKF); *Smitinand* 2533 (BKF, 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 *Dfplatyphylla*, 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, Nat. Pflanzenfam. 16b: 71. 1935; Danser, Blumea 3: 212. 1939; Nova Guinea N.S. 4: 145. 1940.

Erect dendroparasitic 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 monoecious, 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 involucre 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 *Scurrula*, *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*

1. *Phacellaria compressa* Benth., Gen. Pl. 3: 229. 1883; Hook.f., Fl. Brit. Ind. 5: 235. 1886; Hieron., Nat. Pflanzenfam. 3: 216. 1889; Collett & Hems., J. Linn. Soc. 28: 122. 1890; Boerl., Handl. Fl. Ned. Ind.: 181. 1900; Pilger in Engl. & Harms, Nat. Pflanzenfam. 16b: 71. 1935; Danser, Blumea 3: 227. 1939; C.Y.Wu & D.D.Tao, Fl. Yunnan. 4: 288. 1986; P.H.Hô, Câyno Vietnam 2.1: 152. 1992. Type: China, Yunnan, *Parish* s.n. (holotype K!).— *Phacellaria wattii* Hook.f., Fl. Brit. Ind. 5: 236. 1886. Type: India, *Watt* 6154 (holotype K!).— *Phacellaria ferruginea* W. W. Smith, Notes Bot. Gard. Edinb., 10: 49. 1918. Type: China, Tali Range, *Forrest* 11585 (holotype K!).— *Phacellaria caulescens* Collett & Hems., J. Linn. Soc. 28: 122 t. 17. 1890, **syn. nov.** Type: Myanmar, *Collet* 736 (holotype K!).— *Phacellaria tonkinensis* Lecomte, Bull. Mus. Hist. Nat. [Paris] 20: 399. 1914; Lecomte, Fl. Gen. I.-C. 5: 213. 1915; C.Y.Wu & D.D.Tao, Fl. Yunnan. 4: 287. 1986; Tam, Fl. Reipubl. Pop. Sin.: 69. 1988; Hô, Câyno Vietnam 2.1: 153. 1992, **syn. nov.** Type: Vietnam (Annam), *Balansa* s.n. (holotype P!) — *Phacellaria glomerata* C.Y. Wu & D.D.Tao, Fl. Yunnan. 4: 288. 1986, **syn. nov.** Type: China, Yunnan, *Li* 2653 (holotype KUN!).

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 (BKF); 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.

2. *Phacellaria rigidula* Benth. in Benth. & Hook.f., Gen. Pl. 3: 229. 1883; Hook.f., Fl. Brit. Ind. 5: 235. 1886; Hieron., Nat. Pflanzenfam. 3.1: 216. 1889; Boerl., Handl. Fl. Ned. Ind.: 181. 1900; Pilger in Engl. & Harms, Nat. Pflanzenfam. 16b: 71. 1935; C.Y.Wu &

D.D.Tao, Fl. Yunnan. 4: 288. 1986; P.C. Tam, Fl. Reipubl. Pop. Sin.: 69. 1988. Type: India, *Griffith* 2745 (holotype K!).— *Phacellaria gracilis* Danser, Blumea 3: 225. 1939; P.H.Hô, Câyno Vietnam 2.1: 153. 1992, **syn. nov.** Type: Vietnam, *Poilane* 25403 (holotype P!; isotype L!).

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 & Phengkai* 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

A.DC., Prodr. 14: 624. 1857; Hewson & George, Fl. Australia 22: 60. 1984.— *Osyrideae* Rchb., Consp. regni Veg.: 80. 1828; Benth., Gen. Pl. 3: 222. 1883; Pilger in Engl. & Harms, Nat. Pflanzenfam. 16b: 69. 1935.— *Buckleyae* Torr., Am. J. Sci. 45: 170. 1843; A.DC., Prodr. 14: 623. 1857.

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

L., Syst. Nat.: 1101. 1735; Sp. Pl. 2: 1022. 1753; Syst. Vegetab. 14: 881. 1774; A.DC., Prodr. 14: 632. 1857; Hook.f., Fl. Brit. Ind. 5: 232. 1886; Trimen, Fl. Ceylon 3: 474. 1895; Cooke, Fl. Bombay 2: 555. 1906; Benth., Gen. Pl. 3: 227. 1883; Stauffer, Vierteljahrsschr. Naturf. Ges. Zürich 106: 388–399. 1961; Grierson & Long, Fl. Bhutan 1.1: 142. 1983.

Hairless shrub, branches pendulous, bark smooth or faintly striate. *Leaves* spiral, rounded, elliptic, lanceolate, fleshy, glaucous; venation curvipinnate, 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*.

Osyris lanceolata Hochst. & Steud. ex. A.DC., Prodr. 14: 633. 1857; Grierson & Long, Fl. Bhutan 1.1: 142. 1983; P.H.Hô, Cáyco Vietnam 2.1: 154. 1992. Type: Portugal, *Schimper* s.n. (holotype K!).— *Osyris arborea* [Wall. Cat. 4035. 1831]; Hook.f., Fl. Brit. Ind. 5: 232. 1886; Trimen, Fl. Ceylon 3: 474. 1895; Cooke, Fl. Bombay 2: 555. 1906; Collett, Simla Flora: 441. 1902; Burkill, Bot. Sur. Ind. 4: 129. 1910; Lecomte, Fl. Gén. I.-C. 5: 215. 1915; Kanjilal, Fl. Assam 4: 130. 1940. Type: not located.— *Osyris nepalensis* Griffith, Notulae 4: 376. Type: not located.— *Osyris wightiana* [Wall. Cat. 4036. 1831]; Wall. ex

Wight, Icon. 5: 17. 1852; Bot. Survey Ind. 16: 269. 1953; Baehni, Candollea 16: 215. 1958; Hara, Fl. Eastern Himalayas 2: 20. 1971; C.Y.Wu & D.D.Tao, Fl. Yunnan. 4: 293. 1986; Philcox in Dassan. & Clayton, Rev. Fl. Ceylon 13: 199. 1999. Type: India, Madras, *Wight 5* (holotype K!).— *Osyris quadrifida* Benth., Gen. Pl. 3: 227. 1883. Type: sine loc., *Gay s.n.* (holotype K!).— *Osyris arborea* var. *tipitata* Lecomte, Bull. Mus. Nat. Hist. [Paris] 10: 404. 1914, **syn. nov.** Type: sine loc., *Wilson 4443* (holotype P!).— *Osyris arborea* var. *rotundifolia* P.C. Tam, Bull. Bot. Reserv. N.E. For. Inst. 1.3: 71. 1981; Tam, Fl. Reipubl. Pop. Sin.: 24: 64. 1988, **syn. nov.** Type: China, *Pan 60-1145* (holotype SZ, not seen).

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, papillose; 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, papillose 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 & Smitinanad 12635* (AAU, E); Doi Inthanon *Iwatsuki & Fukuoka 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, *Suddee & 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

L., Sp. Pl. 1: 349. 1753; Gen. Pl.: 165. 1754; R.Br., Prodr. Fl. Nov. Holl.: 355. 1810; Miq., Fl. Ind. Bat. 1.1: 77. 1856; A.DC., Prodr. 14: 681. 1857; Cooke, Fl. Bombay: 554. 1906; Roxb., Fl. Indica 1: 462. 1820; Benth., Gen. Pl. 3: 224. 1883; Hook.f., Fl. Brit. Ind. 5: 231. 1886; Pilger in Engl. & Harms, Nat. Pflanzenfam. 16b: 81. 1935; Backer, Fl. Java 2: 78. 1965; Hewson & George, Fl. Australia 22: 61. 1984; Philcox in Dassan. & Clayton, Rev. Fl. Ceylon 13: 201. 1999.— *Fusanus* R. Br., Prodr. Fl. Nov. Holl.: 355. 1810; A.DC., Prodr. 14: 684. 1857; Benth., Fl. Australia 3: 215. 1895.— *Sirium* L., Syst. Vegetab. 14: 160. 1784.— *Sandalum* Rumph., Herb. Amboin. 2: 42, 47 t.11. 1741.— *Eucarya* T.L. Mitchell, Three Expeditions to Australia 2: 100. 1839; Sprague & Summerh., Kew Bull. 11: 196. 1927.

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.

Santalum album L., Sp. Pl. 1: 349. 1753; Sp. Pl. 2: 497. 1762; [*Sandalum album* Rumph., Herb. Amboin. 2: 42, 47 t.11. 1741]; L., Syst. Vegetab. 14: 164. 1784; Lour., Fl. Coch. 2: 87. 1790; Roxb., Fl. Indica 1: 462. 1820; Miq., Fl. Ind. Bat. 1.1: 776. 1856; Bedd., Fl. Sylvat. t.256. 1873; Kurz, Fl. Burm. 2: 329. 1877; Boerl., Handl. Fl. Ned. Ind.: 180. 1900; Cooke, Fl. Bombay: 555. 1906; Pilger in Engl. & Harms, Nat. Pflanzenfam. 16b: 81. 1935; Engl., Syllabus der Pflanzenfam.: 186 t.184. 1964; Kanjilal, Fl. Assam 4: 129. 1940; Backer, Fl. Java 2: 78. 1965; Philcox in Dassan. & Clayton, Rev. Fl. Ceylon 13: 201. 1999; George, Fl. Australia 22: 61. 1984. Type: Timor, *Breynius*, Prodomus fasciculi rariorum plantarum 1 : t5 (1680) (lectotype BM!, selected here); *Bauhin*, Pin. 392; Timor 5 km from Soe, *Kartawinata* 1738 (epitype BO!; designated here).— *Santalum ovata* R.Br., Prodr. Fl. Nov. Holl.: 355. 1810; Blume, Bijdr.: 645. 1825. Type: Melville Bay, *Brown* s.n. (holotype BM!)— *Santalum ovatum* Miq., Fl. Ind. Bat. 1.1: 777. 1856. Type: not located.— *S. myrtifolium* Roxb., Flora Indica 1: 443. 1820. Type: India, *Roxburgh* s.n. (holotype K!).— *Sirium myrtifolium* L., mant. Pl. Alt.: 200, 1771; Syst. Veg.: 14: 160. 1784, **syn. nov.** Type: Linn 138.1 n.v.

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 axial, cauliflorous and on young shoots, pedunculate, peduncles 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. SCLEROPYRUM

Arn., *Mag. Zoo. Bot.* 2: 549. 1838; Miq., *Fl. Ind. Bat.* 1.1: 778. 1856; Hook.f., *Fl. Brit. Ind.* 5: 234. 1886; Trimen, *Fl. Ceylon* 3: 475. 1895; Gamble, *J. As. Soc. Beng.* 75: 275. 1912; Cooke, *Fl. Bombay* 2: 556. 1906; Pilger, *Engl. Bot. Jahrb.* 59: 122. 1924; Pilger in *Engl. & Harms, Nat. Pflanzenfam.* 16b: 72. 1935.— *Pyrularia* A.DC., *Prodr.* 14: 628. 1857, pro parte.— *Scleromelum* K. Schum. & Lauterb., *Fl. Deutsch. Schutz. Sudsee*: 300 t.5. 1900; [*Scleropyron* Benth., *Gen. Pl.* 3: 228. 1883].

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 $\pm$ 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 hypanthium, 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, capitate; ovary present, superior, slender, saggitate, 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***

1. *Scleropyrum maingayi* Hook.f., Fl. Brit. Ind. 5: 235. 1886; Boerl., Handl. fl. Ned. Ind.: 181. 1900; Gamble, J. As. Soc. Beng. 75: 276. 1912. Type: Malay Peninsula, *Maingay* 1891 (holotype K!).

Juvenile stems terete, smooth, shining, initially sparsely hairy then hairless and occasionally pustulate; 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 younger 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 & Smitinand* 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.

2. *Scleropyrum pentandrum* (Dennst.) Mabb., Taxon 26: 533. 1977.— *Pothos pentandrus* Dennst., Schlüssel: 16, 24, 33. 1818; Forts. Alleg. Deutsch. Garten-Mag. 3: 34, 42, 82. 1818; Dillwyn, Review: 33. 1839. Type: India, *Rheede* s.n. (isotype TCD!).— *Sphaerocarya wallichiana* Wight & Arn., Edinb. Phil. J. 15:180. 1833; Roxb., Fl. Indica ed. 1: 371. 1824.— *Scleropyrum wallichianum* (Wight & Arn.) Arn., Mag. Zoo. Bot. 2: 550. 1838; Hook.f., Fl. Brit. Ind. 5: 234. 1886; Collett & Hems., J. Linn. Soc. 28: 121. 1890; Trimen, Fl. Ceylon 3: 475. 1895; Cooke, Fl. Bombay 2: 556. 1906; Lecomte, Fl. Gen. I.-C. 5: 221. 1915; Philcox in Dassan. & Clayton, Rev. Fl. Ceylon 13: 200. 1999.— *Pyrularia wallichiana* A.DC., l.c. 1857; Bedd., Fl. Sylv.: t.304. 1873. Type: India, *Wight* 948 (holotype E!).— *Sphaerocarya moschifera* Blume, Mus. Lugd. Bat. 1: 245. 1850, **syn. nov.** Type: Sumatra, *Korthals* s.n. (holotype L!).— *Pyrularia ceylanica* A.DC., Prodr. 14: 629. 1857. Type: not located.— *Scleropyrum mekongense* Gagnep. in H. Lecomte, Not. Syst.: 196. 1909.— *Scleropyrum wallichianum* var. *mekongense* Lecomte, l.c.: 404. 1914; C.Y.Wu & D.D.Tao, Fl. Yunnan. 4: 294 t.82. 1986, **syn. nov.** Type: Laos, *Spire* 743 (holotype P!).— *Scleropyrum wallichianum* var. *siamensis* Lecomte, Bull. Mus. Hist. Nat. [Paris] 20: 404. 1914, **syn. nov.** Type: Thailand, Chiang Mai, Doi Suthep, *Kerr* 1701 (holotype P!; isotypes AAU!, K!)— *Scleropyrum ridleyi* Gamble, Kew Bull. 1912: 202. 1912 & As. Soc. Beng. 75: 276. 1912, **syn. nov.** Type: Singapore, *Ridley* 4761 (holotype K!).

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 tertiaries percurrent, 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, subsessile 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); Me 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)]. NORTH-EASTERN: 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°03'N, 103°58'E, trail north of park headquarters, *Suddee et al.* 1007 (BKF, TCD); Phetchbun, *Sangkadrang* 3080 (L)]; Loei [Phu Kradung, *Suoatabandhn* 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, *Niyomdhan & Kubat* 1306 (AAU, E, L); *Phengkklai* 4009 (A)]. SOUTH-WESTERN: Kanchanaburi [*Phengkklai* 362 (BKF, E, 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°30'N, 99°45'E, *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, *Sangkhachun* 618 (BKF, L)]; Rayong [12°37' N, 101°10' E, *Smitinand et al.* 6039 (L); *Suoatabandhn* 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, low-land 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 ridleii* 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

Rchb., Handb. Nat. Pflanzensyst.: 167. 1737; Benth., Gen. Pl. 3: 218. 1883; Pilger in Engl. & Harms, Nat. Pflanzenfam. 16b: 84. 1935.

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, extrafloral 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, eliasome sometimes present.

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

7. THESIUM

L., Hort. Cliff.: 41. 1737; Gen. Pl.: 60. 1737; Sp. Pl.: 207. 1753; R.Br., Prodr. Fl. Nov. Holl.: 352. 1810; A.DC., Prodr. 14: 637. 1857; Benth., Gen. Pl. 3: 221. 1883; Hook.f., Fl. Brit. Ind. 5: 229. 1886; Hill, Fl. Capens. 5.2: 136–200. 1915; Pilger in Engl. & Harms, Nat. Pflanzenfam. 16b: 67. 1935; Grierson & Long, Fl. Bhutan 1.1: 140. 1983; George, Fl. Australia 22: 67. 1984.

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.

Thesium psilotoides Hance, J. Bot.: 48. 1886; Forbes, Chinese Botany 1.6: 409. 1888; Lecomte, Bull. Mus. Nat. Hist. [Paris]: 403. 1914; Lecomte, Fl. Gen. I.-C. 5: 214. 1915. Type: China, Canton, *Hance* 13749 (holotype BM!)

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 quincuncially 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, *Pooma* 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

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NON-THAI SPECIMENS EXAMINED

Dendrotrophe buxifolia (Blume) Miq.

- CHINA: Hong Kong, Happy Valley, *Bodinier* 124 (L).
 VIETNAM: Bhudue, *Pierre* 1409 (E, GH).
 CAMBODIA: Cheko, Koh Kong province, *Kira et al.* 387 (KYO).
 MALAY PENINSULA: *Kingdon 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 Boeea* 3615 (A); Laboehan, *si Boeea* 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); Lambir hills, *Dan Bin & Bakar* 3019 (L); *Dayang* 50406 (L); *Polak* 253 (BO). SABAH: 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 Boeea* 3623 (A);
 BANGKA: *Teysmann* s.n. (U); *Teysmann* 3460 (P, U); *Bunnemeijer* 1473 (BO, L); *Bunnemeijer* 1621 (L); *Burger* 25 (L); *Huitema* 39 (L); *Kostermans & Anta* 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, Yai-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)]; Hue [*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, *Soejarto & Madulid* 6168 (A, L); Mt Victoria, *Sulit* 12326 (A, L); Mt Sorgson, *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); *Malvuis* 773 (SING); *Ridley* 359 (SING); *Burkill* 3220 (SING); *Holtum* s.n. (SING); *Hur & Kiah* 7804 (SING); *Kiah* 31858 (BO, L, SING); Kampong Gobek, Kerilla estate, Tamangan, *Shah & Kadim* 557 (BO, L); Gunong Rabong, *Soepadmo* 1077 (BO); Gunong Thana, *Soepadmo* 974 (L)]; Pahang [Fraser's 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); *Holtum* 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 [*Moysey & 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 Dulit, 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, *Wiriadinata* 870 (BO, L); Gunong Majar, Tebakang, *Yii 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); Baram district, *Chai* 35925 (L); Bukit Salong, Hose Mt, Melinau, *Chai* 37238 (L); Gunong Buda, Gunong Mulu national park, *Chai* 39906 (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 Sebuoh, 8 km southwest of Sipitang, *Beaman* 8726 (A, L); 5 02N 115 32E, *Beaman* 8407 (K, L)]; Beaufort district, 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)]; Kepyayan, *Dewol & Talib* 80417 (L); Mandahan forest reserve, *Dewol & Karim* 78036 (L); Pontianak, Kp. Mandor, *Mondi* 283 (L, SING, U); Banjaran 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); Seguntor river, *Wood* 3656 (L)]; Mandahan, Papar, *Husin* 86192 (L); Kimanis, *Talib & Heya* 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 Telamba 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); Lintoeng, Dolok Sangoel, *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 Boeea* 4186 (A); Langgapayung, *si Boeea* 3465 (A, L); Soengi Kanan, Laboehan Batoe, *si Boeea* 3999 (A); Rantau Parapat, Bila, *si Boeea* 2220 (A); Soengi Kanan, Laboehan Batoe, *si Boeea* 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 collettii (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 (Craib) 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); *Poliane* 30928 (P)]; Nam Phan, Nui Dai Ding near Dak, *Poliane* 32822 (P); Nam Phan, north of Kontum on summit of Ngoc Pong, *Poliane* 32149 (P); near Da Lat, *Poliane* 32567 (P); Nam Phan, near Thu Dau Mot, *Chevalier* 20403 (P).

Phacellaria compressa Benth.

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

CHINA: Yunnan, Teng Yueh, *Howell* 325 (E); Yunnan, Dapingdi, *Sino-British Expedition* 1981, 0080 (K).

MYANMAR: Taunggi 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 mountain range, 25°43' N, 100°02' E, *Bartholomew et al.* 207 (E); Yunnan, *Henry* 11085 (K).

***Osyris lanceolata* Hochst. & Steud. ex. A.DC.**

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 Xiengkhouang, *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)]; Pondichery, *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)]; *Haines* 2136 (K), Dehra Dun.

BHUTAN: Samchi district, 26°54' N, 89°06' E, *Grierson & Long* 3511 (E).

PHILIPPINES: Luzon [Laguna province, Makiling national park, *Sulit* 7028 (A)].

JAVA: *Zollinger* 2804 (A); East Java, *Groenhart* 92 (U); Pasoeroean, Malang, *Altona* s.n. (BO). TIMOR: Kapan, Soe, *Darnaedi* 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: Langkwai, north Kedah, *Chan* 6849 (SING).

SUMATRA: Ketambe, Lau Alas valley, Gunong Setan, *de Wilde & de Wilde Duyffjes* 14387 (K).

SARAWAK: Lambir hills, *Ashton* 16764 (BO, L).

JAVA: *Koorders* 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); Telephon, *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 Luoc, *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 Riau, *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 Thamias, *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 Royen & 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

GENUS	SPECIES	DISTRIBUTION
<i>Dendrotrophe</i>	<i>Dendrotrophe buxifolia</i> (Blume) Miq.	Bo, MP, P, S, T
	<i>Dendrotrophe varians</i> (Blume) Miq.	Au, B, Bo, C, Ca, J, L, Mol, NG, P, S, Si, V
<i>Dufrenoya</i>	<i>Dufrenoya collettii</i> (Gamble) Stauffer	B, T
	<i>Dufrenoya platyphylla</i> (Spreng.) Stauffer	B, I, T
	<i>Dufrenoya robusta</i> Stauffer	B, T
	<i>Dufrenoya sessilis</i> (Craib) Stauffer	L, T, V
<i>Phacellaria</i>	<i>Phacellaria compressa</i> Benth.	B, C, I, T, V
	<i>Phacellaria rigidula</i> Benth.	C, T
<i>Osyris</i>	<i>Osyris lanceolata</i> Hochst. & Steud.	Af, C, E I, L, T, V
<i>Santalum</i>	<i>Santalum album</i> L.	J, I*, T*, Ti, NG
	<i>Scleropyrum maingayi</i> Hook.f.	Bo, J, MP, S, T
<i>Scleropyrum</i>	<i>Scleropyrum pentandrum</i> (Dennst.) Mabb.	B, Bo, C, Ca, I, L, MP, NG, S, T, V
<i>Thesium</i>	<i>Thesium psilotoides</i> Hance	L, T

*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*.

Brown 1810	Blume 1850	Miquel 1856	A.D.C. 1857	Benth. 1883	Danser 1940	Stauffer 1969
Santalaceae (F)			Buckleyeae (T)			
<i>Santalum</i>		<i>Santalum</i>	<i>Santaleae</i> (T) <i>Santalum</i>	Osyrideae (T) <i>Santalum</i>		
		<i>Scleropyrum</i>	<i>Scleropyrum</i>	<i>Scleropyrum</i>		
<i>Osyris</i>	<i>Henslowia</i> <i>Exocarpos</i>	<i>Dendrotrophe</i>	<i>Osyris</i> <i>Henslowia</i>	<i>Osyris</i> <i>Henslowia</i> <i>Phacellaria</i>	<i>Dendrotrophe</i> <i>Phacellaria</i> <i>Hylomyza</i> <i>Dendromyza</i> <i>Cladomyza</i>	<i>Amphorogyneae</i> (T) <i>Dendrotrophe</i> <i>Phacellaria</i> <i>Dufrenoya</i> <i>Dendromyza</i> <i>Cladomyza</i>
<i>Thesium</i>			<i>Thesium</i>	<i>Thesieae</i> (T) <i>Thesium</i>		
<i>Exocarpos</i>			<i>Anthoboleae</i> (T) <i>Exocarpos</i>	<i>Anthoboleae</i> (T) <i>Exocarpos</i>		

F = Family; O = Order; T = Tribe