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A Systematic Revision of the Santalaceae R. Br. of Southeast Asia

A Systematic Revision of the Santalaceae R. Br. of Southeast Asia

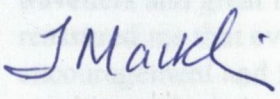
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A Thesis submitted to the University of Dublin, Trinity College, for the Degree of Doctor of Philosophy

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Jill Macklin

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Summary

Systematics is the study of biodiversity and taxonomy concerns the naming and describing of species, which are the basic units of life. Biodiversity studies have taken on a great importance in recent times due to the accelerated destruction of habitats with increased land use pressures and exploitation of natural resources. In particular tropical regions, which harbour over half of the world's biodiversity, have come under increased threat in the last century. These regions are also the least understood and studied regions in the world. The tropical ecosystem is a reservoir of untapped resources and genetic diversity which may be used by future generations in the search for cures for diseases and to counteract the deleterious effects of global climate change. It is becoming increasingly clear that an inventory of tropical species is necessary in order to provide information, which can be used to create conservation measures, and to give detailed information on species numbers which can be used to predict future extinction rates. In addition the study of evolutionary relationships amongst plant species is important for defining conservation criteria, to assist in defining specific relationships and in the production of better classifications.

This study involved a systematic revision of the Santalaceae in Southeast Asia. This region contains approximately 26% of the worlds plant species and is an area where the threat to biodiversity is ever increasing due to logging, shifting cultivation and conversion to plantation. The Santalaceae is a small family of hemiparasitic plants, which means that they are photosynthetic but rely on a host for water and some nutrients. There is a common theme within parasitic plants towards convergences and reductions in floral and reproductive parts. The Santalaceae is no exception and due to the limitation of traditional taxonomic methods specific and familial relationships have remained largely misunderstood. This study shows that Southeast Asia is home to 48 species of Santalaceae in 9 genera and this region is home to a unique group of Santalacean mistletoes. All of the species have been fully described in this thesis with accompanying identification keys. Ecologically the species are generally associated with disturbed habitats and the aerial parasites can display a degree of host specificity. These species generally inhabit montane regions and are usually parasitic on species which are associated with higher elevations such as *Quercus*, *Lithocarpus* (Fagaceae) and *Vaccinium* (Ericaceae).

Pollen morphology is very variable within the family and, with the aid of Scanning Electron Microscopy (SEM), it has been discovered that it can be a useful discriminating characteristic at the generic level within the tribe Santaleae and is very helpful in determining specific boundaries within the Amphorogyneae. In addition within this group pollen morphology can be associated with particular floral characteristics and may be a method for the adoption of selective pollination strategies.

The Santalacean mistletoes are confined to Southeast Asia and the position of generic boundaries within this group have remained controversial. Based on phylogenetic analysis of morphological characters and sequencing of the Internal Transcribed Spacer (ITS) 2 region of nuclear ribosomal DNA *Dendrotrophe* is the basal member of the Santalacean mistletoes. It is postulated that it was probably a progenitor of this group which migrated into Southeast Asia following the collision of India with Laurasia c. 45 Ma. Analysis of morphological characters has also indicated that the eastern Malesian genus *Dendromyza* is paraphyletic with *Cladomyza*, which occupies a similar geographic range and has many similar morphological characteristics.

In the taxonomic treatment of the species 48 species in 9 genera have been described. Identification keys, notes on the ecological requirements and geographical ranges of the species have been provided. *Cladomyza* has been subsumed into *Dendromyza* based on phylogenetic analysis and morphological observations. The taxonomic treatment has also resulted in the description of three species which are new to science, whilst specific boundaries have become broader in several instances due to the increased availability of herbarium material for investigation.

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Summary

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Introduction

This chapter presents an overview of the current state of the world's biodiversity with particular reference to Southeast Asia, which in this thesis, incorporates the countries of Thailand, Laos, Cambodia, Vietnam, Philippines, Malaysia, Brunei, Singapore, Indonesia and Papua New Guinea. This is followed by a discussion of classification systems and species concepts. The following section outlines the project goals and introduces the Santalaceae providing some information on general characteristics and ecology of the Southeast Asian species. Phylogenetic relationships of the order Santalales are explored in the next section with particular reference to the position of the Santalaceae in relation to the other families in the order. The penultimate section provides general information on the geographical and floristic setting in Southeast Asia and gives some detail on climate and vegetation types in the region. This last section is important for understanding geographical distributions and ecological affinities of the Santalaceous species, which will be encountered in later chapters. The final section presents a summary of the aims of the project outlining the various techniques, which have been utilised to explore the relationships and specific boundaries of the Southeast Asian Santalaceae.

Systematics and implications for biodiversity

Systematics is essentially the study of biodiversity, which refers to the numbers of plants, animals and microorganisms in the world, the genes they contain and the ecosystems they form. Biodiversity on Earth is the product of hundreds of millions of years of evolutionary history and is reflected in the variety and diversity of life observable in the world today (Department of the Environment, Sport and Territories (DEST) 1999). In the tropics intensive habitat alteration began after 1500 with the explorations by many European countries seeking to extend their wealth and resources. This continued in the late 19th century with the conversion of many areas into plantations (Heywood & Stuart 1992). The last century saw an unprecedented loss in biodiversity due to increasing population densities and increased exploitation of the world's natural resources (Philips 1988, World Resource Institute (WRI) 2000). Tropical forests are habitats with the greatest abundance and diversity of species in the world. They cover just 7% of the earth's land surface but harbour close to half its total number of species (Pearce & Brown 1994). It has been estimated that in 10 tropical forests, which

represent 3.5% of the total forest cover, 27% of the higher plant species can be found there and of those 14% are endemic to tropical regions (Bryant 1999). Latterly financial problems in developing countries which contain tropical forests and hence the highest proportion of the worlds biodiversity has led to the destruction of large tracts of forests which have been harvested for timber and other resources (WRI 2000). Logging, shifting cultivation and conversion to plantations (Anderson et al 1982, Johns 1992) have mainly caused the destruction of these areas. It seems clear that forest destruction relates directly to economic climates and deforestation has increased at various times through the last century in response to increased value for tropical timber, increasing populations and the falling value of domestic currencies (Capistrano 1994). In particular, in Southeast Asia, fire clearance for crop cultivation has been responsible for the removal of large tracts of forests (Myers 1994, Panayotou & Sungsuwan 1994). The Forestry and Agriculture Organisation of the United Nations (FAO) has estimated that shifting cultivation has been responsible for the removal of 70% of Southeast Asian forests (Whitmore 1998). The inherent poor soil quality of these forests, however, has meant that the clearance of larger and larger areas has been necessary to sustain agriculture (Reid 1992). In Malaysia the establishment of plantations of rubber and palm oil have had a major impact on the tropical ecosystem (Whitmore 1998) and 90% of the forests have been licensed for logging (Johns 1992). In the 1970s Indonesia was the world's leading exporter of tropical timber with a 41% market share but since that time timber prices have fallen and the main agents behind deforestation in that region are the need for agricultural land and the effects of transmigration and resettlement (Osgood 1994, Jepma 1995). The main effect of logging has therefore been seen in its opening up of inaccessible areas which can then be exploited for other uses (Barbier et al 1994).

There is little doubt that the rate of species extinction and hence loss of biodiversity has been increasing rapidly in the last few decades. In the 1980s the FAO estimated that annual tropical deforestation was 11.4 million ha/yr. (Reid 1992) while the World Resources Institute (WRI 2000) has produced a higher estimate of 20.4 million ha/yr. If these figures are correct 35% of tropical higher plant species may be extinct by the year 2040; certainly conservative estimates gauge that between 17 - 35% will be lost or committed to extinction by that time (Reid 1992). In terms of species numbers that means that up to 60,000 plant species may become extinct or receive severe erosion to their gene pool (Heywood & Stuart 1992). The World Conservation

Union (World Conservation Union (IUCN) 2000) estimates that currently 12.5% of vascular plants are threatened with extinction on a global level with figures of 40% recorded for some islands which are more vulnerable ecosystems and have a higher number of endemic taxa. Southeast Asia contains around 26% of the worlds tropical plant species and is also one of the most ecologically threatened areas of the world with one of the highest population densities and unstable political climates in many countries (Bryant 1999). It has been estimated that the region lost one third of its forest cover between 1960 and 1990 (WRI 2000). In northwest Borneo approximately 40% of the endemic species have been lost due to forest clearance and in the Philippines the past 50 years has seen two thirds of the forests removed (Wilson 1992). Based on current rates of extinction 5 - 11% of the plant species in Southeast Asia will be extinct by the year 2015 (Johns 1992). The region also has poorly enforced protected areas and in the Philippines, Myanmar, Laos, Cambodia and Vietnam conservation is not a high priority (Heywood & Stuart 1992, Greene & Paine 1997).

There are however some areas where conservation measures are taken more seriously. In Thailand there was a huge increase in forest disturbance early in the last century and less than 20% of the forest cover remains today (Santisuk et al 1991, Lombardini 1994, Paine et al 1997). A programme for the development of national parks has been in place since the 1960s and by 1991 Thailand had 63 national parks, 32 wildlife sanctuaries and 48 other protected areas which cover 11% of the country. This high figure compares to just 3.5% in neighbouring Malaysia (Gray et al 1991). Unfortunately there are still problems of degradation in preserved areas due to illegal logging and the development of resorts at the edges of the reserves. The fact remains, however, that although the prospects of many plant species in Thailand are not guaranteed, they are improving (Heywood & Stuart 1992). In Papua New Guinea a programme for Wildlife Management Areas has been established whereby landowners can regulate hunting and become involved in habitat protection, under this plan however there is no control over commercial logging if a landowner chooses to follow that avenue (Greene & Paine 1997). The importance of community based projects has emerged as a prerequisite for the protection of forest reserves in Southeast Asia, where the needs of local communities were originally ignored and led to the erosion and destruction of protected habitats by encroaching populations (Paine et al 1997).

One of the problems facing conservationists is that tropical areas are poorly explored and inventories of species are non-existent or incomplete (Heywood & Stuart 1992). On a worldwide scale the IUCN estimates that there are 250,000 flowering plant species (IUCN 2000) but it has so far proved impossible to give an exact number and figures vary between this low figure and up to 500, 000 (Iwatsuki 1996, May 1996). There is a general will to conserve the world's biodiversity as indicated by the signing by 150 governments of the Conservation of Biological Diversity strategy in the Earth Summit in 1992 (Bryant 1999). In approaching assessments of diversity, however, biologists are 'close to travelling blind' and there is an urgent need to catalogue the number of species in the world (Wilson 1992).

So far rates of extinction have been based on generalised and inadequate information (Whitmore 1998). Species inventories are therefore necessary so that areas for conservation can be identified and formulations of extinction rates may be calculated (Reid 1992). In the quest for assessing biodiversity taxonomy and systematics have emerged as essential tools for the effective quantification of diversity (Wilson 1992). It has been stated that "Without taxonomy to give shape to the bricks and systematics to tell us how to put them together the house of biological sciences is a meaningless jungle" (May 1990).

The reason for conserving biodiversity is not just for purely idealistic reasons. In particular the removal of tropical forests can have global as well as local consequences (WRI 2000). The tropical ecosystem is a reservoir of untapped resources, genetic diversity and many plant species have medicinal applications. The destruction of the habitat of perhaps undescribed but medicinally useful plants means that treatments for known and future as yet unknown diseases will be lost (DEST 1999). Tropical forests act as a sink for carbon dioxide (Gaston et al 1998, De Camargo et al 1999). Burning and the removal of these forests increases the level of carbon dioxide in the atmosphere resulting in a heating of the earth surface and consequently changes in global climates (Brown & Pearce 1994, Whitmore 1998, WRI 2000). This could have a serious deleterious effect by increasing sea levels dramatically and affecting crop production in many areas. Apart from the effect that climate change may have on land areas and food production it may also lead to further degradation of the remaining tropical forests exacerbating a worsening situation (Johns 1992, Myers 1994). If climate change is inevitable, and it appears that is so, then the retention of at least some areas of tropical forest may be important for

adaptation to change. The potential gene pool in tropical species could be used to tailor agricultural species to changing environmental conditions (DEST 1999).

It appears therefore that tropical ecosystems and hence a large proportion of the world's biodiversity are under severe threat. In order to control the destruction of these areas systematic revisions, like this study, play a very important role in the monitoring of biodiversity and in providing the basis for conservation measures. The production of species inventories and a better understanding of tropical environments also has an essential part to play in the exploitation of new natural resources and in the control of global climate change.

Classification systems

The basic unit of biodiversity is the species (Claridge et al 1997). Systematics in the naming and description of species (taxonomy), and the investigation of evolutionary relationships amongst and between species (systematics in the strict sense), (Minelli 1993) has emerged as an essential component in maintaining biodiversity (Reid 1992). At its most essential level systematics involves the construction of classifications, which is the hierarchical arrangement of objects within classes, such as individuals into species and species into more inclusive genera and families (Minelli 1993). Classification systems are expected to be easy to use and concise enough so that they are easy to recall; fundamentally they are created as an aid to memory (Judd et al 1999). A good classification aims to put order on biological diversity so that it can be easily comprehended by the human mind and interrelationships between groups of organisms can be distinguished (Claridge et al 1997). Systematics has a long history, as early as 300 BC Theophrastus wrote descriptions of plants and was the first to indicate the difference between Monocotyledon and Dicotyledons (Stearn 1996, Judd et al 1999). It was Caesalpino in 1583 who later suggested that natural classification systems should be based on characters of the flowers, fruit and seed, characters which are still the basic units for any classification system (Minelli 1993). Linnaeus as the 'father of modern botany' standardised the use of the binomial system for naming species, that is, the use of generic and specific epithets (Judd et al 1999). In his sexual system of flowering plants he recognised 24 classes determined by the number of stamens and he further subdivided classes into orders based on the numbers of female reproductive parts. In his Philosophia Botanica (1751) he refined his classification system based on the symmetry of plant parts and some of his groups are still recognised today e.g. Umbelliferae (Apiaceae) and Compositae (Asteraceae) (Rendle 1925).

Although Tournefort in 1694 was the first advocate of grouping species into genera Linnaeus expanded on his work and gave more detailed descriptions of generic characteristics and today's genera are built on the foundations of his thesis (Judd et al 1999). Jussieu (1789) improved on the Linnean system and defined 100 orders of plants in 15 classes (Rendle 1925). His primary division was based on the distinction between Monocotyledons and Dicotyledons and his subdivisions were based on the presence or absence of petals and the relative position of floral parts (Judd et al 1999). This latter characteristic was drawn from the terms hypogynous (perianth and stamens attached below the ovary), perigynous (perianth and stamens attached around the ovary) and epigynous (perianth and stamens inserted above the ovary) of Theophrastus (Rendle 1925). From a philosophical point of view Jussieu's system was based on his belief that there are no natural groups in nature and classifications are man-made devices. His families were therefore based on general rather than absolute differences and gradual transitions from one to another produced continuity in relationships (Judd et al 1999).

The Prodromus of A.P. de Candolle (1824 - 73), which was continued by his son Alphonse, contained descriptions of all known species, at that time, and is an indispensable work in any systematic investigation. A. P. de Candolle reasoned that the relationships between plants were to be ascertained by comparative morphology rather than considerations of function. He divided up the Dicotyledons into Thalamiflorae (hypogynous, petals and sepals distinct), Calyciflorae (perigynous, sepals and petals distinct), Corolliflorae (sympetalous) and Monochlamydeae (perianth undifferentiated into sepals and petals) (Rendle 1925).

All of these classification systems were written before theories of evolutionary relationships were proposed and were produced as practical handbooks, arranged to facilitate determination (Judd et al 1999). Even the work of Bentham and Hooker (1862 - 1883) which postdated evolutionary theory was produced as a guide to the families of flowering plants and largely followed the system of de Candolle as it was not intended to express phylogenetic (evolutionary) relationships (Rendle 1925). All of the early systems also had a common thread in that they recognised a small number of families (Bentham and Hooker took 200 as the upper limit) and smaller groupings at all hierarchical levels following the theme that classifications should be concise and easy to use (Judd et al 1999).

The work of Engler and Prantl at the turn of the 20th century, which began when the theory of evolution was accepted, attempted to incorporate phylogenetic relationships into a classification system (Rendle 1925). It was somewhat unsuccessful, however, due to lack of available information. Theories of what were primitive and advanced characteristics, under their system, do not correspond to modern understanding (Judd et al 1999). A larger number of families were recognised but in interpreting the absence of a perianth as a primitive characteristics and therefore placing the Amentiferae (plants lacking a perianth) at the beginning of their classification they were mistaken.

The advent of phylogenetic theory has led to the reinterpretation of species relationships and differing views on the rank of taxa (should they be genera, tribes or families) has resulted in the acceptance of different numbers of plant families (Cronquist 354, Takhtajan 589, Angiosperm Phylogeny Group (APG) 462) (Judd et al 1999). Current classification systems seek to elucidate relationships between different families based on their phylogenetic status and origin (Heywood 1997). Techniques of molecular analysis have provided powerful tools by which evolutionary relationships between species can be explored and hopefully elucidated (Soltis & Soltis 2000). To that end the Angiosperm Phylogeny Group has recently produced a classification of 462 families in 40 orders based on *rbc*L, *atp*B and 18S rDNA genes (APG 1998, Soltis et al 1999). Despite certain areas of poor resolution and weak support it has been claimed that the general framework of angiosperm classification has now been elucidated and further work in this area should provide a more stable classification system (Soltis et al 1999). Continued work is therefore required in order to provide a balanced reference system which can be used not just in systematics but in many other areas of biology (APG 1998). This work is particularly necessary in light of the prior discussion on the needs of conservation. Only when a stable classification is produced and relationships between families and species are understood can the requirements of conservation on the numbers of species and families in a given area be provided (Hervé & Adoutte 1996, Williams 1996).

Species concepts

If species are the fundamental units of biodiversity and the basis for all classification systems then it is necessary to understand what exactly is meant by a species. 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). In systematic botany, however, the concept of what constitutes a species has been hotly debated over the last century (Minelli 1993). In the preceding century there was not much controversy on the issue and even though Darwin called his treatise on evolution 'On the Origin of the Species' he did not address the subject of species concepts (Judd et al 1999). To Darwin species were simply arbitrary stages in the process of the evolution of divergence (Claridge et al 1997).

In a discussion of species concepts it is first necessary to differentiate between species as a taxon, which is a natural entity recognised and delimited by a taxonomist with an existence in space and time, and a species as category, which is a point in taxonomic hierarchy and the rank which is given to a species taxon (Minelli 1993). The nihilistic approaches of some who claim that there is no such thing as a species or speciation (Nelson 1989) are unhelpful. Claims that no patterns of biological diversity can be distinguished at a hypothetical species level is a defeatist attitude and avoids the question of species interactions and their underlying evolutionary relationships.

Species have been recognised for a very long time and can be traced back to Aristotle who recognised groups of organisms on the basis of their shape and resemblance to each other (Gornall 1997). The criteria for recognising species was proposed by Ray in 1686 who suggested that reproductive characteristics should be used in their delimitation (Minelli 1993). Linnaeus (1753) adopted this theory in his sexual system, which distinguished species on the basis of a few reproductive characters. Linnaeus believed that a species was a fixed system, which exhibited a certain amount of variation, and that it was up to the individual scientist to recognise the limits of that variation (Judd et al 1999). 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).

Historically species were often described from fragmented herbarium material without knowledge of growth form or habitat (Claridge et al 1997). This practice led to the proliferation of species names, many of which, in the light of new evidence, have been reduced to synonomy. These practices undermined the TSC and resulted in a certain instability in species delimitation. As a result many systematists have rejected the concept of a taxonomic species (Minelli 1993). Currently, however, the use of evidence from a wide variety of sources such as morphological, molecular and anatomical studies has strengthened the grounds on which morphological species are described. The International Code of Botanical Nomenclature has also laid down rules for the description and publication of species and the correct interpretation of botanical nomenclature (ICBN 1994).

A criticism, which has been leveled at the TSC, is that it treats species as classes, which cannot evolve. This argument considers that species are not members of a class but parts of an integrated unit, which maintains its identity despite the turnover in its part. Classes cannot change whereas species can evolve through individual members. This criticism of the taxonomic species sees it as an artificial construct, which is unwieldy in the face of evolutionary change (Minelli 1993). There is also an inherent problem with the TSC in that species are all given an equivalent rank which means that there is no differentiation between sexually reproducing species and asexual, apomicts and ecotypic species which hold less significance in terms of their contribution to biodiversity (Gornall 1997). This latter problem has been somewhat overcome by the Biosystematic Species Concept, which interprets intermediate categories between species placing them just above and below the species level (Minelli 1993). The major perceived difficulty with the TSC is that it is not actually a concept but rather a method of description and the amount of difference which is required to differentiate between species is based wholly on subjective judgement (Davis & Heywood 1963). Conventions have however been adopted in the recognition of a species and it is a general requirement that at least two independent characters are used to delimit a new species and that variety within a species must be less that that between species. Morphological variation within and between populations can

also be examined by statistical techniques in order that patterns of variation can be compared and compartmentalised if necessary (Gornall 1997).

Owing to the perceived lack of a theoretical basis for the Taxonomic Species Concept other theories have emerged which have attempted to replace it (Gornall 1997). The attempt to define species by recognising them as reproductive communities dates from the time of Ray and de Buffon, in the 17th and 18th centuries respectively, who viewed species in terms of their gene pool (Minelli 1993). The role of gene flow in determining species boundaries is encapsulated in the Biological Species Concept (BSC) where members of a species form a reproductive community and individual members of a species can recognise each other as potential mates (Mayr 1942, Minelli 1993). This concept of species as reproductive communities is essentially isolationist and does not cover every aspect of reproductive populations. In particular in plants where hybridization and apomixis are common occurrences the theory of a biological species fails (Judd et al 1999). The adoption of biological species in terms of plants is generally unrealistic, as it would lead to the naming of potentially vast numbers of selfing individuals as species, e.g. in *Taraxacum* Weber ex Wigg. (Asteraceae) where there are over 2000 microspecies known to exist (Minelli 1993). In other instances too broad a species concept may be applied in groups such as Maloideae where some genera such as *Crataegus* L., *Malus* Miller and *Cotoneaster* Medikus. (Rosaceae) are known to hybridise (Judd et al 1999). The Recognition Species Concept (RSC) is similar to the Biological Species Concept in that it essentially focuses on the role of gene flow within populations (Claridge et al 1997). Under this system Specific Mating Recognition Systems allow individuals to recognise potential mates and each species is defined by a unique set of recognition signals. Whereas the BSC is isolationist the RSC focuses on cohesive forces in maintaining species integrity (Judd et al 1999). In truth there is little difference between the two theories. The appeal of the two concepts lie in their simplicity, the emphasis on gene flow and the fact that they can be tested by verifying interfertility. Infertility cannot, however, provide proof in plant species where there may be large difference in fertility between individuals and populations (Judd et al 1999).

The desire to eliminate the importance of one set of characteristics over others and the wish to incorporate evolutionary theory into species concepts led to the proposal of a Phylogenetic

Species Concept (PSC) (Claridge et al 1997). Simpson was one of the first to develop this theory by integrating current species with species as segregate evolutionary lineages which include fossils. In the PSC gene flow is not considered as the only important factor in distinguishing between species and genetic drift and descent from a common ancestor are judged to be important contributing factors (Gornall 1997). Over the past few decades several versions of the PSC have been proposed (Claridge et al 1997). Monophyly (evolution from a single common ancestor) is an essential requirement for all of the theories and species are defined on the possession of a set of apomorphic (derived) characteristics (Judd et al 1999). In the related Diagnosable Species Concept (DSC) phylogenetic species are seen the smallest aggregation of lineages diagnosable by a unique combination of character states (Nixon & Wheeler 1990). The concept of what comprises a diagnosable character is however not clarified. For example the presence of a single genetic difference between small populations with no associated morphological difference could, in a similar manner to the BSC, lead to the proliferation of new species which are not readily identifiable (Gornall 1997). The advantage this hypothesis has over the BSC is that it is inclusive of apomictic and asexually reproducing populations and seeks to remain as faithful as possible to what are considered natural groups (Claridge et al 1997). If morphological characters are considered to be diagnostic characteristics then the Diagnostic Species Concept is not so different to the Taxonomic Species Concept as both require that species be recognisable and both attribute species rank to the least inclusive group (Gornall 1997, Minelli 1993). In this respect therefore it also has a similar disadvantage in that it will not be able to reveal complex species associations (Claridge et al 1997). The fact that monophyly is a requirement for this theory has been seen as a draw back as not all the descendents of the most recent common ancestor may be included in the species or in other words paraphyletic species are not accepted (Gornall 1997).

A possible compromise between the Phylogenetic and Taxonomic Species Concept is the Composite Species Concept (CSC) which is based on a more inclusive but abstract theory. The basic tenet of this idea is that a species consists of a set of organisms that belong to several subgroups in a phylogenetic series. Under this system breaks in the genealogical network which would be considered speciation events under the Phylogenetic Species Concept are not automatically accepted as such. It is impossible, however, to tell if the splits in the network will lead to speciation events when they occur as they may be just fleeting aberrations

in small isolated populations. Speciation is therefore retrospective and permanent splits in the network can only be recognised after some considerable time (Kornet 1993). The theory is therefore inclusive of what would be paraphyletic species under the Phylogenetic Species Concept. In terms of its current application this theory is impractical due to its retrospective nature, but it represents an important new way of looking at species when faced with seemingly reticulate character distribution between species with unclear specific boundaries. This theory states that the diversity, which we can observe in the world around us, is just a slice in the evolutionary history of a variety of groups some of which have achieved speciation events and some of which are in the process of speciating (Kornet 1993). The value of this theory is therefore not in its practical application but more in its philosophical considerations and relationship to other species concepts.

All of the various species concepts have something to offer when considering what a species comprises (although the BSC and RSC are probably less useful concepts in terms of plant systematics). 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 seems, therefore, 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). The evidence, which provides proof of what species represent in different groups, is obtained from morphological, molecular, ecological, breeding systems and distribution patterns, incorporating all of the other species concepts. 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. Phylogenetic analysis is particularly important in contributing information on evolutionary relationships between species and genera (Soltis &

Soltis 2000). Taxonomic and phylogenetic evidence has been taken from a variety of sources. Primarily morphological characteristics have been studied but palynological and molecular information has been used to confirm and investigate species identities and relationships.

Project Goals

The aim of this study is to complete a revision of the Santalaceae R. Br. for Southeast Asia. The primary goal is to provide a taxonomic account for the family in Thailand, Indochina (Laos Cambodia and Vietnam) and Malesia (Malaysia, the Philippines and Indonesia). To that end a large amount of herbarium material gathered from European, Southeast Asian and Australian herbaria has been consulted in order to determine specific boundaries and to investigate the extent of infraspecific variation. All available taxonomic literature has been examined to verify and furnish correct specific epithets. The basis for species delimitation has been based largely on morphological characteristics observable on herbarium material with additional information provided from a palynological survey of the Southeast Asian species. Some details of ecology and growth habit have been provided based on field observations accompanying herbarium specimens and consultation of available literature. A secondary aim has been to investigate the phylogenetic relationships between the aerial members of the Santalaceae, which has been accomplished by cladistic analysis of a combination of morphological and molecular characteristics. Finally exploration of infraspecific variation within a single very widespread species has been undertaken in order to test its current classification and to give details of its range of variation. Morphological characteristics have been used in the exploration of infraspecific variation in this species and various techniques of morphometric analysis have been employed in the analysis.

Characteristics of Santalaceae

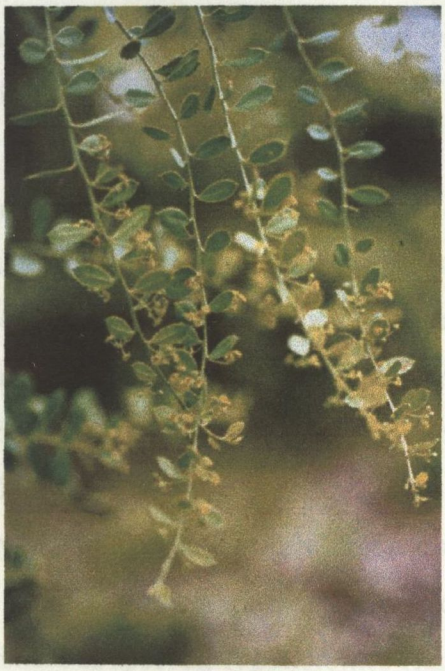
The Santalaceae is a relatively small family of 400 – 540 species, which are contained within 30 - 32 genera (Mabberley 1997, Heywood 1997). The family has a cosmopolitan distribution in tropical and temperate regions with a concentration in arid and semi arid areas. Almost one third of the species (126) and over half the number of genera (16) are located in Southeast Asia and Australia, the rest of the species 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 8 monotypic genera in the family but most of them (5) are restricted to North or South America (Brummitt 1992).

The family contains herbs, shrub, small trees and climbers, in addition Southeast Asia is home to the only known group of branch parasitic Santalaceae. The family is characterised by a hemiparasitic growth habit, which means that individuals are able to photosynthesise but require the presence of a host plant for water and some minerals, which they obtain via a haustorial connection (Nickrent & Starr 1994). The extent to which Santalaceous species are facultative (not always requiring a host plant) or obligate (always requiring a host) hemiparasites (Nickrent & Starr 1994) is not known but studies of *Santalum album* L. which is a small tree indicates that this species is reliant on a host for at least the first stages of growth and development (Bhaskar 1992). In general flowers are small and inconspicuous and borne in dense inflorescences of various kinds. They are odourless or have a faint scent, hermaphrodite or dioecious and radially symmetrical with 3 - 5 undifferentiated perianth lobes (tepals) inserted in a single whorl (**Fig. 1**). Stamen numbers equal the number of perianth segments and are placed one opposite each tepal. The cup-like 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 may act as a secondary attractant. The ovary is unilocular, 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, frugiverous birds being the most common dispersal agents (Herrera 1988). In temperate regions, in the genus *Thesium* L., dispersal is thought to be mediated by ants as the pedicel of the flower contains an eliasome (Reid et al 1995). The seedlings of terrestrial Santalaceae are either epigaeus (cotyledons carried above the soil) or hypogaues (cotyledons remaining below the soil) and cryptocotyly (cotyledons indistinct) has been observed in some of the branch parasitic species (Kuijt 1990). Although some species have hermaphrodite flowers the family is thought to be strictly outbreeding. In *Santalum album* L. the bisexual flowers are homogamous (anthers and stigma receptive at the same time) but studies have shown that some kind of self incompatibility mechanism exists which ensures that self fertilisation is prevented (Sindhuveerendra & Sujatha 1989, Bhaskar 1992). This species was also thought to exhibit an unusual property within the Santalaceae in that the



a. Illustration of *Santalum album* L.
a. stamens are equal to the number of tepals and placed in an opposites position. The nectarial disc alternates with the perianth segments. b. a tuft of hairs emanates from the tepal base behind each stamen



b. Photograph of *Osyris lanceolata* Hochst. & Steudel. This species has pendulous branches and inconspicuous inflorescences which are yellowish green in colour.



c. Photograph of *Osyris lanceolata* Hochst. & Steudel. A close up of the flower. a. open flower with the stamens inflexed over the nectarial disc. b. the nectarial disc turns red / brown withmaturity.

Fig. 1 An illustration of **a.** *Santalum album* and photographs of **b.**, **c.** *Osyris lanceolata* showing the construction of the flower and they inconspicuous nature of the flowers and inflorescences

flowers change colour with age from a pale white creamy colour to dark red and at the same time the receptivity of the stigma decreases. The changing of the perianth colour probably makes the mature flowers invisible to potential pollinators and this coupled with the decline in stigma receptivity ensures maximum pollination of all available flowers (Bhaskar 1992). This current study has revealed that this phenomenon is not restricted to *S. album* and is probably quite common, as changing perianth colour has been observed in several other of the Southeast Asian species of Santalaceae.

In terms of conservation status it is estimated that 9.3% of Santalaceae are threatened with extinction and four species are known to be extinct (IUCN 2000), insufficient data however means that these figures may be an underestimate. Of the number which are threatened with extinction most occur in Australia and the Pacific islands due to changing land practices and the vulnerability of small island populations. The large amount of information on Australian taxa also highlights the fact that details of species conservation status only come from areas where there is sufficient information. Many other regions, which are understudied, may contain species, which are under threat, but without adequate knowledge nothing can be said about their conservation status.

Santalaceae in Southeast Asia

Southeast Asia is home to 48 species of Santalaceae in 9 genera. A number of the genera do not have a strict affinity with the region and are represented by a single species at the limit of their generic range. *Santalum* L. which contains approximately 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 other areas for its valuable, fragrant timber, which is used for intricate carvings. An essential oil, which is obtained by distillation of the heart wood and roots, is also the basis of many perfumes (Lewington 1992). *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 2 species, has a single representative, *O. lanceolata* Hochst. & Steudel, which has a widespread distribution from southern Europe to northern Thailand. The Australian genus *Exocarpos* Labill. which contains 26 species obtains its most westerly extent with *E. latifolius* R. Br., a shrub of coastal regions which is found from the Malay Peninsula to Australia. All of the remaining five genera are confined to

Southeast Asia. *Scleropyrum* Arn. contains four species of small trees, which are found from southern China and India to New Guinea and is characterised by amentiferous inflorescences and pyriform fruits. The other four genera *Phacellaria* Bentham, *Dendromyza* Danser, *Dufrenoya* Chatin and *Dendrotrophe* Miq. are all climbing or branch parasites. This latter group consisting of 40 species also represents the majority of the Southeast Asian Santalaceae. The word dendroparasite has been coined in this study to describe the shrubby, parasitic growth habit of these species and is used interchangeably with mistletoe and branch parasite. To avoid confusion in later chapters, species name are abbreviated so that *Dendromyza* will become *Dm.*, *Dufrenoya* will be *Df.* and *Dendrotrophe* will be *Dt.*

Mistletoe ecology

The canopy dependence of mistletoes makes them a distinct ecological group (Reid et al 1995) and Santalaceous mistletoes have developed an elaborate fruit construction in accord with their aerial habitat (Kuijt 1969). Physiologically the most important limiting factor in the survival of mistletoes is the maintenance of a lower water potential than their host plants and they generally have high transpiration rates in order to do this (Reid et al 1995). Nitrogen is also known to be another growth limiting factor and maintenance of higher transpiration rates may also be a way of acquiring nitrogen from the host xylem (Schultz et al 1984). Incompatibility mechanisms such as physical barriers and chemical cues within a host tree may also be reason why these dendroparasites are often associated with particular plant species (Reid et al 1995). For example *Dufrenoya* is often parasitic on Fagaceae and *Dendromyza* is commonly associated with Ericaceae. In addition many species of *Dendromyza* have secondary haustoria which are external root-like structures which grow from the branches of the parasite and attach to different parts of the host plant, a phenomenon which is fairly common in parasites of the humid tropics (Kuijt 1969). *Phacellaria* is a hyperparasite (parasitic on other mistletoes) on species of Loranthaceae and *Dufrenoya* with a degree of endophytic growth. This means that strands of tissue, emanating from the primary haustorium, ramify through the host cortex and give rise to aerial shoots that emerge through the host bark and through lenticels at different points along a branch (Reid et al 1995). This strategy may be important on long-lived hosts where the parasite can persist after the primary connection has senesced or abscised (Hamilton & Barlow 1963). *Dendrotrophe* is a generalist parasite, in particular *Dt. varians* (Bl.) Miq. which is normally a terrestrial climber is parasitic on a variety of plant species. The generalist

strategy may also be responsible for the widespread distribution of this species from southern China to Australia. The distribution of the other genera, *Dufrenoya* and *Phacellaria* in western Southeast Asia and *Dendromyza* in eastern Malesia may in part be attributed to their particular host associations and the behaviour of avian dispersal agents which have a particular affinity with certain geographical regions (Reid et al 1995). The historical geological instability of the Southeast Asiatic region (Hall 1998) has also certainly contributed to their particular geographic distributions. Due to their specific ecological requirements, complex associations with other organisms and the lack of persistent seed bank mistletoes are particularly sensitive to habitat disturbance (Reid 1991, Nickrent 2000). Their absence from conservation lists and the lack of detail on their ecology, breeding biology in scientific literature indicates that field studies are required in order to determine their particular conservation requirements.

Phylogenetic relationships of the Santalales

The Santalaceae is contained within the order Santalales which is thought to be a monophyletic group and also includes the families Olacaceae, Loranthaceae, Misodendraceae, Opiliaceae and Viscaceae (Nickrent 2000). All members of the order are parasitic although some species of Olacaceae are known to be facultative hemiparasites (Kuijt 1969). Associations, in the group as a whole, includes the shift from a non parasitic to parasitic mode of growth, from bisexual to unisexual flowers, a superior to an inferior ovary and from free central to basal placentation (Nickrent 2000). These are just overall tendencies however and different patterns emerge within the various families. For example within the Santalaceae *Exocarpos* which is considered the most derived genus (Kuijt 1969, Lobreau Callen 1982) has a superior ovary. Determination of relationships amongst parasitic plants has often been problematical owing to frequent reductions in vegetative and floral characteristics (Kuijt 1969, Nickrent & Franchina 1990) and at different times various other families have been placed within the order (Endlicher 1840, Fagerlind 1948, Heywood 1997). The limited number of characters for phylogenetic analysis and the high incidence of reversals and convergent evolution has also meant that relationships between families has often proved difficult to resolve (Nickrent & Franchina 1990).

Historically the Santalales was thought to have been derived from within the Celastrales with affinities to the Proteales, and some authors (Heywood 1997) have maintained this traditional classification. A common ancestor for the Celastrales and the Santalales with both orders

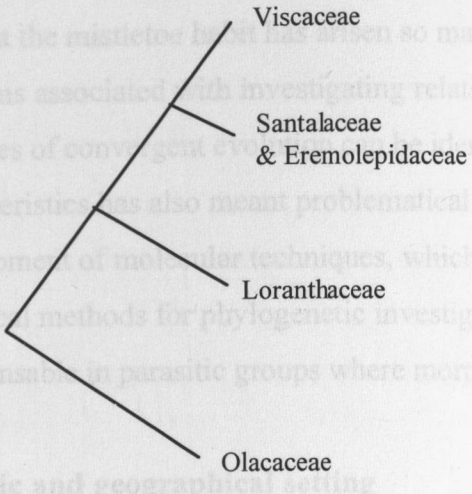
derived from the Saxifragales has been suggested by Takhtajan (1980) whilst Cronquist (1981) has suggested that the Rafflesiales and Santalales share a common ancestor based on the mode of parasitism and the lack of any other possible relatives for the Rafflesiales. A recent classification of the angiosperms using cladistic analysis of molecular markers has however indicated that the Santalales is a sister group to the Caryophyllales and Berberidaceae, with the Saxifragales derived from the clade which contains these groups (Nickrent & Soltis 1995, APG 1998). In this analysis there is no close association between the Celastrales and the Santalales but there is a suggestion that the Santalales and Caryophyllales are derived from the Proteales. Takhtajan (1997) places Rafflesiales in the Magnoliales and Thorne (1992) suggests an allied position for this group with the Magnoliales. A recent molecular study suggests that the family Rafflesiaceae belongs to the group of primitive angiosperms, which includes Chloranthaceae and Hydnoraceae (APG 1998).

The expression of parasitism and embryological studies have largely influenced the classification of the Santalales. Reliance on these characters has, however, been questioned due to the fact that parasitism appears to have arisen independently seven to nine times throughout the angiosperms (Kuijt 1968). Reduction in reproductive characteristics and specialised dispersal and germination patterns has also meant that convergent patterns in ovary construction have occurred in unrelated parasitic families (Nickrent & Franchina 1990). Fagerlind in 1948 proposed one of the first evolutionary trees for the order (Nickrent 2000). The Balanophoraceae was included in this scheme, derived from the Loranthaceae and Heywood also includes it within this order but suggests an affinity with the Haloragaceae (*Gunnera*). Kuijt suggested that the inclusion of the Balanophoraceae in the Santalales was the result of a historical accident in the misinterpretation of ovary structure (Kuijt 1968). Molecular analysis by the Angiosperm Phylogeny Group (1998) suggests an unknown affinity for this strange family of holoparasites, which was originally misidentified as a fungus (Heywood 1997). Grubbiaceae was established by Endlicher (1840) as a distinct family close to the Santalaceae and Bentham (1883) later reduced it to a tribe of dubious affinity within the family. Johri and Bhatnagar chose to follow Endlicher's classification of Balanophoraceae but included it within the subtribe Santalineae which also included the Santalaceae and Olacaceae (Johri & Bhatnagar 1960). Recent classification systems now accept that the Balanophoraceae

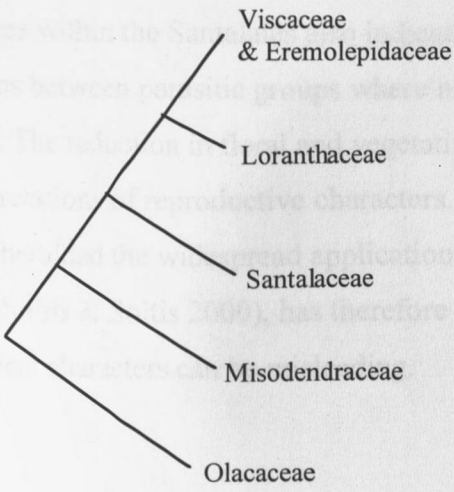
belongs within the Ericales, a fact which has been supported by palynological and molecular evidence (Erdtman 1952, Heywood 1997).

One fact that has been accepted by all authors is that some members of the polyphyletic (derived from more than two ancestral lineages) family Olacaceae are basal within the order (**Fig. 2**) (Kuijt 1968, Nickrent & Franchina 1990, Nickrent et al 1998). In the past the Santalaceae was placed near the Olacaceae with both the Loranthaceae and Viscaceae derivable from it (Bhatnagar & Johri 1983). Current evidence, however, points to a derived position for the Santalaceae between the Loranthaceae and Viscaceae with the latter as the most advanced family within the order (Nickrent et al 1998).

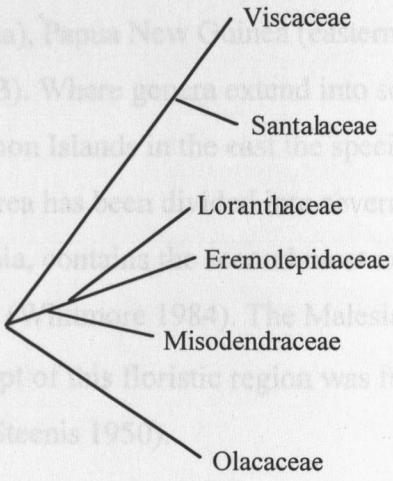
Families that have been included in or split off from the Santalaceae *sensu lato* are the Misodendraceae, Eremolepidaceae and Opiliaceae (Bentham 1883, Johri & Bhatnagar 1960, Wiens & Barlow 1971). It is now considered that the latter family is a sister to the Santalaceae between it and the Loranthaceae (Nickrent 2000). Due to the fact that the ovary of Misodendraceae exhibits free central placentation it was included under the Santalaceae by Bentham (1883). It has quite different floral characteristics from the Santalaceae, however, as the anthers are unilocular and there is a bristle of hairs between each perianth segment which alternate with the stigma (Heywood 1997). Kuijt (1968) therefore placed Misodendraceae as a separate family close to the Olacaceae, a position which has been verified by molecular evidence (Nickrent 2000). Nickrent et al (1998) have also suggested that this small monogeneric family of branch parasites from South America is relictual and evolved on the Gondwanan landmass along with the Loranthaceae. Traditionally Eremolepidaceae has been placed as a distinct family with connections to Viscaceae and Loranthaceae (Kuijt 1968, Bhatnagar & Johri 1983). Wiens and Barlow (1971) were the first to suggest, based on karyological evidence, that the family was part of the Santalaceae. Molecular analysis supports this theory and has repeatedly shown that this group of mistletoes, of South American origin, is monophyletic with the Southeast Asian Santalaceae (Nickrent & Soltis 1995). This and later analyses (Nickrent et al 1998) demonstrates that the Santalaceae is paraphyletic (having more than one common ancestor).



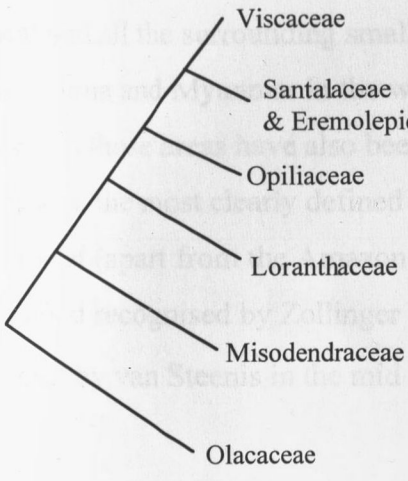
A. Wiens and Barlow (1971)
Karyological data



B. Bhatnagar & Johri (1983)
Embryology



C. Kuijt (1968)
Inflorescence structure



D. Nickrent (2000)
Molecular data

Fig. 2 Four hypothetical phylogenetic trees for the Santalales based on karyology, embryology, inflorescence morphology and molecular data. The most recent classification of the order (**D.**) has been proposed by Nickrent based on a combined cladistic analysis of 18S rDNA and *rbc*L genes. This figure is taken from Nickrent (2000) with some modifications (branch lengths are representations and are not indicative of divergence of relationships).

It appears from current information on the Santalales that branch parasitism has arisen four times within the order (Santalaceae, Misodendraceae, Viscaceae, Loranthaceae) (Nickrent et al 1998). It also highlights the difficulties associated with classification systems when too much weight is placed on a small number of characters, in this case embryology and parasitism. The fact that the mistletoe habit has arisen so many times within the Santalales also indicates the problems associated with investigating relationships between parasitic groups where many instances of convergent evolution can be identified. The reduction in floral and vegetative characteristics has also meant problematical interpretations of reproductive characters. The development of molecular techniques, which have heralded the widespread application of new analytical methods for phylogenetic investigation (Soltis & Soltis 2000), has therefore proved indispensable in parasitic groups where morphological characters can be misleading.

Floristic and geographical setting

This study involves a revision of the Santalaceae in Southeast Asia which incorporates the countries of Thailand, Laos, Cambodia, Vietnam (Indochina), Malaysia, the Philippines, Indonesia (eastern Borneo, Sumatra, Java, Sulawesi, Moluccas, Irian Jaya (western New Guinea), Papua New Guinea (eastern New Guinea) and all the surrounding smaller islands) (**Fig. 3**). Where genera extend into southern India, China and Myanmar in the west and the Solomon Islands in the east the species which occur in those areas have also been addressed. The area has been divided into several floristic regions; the most clearly defined of which, Malesia, contains the second most extensive rainforest (apart from the Amazon basin) in the world (Whitmore 1984). The Malesian region was first recognised by Zollinger in 1857 and the concept of this floristic region was further developed by van Steenis in the mid 20th century (van Steenis 1950).

Phytogeography of Malesia

The delimitation of this area is defined by four contacts with adjacent floral regions where there are changes in floristic composition and numbers of plant genera (van Steenis 1950). The most northerly point of Malesia is at the Isthmus of Kra in Peninsular Thailand where there is a difference of 575 genera between the north and south of this point (Johns 1995). In the north the boundary is defined by the Philippines where 424 genera occur in Philippines which are not represented in the nearest pacific islands. The strongest line of demarcation is in the east

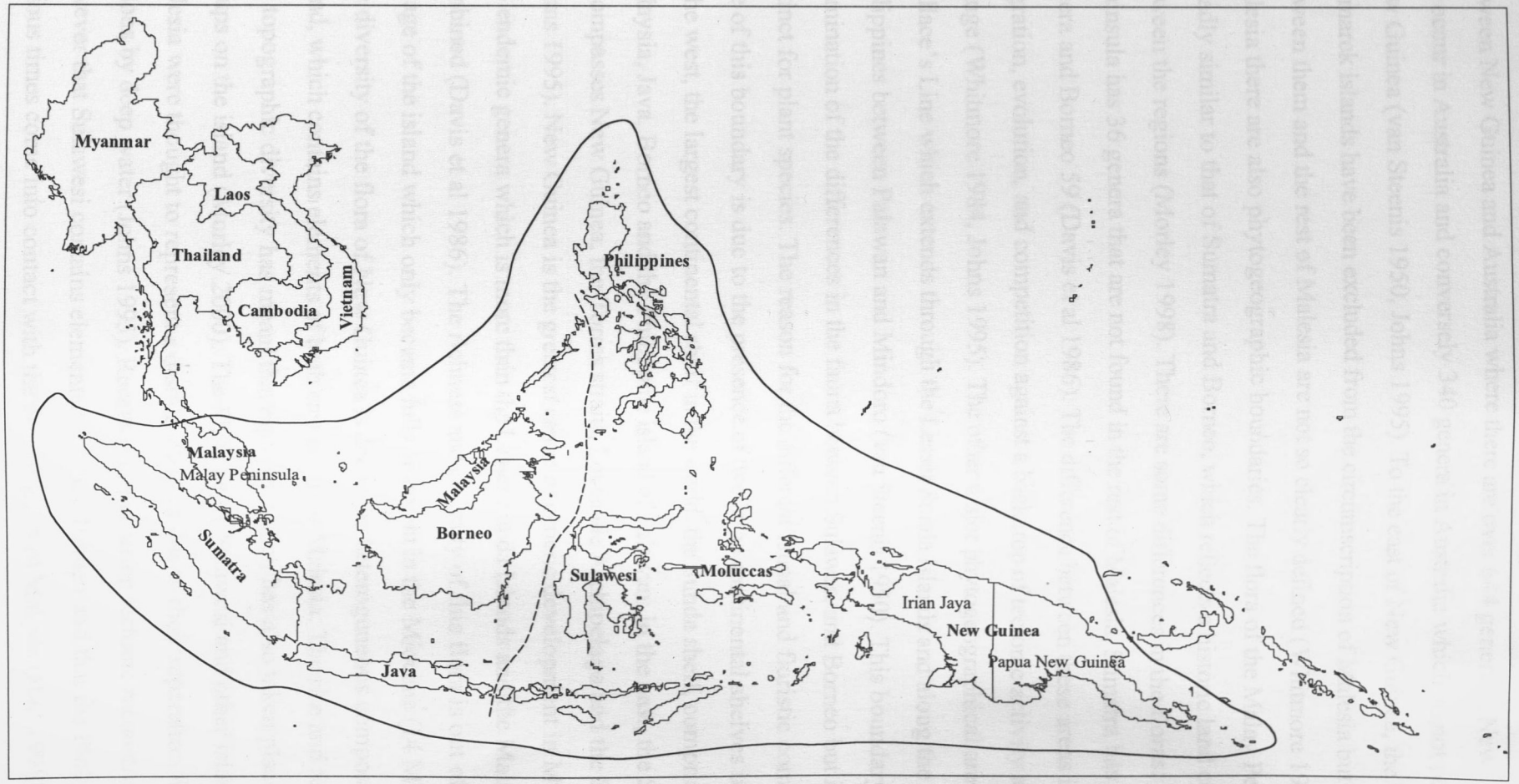


Fig. 3 Outline map of Southeast Asia illustrating the relative positions of the countries which make up this geographic area. The phytogeographical region of Malesia is indicated by a solid line circumscribing the islands of the Malay Archipelago. The dashed line (– – –) indicates the position of Wallace's Line (*sensu* Merrill and Dickerson) which demarcates the division between east and west Malesia.

between New Guinea and Australia where there are over 644 genera in New Guinea which do not occur in Australia and conversely 340 genera in Australia which do not penetrate as far as New Guinea (van Steenis 1950, Johns 1995). To the east of New Guinea, the Solomon and Bismarck islands have been excluded from the circumscription of Malesia but the boundaries between them and the rest of Malesia are not so clearly defined (Whitmore 1984). Within Malesia there are also phytogeographic boundaries. The flora of the Malay Peninsula is broadly similar to that of Sumatra and Borneo, which reflects a historic land connection between the regions (Morley 1998). There are some differences in the floras: the Malay Peninsula has 36 genera that are not found in the rest of Malesia, Sumatra has 17 endemic genera and Borneo 59 (Davis et al 1986). The difference between these areas is due to migration, evolution, and competition against a backdrop of tectonic activity and sea level change (Whitmore 1984, Johns 1995). The other major phytogeographical area is defined by Wallace's Line which extends through the Lesser Sunda Islands and along the west side of the Philippines between Palawan and Mindoro (van Steenis 1950). This boundary was based on examination of the differences in the fauna between Sulawesi and Borneo but is generally less distinct for plant species. The reason for the different faunal and floristic composition either side of this boundary is due to the presence of two large continental shelves in Southeast Asia: in the west, the largest continental shelf in the world, the Sunda shelf, comprises Sumatra, Malaysia, Java, Borneo and the Philippine island of Palawan; in the east, the Sahul shelf encompasses New Guinea, the Torres straits, Louisiade Archipelago and the Solomon Islands (Johns 1995). New Guinea is the greatest centre of generic development in Malesia with some 124 endemic genera which is more than the Lesser Sunda Islands and the Malay Peninsula combined (Davis et al 1986). The richness and diversity of this flora is out of proportion to the age of the island which only became fully emergent in the Miocene (14 Ma) (Hall 1998). The diversity of the flora of New Guinea is due to the heterogeneous composition of the island, which contains elements of both east and west Malesia. The rise and fall of sea levels and topographic diversity has meant that rapid speciation has also taken place in many plant groups on the island (Morley 2000). The Philippines, Sulawesi and other islands of central Malesia were thought to represent a distinct element due to their separation from the other regions by deep water (Johns 1995). Recent evidence using tectonic reconstruction has shown however that Sulawesi contains elements of eastern Borneo and that the Philippines has at various times come into contact with the other regions of Malesia (Hall 1998). The distinct

flora of Sulawesi may therefore be due to contributions from both eastern and western Malesia coupled with high rates of endemism due to accelerated speciation on the extensive areas of ultramafic rock (Johns 1995). The flora of Java is thought to have a closest affinity with that of Sumatra and Borneo but due to anthropogenic interference and different climatic conditions in the east and west of the island it is somewhat distinct with 10 endemic genera (Davis et al 1986). The genera which are mainly absent from Borneo and Sumatra but present in Java occur in Southeast Asia above the Isthmus of Kra reflecting similar climatic conditions in the two distinct regions (van Steenis 1950). The flora of Java is depauperate compared to the rest of Malesia with just 5,011 species compared to 15,000 in Borneo, 10,000 in Sumatra and 7,500 in the Malay Peninsula. This is thought to be due to wide scale forest clearance in Java which also may mean that many of the island's endemic genera are now extinct (van Steenis 1950). This floristically rich region of Malesia which contains perhaps 60,000 flowering plant species (Davis et al 1986) is the subject of the Flora Malesiana project which was conceived by van Steenis and begun in 1948. The aim of the project is to provide taxonomic revisions for all of the families in the region and possibly 70% of them have now been covered. Taxonomic treatments have however concentrated on the smaller groups, as the number of species is not evenly distributed across families only 20% of the species have been published (Roos 1995).

Phytogeography of Thailand and Indochina

The other Floristic regions which are covered in this study are Thailand and Indochina (Laos Cambodia and Vietnam). Peninsular Thailand and Indochina have some floristic similarities to the Malay Peninsula, and as more genera are discovered in Peninsular Thailand the boundary between Malesia and this region becomes less distinct. The area of Thailand is 513,115 km^2, about the area of France; it is 1,600 km from north to south and 780 km at its widest point (Gray et al 1991). It is delineated by the drainage systems of the Chao Phraya river, the Irawaddy of Myanmar and the Mekong, which drains Indochina, and the central Khorat plateau of Thailand. This central plain is an area of low relief and elevation of just 200 - 500 m from north to south (Sternstein 1976). The country is delineated by two mountain systems: the Central Cordillera in the west along the Myanmar border is part of the mountain system originating from the southeast corner of the Tibetan massif (Sternstein 1976). In the east is the Cordillera of Annam, which transverses Laos and Vietnam (Gray et al 1991). Thailand therefore contains six physiographic regions which correspond to the topography and climatic

regions in the different areas (Rundel & Boonpragob 1995). The northern part of the country comprises parallel north - south orientated mountain ranges which alternate with elongate, often wide, alluvial valleys in between. Steep limestone ridges and volcanic plateaux are present in several areas (Sternstein 1976). The highest peak in Thailand, Doi Inthanon, at 2,576 m is found in this region. Southward from this area is the central plain which is one of the most fertile agricultural regions in the country (Gray et al 1991). The northeast of the country is defined by the Khorat Plateau, a sandstone region which cover nearly one third of the country and is a large basin of no more than 500 m in altitude which slopes downwards from north to south (Rundel & Boonpragob 1995). To the north of the central highlands is a complex assemblage of strongly incised plateaus and steep limestone ridges (Sternstein 1976). The southeastern region consists of low hills to the north and mountains to the east, which are a continuation of the Cardamon mountains of Cambodia. The coast around this area is fringed by more than 80 rocky, forested islands (Rundel & Boonpragob 1995). The southwest, along the Myanmar border represents a continuum of the mountains from the north but valleys are narrower and several tributaries of the larger river systems originate here (Sternstein 1976). The peninsular region is a continuation of the western ranges, the backbone of which is formed by short longitudinally orientated ridges which rarely exceed an elevation of 1000 m (Rundel & Boonpragob 1995). On the west side the mountains extend to the sea and the coast is very irregular, studded with narrow terraces and plains and there are more than 275 offshore islands. The eastern side of the peninsula consists of long stretches of coastal plain and beach (Gray et al 1991).

Thailand has a very rich flora of some 12,500 flowering plant species (Parnell 2000) which inspired a growing interest in the flora of the region from the first half of the 20th century. The country has a long history of plant collecting from the first collection of Kaempfer in 1690 (Larsen 1979) until the present day. The flora of the region is currently being revised under the auspices of the Flora of Thailand project which was conceived during the Thai - Danish botanical expedition of 1958 – 1959 (Larsen & Warncke 1966, Santisuk et al 1991). To date 20% of the species have been treated and the project will require approximately a further 35 years to complete (Parnell 2000).

Laos is a land locked country which straddles several biogeographic zones: the Himalayas and China in the north and the Indo – Malayan region which has influenced the floristic composition of the south. The total area of the country is 236,800 km^2 (Counter Intelligence Agency (CIA) 2000) which mainly consists of rugged mountains with some plains and plateaux in the west and south of the country. The highest point in the country is Phou Bia, an extension of the Xiangkhouang plateau, reaching up to 2817 m. Laos has borders with several other countries: Myanmar, Cambodia, China, Thailand and Vietnam. The longest border is with Vietnam, defined by the Cordillera of Annam. The Mekong runs along the border with Thailand and this area consists of flood plains and alluvial terraces. The northwest of the country contains parallel north-west orientated mountain ranges which rarely exceed 1000 m. To the east of this region is a low-lying area which is defined by the Ngum river and the Nam Ngum Reservoir. In the south the Bolovens plateau is surrounded by an irregular assortment of low mountains interspersed by narrow valleys. The southeast is a flat plain demarcated by the Mekong which has its widest point in Laos in this region. The country contains approximately 27,000 km^2 of tropical lowlands and hill evergreen forests which occurs along the Cordillera of Annam and the Bolovens plateau although above 1000 m the forests have been extensively converted to grassland (Davis et al 1986). Due to its relative isolation, surrounded by mountains in the north and east, over 54% of the country has remained forested (CIA 2000) and the flora of the country is relatively unknown.

Cambodia, to the south of Laos with an area of 181,040 km^2, (CIA 2000) is bounded by the Gulf of Thailand in the south and Vietnam in southeast and east. The Tônle Sap or Great Lake and the Mekong dominate the landscape of Cambodia and the latter transverses the country from north to south. This river system largely controls the hydrology of the country. During the northeast monsoon the flow of the river reaches it's maximum in June and floods the adjacent area for four to seven months. At this time the Tônle Sap also achieves its maximum area and increases from 2,600 to approximately 10,000 km^2 (Kingdom of Cambodia 2000). The central plain which covers three quarters of the country is an area of low relief with elevations of less than 100 m. Surrounding this area in the west and south west are the Cardamon mountains and Elephant range which form part of the natural southern border with Thailand. The highest peak in the country, Phnum Aôral (1,810 m), is found in the Cardamon range which consists of northwest orientated mountains separated by narrow valleys. The two

mountain ranges are bordered by a strip of coastal plain which faces the Gulf of Thailand. The northern border with Thailand is defined by the Dongrek mountains which adjoin the Khorat plateau of Thailand. In the east a series of north south orientated mountain ranges, the Chhlong highlands, merge with the southern portion of the Cordillera of Annam in Vietnam. The country is covered by 71,500 km^2 of forests (approximately 40% of the land area) (CIA 2000), 40% of which are probably dry deciduous forests. 30% of the forested area is represented by hill evergreen forests along the Cordillera of Annam (Davis et al 1986).

Vietnam with an area of 329,560 km^2 (CIA 2000) is the largest country in Indochina, bordering the South China sea. The topography of Vietnam is dominated by a low flat deltas in the south and northeast and mountains in the west and north. The borders with Laos, Cambodia and China are defined by the Cordillera of Annam which runs from the north to the south of the country. The north and northwest regions are defined by a high rugged mountains separated by narrow, steep valleys. The highest peak, Fan si Pan (3,143 m), part of the Hoàng Liên range, is located in this region, near the border with southern China. The Red river flows through the northwest and drains the plains of the northeast, flowing into Gulf of Tonkin at Phòng. To the east of the Red river is a randomly orientated assortment of high mountains, interspersed by broad valleys and plains. Along the east coast, bordering the Cordillera of Annam is a narrow stretch of coastal plain and river flood plains which extends to the south of the country. The southeast is dominated by high east - west orientated mountains interspersed with valleys and broad plains. The low lying southern tip of Vietnam is defined by the Mekong, which flows into the South China sea at four points in this region. The country is covered by 78,169km^2 (approximately 25% of the land area) (CIA 2000) of forested areas with tropical rainforest in submontane and montane regions and semi deciduous forests in the northwest and south. The country contains approximately 10,500 plant species, 10% of which are endemic (IUCN 2000, CIA 2000).

Climates in Southeast Asia

Climate and topography are major defining factors in the floristic composition of Southeast Asia. The climate in the region is determined by two major factors: the fact that the region is dominated by islands and peninsulas means that there is a strong maritime influence (Whitmore 1984) and the movement of the Inter Tropical Convergence Zone (ITCZ) is a major factor

influencing seasonality (Rundel & Boonpragob 1995). The Malay Peninsula, southern Philippines, Sumatra, western Java, Borneo and from Sulawesi to New Guinea are under the influence of an equatorial monsoonal climate and Thailand, Indochina and eastern Java and the southern tip of New Guinea have a seasonal monsoon climate (M^{c}Gregor & Nieuwolt 1998).

Those areas which are dominated by an equatorial monsoon climate are influenced by both the Northeast Monsoon and the Southwest Monsoon which bring rainfall and means that these regions receive year round precipitation (Rundel & Boonpragob 1995). Dry seasons are rarely prolonged and seasonality is not an important factor with the result that annual temperature ranges rarely exceed 2°C (M^{c}Gregor & Nieuwolt 1998). In these areas diurnal temperature fluxes exceed the annual range and topography is the important limiting factor in terms of plant distribution as temperature decreases with elevation by approximately 0.65°C per 100 m (M^{c}Gregor & Nieuwolt 1998). Precipitation also increases with increased altitude so that areas of higher elevation have more wet and humid conditions (Whitmore 1998).

Seasonality in the other regions of Southeast Asia is controlled by the movement of the ITCZ which separates the flow of air from north to south and causes the monsoonal climates. From January it moves northward passing the Malay Peninsula in April reaching its highest latitude around August, it then retreats and passes again over the Malay Peninsula around November (Rundel & Boonpragob 1995). The northeast monsoon is the driest time over this region from December to February and winds from the north bring relatively cool air over Thailand and northern Indochina (M^{c} Gregor & Nieuwolt 1998). Exceptions are the southeastern coast and the peninsula of Thailand and the southern regions of Vietnam, southwest Cambodia and part of central Laos when the northeast winds bring heavy precipitation and it is the wettest time of the year (Gray et al 1991). Maximum temperatures in Thailand in December are lower by up to 8°C than in May or June (Gray et al 1991). In contrast to equatorial monsoonal climates annual temperature varies considerably from 18 - 20°C in the coldest months, with minimum temperatures in northern Vietnam reaching as low as 10 -12°C, to 33 - 40°C in the warmest parts of the year (Sternstein 1976, Vidal 1979). The southwest monsoon begins in May with a maximum intensity in August and ends in October. This monsoon brings more rainfall than the previous one with a peak in precipitation in August or September in northern Thailand and a couple of months later in central and southern districts (Rundel & Boonpragob 1995). Mean

annual precipitation for the country as a whole is 1550 mm but in the peninsular region and the southeast coast it is much higher (up to 4000 mm) due to the influence of the northeast monsoon (Gray et al 1991). The north of the Thailand and Vietnam have the lowest annual rainfall with 1300 mm per year but, within this seasonal climatic region, topography can exert influence over local precipitation (Rundel & Boonpragob 1995).

Vegetation communities of Southeast Asia

Temperature, rainfall, soil conditions and tectonic history have influenced the vegetation types in Southeast Asia (Whitmore 1984). In northern Thailand and northern Vietnam where more seasonal conditions prevail there is an increase in temperate taxa at higher elevations (M^{c}Gregor & Nieuwolt 1998). In contrast, in southeast and Peninsular Thailand, coastal areas of Vietnam, southern Cambodia and most of Malesia where there is general unseasonality, higher temperatures (in Malesia) coupled with increased precipitation means tropical rainforest vegetation dominates the landscape (Whitmore 1998). Ecologically and commercially the occurrence of dipterocarp forest is significant particularly in western Malesia (Whitmore 1984). In Southeast Asia Santalaceae occupy a variety of habitats. The dendroparasitic genera are confined to montane regions with the exception of *Dendrotrophe* which occurs from coastal to mountainous areas with a preponderance in the lowland and disturbed habitats of western Malesia. It is also associated with heath vegetation and freshwater peat swamps from southern Thailand to Borneo. *Scleropyrum* also occurs at a wide range of elevations but predominately in disturbed vegetation of evergreen forest and in dry evergreen and dry dipterocarp forests in Thailand and Indochina. Both *Osyris* and *Thesium* inhabit montane regions in open grassy ecosystems where there is usually evidence of disturbance. *Santalum* and *Exocarpos* occupy lower elevations in coastal habitats, although *Santalum* can be found at higher elevations in it's native Java. The habitat in which each species occurs is indicated after the taxonomic description of each one in **Chapter 5**. In order to understand the ecological requirements and geographical distributions of the genera it is necessary to give a brief outline of the different vegetation types in which the various genera can be found and the locations in which they occur.

Tropical evergreen rainforests, which are a feature of the Indo - Malay vegetation, grade into other vegetation types at the edge of their distribution, a phenomenon which is influenced by

climate and local topography (Rundel & Boonpragob 1995). Peninsular Thailand is generally considered to be the northern limit of this vegetation type with outliers in the southeast of the country, in southwest Cambodia and southern Vietnam (Whitmore 1984, Morley 2000). Towards the sub tropical regions mixed deciduous and deciduous forests are more abundant and these may grade into cool temperate rainforest a higher latitudes (Whitmore 1998). Mixed deciduous forests are subjected to annual periods of moisture stress for 5 - 6 months of the year (Sternstein 1976) and are restricted to Thailand, Myanmar, and Indochina and would probably have once occurred in eastern Java (Morley 2000). They resemble tropical evergreen forest in respect of their closed, high canopy and the diversity of tree species which occur in them. They differ from tropical evergreen rainforest in the fact that there is a higher proportion of deciduous species (Rundel & Boonpragob 1995). These forests, which occur between 400 - 600 m, have been heavily disturbed by logging for Teak (Vidal 1979). They are therefore replaced in many areas by deciduous dipterocarp forests and agriculture. Deciduous dipterocarp forests are lower in stature and are more open than mixed deciduous forests and merge with savannah vegetation (Gray et al 1991). In Laos, Cambodia and Vietnam this vegetation type has been termed Fôret Claire a Dipterocarpaceae and it covers large areas of Thailand and Indochina (Rollet 1972). Like mixed deciduous forest it is characterised by a distinctive dry season but it generally occurs on drier, sometimes steeper slopes (Rundel & Boonpragob 1995). Fires are frequent in dry dipterocarp forests and generally occur at intervals of 1 - 3 years, Vidal (1979) has therefore termed them an edapho-anthro-climax vegetation. Frequent burning and topographic factors demarcates this vegetation type from mixed deciduous forest (Rundel & Boonpragob 1995). The dry evergreen forests of Thailand and Indochina are floristically derived from southern Malesian elements (Whitmore 1984). They can be found in the south and west areas of the Khorat plateau and along galleries and ridges throughout Thailand and Indochina and occur where local soil conditions create a mesic environment (Rundel & Boonpragob 1995). Dipterocarpaceae are the most important tree species in these forests and they generally occur at higher elevations than mixed deciduous forests (Santisuk 1997). Lianas are common in the understories of these habitats and soil conditions are generally acidic. Bamboos are common in areas, which have been subjected to disturbance, and the distribution of this forest type has been highly influenced by anthropogenic factors (Rundel & Boonpragob 1995). With increasing elevation floristic

composition of all of these forests change to lower montane rainforest, upper montane rainforest and finally alpine vegetation (Whitmore 1984, Morley 2000).

Lower montane or hill evergreen forest occurs at elevations from 800 - 1000 m in Thailand and Indochina (Sternstein 1976, Vidal 1979) and usually between 1500 - 3000 m in Malesia where it is common on limestone mountains (Whitmore 1984). Temperate taxa such as *Quercus*, *Castanopsis* and *Larix* dominate the canopy and *Rhododendron* is a common understorey shrub (Gray et al 1991). In Thailand this vegetation type covers just 9 - 10% of the country and is restricted to the northern part of the country (Rundel & Boonpragob 1995). It also occurs at high elevations in New Guinea and Sarawak in western Borneo and is better developed in western rather than eastern Java (Morley 2000). In the mesic environments of these forests epiphytes are common and at the higher elevation bryophytes form a rich carpet on acidic peaty soils (Gray et al 1991). Above 2000 m the vegetation becomes more stunted, mosses and ferns are more luxuriant and *Nothofagus* is the dominant canopy tree (Whitmore 1984). These forests are found in upper montane vegetation, above 2000 m in Thailand and Indochina (Gray et al 1991) and 3000 m in Malesia (Whitmore 1998). Temperate taxa such as Ericaceae are again quite common and at lower elevations (between 3 - 3400 m in Malesia) and Elaeocarpaceae and Podocarpaceae are frequent (Whitmore 1984). Above this point the vegetation is short, dense and distinctively sub alpine with small leaved species such as *Vaccinium* and *Olearia* being the most common species. Above the tree line the alpine vegetation is a complex mosaic of stunted shrubs, moss tundras and alpine grassland determined by soil conditions (Whitmore 1984). The soil in upper montane and alpine forests is generally peaty and waterlogged reflecting lower temperatures and decreased biological activity in the soil (Mangen 1993). *Sphagnum* and other mosses occur in these areas and serve to increase peat formation (Whitmore 1984). Big daily temperature fluctuations and the cooler moister environmental conditions means that this vegetation type is clearly demarcated from lower montane forests (Whitmore 1998). In general montane forests have an affinity at the family level with warm temperate forests of southern China and Japan (Whitmore 1984). In other areas of lower elevation the different vegetation types can grade into each other. In Thailand and Indochina forests of *Pinus khaysia* or *Pinus merkusii* can occur in small pockets from 200 - 1200 m (Santisuk 1997), representing the most southern point of the natural distribution of *Pinus* (Gray et al 1991). They are a sub climax vegetation type, which is often

subjected to burning (Vidal 1979). Pine forests occur as pure stands in northern Thailand, most notably on Phu Kradung and Nam Nao in the northeast, and in Laos in Xieng Khouang (Vidal 1979). At higher elevations and stages of succession they occur mixed with *Quercus* or *Lithocarpus* (Vidal 1979, Gray et al 1991). The vegetation zones are most clearly defined in New Guinea where forests can extend without disturbance from sea level to the high mountain tops (Mangen 1993).

Secondary forest occurs as the result of disturbance and forms most frequently due to anthropogenic interference by logging, fire and abandonment of plantations (Morley 2000). The vegetation is depauperate and pioneer species are usually light demanding and often form monospecific stands. In Southeast Asia *Macaranga* is the most typical species of this vegetation type and above 1000 m *Homolanthus* and tree ferns may be common invaders (Whitmore 1984). If disturbance within an area is constantly repeated open grasslands will form. Extensive stands of bamboo are also a common feature of secondary vegetation and are particularly common in Thailand and Indochina in the seasonal climatic regions where the burning of vegetation is easier (Whitmore 1998).

In lowland regions on siliceous soils which are free draining, kerangas or heath forest forms (Morley 2000). The vegetation is generally depauperate and the canopy is low and stunted, often red or brown in colour. In a similar manner to upper montane rainforest the vegetation is sclerophyllous and bryophytes are frequent (Whitmore 1984). The soil is also acidic and in some areas an iron pan can form which impedes drainage and produces waterlogged conditions (Whitmore 1998). In coastal areas this vegetation type can be found occasionally in Thailand and Indochina, Sumatra and the Malay Peninsula. It is most extensive in Borneo where it is also found inland on raised tertiary terraces of poorly consolidated, coarse sand (Morley 2000). This type of vegetation is very sensitive to disturbance and in many coastal areas it has been converted to padang which is a slow growing community of savannah and shrubs (Whitmore 1984). Small areas of heath forest have also been recorded from Sulawesi and central New Guinea (Mangen 1993).

Peat swamp forests occur in areas where there is impeded drainage and in coastal areas they occur behind mangroves (Morley 2000). They have their greatest extent in southern Thailand,

Sumatra, Malaysia, Borneo and western New Guinea (Whitmore 1998). In inland areas they occur in low-lying water sheds and have accumulated in a similar manner to temperate bogs (Morley 2000). On thick peats, like heath forest, the vegetation is sclerophyllous but in certain areas, on shallow peaty soil, the structure is similar to lowland forests (Whitmore 1984). There is often a gradient in vegetation types from the centre to the periphery of peat swamp vegetation (Morley 2000). At the centre, a low stunted forest with species which are adapted to low nutrient availability are predominant, these are then gradually replaced towards the edges by species from the surrounding lowland community (Whitmore 1998).

Summary of aims

In summary this study seeks to present a revision of Santalaceae in Southeast Asia covering the floristic regions of Thailand, Indochina and Malesia. A number of techniques have been employed to investigate species delimitations and relationships. Herbarium material from all of the major European and Southeast Asian herbaria have been examined to examine specific boundaries and to construct taxonomic descriptions and keys to the genera and species. This material has also been used to construct a phylogenetic hypothesis of the dendroparasitic genera in Southeast Asia. Molecular analysis has also been undertaken on a subsample of the genera in order to make comparisons with morphological phylogenetic analysis and to examine character evolution in terms of fruit and inflorescence morphology. Examination of pollen using Scanning Electron Microscopy and Light Microscopy has been undertaken for all of the 48 taxa in order to provide additional taxonomic information, to examine specific relationships in the region and to make comparisons between the dendroparasites and the family Viscaceae. Finally infraspecific relationships within *Dendrotrophe varians* has been explored to test the current classification of the species and to examine patterns in regional variation.

Pollen Morphology and Evolutionary Trends in Southeast Asian Santalaceae

Introduction

The taxonomy and phylogeny of the Santalaceae is complex and has remained obscure because of the limitations of traditional taxonomic methods. Throughout the family flowers are small, inconspicuous and uniform and offer few useful characters for taxonomic investigation (Kuijt 1969). The paucity of floral characters has created many problems and the delimitation of species can become quite difficult when only these characteristics are taken into account. It has long been acknowledged that pollen morphology is of great importance in the taxonomy and understanding the evolutionary relationships between members of the Santalaceae (Feuer 1977, Lobreau Callen 1982). Swamy was perhaps the first to examine in detail the wood anatomy and pollen exo- and endomorphology of the family (Swamy 1949). He recorded features of the sculpturing elements of the ektexine and the shape and size of the endoaperture in several species. *Choretrum* and *Leptomeria* in the Amphorogyneae were designated the most primitive members of the Santalaceae with diffuse vessel distribution and isopolar pollen grains with a diffuse or finely granular exine ornamentation. Due to the limitations of the light microscope, however, the exine ornamentation of the pollen of many species was incorrectly assigned.

The use of the Scanning Electron Microscope (SEM) has made enormous advances possible in the study of the fine micromorphology of the pollen grain and has revealed many characters of taxonomic importance which cannot be accurately observed with the light microscope (Harley & Ferguson 1990). Its use in comparative morphological and systematic studies has in many ways revolutionised this area. Now the employment of SEM in any study involving pollen morphology is routine and is an "essential part of the illustrative method that holds its own unique position in elucidating exine structure and ornamentation" (Harley & Ferguson 1990).

Based on both palynological and wood anatomical studies of the Santalaceae it has long been advised that the family is in need of revision (Erdtman 1952, Metcalf & Chalk 1950). A detailed SEM study of the pollen morphology of the Santalaceae revealed the great variety of shape and exine ornamentation in the family (Feuer 1977). The range of sculpturing patterns of the ektexine was revealed, particularly in the tribe Amphorogyneae which had been largely ignored in previous studies. The investigation of such a large group however, necessitated

examination of a small number of samples from each genus within the family. On this large scale general trends and correlations between shape change and sculpturing patterns of the pollen grains were determined. In particular it was discovered that highly sculptured, spherical grains are associated with simple apertures whilst less sculptured grains with an elongated polar axis are associated with compound apertures. No phylogenetic inferences were made in this study and it was left to later researchers to identify the primitive condition as being represented by a highly sculptured ektexine accompanied by a reduction in the endexine (Lobreau-Callen 1982). The elongation of the polar axis with accompanied elaboration of the endoaperture was deemed therefore to represent the derived condition in the family. The elucidation of phylogenetic relationships was based on overlaying pollen morphology onto the traditional hierarchical classification rather than independent assessment of evolutionary position based on pollen morphology. Pollen morphology within the tribe Amphorogyneae was therefore assumed to be basal with all other forms derivable from it.

There is no doubt that the work of previous researchers has contributed greatly to the appreciation of the value of pollen morphological studies in the Santalaceae. The recognition of trends in shape, sculpturing and endomorphology by Feuer and the evolutionary synthesis of Lobreau Callen have provided an invaluable template for any study of pollen construction and organisation within the family.

Studies at the familial level are of vital importance in determining overall trends and relationships between genera but by their very nature they prohibit the examination of the full range of morphological variation in pollen characteristics within any one genus. The full complexity and the different types of pollen construction within a single genus has not until now been explored. The correlation between macromorphological characteristics and pollen morphology has also not been investigated.

This study concentrates on one geographical region and therefore overall phylogenetic implications may not be assessed. It does however, uniquely present a detailed analysis of the variation which exists at the infrageneric level within the Santalaceae. The four tribal classifications Anthoboleae, Santaleae, Thesieae and Amphorogyneae are represented in Southeast Asia (**Table 1**). Of the 48 species in Southeast Asia 40 belong to the tribe

Table 1: Summary of the genera of Santalaceae in Southeast Asia. The majority of the species (40) are contained within the tribe Amphorogyneae. The other tribes Santaleae and Anthoboleae make up the remaining 8 species.

Tribe	Genus	No. of species	Distribution	Habit
Amphorogyneae	*Dendromyza*	21	Malay Peninsula-Australia	Dendroparasite
Amphorogyneae	*Dendrotrophe*	4	Southern China - Australia	Shrub/climber/ dendroparasite
Amphorogyneae	*Dufrenoya*	11	Southern India/China– Northern Borneo	Dendroparasite
Amphorogyneae	*Phacellaria*	4	Southern China– Malay Peninsula	Dendroparasite
Santaleae	*Osyris*	1 (2 worldwide)	Southern Europe– Northern Thailand	Shrub
Santaleae	*Santalum*	1 (25 worldwide)	Timor- Pacific Islands	Tree
Santaleae	*Scleropyrum*	4	Southern India – New Guinea	Tree
Anthoboleae	*Exocarpos*	1 (26 worldwide)	Malay Peninsula - Australia	Shrub/tree

Amphorogyneae and are characterised by a climbing or dendroparasitic growth habit. They are contained within the four genera *Dendrotrophe*, *Dufrenoya*, *Dendromyza* and *Phacellaria* and form a monophyletic group. Relationships among and between these species in terms of pollen morphology will be explored in detail. The fact also that all of the tribal classifications within the family are present in Southeast Asia provides added scope for comparisons of general characteristics of the different tribes. The tribe Thesieae has however been excluded on the basis that pollen evolution within this tribe does not conform to the scenario in the family as a whole.

Materials and Methods

Not all species could be examined due to the paucity of mature flowers on the herbarium specimens and also because several species are represented by fruiting specimens only. A list of the species and the herbarium sheets from which pollen was taken is given in **Table 2**.

Table 2 List of species and herbarium specimens from which pollen was sampled.

Species	Collector, Field no., Country	Herbarium
Dendrotrophe amorpha	Sleumer 6970, New Guinea	CANB
Dendrotrophe buxifolia	Balgooy 2200 Malay Peninsula	L
	Kerr 15916, Thailand	L
Dendrotrophe varians	Kerr 11853, Thailand	GH
Dendrotrophe varians	Maxwell 85-60, Thailand	GH
Dendromyza acrosclera	Womersley 17967, New Guinea	B0
	Brass 4240a, New Guinea	GH
	Croft 61725, New Guinea	CANB
Dendromyza angustifolia	Balgooy 105, New Guinea	CANB
	Brass 30105, New Guinea	GH
Dendromyza cucullata	Ledermann 12911, New Guinea	B
Dendromyza cuneata	Hoogland 5448, New Guinea	GH
D. cuneata var *fruticosa*	Balgooy 200, New Guinea	CANB
Dendromyza crassifolia	van Royen 8173, New Guinea	BO
	Van Royen 7866, New Guinea	L
Dendromyza dendromyzoides	Sleumer 4356, 4357, New Guinea	L
Dendromyza erecta	Lam 1974, New Guinea	L
	Schodde 2111, New Guinea	CANB
Dendromyza kaniensis	Schodde 1508, New Guinea	CANB
	Mendum 92189, New Guinea	E
Dendromyza ledermanii	Schodde 2861, New Guinea	CANB
Dendromyza microphylla	Craig 102, New Guinea	CANB
	Kalkmann 4485, New Guinea	L
Dendromyza multinervis	Kostermans 1140, Moluccas	L
Dendromyza pachydisca	Ramos 38974, Philippines	GH
Dendromyza reinwardtiana	Schodde 31603, New Guinea	CANB
Dendromyza stellata	Buwalda 5421, Moluccas	L
Dendromyza trinervia	Brass 23305, New Guinea	L
Dendromyza uncinata	Brass 13409, New Guinea	BO
Dufrenoya collettii	Beusekon 2372, Thailand	CANB
	Santisuk 1469, Thailand	GH
Dufrenoya euryphylla	van Steenis 4872, Java	BO
Dufrenoya granulata	Hooker s.n. India	K
	Ludlow 118625, Bhutan	E
Dufrenoya oresitropha	Whitmore 12651, Malaysia	K
	Holttum 11368, Malay Peninsula	BO
Dufrenoya papillosa	de Wilde 14303, Sumatra	L
Dufrenoya platyphylla	Niyomdham 448, Nepal	P
Dufrenoya poilanei	Petelot 3384, Vietnam	GH
Dufrenoya robusta	Koyama 31633	GH
	Kerr 10393, Thailand	L
Dufrenoya sessilis	Smitinand 9734, Thailand	BKF
Dufrenoya sphaerocarpa	Clemens 40831, Borneo	B
	Carr 28747, Borneo	SING
	Nur 32813 Malaysia	L
Phacellaria compressa	Maxwell 91/242, Thailand	GH
Phacellaria malayana	Robinson s.n., Malay Peninsula	K
Phacellaria rigidula	Beusekom 2564, Thailand	BKF
Osyris lanceolata	Geesink 8134, Thailand	BKF
Santalum album	Smitinand 89/49, Thailand	BKF
Scleropyrum aurantiacum	Hoogland 5001, New Guinea	CANB
	Clemens 753, New Guinea	GH
Scleropyrum brevistachyum	Brass 1498, New Guinea	GH
Scleropyrum maingayi	Kerr 5012, Thailand	L
Scleropyrum pentandrum	Smitinand 14567, Thailand	BKF
Exocarpos latifolius	Bermee s.n., Timor	

Polleniferous material was taken from mature anthers of identified specimens and subjected to acetolysis following the method of Erdtman (Erdtman 1960) with some modifications advised by the Kew protocol (**Table 3**). The timing of the length of acetolysis was gauged by lengthy experimental tests until the optimum time was achieved. The importance of the careful removal of the pollen from anthers before applying the experimental protocol must be stressed. In many cases the pollen was securely enclosed within the anthers and could only be removed with a needle and fine forceps. Crushing the anthers in glacial acetic acid or simply grinding them as recommended by Erdtman (Erdtman 1952, 1960) did not achieve satisfactory results. Light microscopy facilitates the examination of the internal construction of the pollen grain. Samples for light microscopy were therefore prepared using some of the acetolysed material and also unacetolysed material rehydrated in distilled water and detergent. The size of the pollen grains was determined from SEM photographs and were basically equivalent to measurements taken under the light microscope. Where possible, several samples of pollen from each species was examined to check for infraspecific variation in exine ornamentation.

Table 3: Acetolysis method of pollen preparation following the method of Erdtman (1960) with some modifications advised by the Kew protocol.

1. Remove flower bud from herbarium sheet; place in a watch glass with water and detergent. Heat for a couple of minutes on a hot plate
2. Dissect out pollen from the anthers with a fine forceps and needle under a dissection microscope.
3. Wash through a fine sieve with distilled water to remove anther debris. Collect pollen in a centrifuge tube.
4. Centrifuge at 3000 rpm for 10 min. Discard supernatant*
5. Add glacial acetic acid until tube is 2/3 full. Repeat 4
6. Add 10 mls of acetolysis mixture (9:1 acetic anhydride: conc. sulphuric acid)** to tube and place in a water bath at 100°C for 1 minute***
7. Remove tube from waterbath and repeat 4
8. Add glacial acetic acid and stir for 5 min. Repeat 4
9. Add distilled water and stir for 5 min. Repeat 4 (repeat washing procedure 3 times)
10. Add 95% ethanol to tube and then transfer to screw top tube (5 ml)
11. At this point the sample is split into two
12. For SEM: Pipette pollen suspension onto SEM stub and cover with a beaker until dry
13. For Light Microscopy: Add mineral oil to the sample and mix thoroughly. Place sample in an oven at 60°C overnight or until all of the alcohol has evaporated

* From this point all procedures must be carried out in a fume cupboard and gloves must be worn

  Glacial acetic acid is an irritant

** Acetolysis fluid is highly corrosive and is also explosive in contact with water. The sulphuric acid should be added to the glacial acetic acid and not the other way round. The reaction is exothermic so care should be taken and the sulphuric acid should be added slowly.

*** Longer times may be used depending on the pollen type under study. If the exine is robust it can withstand longer times in the acetolysis fluid.

Samples for SEM analysis were coated in a gold palladium mixture and photographs were taken using SEM at an accelerating voltage of 15kV. For light microscopy a small amount of mineral oil containing pollen in suspension was placed onto a glass slide and a coverslip was placed on top. The edges of the coverslip were then sealed with clear nail varnish to prevent the sample from drying out.

Results

The nomenclature which has been used in the pollen descriptions of each species is based on that which has been adopted in later chapters resulting from phylogenetic and taxonomic investigations (**Chapter 3**, **Chapter 5**). Not all of the pollen types have been illustrated following the descriptions. Those that have been illustrated represent the overall picture within the Southeast Asian species and are the best images which were obtained using SEM and LM.

Pollen Descriptions

Santalaceae R.Br.

Pollen grains isopolar to subisopolar, 3 - aperturate: tricolpate; colporate; porate. Polar length ranging from 11 – 24 μm, oblate to prolate in shape. Exine ornamentation very variable: rugulate, striate, perforate, microechinate, echinate, verrucate. Endoaperture elliptical, rectangular.

Tribe Amphorogyneae

Pollen grains isopolar, tricolpate, colporate. Polar length 11 – 17 μm. Exine sculpturing rugulate, striate, perforate, microechinate, echinate. Endoaperture absent, elliptical.

Dendromyza Danser

Pollen grains isopolar, tricolporate, polar length 11 – 17.5 μm. Exine sculpturing distinctly rugulate, echinate, microechinate. Endexine thin; endoaperture following the margins of the colpi, absent or elliptical.

Dendromyza acrosclera (Danser) Macklin (**Fig. 4.2**)

Grains sub prolate in equatorial view, length 17.5 μm, width 16 μm. The exine sculpturing is uniformly rugulate, similar to *Dendromyza reinwardtiana.* Colpi shallow, 13 μm long, not contracted at the pore, pore indistinct. The endexine and the ektexine are of uniform thickness. There is evidence of thickening along the margins of the colpi.

Dendromyza angustifolia (Stauffer) Macklin (**Fig. 4.3**, **4.4**, **13**)

Grains prolate in equatorial view, length 15.7 μm width 12 μm. The exine sculpturing is uniformly rugulo-striate. Colpi shallow, 12 μm long, not contracted at the pore, pore indistinct. The endexine is thin, the ektexine becomes thicker towards the pore; the

endoaperture is elliptical in equatorial view with irregular margins and appears to transverse the equator of the grain. There is evidence of thickening along the margins of the colpi.

Dendromyza cucullata (Danser) Stauffer

Grains spheroidal in equatorial view, length 12.5 μm, width 12.5 μm. The exine sculpturing is entirely weakly rugulate. Colpi deep and not contracted at the pore, pore indistinct. The endexine becomes thinner at the pore, the ektexine is of uniform thickness; the endoaperture is elliptical in equatorial view. There is evidence of thickening along the margins of the colpi.

Dendromyza crassifolia (Gibbs) Stauffer (**Fig. 4.5**, **4.6**)

Grains prolate in equatorial view, length 14 μm, width 13 μm. There are differences in the sculpturing of the mesocolpium and the polar regions: the mesocolpium is rugulo-striate, the striate pattern becoming more pronounced along the margins of the colpi and at the poles. Colpi broad, shallow, 11.4 μm long, rounded at the ends, pore distinct. The endexine becomes thicker at the pore, the ektexine is of uniform thickness; the endoaperture is irregularly elliptical in equatorial view. There is no difference in thickness between the colpi and the mesocolpium.

Dendromyza cuneata (Danser) Macklin (**Fig. 13**)

Grains spherical to elongate, length 12.5 μm, width 12 μm. The exine ornamentation is entirely rugulo-striate. Colpi shallow, 11 μm long, not contracted at the pore, pore indistinct. The endexine becomes thinner at the pore, the ektexine is of uniform thickness; the endoaperture is irregularly elliptical in outline. There is evidence of thickening along the margins of the colpi.

Dendromyza dendromyzoides (Stauffer) Macklin (**Fig. 5.1**)

Grains spheroidal in equatorial view, length 17 μm, width 16 μm. The exine sculpturing is entirely echinate, the spines are narrow, 1.4 μm in length, some of the appear to be bent over and flattened. Colpi faint, approximately 3/4 of the polar length, 11 μm long, pore indistinct. The endexine is of uniform thickness, the ektexine becomes thinner towards the pore; the endoaperture is absent. There is no difference in thickness between the colpi and the mesocolpium.

Dendromyza erecta (Danser) Macklin

Grains spheroidal in equatorial view, length 12.5 μm, width 12.5 μm. The exine sculpturing is entirely microechinate; the echinae are 0.7 μm in length. Colpi long and deep, pore indistinct. The endexine becomes thicker towards the pore, the ektexine is of uniform thickness; the endoaperture is absent. There is no difference in thickness between the colpi and the mesocolpium.

Dendromyza kaniensis (Pilger) Stauffer (**Fig. 5.2**, **5.3**, **Fig. 13**)

Grains oblate spheroidal in equatorial view, length 12.6 μm, width 12.6 μm. The sculpturing pattern on the exine is uniformly echinate, the echinae are 1.1 μm in length and all erect. Colpi very short and shallow, 1/2 the polar length, 5.7 μm long, pore indistinct but more obvious than in the other echinate species. The endexine and ektexine are of uniform thickness. There is no difference in thickness between the colpi and the mesocolpium.

Dendromyza ledermanii (Pilger) Stauffer (**Fig. 5.4**, **5.5**)

Grains spheroidal in equatorial view, length 11 μm, width 11 μm. The sculpturing of the exine is very similar to *Dendromyza reinwardtiana,* the mesocolpium is entirely rugulate becoming micropunctate and psilate along the margins of the colpi. Colpi broad, 10 μm long, contracted at the pore, pore indistinct. The endexine is thinner at the pore, the ektexine is of uniform thickness; the endoaperture is irregularly rectangular in equatorial view. There is evidence of thickening along the margins of the colpi.

Dendromyza microphylla (Lauterb.) Macklin (**Fig. 6.1**, **6.2**)

Grains spherical in equatorial view, length 13 – 15 μm width 13 – 15 μm. The exine sculpturing is entirely microechinate; the echinae are 0.7 μm in length. Colpi very faint and only become distinct when the grains collapse, shallow, approximately 1/2 the polar length, 6.5 - 7.5 μm long, pore indistinct. The endexine and ektexine are of uniform thickness; the endoaperture is absent. There is evidence of thickening along the margins of the colpi.

Dendromyza multinervis (Danser) Macklin (**Fig. 6.3**, **6.4**)

Grains prolate in equatorial view, length 15 μm, width 12 μm. The exine ornamentation is uniformly rugulo-striate. Colpi broad, 12.7 μm long and blunt rather than rounded towards the ends, contracted at the pore, pore indistinct. The endexine becomes thinner in the region of the

pore, the ektexine is of uniform thickness; the endoaperture is irregularly rectangular in equatorial view. There is evidence of thickening along the margins of the colpi.

Dendromyza pachydisca (Danser) Macklin

Grain spheroidal in equatorial view, length 17.5 μm, width 17.5 μm. The exine sculpturing is entirely microechinate. Colpi faint and shallow, approximately 1/2 the polar length, 8 μm long, pore is indistinct. The endexine and ektexine are of uniform thickness. There is no difference in thickness between the margins of the colpi and the mesocolpium.

Dendromyza reinwardtiana (Bl.) Danser (**Fig. 6.5**)

Grains spheroidal in equatorial view, length 12 μm, width 12 μm. There is a difference in exine sculpturing between the mesocolpium and polar regions: the mesocolpium is pronounced rugulate becoming micropunctate and psilate along the margins of the colpi and the poles. Colpi narrow, 11 μm long, contracted at the pore, pore indistinct. The endexine and ektexine are of uniform thickness There is evidence of thickening along the margins of the colpi.

Dendromyza stellata (Stauffer) Macklin

Grains spheroidal in equatorial view, length 13 μm, width 13 μm. The exine sculpturing is entirely microechinate, the echinae are 0.7 μm in length. Colpi very faint, shallow, 1/2 the polar length, 5 μm long, not contracted at the pore, pore distinct. The endexine becomes thicker at the pore, the ektexine is of uniform thickness; endoaperture absent. There is no difference in thickness between the colpi and the mesocolpium.

Dendromyza trinervia (Stauffer) Macklin

Grains spheroidal in equatorial view, length 15 μm, width 16 μm. The sculpturing of the exine is entirely echinate, the echinae are 1 μm in length. Colpi long, shallow, 2/3 of the polar length, 10 μm long. The endexine is of uniform thickness and the ektexine becomes thinner at the pore. There is evidence of thickening along the margins of the colpi.

Dendromyza uncinata (Danser) Macklin

Grains spherical in equatorial view, length 12.5 μm, width 12.5 μm. The exine sculpturing is entirely microechinate, the echinae are 0.7 μm in length. Colpi faint, approximately 1/2 the

polar length, 7 μm long, pore indistinct. The endexine and ektexine are of uniform thickness; endoaperture absent. There is no difference in thickness between the colpi and the mesocolpium.

Dendrotrophe Miq.

Pollen grains isopolar, tricolporate, polar length 13 – 17 μm. Exine sculpturing rugulate, perforate, echinate. Endexine thin; endoaperture shallow, following the margins of the colpi.

Dendrotrophe amorpha Stauffer (**Fig. 12**)

Grains spheroidal in equatorial view, length 15.5 μm, width 15 μm. The exine sculpturing is uniformly echinate. The densely packed spines are 1.2 μm in length. Colpi 8 μm long, shallow and rounded at the ends, not contracted at the pore, which is rectangular in outline and distinct. The endexine is of uniform thickness and ektexine becomes thinner at the pore. There is no evidence of thickening along the margins of the colpi. (The colpi of *D. amorpha* pollen are much more distinct than in any of the other species with echinate pollen grains).

Dendrotrophe buxifolia (Bl.) Miq. (**Fig. 7.1, 7.2, 12**)

Grains spheroidal in equatorial view, tricolpate, colporate, length 13 μm, width 13 μm. The exine sculpturing is uniformly microperforate. Colpi 10 μm long, shallow and not contracted at the pore which is still not very obvious. The endexine and the ektexine are of uniform thickness. There is no evidence of thickening along the margins of the colpi.

Dendrotrophe varians (Bl.) Miq. (**Fig. 7.3, 7.4, 12**)

Grains sub prolate in equatorial view, length 17 μm, width 16 μm. Difference in sculpturing of the exine between the mesocolpium and polar region: mesocolpium rugulate, polar region and margins of the colpi microperforate to psilate. Colpi 12 μm long, narrow and contracted in the region of the pore, pore indistinct. The endexine is of uniform thickness, the ektexine becomes thinner at the pore. There is evidence of thickening along the margins of the colpi.

Dufrenoya Chatin

Pollen grains isopolar, tricolporate, polar length 11 – 17 μm. Exine sculpturing weakly or distinctly rugulate, echinate. Endexine thin; endoaperture shallow, following the margins of the colpi.

Dufrenoya collettii (Gamble) Stauffer (**Fig. 7.5, 7.6**)

Grains spheroidal in equatorial view, length 14 μm, width 14 μm. Sculpturing differences between mesocolpium and polar region is slight: mesocolpium rugulate tending towards microperforate, becoming less pronounced along the margins of the colpi and in the polar region. Colpi narrow, 11 μm long, contracted and overlapping at the pore, pore indistinct. The endexine is of uniform thickness and the ektexine becomes thinner at the pore. There is evidence of thickening along the margins of the colpi.

Dufrenoya euryphylla (Danser) Stauffer

Grains spheroidal, length 14 μm, width, 14 μm. The exine sculpturing is entirely weakly rugulate, similar to *Dufrenoya collettii*. Colpi narrow. The endexine becomes thinner beneath the pore and the ektexine is of even thickness. There is evidence of thickening along the margins of the colpi.

Dufrenoya granulata (Hook.f. et Th.) Stauffer

Grains prolate spheroidal in equatorial view, length 17.5 μm, width 15 μm. The exine sculpturing is entirely weakly rugulate. Colpi narrow. The endexine is of even thickness and the ektexine becomes thinner at the pore. There is evidence of thickening along the margins of the colpi.

Dufrenoya oresitropha (Danser) Stauffer

Grains spheroidal in equatorial view, length 11μm, width 11μm. Exine sculpturing is uniformly echinate. The echinae are 1.2 μm in length, well spaced and some of the spines appear broken and bent over. Colpi narrow, 9 μm long, tapering and almost meeting at the poles, not contracted at the pore which is quite distinct and rectangular in outline. The endexine becomes thin at the pore, the ektexine is of uniform thickness. There is evidence of thickening along the margins of the colpi.

Dufrenoya papillosa Stauffer

Grains prolate spheroidal in equatorial view, length 12 μm, width 10.5 μm. There is a difference in exine sculpturing between the mesocolpium and the polar region: the sculpturing of the mesocolpium is similar to *Dufrenoya sessilis* except that at the margins of the colpi and the poles the sculpturing becomes micropunctate to psilate. Colpi shallow and narrow, 10.7

μm long, flared at the pore, pore distinct, rectangular in outline. The endexine becomes thicker beneath the pore, the ektexine is of uniform thickness. There is evidence of thickening along the margins of the colpi.

Dufrenoya platyphylla (Sprengel) Stauffer (**Fig. 8.1, 8.2**)

Grains prolate spheroidal in equatorial view, length 14 μm, width 12.6 μm. Exine sculpturing is rugulate, similar to *Dufrenoya collettii*. There is a slight difference in sculpturing at the poles and margins of the colpi where it becomes more microperforate to psilate. Colpi narrow, 12 μm long, and rounded at the ends, contracted at the pores where the margins appear to overlap, pore indistinct. The endexine is of uniform thickness and the ektexine becomes thinner at the pore. There is evidence of thickening along the margins of the colpi.

Dufrenoya poilanei Stauffer (**Fig. 8.3, 8.4**)

Grains spheroidal, length 13 μm, width 12.6 μm. The exine sculpturing is uniformly echinate. The echinae are crowded and 1 μm in length. Colpi narrow, deep, 10 μm long and rounded at the ends, not contracted at the pores which are distinct but uneven in outline. The endexine is of uniform thickness and the ektexine becomes thicker at the pore. There is evidence of thickening along the margins of the colpi.

Dufrenoya robusta Stauffer (**Fig. 8.5, 8.6**)

Grains spheroidal in equatorial view, length 11 μm, width 11 μm. Exine sculpturing is uniformly echinate, the echinae are crowded and 1.1 μm in length. Colpi broad, deep, 10 μm long and tapering towards the ends, not contracted at the pore which is distinct and rectangular in outline. The endexine and ektexine are of uniform thickness. There is very obvious thickening along the margins of the colpi.

Dufrenoya sessilis (Craib) Stauffer (**Fig. 9.1, 9.2**)

Grains spheroidal in equatorial view, length 12.5 μm, width 12 μm. The exine sculpturing is uniformly rugulate, similar to *Dendromyza reinwardtiana* where the rugulate nature of the sculpturing tends towards small echinae. Colpi narrow, 9 μm long, contracted at the pore in a similar manner to *Dufrenoya collettii*, pore indistinct. The endexine becomes thicker at the pore and the ektexine is of uniform thickness. There is evidence of thickening along the margins of the colpi.

Dufrenoya sphaerocarpa (Danser) Stauffer

Grains spheroidal – sub prolate in equatorial view, length 15 μm, width 14 - 15 μm. The exine sculpturing is entirely rugulate, similar to *Dufrenoya colletti*. Colpi broad, deep, 11 μm long, contracted at the pore. The endexine is of uniform thickness and the ektexine becomes thicker at the pore. There is evidence of thickening along the margins of the colpi.

Phacellaria Bentham

Pollen grains isopolar, tricolporate, polar length 11 – 14 μm. Exine sculpturing weakly rugulate. Endexine thin; endoaperture shallow, following the margins of the colpi.

Phacellaria compressa Bentham (**Fig. 9.3**, **9.4**)

Grains prolate in equatorial view, length 13 μm, width 11 μm. The exine sculpturing is almost entirely weakly rugulate becoming only slightly less pronounced in the polar region and along the margins of the colpi. Colpi narrow, 9 μm long, contracted at the pore. The endexine and ektexine are of uniform thickness. There is evidence of thickening along the margins of the colpi.

Phacellaria malayana Ridley

Grains spherical in equatorial view, length 11 μm, width 11 μm. The sculpturing pattern is very similar to *Phacellaria rigidula* being entirely weakly rugulate. Colpi shallow, 10 μm long and contracted at the pore where the margins almost appear to overlap. The endexine and ektexine are of uniform thickness. There is evidence of thickening along the margins of the colpi.

Phacellaria rigidula Bentham (**Fig. 12**)

Grains elongate in equatorial view, length 14 μm, width 11 μm. The exine sculpturing is entirely weakly rugulate. Colpi narrow, 12.7 μm long and appear to almost overlap in the region of the pore, pore indistinct. The endexine is of uniform thickness and the ektexine becomes thinner at the pore. There is evidence of thickening along the margins of the colpi.

Tribe Santaleae

Pollen grains isopolar, prolate, tricolporate, porate. Polar length 19 – 24 μm. Exine sculpturing rugulate, perforate, verrucate. Endoaperture indistinct or rectangular.

Osyris L.

Osyris lanceolata Hochst. & Steud. ex A.DC. (**Fig. 10.1, 10.2**)

Grains prolate in equatorial view, length 19 μm, width 17 μm. The exine sculpturing is uniformly perforate. Colpi narrow, 3/4 of the polar length, 15 μm long and tapering at the ends, not contracted at the pores, pore distinct. The endexine is of uniform thickness and the ektexine becomes thinner near the pore; the endoaperture follows the margins of the colpi.

Santalum L.

Santalum album L. (**Fig. 10.3, 10.4**)

Grain prolate in equatorial view, triporate, length 24 μm, width 19 μm. The exine sculpturing is dimorphic: the polar regions are entirely psilate and this pattern is continuous in three longitudinal bands around the pollen grain, the mesocolpium is verrucate. A layer of ektexine excludes the pore; The endexine is thick, both ektexine and endexine become thickened at the pore; the endoaperture is rectangular in outline in equatorial view and thickened along the margins.

Scleropyrum Arn.

Pollen grains isopolar, tricolporate, polar length 23 - 24 μm. Exine sculpturing microperforate, distinctly rugulate. Endexine thick; endoaperture following the margins of the colpi.

Scleropyrum aurantiacum (Lauterb. & K.Schum.) Pilger (**Fig. 11.1, 11.2, 11.3, 13**)

Grains sub prolate in equatorial view, length 23 μm, width 22 μm. The exine sculpturing is pronounced rugulate except along the margins of the colpi and the polar regions where this pattern becomes less pronounced. Colpi broad, 3/4 of the polar length, 17μm long, not contracted at the pore, pore distinct. The endexine is of uniform thickness and the ektexine becomes thinner towards the pores. There is evidence of thickening along the margins of the colpi.

Scleropyrum maingayi Hook.f. (**Fig. 11.4**)

Grains sub prolate in equatorial view, length 24 µm, width 20 µm. The exine sculpturing is faintly rugulate becoming microperforate and eventually psilate along the margins of the colpi and at the poles. Colpi narrow, 4/5 of the polar length, 20 µm long, not contracted at the pores, pore distinct. The endexine and ektexine are of uniform thickness. There is evidence of thickening along the margins of the colpi.

Scleropyrum pentandrum (Dennst.) Mabberley (**Fig. 11.5, 11.6**)

Grains sub prolate in equatorial view, length 24 µm, width 23 µm. The exine sculpturing is sparsely microperforate, becoming psilate at the poles and along the margin of the colpi. Colpi broad, 3/4 of the polar length, 18 µm long, not contracted at the pore, pore distinct. The endexine and ektexine are of uniform thickness. There is evidence of thickening along the margins of the colpi.

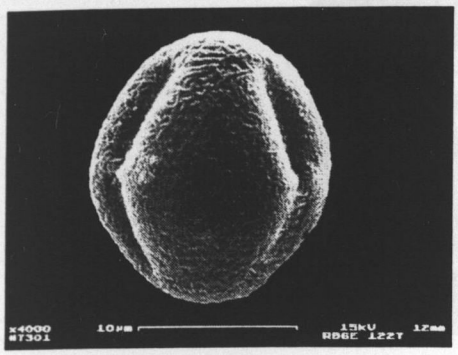
Tribe Anthoboleae

Pollen grains isopolar, prolate, tricolporate. Polar length 19 µm. Exine sculpturing striate. Endoaperture elliptical, transversing the grain in equatorial view.

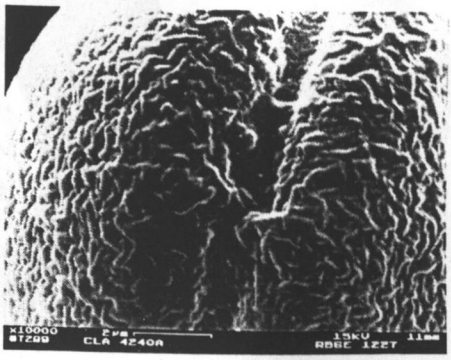
Exocarpos Labill.

Exocarpos latifolius R.Br. (**Fig. 10.5, 10.6, 13**)

Grains prolate, length 19 µm, width 10 µm. The exine sculpturing is entirely striate. Colpi shallow, 7 µm long, pore distinct. The endexine is thick and the ektexine becomes much thickened at the pores; the endoaperture is elliptical, transversing the equator of the pollen grain forming a kind of girdle around it, the margins of the endoaperture are somewhat thickened.



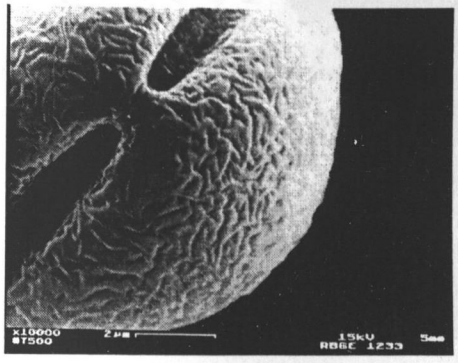
1. *Dendromyza acrosclera*
Equatorial view



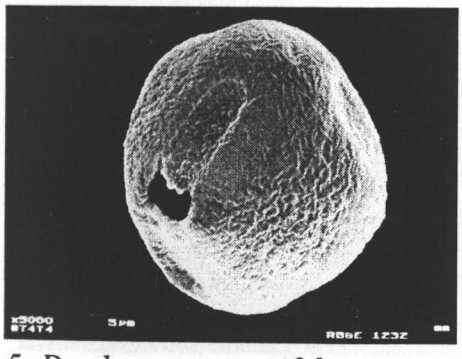
2. *Dendromyza acrosclera*
Close up of mesocolpium and pore



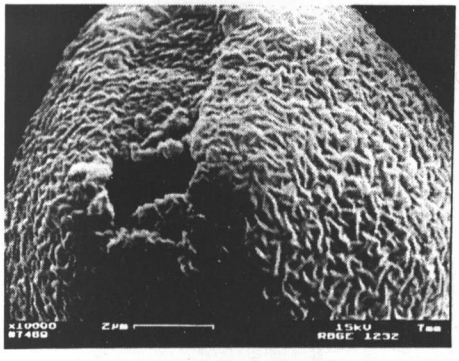
3. *Dendromyza angustifolia*
Equatorial view



4. *Dendromyza angustifolia*
Close up of mesocolpium and pore

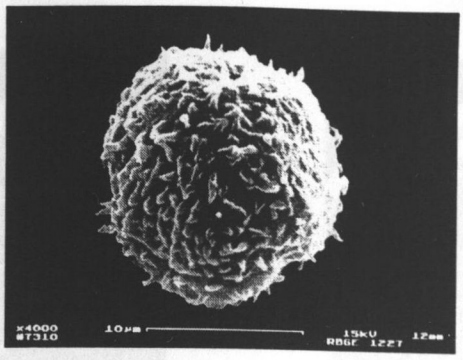


5. *Dendromyza crassifolia*
Equatorial view

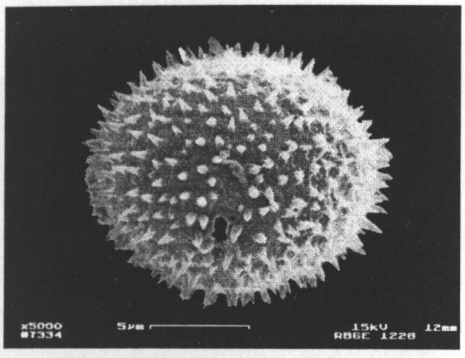


6. *Dendromyza crassifolia*
Close up of mesocolpium and pore

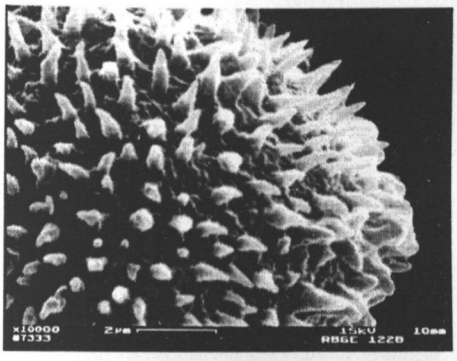
Fig. 4 SEM images of: 1. *Dendromyza acrosclera* x 4000;
2. *Dendromyza acrosclera* x 10000 3. *Dendromyza angustifolia* x 5000;
4. *Dendromyza angustifolia* x 10000; 5. *Dendromyza crassifolia* x 5000;
6. *Dendromyza crassifolia* x 10000



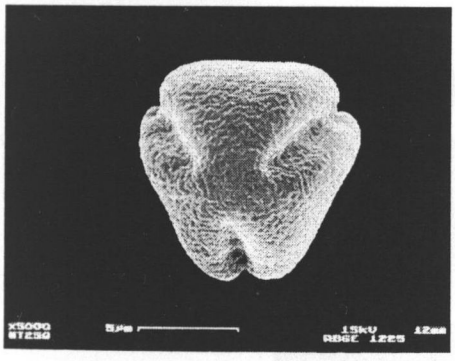
1. *Dendromyza dendromyzoides*
Polar view



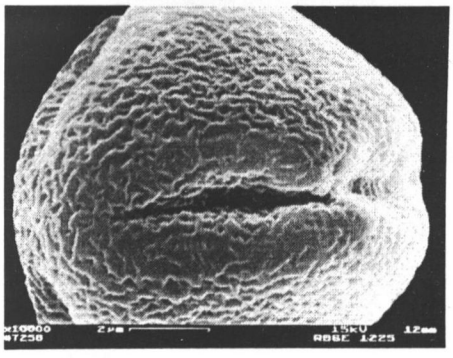
2. *Dendromyza kaniensis*
Equatorial view



3. *Dendromyza kaniensis*
Close up of mesocolpium

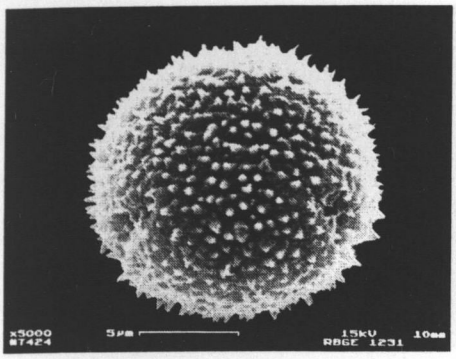


4. *Dendromyza ledermanii*
Polar view

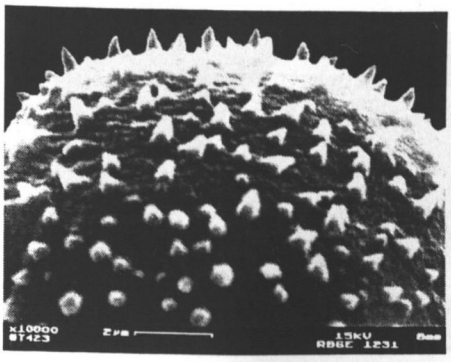


5. *Dendromyza ledermanii*
Close up of mesocolpium and colpus

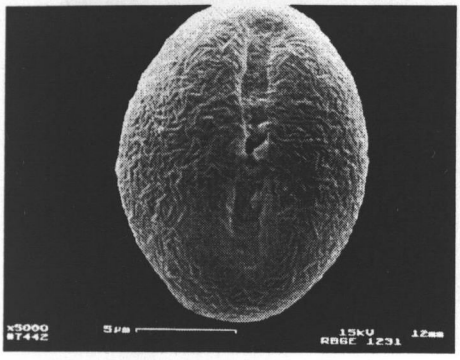
Fig. 5 SEM images of: 1. *Dendromyza dendromyzoides* x 4000;
2. *Dendromyza kaniensis* x 5000; 3. *Dendromyza kaniensis* x 10000;
4. *Dendromyza ledermanii* x 5000; 5. *Dendromyza ledermanii* x 10000.



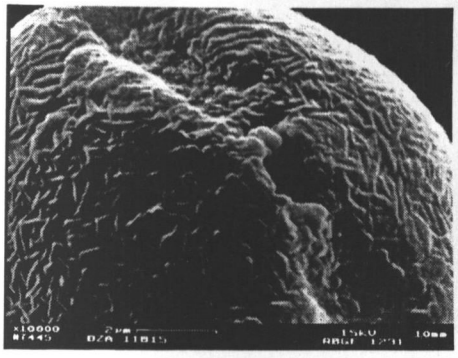
1. *Dendromyza microphylla*
Polar view



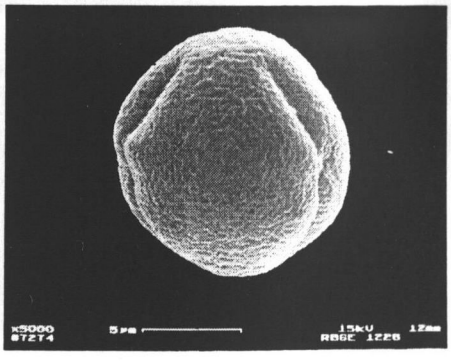
2. *Dendromyza microphylla*
Close up of mesocolpium



3. *Dendromyza multinervis*
Equatorial view

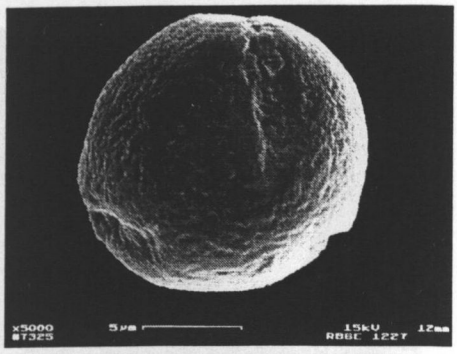


4. *Dendromyza multinervis*
Close up of mesocolpium and pore

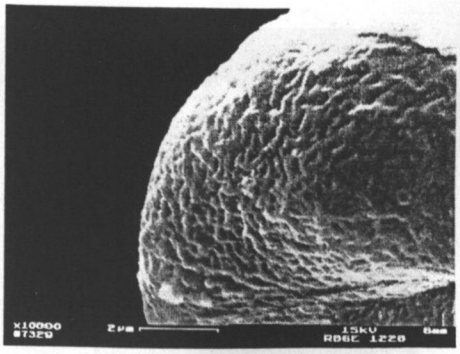


5. *Dendromyza reinwardtiana*
Equatorial view

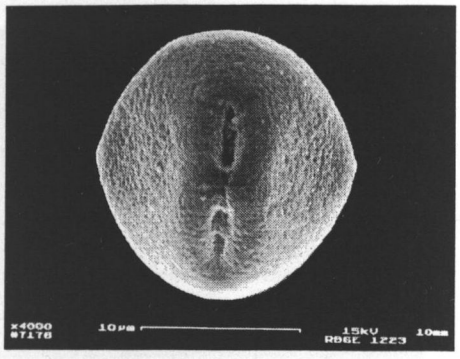
Fig. 6 SEM images of: 1. *Dendromyza microphylla* x 5000; 2. *Dendromyza microphylla* x 10000; 3. *Dendromyza multinervis* x 5000; 4. *Dendromyza multinervis* x 10000; 5. *Dendromyza reinwardtiana* x 5000.



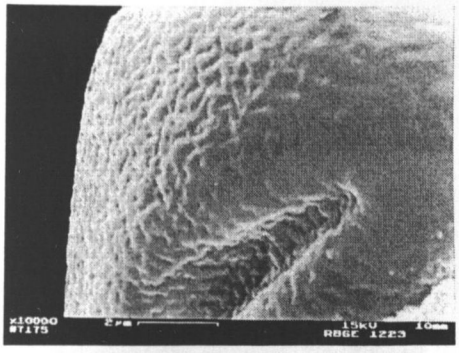
1. *Dendrotrophe buxifolia*
Polar view



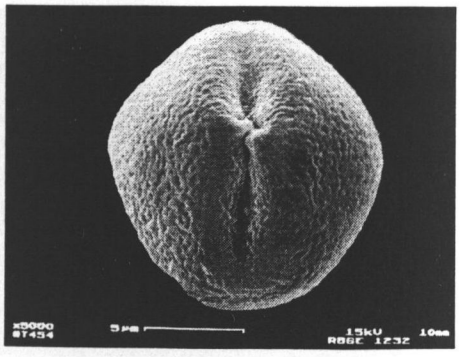
2. *Dendrotrophe buxifolia*
Close up of mesocolpium and colpus



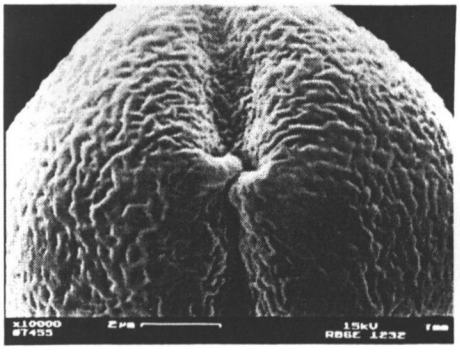
3. *Dendrotrophe varians*
Equatorial view



4. *Dendrotrophe varians*
Close up of mesocolpium and colpus

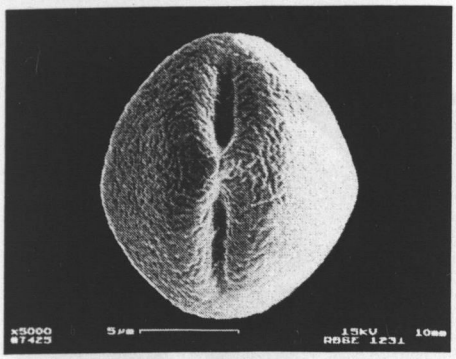


5. *Dufrenoya collettii*
Equatorial view

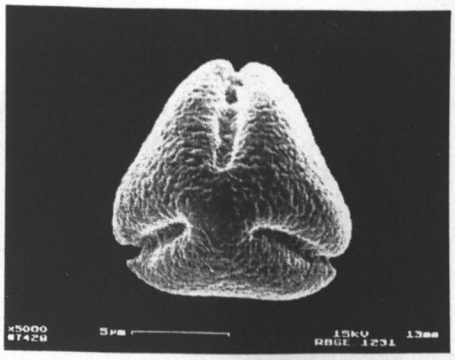


6. *Dufrenoya collettii*
Close up of mesocolpium and pore

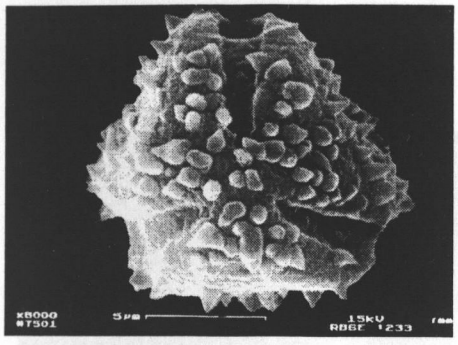
Fig. 7 SEM images of: 1. *Dendrotrophe buxifolia* x 5000;
2. *Dendrotrophe buxifolia* x 10000; 3. *Dendrotrophe varians* x 4000;
4. *Dendrotrophe varians* x 10000; 5. *Dufrenoya collettii* x 5000;
6. *Dufrenoya collettii* x 10000;



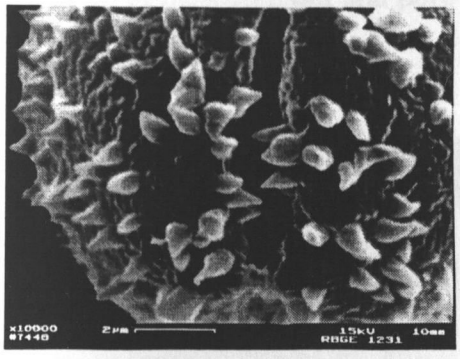
1. *Dufrenoya platyphylla*
Equatorial view



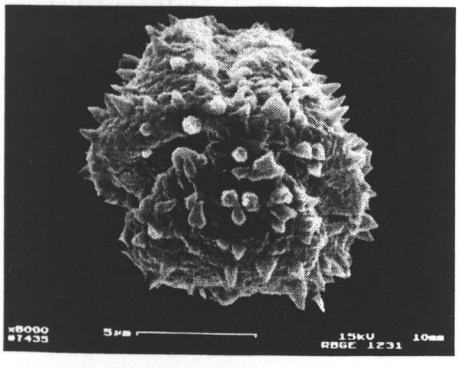
2. *Dufrenoya platyphylla*
Polar view



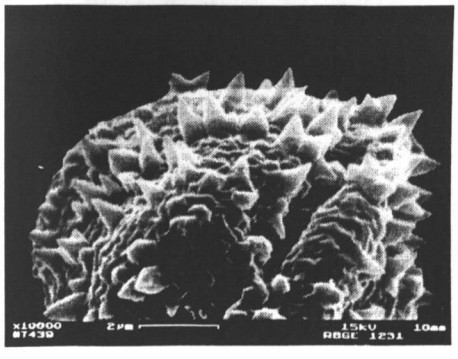
3. *Dufrenoya poilanei*
Polar view



4. *Dufrenoya poilanei*
Close up of mesocolpium and colpus

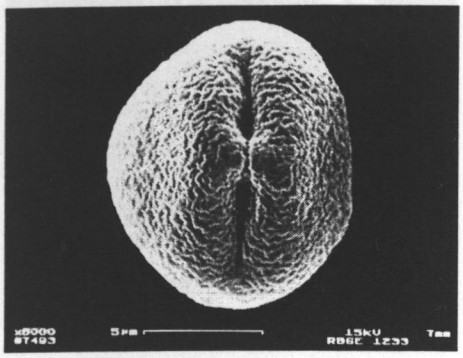


5. *Dufrenoya robusta*
Polar view

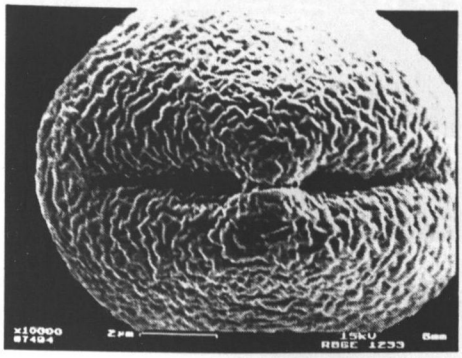


6. *Dufrenoya robusta*
Close up of mesocolpium and colpus

Fig. 8 SEM images of: 1. *Dufrenoya platyphylla* x 5000;
2. *Dufrenoya platyphylla* x 10000 3. *Dufrenoya poilanei* x 5000;
4. *Dufrenoya poilanei* x 10000; 5. *Dufrenoya robusta* x 5000;
6. *Dufrenoya robusta* x 10000;



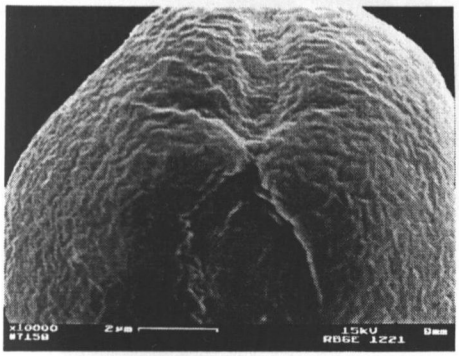
1. *Dufrenoya sessilis*
Equatorial view



2. *Dufrenoya sessilis*
Close up of mesocolpium and pore

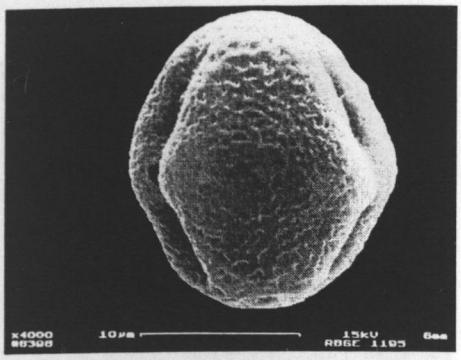


3. *Phacellaria compressa*
Equatorial view

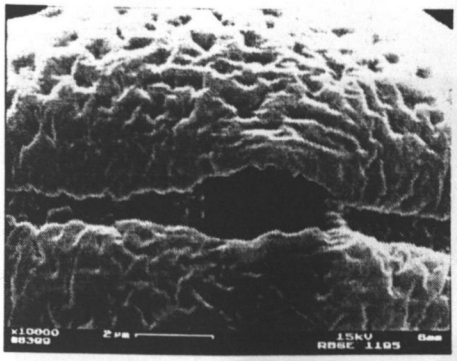


4. *Phacellaria compressa*
Close up of mesocolpium and pore

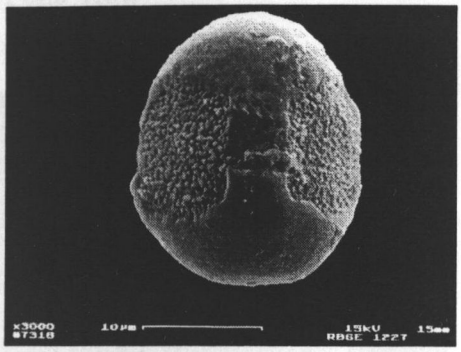
Fig. 9 SEM images of: 1. *Dufrenoya sessilis* x 5000;
2. *Dufrenoya sessilis* x 10000; 3. *Phacellaria compressa* x 5000;
4. *Phacellaria compressa* x 10000.



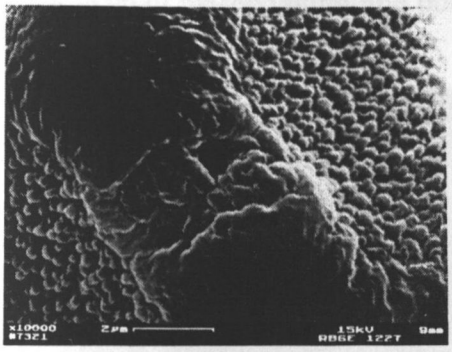
1. *Osyris lanceolata*
Equatorial view



2. *Osyris lanceolata*
Close up ofmesocolpium and pore



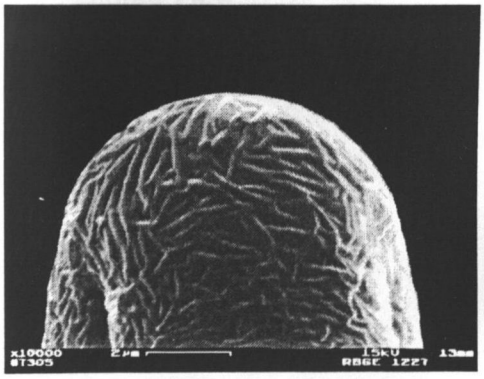
3. *Santalum album*
Equatorial view



4. *Santalum album*
Close up of mesocolpium and pore

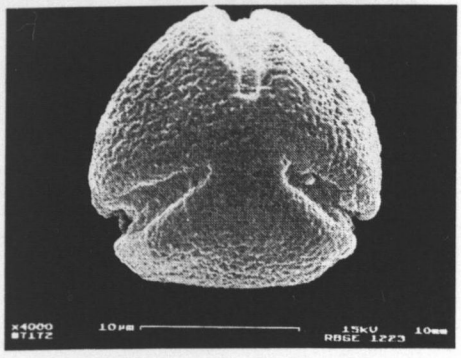


5. *Exocarpos latifolius*
Equatorial view

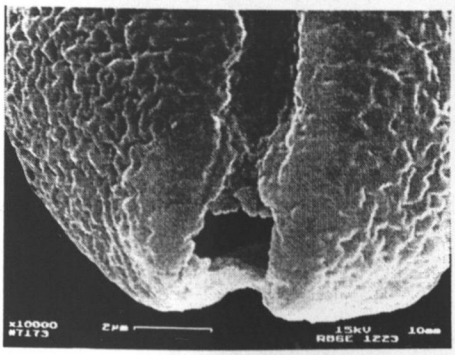


6. *Exocarpos latifolius*
Close up of mesocolpium

Fig. 10 SEM images of: 1. *Osyris lanceolata* x 4000; 2. *Osyris lanceolata* x 10000;
3. *Santalum album* x 3000; 4. *Santalum album* x 10000;
5. *Exocarpos latifolius* x 4000; 6. *Exocarpos latifolius* x 10000.



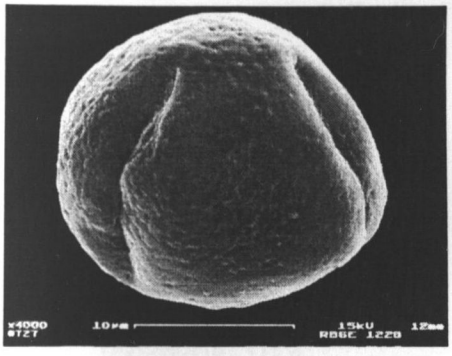
1. *Scleropyrum aurantiacum*
Polar view



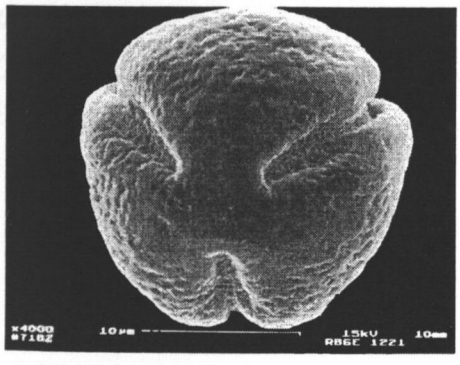
2. *Scleropyrum aurantiacum*
Close up of mesocolpium and pore



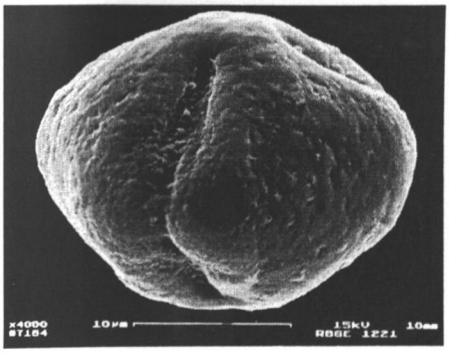
3. *Scleropyrum aurantiacum*
Equatorial view



4. *Scleropyrum maingayi*
Equatorial view



5. *Scleropyrum pentandrum*
Polar view

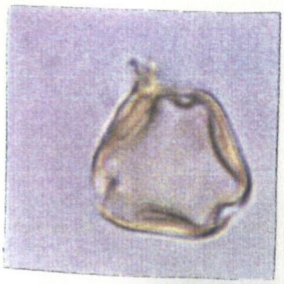


6. *Scleropyrum pentandrum*
Equatorial view

Fig. 11 SEM images of: 1. *Scleropyrum aurantiacum* x 4000;
2. *Scleropyrum aurantiacum* x 4000; 3. *Scleropyrum aurantiacum* x 10000
4. *Scleropyrum maingayi* x 4000; 5. *Scleropyrum pentandrum* x 4000;
6. *Scleropyrum pentandrum* x 4000.



1. *Dendrotrophe buxifolia*
Polar view



2. *Dendrotrophe varians*
Polar view

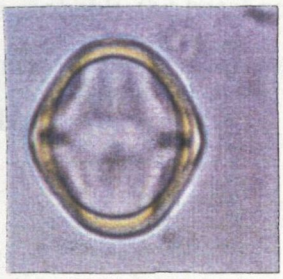


3. *Dendrotrophe amorpha*
Polar view

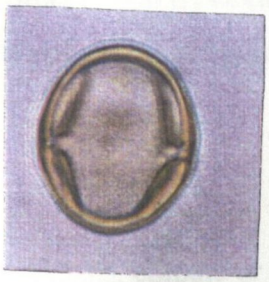


4. *Phacellaria rigidula*
Equatorial view

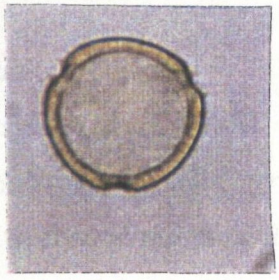
Fig. 12 Light microscopy images of: 1. *Dendrotrophe buxifolia* x 1000;
2. *Dendrotrophe varians* x 1000; 3. *Dendrotrophe amorpha* x 1000;
4. *Phacellaria rigidula* x 1000.



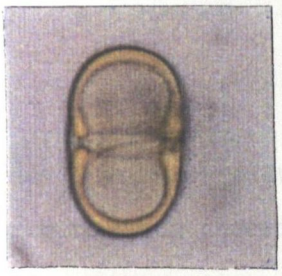
1. *Dendromyza angustifolia*
Equatorial view



2. *Dendromyza cuneata*
Equatorial view



3. *Dendromyza kaniensis*
Polar view



4. *Exocarpos latifolius*
Equatorial view



5. *Scleropyrum aurantiacum*
Polar view

Fig. 13 Light microscopy images of: 1. *Dendromyza angustifolia* x 1000; 2. *Dendromyza cuneata* x 1000; 3. *Dendromyza kaniensis* x 1000; 4. *Exocarpos latifolius* x 500; *Scleropyrum aurantiacum* x 1000.

Summary of results

The species can be split into four categories based on pollen micromorphology. The first group represents probably the basal condition from which all other pollen types can be derived. A summary of the comparison of the different generic pollen characteristics is presented in **Table 4**.

Group 1

Exine ornamentation rugulate or punctate, grains spherical or elongate, colpate or colporate; endoaperture shallow in polar view, following closely the contours of the colpi:

Dendrotrophe, Dufrenoya, Dendromyza, Phacellaria, Scleropyrum, Osyris. This is macromorphologically a very diverse group representing all of the stem parasites and also two terrestrial arborescent and shrubby genera.

Sub section 1.1

Exine ornamentation punctate:

Scleropyrum, Osyris, Dendrotrophe

The species of *Scleropyrum* and *Osyris* have pollen grains which are minutely rugulate and perforate respectively and resemble the other species in endomorphological characteristics but are much larger (19 – 24 μm) and are also distinctly prolate.

Sub section 1.2

Exine ornamentation rugulate:

Scleropyrum, Dendrotrophe, Dendromyza, Dufrenoya, Phacellaria.

There are two types of rugulate exine sculpturing. Pollen grains with strongly rugulate ornamentation which is almost scabrate, are usually spheroidal in shape and represent most of the species of *Dendromyza*. The remainder of the species have pollen with weakly rugulate exine ornamentation. There is no discernible trend in shape but most of the species of *Dufrenoya* are found here and also *Dendrotrophe varians*.

Group 2

Exine ornamentation echinate, grains spheroidal, oblate, colporate; endoaperture highly reduced or absent:

Dendromyza, Dufrenoya, Dendrotrophe

In this group exine sculpturing is correlated with grain shape and also in the reduction in the length of the endoaperture. Interestingly, there is also a reduction in the aperture and the colpi

Table 4: Comparison of pollen characteristics between genera. The tribe Santaleae (*Osyris*, *Santalum*, *Scleropyrum*) have generally larger pollen grains with an elongate polar axis. *Exocarpos* is similar to *Dendromyza* in terms of exine sculpture but in other aspects is similar to the Santaleae. Amphorogyneae (*Dendrotrophe*, *Dendromyza*, *Dufrenoya*, *Phacellaria*) have much smaller pollen with generally more variable exine ornamentation.

Characters / **Genus**	**Polar length (µm)**	**Exine sculpturing**	**Endoaperture**	**Differences in sculpturing pattern between colpi and mesocolpium**	**Colpi contracted at pores**	**Grain shape**
Dendromyza	11 – 17 µm	rugulate / punctate / striate	shallow / elliptical/ absent	+	+	Spheroidal / sub prolate
Dendrotrophe	13 – 17 µm	rugulate / echinate /	shallow/ absent	+	+	Spheroidal/
Dufrenoya	11 – 15 µm	rugulate/ echinate	shallow	+	+	Spheroidal
Phacellaria	11 – 13 µm	rugulate	shallow	—	+	Spheroidal
Osyris	19 µm	perforate	rectangular	—	—	Prolate
Santalum	24 µm	verrucate	shallow	+	—	Prolate
Scleropyrum	23 – 24 µm	rugulate / punctate	shallow	+	—	Prolate
Exocarpos	19 µm	striate	transversal	—	—	Prolate

+ = yes

— = no

are very much reduced in length. This group contains mainly species of *Dendromyza* representing over half of the number of species in this genus.

Group 3

Exine ornamentation striate, grains prolate, colporate; endoaperture elliptical or transvering the pollen grain in equatorial view:

Dendromyza, Exocarpos

In this group there is a definite trend in the elongation of the polar axis accompanied by a reduction in the length of the colpi and an elaboration of the endoaperture. In species of *Dendromyza* the colpi are more elongate and the endoaperture is elliptical and an easily identifiable progression to the situation in *Exocarpos* can be observed. In this genus the colpi are shorter and the endoaperture is extensive, transversing the equator of the pollen grain. The striate exine sculpturing in *Dendromyza* may represent a precursor to the type of pollen construction found in *Exocarpos*. In general also the pollen grains in this group are larger than any of the other types found in this genus.

Group 4

Exine ornamentation verrucate, grains prolate, porate; endoaperture rectangular and thickened in equatorial outline:

Santalum

This latter group, represented by just one genus, is quite different in terms of pollen morphology to the other groups. The absence of colpi and the verrucate sculpturing of the exine is unique to the Southeast Asian species. Zonation of the sculpturing pattern is also clearly defined here. The polar region and the area which was once occupied by the colpi is completely psilate and presents a distinctive band around the pollen grain.

Infrageneric relationships

Dendrotrophe

The pollen morphology of the species in this genus is quite diverse. The rugulate nature of *D. varians* pollen is common within the tribe Amphorogyneae whilst the punctate condition of *D. buxifolia* is uncommon. The echinate exine sculpturing of *D. amorpha* is more similar to that observed in *Dendromyza*. As suggested by its name this species is anomalous for the genus. It is the only strict dendroparasite in the genus and is characterised by umbellate male

inflorescences. The nature of the endoaperture is however different to *Dendromyza* which suggests that echinate exine ornamentation has arisen several times in the tribe.

Dendromyza

The species in this group exhibit a wide range of exine ornamentation. A large number of species have echinate pollen grains, a characteristic which is also associated with other floral features such as mode of anther dehiscence and the absence of glandular hairs. The rugulate condition of *D. reinwardtiana* and *D. ledermanii* is exaggerated and tends towards scabrate and is quite similar to that observed in some species of *Dufrenoya*. The striate pollen type is associated with an elongated polar axis and an elliptical endoaperture and in many respects approaches the condition seen in *Exocarpos*. Microechinate pollen grains are unique to this genus and have similar macromorphological characteristics to the species with echinate pollen.

Dufrenoya

The exine ornamentation of the majority of the species in this genus is rugulate. There are however slight variations within this pattern from weakly to pronounced rugulate and also in the unequal distribution of sculpturing along the colpi and polar regions of some species. Three species have echinate sculpturing similar to *D. amorpha* and *Dendromyza sp.*, but the form of the endoaperture is again different. It is possible therefore that echinate sculpturing is associated with the aerial parasitic growth habit.

Phacellaria

The exine sculpturing of all of the species in this genus is uniformly rugulate. The similarity in exine ornamentation across the genus corresponds with floral and inflorescence morphology which is very similar in all species. In terms of pollen morphological trends *Phacellaria* is more similar to species of Santaleae where pollen structure is relatively uniform throughout the species but definitive at the genus level.

Scleropyrum

Species have either rugulate or punctate, tending towards psilate, pollen grains. The morphology of the endexine and the endoaperture is very similar to that observed in the Amphorogyneae (*Dendrotrophe*, *Dufrenoya*) but in general the grains are much larger and may be elongated.

Osyris, Santalum, Exocarpos

Only one species from each genus is represented in the study area and therefore infra generic relationships cannot be ascertained. In general however *Osyris* is quite similar to *Scleropyrum* in internal morphology whilst *Santalum* and *Exocarpos* are quite different. The striate exine ornamentation of *Exocarpos* is quite similar to that observed in some species of *Dendromyza*. The construction of the endoaperture and the endexine is however more complicated. *Santalum* exhibited the greatest dimorphism in terms of exine sculpturing and the verrucate nature of the intercolpium is unique in the Southeast Asian species.

Discussion

The Santalaceae which are found in Southeast Asia do not in general represent a homogenous group. Out of the eight genera which are recorded for this geographical region three are represented by only one species, (*Santalum, Osyris, Exocarpos*). There is a good representative sample however, of what have been considered 'primitive' and 'advanced' genera and all of the tribal classifications of the Santalaceae are found in this geographical region. The remaining five Southeast Asian genera are fully represented, however, and at least four of them (*Dendromyza, Dufrenoya, Dendrotrophe, Phacellaria*) form a monophyletic group (**Chapter 3**). These genera represent the majority of the species in the Southeast Asiatic region and exhibit a wide variety of pollen exo- and endomorphological features. They belong to the tribe Amphorogyneae which traditionally contains the species which have retained the most plesiomorphic characteristics in the Santalaceae.

Sculptural elements

Within the Tribe Santaleae represented here (*Santalum, Scleropyrum, Osyris*) there does not appear to be much variation in the exine ornamentation of the different species. The differences between the genera, however, are quite distinct and taxonomically the surface sculpture of the exine appears to be a very good character allowing generic segregation (**Fig. 10, 11**). Dimorphic exine ornamentation is a feature of many of the species and in particular the sculpturing of *Santalum* is unique among the Southeast Asian Santalaceae in being distinctly verrucate at the mesocolpium and psilate at the poles and around the apertures.

The sculpturing differences observed in the Amphorogyneae are quite different to the Santaleae. In this former tribe exine ornamentation is certainly a specific characteristic and

generic boundaries cannot be distinguished based solely on pollen exomorphology. This group is represented by four genera: *Dendrotrophe, Dufrenoya, Phacellaria* and *Dendromyza*. Pollen ornamentation may be microperforate, rugulate, striate, microechinate and echinate. Echinate grains are unique to this group and are a strong feature in several of the genera. There is a high frequency of echinate sculpturing in the genus *Dendromyza* where up to 50% of the species have microechinate or echinate grains. The adoption of this type of exine ornamentation is associated with a spheroidal or oblate shape and a reduction in the length of the colpi (**Fig. 5, 6**). The endoaperture is also simplified in many of the echinate species and may be absent in some (**Fig. 13**). There is a degree of dimorphism in exine ornamentation in this group but it is not so pronounced as in the Santaleae. In particular the species with echinate or striate pollen grains have uniform exine sculpturing whilst dimorphic sculpturing is more common in species with rugulate pollen grains.

The tribe Anthoboleae is represented by a single species *Exocarpos latifolius* but it seems to fit very well with the other Southeast Asian species. Traditionally this group is thought to possess highly apomorphic characteristics and the species are generally thought to be the most derived members of the family. The exine sculpture is uniformly striate and pollen grains are elongated. There are a number of species of *Dendromyza* which have similarly striate pollen grains with uniform sculpturing but in endomorphological terms they are not so elaborate as *E. latifolius* (**Fig. 13**).

Associated shape and endomorphological features

It has been seen that in general echinate exomorphology is associated with a reduction in the polar axis and the loss of several apertural characteristics. The rugulate nature of the ektexine in *D. varians* and the majority of species of *Dufrenoya* is associated with a shallow endoaperture (**Fig. 12**). In this group the shape of the pollen varies and the grains may be spherical or elongated. In addition the exine extends over the pore in many cases. The same sculpturing pattern is observable in the Santaleae in *Scleropyrum sp.* and is again associated with a shallow endoaperture, although the grains are much bigger and the pore is not protected by the exine. The occurrence of striate pollen grains is not common in the family and is represented in the Amphorogyneae by *Dendromyza* and in the Anthoboleae by *Exocarpos*. This sculpturing pattern is correlated with elongation of the polar axis and equatorially an elongation and elaboration of the endoaperture.

The endexine in the majority of the species of the Santaleae and Amphorogyneae is almost uniformly thin with slight changes in thickness at the pores. This is especially true for those species with rugulate ektexine sculpturing. In *Santalum* the endexine is dramatically thicker at the pores and forms a wedge shape, there is also a thickening along the endoaperture. In *Exocarpos* also there is also a thickening of the endoaperture at the pores and thinning at the poles. In Amphorogyneae the condition is generally the same as the Santaleae *Scleropyrum* and *Osyris*. Echinate pollen grains are characterised by a uniform endexine and the absence of an endoaperture. In the species with striate pollen grains the endexine may become slightly thickened in the pore region and the endoaperture is elliptical with uneven margins in equatorial outline.

The change in pollen grain size, shape and internal construction may be related to the Wodehouse effect (Muller 1979). When anthers dehisce and pollen grains are released they are immediately subjected to the desiccating influences of the external environment. When they come into contact with the surface of the stigma, however, they are subjected to rehydration and pulling and stretching of the exine (Heslop-Harrison 1976). To counterbalance this effect strategies have arisen to accommodate changes in water potential within the pollen grain. This adjustment is known as harmomegathic accommodation (Punt 1986). In general large pollen grains have to accommodate larger changes and need more elaborate colpi which can bend and fold with changes in water potential, they also require more robust exines to minimise damage caused by such stretching and folding (Blackmore & Barnes 1986). Smaller pollen grains on the other hand, due to their small volumes, have less need for such accommodation and therefore have thinner exines and may lack colpi. This effect can be seen most clearly in the pollen of *Santalum album* on one hand and the majority of dendroparasitic species on the other. The pollen grains of *S. album* are large, the exine is thickened and the endoaperture is quite large and elaborate. In the majority of dendroparasitic species the pollen is small, the exine is thin and elastic and endexine and endoapertures are either much reduced or absent. The covering of the pore by the exine is also a strategy employed by many of these species (*Dufrenoya*, *Dendromyza*, *Phacellaria*) probably to minimise desication, therefore involving a transfer of harmomegathic accommodation to the exterior of the pollen grain.

There seems to be an interaction between sculptural patterning and adjustment to changes in water potential in the pollen of the Santalaceae. Echinate pollen grains have evolved to

transfer volume accommodation from colpi folding to aperture elasticity (Blackmore 1982) whereas elongation of the polar axis is associated with striate exine ornamentation and the transfer of harmomegathic function to internal structures (Thanikaimoni 1986). In the Santalaceae the adoption of both strategies has occurred. In *Exocarpos* and some species of *Dendromyza* the elongation of the polar axis is associated with striate exine ornamentation and elaboration of the endoaperture. The echinate nature of the pollen of *Dufrenoya*, *Dendromyza* and *Dendrotrophe* is associated with the reduction in endoapertures, this phenomenon is particularly pronounced in *Dendromyza* where endoapertures are virtually absent.

Associated characteristics

There are certain associated pollen characteristics observable within the Amphorogyneae represented here, the pollen exo- and endomorphology is so varied that many of the tendencies observed in this group may be applicable to the entire family. One trend is the adoption of echinate grains with the reduction of apertures while another is the elongation of the polar axis accompanied by the simplification of exine ornamentation and elaboration of the endoaperture. The hypothetical ancestral condition seems to be the intermediate rugulate condition of which there are two different types. Those with the more pronounced rugulate condition are generally spherical and associated with the Eastern Malesian genera while the weakly rugulate species are generally found in western Southeast Asia and are variable in shape. It would not be difficult to imagine that this basal form could give rise to the echinate and striate condition. It is interesting that both *Scleropyrum* and *Osyris* have rugulate and punctate grains respectively but their grains are much larger than the other species with this type of exine sculpturing. (**Fig. 14**). *Scleropyrum*, *Santalum* and *Osyris* are shrubby or arborescent genera and have the largest pollen grains demonstrating that pollen size may be related to growth habit. Conversely the dendroparasitic genera have much smaller pollen grains. It is thought that pollen grain size may be correlated with plant nutrition (Richards 1997). The terrestrial species of Santalaceae have a wider choice and variety of hosts and therefore can allocate greater resources to pollen production, resulting in larger pollen grains. The aerial parasites on the other hand occupy a more difficult environment with possibly limited resources and have smaller pollen. The different trends in pollen shape within *Dendromyza* can also be observed in **Fig. 14**. Some species approach *Exocarpos* in terms of pollen shape and size and these are all species with striate exine ornamentation.

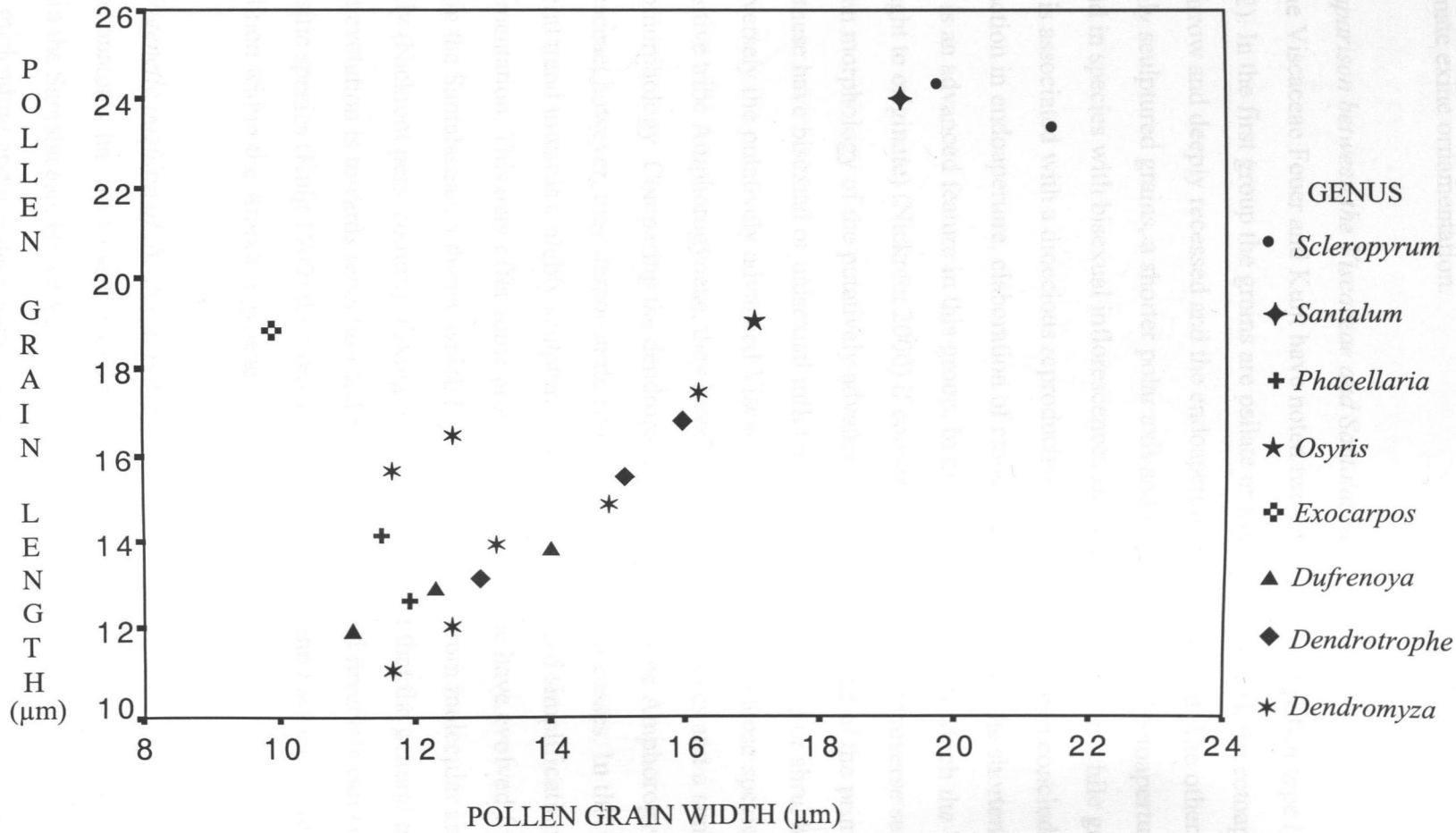


Fig. 14 Scatter plot of pollen grain length v width. The arborescent genera (*Scleropyrum*, *Santalum*) have much larger pollen than the dendroparasitic genera (*Dufrenoya*, *Phacellaria*, *Dendrotrophe* & *Dendromyza*). *Exocarpos* shows a rather different trend and is more similar to some *Dendromyza sp*.

There are other species which approach a spherical or oblate shape and all of these have echinate exine ornamentation.

Comparison between the Viscaceae and Santalaceae

In the Viscaceae Feuer and Kuijt have noted two basic groups of pollen type (Feuer & Kuijt 1982). In the first group the grains are psilate or slightly sculptured, the ectoaperture is narrow and deeply recessed and the endoaperture is well defined. The other group has highly sculptured grains, a shorter polar axis and shallow endo and ectoapertures. Group one is found in species with bisexual inflorescences and a monoecious habit while group two is associated with a dioecious reproductive condition. It has been concluded that the reduction in endoaperture, elaboration of exine ornamentation and the shortening of the polar axis is an advanced feature in this group. In the Santalaceae, (from which the Viscaceae are thought to originate) (Nickrent 2000) if convention is followed, the reverse seems to be true. Pollen morphology of the putatively advanced species follows that of the primitive Viscaceae and these have bisexual or unisexual inflorescences and arborescent or shrubby growth habit. Conversely the putatively advanced Viscaceae are very similar to those species of the primitive tribe Amphorogyneae, they have unisexual inflorescences and a simple pollen endomorphology. Comparing the dendroparasitic species of tribe Amphorogyneae with the Viscaceae, however, may demonstrate similar evolutionary processes. In this group there is a general trend towards a highly sculptured exine with associated simplification of exine ornamentation. This may offer some proof that the Viscaceae have evolved from this group within the Santalaceae, a theory which has been postulated from molecular analysis of the family (Nickrent pers. comm.). Taking into account the fact that the general trend in parasitic plant evolution is towards reduction and many reductions and reversals can be observed in parasitic species (Kuijt 1969) the loss of aperture and endexine may therefore be a derived condition within the Amphorogyneae.

Phylogenetic position of the aerial parasites

Wood anatomy has been used to justify the primitive status of the tribe Amphorogyneae within the Santalaceae. However, the information on the wood anatomy of the family may be very misleading and it is necessary to discuss some aspects of the wood anatomical studies to clarify this point. The status of the tribe Amphorogyneae as primitive within the Santalaceae is based largely on the structure of the wood as described by Swamy (1949). The wood

construction of this group based on his investigations is thought to be diffuse porous and a high proportion of vascular tracheids is a common feature. As the occurrence of tracheids is essentially a plesiomorphic and generally irreversible characteristic (a few exceptions are noted) the basal status for this tribe seems warranted. There are cases however where the retention of this primitive condition may occur or where reversals have arisen (Baas & Wheeler 1996). Compensation may be made by the tendency of other vegetative structures to evolve more rapidly, possession of a xeromorphic leaf structure could be an example of this (Carlquist 1996). The species of Amphorogyneae that were examined by Swamy have small xeromorphic leaves (as do many other members of the Amphorogyneae), so an explanation may be given for the retention of vascular tracheids with the adaptation of other vegetative structures. Tracheids may also have an adaptive role in extreme environments, examples are given for species of Proteaceae and Rosaceae which are found in Mediterranean environments where the proportion of tracheids in the wood is increased in the very hot parts of the year (Carlquist 1985). The species studied by Swamy is climbing or dendroparasitic and is part of a group representing the only branch parasites in the family. The habitat and growth form of this plant implies that it occupies an extreme environment and is subjected to water stress. The possession of tracheids can therefore be seen as an adaptive characteristic. As tracheids are also shorter than vessels they may infer greater mechanical strength and water use efficiency in the long twining stems of a liana. Wood anatomy, which has been employed to attribute a primitive status to the Amphorogyneae, may therefore be redundant.

The wide variety of pollen morphology within the dendroparasites may be due to the relaxation of selection pressures in their branch parasitic ecological niche (Feuer 1977). In particular the variation within *Dendromyza* may indicate that this has occurred. In relation to other characteristics the majority of species are dioecious with elaborate fruit structure. This coupled with increased host specificity is indicative that the dendroparasites, in particular *Dufrenoya*, *Dendromyza* and *Phacellaria* hold a derived position within the Amphorogyneae.

Relationship between exine ornamentation and floral morphology in Amphorogyneae

The basic Santalaceous flower is radially symmetrical with a substantial nectarial disc which covers the surface of the receptacle. The nectary produces copious amounts of nectar, may be slightly fragranced and is the chief attractant to prospective pollinators. The type of nectar produced is thought to influence pollinator preference. The highly viscous nature of the nectar

in Santalaceous flowers is most suited for feeding by insects with relatively unmodified mouth parts (Richards 1997). Frequently there is a tuft of glandular hairs behind each anther, emanating from the inner tepal surface and at anthesis the anthers usually become inflexed over the nectarial disc. The anthers may then lie at the tip of the style or below it. In all cases where this occurs access to the nectary is partially occluded by the anthers. It has been observed that the chief pollinators of *Santalum album* are syrphid flies and bees which insert their probosci between the anthers and the stigma to gain access to the nectar (Bhaskar 1992). In the Mediterranean flies are also the chief pollinators of *Osyris alba* L. The post staminal hairs are seen to produce an oily viscous fluid which may act as an additional attractant. These hairs have conidia at their tip which is known to stimulate pollen collecting activity in bees (Vogel 1978). The fact that they produce a lipid rich fluid means that they may also be sucked by visiting insects who then inadvertently collect pollen on their mouth parts (Aronne et al 1993). A similar strategy has arisen in *Sternbergia* (Amaryllidaceae) and has resulted in the diversification of pollinators. In this species nectar is produced basally in the flower which attracts bees whilst hairs at the tips of the perianth are visited by syrphid flies (Dafni & Werker 1982). In the Santalaceae the nectary covers the surface of the receptacle and therefore the inflexing of the stamens over the centre of the flower may also act to guide pollinators towards the stigma in hermaphrodite flowers. In dioecious flowers staminodes may produce the same effect in female flowers whereas in those species without staminodes the stigma may be very large taking up almost the entire inner portion of the perianth (*Dufrenoya robusta, D. poilanei*) or it may consist of several separate stigmas which are outspread (*Dendromyza*) which increases the chance that they will come into contact with visiting insects.

The Amphorogyneae exhibits the greatest range of pollen exine ornamentation. In particular the dendroparasitic species have elaborated to produce rugulate, striate, echinate and microechinate pollen grains. The genera in this tribe also possess the widest variability in terms of floral morphology: hairs may or may not be present behind the anthers and the anthers can differ in terms of shape and mode of dehiscence. In the genus *Dendromyza* there appears to be a correlation between anther dehiscence, the presence or absence of glandular hairs and pollen exine ornamentation. In those species which have rugulate or striate pollen grains glandular hairs are usually present and anther dehiscence is invariably longitudinal. In contrast species with transversally dehiscing anthers lack post staminal hairs and the anther dehiscence is transverse (**Table 5**). In the first group the glandular hairs may act to aggregate

the pollen into clumps within the dehisced anther and the hairs may also provide an attractant to specific pollinators. In the latter group the glandular hairs are absent but often luminous dots appear on the tepal surface concentrated around the anther or pale lines can be present. These may act as guides towards the nectary as color patterns can strongly influence pollinator behavior once they reach a flower (Wasar 1983). A cluster of druses can also be observed at the centre of dehisced anthers which may act as a reward for pollinators in replacement of the lipid rich fluid of the glandular hairs. It is known that several species can produce food bodies of this kind, which act as rewards for beetles and some flies and bees (Richards 1997). The fact that these species have echinate pollen grains and offer a possible alternative reward to pollinators is suggestive of a selective pollination strategy. Some species may be attracted to those plants with glandular hairs whilst others may select those without. The different pollination strategies may therefore act to reinforce reproductive barriers between species. There is however no data on pollinators for this genus and the selective partitioning of pollinators can only be a suggestion at this stage.

Table 5: Comparison of floral structure and exine ornamentation in the genus *Dendromyza*. Those species with echinate pollen grains generally have transversally dehiscing anthers and lack glandular hairs behind the anthers.

Species	Anther dehiscence	Glandular hairs	Exine ornamentation
Dm. reinwardtiana	L	—	rugulate
Dm. ledermanii	L	+	rugulate
Dm. crassifolia	L	+	rugulo-striate
Dm. multinervis	L	+	rugulo-striate
Dm. cuneata	L	+	rugulo-striate
Dm. angustifolia	L	+	rugulo-striate
Dm. cucullata	L	+	rugulate
Dm. acrosclera	T	+	rugulate
Dm. microphylla	T	—	microechinate
Dm. uncinata	T	—	microechinate
Dm. stellata	T	—	microechinate
Dm. dendromyzoides	T	—	echinate
Dm. kaniensis	T	—	echinate
Dm. trinervia	L	+	echinate
Dm. pachydisca	T	—	echinate

L = longitudinal dehiscence
T = transversal dehiscence

The other genus within the tribe which appears to have correlated floral and pollen morphological characteristic is *Dufrenoya*. In this case however a slightly different trend emerges in that all of the species with echinate pollen grains have longitudinally dehiscing

anthers but they still lack post staminal hairs, the pollen of these species is however usually brightly coloured and more profuse than in species with transversally dehiscing anthers. It is known that some flavanoids which contribute to the colour of pollen grains may impart a certain taste or fragrance which will encourage or dissuade pollinating insects (Thanikaimoni 1986) and in this case the numerous brightly coloured pollen grains may act as an attractant. *Dufrenoya* occurs in a different geographic location to *Dendromyza* and therefore different pollinators may be involved. Therefore two seemingly differing strategies of floral morphology appear to have resulted in echinate pollen grains.

It has also been postulated that electrostatic forces may be implicated in exine ornamentation. It is assumed that the stigma is positively charged whilst the pollen grain has a negative charge. Smooth grains will lose their electric charge very rapidly when they come into contact with the stigmatic surface, whilst echinate grains because they are kept at a short distance from the surface of the stigma will retain their charge longer and hence their electrostatic attraction. The same thing is postulated for pollinator – pollen attraction (Punt 1986). Echinate grains may therefore have a greater adherence to pollinators and also to stigmatic surfaces than smooth pollen grains, and this may offers a degree of selective advantage. Within the dendroparasites as a whole there is a a high proportion of species with echinate pollen indicating that some kind of selective process, for this pollen type, may be in operation.

Pollen morphology in relation to molecular phylogeny

The pollen morphology of all the members of the Santalales has been explored in some detail and evolutionary relationships between families have been postulated based on the evidence of pollen morphology. In particular a close relationship between the Eremolepidaceae and the Santalaceae was suggested on the basis of pollen morphology (Feuer 1981, Lobreau Callen 1982). This hypothesis has been borne out by recent molecular evidence which suggests that the Eremolepidaceae forms a monophyletic group with the Santalaceae (Nickrent 2000). This same molecular analysis using *rbc*L and 18S gene sequences has suggested that the family Santalaceae is in fact paraphyletic, the Eremolepidaceae and Southeast Asian genera forming a separate clade from *Thesium* and mainly South American species.

Based on previous studies of pollen morphology it was also postulated that the Santalaceae is in need of revision and that characteristics of the pollen morphology of certain genera are

anomalous for the family (Erdtman 1952, Fernández 1993). The study of Lobreau Callen (1982) indicated a trend within a certain group of the Santalaceae towards heteropolar pollen grains. This group included *Thesium*, *Jodina* and *Comandra*. Comparing the trends in pollen morphology to the molecular evidence it appears that this particular pollen type forms a separate clade from the rest of the Santalaceae. In other words pollen morphology follows closely the molecular evidence. In recent years there has been a trend to concentrate solely on molecular data when inferring phylogenies and pollen morphology has often been seen as unreliable. If however, the data are re-examined and comparisons are made between molecular phylogenies and pollen morphology, morphological trends within groups may be determined and relationships reinforced.

Conclusions

The basic pollen structure of the Southeast Asian Santalaceae is the rugulate condition observed in *Dendrotrophe*, *Dufrenoya* and *Scleropyrum* with either trends towards the elaboration of the exine, a shortening of the polar axis and the loss or reduction of the apertures or a simplification of the exine ornamentation with the associated elongation of the polar axis and elaboration of the endoaperture. The echinate condition observed in many of the species of *Dendromyza* is possibly a derived condition as is the elaboration of the endoaperture of the species with striate sculpturing elements. The size differences between the genera is associated with habit, as species with larger pollen grains are generally arborescent, while those with smaller grains are aerial parasites. These species in general also have smaller flowers, more elaborate fruit and their degree of parasitism is more pronounced and often host specific. Within the Amphorogyneae pollen morphology is also correlated with differences in floral morphology. In particular in *Dendromyza* echinate exine ornamentation is associated with the loss of glandular hairs and transverse anther dehiscence. There is a strong relationship between the Viscaceae and the branch parasites in the Santalaceae in terms of the evolution of exine structure, and molecular evolution parallels pollen morphology in this group. In taxonomic terms it has been demonstrated that pollen morphological characteristics are very useful at the generic level in the Santaleae while amongst the branch parasitic species of the Amphorogyneae they are extremely useful at a species level.

Glossary of Pollen Terms

Aperture: a thin or missing part of the pattern of the exine

Colpi: longitudinal apertures, or furrows usually narrowly elliptical in shape

Colporate: pollen grain with colpi and approximately circular openings or pores (porate: with three pores only)

Echinate: with projecting spines grater than 1μm in length

Ektexine: the outer sculptured layer of a pollen grain (stains intensely with basic fuschin)

Endexine: inner unsculptured layer of a pollen grain (stains only slightly with basic fuschin)

Endoaperture: an aperture which is a feature of the endexine

Exine: the outer, usually resistant layer of the pollen grain

Isopolar: pollen grains in which the proximal and distal faces are the same

Mesocolpium: the area bordered by two colpi

Microechinate: with projecting spine less than 1μm in length

Microperforate: with surface pitted holes less than 1 μm in diameter

Perforate: with surface pitted holes greater than 1μm in diameter

Polar axis: a perpendicular line connecting the poles of a pollen grain

Pore: isodiametric holes (in Santalaceae placed along the colpi) which may also be slightly elongated with rounded ends

Prolate: the ratio between polar axis and equatorial diameter is: 1.33 – 2

Prolate spheroidal: the ratio between the polar axis and equatorial diameter is 1.14 – 1.00

Psilate: smooth, without adornment

Rugulate: with shallowly projecting elements which are irregularly distributed

Scabrate: exaggerated rugulate, where the projecting elements have dimensions no greater than 1 μm.

Striate: with projecting elements which are arranged approximately parallel to each other

Sub prolate: the ratio between the polar axis and equatorial diameter is 1.14 – 1.33

Verrucate: with wart – like projections

(Moore et al 1991, Erdtman 1952, Faegri & Iversen 1950)

Phylogenetic Relationships of the Santalacean Dendroparasites

Introduction

There are approximately 1400 species of mistletoes (dendroparasites) known world-wide which belong to the order Santalales and are characterised by possessing a shrubby epiphytic growth habit (Kuijt 1990, Reid et al 1995). Almost 90% of dendroparasites are contained in the families Loranthaceae and Viscaceae and the majority of the remaining species are contained in the Santalaceae (Reid et al 1995). Southeast Asia is home to this unique group of Santalean mistletoes, which consists of a complex of 40 species contained in 4 - 5 genera covering the geographic area from southern India and China to the northern tip of Australia. These species occupy a unique place within the Santalaceae with regard to their growth habit and have developed elaborate modifications in their fruit and pollen morphology in response to their aerial habitat (Kuijt 1968). The species are mostly dioecious and are very similar in terms of vegetative, and to a certain extent, floral morphology. The dioecious condition and the paucity of taxonomically informative characters creates difficulties in terms of generic and species identification and delimitation. It has generally been accepted that within the Santalaceae as a whole sub-familial classifications are imperfectly defined (Kuijt 1968). In particular, with regard to the position of the Santalacean dendroparasites, "one is left with an uneasy feeling that the systematics of the group is partly unresolved" (Kuijt 1990).

The tribe Amphorogyneae contains an assemblage of 11 genera and 70 species, which are confined to Southeast Asia, particularly eastern Malesia and Australia. The circumscription of the tribe is based on the possession of an inferior ovary, clustered inflorescences and small hermaphrodite flowers (Stauffer 1969) and there are certain tendencies within the group towards stem parasitism and host specificity. The majority of the members are terrestrial species from Australia and some are narrow endemics in that region (Hewson & George 1984). The mistletoe species are believed to occupy a derived position in the tribe as nearly all are dioecious with increased host specificity (Swamy 1949, Stauffer 1969, Loubreau-Callen 1982).

Blume (1850) initially described eight species of dendroparasites within a single genus *Henslowia* (now *Dendrotrophe*). The circumscription of the genus was based on the species possessing a climbing or dendroparasitic growth habit and geographic location *i.e.* species were confined to Southeast Asia. Species delimitation was based on leaf size and fruit shape and size. Blume and subsequent researchers (De Candolle 1857, Bentham 1883, Pilger 1935) did not, however, recognise the internal complexity of their fruit structure (Danser 1940) which was masked by a superficially simple morphology.

It was not until the 20th century that the complexity and variety of internal fruit morphology of the Santalacean dendroparasites was fully recognised. In 1940 Danser removed the simple exocarp of a number of the species and discovered a wealth of thentofore hidden morphological variation. His investigation showed that the construction of the fruits of these mistletoes was much more complex than originally believed, and like the Loranthaceae and Viscaceae strategies for fruit dispersal and seedling establishment, had arisen in response to an aerial habitat. His seminal paper (Danser 1940) described 3 new genera: *Hylomyza* (now *Dufrenoya* Chatin), *Dendromyza* and *Cladomyza* and 10 new species of Santalaceae. Danser also recognised their close relationship to the genus *Phacellaria* Benth., a small genus of leafless dendroparasites distinguishable from *Henslowia* by vegetative morphology only. Danser's rationale for splitting *Henslowia* was based on fruit morphology, as the species seemed to fall easily into four categories based on the internal construction of the fruits. He also considered that if *Henslowia* was maintained as a genus *Phacellaria* would have to be subsumed within it which was not appropriate due to the leafless habit and host specificity of the genus. The basic differences, as indicated by Danser, between the five dendroparasitic genera (including *Phacellaria*) were described as follows:

Cladomyza Danser

Fruit ovoid, mesocarp delicate, with woolly or silky indument attached all over the surface of the endocarp, and ascending and attaching the apex of the endocarp to the exocarp. Numerous long, ciliate fibres also present, forming a bundle of "tails" at the apex of the endocarp.

Endocarp 4 – 5 lobed, hard with a solid beak at the apex. Internally incompletely 4 - 5 chambered at the apex, becoming completely so until the base (**Fig. 15.1**, **15.2**).

Dendromyza Danser

Fruit ovoid, numerous long, fibrous strands at the apex of the endocarp forming a bundle of "tails" as in *Cladomyza*. Endocarp not hard with 5 shallow grooves along which it may easily split into five equal parts. Internally endocarp unilocular (Fig. **15.3**).

Dendrotrophe Miq.

Fruit globose to elliptical, mesocarp fleshy. Endocarp hard, rough or tuberculate outside, the larger tubercles usually in about 10 longitudinal rows. Internally endocarp completely 5 chambered at the base and apex otherwise incompletely 5 - 10 chambered; transverse chambers present through out the endocarp. Seed ruminate and in general morphology reminiscent of Juglans (**Fig. 16.1**, **16.2**).

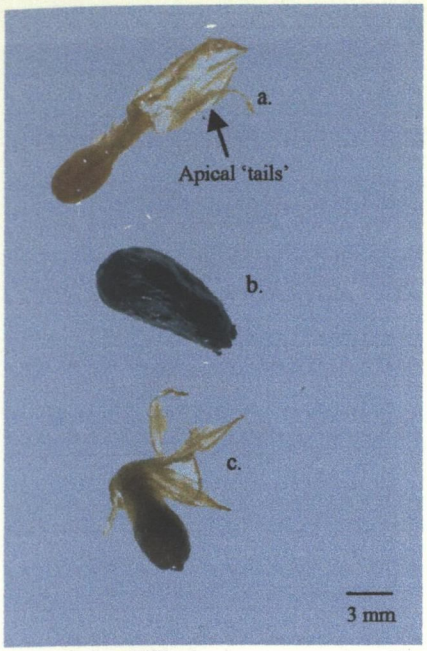
Dufrenoya Chatin (*Hylomyza* of Danser)

Fruit ovoid or globose, mesocarp with radial membranous fibres attached to the endocarp and lying against the interior wall of the exocarp. Endocarp not hard, externally longitudinally grooved or not. Internally completely 5 chambered at the apex and the base, incompletely so elsewhere (**Fig. 16.3**, **16.4**).

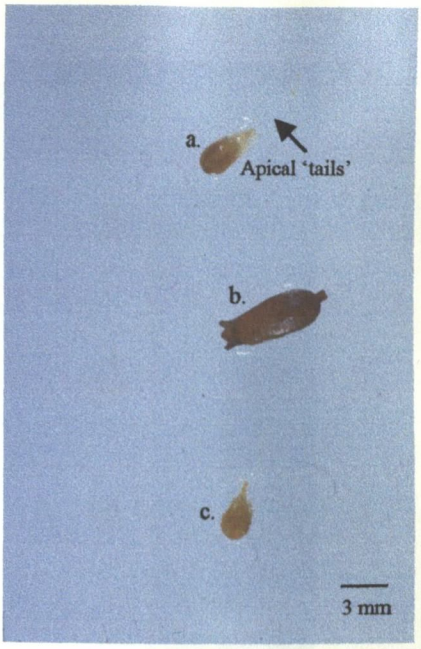
Phacellaria Bentham

Same construction as *Dufrenoya* but endocarp not chambered at the base. The radial fibres of the mesocarp may be more hair like than membranous (**Fig. 15.4**).

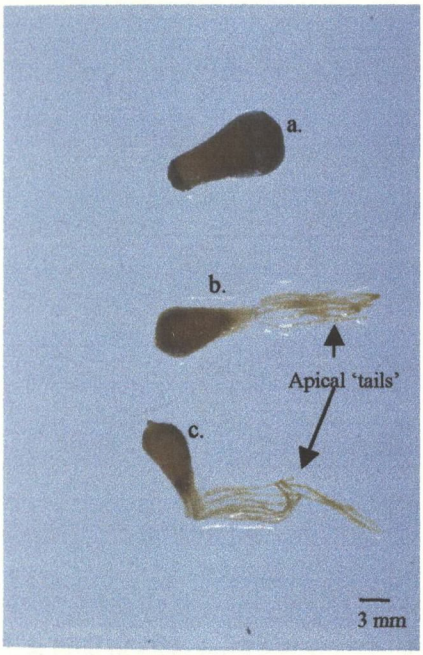
The genera, as described by Danser, appear to be quite distinct and have been maintained to the present day. Certain reservations may, however, be expressed about the naturalness of the groupings and the validity of maintaining certain generic boundaries: examination of the fruits of some species of *Dufrenoya* has shown that they are almost identical to *Phacellaria* (**Fig.**



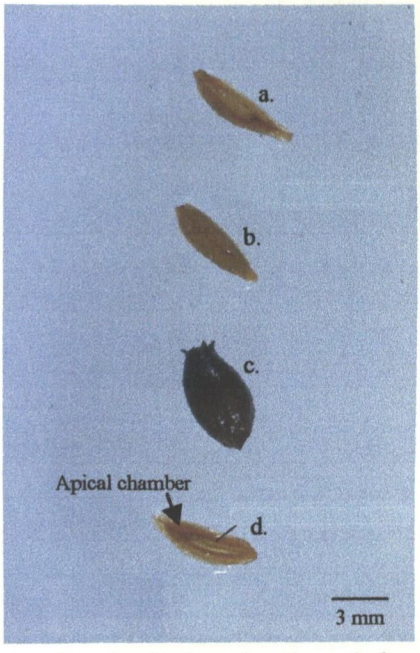
1. a. Fruit of *Cladomyza acrosclera* Danser when the exocarp is removed. note toe pilose apical 'tails' on the endocarp. **b.** fruit. **c.** same as **a**. The mesocarp is sericeus at the apex of the endocarp.



2. a. Fruit of *Cladomyza kaniensis* (Pilger) Stauffer when the exocarp is removed. Note the apical 'tails' of this species are fine and filamentous. **b.** fruit. **c.** same as **a.** The mesocarp is fine, sericeus at the apex of the endocarp.

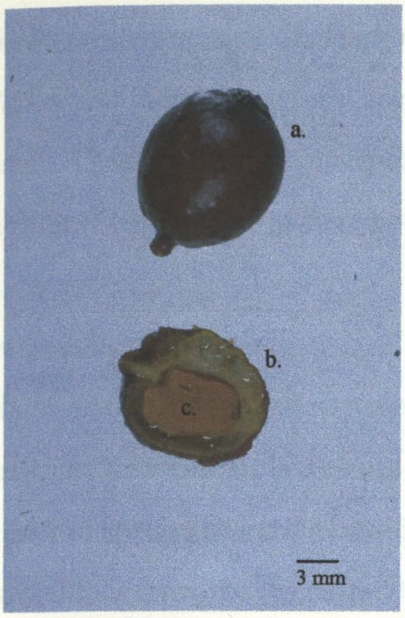


3. a. Fruit of *Dendromyza ledermanii* (Pilger) Stauffer **b.** fruit when the exocarp is removed. Note the long apical 'tails' at the apex of the endocarp **c.** same as **b.** the apical 'tails' are not pilose.

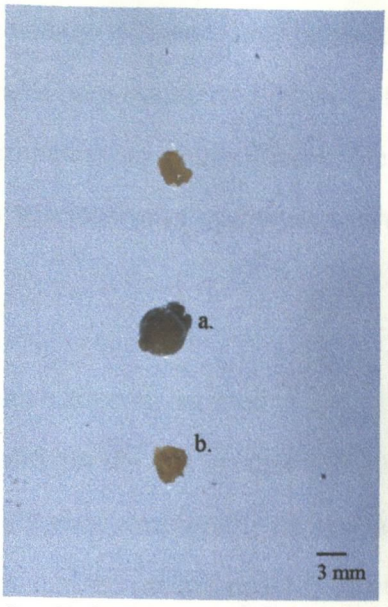


4. a. Longitudinal section through the endocarp of *Phacellaria rigidula Bentham* **b.** fruit when the exocarp is removed. Note the short, sericeus mesocarp. **c.** fruit **d.** same as **a.** Note the chamber at the apex of the endocarp.

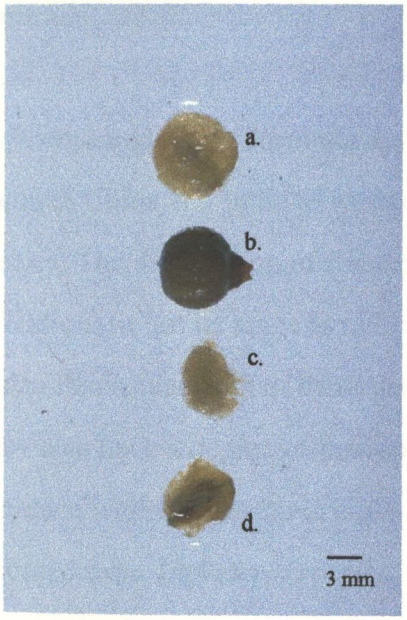
Fig. 15 Fruits and longitudinal sections through the endocarp of species of *Cladomyza*, *Dendromyza* and *Phacellaria*: **1.** *Cladomyza acrosclera*; **2.** *Cladomyza kaniensis*; **3.** *Dendromyza ledermanii*; **4.** *Phacellaria rigidula*.



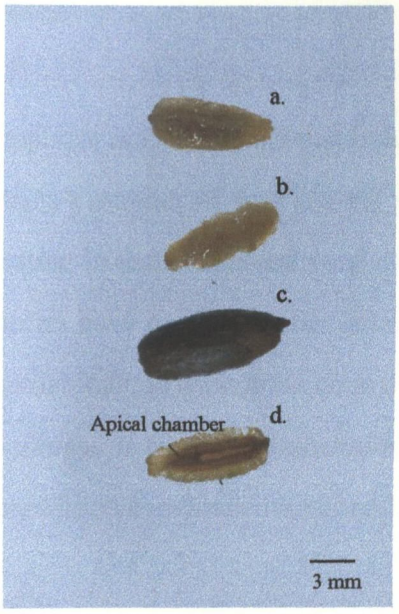
1. a. Fruit of *Dendrotrophe varians* (Bl.) Miq. **b.** longitudinal section through endocarp, which is chambered in the apex and the base and also has transverse chambers.**c.** the seed is ruminate and fills the entire cavity of the endocarp.



2. a. Fruit of *Dendrotrophe buxifolia* (Bl.) Miq. Which is much smaller than *Dendrotrophe varians* (Bl.) Miq. **b.** longitudinal section through endocarp which has the same structure as *D. varians*.



3. a. Fruit of *Dufrenoya collettii* (Gamble) Stauffer when the exocarp is removed. Note the membranous mesocarp.**b.** fruit **c.** part of the mesocarp **d.** transverse section through the endocarp. Note the mesocarp wraps around the endocarp and the endocarp is chambered.



4. a. Fruit of *Dufrenoya oresitropha* (Danser) Stauffer when the exocarp has been removed. Note the short sericeus mesocarp. **b.** part of the mesocarp **c.** fruit **d.** longitudinal section through the endocarp. Note the mesocarp is vertically orientated and the endocarp is chambered in the apex only.

Fig. 16 Fruits and longitudinal sections through the endocarp of species of *Dendrotrophe* and *Dufrenoya*: **1.** *Dendrotrophe varians*; **2.** *Dendrotrophe buxifolia*; **3.** *Dufrenoya collettii*; **4.** *Dufrenoya oresitropha*.

15.4); that not all of the species *Cladomyza* have an indument on the endocarp; that often the apical "tails" in species of *Dendromyza* are ciliate and the endocarp may be as robust as *Cladomyza*. Indeed on several occasions species have been transferred between the two latter genera. These differences in respect of generic delimitation are exemplified in the work of Stauffer (Stauffer 1969) where he transferred four species from *Cladomyza* to *Dendromyza*.

Geographic distributions

Dendromyza and *Cladomyza* have distributions which are concentrated in eastern Malesia, in particular New Guinea is a centre of species diversity for the two groups with less than one quarter of species occurring outside this island. Only very occasionally do species distributions cross the sea barrier between Sulawesi and the eastern coast of Borneo. More specifically only one species of each genus occurs beyond the Moluccas. *Cladomyza* has one species which is found in the Philippines and northeast Borneo whilst *Dendromyza* also has one species with a much broader distribution, which has been recorded as far as the Malay Peninsula.

Dufrenoya and *Phacellaria* occupy very similar geographical ranges. *Dufrenoya* is found from southern China and India to western Borneo and contains a number of very closely related species. The distribution of *Phacellaria* is very interesting in that it follows very closely that of *Dufrenoya* but its range is rather contracted and species have not been recorded east of the Malay Peninsula. Both of these genera occur in similar habitats, in montane evergreen forest. They also have a degree of host specificity in that *Dufrenoya* is found in association with Fagaceae whilst *Phacellaria* is always parasitic on Loranthaceae and has occasionally been recorded from *Dufrenoya* species.

The final genus, which makes up this eclectic group, is *Dendrotrophe*. Of all the genera thus far described it has the broadest geographical distribution from southern China to the north coast of Australia. It is also the least specific in terms of host associations and in terms of growth

habit. Several of the species of this group are climbers, which have the capacity to become dendroparasites secondarily, and just one of its four species is a true mistletoe.

Evolutionary position

It has been postulated that the original Santalacean ancestor was a type of root parasite, the descendents of which became secondarily aerial (Kuijt 1969) and the tribe Amphorogyneae (which includes the dendroparasitic species) represents the primitive position in the Santalaceae (Swamy 1949, Lobreau-Callen 1982). Another point of view is that the Santalacean dendroparasites are a highly evolved group within the family based on their growth habit and host specificity (P. Baas pers. comm.). A question has also been raised concerning the position of this group in relation to the Viscaceae. Viscaceae is considered to be the most advanced family in the Santalales with the highest number of apomorphies in terms of host specificity and reduction in vegetative and reproductive parts (Kuijt 1968, 1969, Nickrent et al 1998). It is now believed that the Viscaceae is derived from the Santalaceae and in particular that it has arisen from within the Santalacean dendroparasites, its closest relative being *Dufrenoya* (Nickrent 2000). Proof for this suggestion has so far not been produced but pollen analysis indicates a close relationship between the two groups (**Chapter 2**) and it does seem a likely theory.

Questions to be addressed

To date there has been no phylogenetic investigation of the Santalacean mistletoes. The generic boundaries between certain groups are far from clear and the justification for maintaining them has been brought into question. It seems necessary to test the current classification and simultaneously investigate the phylogeny of the group. The question is: are there truly five genera of dendroparasitic Santalaceae? If there are fewer how many true groups are there and what are their relationships to each other? Another pertinent question remains over the origin of this group in Southeast Asia; do they have an Old World origin or are they derived from Gondwanan stock? Some clues to the answers to the first question may be obtained from the

classification of Danser, such as the close relationships between *Cladomyza* and *Dendromyza* (Danser 1940).

In order to investigate the uncertainty of the generic relationships and to obtain some estimate of the phylogeny of the group a cladistic analysis seemed to be the most appropriate avenue to follow. To increase the strength of the study, two sets of data: morphological and molecular were used. Using two contrasting, but complementary sets of evidence, helps to detect differences between groups which may not be detected by using one alone (Hillis 1987, Doyle et al 1994). The morphological data set could also be used to test the robustness of the characters currently used to distinguish the genera and to provide a set of reliable qualitative characters, which may be reliably employed in generic identification. The molecular data may point to areas of ambiguity in the morphological analysis and be more useful in determining stable phylogenetic relationships in a group (Donoghue & Doyle 1989).

Cladistic theory

Classification involves the grouping of organisms on the basis of those shared derived characters which are assumed to indicate common ancestry (Thompson 1996). Using cladistics to infer phylogenies can be broken down into two distinct areas: evolutionary theory, and the algorithms which can be used to explain that theory (Swofford et al 1996). In any discussion on cladistics it is necessary to decouple the philosophical considerations from the actual procedures involved in order that a full comprehension of the process may be achieved.

Theoretical considerations

The principles of cladistic analysis which were originally called phylogenetic systematics was introduced by Hennig in 1950 but it did not become well known until the English version of his book was published in 1966 (Patterson 1987). The theory behind the search for genealogical relationships between species, using cladistics, can be broken down into five basic assumptions:

1. Life is hierarchical

2. It is possible to discover that hierarchy

3. In constructing a phylogeny homologous structures must first be identified

4. The maximisation of character congruence can be used to discern between homology and homoplasy

5. Parsimony is the arbiter of congruence

(Sieberg 1997)

Hierarchical constructs emphasise the distinctiveness of classes or individuals, each of which has a particular property, but which is connected above and below it to other members of a group by common attributes (Rieppel 1988). It seems natural to assume that life is hierarchical and that there is order in nature. Without that assumption it would not be possible for the human mind to comprehend and make sense of the variety which exists in the natural world. The search for hierarchical structure in life is not unique to cladistics. In biology organisms have been long classified based on their morphological similarity (Ridley 1996). In botany plants have been arranged into orders, families, tribes and at the lower level species, subspecies and varieties. The hierarchical arrangement of groups and individuals is based on theories of stability in structure and form. Hierarchy is innately characterised therefore by a resistance to change (Rieppel 1988). In terms of human understanding, therefore, creating hierarchical arrangements is a convenient way of ordering nature, a type of filing system, or stock taking of the world around us. In the past it has been postulated that the type of hierarchy which we find understandable may not actually be reality, that the order which we observe is as a result of human perception and the reality of that structure is incomprehensible to human cognition (Sneath & Sokal 1973). If this were true however then there would be no point in attempting to understand a reality, which is beyond our perception. Rather it may be preferable to accept the hierarchical structure of life with the proviso that not all aspects of it have yet been discovered.

If life is hierarchical and the structure of that hierarchy can be known the question arises how can it be discovered? Many classifications have been constructed based on the concept of morphological similarity. Linnaeus divided up the plant kingdom based on numbers of

reproductive parts (Linnaeus 1753). His system was not phylogenetic but it does indicate the errors which can occur when morphological similarity is equated with phylogenetic relationships (Hennig 1966). How then can hierarchical classifications be described if morphological resemblance between species is discounted? Cladistic theory and methodology offers an opportunity to discover the natural classes of organisms. It is not that similarities of form are discounted in phylogenetic systems but rather how those properties of one organism are related to similar features in another.

This statement leads to one of the most important and useful properties of phylogenetic classifications: the concept of homology. Homology breaks up the simple perception of resemblance into the concept of shared characteristics between organisms which are derived from common ancestry (Rieppel 1988). In essence they are observable features of organisms which can be traced back to the same feature in the common ancestor of that organism (Eggleton & Vane Wright 1994) *i.e.* similarities due to common descent (Doyle & Davis 1998). In phylogenetics the investigation of homologies between organisms is an attempt to distinguish superficial similarity from true similarity (Scotland 1992). It is a relative concept and involves the deconstruction of organismal structure into its constituent parts. The concept of homology was first postulated by Saint-Hilaire in the 19th Century under his law of connectivity which stated that absolute similarity between structures was irrelevant, rather their topographical relationships are important (Rieppel 1988). In cladistics homologies must be looked for before they are discovered and tested before they are accepted. This may be one of the supreme values of a cladistic phylogenetic study as it necessitates the thorough investigation of morphological characters. It is of little value to say that a group of organisms share a common characteristic if the basis of that feature is not understood. If simply overall likeness is accepted then features in organisms which are visually different but which are ancestrally linked may be overlooked.

When characters are placed together which are not homologous they are deemed to be homoplasic. That is they are characters which are superficially similar but do not share a

common ancestry (Eggleton & Vane Wright 1994). The possession of wings by a birds and bats, for example, may be considered a homoplasic trait as both structures have arisen independently in the respective animals. They are an example of a convergence, a functional rather than a true similarity. Homoplasy may therefore arise when structures are incorrectly identified or when they are analogous.

In a cladistic analysis there are basically two different types of homologies, shared ancestral characteristics (sympleisiomorphy) and shared derived characters (synapomorphy) (Scotland 1992). The common possession of characteristics, which have remained unchanged for long periods of time, cannot be evidence of close relationships; therefore sympleisiomorphic characters are not informative for establishing evolutionary relationships (Hennig 1966). The possession of shared derived characters are, however, indicative of phylogenetic relationships between groups of organisms. In essence the presence of common apomorphic traits in a group is an indication of that they have a shared ancestry *i.e.* that they are a monophyletic group. Of course concepts of what indicates a plesiomorphic or apomorphic characteristic are all relative. The presence of sepals and petals in one group of plants may be considered as a synapomorphy but at a different level in the same group it may be considered a sympleisiomorphy. The idea of relativity is where difficulties arise, what constitutes a monophyletic group at one hierarchical level is paraphyletic (having more than one common ancestor) at another (Minelli 1993). At the outset of cladistic theory only monophyletic groups were considered to be real, this trenchant position has however been softened recently and now the existence of paraphyletic groups is permitted in cladistic theory (Swofford et al 1996).

Originally ancestral states were determined subjectively and influenced by individual bias. The use of outgroup comparison has increased objectivity and provided a relatively simple and reliable method for determining synapomorphies. In this procedure characters which are being used to create a phylogeny are compared to another group of organisms which is believed to be distinct and not members of the group under investigation. For a given character the state

occurring unambiguously in the outgroup represents the plesiomorphic condition, when different character states occur in the outgroup algorithms exist to calculate the plesiomorphic state (Maddison et al 1984). In this way a degree of subjectivity is removed from a phylogenetic investigation. It is not up to an individual researcher to decide which character states represent the plesiomorphic condition rather this is decided by comparison to the outgroup taxa.

Parsimony as the arbiter of character congruence

It has been said that homology must be maximised in order to discover true phylogenies. This final concept is often achieved through parsimony which is perhaps the most controversial of cladistic assumptions. William Ockham, in the early 14th century, was the first proponent of parsimony (Rieppel 1988). He was searching for a relation which could be used to describe the uniformity and reliability of natural laws (Camin & Sokal 1965). According to Ockham if an event may be explained by more than one theory the most economical explanation is the one that should be accepted. To Ockham parsimony was a way of testing competing theories, in terms of cladistic analysis parsimony is a method which restricts the numbers of changes on an evolutionary tree. In this sense cladistic analysis is implicitly Bayesian, it is a view of the phylogeny of a group taken as a snap shot in time and Bayesian generalisations and inferences are needed throughout the analysis (Zander 1998). Taking that aside, in essence the shortest or most parsimonious tree often indicates the most likely explanation of evolutionary relationships (Kitching et al 1998). Herein lies another problem of accepting the theory of parsimony in a cladistic sense. If an evolutionary tree is drawn and a number of the characters appear to be incongruent *i.e.* homoplastic, then that pattern of evolution is rejected in the strict cladistic sense. From population biology studies, however, it is known that evolution may not proceed in a strictly parsimonious fashion and speciation may occur through reticulate evolution. In this case the parsimonious model will not reveal true relationships. It is now accepted that natural systems may not fit the parsimonious, hierarchical structure and that the phylogeny of a group may be allowed to reject the most parsimonious solution (Swofford et al 1996). In rejecting or accepting cladistic theory one may consider the Aristotelian theory that

an individual changes through time but the fact of belonging to a species means that, at another level, it is beyond the constraints of time and space. In the Platonic sense it is being rather than becoming (Rieppel 1988). On one level the cladistic model of parsimony only considers the 'being' part of the equation of existence, whereas in reality both are inextricably linked. In reality, therefore, the inference of a phylogeny by cladistic analysis can only involve "making the best estimate of evolutionary history" (Swofford et al 1996). Every attempt is made to improve on the classification of a group of organisms but cladistics does not claim to have discovered a single true phylogenetic solution.

The use of molecular data in phylogenetic studies

Molecular data was first utilised in systematic studies at the beginning of the last century (Li 1997). Since that time, and in particular with the recent advent of the Polymerase Chain Reaction (PCR), it has been refined to the point where molecular analysis in systematic studies is almost routine (Palumbi 1996, Wolfe & Liston 1998). In particular, the area of phylogenetic analysis has benefited from the new insights provided by molecular studies. The construction of phylogenies from molecular data is achieved by either using genomic arrangements or by the sequencing of DNA and using the four bases, ATGC, as characters (Judd et al 1999). Regularly sequence data is used in phylogenetic studies and particular genes or gene regions may be chosen to study a phylogeny of a group depending on the level of hierarchy of interest. Studies involving the cooperation of numerous researchers have examined the high level classification of the angiosperms in order to elucidate relationships between plant families and to identify the closest living relatives to this group (APG 1998, Soltis et al 1999, Qiu et al 1999). At lower levels of classification sequencing data has been used to resolve relationships between species and genera (Mes et al 1997, Nickrent et al 1994, Baldwin 1992, Miao et al 1995) to name but a few. The reason for this is that different genes have been identified which evolve at varying rates, for example the *rbc*L gene has evolved quite slowly and may be used when looking at relationships at the familial or ordinal level (APG 1998, Soltis & Soltis 1998). On the other hand the Internal Transcribed Spacer (ITS) region of the nuclear ribosomal DNA has

evolved more rapidly and may be used when generic or specific relationships are of interest (Baldwin 1992, Baldwin et al 1995).

In one sense the use of molecular characters in a phylogenetic analysis is similar to morphological data in that it involves searching for similarities between gene regions. In morphological data sets this would be equivalent to searching for homology, in molecular analysis homologous DNA regions are termed orthologous (Eggleton & Vane Wright 1994). The actual alignment of gene regions is termed positional homology, which effectively is determined by the physical process by which gaps are inserted in a sequence to infer deletion and replication events. Gene sequences are therefore aligned to minimise the maximum number of character state changes. In particular alignment of ITS sequences can be difficult if a high number of gaps have to be inserted to infer insertion or deletion mutations (Nickrent et al 1994, Baldwin et al 1995). Molecular characters are thought to be more reliable than morphology in terms of homology because they are less influenced by environmental influences and are therefore less subject to homoplasy. Molecular sequences are however not free from error. Multiple copies of genes are present in all organisms and these may vary from one another especially after a recent hybridization or duplication event. It may be difficult, therefore, to distinguish between truly homologous or orthologous sequences and paralogous sequences which are due to duplication (Eggleton & Vane Wright 1994) and xenologous sequences which are due to lateral transfer of gene regions due to viruses (Patterson 1987). In general the discovery of homology in molecular data differs from its application to morphological characters in that character states are observed first and then characters are defined by alignment procedures (Doyle & Davis 1998).

Comparisons between morphological and molecular data

The use of molecular data to infer phylogenies should not be viewed as a rival to morphological data; rather the two should be viewed as complimentary sets of information (Moritz & Hillis 1996). The external morphology of taxa is the basis for any classification as it is the means by which it can be identified and the characters in a morphological analysis can be quickly

identified (Nickrent & Starr 1994). In contrast the molecular data set is more abstract and a step removed from the outer recognisable structure of an organism. It may however be extremely useful in groups where a large amount of convergence between morphological characters is thought to occur or where very few morphological characters can be identified. This is exemplified in ordinal classifications where morphological coherence between characters lack evolutionary coherence or are unrecognisable from one group to another (APG 1998). In general studies that incorporate both kinds of data will provide a superior description and interpretation of biological diversity (Moritz & Hillis 1996, Donoghue and Strauss 1988, Donoghue & Sytsma 1988). Congruence between morphological and molecular phylogenies provides strong evidence that an underlying phylogenetic signal has been discovered. For example in a study of the phylogenetic relationships between species of Monanthes (Crassulaceae) the combination of morphological and molecular data resulted in higher resolution of species relationships (Mes et al 1997). Conflict between studies can however indicate that there are theoretical or procedural problems involved in the analysis or that more data is required to elucidate relationships (Hillis 1987). Some researchers have advocated combining data sets of different origins to infer phylogenies (total evidence) whilst others have advocated separate analyses followed by comparative assessment of the results (Johnson & Soltis 1998). Both approaches have merits and disadvantages and in general the adoption of both practices may be advocated to provide a more complete picture of phylogenetic relationships.

Perhaps one of the supreme beneficial uses of molecular data is in comparative morphology where the mapping of morphological characters onto a molecular phylogeny can be used to infer the origin and development of particular features (Mickevich & Weller 1990, Soltis et al 1999, Soltis & Soltis 2000). The mapping of morphological characters onto a molecular phylogeny of Rosaceae has indicated the origin of a particular fruit type (Morgan et al 1994) and the evolution of the double corolla in Clermontia (Campanulaceae) (Albert et al 1998). In particular, mapping of morphological characters has shown that simple changes in gene regulation may have widespread morphological effects (Wendel & Doyle 1998). In addition,

recent higher level classifications using molecular markers have provided large data sets which can now be used as a basis for the investigation of the homology of characteristics such as floral structure and organisation (Soltis et al 1999).

Characters used to determine phylogenies

The classical definition of a character is that it is a diagnostic feature (Grant Inglis 1991). The characters, which are used, are selected on the criteria that they are independent variables whose values are assumed to consist of mutually exclusive character states. In practice the characters utilised are qualitative, presence / absence characters which can be binary (value of 0 or 1) or multistate (0, 1, 2 etc.). In reality there is possibly no such thing as a qualitative character, based on Leibniz's theory of continuity all natural phenomena are related by an unbroken chain of causality (Rieppel 1988). If this is true then the morphological characters that we term qualitative are artificially defined and the perception of discontinuity of character states is an artefact due to missing information (Stevens 1991). The distinction between qualitative and quantitative characters therefore refers to the mode of expression rather than any intrinsic property of the data (Kitching et al 1998). There is an assumption also that the characters are independent and uncorrelated. It is known from morphometric studies that in nature many characters are in fact correlated and that autocorrelations *i.e.* interdependence among variables are frequent (Legendre & Legendre 1998). In such studies characters which are highly correlated have a greater effect on the outcome of an analysis and may bias it in favour of those characters. It is not known what effect the interaction of such characters may have in a phylogenetic analysis and there is no way of testing for character correlations in such instances (Swofford et al 1996). By ignoring the probability of correlations in a data set there is a chance of type 1 error occurring and the wrongful rejection of the null hypothesis that autocorrelations are not present in a group of characters (Forthofer & Lee 1995).

The transformation between character states in an analysis is achieved by the outgroup comparison. By this procedure character states are polarised and are either declared to be plesiomorphic character states or apomorphic character states. When using multistate

characters in a cladistic analysis it is possible to make their transformations unordered or ordered, or in other words one may specify the direction of character transformation. The first cladistic programs (Farris 1970) assumed that character state changes are ordered (Wagner parsimony). Under this criterion transformation between character states that are not immediately connected implied passage through intermediate stages (Kitching et al 1998). It is equally possible to employ unordered character state changes where any state may transform directly to any other state and all changes in character state transformation are equally possible (Fitch parsimony) (Swofford et al 1996). In morphological studies both types of transformations can be employed whilst Fitch parsimony is usually utilised in molecular studies (Williams 1992). In the majority of instances, however, in the analysis of both types of data, unordered character state changes are favoured. If the direction of change is specified then a subjective bias may be introduced into an analysis and use of unordered characters maintains a degree of objectivity.

Maximium Likelihood

Maximum likelihood is used in phylogenetic analysis of molecular data and involves the creation of a probabilistic model of evolution. Under this criterion an evolutionary model is specified and trees are constructed and compared to the model. The tree whose branch lengths correspond most closely to the specified model is then taken as the best estimate of phylogeny. The calculation of branch lengths is therefore important in this technique and one of its basic tenets is that changes are more likely along long branches than short ones (Swofford et al 1996). The problems associated with rate heterogeneity in sequence data, which lead to the underestimation of branch lengths can, therefore, be overcome under the maximum likelihood criterion (Swofford et al 1996). More precise estimations of branch length are achieved by allowing substitution rates to follow a gamma distribution, which means that some sites are assumed to be invariable (under selective constraint) and others are allowed to vary (Sullivan et al 1999). The maximum likelihood model also allows for the calculation of the transition (T $\leftrightarrow$ C, A $\leftrightarrow$ G) and transversion (T $\leftrightarrow$ A, T $\leftrightarrow$ G, C $\leftrightarrow$ A, C $\leftrightarrow$ G) ratio which can again increase the likelihood of discovering correct branch lengths (Yang & Kumar 1996).

One of the difficulties with maximum likelihood is that the number of trees to be compared increases exponentially with the addition of taxa and it can therefore take a prohibitive amount of computing time. In practice this technique is most useful for a small number of taxa where evolution is mediated by small, clearly defined groups of character state transitions whose probabilities may be estimated (Quicke 1995).

Tree searching algorithms in parsimony and Maximum Likelihood analysis

The most popular set of methods which are currently used to construct phylogenies are based on the maximum parsimony optimality criterion (Forey 1992), the results of which are dichotomously branching evolutionary trees or cladograms. There are several different types of search algorithms which can be used in parsimony analysis (which are also employed in maximum likelihood), each of which can be used depending on their suitability for a particular data set. Neighbor Joining is the most commonly used phenetic method and involves measuring phenetic differences between taxa. Phenetic algorithms and maximum likelihood produce a single tree whilst parsimony produces differing numbers of trees depending on the criterion selected.

Exhaustive search

The most comprehensive search, the exhaustive search method, is only generally feasible for situations of ten taxa or less as the procedure involves searching through all of the possible arrangements in order to find the shortest trees (Quicke 1995). One of the really big advantages of this particular method is that it displays the distribution of trees of different length. It is therefore possible to examine the frequency and numbers of suboptimal trees which may in fact provide better phylogenies (Swofford et al 1996). As the number of trees increases exponentially to the number of taxa and the amount of characters the time required for an exhaustive search may be prohibitive.

Branch and Bound search

The branch and bound search looks for all optimal tree solutions. It does so by building trees in a stepwise manner. Under this procedure as taxa are joined together relative tree lengths are calculated. If, at any point, a particular arrangement of taxa exceeds the current minimum tree length it is discounted because the tree length cannot be reduced by the addition of subsequent taxa (Swofford et al 1996). This algorithm which searches for all of the optimal trees is very efficient for about 20 - 25 taxa and possibly more once the data is clearly defined and relatively free of homoplasy (Quicke 1995). Problems arise however when more taxa are added to a data set as bigger data matrices require longer search times and also the chances of convergence between characters increases (Kitching et al 1998).

Heuristic search

In the majority of cases, therefore, with bigger data sets a heuristic search algorithm is used which involves using approximate methods to find optimal trees. Heuristic literally means allowing or assisting to discover and proceeding to a solution by trial and error (Thompson 1996). In cladistic terms this means sampling of a data set in order to find the shortest tree. Unlike the previous methods a heuristic search therefore does not search all possible trees and cannot guarantee finding the most parsimonious solution.

There are two stages in a heuristic search: an initial tree building stage followed by a series of rearrangements to improve or in other words decrease the tree length. The initial or starting trees are obtained by stepwise addition where initially three taxa are selected to form a tree and subsequent taxa are added in a stepwise manner so that only trees of minimal length are saved (Kitching et al 1998). In one of the most commonly used computer packages, Swofford's PAUP (Phylogenetic Analysis Using Parsimony) (Swofford 1999), initial starting trees are obtained by comparing all triplets of taxa and starting with the one which is the shortest length. At each subsequent step all of the other taxa are considered for addition to the tree and the one which provides the most economical solution in terms of tree length is retained. Once the starting trees have been obtained rearrangements of the branches is attempted in order to

try and decrease the tree length further (Swofford et al 1996). There are several different methods of branch rearrangement that can be utilised but Nearest Neighbor Interchange (NNI) and Tree Bisection and Reconnection (TBR) are two of the most commonly employed algorithms. In the first instance branches which lie beside each other are exchanged and rearrangements are possible for interior branches only (Swofford et al 1996). The second method of rearrangement is more comprehensive in that a subtree (a small portion of the original tree) is separated and placed in a different location on the tree in such a way that it may minimise tree length. By this procedure all possible rearrangements of branches are tried, not just Neighboring ones (Kitching et al 1998).

Heuristic searches are employed for larger data sets where exhaustive and branch and bound searches are unfeasible. Generally the TBR rearrangement method is preferred over NNI as it allows for the testing of all possible branch arrangements, although in certain cases when there is a lot of noise in the data it is impracticable and the NNI approach is preferred. As both procedures may ultimately give the same outcome, and when computing time is taken into account the use of NNI is acceptable. The main problem with heuristic search methods is that they may become trapped in local optima. Under this scenario the starting trees which were obtained are not the shortest ones and branch swapping on those trees will never find the optimal solution (Forey 1992). In order to overcome this problem a large number of replicates are included (usually over 1000) in the analysis.

Tree statistics

Once a phylogenetic tree, or a number of trees, have been obtained by one of the above methods there are certain statistics which are attached to the solution to provide information on the quality, reliability and suitability of the data to the analysis. The first statistic which can be obtained for a given tree is its length. This figure is a function of the number of characters in the data matrix and the tree length increases relative to the increase in the number of characters. The production of relatively long trees can be the result of a large number of character state changes and may indicate a lack of congruency between the data and the

analysis. The second category of information which may be attributed to a given tree is the consistency index (CI). This is calculated as CI = m/s where m is the minimum number of character state transformations and s is the actual number of transformations (Siebert 1992). The consistency index is high when there is a lot of congruency between characters in a data set and low when the amount of apparent homoplasy is significant. If there is no homoplasy at all CI = 1 and low values of CI indicate a large amount of incongruence in the data. In morphological data sets CI values between 0.25 - 0.35 are common indicating a high number of unreliable characters. It has been proposed, however, that the distribution of homoplasic characters in a data set may provide some phylogenetic signal (Archie 1989). It has been shown that the CI value is influenced by the number of characters in a data set and should be used cautiously when determining the acceptability of a data set to the parsimony method (Quicke 1995). Another figure which can be calculated for a phylogenetic tree is the retention index (RI). RI = (g-s)/(g-m), where g is equivalent to the greatest number of character state transitions. This means that the RI accounts for the proportion of apparent synapomorphy that can be attributed to homology (Siebert 1992). A high value for RI occurs when the changes occur predominately on internal nodes and low when the changes occur on branches leading to the terminal taxa (Swofford et al 1996). The RI is more reliable for judging the amount of homoplasy in a data set than the CI as it is not sensitive to the size of the data matrix. The final tree statistic which is necessary to the interpretation of a tree is the rescaled consistency index, RC, which the product of the retention index and the consistency index. This final value is possibly the most useful as it takes into account the effect in the different value of g for characters which may otherwise exhibit similar levels of homoplasy. Autapomorphies and totally homoplasic characters are therefore excluded from the calculation, preventing them from artificially increasing the measure of fit (Forey 1992).

Character weighting

In most initial cladistic analysis characters are given equal weight, that is they are all thought to contribute equally to the evolutionary relationships between taxa. Indeed there is one school of thought which says that if characters are equivalent to synapomorphies then weighting will be

philosophically problematic and imply that some synapomorphies are of greater value than others (Siebert 1992). This philosophical dilemma may however be resolved if one thinks that not all character homologies are necessarily recognised in a study and that some characters may not behave in accordance to the rules of parsimony. If one also considers that parsimony analysis will assign more weight naturally to multistate characters (because they contribute more to the length of a tree) then character weighting seems not only acceptable but inevitable (Quicke 1995). In general, therefore, the problem has been seen as not whether to weight but what value and to which characters weights should be assigned. The most obvious kind of weighting that is introduced in a data set is *a priori*; that is, disregarding characters before analysis, effectively giving them a value of zero weight (Fitch 1984). The most objective form of character weighting which is currently employed is a type of *a posteriori* weighting called successive weighting which was first proposed by Fitch in 1969 (Siebert 1992). In this process initial trees of equal length are obtained and then the characters are reweighted based on a measure of there fit on the cladistic tree *i.e.* on the consensus and retention indices or the rescaled consistency index. The reweighting is reiterated until a stable number of trees have been obtained (Eggleton & Vane Wright 1994). In a certain sense character reweighting approaches compatibility or 'clique' analysis which advocates the use of a small number of compatible characters, a 'clique', to estimate phylogenetic relationships between species. The reason for using a small set of characters is that characters which do not reflect evolutionary relationships in a group are likely to be in conflict with those that do, in other words homoplasous characters do not assist in defining evolutionary relationships (Quicke 1995). Up to a point this is true but characters which exhibit some degree of homoplasy may be useful in assessing evolutionary relationships between species. The fact also that certain characters do not conform to parsimony does not necessarily mean that they are not meaningful. Successive weighting may therefore be seen as a compromise between the extremes of no weighting at all and compatibility analysis which uses an extreme form of weighting, that of removing characters altogether. In terms of which type of tree statistic to use in successive weighting there are no hard and fast rules. Of the three most commonly used indices perhaps the rescaled consistency index is the most comprehensive as it is able to assign zero weight to certain

characters, a feature which is not available when using the other indices (Siebert 1992, Kitching et al 1998).

Problems associated with parsimony analysis

Once a phylogenetic tree has been obtained and the tree statistics examined it may become apparent that the data has not performed well under the parsimony criterion. There are several reasons why a parsimony analysis may not reflect the best estimate of a phylogeny. If the number of taxa and characters are large then a heuristic search is the only appropriate method which can be realistically persued. Heuristic searches, may however, be prone to becoming lodged in local optima which do not reveal the most parsimonious trees.

Errors may also be present in the data matrix which are exacerbated in the analysis and generally all types of analyses are subject to both random and systematic error. Random error can occur when there is missing information *i.e.* missing taxa in a given phylogeny. As taxa are added to a data set the random error decreases. The degree of this kind of error present in an analysis cannot be ascertained, as the numbers of unknown taxa in a group cannot be surmised. Systematic error on the other hand can happen when a particular data set is unsuited to the criteria of parsimony *i.e.* that the characters display a lot of apparent homoplasy. This type of error in a phylogeny has been termed "entering the Felsenstein zone" (Swofford et al 1996). In evolutionary reconstructions which have this kind of problem the chances of obtaining a more precise but incorrect phylogeny increases as more taxa are added. It may be difficult to determine to what extent the topology of a given tree may be influenced by systematic error. It tends to be associated however with relatively long branch lengths in a cladogram. When two or more taxa diverge considerably the branches which lead to them undergo extensive substitutions which may display many parallel changes. If changes in tree topologies are associated with the most divergent taxa *i.e.* those which have the longest branch lengths then it may indicate that the result of the analysis is not a true indictor of phylogeny (Williams 1992, Sanderson et al 2000). The use of maximum likelihood has been seen to be more successful than parsimony in estimating phylogenies in which there are unequal substitution rates (Yang

& Kumar 1996, Sullivan et al 1999) and it is also less susceptible to sampling error (Robinson et al 1998). In practice, however, all methods of phylogenetic reconstruction are susceptible to the problem of long branch attraction in divergent groups when sampling is low (Russo et al 1996).

Many assumptions are made in the course of a cladisitc analyses from the first acceptance of the hierarchical, dichotomously branching nature of evolution to the problems associated with parsimony criteria and random and systematic errors therein. Cladistic methods and in particular those which utilise parsimony are however currently among the most consistent methods available for deducing phylogenies.

In general terms all scientific methods may be considered as a system of competing theories each of which can contribute to the explanation of the processes in nature but which also have their specific drawbacks (Rieppel 1988). One of the strengths of cladistics is the fact that in the modern sense of its usage many of its shortcomings are known and it does not claim to reveal the complete truth about evolutionary processes. Rather it offers an estimate of phylogeny which can either be rejected or accepted by a particular group of organisms. In fact, the falsification of a particular theory of evolution may provide a fertile prelude to the considerations of other possible evolutionary scenarios. When Ockham first proposed his parsimony theory he did not claim that it was the truth rather that it provided a comprehensible and repeatable method for evaluating scientific theories.

Phenetic methods for measuring similarity

Phenetics is the study of morphological variation amongst species or OTUs (Operational Taxonomic Units) using a series of mathematical equations (Sneath & Sokal 1973). Unlike cladistics phenetics has never claimed to be able to reconstruct evolutionary history but presents a large number of ways of testing similarity relationships in a data matrix (Patterson 1982). It can also suggest phenetic relationships between groups of species which may be useful in taxonomic classifications. In a phenetic data set all of the characters and character

states are considered to have an equal weight (Wiley 1981) so no potential subjective bias is imposed on the data (except of course in the initial choice of characters to be analysed).

Neighbor Joining (NJ)

The principle of this method is to find combinations of Neighboring taxa sequentially which are chosen so as to minimise total tree length, and this involves divisive pair-wise clustering by star decomposition. As the name indicates star decomposition begins with the connection of all of the taxa at a single internal node, like the spokes of a bicycle wheel (Li 1997). The following description of the procedures involved follows that given by Swofford et al (1996). Initially taxa are joined together so that the length of the first tree is minimised, as in stepwise addition. Further pairs of taxa are considered for addition to the tree on the basis that they do not increase tree length. Each time that a taxon is connected the number of branches at the internal node is decreased by one. The result of the Neighbor Joining process is a single tree, which has both the advantage and disadvantage of providing a single solution for the data matrix. The attraction of the single solution is that the numerous other trees which can be the product of a heuristic search do not have to be considered. This may also be a considerable drawback as a single solution although a neat one does not provide any information on other possible reconstructions. NJ, like step-wise addition is prone to local optima and the chances of obtaining an incorrect tree by this technique are compounded. The most fundamental drawback of both of these procedures is that they proceed directly to a single solution without considering any other alternative solutions (Swofford et al 1996). When the maximum likelihood criterion for estimating branch lengths are employed in NJ they may, however, be more useful in determining relationships between taxa than parsimony. This is particularly true in the case where there are unequal substitution rates in sequence data (Kuhner & Felsenstein 1994).

Testing classifications produced by cladistic and phenetic analyses

A data matrix is assumed to have a structure and in cladistic and phenetic analyses that structure is presumed to be hierarchical. Any random set of data may, by chance, however,

contain a degree of hierarchy. In order to test the hierarchical nature of a matrix it may be necessary to subject it to a test in order to estimate if it does in fact have the structure expected by both analyses (Faith & Cranston 1991). This may be of particular benefit when using a combined data matrix of morphological and molecular characters where the data is from two different sources and will usually exhibit different rates of evolution. One way to test for hierarchy in a given data set is to carry out a permutation test (PTP) which destroys the actual structure of the matrix and compares the results to distributions in a particular set of test matrices. In this procedure character states are firstly randomised with respect to taxa whilst the number of occurrences of the character states remains constant. The results of the randomisation are compared to the test matrices and the null hypothesis that there is no hierarchical structure in a particular data set is either rejected or accepted. If the matrix has a hierarchical structure then it will occur in the extreme 5% of the test distribution (Swofford et al 1996). If it does not there is a probability that the structure of the matrix has occurred by chance. The result of a permutation test is therefore given as a probability; if the probability that the data follows the test distribution is greater than 5% then it may have a random structure and should be analysed with caution.

Bootstrapping

Once a tree or a series of trees has been obtained it is necessary to test if the relationships that are expressed in the phylogeny are true reflections of evolution, or if they have occurred by chance in the analysis. Bootstrapping is a way of testing the internal branch support of a given set of trees and hence the strength of evolutionary relationships (Li 1997). It is basically a resampling technique where characters are sampled randomly from the data set until a new one which contains the original number of characters is obtained. In this way some characters may never be sampled whilst others may be sampled more than once. A large number of such samples are produced and their trees compared. The proportion of such trees that support a given internal branch on a phylogenetic tree is noted (Swofford et al 1996). The bootstrap value is given as a percentage and high percentages will indicate that the relationships between a given group of species is highly supported whilst low percentages indicate that the

relationships may be considered dubious and may have occurred purely by chance. As a general rule a bootstrap value which supports a clade with a value greater than 70% indicates stability in relationships, and hence that a clade has a higher probability of being monophyletic (Olmstead & Palmer 1994).

Characters selected for morphological analysis

The 52 characters which were selected included 21 fruit morphological characters as they are considered crucial under the current generic classification. A minimum number of multistate characters were chosen to minimise the influence they may have on the analysis.

Fruit characters

1. Endocarp smooth/endocarp rough 0/1
2. Mesocarp fleshy/mesocarp pilose 0/1
3. Mesocarp covering entire endocarp/mesocarp not covering entire endocarp 0/1
4. Apical 'tails' absent on the endocarp/apical 'tails' present on the endocarp 0/1
6. Endocarp not spherical/endocarp spherical 0/1
7. Endocarp not elliptic/endocarp elliptic 0/1
8. Endocarp not ovoid/endocarp ovoid 0/1
9. Endocarp not obovoid/endocarp obovoid 0/1
10. Apex of endocarp not apiculate/apex of endocarp apiculate 0/1
11. Base of endocarp not apiculate/base of endocarp apiculate 0/1
12. Apex of endocarp not cuspidate/apex of endocarp cuspidate 0/1
13. Endocarp not lobed/endocarp lobed 0/1
14. Endocarp not angular/endocarp angular 0/1
15. Endocarp not chambered in the upper portion/endocarp chambered in upper 0/1
16. Endocarp not lobed in the upper portion/endocarp lobed in upper 0/1
17. Endocarp not lobed in the middle portion/endocarp lobed in middle 0/1
18. Endocarp not lobed in the base/endocarp lobed in base 0/1
19. Endocarp not chambered in the base/endocarp chambered in base 0/1
20. Transverse chambers not present in the endocarp/transverse chambers present 0/1
21. Endocarp not splitting easily/endocarp splitting easily 0/1

Inflorescence characters

22. Inflorescence pedunculate/inflorescence sessile 0/1
23. No involucral bracts at the apex of the peduncle/involucral bracts at apex 0/1
24. Inflorescence bracts caducous/inflorescence bracts persistent 0/1
25. Flowers not dioecious/flowers dioecious 0/1
26. Inflorescence not monoecious/inflorescence monoecious 0/1

27. Inflorescence not cauliflorous/inflorescence cauliflorous 0/1
28. Inflorescence not racemose/inflorescence racemose 0/1
29. Inflorescence not umbellate/inflorescence umbellate 0/1
30. Inflorescence not sessile/inflorescence sessile 0/1

Vegetative characters

31. Plant not terrestrial climber/plant terrestrial climber 0/1
32. Plant not dendroparasitic/plant dendroparasitic 0/1
33. Plant not leafless/plant leafless 0/1
34. Bark not fissured/bark fissured 0/1
35. Bark not muricate/bark muricate 0/1
36. Bark not papillose/bark papillose 0/1
37. Bark not tuberculate/bark tuberculate 0/1

Floral characters

38. Flowers not pedicellate/flowers pedicellate 0/1
39. Glandular hairs present on inner surface of tepal/glandular hairs absent 0/1
40. Anther dehiscence longitudinal/anther dehiscence transverse 0/1
41. Anther locules equal/anther locules unequal 0/1
42. Stigma lobed (0), entire (1), separate (2)
43. Staminodes present in the female flower/staminodes absent 0/1

Pollen characters

44. Grain spherical/grain elongate 0/1
45. Colpus not constricted/colpus constricted 0/1
46. Pore not distinct/pore distinct 0/1
47. Exine sculpturing not perforate/exine sculpturing perforate 0/1
48. Exine sculpturing not rugulate/exine sculpturing rugulate 0/1
49. Exine sculpturing not echinate/exine sculpturing echinate 0/1
50. Exine sculpturing not microechinate/exine sculpturing microechinate 0/1
51. Grain surface not psilate at polar region/psilate at polar region 0/1
52. Grain surface not psilate along colpi margins/psilate along colpi margins 0/1

Where character states were unknown or inapplicable they were indicated by a question mark. This is a standard procedure which is employed to avoid biasing the results by assuming questionable homologies (Kitching et al 1998). Characters with a large number of inapplicable character states were kept to a minimum as their presence may lead to spurious theories of

character evolution and the generation of multiple, equally most parsimonious trees (Doyle et al 1994).

In the final analysis two of the characters were excluded as uninformative by the statistical package used (PAUP 4.0 Beta 2 (Swofford 1999): character 31 which referred to plants with a climbing habit and character 35 which accounts for those species with muricate bark.

The importance of the concept of homology was exemplified in the assessment of character 4. The presence of apical 'tails' at the apex of the endocarp is a defining characteristic for species of *Dendromyza* and *Cladomyza*. There are two exceptions in other genera where this phenomenon occurs in a single species (*Dendrotrophe amorpha* Stauffer, *Dufrenoya platyphylla* (Sprengel) Stauffer)). In an initial cladistic analysis these species were scored for the presence of apical 'tails' and subsequently appeared within the *Dendromyza/Cladomyza* clade although they differed considerably in other characteristics. A careful re-examination of this character revealed that it has a different origin in *Dendromyza/Cladomyza* compared to *Dendrotrophe* and *Dufrenoya*. In the former case the 'tails' are intimately associated with the internal structure of the endocarp. In the fruits of these species there are long flexible fibres which are free structures in the endocarp, they lie along its inner surface and extend into the basal locules. These fibres extend through narrow openings at the apex of the endocarp to the exterior surface. The 'tails' arise from the apices of these fibres in groups of three. In *Dufrenoya* the longitudinal fibres are present in the endocarp but in this case they do not extend to the outer surface, instead they are connected internally at the apex of the endocarp and are components of the apical chambers of the endocarp. The 'tails' observed are not connected to these fibres but are in fact attached to the outer surface of the endocarp near to but not actually at the apex. A similar situation arises in *Dendrotrophe*. The difference here is that the internal fibres are attached to the inner wall of the endocarp and are hardly distinguishable from it. The 'tails' in the species of *Dendrotrophe* and *Dufrenoya* are therefore not homologous with those of *Dendromyza/Cladomyza*; they are components of the mesocarp rather than the endocarp and have arisen separately in both cases. This is an example of convergent evolution. The

presence of 'tails' on the endocarp is a selectively advantageous feature in species which occupy an aerial habitat most probably they provide an extra anchor for the germinating seedling in such a hostile and precarious environment.

Selection of molecular characters

Different genes and DNA regions evolve at different rates. The plastid genome varies little in size structure and content amongst angiosperm taxa (Olmstead & Palmer 1994) and is often used to determine phylogenetic relationships at the familial and ordinal level. In contrast the nuclear genome is much larger and complex and includes many repeated and non-coding sequences. The advent of PCR technology has enabled the isolation and investigation of rapidly evolving but unambiguously alignable nuclear gene regions for intergeneric and even infraspecific studies (Baldwin et al 1995).

Traditionally ribosomal genes are used as they are present in high copy numbers of hundreds or thousands at the nucleolar organiser region on one or more chromosomes of a haploid set (Bachmann et al 1995) and are therefore easy to isolate. In particular the Internal Transcribed Spacer (ITS) region has favourable attributes for intergeneric and interspecific studies in many taxa due to its conserved length, which means it is easily comparable across species. The fact that it undergoes rapid concerted evolution, which often avoids the sequencing of paralogous genes, is also a considerable advantage (Soltis & Soltis 1998). The ITS region is also quite small (< 700 bp) and is flanked by highly conserved regions which makes it easy to amplify (Baldwin et al 1995). The entire ITS region actually consists of two subregions in the rDNA, the first, ITS1, is between the 18S subunit and the smaller 5.8 subunit and the second ITS2, is between the 5.8 and larger 26S subunit (Baldwin 1992). ITS1 is usually slightly longer, 200-300bp, than ITS2, 200-250bp (Soltis & Soltis 1999) but this does not always hold true (Nickrent et al 1994).

In this study the ITS region was selected for study because of its utility in investigations of intergeneric classifications. The best DNA extractions are obtained from fresh or silica gel-dried

plant material as the DNA will be largely intact. Nearly all of the species in this study are dendroparasitic and therefore inaccessible by routine collecting procedures, they are also generally confined to small geographic areas and are difficult to find. It proved impossible to get fresh or silica-dried gel specimens of any of the plant species except for the outgroup taxa. Herbarium material was therefore used as a source of DNA. The general guidelines for the selection of herbarium material for a molecular analysis is that it has not been treated with alcohol or any other chemicals and that it is free of fungal hyphae and other contamination. This narrows considerably the number of specimens which can be used for analysis. Due to the fact that the DNA can become degraded and fragmented with time and due to exposure to light and chemicals the more recent collections are the most likely ones to contain relatively undegraded DNA. This is not always the case however, and successful isolation of DNA may depend more on the mode of preservation or species specific compounds which effect DNA preservation or hamper PCR amplification (Soltis & Soltis 1999). It is hard to predict whether intact DNA, of sufficient length for sequencing, can be obtained from herbarium material. In this case it was found that shorter regions of DNA (ITS 2) could be amplified successfully from herbarium specimens whereas amplification of the whole region was not possible.

Materials and Methods

Morphological analysis

The discrete character scores were inputted into a data matrix (**Appendix 1**) and analysed using PAUP 4.0 Beta 2 (Swofford 1999). The data was analysed by maximum parsimony using the heuristic search option. Starting trees were obtained by stepwise addition using a random addition sequence with two thousand random repeats. Nearest Neighbor Interchange (NNI) branch swapping was carried out on the trees generated from the stepwise addition process and a single tree was saved at each step. The characters were subsequently reweighted using the rescaled consistency index until the number of trees obtained stabilised. The data was also analysed using Neighbor Joining. Bootstrapping was carried out on the data using two thousand replicates, to test the reliability of the results.

Molecular analysis

Suitable herbarium material was selected and between 0.1 and 0.15 g proved to be the optimal amount of material required for extraction. A slightly larger amount 0.2-0.23 g was obtained from the silica-dried gel outgroup specimens. Total DNA was isolated using the 2 x CTAB method (**Table 6**).

Table 6: CTAB method of DNA extraction from herbarium specimens (modified from Doyle & Doyle 1987)

Preheat pestle and mortar and 5 mls* of 2 x CTAB extraction buffer (in 15ml capped centrifuge tube) to 65°C in a water bath
Weigh out 0.1 – 0.15 g of herbarium material (0.2 – 0.25 g silica gel-dried material)
Grind material in a preheated mortar using a small amount of extraction buffer
Add remaing buffer and grind further until material has disintegrated into a slurry
Pour the buffer-plant mixture back into the centrifuge tube and incubate for 10 min. At 65°C
Add 5mls of CI (24 Chloroform: 1 Isoamyl alcohol), and shake, untighten lid briefly to release gas and then re-tighten
Place on a shaker for 30 min.
Release gas build up once again and centrifuge tubes at 4000 rpm for 10 min.
Transfer the aqueous upper phase which contains the DNA, using a transfer pipette, into a fresh 15 ml tube.
Add equal volumes of `ice-cold isopropanol and invert tube gently to mix
Place sample in freezer for a minimum of three weeks to precipitate the DNA**
Centrifuge tubes at 2000 rpm for 10 min. to pellet the DNA
Decant off supernantant and add 3 mls of 70% ethanol, mix gently
Centrifuge again at 2000 rpm for 10 min.
Decant supernanant and gently place the tube upside down for 5 min. on a paper towel to drain the excess ethanol
Turn the tube the right way up and let the pellet dry in a fume hood for a further hour to remove all traces of ethanol
Resuspend the pellet in 0.5 ml of TE buffer (10mM Tris HCl pH 8.0; 1mM EDTA)
Label a 1.5 ml microcentrifuge tube with permanent marker
Transfer DNA from the 15ml tube into the labelled 1.5 ml tube and store DNA in freezer until use

*Amounts of all chemical were doubled for the silica gel dried material
**For fresh and silica dried gel material this time can be reduced to beween a few hours to a few days.
CTAB buffer = 20g hexadecyltrimethlammanium bromide (CTAB)
140 ml 5M sodium chloride
25 ml 2M Tris HCl, pH 8.0
add H20 until 1L

DNA was further purified using spin columns (**Table 7**). A Polymerase Chain Reaction to amplify the ITS 2 DNA region was carried out (**Table 8**) in a Perkin Elmer 480 DNA thermal cycler using the following primers:

ITS 3: (5' to 3') GCA TCG ATG AAG AAC CGA GC (White *et al*)

AB102: (5'to 3'): TAG AAT TCC CCG GTT CGC TCG CCG TTA (Sun *et al*)

The thermal cycling parameters for both regions comprised 40 cycles, each with a 1 minute denaturing temperature at 97°C, annealing was at 50°C for 2 minutes with extension at 72°C for 3 minutes. The DNA obtained was less than 1 ng/mmol and the amount of template required for the analysis was 6µl which is suitable for herbarium material. Leaving the temperature at

50°C is the optimum annealing temperature for the primers and was necessary to prevent other smaller fragments of DNA and contaminants from being processed during the PCR. The number of cycles for the reaction was optimised at 40 for both the herbarium and the silica dried gel material. The addition of betaine PCR reagent was a crucial breakthrough in producing a successful reaction as it reduces base pair composition dependence on DNA strand melting (Sigma-Aldrich Inc. Missouri).

Table 7: Clean up of DNA samples using spin columns
Following the Concert Rapid PCR Purification System (Life Technologies UK) Preheat 30 mls (per sample) of TE buffer to 65°C Add 400µl of binding solution (HI) to the amplification reaction and mix thoroughly Place a spin cartridge into a 2ml tube. Load samples into the spin cartridge and centrifuge at 12000 g for 1 min Discard the flow through and add 700µl of wash buffer (H2) to the spin cartridge. Centrifuge twice at 12000g for 1 min Place the spin cartridge into a 1.5 ml recovery tube. Add 30µl of warm TE buffer directly to the centre of the spin cartridge. Incubate at room temperature for 1 min and the centrifuge at 12000 g for 2 mins Label the tube with a permanent maker and place samle in the freezer until required

Table 8: Reagents and quatities for PCR reaction master mix (quantities are for each
sample) The order of addition of each reagent should be followed DNA 6 µl (50 ng) PCR buffer 10µl* 20µl of 5M Betaine Water 48.5 µl DNTPs 2 µl (deoxyribonucleotides) (0.1 mM) ITS 3 primer 1.5 µl (150 ng) AB102 primer 1.5 µl (150 ng) MgCl2 10µl (2.5 mM) Taq polymerase in storage buffer** 0.5 µl

* PCR buffer: 10 x 500 mM KCl; 100 mM Tris-HCl (pH 9.0); 1% Trition X-100
** Taq storage buffer: 50mM Tris-HCl (pH 8.0); 100 mM NaCl; 0.1 mM EDTA; 1 mM DTT; 50% glycerol; 1% Triton X-100

Amplified double stranded DNA fragments were subjected to a sequencing reaction (**Table 9**). The sequencing parameters comprised 25 cycles of a rapid thermal ramp to 96°C for 10 sec., a further rapid thermal ramp to 50°C for 5 sec. and a final rapid thermal ramp to 60°C for 4 min. The sequences were then cleaned to remove primers and excess big dye terminators (**Table 10**). Sequencing reactions were run on an ABI 377 automated DNA sequencer at the Royal Botanic Gardens, Kew, UK.

Table 9: Reagents and quantities for DNA sequencing reaction
Perkin Elmer dye deoxy cycle sequence mix 1µl
Sterile deionised water 1.8 µl
Sequence buffer 3.5 µl*
Primer 0.7 µl (5 ng)
PCR product 3 µl (600 ng)

* Sequence buffer: 200 mM Tris; 5 mM MgCl2 pH 9.

Table 10: Clean up of cycle sequencing reaction (quantities are per sample)
Make up a master mix for the required number of samples with 50µl ethanol and 2µl Sodium acetate
Place 52µl of master mix into the required number of 1.5 µl tubes
Add sequnecing reaction mixture to the tubes
Leave for 5 mins at room temperature
Place on ice for 5-10 mins
Spin for 25 mins at 10,000 g
Drain off ethanol onto a tissue
Wash samples with 300µl of 70% ethanol
Spin for 15 mins
Drain off ethanol well onto tissue
Lie sample on its side between two tissues and leave overnight for all ethanol to evaporate and the sample to become completely dry

Data analysis

Sequencing editing and assembly of the complementary DNA strands was carried out using Sequencher 3.1 (Gene Codes Corp Inc. Ann Arbor Michigan). The sequences were transformed into Nexus format and initial alignment was achieved by using the Clustal W 1.6 (Higgins et al 1992) auto alignment program (**Appendix 2**). This software package works on the basis of global alignment by creating an initial tree from the original data, this tree is then used to produce further alignments until the process produces a stable alignment (Hillis et al 1996). A further program, Sequence Alignment Editor (Se-Al) (Rambaut 1998), was then used to improve on the results of the Clustal procedure. Se -Al is useful when working with nucleotide sequences as the different bases ATGC are colour-coded making visual alignment easier. A Blast search was carried out on all of the sequences using the Entrez browser in the National Centre for Biotechnology Information (NCBI) and the nearest matches were angiosperm taxa and algae in the conserved regions at each end of the sequences.

Sequence data for two additional outgroup taxa: *Viscum cruciatum*, seq. ID.: AF 180532 [GI 5924278] Geobotanisches Institut, Zürich, Switzerland and *Korthalsella japonicum*, seq. ID.:

AF 051975.1 [GI 3093827] University of Oklahoma, USA, were obtained from Genbank at the same website (http://www.ncbi.nlm.nih.gov/) (**Appendix 3**).

The data matrix was imported into PAUP and subjected to maximum parsimony analysis using the branch and bound search option. The matrix was subsequently reweighted using the rescaled consistency index and the analysis repeated until the tree length stabilised. The data was also analysed by Neighbor Joining using the Hasegawa, Kishino & Yano (HKY '85) distance measure which allows for unequal base frequencies (Swofford et al 1998), the number of invariable sites was set to 0.25 after examination of the base distributions and the gamma distribution was set to 0.5 to allow for unequal sustitution rates. A gamma distribution of this nature allows for some regions to be highly conserved and others to vary considerably (Sullivan et al 1999). Maximum likelihood was carried out under the same criteria, different frequencies of individual nucleotides were calculated by empirically observed frequencies and the transition/transversion rate ratio was calculated during the analysis. The heuristic search option using TBR swapping algorithm was used to generate the maximum likelihood tree. Bootstrapping was carried out to test the internal support of the resulting trees. Separate analyses were carried out including the sequences obtained from Genbank.

Morphological and molecular data combined

Species from the morphological data matrix which were also present in the molecular data set were combined using the interleave option in PAUP. The interleaved data was subsequently subjected to maximum parsimony analysis using the branch and bound search option. The data was also analysed by the Neighbor Joining. Bootstrapping was carried out to test the internal support of the resulting trees as before.

Results

Morphological analysis

Parsimony results

The heuristic search utilised 49 parsimony informative characters and revealed 36 most parsimonious trees of length 229 steps. The consistency index for the trees was 0.23 whilst the retention index was 0.65. The higher value for RI over CI indicates that the relationships between the genera had been well resolved. The rescaled consistency index was 0.15. The topology of the trees were always very similar as indicated by the 50% majority rule consensus tree. The monophyly of the dendroparasitic taxa was confirmed in this analysis and the ingroup divided into a number of groups that are generally congruent with the current generic classification (**Fig 17**). *Dendrotrophe* is a monophyletic group, and is sister to the other genera. *Dufrenoya* is a sister to the other dendroparasites and *Phacellaria* forms a sister clade to *Dendromyza* and *Cladomyza*. The latter two genera form a well supported monophyletic group with 84% bootstrap support. One species of *Dendromyza*, *Dm. crassifolia* was placed within *Cladomyza* as the nearest relative to *C. angustifolia* with a bootstrap support of 70% for that relationship. The highest bootstrap supports were for the outgroup, 86%, and *Phacellaria* 92%. The support for the separation of *Dufrenoya* from the other dendroparasites had lower bootstrap support (63%). There was resolution within *Dufrenoya* with the separation of those species with entire stigmas, longitudinally dehiscing anthers and echinate pollen grains (*Df. granulata*, *Df. poilanei*, *Df. robusta*, *Df. oresitropha*) from the other species. There was, however, a lack of bootstrap support for this association. The separation of *Dufrenoya* from *Dendromyza* and *Cladomyza* was supported but the separation of the latter two genera did not have support. There was some support for species associations below the generic level in *Dendromyza* and *Cladomyza*: *C. angustifolia* and *Dm. crassifolia* had 70% bootstrap support; *C. kaniensis* and *C. pachydisca* had 82% support. These species are united on the fact they have transverse dehiscing anthers, echinate pollen grains and umbellate male inflorescences. In *Dendromyza* there was 59% support for the *Dm. puberula*, *Dm. multinervis*, *Dm. salomonia* association. These species are morphologically similar as they all have umbellate male inflorescences and elliptical fruits. The association

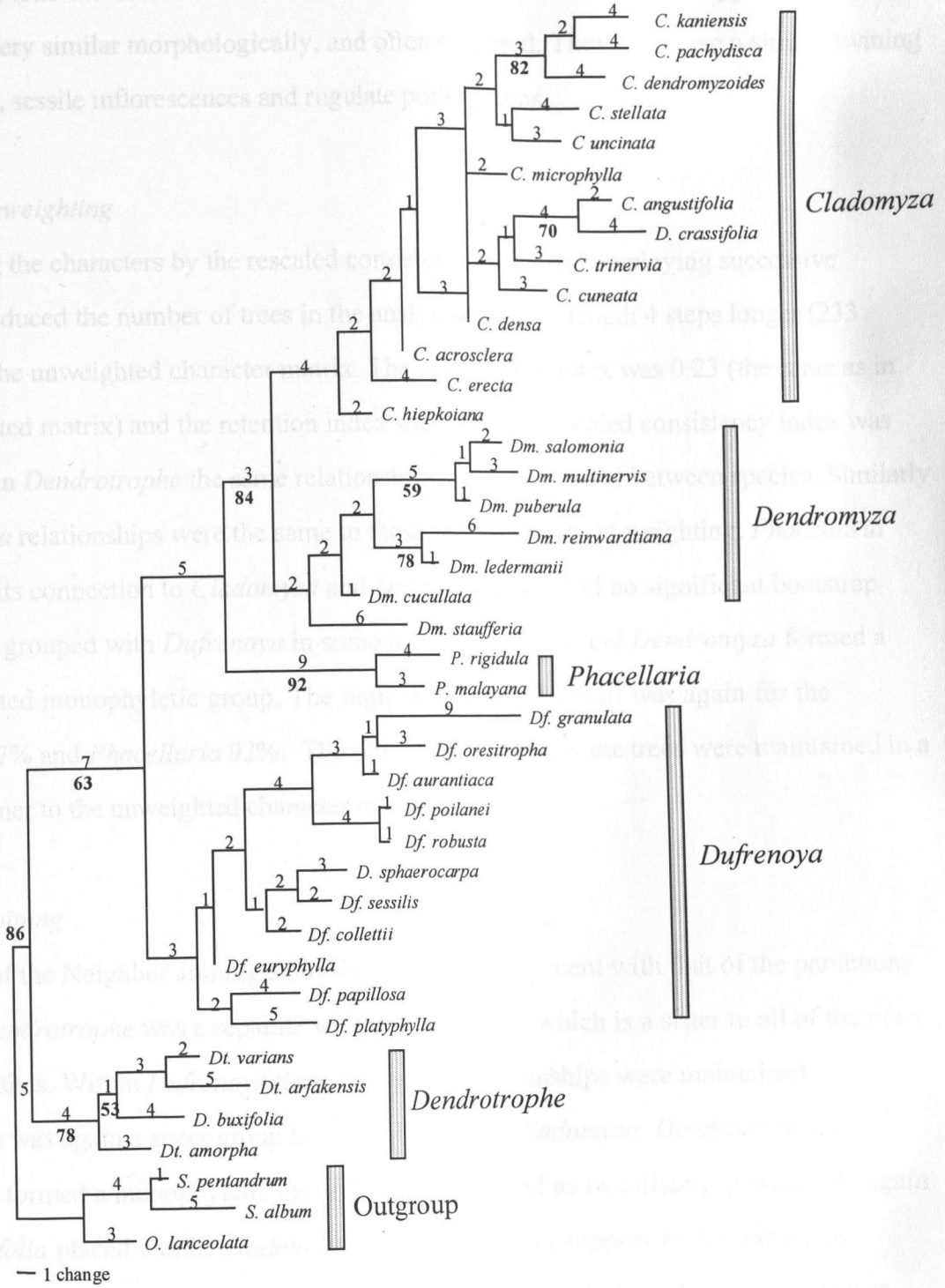


Fig. 17 Parsimony tree of morphological data for Santalacean dendroparasites and outgroup taxa.

One of the 203 maximally parsimonious tree using heuristic search options for 49 morphological characters. Tree length: 229; CI: 0.23; RI: 0.65. Values above branches are steps and bootstrap percentages are indicated in bold below the branches.
Dendrotrophe is sister to the other dendroparasites; *Dufrenoya* is sister to *Phacellaria* and *Dendromyza*. There are long branch lengths associated with *Phacellaria*.

between *Dm. ledermanii* and *Dm. reinwardtiana* received 78% bootstrap support. These two species are very similar morphologically, and often confused. They both have a similar twining growth habit, sessile inflorescences and rugulate pollen grains.

Character reweighting

Reweighting the characters by the rescaled consistency index and employing successive weighting reduced the number of trees in the analysis to 9, of a length 4 steps longer (233 steps) than the unweighted character matrix. The consistency index was 0.23 (the same as in the unweighted matrix) and the retention index was 0.63, the rescaled consistency index was again 0.15. In *Dendrotrophe* the same relationships were maintained between species. Similarly in *Dufrenoya* relationships were the same to those obtained without weighting. *Phacellaria* maintained its connection to *Cladomyza* and *Dendromyza* but had no significant bootstrap support and grouped with *Dufrenoya* in some trees. *Cladomyza* and *Dendromyza* formed a well supported monophyletic group. The highest bootstrap support was again for the outgroup, 87% and *Phacellaria* 92%. The other relationships in the trees were maintained in a similar manner to the unweighted character matrix.

Neighbor Joining

The result of the Neighbor Joining analysis was highly congruent with that of the parsimony analysis. *Dendrotrophe* was a separate well resolved genus which is a sister to all of the other dendroparasites. Within *Dufrenoya* the same species relationships were maintained. *Phacellaria* was again a sister group to *Dendromyza* and *Cladomyza*. *Dendromyza* and *Cladomyza* formed a monophyletic group but also separated as two distinct genera with again *Dm. crassifolia* placed within *Cladomyza*. There was poorer support for the outgroup separation in NJ but this figure is still high at 80%. The monophyly of *Dendrotrophe* was maintained with a 79% bootstrap value. The separation of *Dufrenoya* from the other dendroparasites received just 62% support, which is higher than the parsimony analysis. *Phacellaria* received the highest support for monophyly with a bootstrap percentage 99% (**Fig. 18**).

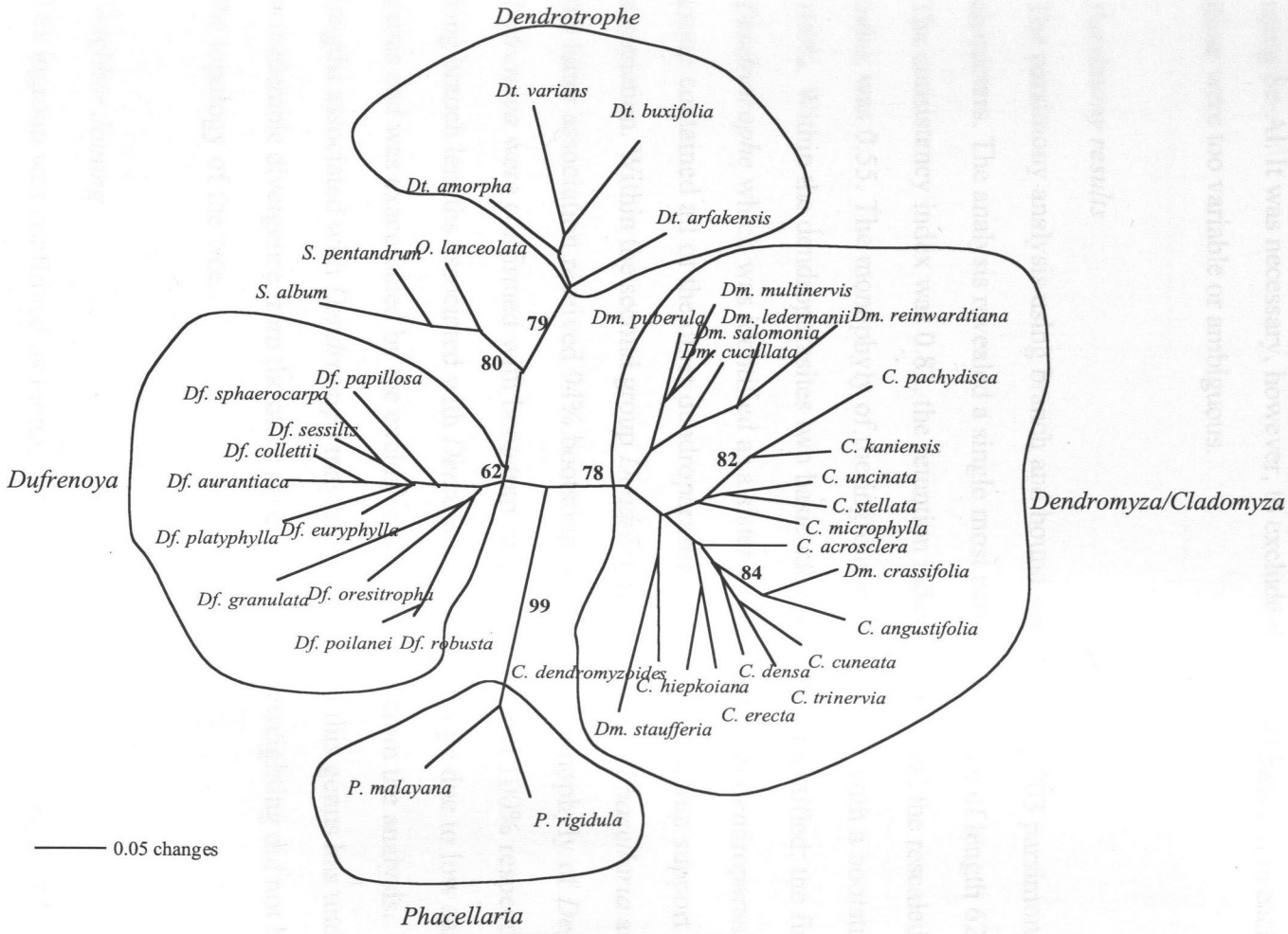


Fig. 18 Neighbour Joining tree of morphological characters for Santalacean dendroparasites

Numbers in bold beside the branches are bootstrap percentages. *Cladomyza* and *Dendromyza* are sisters and there is no support for the separation of these two genera. There is a long branch length associated with *Phacellaria* and it is almost equidistant between *Dufrenoya* and *Dendromyza*. 4 major clades have been identified: *Dendrotrophe*; *Dufrenoya*; *Phacellaria* and *Dendromyza/Cladomyza*.

Molecular analysis

Complete sequences of ITS 2 were obtained for nine taxa, including three outgroup species. An objective alignment was obtained by using Clustal W 1.6 and only minor changes were made using Se-Al. It was necessary, however, to exclude the first 49 bases from each sequence as these were too variable or ambiguous.

Parsimony results

The parsimony analysis using branch and bound search utilised 203 parsimony informative characters. The analysis revealed a single most parsimonious tree of length 621 steps (**Fig. 19**). The consistency index was 0.82, the retention index was 0.66 and the rescaled consistency index was 0.55. The monophyly of the ingroup was confirmed with a bootstrap support of 100%. Within the dendroparasites two basic subgroups were identified: the first contained *Dendrotrophe* which was identified as a sister group to the other dendroparasites. The second group contained all of the other dendroparasites with 97% bootstrap support for that association. Within the second group *Dendromyza* was sister to *Phacellaria* and *Dufrenoya*, the latter association received 94% bootstrap support. The monophyly of *Dendrotrophe* and *Dufrenoya* were confirmed with bootstrap support of 99% and 100% respectively. There were long branch lengths associated with *Dendromyza* which may be due to low sampling for this genus and was exacerbated by the exclusion of *Cladomyza* from the analysis. The long branch lengths associated with *Dendromyza* may also indicate that this genus has undergone considerable divergence from the other genera. Character reweighting did not have any effect on the topology of the tree.

Neighbor Joining

The ingroup was confirmed as monophyletic with 75% bootstrap support for that association. *Dendrotrophe* was sister to the other dendroparasites and there was weaker support for the association between *Dufrenoya*, *Phacellaria* and *Dendromyza* (65%) (**Fig. 20**). There was strong support (70%) for the monophyly of *Dufrenoya*. *Dendromyza* and *Phacellaria* were associated with each other in the tree but were also very divergent from each other, as well as

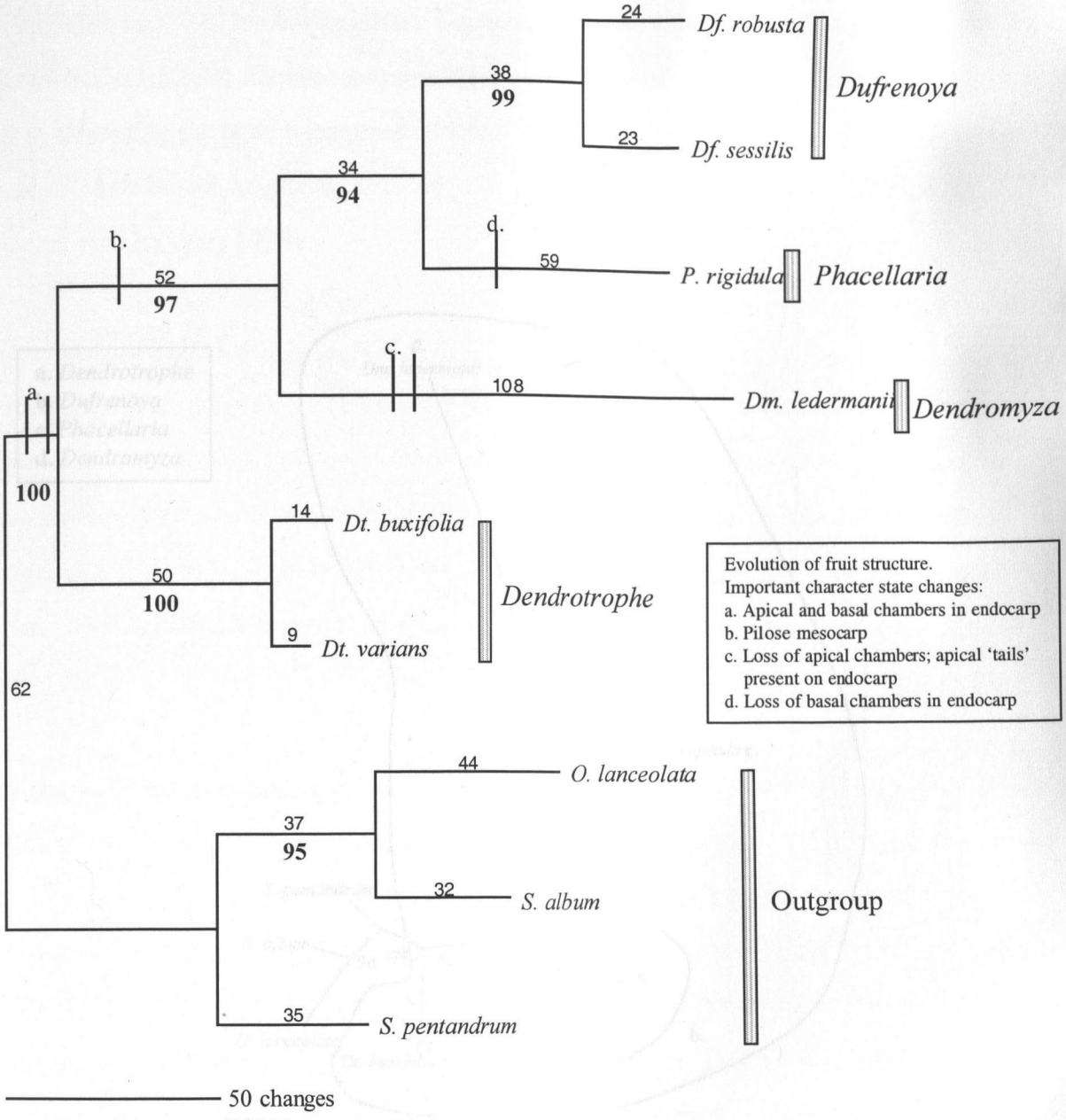


Fig. 19 Parsimony tree of ITS sequence data for Santalacean dendroparasites and outgroup taxa.

Single maximally parsimonious tree using branch and bound search option. Tree length: 621; CI: 0.82; RI: 0.66. Values above branches are steps and bootstrap percentages are indicated in bold below the branches. *Dendrotrophe* is a sister to the other dendroparasites; *Dendromyza* is a sister to *Phacellaria* and *Dufrenoya*. There are long branch lengths associated with *Dendromyza* and *Phacellaria*.

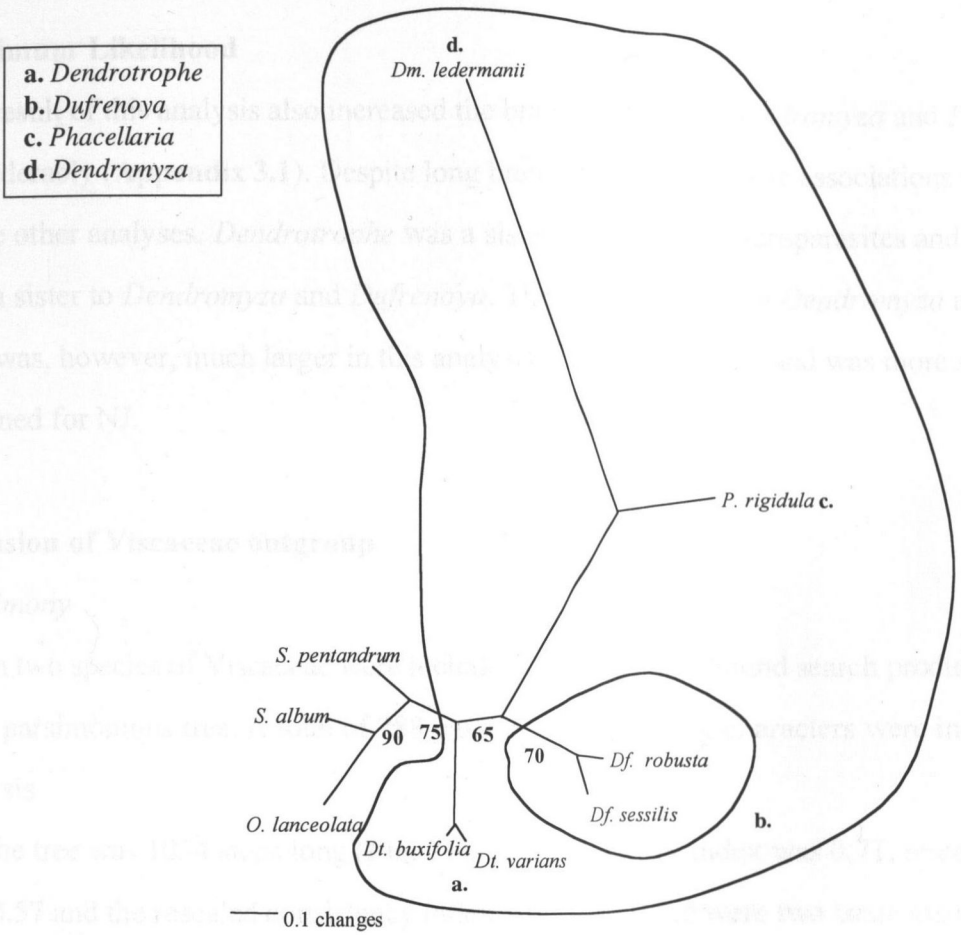


Fig. 20 Neighbour Joining tree of ITS sequence data for Santalacean dendroparasites and outgroup.

Numbers in bold beside the branches are bootstrap percentages. The dendroparasites are identified as a monophyletic group. Other supported groups are *S. pentandrum*, *S. album* and *O. lanceolata*;*Dufrenoya*, *Phacellaria*, *Dendromyza*. There are long branches associated with *Phacellaria* and *Dendromyza* which may be due to undersampling

from the other taxa. The branch length for *Dendromyza* and for *Phacellaria* increased due to the fact that the HKY'85 distance measure allowed for unequal substitution rates and was better at estimating the branch lengths of the individual taxa than parsimony. Parsimony tends to underestimate branch lengths and the longer the branch the more the increase in the error associated with it (Yang 1996).

Maximum Likelihood

The result of this analysis also increased the branch lengths of *Dendromyza* and *Phacellaria* considerably (**Appendix 3.1**). Despite long branch lengths, the basic associations were similar to the other analyses. *Dendrotrophe* was a sister to the other dendroparasites and *Phacellaria* was a sister to *Dendromyza* and *Dufrenoya*. The distance between *Dendromyza* and the other taxa was, however, much larger in this analysis than in parsimony and was more similar to that obtained for NJ.

Inclusion of Viscaceae outgroup

Parsimony

When two species of Viscaceae were included the branch and bound search produced a single most parsimonious tree. A total of 288 parsimony informative characters were included in the analysis

and the tree was 1034 steps long (**Fig. 21**). The consistency index was 0.71, retention index was 0.57 and the rescaled consistency index was 0.45. There were two basic associations within the ingroup: in the first *Dendromyza* was placed as a sister group to *Phacellaria* whilst all of the other species including the 'Santalacean outgroup' were placed closer to each other. Within the latter section *Dufrenoya* was a sister group to *Dendrotrophe* which in turn was sister to the 'Santalacean outgroup' species. The bootstrap values which supported this tree were generally high: there was 100% support for monophyly of the Santalaceae. There was also 100% support for the association of *Dendrotrophe* with the 'Santalacean outgroup'. There was, however, little bootstrap support (55%) for the association between *Dendromyza* and *Phacellaria*.

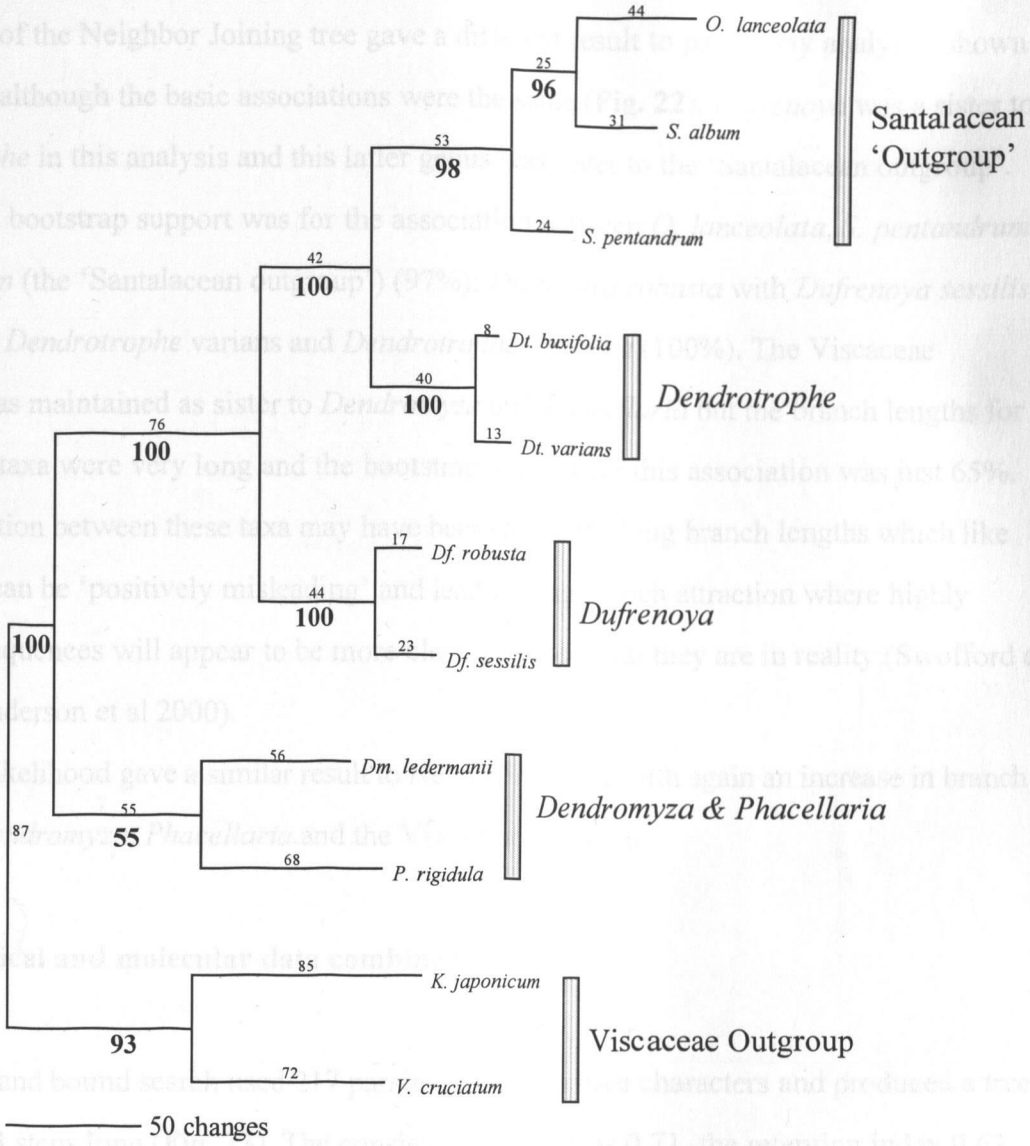


Fig. 21 Parsimony tree of ITS sequence data for Santalaceae and Viscaceae outgroup taxa.

Single maximally parsimonious tree using branch and bound search option. Tree length: 1034; CI: 0.71; RI: 0.57. Values above branches are steps and bootstrap percentages are indicated in bold below the branches. Santalaceae is monophyletic. *Dendromyza* is sister to *Phacellaria*. branch lengths of *Dendromyza*, *Phacellaria* and Viscaceae are all very long indicating that the topology of the tree may be spurious.

Neighbor Joining

The results of the Neighbor Joining tree gave a different result to parsimony analysis (shown in Fig. 21), although the basic associations were the same (**Fig. 22**). *Dufrenoya* was a sister to *Dendrotrophe* in this analysis and this latter genus was sister to the 'Santalacean outgroup'. The highest bootstrap support was for the association between *O. lanceolata*, *S. pentandrum* and *S. album* (the 'Santalacean outgroup') (97%); *Dufrenoya robusta* with *Dufrenoya sessilis* (100%) and *Dendrotrophe* varians and *Dendrotrophe buxifolia* (100%). The Viscaceae outgroup was maintained as sister to *Dendromyza* and *Phacellaria* but the branch lengths for all of these taxa were very long and the bootstrap support for this association was just 65%. The association between these taxa may have been due to the long branch lengths which like parsimony can be 'positively misleading' and lead to long branch attraction where highly divergent sequences will appear to be more closely related than they are in reality (Swofford et al 1996, Sanderson et al 2000).

Maximum likelihood gave a similar result to Neighbor Joining with again an increase in branch length of *Dendromyza*, *Phacellaria* and the Viscaceae outgroup.

Morphological and molecular data combined

Parsimony

The branch and bound search used 217 parsimony informative characters and produced a tree that was 703 steps long (**Fig. 23**). The consistency index was 0.71, the retention index 0.63 and the rescaled consistency index 0.50. The results of this analysis were similar to those of the analysis of strictly molecular characters. *Dendromyza* was a sister to *Dufrenoya* and *Phacellaria*. The distance between *Dendromyza* and *Phacellaria* was hardly increased by the introduction of extra morphological characters but the distance between *Phacellaria* and *Dufrenoya* increased to a greater degree. The monophyly of the dendroparasites was again confirmed by 100% bootstrap support. The other bootstrap values were similar to those obtained by strict molecular analysis.

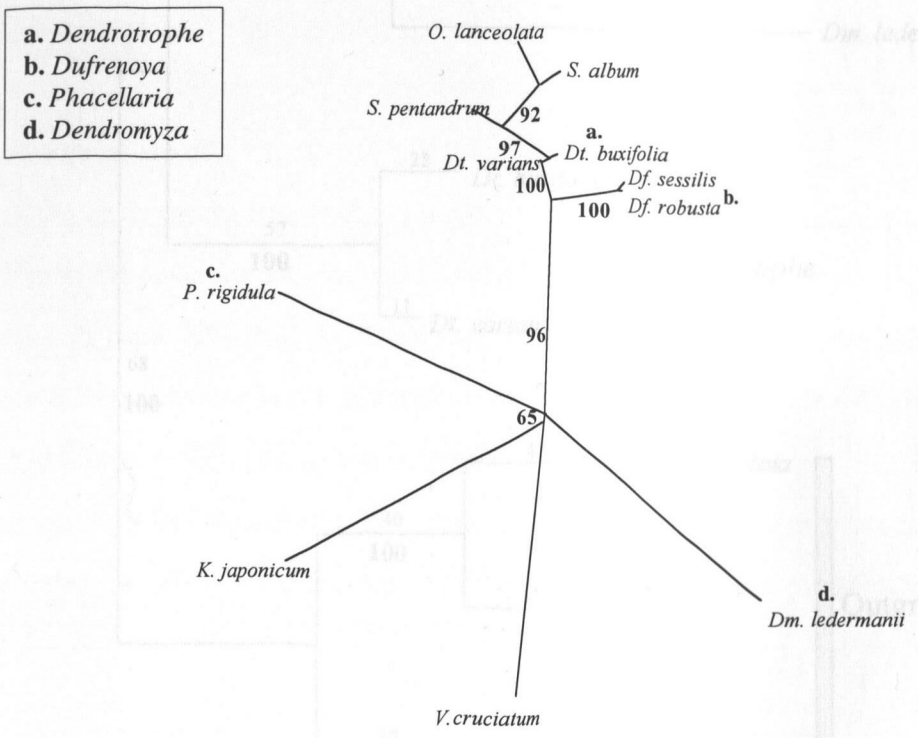


Fig. 22 Neighbour Joining tree of ITS sequence data for Santalaceae and Viscaceae.

Numbers in bold beside the branches are bootstrap percentages. The long branches associated with *Phacellaria*, *Dendromyza* and Viscaceae may be due to undersampling and could be broken up by inclusion of additional taxa.

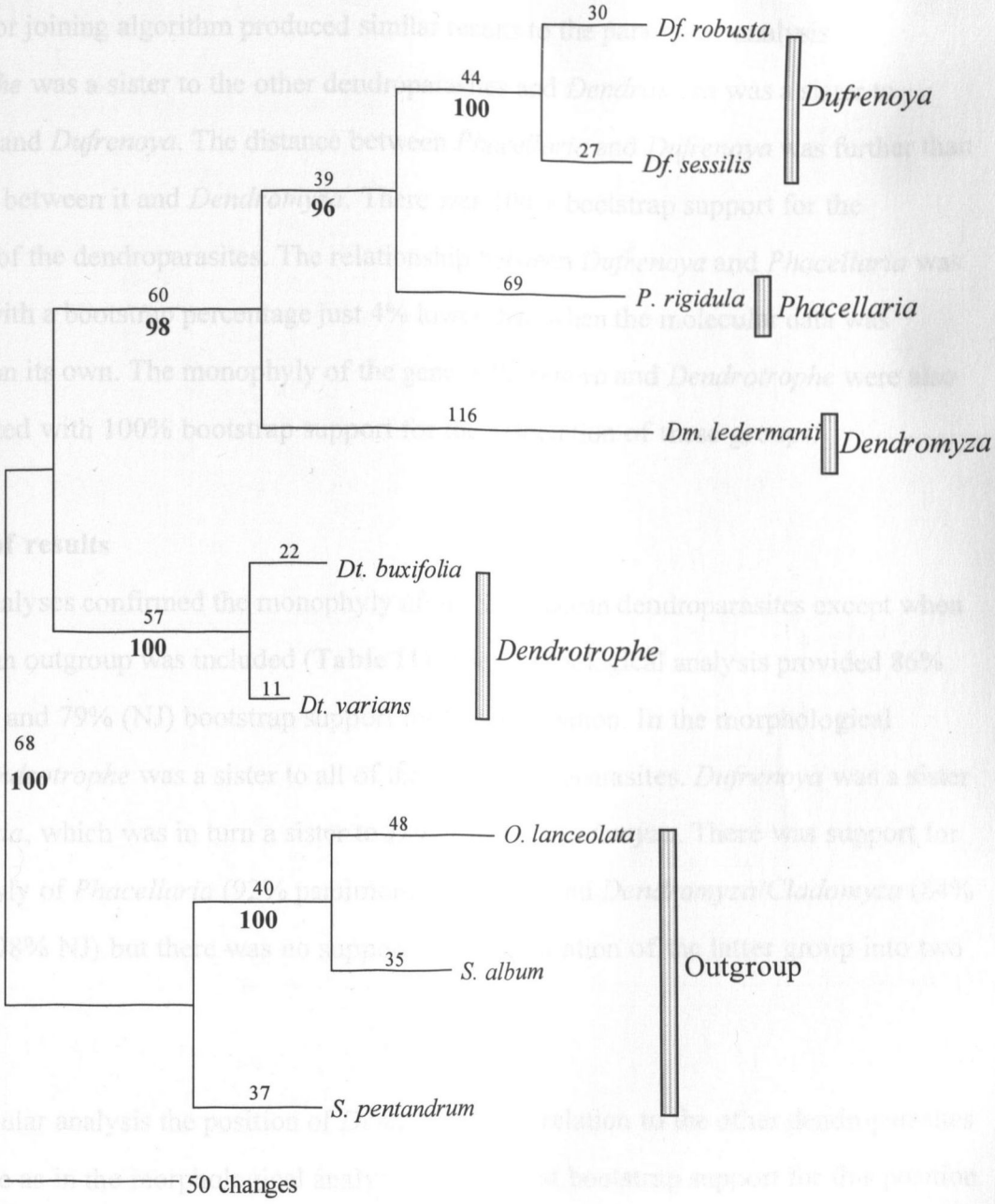


Fig. 23 Parsimony tree of ITS sequence data and morphological characters for Santalacean dendroparasites and outgroup taxa.

Single maximally parsimonious tree using branch and bound search option. Tree length: 703; CI: 0.71; RI: 0.63. Values above branches are steps and bootstrap percentages are indicated in bold below the branches. Addition of morphological characters has no effect on tree topology which is the same as for the strictly molecular analysis. *Dendrotrophe* is sister to all of the other dendroparasites; *Dendromyza* is sister to *Phacellaria* and *Dufrenoya*. Note long branch length for *Dendromyza*.

Neighbor Joining

The Neighbor joining algorithm produced similar results to the parsimony analysis. *Dendrotrophe* was a sister to the other dendroparasites and *Dendromyza* was a sister to *Phacellaria* and *Dufrenoya*. The distance between *Phacellaria* and *Dufrenoya* was further than the distance between it and *Dendromyza*. There was 100% bootstrap support for the monophyly of the dendroparasites. The relationship between *Dufrenoya* and *Phacellaria* was confirmed with a bootstrap percentage just 4% lower than when the molecular data was considered on its own. The monophyly of the genera *Dufrenoya* and *Dendrotrophe* were also well supported with 100% bootstrap support for the association of these groups.

Summary of results

All of the analyses confirmed the monophyly of the Santalacean dendroparasites except when the Viscacean outgroup was included (**Table 11**). The morphological analysis provided 86% (parsimony) and 79% (NJ) bootstrap support for this association. In the morphological analyses *Dendrotrophe* was a sister to all of the other dendroparasites. *Dufrenoya* was a sister to *Phacellaria*, which was in turn a sister to *Dendromyza/Cladomyza*. There was support for the monophyly of *Phacellaria* (92% parsimony; 99% NJ) and *Dendromyza/Cladomyza* (84% parsimony, 78% NJ) but there was no support for the separation of the latter group into two genera.

In the molecular analysis the position of *Dendrotrophe* in relation to the other dendroparasites was the same as in the morphological analysis. The highest bootstrap support for this position was obtained by parsimony (100%) but the value obtained by NJ (75%) was also high. The difference between the morphological and molecular results was that in parsimony analysis of the DNA matrix *Dendromyza* was a sister to *Phacellaria* which was in turn a sister to *Dufrenoya* (94%) and this latter genus was the most derived group. There were some inconsistencies in the molecular analysis, however, between parsimony and NJ. In NJ *Dendrotrophe* was sister to *Dufrenoya* (65%) (like morphological analysis) and *Phacellaria* was a sister to *Dendromyza*, although there was little support for this association.

Table 11 Summary of results of phylogenetic analyses for Santalacean dendroparasites using morphological and molecular characters. The morphological analysis suggests a derived position of the genus *Dendromyza* and the majority of the analyses postulate *Phacellaria* as a sister to this group. Molecular analysis differs slightly by suggesting the most derived position for *Dufrenoya*. All analyses confirm the basal position of *Dendrotrophe*. Below is a summary of the main relationships for each analysis.

Analysis	Data Matrix		
	Morphology	Molecular	Addition of Viscaceae
Parsimony	Monophyly of dendroparasites 86% bootstrap. *Dendrotrophe* sister to *Dufrenoya* and *Phacellaria* sister to *Dendromyza* (84% support).	Monophyly of dendroparasites 100% bootstrap. *Dendrotrophe* sister to *Dendromyza* and *Phacellaria* sister to *Dufrenoya* (99% support).	Monophyly of Santalaceae 100% bootstrap. *Dendrotrophe* sister to *Dufrenoya* *Phacellaria* sister to *Dendromyza* (55% support).
Neighbour Joining	Monophyly of dendroparasites 79% bootstrap. *Dendrotrophe* sister to *Dufrenoya* and *Phacellaria* sister to *Dendromyza* (78% support).	Monophyly of dendroparasites 75% bootstrap. *Dendrotrophe* sister to *Dufrenoya* *Phacellaria* sister to *Dendromyza**.	Dendroparasites monophyletic but poor support (65% support) for this hypothesis. *Dendrotrophe* sister to *Dufrenoya* (96% support) *Phacellaria* sister to *Dendromyza**.

Constant relationships: *Dendrotrophe* as basal to other dendroparasites (all); *Dendrotrophe* sister to *Dufrenoya* morphology; molecular NJ, addition of Viscaceae parsimony and NJ; *Phacellaria* sister to *Dendromyza* (morphology NJ, molecular NJ, Addition of Viscaceae parsimony and NJ)
* long branches and no internal support for relationships.

The addition of the Viscaceae outgroup produced a similar result in both parsimony and NJ. The difference between this analysis and the others was that *Dendrotrophe* was placed as sister to the Santalacean species which had been considered as outgroup taxa in the previous analyses and *Dendromyza* and *Phacellaria* became sister taxa to the Viscaceae outgroup. A common theme throughout all of the analyses of molecular characters (and to a certain extent in the morphological character analysis) was the long branch lengths associated with *Dendromyza* and *Phacellaria*. *Dendromyza* was very divergent from the other taxa an in particular NJ and maximum likelihood increased the branch length of this taxa. This is because simplistic models like parsimony tend to underestimate branch lengths whereas the distance measure used in NJ (HKY '85) and maximum likelihood give a more precise measure of branch lengths. These models can, however, experience the same problems as parsimony in the misplacement of taxa with long branch lengths. This may explain why *Dendromyza* and *Phacellaria* were placed near the base of the evolutionary trees in all the analyses. Addition of more taxa would help to resolve this problem by breaking up the lineages (Robinson et al 1998).

Discussion

Morphological analysis

The parsimony analysis defined four or five basic groups, which generally correspond to the current classification system of Danser (1940). *Dendrotrophe*, *Dufrenoya* and *Phacellaria*, are all clearly defined monophyletic groups. (**Fig. 17**).

Dendrotrophe

Dendrotrophe is basal and appears a sister to all of the other dendroparasites in both the morphological and molecular analyses. This is not surprising based on its geographic distribution, which extends from southern China to New Guinea, and the fact that species are either climbers or dendroparasites. Below the genus level there was no particular separation based on geographic area although it does appear that there is a close relationship between *Dt. varians* and *Dt. arfakensis*. This relationship is borne out by fruit morphology and growth habit. The latter species was originally named as a variety of *Dt. varians* but the parsimony

analysis confirmed that it warrants a separate species status. The position of *Dt. amorpha* as basal within the group in the parsimony analysis had not been expected. As its name suggests this species contains many features which are atypical for the genus: it is a true dendroparasite, has an umbellate male inflorescence and echinate pollen grains. Its position therefore may be attributed to a convergent evolutionary history with the other stem parasites where this type of inflorescence structure and pollen morphology is more common.

Dendromyza and *Cladomyza*

Within the group of true dendroparasites *Dendromyza* was a sister to *Cladomyza*. Both of these genera have a centre of diversity in New Guinea but one species of *Dendromyza* is widespread in eastern Malesia and can be found as far west as the Malay Peninsula. This would suggest that perhaps this group originated on the coastal region of northern Australia and spread through the eastern islands of the Philippines into western Malesia. One species of *Dendromyza*, *Dm. crassifolia*, appears as a close sister to *C. angustifolia* and this relationship is supported by a high bootstrap value, indicating that boundaries between the two genera are unstable. Morphologically both groups are also very similar and in terms of floral morphology it is impossible to draw a division between the two genera. Fruit morphological characters have been traditionally used to distinguish *Dendromyza* from *Cladomyza*, but again there appears to be a gradual transition from chambered to unilocular fruits. On strictly morphological grounds, therefore, it does not seem possible to maintain the genera as separate entities. In this analysis there was also no bootstrap support for the separation of *Dendromyza* from *Cladomyza*, which points to the possibility that the genera may in fact be artificial constructs, and would be better combined as a monophyletic group. The pattern of association between the genera was also found with reweighting, when another species of *Cladomyza* joined with the *Dendromyza* clade.

Phacellaria

Phacellaria was placed as a sister group to the *Dendromyza/Cladomyza* clade and to *Dufrenoya*. The grouping of *Phacellaria* as a separate genus is supported by a high bootstrap

value suggesting that it forms a strong monophyletic group. Its relationship to the other dendroparasites has not been well resolved and it changed position in relation to the other genera as either sister to both *Dendromyza/Cladomyza* or as a basal group within the true dendroparasites. Based on morphological features there is a suggestion that genus is a derived group within the stem parasites. This is borne out by the fact that leaves are reduced to scales, it has high host specificity and exhibits a degree of endophytic growth. In terms of fruit structure and geographic distribution it is most similar to *Dufrenoya* but due to the reduction in inflorescence size and floral organs it lacks several of the features which can be found in this genus. The long branch lengths which are associated with this genus indicates that it has evolved a lot of unique characteristics compared to the other genera.

Dufrenoya

Dufrenoya appeared to form a clear monophyletic group, although the bootstrap support for this association is low, and it is basal to *Phacellaria*, *Dendromyza* and *Cladomyza*. This genus consists of a group of closely related species which are generally confined to montane evergreen forest with the greatest species diversity in the montane regions of Vietnam. Within the genus there was separation of species which have a particular floral morphology. Theses species *Df. poilanei*, *Df. granulata*, *Df. robusta* all have entire stigmas, lack both post staminal hairs and staminodes and have echinate pollen grains. They are also generally associated with the montane regions of northern Vietnam and Bhutan and form a unique group within *Dufrenoya*.

Molecular analysis

The molecular analysis was carried out on a small subset of taxa but there was a certain amount of congruency with the morphological analysis (**Fig. 19**). The trees obtained were much longer but this was due to the four-fold increase in the number of characters. The strong bootstrap support values for many of the clades in the parsimony analysis helped to define the groups, although the problems of long branch attractions could mean that this support was positively misleading. From this analysis the position of *Dendrotrophe* in relation to the other

dendroparasites was well resolved, it is phylogenetically basal to the other ingroup taxa reflecting the results of the morphological analysis. The parsimony analysis of molecular data also indicated that *Dendromyza* was sister to the other dendroparasites, which is in conflict to the morphological analysis where it is the most derived group. *Dendromyza* had, however, much longer branch lengths associated with it than the other taxa. Long branches indicate many changes occurring in a single lineage so as the number of those changes increases those which can be attributed to homoplasy also has a chance of increasing. It is known that the presence of long branch lengths can lead to spurious results and the misplacement of taxa (Wendel & Doyle 1998, Williams 1992). The placing of this group as basal to the other stem parasites, therefore, may have been because it does not fit very well on the tree. With parsimony, in particular, taxa with long branches will tend to be placed near the base of a tree. Sanderson et al (2000) found a similar problem in an investigation of the phylogeny of seed plants. In this study long branch lengths associated with Gnetales meant that it was incorrectly placed at the base of the phylogenetic tree near to ferns. The position of *Dendromyza* in relation to the other taxa is, therefore, best observed in the NJ analysis where the long branch lengths show clearly that it is very divergent from *Dufrenoya* and *Dendrotrophe*. The long branch lengths associated with *Dendromyza* may have occurred for two reasons. Firstly, there could certainly be an element of random error involved. In an earlier section it has been explained that random error can occur due to undersampling. In this case only one species out of a potential twenty one (if *Cladomyza* is included) was successfully sequenced. If other taxa were added to the analysis the genetic distance between this group and the other genera may be lessened (Robinson et al 1998). On the other hand this group is of eastern Malesian origin, most likely originating on the northern coast of Australia which is now part of New Guinea (Hall 1998). It has therefore been geographically isolated from the other genera for a considerable time and has accumulated many unique genetic differences.

The position of *Phacellaria* also changed between the morphological and molecular analyses. In the parsimony analysis of molecular characters where it was placed it as a sister group to *Dufrenoya*. If the branch lengths between *Phacellaria* and *Dufrenoya* and *Phacellaria* and

Dendromyza are examined, however, it seems that *Phacellaria* is almost equidistant between the two. NJ confirmed the divergent nature of *Phacellaria* and this analysis also places it closer to *Dendromyza*. The long branch lengths associated with this genus may help explain why its position was unstable in both the morphological and molecular parsimony analysis. Like *Dendromyza*, the random error explanation may be involved. If however the group itself is considered there may be another reason for the separate nature of this genus. As pointed out in the morphological analysis, all the species of *Phacellaria* have undergone reductions in terms of vegetative and reproductive characters and it is also the most specialised in terms of host preferences and growth habit. It may be, therefore, that it has evolved and accumulated a high number of genetic differences compared to the other genera. If true, this would also explain why *Phacellaria* is unstable in the morphological analysis, being too distinct from the other taxa.

The inference that *Phacellaria* is a sister to *Dufrenoya* complies with geographic distribution patterns. Both of these genera occur in western Malesia and occupy similar habitats, although the range of *Phacellaria* is narrower than that of *Dufrenoya*. Morphological analysis suggested a derived position for *Phacellaria* but the parsimony analysis of molecular characters did not. This may have more to with the limitations of parsimony which has difficulty in placing species with long branches. The NJ analysis (which accounts for unequal rates of character evolution) of the same data matrix demonstrated that this genus is quite divergent from *Dufrenoya* and has a closer association with *Dendromyza* but long branch length attraction may be responsible for that association.

Due to the uncertainty of the placement of both *Dendromyza* and *Phacellaria* in the molecular analyses it is difficult to draw any conclusions about their phylogenetic position based on these data. In general, however, the analysis of molecular characters does indicate strong support for the monophyly of *Dufrenoya* which was missing from the morphological analysis and it also confirmed that *Dendrotrophe* is a sister to all of the other dendroparasites except when Viscaceae was added as an outgroup.

Combined morphology and molecular analysis

When the morphological data was combined with the sequence data the relationships between the genera were reinforced. In particular the distance between *Phacellaria* and *Dendromyza* was not increased substantially (**Fig. 23**). *Dendromyza* appeared, however, to be even more divergent from the other taxa based on the combined analysis, giving weight to the fact that the progenitors of this species may have become isolated from the other dendroparasites for some considerable time.

Effect of addition of Viscaceae outgroup

A new outgroup consisting of two species of Viscaceae, *Korthalsella japonicum* and *Viscum cruciatum*, was introduced into the molecular analysis. The Viscaceae is a group of highly specialised stem parasites which have been traditionally placed as a genus within the Loranthaceae (Mabberley 1997, Heywood 1998). Recent molecular evidence based on a combined analysis of 18S rDNA and plastid rbcL has shown that the Viscaceae is a distinct family which has arisen from an element within the Santalaceae, with the Santalacean dendroparasites as its most obvious progenitors (Nickrent et al 1998).

The inclusion of this outgroup led to some changes in tree topology in the parsimony and NJ analysis and resulted in the 'Santalacean outgroup' forming a monophyletic sister group to *Dendrotrophe*, effectively including it as part of the ingroup. An examination of the unrooted NJ tree elucidated this relationship further (**Fig. 22**). It appears that the Viscaceae taxa plus *Dendromyza* and *Phacellaria* have very long branch lengths which meant that they came out together and forced the remaining taxa together. The NJ analysis also indicated a relationship between Viscaceae, *Dendromyza* and *Phacellaria*. The low bootstrap support for this association, the star-shaped nature of the NJ tree plus problems associated with the presence of taxa with long and short branch lengths indicates that this is a spurious relationship (Russo et al 1996). It still seems quite possible that the Viscaceae have arisen from within the Santalacean dendroparasites but based on this analysis it is not possible to determine exactly

where the closest alliance lies. The inclusion of more taxa and outgroups to break up the lineages would certainly assist in elucidating the relationship between the Viscaceae and the Santalacean dendroparasites further.

Mapping morphological characters onto the molecular tree

The fact that so few taxa were included in the molecular analysis means that tracing the evolution of morphological characters may only be done in the most general way. The fact that the relationships between the taxa are generally consistent with the morphological analysis means that general trends in terms of the evolution of morphological characteristics can be proposed.

The evolution of fruit structure

Based on the molecular and morphological analysis it appears that the possession of a fleshy mesocarp is the ancestral condition in this group. In *Dendromyza* it becomes reduced and is replaced by the apical 'tails' on the endocarp (**Fig. 19**, **15**). It is possible that the origin of a pilose mesocarp stems from *Dufrenoya*. The fact that this became reduced again in *Dendromyza* and later regained means that several reversals in this characteristic may have occurred to give the pilose condition which is observed in some species of *Dendromyza/Cladomyza*. The presence of this type of mesocarp, however, can certainly be thought of as a derived condition.

The presence of chambers in the endocarp is also a character which appears to have undergone some degree of change throughout the different lineages. It appears that the plesiomorphic character state is the possession of both apical and basal chambers, which is the condition in *Dendrotrophe* (**Fig. 19**, **16.1**, **16.2**). The presence of both apical and basal chambers also appears to be the pleisiomorphic state in *Dufrenoya* where the derived condition is the absence of basal chambers. In *Phacellaria* the basal chambers have also been lost. In *Dendromyza/Cladomyza*, species can either lack basal and apical chambers or have basal chambers only, and based on the morphological analysis it appears that the latter condition is

the derived state. It appears, therefore, that the ancestral condition has given rise to the variety of structures which can be observed in all of the other genera (**Fig. 19**).

If it is postulated that an ancestor of *Dendrotrophe* gave rise to two separate lineages, one in eastern Malesia (*Dendromyza/Cladomyza*) and another in western Malesia (*Dufrenoya* and *Phacellaria*), then the situation may be simplified. The condition that is observed in species of *Dufrenoya* which lack basal chambers in the endocarp is a derived one and is similar to that observed in *Phacellaria*. The other lineage in eastern Malesia gave rise to the condition that is observable in *Dendromyza/Cladomyza*. The long branch lengths which separate *Dendromyza* from the other genera suggests that it has accumulated a lot of genetic differences and would also suggest that it has been isolated from the western Malesian taxa for a long time.

Character distribution and evolution

The low bootstrap values obtained from the morphological analyses reflect the instability of the groupings and homoplasy in the data set. At least nine of the characters have more than five character state changes on any tree and two characters account for ten steps each. The characters, which contribute most to the length of the tree, are not confined to a single suite. In terms of fruit structure, as demonstrated from mapping characters on to the molecular tree, there are many instances of reversals and possible convergences. The presence of basal chambers in the endocarp has previously been considered important in generic delimitation and it is thought to have high phylogenetic significance, this analysis indicates that it is not a stable character. Another character, the ease with which the endocarp disintegrates, clearly may have an adaptive value. In order that a seedling may become established quickly on a host it should not have a hard outer covering. A thin walled endocarp which splits open easily could raise the fitness of a species in the harsh aerial environment by allowing rapid germination. This character may have arisen several times in response to selective environmental pressures.

In terms of floral structure the presence of post staminal hairs can be considered as a character which exhibits a high degree of homoplasy. The presence of such hairs is usually considered a

diagnostic character for the family. These hairs, which emanate from the inner surface of the tepals, emit an oily fluid, which has been thought to act as an attractant to pollinators (Aronne et al 1993). Therefore, the presence of such hairs may have an adaptive significance in attracting certain insect species to the flowers. Species that lack such hairs usually have echinate pollen grains indicating they may attract different types of pollinators and have developed a different type of pollination strategy. The diversification in pollen morphology may therefore act as a mechanism of reinforcing reproductive isolation between species.

The *Dendromyza/Cladomyza* group contributes the most to the number of character state changes on the tree. This group contains the largest number of species and possesses the greatest variability in terms of both pollen and fruit morphology. They have a centre of diversity in New Guinea and are confined to the high mountainous areas of this region. The upland areas in New Guinea have emerged quite recently (c. 14 Ma) (Hall 1998, Morley 2000) and this coupled with the rapid character evolution in this group may indicate that the species have undergone a rapid and recent radiation. It may be postulated that this group is at a relatively 'young' stage of evolution and have radiated only recently.

The concentration of species in New Guinea and their morphological diversity opens the debate on the circumstances which lead to speciation. There are several theories that can be invoked on methods of speciation. In general the theories first involve isolation either geographically or ecologically of populations with subsequent differentiation, both genetic and morphological. In the final stage of speciation there is actual reproductive isolation where if the original populations come into contact again they will not be able to interbreed or if they do their offspring will have a poor fitness (Judd et al 1999). The most common type of isolation which leads to speciation is termed peripatric speciation where small local populations at the edge of a species range become isolated from the rest of the species range (Judd et al 1999). In general although physically isolating mechanisms are important in the speciation process it is the development of reproductive isolating mechanisms which maintain species integrity (Minelli 1993).

In general, controversy arises in regard to what actually causes morphological and genetic differentiation to occur. In Darwinian terms natural selection drives speciation. In other words speciation is controlled externally by environmental conditions (Ridley 1996). An explanation of the high levels of homoplasy evident in the morphological characters of the Santalacean dendroparasites may be due to the highly selective nature of the aerial habitat. It is clear that certain characteristics may be of a higher selective value in such an environment. In terms of fruit structure the possession of apical 'tails' on the endocarp and the presence of a pilose mesocarp seem to be important in the establishment of the young plants.

Although natural selection is obviously an important part of the speciation process, random genetic drift has a vital role in the differentiation of populations. This involves the accumulation of essentially neutral genetic mutations which may spread throughout a population. The mutations may not have a selective value in the short term but they may have a major impact in the long term (Briggs & Walters 1997). This neutral theory of speciation is based on the idea that internal mechanisms in an organism, which are not influenced by environmental conditions, control speciation processes. Therefore any characters, which appear to have a selective value, have arisen purely by chance.

The shift balance or adaptive topography theory of Wright presents a compromise between the extremes of these two evolutionary theories. In this scenario random genetic drift has a role to play in encouraging genes to explore the terrain around them. As this happens, natural selection acts in tandem by fixing gene frequencies which have arisen through random genetic drift, which infer a selective advantage (Ridley 1996). It is logical that both random drift and natural selection have roles to play in the speciation process. Especially in small isolated populations where the gene pool is small mutations may accumulate rapidly. If the environment is also physically harsh or extreme natural selection may also have a greater role to play in selecting the fittest individuals for that particular habitat. This may be seen as a circular process in small populations where random genetic drift occurs within a limited range

of genetic variability, natural selection then comes into play selecting those individuals who are best adapted to the environment. As selection continues the gene pool decreases and random genetic drift increases driving the speciation process.

In New Guinea the terrain is very variable and populations can easily become isolated in the high mountain ranges. This coupled to the extreme environment *Dendromyza* and *Cladomyza* inhabit and the dispersal mechanisms which they operate may have a greater role to play in the convergent evolution which seems to be a common theme throughout the parsimony reconstruction. Certainly many of the species in these genera are locally abundant and are concentrated in small geographic areas. Their poor dispersibility and the fragmentation of the environment which they inhabit effectively isolates populations from Neighboring ones so random genetic drift may become important in character evolution. All of the taxa are descended from a common ancestor and therefore in theory at least they all have access to a common gene pool (Nickrent et al 1994). In species with small, isolated populations it is easier for traits to become fixed than in larger, widespread species where there is a continuous exchange of genetic information. This appears to be shown by the almost random distribution of characters in the phylogenetic reconstruction.

Evolution of Inflorescence structure

Inflorescence morphology is a distinctive characteristic of many Santalaceae genera. Investigation of South American and African species has indicated that the inflorescence is an important component of generic delimitation (Stauffer 1961) but the evolutionary implications of the distribution of inflorescence types has not been considered for any group. The inflorescence structure of the dendroparasitic genera has not been studied in any great detail except for *Phacellaria* (Danser 1939) and no intergeneric comparisons have been made.

In the Santalacean dendroparasites there is dimorphism in terms of inflorescence morphology in that the female inflorescence is uniformly one-flowered and either solitary or in groups of two to three. This basic construction is reflected in many of the Australian species, which have

hermaphrodite flowers. The male inflorescence, however, exhibits a degree of diversity. Male inflorescence morphology may be used to define certain if not all genera with either a racemose, umbellate or sessile inflorescence. In the parsimony analysis of the morphological and molecular data *Dendrotrophe* appears to be basal to all of the other genera. The male inflorescence of this genus is quite variable; in *Dt. varians* and *Dt. arfakensis* it consists of terminal and axial determinate racemes but in *Dt. amorpha* the inflorescence is umbellate, which may be a derived condition. Perhaps the most interesting species in this group is *Dt. buxifolia* where the male inflorescence is paniculate, the rachis has a single terminal flower and side shoots, from which flower buds emerge. Each of the side shoots is surrounded at the base by an involucre of bracts and has the capacity to repeat the structure of the main axis. Based on the phylogenetic reconstruction it appears therefore that the racemose inflorescence is the basic unit of inflorescence that has led to the other forms. This contrasts with the situation in the Loranthaceae where the reverse situation has been postulated, with the single flowered inflorescence as the ancestral condition (Kuijt 1981).

It is possible to derive the various inflorescence types of this group from *Dendrotrophe* (**Fig. 24**) and particularly *Dt. buxifolia*. If the main axis of the panicle is compressed then a situation like that in *Dm. ledermanii* may be achieved: a single flower surrounded by an involucre of bracts with a flower bud then developing in the axil of each bract each of which is also surrounded by an involucre of bracteoles. Reduction in the bracteoles would give rise to an inflorescence similar to that of the *C. microphylla* and reducing the number of flowers to one would lead to the situation in *Dm. reinwardtiana*. In *Dendromyza/Cladomyza*, however, the pattern is still unclear, as it appears that many reversals have taken place with the subsequent loss and gain of floral bracts and flowers. The sessile inflorescence of *Phacellaria* is however strikingly similar in many respects to the *Dendromyza/Cladomyza* group, and in particular to those inflorescence which have multiple bracts and bracteoles. The difference is that in *Phacellaria* the inflorescences are truly sessile and can spread along the stems by the repetition of the basic inflorescence structure. This is made possible by the leafless nature of the species but in *Dendromyza/Cladomyza* this type of inflorescence expansion is not possible and is

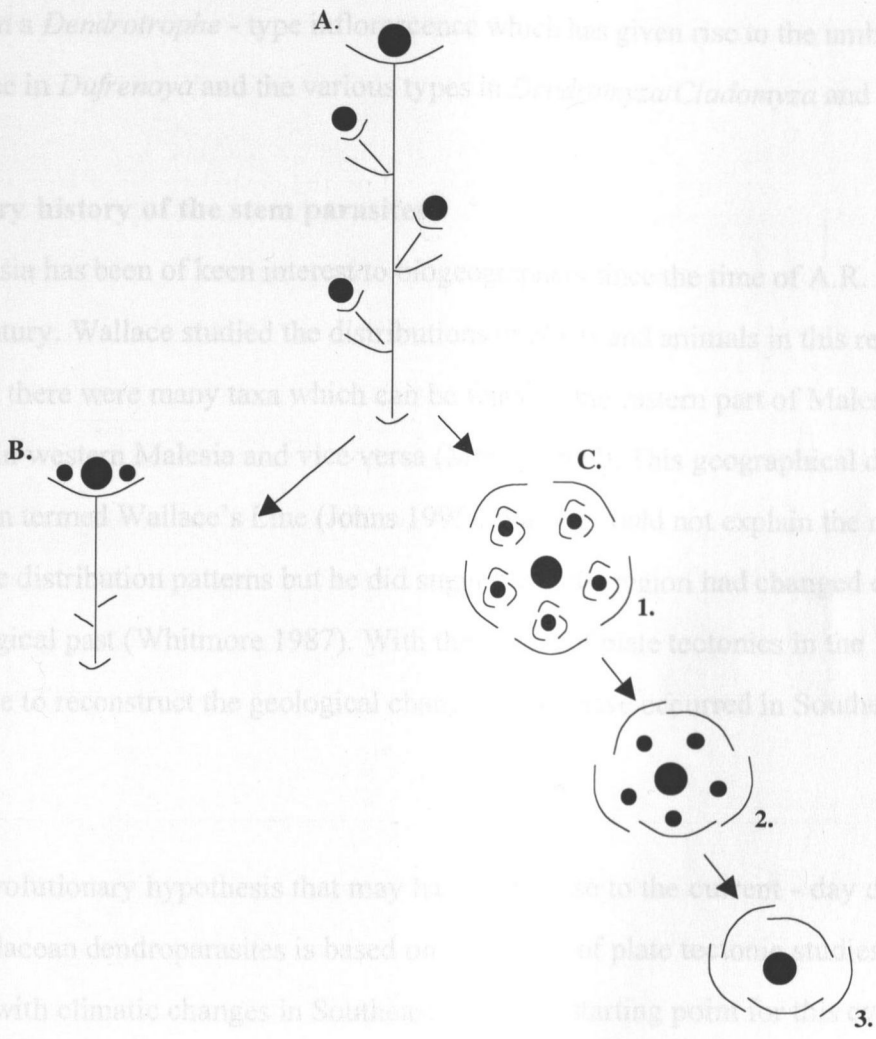


Fig. 24 Diagrammatic representations of inflorescence structure in the aerial members of the Santalaceae. **A.** the inflorescence of *Dendrotrophe buxifolia* is paniculate and it is possible to derive all of the other inflorescence types from this scheme. **B.** the inflorescence of *Dufrenoya* is umbellate and the axial flowers are each subtended by a single bract. **C.** The various inflorescence types of *Dendromyza* as viewed looking down on them. **1.** Is similar to that observed in *Dendromyza ledermanii*; **2.** Is similar to *Cladomyza microphylla* and **3.** resembles *Dendromyza reinwardtiana.* The inflorescences of *Dendromyza sp.* are generally sub sessile but in some cases they may be shortly pedunculate and in that case they are superficially similar to *Dufrenoya.* In addition the inflorescences of *Phacellaria sp.* are strikingly similar to *Dendromyza*, particularly **C.1.**

constrained by leaf phyllotaxy. The similarities between the inflorescence structure of *Phacellaria* and *Dendromyza/Cladomyza* may suggest a closer relationship between them, which was suggested by fruit morphology.

In summary the basic male inflorescence structure in the dendroparasitic species seem to be derived from a *Dendrotrophe* - type inflorescence which has given rise to the umbellate inflorescence in *Dufrenoya* and the various types in *Dendromyza/Cladomyza* and *Phacellaria*.

Evolutionary history of the stem parasites

Southeast Asia has been of keen interest to biogeographers since the time of A.R. Wallace in the 19th century. Wallace studied the distributions of plants and animals in this region and realised that there were many taxa which can be found in the eastern part of Malesia which are not present in western Malesia and vice versa (Morley 1998). This geographical division of taxa has been termed Wallace's Line (Johns 1995). Wallace could not explain the reason for these strange distribution patterns but he did suggest that the region had changed dramatically in the geological past (Whitmore 1987). With the advent of plate tectonics in the 1960s it has been possible to reconstruct the geological changes which have occurred in Southeast Asia (Hall 1998).

The basic evolutionary hypothesis that may have given rise to the current - day distributions of the Santalacean dendroparasites is based on the results of plate tectonic studies and its association with climatic changes in Southeast Asia. The starting point for this evolutionary hypothesis is the origin of an ancestral taxon on the Gondwanan landmass. Palynological evidence has suggested that the Santalaceae originated on the continent of Australia and subsequently migrated to other areas (Truswell et al 1987). This is however a biased scenario perhaps resulting from the relatively large number of palynological samples of Australian origin. As late as the tertiary Australia was part of the Gondwanan landmass and migration routes along the southern shores of the Tethys sea would have allowed for the exchange of taxa between Australia and the rest of Gondwana (Morley 1998). Molecular and morphological

evidence from this study suggests that the basal group within the Santalacean dendroparasites is *Dendrotrophe*. The current distribution of this genus is widespread with one species *Dt. varians*, occurring throughout southeast Asia from southern China to Australia, a single species distributed from southern China to Borneo whilst another two species are rare endemics in the Vogelkop of New Guinea. If an ancestor of *Dendrotrophe* is the progenitor of the other stem parasites then it seems most likely that this species was widespread throughout eastern Gondwana during the tertiary.

India separated from Gondwana and collided with Eurasia approximately 50 Ma (Barlow 1981, Whitmore 1998). This event is probably the most important incident in the floristic history of the region and explains the current floristic diversity and species richness (Hall 1998) of the area. The pre-collision flora of the Indian subcontinent contained an African, an ancient Gondwanan and elements of the Australian floras. It now seems likely that an ancestral form of *Dendrotrophe* was contained within this eclectic mix of taxa. Due to the favorable climatic conditions which ensued in the time after the collision there was widespread dispersal of the Gondwanan flora into Sundaland which consisted of continental Southeast Asia and the islands of the Malay archipelago as far as the southern arm of Sulawesi (Morley 1998).

Dendrotrophe

The ancestral *Dendrotrophe* taxon presumably migrated with the Gondwanan flora into Southeast Asia and spread throughout the region. The species of this group have low host specificity and are common in disturbed secondary vegetation indicating high adaptability. There is also considerable morphological variability in the current day taxa of this group which contains shrubs, lianas and a single dendroparasitic member. My suggestion is that possibly an ancestral lineage similar to *Dt. varians* was widespread through eastern Gondwana in the tertiary and evolved into all of the present day dendroparasites. This is supported by the molecular evidence and also by the current distribution of *Dendrotrophe*. This species traveled to Southeast Asia on the Indian microcontinent and subsequently spread throughout the area.

The distribution of the genus in western and eastern Malesia suggests that they differentiated post separation of Australia from Gondwana.

Dufrenoya

Widespread elevated areas were a common feature of the cretaceous and early tertiary landscape of Southeast Asia (Morley 2000). Mountain building, which was a consequence of the collision of India with Eurasia, led to changes in climate and the creation of new habitats and *Pinus* savannah was a common feature at the time, indicative of cooler temperatures (Whitmore 1998). The mountain ranges provided the main dispersal route for northern temperate taxa from Asia via the Malay Peninsula (Whitmore 1987, Morley 1998). It seems likely that *Dufrenoya* evolved in this environment. The present day distribution of this genus is from southern India and northern Vietnam to west Borneo. It is found in association with what are generally recognised as northern temperate taxa such as *Quercus* and *Castanopsis*, in the high montane evergreen forests of those regions. The distribution of *Dufrenoya* can therefore be explained by migration in tandem with those species into Southeast Asia.

Dendromyza/Cladomyza

Australia separated from Gondwana at the same time as India and moved northwards, also at approximately the same rate (Hall 1998). From molecular evidence it is probable that the *Dendromyza/Cladomyza* species assemblage was derived from the *Dendrotrophe* stock which was stranded in the northern part of the Australian continent which collided with northern New Guinea in the Miocene (Duffels & De Boer 1990, Polhemus & Polhemus 1998). The large genetic distance between this group and *Dufrenoya* could also be explained in these terms. If *Dendromyza* arose separately from an ancient *Dendrotrophe* stock in New Guinea then it has been separated from the western Southeast Asian taxa for some considerable time. It had been assumed that Australia has remained isolated from the time of its separation from Gondwana to the present day but in fact approximately 25 Ma New Guinea, which was part of northern Australia, collided with the leading edge of the Philippines, Halmahera arc system. This docking of New Guinea provided a dispersal route to the east for the Sundanian flora and to

the west for the Australian flora (Hall 1998). The molecular evidence does not suggest that *Dendromyza* was part of the Sundanian flora which became stranded in southern Sulawesi which subsequently migrated into New Guinea after the opening of the Makassar strait between Sulawesi and Borneo. The genetic distances between it and the other taxa are too great to suggest that they have diverged in recent geological times. The present day distribution of *Dendromyza/Cladomyza* is centered on New Guinea. Just one species, *Dm. reinwardtiana*, is found as far as the southern most point of the Malay Peninsula and southern Philippine islands. It may be possible that *Dm. reinwardtiana* migrated into the Philippines and subsequently into the rest of western Malesia at this time, which would explain the east-west distribution pattern of this species.

Many of the islands of eastern Indonesia including Irian Jaya and eastern Sulawesi may be relatively young with uplift taking place only in the middle Miocene, approximately 15 Ma (Barlow 1983, Truswell et al 1987). The increase in upland areas provided a variety of habitats and it is possible that the radiation of *Dendromyza/Cladomyza* began at this stage. The extreme variability in terms of morphological characteristics of this group could be therefore explained by a recent speciation events subsequent to isolation following mountain building in New Guinea (van Welzen 1995). Higher speciation rates for this group may also be explained by sea level changes which occurred at intervals throughout the last 14 Ma. The changes in sea level and associated temperature difference means that during colder conditions species will have migrated down mountain sides and then expanded back up during warmer conditions (Ridder-Numan 1995, 1998). It is possible that populations became stranded in different locations during cold spells following warmer periods of high sea levels, and genetic drift within those isolated populations led to speciation. During glacial maxima sea levels may have been lower by 180 m compared to the present, due to the fact that much water was trapped in the extended polar ice caps (Whitmore 1998). The submergence and recolonisation of continental shelves by populations of different genetic make up during periods of fluctuating sea levels (Morley 2000) may also have added to the increased divergence of this group from the other genera. The presence of *Dm. reinwardtiana* in northern Australia can be explained by the

expansion of tropical forests in Australia approximately 8000 Ya and the migration of species into that area from New Guinea and the rainforest refugia of Queensland (Barlow 1981, Johns 1995).

Phacellaria

In the morphological analysis *Phacellaria* was derived from an element within *Dufrenoya*. It was placed as a sister to *Dendromyza/Cladomyza*, but its position did change quite considerably from one analysis to another. The molecular parsimony analysis indicated a stronger relationship with *Dufrenoya* but the genetic distance between the two genera was large (**Fig. 19**) and it may have been misplaced due to long branch lengths as explained before. When the Viscaceae outgroup was included in the molecular analysis *Phacellaria* was found to be more closely associated with *Dendromyza*, although the support for this relationship was not strong (**Fig. 21**). *Phacellaria* and *Dendromyza* differ quite considerably in terms of fruit morphology and geographic distribution. If the molecular parsimony analysis is to be accepted, however, *Phacellaria* is derived from a common ancestor to *Dendromyza/Cladomyza*, which was possibly introduced into Southeast Asia after the mid-Miocene collision of Australia with the Philippines and Sulawesi. If this is true then an ancestor of this genus must have dispersed into the Malay Peninsula and subsequently Thailand and China via the Philippines and Borneo.

The current distribution of this species is in the montane evergreen forests of continental Southeast Asia. It occupies almost the same habitat as *Dufrenoya* but has a more restricted distribution than this genus. Both genera are also very similar in terms of fruit structure and this was reflected in both the morphological and molecular parsimony analysis. *Phacellaria* is, however, more host specific and favours mainly Loranthaceae and occasionally some species of *Dufrenoya*. Therefore, *Phacellaria* may in fact be derived from a common ancestor of *Dufrenoya*. The narrower geographical range of *Phacellaria* reflects more specific host requirements within the mountain ranges of western Southeast Asia. The distribution pattern of *Phacellaria* suggests conclusively that, like *Dufrenoya*, it is tracking the distribution of

certain host taxa and the lack of bootstrap support for the relationship between the two genera, despite their morphological similarity, may be due to a convergent evolution based on habitat preferences. The evidence suggests that *Phacellaria* is related to *Dufrenoya* but the morphological analysis and the genetic difference between the two also suggests a relationship to *Dendromyza/Cladomyza*.

Conclusions

The Santalacean dendroparasites are a group of highly specialised plants which show varying degrees of host specificity. Due to the constraints and selection pressures, which ensue from their aerial habitat, it was suspected that convergent evolution would play an important role in the phylogeny of the species. It has been shown that in other parasitic plants that convergences are extremely common and that rates of molecular evolution are high (Nickrent & Starr 1994, Wolfe & de Pamphilis 1998) relative to non-parasitic species. The morphological analysis indicated that the distribution of character states was highly variable on the evolutionary tree, the variability in DNA sequences and associated long branches indicated that the genera have undergone a high degree of molecular divergence. The high rates of divergence can be attributed to selectivity of highly specialised habitats, as a consequence of random genetic drift which is increased in small isolated populations and the acquirement of novel morphological adaptations which can lead to rapid diversification (Wendel & Doyle 1998). Rate acceleration in genetic evolution has not been demonstrated for any members of the Santalaceae to date (Nickrent et al 1998) but it has been demonstrated for the closely related Viscaceae (Nickrent et al 1994). This study may therefore be the first example of increased evolutionary rates in the Santalaceae.

In general the distribution of fruit and inflorescence characteristics were unstable in the analysis but certain trends in construction have been identified along with an evolutionary hypothesis of inflorescence construction. It has been ascertained that *Dendrotrophe* is likely to represent the basal genus to all the other stem parasites based on both morphological and molecular analysis. It is postulated that an ancestor of *Dt. varians* was widespread throughout

eastern Gondwana during the tertiary and subsequently migrated into South East Asia. All of the other dendroparasites are of Southeast Asian or Australian origin.

The analysis of molecular characters demonstrated that there were long branch lengths associated with both *Phacellaria* and *Dendromyza*, which meant that relationships between these two genera could not be reliably elucidated, but the NJ analysis of molecular characters gave a similar pattern to the morphological analysis. Inclusion of more taxa to the molecular analysis would help, in particular, to solve the relationship of *Phacellaria* to the other dendroparasites.

The close relationship between *Dendromyza* and *Cladomyza* has indicated that their generic boundaries may be artificial constructs and the two genera should be combined. Fruit morphology and biogeographical evidence also reinforces this.

In conclusion phylogenetic analysis indicates that the Santalacean mistletoes form a monophyletic group. Comparison between morphological and molecular analyses indicate that *Dendrotrophe* is a sister to *Dufrenoya*, *Phacellaria*, *Dendromyza* and *Cladomyza* and the latter two genera should be combined. The long branch lengths associated with *Phacellaria* and *Dendromyza/Cladomyza* indicate accelerated molecular evolution combined with undersampling. Further work is required to fully resolve the relationship of *Phacellaria* to the other dendroparasites and to discover the closest relative to the Viscaceae.

Infraspecific Variation in *Dendrotrophe varians* (Bl.) Miq.

Introduction

The majority of Southeast Asian Santalaceae are confined to narrow geographical ranges in mountainous regions. The species are often associated with particular habitats and many of the aerial parasites have quite specific host associations (**Chapter 5**). Genera are also generally confined to either western or eastern Southeast Asia and few species are known to cross the deep waters between Borneo and Sulawesi. This is particularly evident within the dendroparasites of tribe Amphorogyneae. Two of the genera are restricted to continental Southeast Asia with some extension as far as northern Borneo and one other is of eastern Malesian affinity. The remaining genus, *Dendrotrophe* Miq., which can be included with this group, has a very widespread distribution from southern China to Australia. In particular one species *Dendrotrophe varians* (Bl.) Miq. occurs across the entire geographic range of the genus.

Dendrotrophe was first described by Blume under the name *Henslowia* in 1850. The species were distinguished on the basis of leaf shape, the presence or absence of inflorescence bracts and fruit shape. As further species were described additional vegetative characteristics such as petiole length, peduncle and pedicel length were deemed to be important distinguishing specific characteristics. Throughout the taxonomic history of the genus, however, it was acknowledged the species were closely allied and usually difficult to distinguish (Champion 1853, Hooker 1886, Danser 1940). By the middle of the 20th Century a total of 14 species of *Dendrotrophe* had been described; the consensus being that the genus contained up to 20 species some of which were undescribed (Gamble 1912, Pilger 1935). Some of these were described in isolation for example from South Australia or the Nicobar Islands (Kurz 1879, Smith 1951). In addition as the plants are dioecious it was not uncommon that new species were named from either male or female plants. This, along with the misinterpretation of vegetative and reproductive structures (Champion 1853, Smith 1951), compounded the proliferation of new species names.

Almost all of the species which were described were characterised by a climbing or terrestrial growth habit, relatively large leaves and a racemose male inflorescence. Many of the characteristics which were used to describe the numerous species were based on unreliable

vegetative characteristics such as leaf size, consistency and colour. Reproductive characters were based on quantitatively varying attributes rather than qualitative differences. Hooker in the Flora of British India (1886) stated that the characters which were used to describe the species "are utterly insufficient and from imperfect specimens. I am at a loss to identify the Indian satisfactorily from the Archipelagan species". **Table 12** outlines the diagnostic characteristics which were traditionally used to identify the species. Although many authors agreed on the close relationship between the component members of *Dendrotrophe* a critical evaluation of the group did not take place until the 1960s. At this point twelve of the species

Table 12: Characters used to historically to discriminate between species of *Dendrotrophe*. Up until the mid 20th century it was considered that there were approximately 20 species in the genus all of which were based on mainly size differences in vegetative and inflorescence characteristics.

Diagnostic character	Authority
Leaf shape	Blume 1850; Miquel 1856; A. De Candolle 1857 Lecomte 1914; Pilger 1935
Leaf texture	Gamble 1912
Leaf colour	Hooker 1886; Hemsley 1891
Number of primary veins	Gamble 1912; Stauffer 1969
Proinence of secondary veins	Gamble 1912; Lecomte 1914
Petiole length	Hooker 1886
Inflorescence bracts present/absent	Blume 1850; Miquel 1856
Inflorescence umbellate or racemose	Miquel 1856; Hooker 1886; Lecomte 1914
Peduncle length	Gamble 1912
Size of flowers	Hooker 1886
Length of pedicel	Hemsley 1891; Lecomte 1914
Fruit size	Blume 1850; A. De Candolle 1857; Gamble 1912
Fruit shape	Blume 1850; Miquel 1856; A. De Candolle 1857 Hooker 1886
Surface sculpture of the endocarp	A. De Candolle 1857

were designated as synonyms of *Dt. varians*, a further two were retained as separate species and several varieties were described (Stauffer 1969). The combination of the majority of species under *Dt. varians* has resulted in its very widespread present-day distribution.

Dendrotrophe varians as currently defined, unlike many other Santalaceae, is represented by a very substantial collection of herbarium material. Examination of that material revealed that although there was indeed continuous variation within the species a certain amount of regional differentiation could be detected. There were indications of the existence of an Indochinese element with larger elliptic fruits and narrowly elliptical leaves whilst individuals in Borneo appeared to have smaller fruits and broader leaves. Within the species fruit shape varies from spherical to elliptical and obovoidal. The same variability is expressed in leaf shape which may be elliptic, obovate or orbicular with the number of primary veins ranging from 3 – 5 – 7 – 9. The range of infraspecific variation coupled with the association between geographic location and plant form required further investigation. The presence of a large number specimens in the herbarium also provided an ideal opportunity to test the current classification.

The use of phenetic techniques involving the examination of quantitative characters seemed to offer the widest range of statistical analyses which are suitable for the investigation of infraspecific variation. They have been used extensively in studies of within species variation in other plant groups (Marholt 1992, Neuffer & Hurka 1999, Selvi 1998, Neuffer & Hoffrogge 2000). The choice of characters to be utilised in this analysis was based on the traditional characteristics which had been used historically to describe species. Further new characters were also added to the data matrix and also some categorical characters were selected.

Morphometric theory

Morphometrics or phenetics encompasses a suite of statistical analyses which can be used to group individuals based on estimates of overall morphological similarity (Siebert 1992). The techniques all focus on the idea that measurements of individuals can be used to group them into taxa and essentially each individual member of a group is more similar to other members of that group than to any individual of another (Kent & Coker 1992). The techniques all involve the use of mathematical equations which aim to take large and complex data sets of measurements and simplify them so that patterns of variation within and between groups of

taxa can be easily illustrated and statistically tested. One of the premises of morphometrics is that the more measurements of an object or individual are made the better it can be described (Sneath & Sokal 1973). That the shape of an organism can be characterised by a set of measurement variables is implicit in the theory of morphometric analysis. In the absence of genetic information morphological data can be used to characterise an organism by its shape as it is a major component of any organism, providing information on growth and adaptation. 'Basically the shape of an organism is the major criteria we use to distinguish one species from another' (Rosas 1997). Morphometric techniques seek, in essence, to simplify the complex shape of an organism and illustrate it in a way that can be easily identifiable and distinguishable by the human eye. It has been suggested that ideally more than 60 characters should be measured for each individual (Gower 1988). The idea behind this is that an organism consists of a very large number of characters and those that are selected for a given analysis are a sample of all available characters In reality, however, it is not always possible to reach this suggested figure.

There are two complementary types of morphometric techniques that can be used to describe and group organisms into recognisable groups: Ordination and Classification. Both methods are similar in that they aim to group individuals on the basis of their particular attributes and to seek patterns and order in a data set (Kent & Coker 1992). They are also theoretically objective and repeatable utilising unweighted characters in their respective analyses (Patterson 1982).

Ordination

Ordination comprises a group of methods which seeks to simplify the components of an organism whilst conserving the geometry of the object in question (Legendre & Legendre 1998). The techniques that are used define shape numerically by measurement of lengths and widths of individual organs of an organism. These are then positioned in a space that contains fewer dimensions than the original, complex data set (Philips 1983). There is a whole array of ordination techniques which can be employed to explain a data set but probably the most simple method that can be used is Principal Components Analysis (PCA). PCA is a multivariate technique that can reveal patterns and groupings of individuals based on two or more set of measurements. It uses mathematical formulae to extract a series of axes or

components which are linear combinations of the original measurements (Siebert 1992). The number of axes which are extracted are therefore equal to the number of characters and the components of the analysis are simplified so that they may be viewed in two dimensions (Legendre & Legendre 1998). The first axis or principal component is chosen to represent the largest proportion of variability of the organism in reduced space and the subsequent axes present the rest of the variation in a descending order of magnitude (Sokal & Rohlf 1998).

PCA provides information on the role characters play in the formation of the principal axes and can also be used to show relationships amongst the original characters in reduced space (Legendre & Legendre 1998). Two of the basic tenets of this kind of analysis are that the data is quantitative, continuous and is normally distributed. Normally distributed data is such that it follows the normal curve of errors or has a Gaussian distribution (Forthofer & Lee 1995). It is assumed that most biological data will follow a normal distribution but this is not always the case. Examination of character distribution by histogram and normal probability plots will reveal the nature of the data distribution and may require some measure of transformation so that the data will conform to an approximately normal distribution. The reason why the data must be normally distributed is that in a PCA analysis major deviations may cause the first principal component to only separate out a few taxa which exhibit extreme deviation from the mean (Legendre & Legendre 1998). This will cause abnormal weight to be placed on them hence obscuring the main axis of variation. Checking data for normal distributions by examining histograms and normal probability plots may be a long and tedious task. It does however have added benefits in that it can indicate spurious measurements or incorrect data input.

Most statistical tests are based on the premise that variables are independent (Legendre & Legendre 1998). In the natural world, however, it is often the case that there may be a lack of independence between variables, as they are autocorrelated. For example leaf length may be correlated with petiole length or the width of a pedicel may be correlated with fruit size, as larger fruits require greater support. In PCA, as with any other type of ordination procedure, it is therefore prudent to eliminate data which may be highly correlated. If highly correlated data is used in an ordination it will cause extra importance to be given to some characters which may lead to a type 1-error occurring *i.e.* the false rejection of the null hypothesis (Forthofer & Lee 1995). If correlations do not occur frequently in a data matrix those characters can be

removed before the analysis. If however there are many characters which are highly correlated this could result in a net loss of information (Legendre & Legendre 1998). In this kind of scenario therefore the best approach would be to analyse the data whilst acknowledging the presence of correlations.

The output from a PCA is a set of principal components which account for the variation between individuals on successive principal axes. The eigenvalues, which are given for each principal axis, are linear combinations of the original variables (SPSS 6.1Professional Statistics 1994). Each taxon has a series of eigenvectors associated with it and the multiplication of the eigenvectors by the characters gives a series of values which can be plotted in reduced space. The plots can be then used to explore relationships between taxa in order to visualise those relationships in one, two or three dimensions. The importance of the characters which account for the variation between taxa can also be examined, as those characters which have high eigenvalues will influence the data in reduced space (Sokal & Rohlf 1998). Usually the first two or three axes account for the majority of the variation and the other principal components can be discarded. Often it is not clear however how many axes are of importance and some debate has existed on exactly how many axes should be considered from an analysis. It has been suggested, for example, that the first principal axis is related to size and only the subsequent axes should be considered (Siebert 1992). Others have advocated that in the presence of a large number of taxa the first two axes do not account for a large proportion of the variation and only axes of a higher order should be examined (Legendre & Legendre 1998). The default option on the statistical package which has been used in this analysis is the Kaiser – Guttmann criterion in which only eigenvalues over 1 should be considered as significant. Even the guide to the program, however, does not recommend that this criterion should be accepted (SPSS Professional Statistics 6.1 1994). It is now generally recommended that the broken stick model of Frontier should be used to determine how many axes are significant in a PCA (Jackson 1983, Legendre & Legendre 1998, Parnell & Needham 1998). The model is based on considering eigenvalues from a random data set. It assumes that if the sum of eigenvalues is divided randomly then their expected distribution will follow a broken stick model. If eigenvalues obtained after an analysis exceed those generated by the model they are considered to be significant or in other words they have not occurred by chance (Jackson 1983).

Among the panoply of ordination techniques Canonical Discriminant Analysis (CDA) is another straightforward way of examining relationships between taxa. It is a type of canonical analysis and therefore involves comparing the centroids of groups (Legendre & Legendre 1998). The important property of CDA is that it involves testing known groups and can therefore be used to test an *a priori* hypothesis about the variance in and between predetermined groups of taxa (Sokal & Rohlf 1998). In essence it finds linear combinations of the variables which best discriminate between specific groups (SPSS Professional Statistics 6.1 1994). Like PCA, CDA requires that the data be normally distributed and uncorrelated. CDA is however thought to be quite statistically robust and less sensitive to deviations from normality than PCA (Legendre & Legendre 1998). The groups that are selected for CDA may be known species or they may be groups which have been indicated by a cluster analysis. The output from a CDA is a group of discriminant functions which can be plotted to examine relationships within and between taxa. One of the useful features of this technique is that it can indicate when an individual has been misclassified (incorrectly assigned to a group). It will then suggest the next best group to which it can be assigned. If the position of an individual is unknown it can also be added to an analysis and assigned to an appropriate group (Sokal & Rohlf 1998). The disadvantage of CDA is that it will tend to force an object into a group whether it belongs there or not. For example if three groups are specified for CDA when there are in fact four or five natural divisions all of the individuals will be placed in one of only three categories.

Cluster analysis

The other main branch of morphometric analysis is known as cluster analysis. It encompasses a group of algorithms which can be used to group or classify objects based on their similarity or dissimilarity and it aims to group individuals together on the basis of their attributes (Sneath & Sokal 1973). The end product is a classification in which, ideally, every individual within a group is more similar to the others of that group than individuals from another group (Kent & Coker 1992).

As a method of classification cluster analysis became very popular during the 1970s and a number of different clustering techniques proliferated at that time (Sneath & Sokal 1973). The different clustering strategies correspond to different definitions of what a group should

represent. The type of algorithm which is chosen depends on certain preheld views of the distribution of taxa in space and the shape or type of classification desired (Legendre & Legendre 1998). Sneath and Sokal (1973) have described cluster analysis as consisting of "sets of taxa or operational taxonomic units (OTUs) in phenetic hyperspace that exhibit neither random nor regular distribution patterns and that meet one or more various criteria imposed by a particular cluster definition".

Essentially cluster analysis as it is currently employed is, like ordination, a technique for data reduction and exploration. It is a tool which can be used to search for pattern and order in a data set. Clustering techniques are either agglomerative in that they start with individual samples and progressively combine them in terms of similarity (SPSS Professional Statistics 1994) or divisive so they begin with one large cluster and sequentially divide it into smaller groups (Sneath & Sokal 1973). The first step in an agglomerative schedule begins with the construction of an association matrix which separates pairs of taxa on the basis of a distance measurement such as squared Euclidean distance (Sneath & Sokal 1973). The taxa are then clustered into larger and groups until a single cluster containing all the individuals or OTUs is obtained (Legendre & Legendre 1998). In this analysis an agglomerative schedule was employed and two different clustering algorithms were used: Furthest Neighbour Sorting and Ward's method.

As the name suggests Furthest Neighbour Sorting is a method which can be employed to maximise differences between groups. Basically in this analysis the fusion of clusters depends on the most distant pair of objects. Initially individuals are paired and an object may only join a cluster when it shows a similarity to all objects within the cluster. As a cluster grows, therefore, it becomes more difficult for new individuals to join it (Sneath & Sokal 1973). In practice furthest neighbour sorting tends to produce rather spherical clusters (Legendre & Legendre 1998).

The principal of Ward's method of agglomerative clustering is that the fusion of a cluster to a group depends on the mean point or centroid of the group. Initially each cluster consists of a single individual with a mean point of zero and as clusters form their centroids move further

away from their actual mean point. At each step the pair of objects which minimise the sum of the squared distances between cluster centroids is added (Legendre & Legendre 1998).

A perceived problem with cluster analysis is that depending on the algorithm used different classifications can be obtained from the same data set. It is therefore up to the individual researcher to decide a priori the concept of what constitutes a group before the analysis.

Materials and Methods

Herbarium specimens from **A, AAU, BKF, BO, CANB, E, K, L, P, SING, U, KYO** were used in the analysis. A total of 30 quantitative characters were selected for analysis (**Table 13**). Some characters were measured only for male plants: character 10 (bract length), character 11 (bract width at the midpoint), character 12 (bract width at the base). These were measured in the male specimens only because in the female plants with fruits the bracts fall at an early stage of fruit development. The width of the receptacle (character 15) was also measured for the male plants only as flowers and fruits are not present at the same time on the female plant and this character can vary quite radically within an individual female specimen depending on the age of the flower. The length and width of the style was measured in the male plants as a style and ovary is present but the ovary is abortive. Characters 24 –30 (fruiting characteristics) were only applicable for female plants. In addition as the fruits are largely sessile measurements of pedicel length and width (characters 13, 14) were not made for these individuals. Measurements of the dimensions of the stamens (characters 18 – 21) were made for the female plants, as they possess rudimentary male organs.

A total of 13 qualitative characters were selected for inclusion in the analysis (**Table 14**). Some characters were only applicable to male individuals (characters 9 – 11). Bracts could only be examined in the male plants for the same reason they were not included in the analysis of quantitative characters. In terms of inflorescence morphology character 9 was only applicable to male specimens as the female inflorescence is always 1 – flowered and does not vary. Characters 13 and 14 (fruit characters) were only applicable to female specimens. Measurements were taken from herbarium specimens of 80 female plants and 50 male plants (**Appendix 4**). In the final analysis however, 75 female and 45 male specimens were analysed due to missing data for some of the characters. The specimens were selected for measurement

on the basis that they had some intact leaves and had fully matured flowers (male specimens) and mature fruits (female specimens). Herbarium specimens were also selected so that the entire geographic range of the species was fully represented.

The 30 quantitative characters were inspected for normal distributions using histograms, normal probability plots and regression analysis. In each case a r^2 value exceeding 90% was used as a cut off point for a normal distribution. The majority of the characters were not normally distributed and it was necessary to transform them using $\log_{10}$ and square root functions. In the male specimens the following characters were transformed: leaf length (1), leaf width at the midpoint (2), leaf width at the base (3), distance between primary veins (4), petiole length (6), bract length (10), bract width mid point (11), bract width at the base (12), anther length (20) were transformed by the square root function; tepal width mid point (17) and filament length (18) were $\log_{10}$ transformed. Of the female specimens petiole length (6), tepal width (17), fruit width (25), endocarp length (26), were transformed by square root. Peduncle width (9) and filament length (18) were transformed by the reciprocal square function and the following characters were $\log_{10}$ transformed: peduncle length (8), tepal length (16), style length (22), length of apical chamber (30) (**Appendix 5, 6**). Three characters could not be transformed to a normal distribution because of their categorical nature and unusual distribution: filament width (19), anther width (21), style width (23).

The data for male and female plants were analysed individually and the results compared. Within each separate analysis the data was examined in two different ways. In the first, all of the data was examined together and in the second the leaf characters were excluded. In the analyses 19 characters were included for the female specimens when all of the characters were included and 14 when the leaf characters were excluded. 17 characters were included in the total analysis of the male specimens and 12 characters were analysed when the vegetative characters were removed.

A number of different analyses were carried out. Firstly the data was subjected to cluster analysis using an agglomerative schedule and squared Euclidean distance measurement. Two different clustering techniques were used: Furthest Neighbour Sorting and Wards method. All

Table 13: List of 30 quantitative measurements taken from herbarium specimens of *Dendrotrophe varians*

1 = measured for male specimens only; 2 = measured for female specimens only

Character (mm)	Explanation of character
1. Leaf length	length along the mid rib from the apex of the petiole
2. Leaf width mid point	leaf width at the mid point of the lamina
3. Leaf width base	leaf width at the base above the petiole
4. Distance between first two primary veins	distance taken from the mid point of the leaf between the inner most primary vein and the one adjacent to it.
5. Angle of second primary vein	angle taken from the base of the leaf between the inner most primary vein and the one adjacent to it
6. Petiole length	
7. Petiole width	
8. Peduncle length	
9. Peduncle width	
10. Bract length[1]	
11. Bract width at mid point[1]	
12. Bract width at the base[1]	
13. Pedicel length[1]	
14. Pedicel width[1]	
15. Receptacle width[1]	
16. Tepal length	
17. Tepal width	tepal width at the midpoint
18. Filament length	
19. Filament width	
20. Anther length	
21. Anther width	
22. Style length	
23. Style width	width of the style at the base
24. Fruit length[2]	
25. Fruit width mid point[2]	
26. Endocarp length[2]	
27. Endocarp width 1[2]	endocarp width 1/3 from apex
28. Endocarp width 2[2]	endocarp width at the midpoint
29. Endocarp width 3[2]	endocarp width 1/3 from the base
30. Length of apical chamber[2]	distance from apex of endocarp to base of chamber

Table 14: List of 13 qualitative and categorical characters taken from herbarium specimens of *Dendrotrophe varians*

1 = characters applicable to male plants only; 2 = characters applicable to female plants only

Character	Explanation of character
1. Bark fissured	longtidudinal fissures absent (0); present (1)
2. Bark pustualte	bark smooth (0); bark pustulate (1)
3. Side shoots bracteate	bracts present at the base of the branches (1); absent (0)
4. Shape of leaf apex	apex acute (0); apex; obtuse (1)
5. Shape of leaf base	base attenuate (0); base rounded (1)
6. Number of primary veins	
7. Primary veins raised on upper leaf surface	
8. Primary veins raised on lower leaf surface	
9. Inflorescences umbellate or racemose[1]	inflorescence racemose but crowded at the apex of the peduncle (0); inflorescence a true umbel (1)
10. Bracts membranous[1]	
11. Bracts fleshy[1]	
12. Endocarp tuberculate[2]	endocarp rugulate (0); endocarp tuberculate (1)
13. Number of chambers in the endocarp[2]	number of chambers in the endocarp when viewed in longitudinal section

of the analyses were carried out on untransformed inflorescence data. In the analysis where all of the characters were included, the data was standardised by z scores (variables had a mean of zero and a standard deviation of 1). This procedure was carried out to adjust for the difference in scale between leaf and floral characters. Three clusters were saved for each analysis. The data was then analysed by Canonical Discriminant Analysis (CDA) using the three groups indicated by the cluster analysis. This technique was employed to test if the groups indicated by the cluster analysis were statistically significant. Both stepwise and non stepwise addition of characters was carried out. All groups were classified equal and analysis was carried out using the within groups covariance matrix. Principal Components Analysis was also carried out on the data to investigate if the groups indicated by the cluster analysis were maintained by PCA. This method was also used to see which characters were important in distinguishing groups of individuals. PCA also has an advantage over CDA in that it does not constrain the data in any way and force it into a particular group. The results of the PCA and CDA were compared for similarities.

Results

The qualitative characters which were selected for analysis were found to be generally unreliable (**Table 14**). Characters 1, 2 were not suitable as they could only be measured on a small number of specimens that had branches of sufficient age. The presence of bracts at the base of the branches was found to be insufficiently variable to include in the analysis (character 3). Whether the primary veins were distinct on the upper or lower surface of the leaf was a character which varied within an individual and therefore characters 7, 8 were not suitable for inclusion in the analysis. The consistency of the bracts in the inflorescence (character 10, 11) also exhibited a similar variation. The surface morphology of the endocarp (character 12) was a character which varied continuously throughout the species and therefore could not considered a qualitative character. Of the other characters the number of primary veins and their angles relative to each other could not be included in the continuous data analysis because they did not exhibit a sufficient range of variability. They were included in an initial analysis and had a disproportionate effect on the results because of their categorical nature. As with data, which is not normally distributed, they were given a greater emphasis than any other character and the groups which they produced did not follow any recognisable pattern.

The cluster analysis for both male and female plants gave the same results when either Furthest Neighbour Sorting or Ward's method was used. The topographies of the dendrograms were slightly different but the same groups of individuals were associated with each other. On closer examination however, the results of the Furthest Neighbour Sorting were discarded. Even though the dendrograms were superficially similar to Ward's method the three clusters that were saved were highly unequal with one large group and two very small groups containing one to two taxa each. This became apparent in CDA when the graph of discriminant scores showed a highly skewed distribution of individuals.

Female Population

Three clusters were saved from the analysis using Ward's method. In the all character analysis (**Fig. 25**) the first cluster, which was the largest, contained a mixture of Malesian and Indochinese taxa (Group 1). The second represented mainly Indochinese specimens

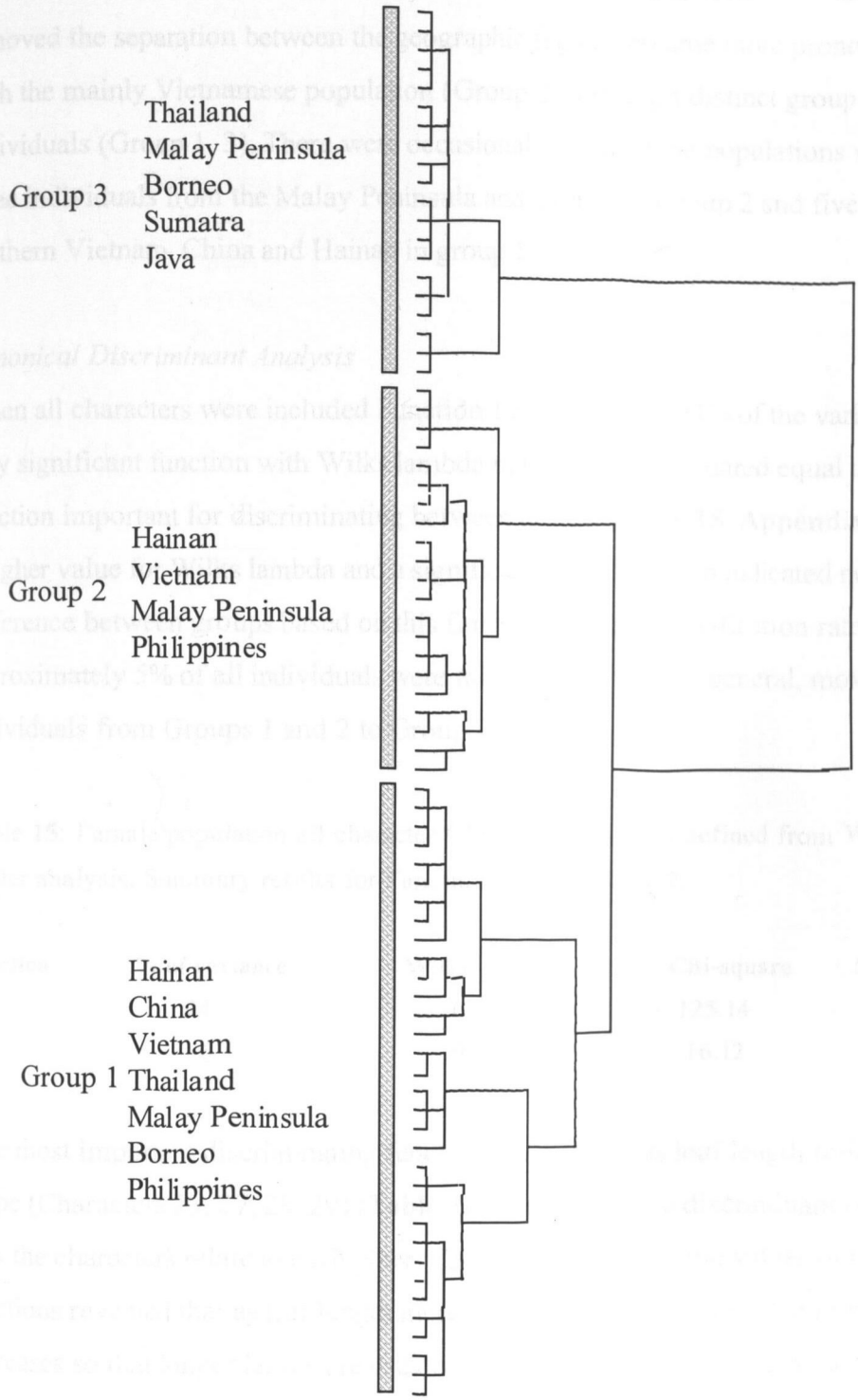


Fig. 25 Dendrogram using Ward's Method of cluster analysis for female individuals of *Dt. varians*. Analysis carried out on measurements of vegetative and floral characters standardised by z scores to compensate for differences in scale between leaf and floral structures. Three groups saved as indicated on the dendrogram. Group 1 contains a mixture of individuals from all geographic areas. Groups 2, 3 correspond to distinct geographic regions with some overlap in the Malay Peninsula.

(Group 2), whilst the third consisted of mainly Malesian individuals (Group 3). This group also contained a Thai element which corresponds to the Peninsular region of the country and areas which have climatic similarities to the Malay Peninsula. When vegetative characters were removed the separation between the geographic regions became more pronounced (**Fig. 26**) with the mainly Vietnamese population (Group 2) forming a distinct group from the Malesian individuals (Group 1, 3). There were occasional mixing of the populations with the presence of three individuals from the Malay Peninsula and Borneo in Group 2 and five individuals from northern Vietnam, China and Hainan in group 1.

Canonical Discriminant Analysis

When all characters were included Function 1 accounted for 94% of the variance and was the only significant function with Wilks lambda of 0.13 and Chi squared equal to 125 making this function important for discriminating between groups (**Table 15, Appendix 7**). Function 2 had a higher value for Wilks lambda and a significance of 0.58 which indicated no significant difference between groups based on this function. The misclassification rate was quite low, approximately 5% of all individuals were misclassified with, in general, movement of individuals from Groups 1 and 2 to Group 3.

Table 15: Female population all character CDA using 3 groups defined from Ward's method of cluster analysis. Summary results for Function 1 and Function 2.

Function	% of variance	Wilks' lambda	Chi-square	Significance
1	94	0.133	125.14	0.0000
2	6	0.771	16.12	0.5841

The most important discriminating function coefficient was leaf length followed by endocarp shape (Characters 25, 27, 28, 29) (**Table 16**). The sign of the discriminant coefficient indicates how the characters relate to each other. Comparison between the values of the different functions revealed that as leaf length increases the distance between the primary veins decreases so that longer leaves are usually narrower. Also as leaf length increases endocarp size increases. Characters, which were correlated with function 1, were mainly fruit characters (endocarp width 1, endocarp width 2, endocarp length and fruit width). Fruit width had a positive correlation value with a negative discriminant function coefficient. This occurred as

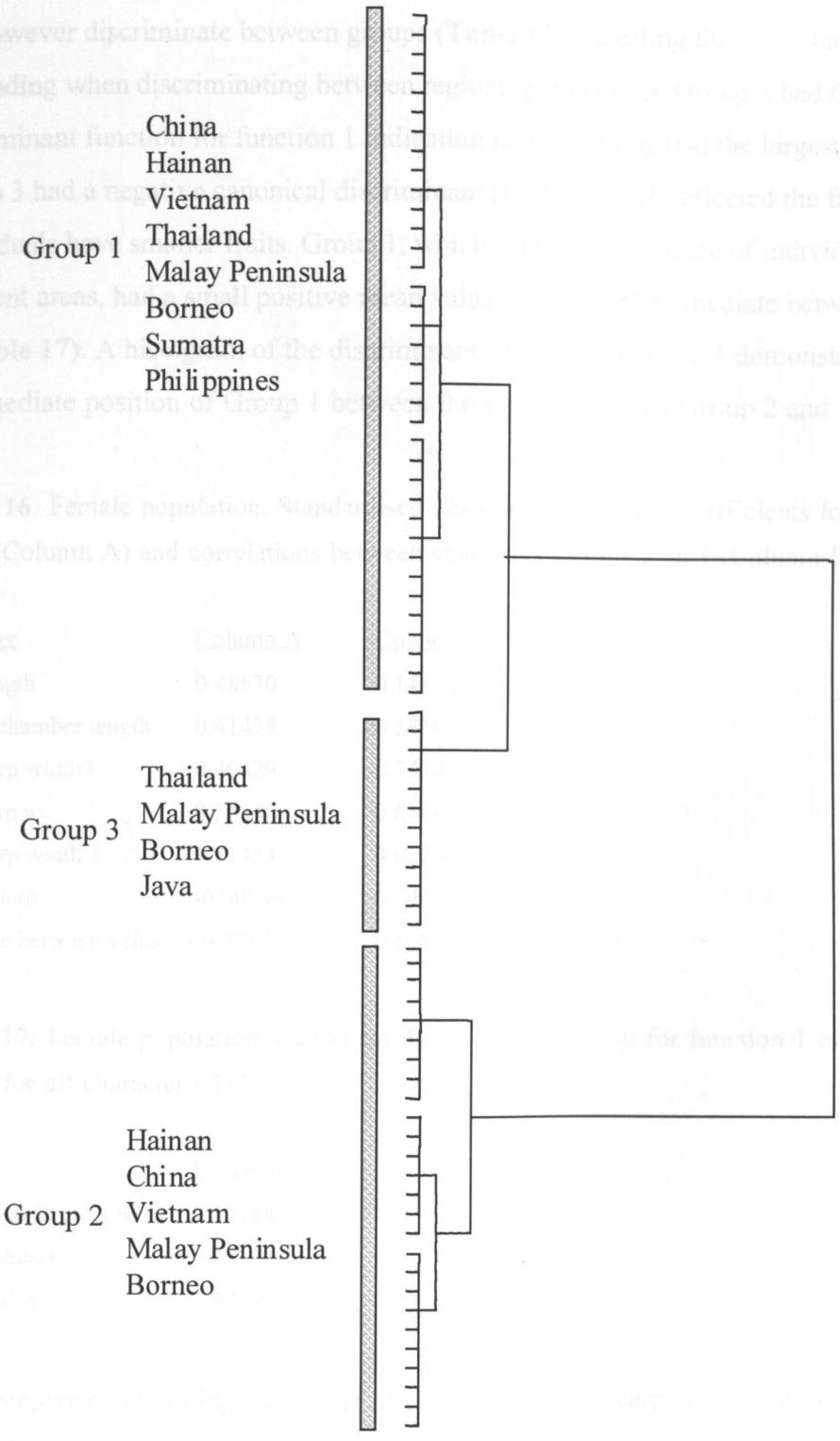


Fig. 26 Dendrogram using Ward's Method of cluster analysis for female individuals of *Dt. varians*. Analysis carried out on measurements of inflorescence characters. Three groups saved as indicated on the dendrogram. Group 1 contains a mixture of individuals from all geographic areas. Groups 2, 3 correspond to distinct geographic regions with some overlap in the Malay Peninsula and northern Borneo.

fruit width is highly correlated with the width of the endocarp. Vegetative characteristics were associated with function 2 and contributed to the variation in this function. Function 2 does not however discriminate between groups (**Table 15**) indicating that leaf characteristics may be misleading when discriminating between regional populations. Group 2 had the highest mean discriminant function for function 1 indicating that this group had the largest fruits whilst Group 3 had a negative canonical discriminant function which reflected the fact that these individuals have smaller fruits. Group 1, which contained a mixture of individuals from different areas, had a small positive mean value which was intermediate between Groups 2 and 3 (**Table 17**). A histogram of the discriminant scores for function 1 demonstrates the intermediate position of Group 1 between the two extremes of Group 2 and 3 (**Fig. 27**).

Table 16: Female population. Standardised discriminant function coefficients for all character CDA (Column A) and correlations between characters and function 1 (Column B).

Character	Column A	Column B
Leaf length	0.48630	0.14112
Apical chamber length	0.41439	0.38308
Endocarp width3	0.40429	0.34347
Endocarp w	0.35340	0.61417
Endocarp width 2	0.21433	0.66246
Fruit width	-0.00589	0.59409
Distance between veins	- 0.7777	0.10612

Table 17: Female population. Canonical discriminant function for function 1 evaluated at group means for all character CDA.

Group	Function 1
1 (Malesia & Indochina)	0.00188
2 (Indochina)	2.81294
3 (Malesia)	- 2.95668

In the stepwise discriminant analysis five characters (endocarp width, leaf length, peduncle length, leaf width 1 and anther length) were selected as the most important discriminating characteristics between groups but the misclassification rate was much higher (13%) than when all of the characters were inputted simultaneously. Some vegetative characters were selected as

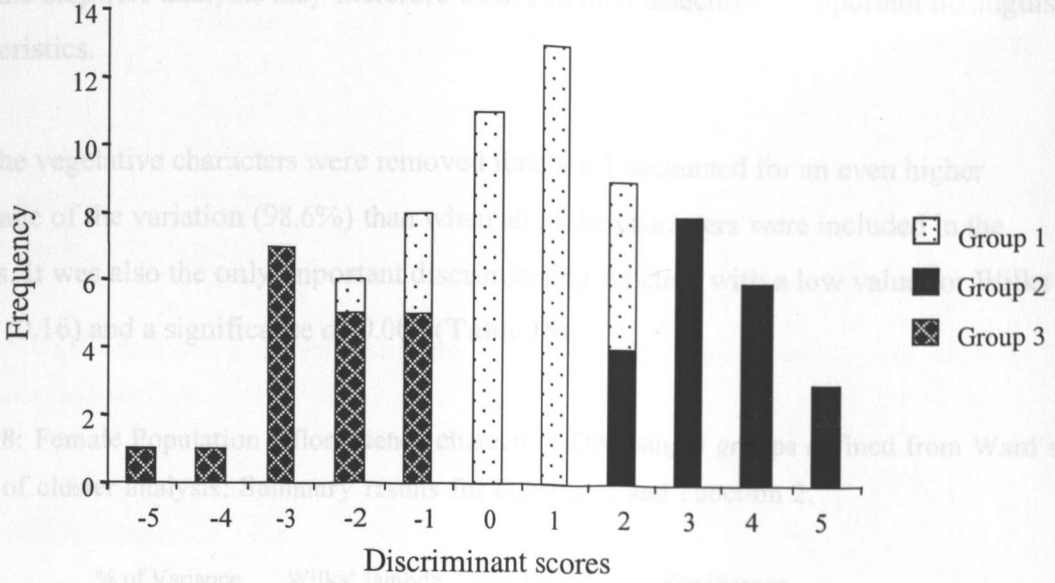


Fig. 27 Histogram of frequency of discriminant scores for first discriminant function. Analysis for female individuals of *Dt. varians* using vegetative and floral characters. Groups were specified from a cluster analysis using Wards method (**Fig. 25**) where three groups were saved.

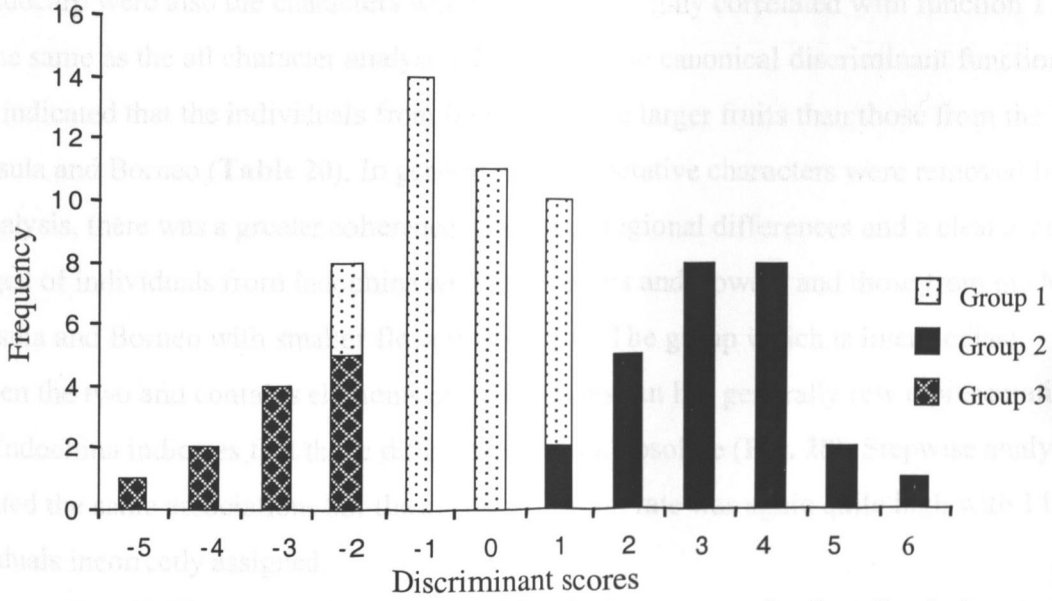


Fig. 28 Histogram of frequency of discriminant scores for first discriminant function. Analysis for female individuals of *Dt. varians* using inflorescence characters. Groups were specified from a cluster analysis using Wards method (**Fig. 26**) where three groups were saved

important discriminating factors in this analysis. In the simultaneous analysis leaf characters were not shown to be significant in distinguishing between groups. The higher misclassification rate in the stepwise analysis may therefore be due to their selection as important distinguishing characteristics.

When the vegetative characters were removed function 1 accounted for an even higher percentage of the variation (98.6%) than when all of the characters were included in the analysis. It was also the only important discriminating function with a low value for Wilks lambda (0.16) and a significance of 0.000 (**Table 18**).

Table 18: Female Population inflorescence character CDA using 3 groups defined from Ward's method of cluster analysis: Summary results for Function 1 and Function 2.

Function	% of Variance	Wilks' lambda	Chi-square	Significance
1	98.6	0.157	119.49	0.0000
2	1.4	0.934	4.38	0.9865

The misclassification rate of individuals was slightly higher (5.5%) in this analysis. Fruit width took on the highest discriminating function coefficient followed by style length, which did not appear in the previous analysis, and endocarp width. The width of the fruits and the shape of the endocarp were also the characters which were most highly correlated with function 1 which was the same as the all character analysis (**Table 19**). The canonical discriminant function again indicated that the individuals from Indochina have larger fruits than those from the Malay Peninsula and Borneo (**Table 20**). In general, when vegetative characters were removed from the analysis, there was a greater coherence in terms of regional differences and a clearer picture emerged of individuals from Indochina with larger fruits and flowers and those from the Malay Peninsula and Borneo with smaller flowers and fruits. The group which is intermediate between the two and contains elements of both regions but has generally few representatives from Indochina indicates that those differences are not absolute (**Fig. 28**). Stepwise analysis indicated the same associations but the misclassification rate was again quite high with 11% individuals incorrectly assigned.

Table 19: Female Population. Standardised discriminant function coefficient for inflorescence CDA (Column A) and correlations between characters and function 1 (Column B).

Character	Column A	Column B
Fruit width	0.61277	0.77716
Style length	0.34524	- 0.12599
Endocarp width	0.32073	0.76081
Endocarp width 2	0.22793	0.55181
Endocarp length	0.04754	0.47958

Table 20: Female Population. Canonical discriminant function for function 1 evaluated at group means for inflorescence character CDA.

Group	Function
1(Malesia and Indochina)	- 0.77890
2 (Indochina)	2.67656
3 (Malesia)	- 3.46252

Principal Components Analysis

When all of the characters were analysed by PCA the first two principal components, as indicated by Frontiers broken stick model, were significant and accounted for 49% of the total variation (**Appendix 8**). The characters, which were significant in distinguishing between groups, were the same as for the discriminant analysis. On axis 1 fruit width and the shape of the endocarp had the highest eigenvalues (fruit width, endocarp width 2, endocarp width 1, endocarp length). On factor two leaf characteristics (leaf width 1, leaf width 2, distance between veins and leaf length) were the most important distinguishing features (**Table 21**). When the groups indicated by the cluster analysis were indicated on a scatter plot of axis 1 and 2 a similar pattern appeared to the discriminant analysis with Group 1 as an intermediate between Groups 2 and 3 but both of these, and in particular Group 3, overlapping with Group 1 (**Fig. 29**). Correlated characters may however have influenced the analysis. Endocarp width is correlated with fruit width and endocarp length is associated with fruit length. The most highly correlated characters had the highest eigenvalues or in other words contributed to the greatest amount of variation. When the leaf characters were removed the first two axes account for 55% of the variation and are the only significant axes (**Table 21**). The characters which are

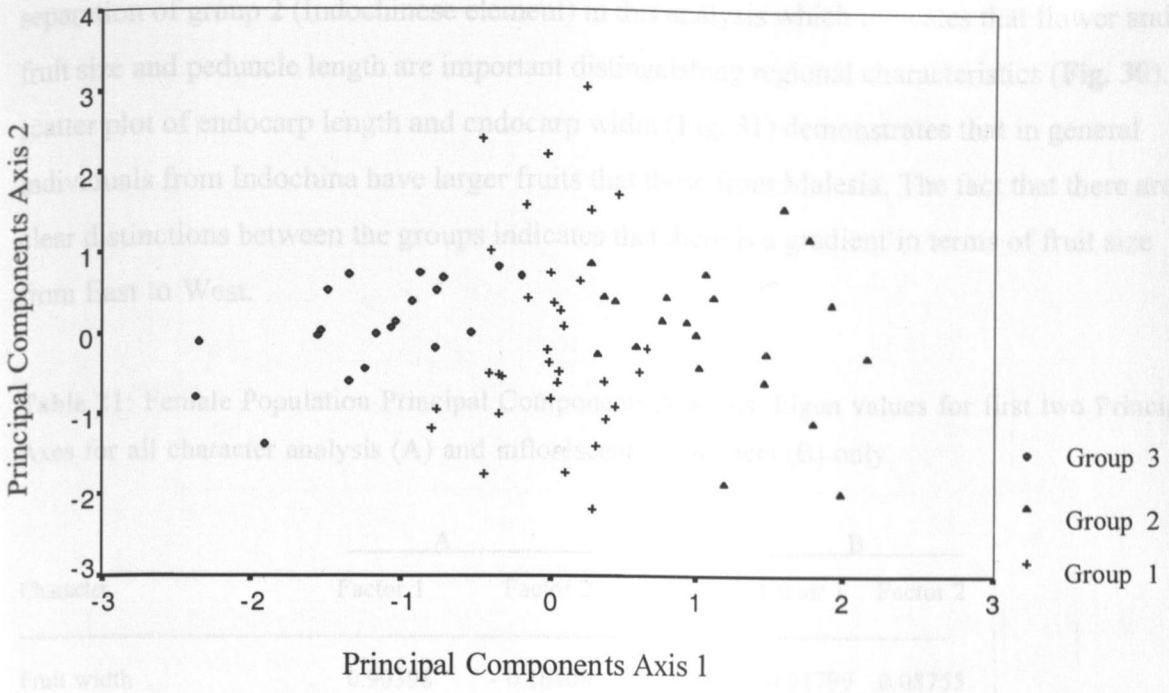


Fig. 29 Scatter plot of first two principal axes from PCA of female individuals of *Dt. varians* using vegetative and floral characters. Groups indicated correspond to those specified by cluster analysis using Ward's method (**Fig. 25**).

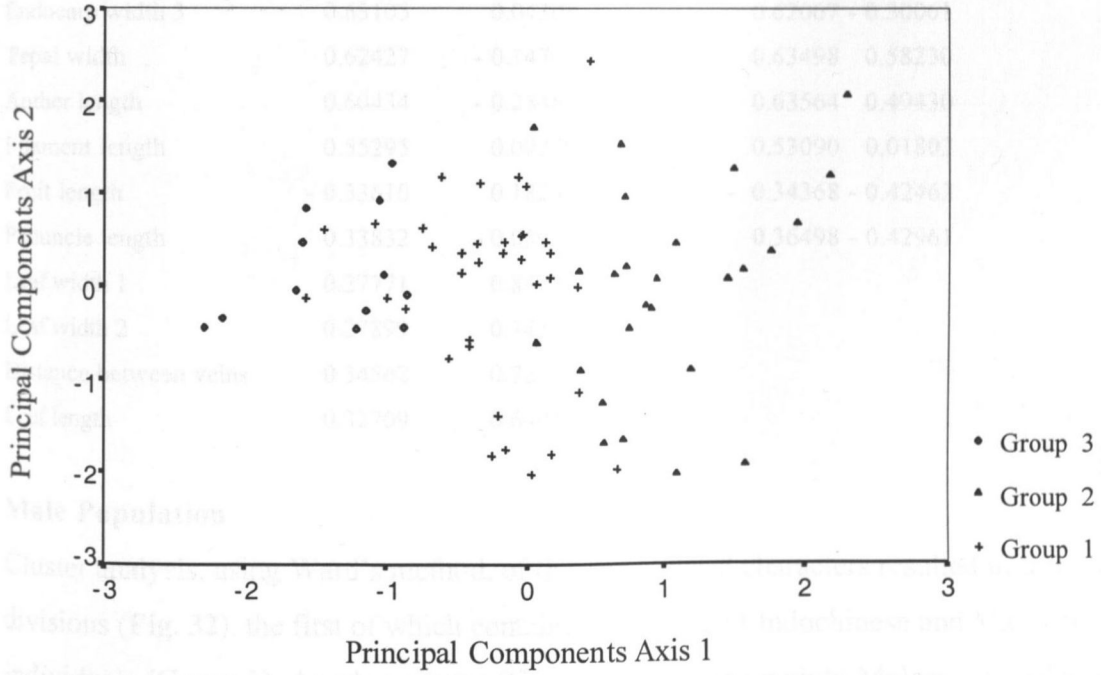


Fig. 30 Scatter plot of first two principal axes from PCA of female individuals of *Dt. varians* using inflorescence characters. Groups indicated correspond to those specified by cluster analysis using Ward's method (**Fig. 26**).

highly correlated (fruit width, endocarp width) contribute most to the variation on axis 1 and peduncle length and fruit length contribute to the variation on axis two. There was a greater separation of group 2 (Indochinese element) in this analysis which indicates that flower and fruit size and peduncle length are important distinguishing regional characteristics (**Fig. 30**). A scatter plot of endocarp length and endocarp width (**Fig. 31**) demonstrates that in general individuals from Indochina have larger fruits that those from Malesia. The fact that there are no clear distinctions between the groups indicates that there is a gradient in terms of fruit size from East to West.

Table 21: Female Population Principal Components Analysis. Eigen values for first two Principal Axes for all character analysis (A) and inflorescence characters (B) only

	A		B	
Character	Factor 1	Factor 2	Factor 1	Factor 2
Fruit width	0.90398	- 0.16908	0.91799	0.08755
Endocarp width 2	0.88842	- 0.07442	0.88870	- 0.18143
Endocarp width 1	0.88184	- 0.21887	0.90671	0.04400
Endocarp length	0.86354	- 0.03232	0.85674	- 0.18360
Length of apical chamber	0.65579	- 0.19781	0.67810	0.20404
Endocarp width 3	0.63105	0.04308	0.62067	- 0.30061
Tepal width	0.62427	- 0.14704	0.63498	0.58230
Anther length	0.60434	- 0.23487	0.63564	0.49430
Filament length	0.55295	0.09200	0.53090	0.01803
Fruit length	- 0.33610	0.18295	- 0.34368	- 0.42462
Peduncle length	0.33832	- 0.05921	0.36498	- 0.42961
Leaf width 1	0.27771	0.84733		
Leaf width 2	0.27899	0.74547		
Distance between veins	0.34562	0.72251		
Leaf length	0.32709	0.64030		

Male Population

Cluster analysis, using Ward's method, of the standardised characters resulted in three major divisions (**Fig. 32**), the first of which contained a mixture of Indochinese and Malesian individuals (Group 1). Another cluster (Group 3) contained mainly Malesian populations with

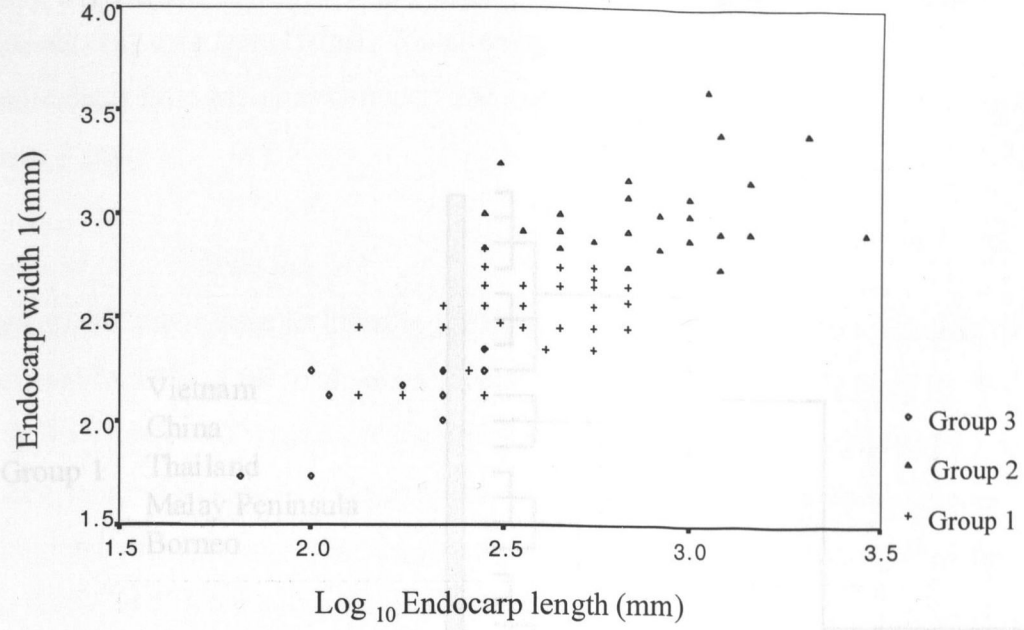


Fig. 31 Scatter plot of endocarp length against endocarp width. The groups indicated correspond to those indicated by cluster analysis of inflorescence characters using Ward's method. Group 2 represents individuals from Indochina which have larger fruits. Group 3 relates to plants which are confined to Malesia. Group 1 cover the entire geographic range with individuals of intermediate characteristics

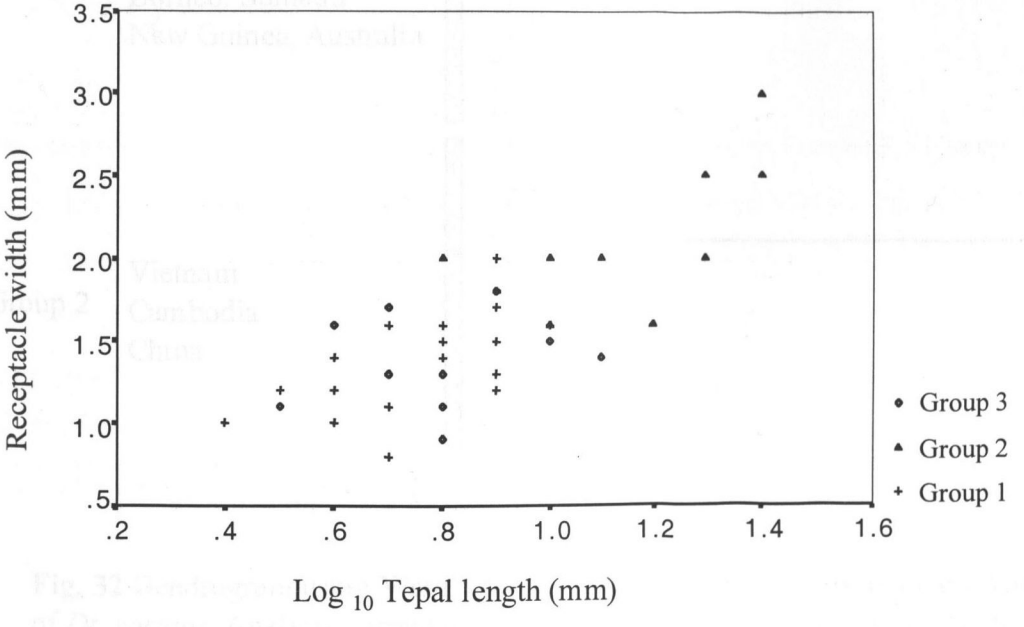


Fig. 38 Scatter plot of tepal length against receptacle width for male individuals. The groups indicated correspond to cluster analysis of all characters using Ward's method. Group 2 contains individuals from Indochina, which have larger flowers. Groups 1 and 3 correspond to plants which are generally confined to Malesia and have smaller flowers.

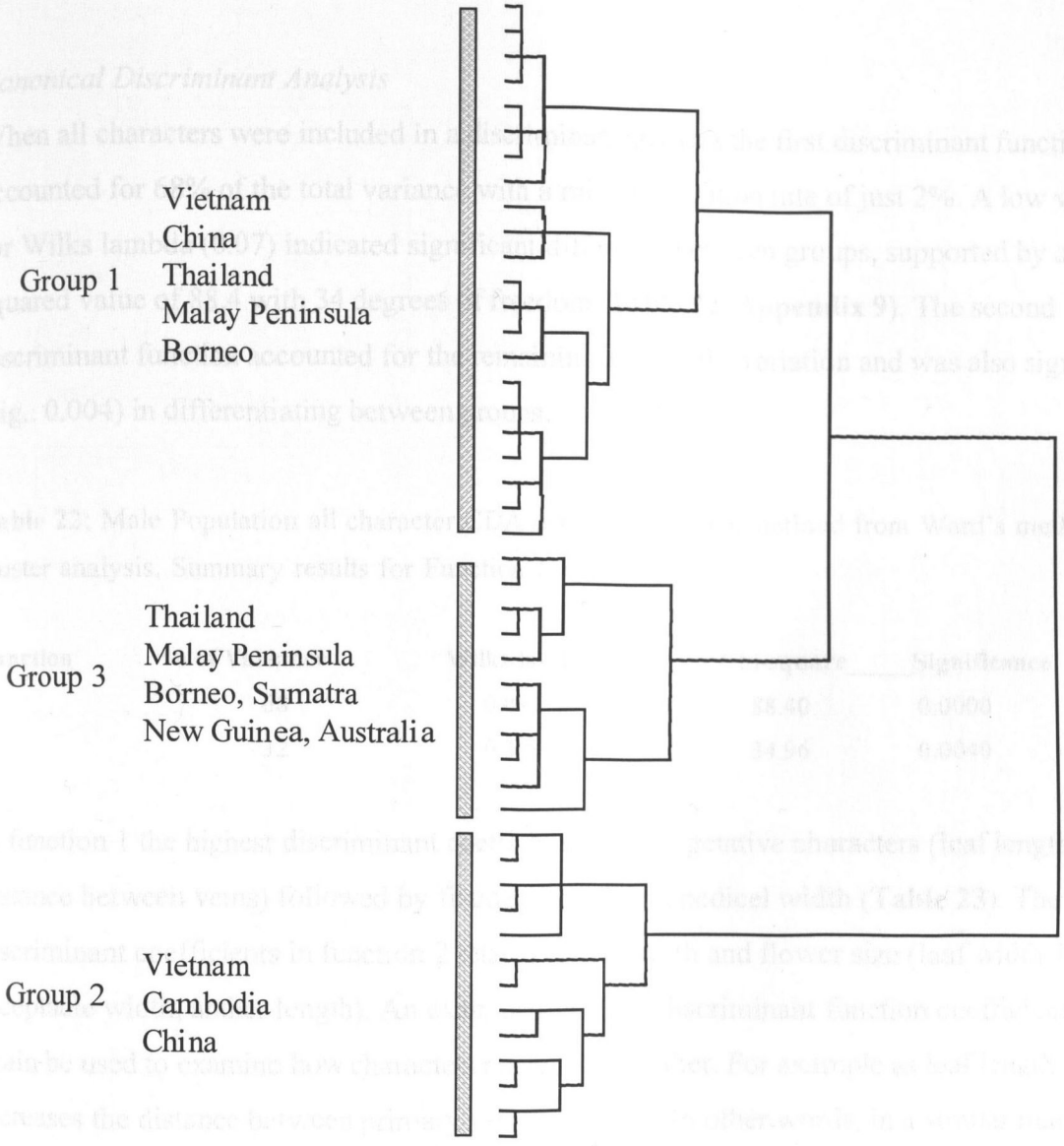


Fig. 32 Dendrogram using Ward's Method of cluster analysis for male individuals of *Dt. varians*. Analysis carried out on measurements of vegetative and floral characters standardised by z scores to compensate for differences in scale between leaf and floral structures. Three groups saved as indicated on the dendrogram. Group 1 contains a mixture of individuals from all geographic areas. Groups 2, 3 correspond to distinct geographic regions.

some specimens from Thailand and the final group (Group 2) represented individuals from Indochina and China. When vegetative characters were removed (**Fig. 33**) one small cluster contained only taxa from Hainan, China and northern Vietnam (Group 2), another comprised of individuals from Malesia (Group 3) and one large group contained individuals from both regions (Group 1).

Canonical Discriminant Analysis

When all characters were included in a discriminant analysis the first discriminant function accounted for 68% of the total variance with a misclassification rate of just 2%. A low value for Wilks lambda (0.07) indicated significant difference between groups, supported by a Chi squared value of 88.4 with 34 degrees of freedom (**Table 22**, **Appendix 9**). The second discriminant function accounted for the remaining 32% of the variation and was also significant (sig.: 0.004) in differentiating between groups.

Table 22: Male Population all character CDA using three groups defined from Ward's method of cluster analysis. Summary results for Function 1 and Function 2

Function	% of Variance	Wilks lambda	Chi-square	Significance
1	68	0.080	88.40	0.0000
2	32	0.368	34.96	0.0040

In function 1 the highest discriminant coefficients were vegetative characters (leaf length, distance between veins) followed by filament length and pedicel width (**Table 23**). The highest discriminant coefficients in function 2 related to leaf width and flower size (leaf width 1, receptacle width, anther length). An examination of the discriminant function coefficients can again be used to examine how characters relate to each other. For example as leaf length increases the distance between primary veins decreases. In other words, in a similar manner to the female population, longer leaves are generally narrow and shorter leaves will be broad. In terms of reproductive characters, as pedicel length increases so too does flower size.

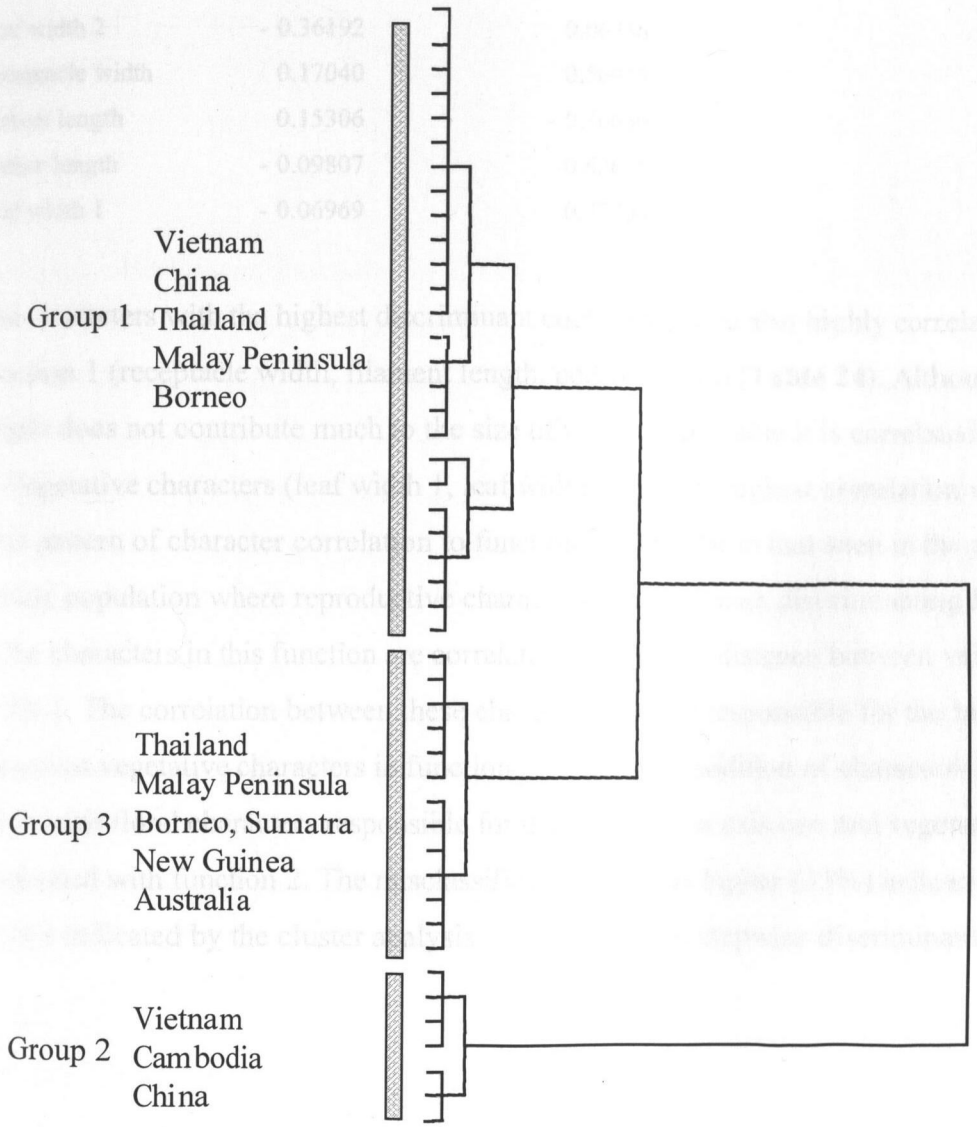


Fig. 33 Dendrogram using Ward's method of cluster analysis for male individuals of *Dt. varians*. Analysis carried out on measurements of inflorescence characters. Three groups saved as indicated on the dendrogram. Group 1 contains a mixture of individuals From all geographic areas. Group 3 contains individuals mainly from Malesia and the smaller Group 2 corresponds to the geographic area of Indochina and China

Table 23: Male Population. Standardised discriminant function coefficient for all character CDA for Function 1 and Function 2

Character	Function 1	Function 2
Distance between veins	- 0.75633	- 0.03065
Leaf length	0.72413	- 0.05323
Filament length	0.56170	- 0.38518
Pedicel width	0.53471	- 0.04039
Leaf width 2	- 0.36192	0.06336
Receptacle width	0.17040	0.56015
Pedicel length	0.15306	- 0.10650
Anther length	- 0.09807	0.62631
Leaf width 1	- 0.06969	0.72704

The characters with the highest discriminant coefficient were also highly correlated with function 1 (receptacle width, filament length, pedicel width) (**Table 24**). Although pedicel length does not contribute much to the size of the function value it is correlated with function 1. Vegetative characters (leaf width 1, leaf width 2) had the highest correlation with function 2. This pattern of character correlation to function was similar to that seen in the analysis of the female population where reproductive characters were the main discriminating factors. Three of the characters in this function are correlated: leaf length, distance between veins and leaf width 1. The correlation between these characters may be responsible for the high importance placed on vegetative characters in function 2. A stepwise addition of characters gave a similar result with floral characters responsible for the variation on axis one and vegetative characters associated with function 2. The misclassification rate was higher (33%) indicating that the groups indicated by the cluster analysis were unsuited to stepwise discriminant analysis.

Table 24: Male Population. Correlation between characters and canonical discriminant functions for all character analysis.

Character	Function 1	Function 2
Receptacle width	0.48813	0.36167
Filament length	0.46654	0.08935
Pedicel length	0.42051	0.14321
Pedicel width	0.38715	0.18184
Leaf width 1	- 0.34689	0.53671
Leaf width 2	- 0.34982	0.44106
Anther length	0.17736	0.44063
Leaf length	- 0.14307	0.36761

The mean discriminant functions for Group 3 (Malesia) were small for function 1 indicating that this group represents individuals with small, shortly pedicellate flowers. In function 2 however the mean function value was high which implies that this group also represents individuals with larger leaves. Group 2 had a high canonical discriminant function value for function one indicating that individuals from Indochina have generally larger flowers with longer pedicels. The difference in leaf size between these individuals and Group 3 is however not markedly different as indicated by the low positive value for function 2. Group 1 is intermediate between the two other groups in terms of flower size but contains taxa with narrower leaves (**Table 25**). A scatter plot of function 1 against function 2 again illustrates the intermediate position of Group 1 between the Indochinese and Malesian elements (**Fig. 34**).

Table 25: Male Population. Canonical discriminant function for function 1 and function 2 evaluated at group means for all character CDA.

Group	Function 1	Function 2
1 (Malesia and Indochina)	- 0.26441	- 1.30990
2 (Indochina)	2.55758	0.97834
3 (Malesia)	- 2.49377	1.46358

When the leaf characters are removed function 1 accounted for almost all of the variation (95%) between groups and the misclassification rate was reduced to just 3.8%. A low

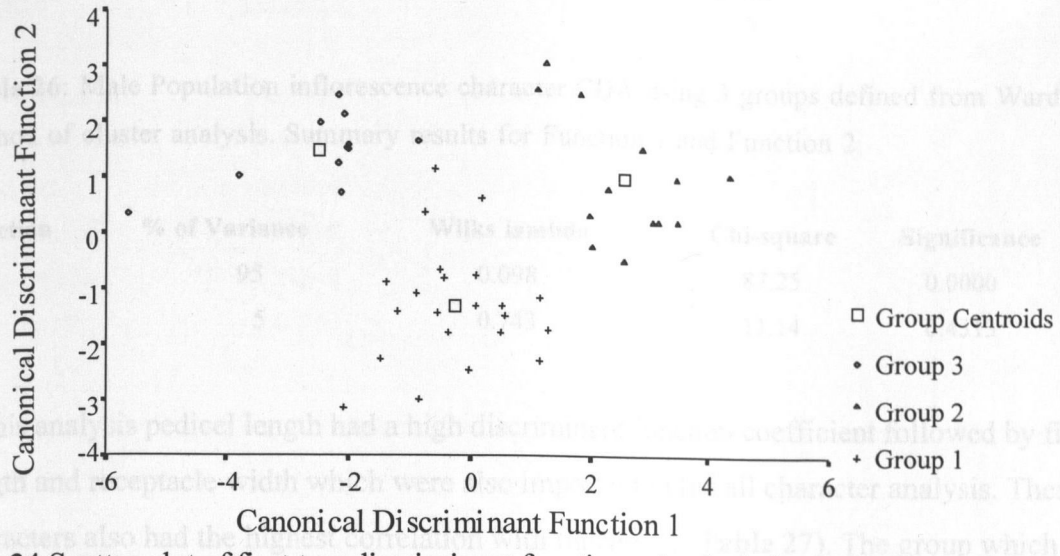


Fig.34 Scatter plot of first two discriminant functions. Analysis for male individuals of *Dt. varians* using vegetative and floral characters. Groups were specified from a cluster analysis using Ward's method (**Fig. 32**) where three groups were saved.

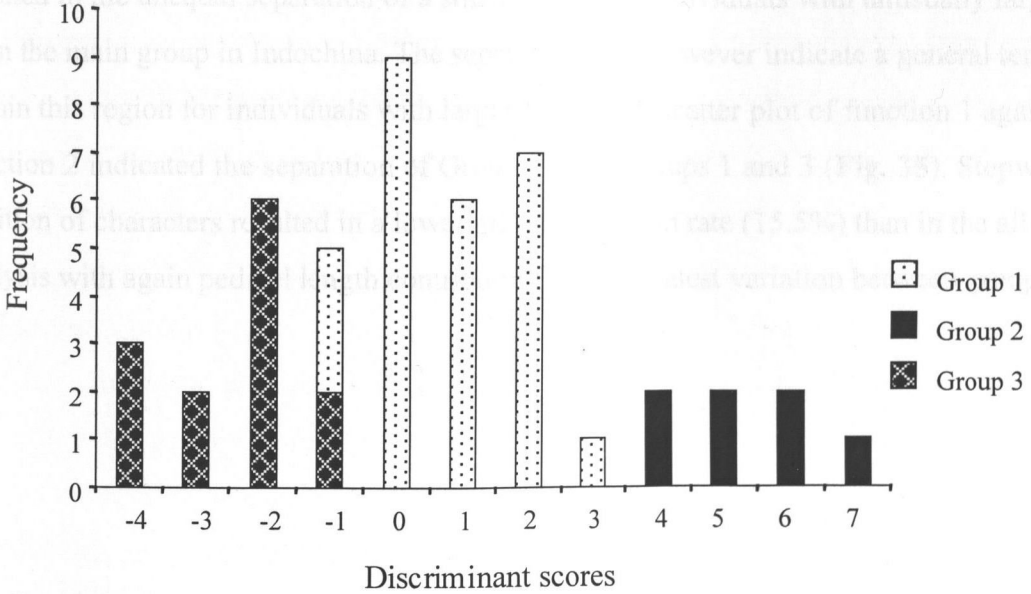


Fig. 35 Histogram of frequency of discriminant scores for first discriminant function. Analysis for male individuals of *Dt. varians* using inflorescence characters. Groups were specified from a cluster analysis using Ward's method (**Fig. 33**) where three groups were saved.

value for Wilks lambda (0.1) with a high Chi squared value (87.2) meant that this function was highly significant. Function 2, on the other hand, was not significant and did not contribute to the between group differences (**Table 26**).

Table 26: Male Population inflorescence character CDA using 3 groups defined from Ward's method of cluster analysis. Summary results for Function 1 and Function 2.

Function	% of Variance	Wilks lambda	Chi-square	Significance
1	95	0.098	87.25	0.0000
2	5	0.743	11.14	0.4313

In this analysis pedicel length had a high discriminant function coefficient followed by filament length and receptacle width which were also important in the all character analysis. These three characters also had the highest correlation with function 1 (**Table 27**). The group which contained a small number of taxa from Indochina (Group 2) had the highest mean discriminant function which implies that this group contains individuals with large flowers. At the other extreme the group, which consisted of all Malesian taxa (Group 3), had the lowest canonical discriminant function and therefore represents those individuals with smaller flowers. The largest group (Group 1) which contained a mixture of specimens from both regions was intermediate between the two (**Table 28**). The smaller sample size of male plants may have resulted in the unequal separation of a small number of individuals with unusually large flowers from the main group in Indochina. The separation does however indicate a general tendency within this region for individuals with larger flowers. A scatter plot of function 1 against function 2 indicated the separation of Group 2 from Groups 1 and 3 (**Fig. 35**). Stepwise addition of characters resulted in a lower misclassification rate (15.5%) than in the all character analysis with again pedicel length contributing to the greatest variation between groups.

Table 27: Male Population standardized discriminant function coefficient for inflorescence characters CDA (Column A) and correlations between characters and Function 1 (Column B).

Character	Column A	Column B
Pedicel length	0.89929	0.66264
Filament length	0.65352	0.42567
Receptacle width	0.44396	0.43811
Tepal width 2	- 0.39844	0.13215
Anther length	0.20208	0.16491
Pedicel width	- 0.19648	0.19964
Tepal length	- 0.07262	0.33425

Table 28: Male Population. Canonical discriminant function for function evaluated at group means for inflorescence characters CDA.

Group	Function 1
1 (Malesia and Indochina)	0.19164
2 (Malesia)	- 3.00459
3 (Indochina)	4.86814

Principal Components Analysis

When all of the characters were included in the analysis the first two axes accounted for 51% of the variance. They were also the only significant axes according to Frontiers broken stick model (**Appendix 10**). On axis 1 the characters which had the highest eigenvalues and therefore contributed to the greatest between groups variation were floral characteristics (receptacle width, tepal length, filament length and pedicel length) (**Table 29**). These characters correspond to those indicated by the discriminant analysis. In a similar manner to the discriminant analysis the vegetative characters contributed to the variation on axis 2 (leaf w1, leaf length, distance between veins, leaf width 2). Leaf width 1 is however correlated with two other leaf characters, distance between veins and leaf length, which may account for the high eigenvalues for vegetative characters on axis 2. When the clusters indicated by Ward's method were superimposed on a scatter plot of axis 1 and axis 2 a similar pattern emerged to the discriminant analysis (**Fig. 36**). The groups that comprise taxa from Indochina on one hand and Malesia on the other are at the extremes of the group which consists of a mixture of individuals from both areas.

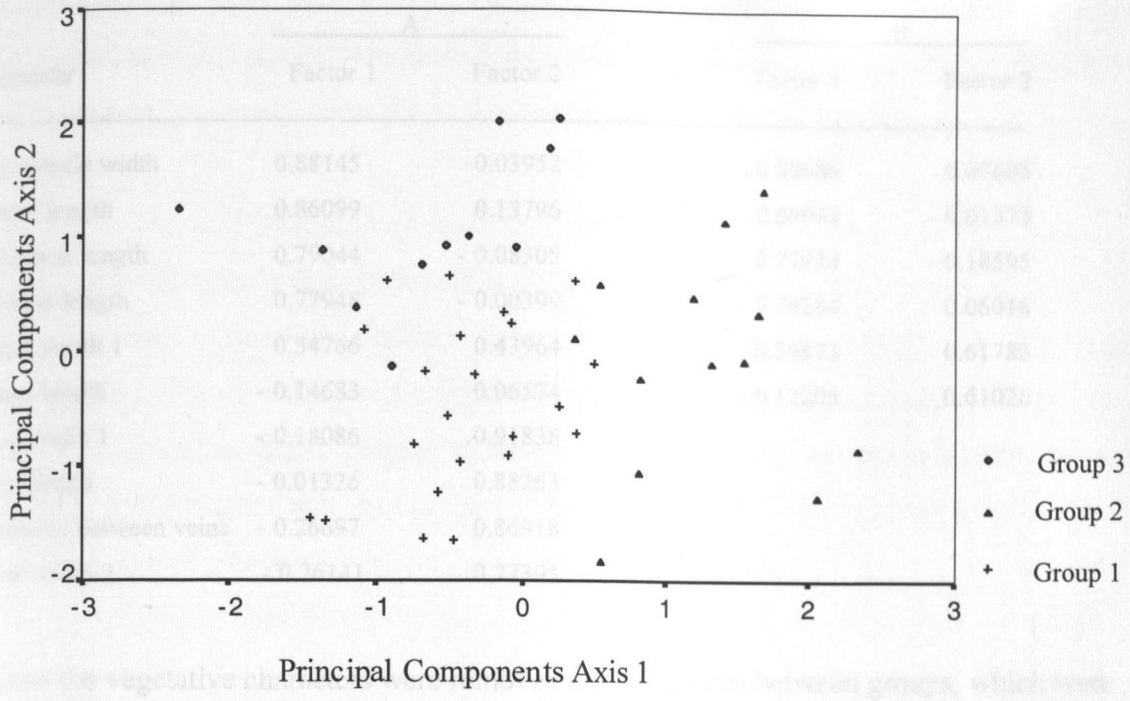


Fig. 36 Scatter plot of first two principal axes from PCA of male individuals of *Dt. varians* using vegetative and floral characters. Groups correspond to those indicated by cluster analysis using Ward's method (**Fig. 32**).

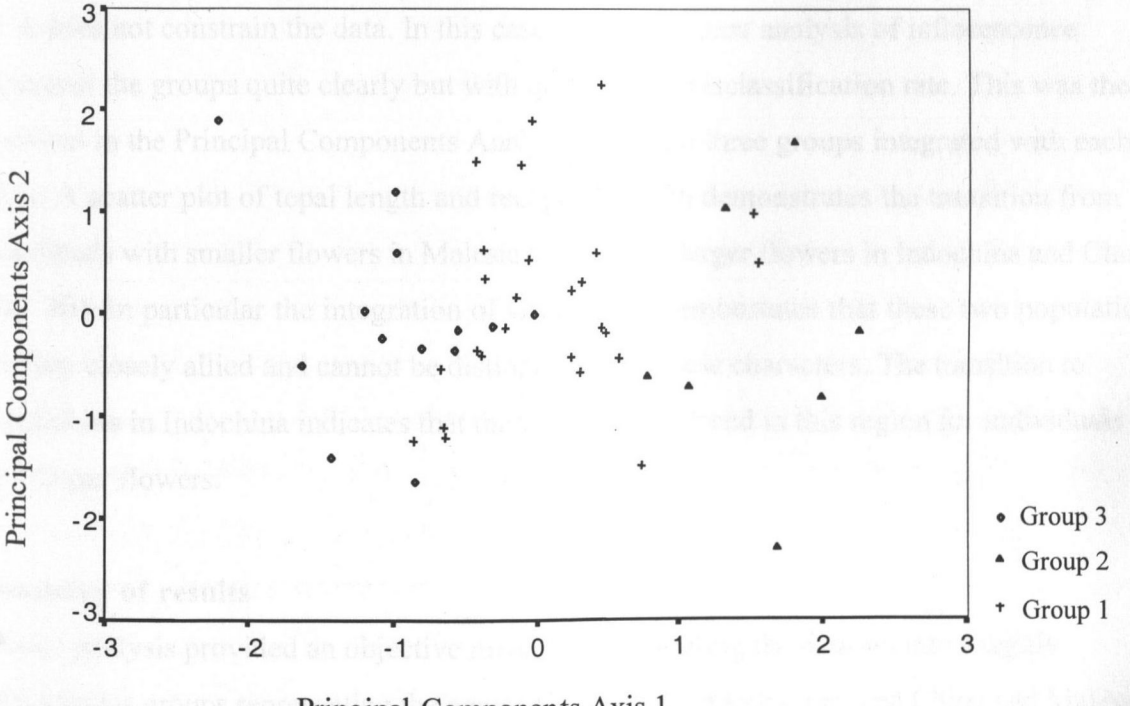


Fig. 37 Scatter plot of first two principal axes from PCA of male individuals of *Dt. varians* using inflorescence characters. Groups correspond to those indicated by cluster analysis using Ward's method (**Fig. 33**).

Table 29: Male Population Principal Components Analysis. Eigen values for first two Principal Axes for all character analysis (A) and inflorescence characters (B) only

	A		B	
Character	Factor 1	Factor 2	Factor 1	Factor 2
Receptacle width	0.88145	0.03952	0.88686	0.07605
Tepal length	0.86099	0.13796	0.86941	- 0.01575
Filament length	0.79044	- 0.08305	0.77414	- 0.18595
Pedicel length	0.77948	- 0.00399	0.76284	0.06016
Bract width 1	0.54766	0.43964	0.59823	0.61783
Bract length	- 0.14683	0.06574	- 0.12206	0.61026
Leaf width 1	- 0.18086	0.91838		
Leaf length	- 0.01326	0.88263		
Distance between veins	- 0.26697	0.86918		
Leaf width 2	- 0.26141	0.77393		

When the vegetative characters were removed the differences between groups, which were indicated by the discriminant analysis, disappear to a certain extent and there is no clear pattern of regional variation (**Fig. 37**). This demonstrates the basic difference between the two techniques, CDA will always assign an individual to one a specified number of groups whereas PCA does not constrain the data. In this case the discriminant analysis of inflorescence separated the groups quite clearly but with quite a high misclassification rate. This was then mirrored in the Principal Components Analysis where all three groups integrated with each other. A scatter plot of tepal length and receptacle width demonstrates the transition from individuals with smaller flowers in Malesia to generally larger flowers in Indochina and China (**Fig. 38**). In particular the integration of Groups 1, 3 demonstates that these two populations are very closely allied and cannot be distinguished on these characters. The transition to populations in Indochina indicates that there is a general trend in this region for individuals with larger flowers.

Summary of results

Cluster analysis provided an objective manner for separating the data set into roughly homogenous groups representing the geographic regions of Indochina and China and Malesia. The different clustering techniques, which were employed, gave similar results indicating a

strong phenetic signal in the data. The inclusion of solely inflorescence characters in the analyses resulted in a better separation of geographical regions for female individuals but this did not hold true for the male individuals. The difference between the analysis of male and female plants in this respect may have been be due to the lower sampling density for male individuals and the fewer floral characters available for measurement.

In general Canonical Discriminant Analysis provided the best separation of Chinese and Indochinese individuals from populations in Malesia. The overlap between geographical regions in terms of floral and vegetative characters indicated however that the separation is not absolute. In particular Principal Components Analysis indicated a closer affinity between individuals from the various geographic regions, which was not apparent in the Discriminant Analysis. The reticulate nature of character distribution may be due to historical climatic factors as well as genetic drift within isolated small populations.

Discussion

The absence of qualitative characters, which can be used to discriminate between individuals in this analysis, indicates that the current classification of *Dt. varians* as a widespread but variable species is correct. The fact that a large number of taxa have been described which are synonymous with this species illustrates the wide range of variation in terms of vegetative and reproductive characters *Dt. varians* is capable of exhibiting.

The paucity of quantitative characters which could be measured (female plants 19 characters, male plants 17 characters) (**Table 13**) also demonstrates the difficulty when working with parasitic species where vegetative and floral characteristics are reduced and generally uniform. The small number of characters in this analysis also calls into question the reliability of the results as the number used falls far short of the 60 which is recommended for morphometric analyses. Another difficulty in interpretation of the analyses arises with the presence of autocorrelations in the data. A number of vegetative (leaf length and width) and inflorescence characters (fruit width and endocarp width) were highly correlated and these characters turned out to be the most important discriminating characteristics. The fact that these characters contributed to most of the variation between groups may have been because in CDA and PCA correlated characters are given extra weight (Legendre & Legendre 1998). The results may

therefore have been strongly biased by the inclusion of these characters. On balance they were not removed from the analyses due to the general paucity of characters which could be measured. Despite the presence of correlations, however, and the few number of characters which could be measured, the general variability of *Dt. varians* has been demonstrated and some tendencies within particular geographic regions have been demonstrated.

Variation and relationship to phenotypic plasticity and genetic canalisation

The current distribution of *Dt. varians* is from southern China to northern Australia which marks it as the most widespread species of Santalaceae in Southeast Asia. The majority of Santalaceae occur in narrow habitats. In particular the dendroparasites, to which *Dt. varians* is allied, are often associated with particular plant species or plant communities. *Dendrotrophe varians* however does not appear to conform to this pattern and can be found in a variety of locations from beach and peat swamp vegetation to the stable environment of montane evergreen forests. It therefore appears to have wide habitat preferences and has adapted to diverse environmental conditions. Closer examination indicates, however, that at lower elevations *Dt. varians* occurs in marginal habitats or those that require some kind of adaptation to nutrient limitation or water stress. For example in Borneo it is often found in kerangas or heath forest which corresponds to a sclerophyllous vegetation type formed on free draining siliceous soils (Morley 2000). It is also occasionally found in peat swamps where there is low nutrient availability due to the slow decompositional nature of the soil (Moore et al 1991).

Phenotypic plasticity has been defined as the existence within a population of a genotype that can exhibit morphological, physiological or behavioral variation when allowed to develop in different environments (Guntrip & Sibley 1998). The potential responses a plant may display under different environmental conditions depends on the life history and genetic background of the individual, other contributory factors include the predictability of the environment and genetic drift (Zhivotovosky et al 1996). The fact that *Dt. varians* occurs in diverse habitats may then be attributed to a high potential genetic variability which have enabled it to survive under a variety of environmental conditions. The fact that it is also a hemiparasite and therefore relies on other plants for some water and nutrients may have also reduced selection pressures, which would have excluded it from particularly extreme environments.

In most cases in the Santalaceae niche partitioning and the exploration of new ecosystems has led to speciation events (*Dendromyza*, *Dufrenoya*). *Dendrotrophe varians* has instead adopted a generalist strategy which means that it exhibits a range of growth forms in a wide range of ecosystems (van Tienderen 1997, Stanton et al 2000). The proof that *Dt. varians* is a generalist species is reinforced by the fact that it co exists with several other species from the same genus: *Dt. buxifolia* from southern Thailand to Borneo and *Dt. arfakensis* in New Guinea.

The fact that the integrity of this species has been maintained despite a variety of selection pressures may be due to genetic canalisation which is the reduced expression of genetic variation at the level of the phenotype or in other words imperfect adaptation (Kawecki 2000). The existence of canalisation has be deduced from the fact that in natural populations, and to a certain extent in controlled environments, most characters exhibit a degree of variability and individuals are not perfectly adapted to their surroundings. If populations become perfectly adapted to a particular environment their potential genetic variability will be reduced and they will not be able to respond if environmental conditions change suddenly. The advantage of canalisation or maladaptation is that as an environment changes the population can adjust to it, albeit imperfectly. Decreasing the response to selection therefore increases the chance of survival in changing environments.

In *Dt. varians* the effect of canalisation may be observed through the fact that groups of morphologically similar individuals do not appear to correspond to any particular vegetation type and there was no relationship between environmental conditions or altitude in any of the characters which were measured in this analysis. Of course certain responses to environment such as plant height and flowering phenology were not measured but the overall picture appears as a reduced response to environmental conditions. The reduced sensitivity to environmental selection pressures may have also been responsible for the paucity of speciation events within *Dendrotrophe* as a whole.

Relationship to climate and geological factors

The variability within *Dt. varians* may not therefore be attributed to environmental factors and it is more likely due to geographic isolation of populations and the historical geological instability of Southeast Asia. The fact that there are no absolute measures of quantitative

difference between populations from different geographic regions may be due to changes in sea levels and climatic conditions which resulted in the isolation and reintegration of populations through time. The same phenomenon has been observed in *Aquilegia* L. in the southwest USA and Mexico where populations were found to be genetically distinct due to lack of gene flow between them (Strand et al 1996). Throughout geological time however changing environmental conditions have periodically resulted in the isolated populations coming into contact with each other. In *Aquilegia* L. the lack of gene flow between populations has led to diverse forms occupying each geographic area. In *Dt. varians* the effect of genetic drift may be responsible for the variation which can be observed within different geographical regions. The fact that the species as a whole possesses the same genetic variability the emergence of similar forms in geographically distant areas is not therefore surprising.

Despite the fact that there is considerable variability in the species as a whole there are certain trends within specific geographic areas which indicates that isolation has resulted in the differentiation of particular morphological traits. In particular in the Discriminant Analysis it appeared that although the species as a whole is quite homogenous certain trends in morphological characters could be observed between different regions. In Indochina and China there is a tendency towards larger flowers and fruits and to a certain extent longer, narrower leaves. In Borneo and eastern Malesia on the other hand flowers and fruits are generally smaller.

The whole of the Southeast Asia has been subjected to considerable geological and environmental fluctuations, which has resulted in it being one of the most floristically rich and diverse areas in the world (Morley 2000). It has been postulated that an ancestor of *Dt. varians* migrated from the Indian subcontinent following the mid Eocene (45 Ma) collision of Gondwanaland with Laurasia (**Chapter 3**). Favourable climatic conditions at that time resulted in the migration of many taxa, along mountain ranges, via the Malay Peninsula into Borneo and Java (Morley 1998) and is certainly possible that a precursor of *Dt. varians* was amongst them. If this theory is true the species has a long history in Southeast Asia. In the early Miocene (25 –23 Ma) there was considerable subsidence in the region reducing the land area considerably and resulting in the migration of upland plants into lowland regions, cooler periods during that time may also have resulted in the migration of montane taxa into lowland

areas (Morley 2000). If *Dt. varians* was amongst the montane contingent which migrated into Southeast Asia it may have moved to lower elevations at that time. The fact that there are populations which occur in montane regions which have been postulated as refugia (northwest Borneo, northern Sumatra and the southern Malay Peninsula) during generally unfavourable climatic conditions (Brandon Jones 1996, Morley 2000) may indicate that this has occurred. At a later stage in the mid Miocene (16 Ma) there were record high sea levels and warm climatic conditions in Southeast Asia which may have led to the separation of Borneo from the Malay Peninsula. There are certainly indications that large portions of Vietnam were submerged in shallow sea at that time (Morley 2000). Fresh water swamps, which are now represented in smaller isolated pockets throughout the region, were also particularly widespread at that time. Throughout the Miocene (25 - 5 Ma) although the climate was generally warm and wet there were short-lived dry spells which supported a more open savannah vegetation (Morley 1998). In terms of *Dt. varians* the changing environmental conditions may have been responsible for forcing the species to explore new habitats such as kerangas and peat swamps.

In more recent geological time dryer cooler climatic conditions in the Pliocene (5 Ma – Present) resulted in the reformation of a land bridge between the Malay Peninsula, Indochina and Borneo which provided the opportunity for the reintegration and genetic exchange between the two populations (Hall 1998). In particular in the last 3 million years there has been considerable fluctuations in temperature and climatic conditions in Southeast Asia. It has been postulated that the diversification of the floristic composition has been ameliorated as a result of successive reformation of lowland vegetation communities following the submergence and emergence of these areas following periods of sea level lowstand and highstand (Morley 2000, Ridder Numan 1995, 1998). The variation within *Dt. varians* may also be attributed to the response to sea level changes, particularly as its present day distribution is concentrated in lowland areas. With the fluctuations in land areas populations may have become isolated and subsequently reintegrated. The genetic composition of the species would also have changed as new populations were established from different genotypes. The movement of communities from montane regions to lowland areas during cooler phases would also have resulted in gene flow between populations at different altitudes.

Conclusions

The general picture, which has emerged from this analysis, is of a very variable species which has adopted a generalist strategy of adaptation to diverse environmental conditions. The lack of a coherent pattern in terms of morphological characteristics in relation to habitat may be due to the genetic effect of canalisation which reduces phenotypic expression in specific environments. The effect of genetic drift within isolated populations has also resulted in a variety of expression of morphological characteristics in similar geographic locations. The species has been present in Southeast Asia for a considerable time and the climatic, sea level changes and tectonic activity have also had an effect on the variability of the species and may explain why it occurs in a variety of diverse habitats. The trends which have been observed in this study in terms of fruit and flower size in Indochina and Malesia are a reflection of the isolation and subsequent homogenisation of the species in response to changing environmental and tectonic conditions over a long period of time.

Taxonomic history

Species of Santalaceae have often been ascribed to diverse families due to the reduction and uniformity of floral characteristics. The variable position of the ovary along with misinterpretation of reproductive structures has meant that genera have moved between different tribes and the delimitation of the family has expanded and contracted within different taxonomic treatments. For example in an extreme case, the tribe Anthoboleae was described as a separate family within the gymnosperms (Gagnepain & Boureau 1947). An outline of the taxonomic evolution of the family with particular reference to the Southeast Asian genera is given in **Table 30**.

Linnaeus recognised three genera of Santalaceae in his first edition of Species Plantarum (Linnaeus 1753). *Osyris* he placed in Dioecia Triandria and *Thesium* he assigned to Pentandria Monogynia. *Santalum* was described from the Prodromus fasciculi rariorum plantarum of Breynius (1680). Linnaeus, however, mistook the origin of *S. album* as being from India rather than eastern Malesia and this error has persisted in many writings to the present day. The confusion surrounding the origin of this species arose due to the fact that *Santalum* has been historically cultivated in India for its valuable aromatic oil and timber.

Jussieu (1789) was the first person to group together four Santalaceous genera under Eleagni which also included elements of what is now the Elaeagnaceae and other members of the Proteales. The features of this group include many of the characteristics which can be used to delimit the Santalaceous tribe Santaleae *i.e.* the absence of a corolla (all Santalaceae), a semi-inferior ovary, alternate leaves, a simple style and unisexual flowers. Jussieu placed *Santalum* with the Onagreae which included many members of the Myrtales. The lobes of the nectarial disc in *Santalum* are prolonged between the perianth segments and the disc is usually brightly coloured. Jussieu interpreted the nectary of *Santalum* as being the corolla and the perianth he considered to be a calyx. Although this interpretation is incorrect it has been suggested since that the nectary of the Santalaceous flower is derived from a corolla (Kuijt 1969).

Table 30: The taxonomic evolution 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*, *Dendromya*, *Dufrenoya*, *Phacellaria*) and is now contained within a separate tribe: Amphorogyneae.

Linnaeus 1753	Jussieu 1789	Brown 1810	Blume 1850	Miquel 1856	A. De Candolle 1857	Bentham 1883	Danser 1940	Stauffer 1969
Octandria Monogynia	**Onagrae** (O)	**Santalaceae** (F)			**Buckleyeae** (T)			
Santalum	*Santalum*	*Santalum*		*Santalum*	**Santaleae** (T) *Santalum*	**Osyrideae** (T) *Santalum*		
Dioecia Triandria	**Elagineae** (O)			*Scleropyrum*	*Scleropyrum*	*Scleropyrum*		
Osyris	*Osyris*	*Osyris*			*Osyris*	*Osyris*		**Amphorogyneae** (T)
			Henslowia	*Dendrotrophe*	*Henslowia*	*Henslowia* *Phacellaria*	*Dendrotrophe* *Phacellaria* *Hylomyza* *Cladomyza* *Dendromyza*	*Dendrotrophe* *Phacellaria* *Dufrenoya* *Cladomyza* *Dendromyza*
Pentandria Monogynia						Thesieae (T)		
Thesium	*Thesium*	*Thesium*			*Thesium*	*Thesium*		
					Anthoboleae (T)	**Anthoboleae** (T)		
		Exocarpos		*Exocarpos*	*Exocarpos*	*Exocarpos*		

F = Family; O = Order; T = Tribe

In his Flora Nova Hollandia Brown (1810) described elements of the Eleagni plus *Santalum* as a new family, Santalaceae. 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 a unilocular ovary with pendulous ovules. Two Australian genera were also newly described by Brown at that time. The genera *Exocarpos* and *Anthobolus*, which are also of Australian origin, were recognised as allied to the Santalaceae but differentiated by a superior ovary with a single ovule. *Olax* (Olacaceae) was also considered as an allied genus which differed by the possession of a calyx and corolla. Allied families, at that time, included Thymelaceae and Proteaceae. Brown's description was comprehensive and contains most of the essential elements of the Santalaceae as known today. The parasitic nature of the family and the variable position of the ovary, were however not recognised by him.

Arnott described the Southeast Asian genus *Scleropyrum* (1838) from *Tirri itticanni* of Rheede's Hortus Malabaricus which was written between 1678 – 1684. In this comprehensive work Rheede described 690 plant species in 12 volumes with 793 illustrations which included depictions of fruiting specimens and analyses of flowers, fruits and seeds. This work is considered as the first comprehensive account of the plant resources of the Indian subcontinent (Nicholson et al 1988).

In 1850 Blume separated the Southeast Asian genus *Henslowia* from *Viscum* of the Loranthaceae. He also included *Scleropyrum* in his description of Malesian plants. 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. The separation of *Henslowia* from *Viscum* also indicated a relationship bewteen the Santalaceae and Viscaceae. Blume described 8 species of *Henslowia* which was later reduced to six by Miquel (1856) who realised that the genus name was a homonym of *Henslowia* Wallich (1832). Miquel renamed *Henslowia* Bl. as *Dendrotrophe* and the species he described now include elements of the genera *Dendromyza* and *Dendrotrophe*.

In his Prodromus Alphonse de Candolle (1857) treated 208 species in 18 genera of Santalaceae, producing the first comprehensive account and detailed description 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 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. He described four tribes, the first Anthoboleae, corresponded to that of de Candolle whilst two others, Osyrideae and Thesieae, contained elements of the Santaleae. The last tribe, Grubbieae, was accepted as anomalous within the Santalaceae and placed with it based on the fact that the species contained in it were parasitic. Grubbiaceae is now considered as a small monogeneric family from South Africa with greater affinities to the Ericales than the Santalales (Heywood 1997). The characters which Bentham used to delimit the first three tribes are still used today in the supra-generic 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. The Osyrideae was further subdivided based on the shape of the nectary and the morphology and mode of dehiscence of the anthers.

Pilger (Pilger 1935) did not deviate much from the scheme of Bentham but excluded *Myzodendron* and *Grubbia* in his conspectus of the family. In his scheme the Osyrideae was also further subdivided in a more comprehensive way based on the presence or absence of glandular hairs in the flowers, the distribution of the sexes, the topography and mode of dehiscence of the anthers and the structure of the inflorescence. The scheme was, however, rather artificial and cumbersome, as the reticulate distribution of characteristics within genera was not identified.

Focusing on the Southeast Asian species, Danser completed a revision of *Phacellaria* in 1939, describing in great detail the inflorescence morphology of the species and 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. Danser described eleven new species of stem parasites in his revision, and later added a further eight in his investigation of the eastern Malesian genera *Dendromyza* and *Cladomyza* (Danser 1940, 1955). In this paper the variation in fruit structure of *Cladomyza* was illustrated and a key to the species was provided. The changes in specific boundaries and the addition of more material to herbarium collections has meant that this key is now obsolete. The species of *Dendromyza* and *Cladomyza* which were described by Danser were often based on incomplete material which lacked either male or female inflorescences and sometimes species were described from a single, poorly preserved specimen. Several species have consequently been reduced to synonyms as more material is collected and the variation within species is better understood.

A tribal revision of the Anthoboleae was produced in 1959 by Stauffer (Stauffer 1959) who also investigated elements of the African and South American Santalaceae (Stauffer 1961). Stauffer was probably the most important contributor to the taxonomy of the family in the middle part of the 20th century. His investigations of groups of South African genera involved detailed descriptions of their inflorescence and floral morphology. The studies were however conducted in isolation from each other and relationships between the groups and to other members of the Santalaceae were not discussed. In his study of the South American genera Stauffer concluded that the boundaries between the Thesieae and the Osyrideae could not be justified as the variability within Thesieae was such that several characteristics overlapped with the Osyrideae. The two tribes have however been maintained as separate entities and the suggestion that the boundaries between the tribes are artificial has not been investigated.

In 1969 Stauffer furthermore described the tribe Amphorogyneae from the Osyrideae which includes all of the stem parasitic genera 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. In more recent times descriptions of the family have sometimes excluded the Amphorogyneae, although this may be due to the fact that it was published in the German language and not widely distributed. Questions still arise however as to the status of this tribe and further investigations are required to establish its exact status. This could only be achieved however in the context of a full familial revision. The tribe Osyrideae as recognised by Bentham has also been reduced to a synonym of Santaleae as described by de Candolle (Hewson & George 1984, Heywood 1997).

In general it can be said that the Santalaceae as a whole has not been thoroughly investigated. Embryological studies in the 1950s and 1960s indicated that several genera exhibited characters which were not consistent with the family (Bhatnagar 1960, Johri & Agarwal 1965). Recent molecular evidence has now demonstrated that the family is indeed paraphyletic with the Southeast Asian genera forming a monophyletic group with a small family of aerial parasites, Eremolepidaceae, from South America. At present, the most recent classifications of Mabberley (1997) and Heywood (1997) recognise three tribes: Santaleae, Anthoboleae and Thesieae with between 400 – 540 species in 34 –35 genera. The majority of the species (325) are attributed to *Thesium*. This genus is however notoriously difficult and complex and has never been subjected to a comprehensive revision. It is probable therefore that the more conservative estimate comes closer to the true number. An entire familial revision is now required to establish the boundaries of the family and a review is necessary of the tribes Santaleae and Amphorogyneae.

Characters of taxonomic importance

Within the Southeast Asian taxa there are several disparate groups and the characteristics which have been used to define them are often variable. In terms of generic boundaries at least five of the genera are easily identifiable and can be easily distinguished using a combination of vegetative and floral characteristics (**Table 31**). The genera within tribe Amphorogyneae, however, are not so easily distinguishable and many of the characteristics used to identify Santalaceous genera are not applicable to the genera in this tribe. These characters are used rather in infra-generic classification.

Habit

The growth habit of the species is variable and their ecology can be of significant importance at the tribal and to a certain extent generic level. Tribes Santaleae and Anthoboleae contain arborescent and shrubby genera whilst Thesieae is represented by one small herbaceous species. The tribe Amphorogyneae, however, contains four genera which are all climbing or branch parasites. Within this group the genus *Dendrotrophe* contains species which are very variable in their growth habit and almost all of the species can be terrestrial, climbing or dendroparasitic and only one species is consistently dendroparasitic. The other three genera *Dufrenoya*, *Phacellaria* and *Dendromyza* are all aerial parasites with shrubby and climbing growth forms and display a degree of host specificity. *Phacellaria* may also possess the capability for some endophytic growth and shoots have been observed to emerge through lenticels along the branches of a host plant. The presence of secondary haustoria on the stems is diagnostic for *Dendromyza* and geographically this genus is mostly confined to eastern Malesia.

Stems and branches

Branching is dichotomous although characteristically amongst the aerial parasites several branches may arise from a single thickened node. Within the majority of the species the juvenile branches are constricted and bracteate at the base and the nodes appear articulated or jointed, although this articulation is usually confined to the Amphorogyneae. A typical feature of all the genera is the flattening of juvenile branches towards the apex. This may provide a wider area for photosynthetic activity, particularly as many of the species are only sparsely leafy. These flattened stems are usually longitudinally grooved and older branches can be quite

Table 31 Distribution of characters between genera. These characteristics are the most important in generic delimitation and can be used in combination to assign species to genera. Tribe Amphorogyneae is generally not so easy to identify and fruit characters play an important role in generic identification.

Tribe	Genus	Habit	Leaf venation	Inflorescence branching	Sexual distribution	Ovule number	Fruit shape	Mesocarp consistency
Amphorogyneae	*Dendromyza*	Dendroparasite	Curvipalmate	Umbellate/sessile cluster/ 1 - flowered	Monoecious/ Dioecious	Four/five	Ovoid	Membranous/sericeus/ apical tails present
Amphorogyneae	*Dendrotrophe*	Shrub/climber/ dendroparasite	Curvipalmate	Racemose (raceme/panicle/ umbel)	Hermaphrodite/ Dioecious	Four - six	Globose/ ellpitic	Fleshy
Amphorogyneae	*Dufrenoya*	Dendroparasite	Curvipalmate	Umbellate	Dioecious	Four - six	Obovoid/ ovoid	Membranous/ sericeus
Amphorogyneae	*Phacellaria*	Dendroparasite	absent	sessile	Monoecious/ Dioecious	Four - six	Oblong/ ovoid	Sericeus
Santaleae	*Osyris*	Shrub	Curvipinnate	Cymose	Dioecious	Three	Globose	Fleshy
Santaleae	*Santalum*	Tree	Compound rectipinnate	Cymose	Hermaphrodite	Four/ five	Globose	Fleshy
Santaleae	*Scleropyrum*	Tree	Pinnate (multi-arcuate)	Racemose (catkin)	Dioecious	Three	Pyriform	Fleshy
Anthoboleae	*Exocarpos*	Tree	Curvipalmate	Racemose (spadix)	Hermaphrodite	One	Globose	Fleshy (thin)
Thesieae	*Thesium*	Herb	absent	1 - flowered	Hermaphrodite	Four	Globose	Fleshy (thin)

distinctly different to the young growth. They are generally terete, smooth or with longitudinal fissures which can be a different colour to the outer bark. Within *Dendromyza* and *Dufrenoya* the stems may also be pustulate and the bark may be muricate with peg–like projections or have a papillose indument. *Scleropyrum* has one species whose trunk and branches are armed with spines which may be several centimetres long and are a defining characteristic.

Leaves

The leaves are generally spirally arranged or may be alternate and rarely opposite. They are usually fleshy, always with entire margins, elliptic to orbicular in shape and may be mucronate at the apex. In *Thesium* the leaves are reduced to phylloclades, whilst in the Santaleae and Anthoboleae the leaves are generally larger with pinnate and palmate venation respectively (in Australia the Anthoboleae often have reduced leaves). In the Amphorogyneae there is considerable variation in leaf dimensions. Some species have leaves of similar size to *Scleropyrum* and *Santalum*, whilst in the majority of species they are much smaller, and in extreme cases, bract-like e.g. in the genus *Phacellaria*, photosynthetic activity is carried out by the stems and minute bracts. Within the rest of the Amphorogyneae leaf venation is curvipalmate with 3 - 11 primary veins (**Fig. 39**). In some species the leaf is greatly thickened and the veins can become obscured. In general however 3 - 5 primary veins are usual. The genus *Dendromyza* exhibits the greatest variation in leaf shape and size from large leaves up to 80 mm long to bract-like leaves.

Hair covering

The presence of an indument on the leaves or stems is generally of little diagnostic value as most of the Santalaceae are primarily glabrous. In Southeast Asia, however, the genus *Scleropyrum* has an indument of simple hairs on its leaves, inflorescences and young stems. Previously the density of this indument has been used to delimit the species within this genus. On careful examination, however, the quantity of indument appears to be continuously variable throughout the species. In the Anthoboleae *Exocarpos* possesses an indument of tufted hairs on its stems, leaves and inflorescences, the perianth of the flowers are also densely papillose. The majority of the Amphorogyneae are glabrous with a few notable exceptions. One species each of *Dendromyza* and *Dufrenoya* have papillose stems and inflorescences.

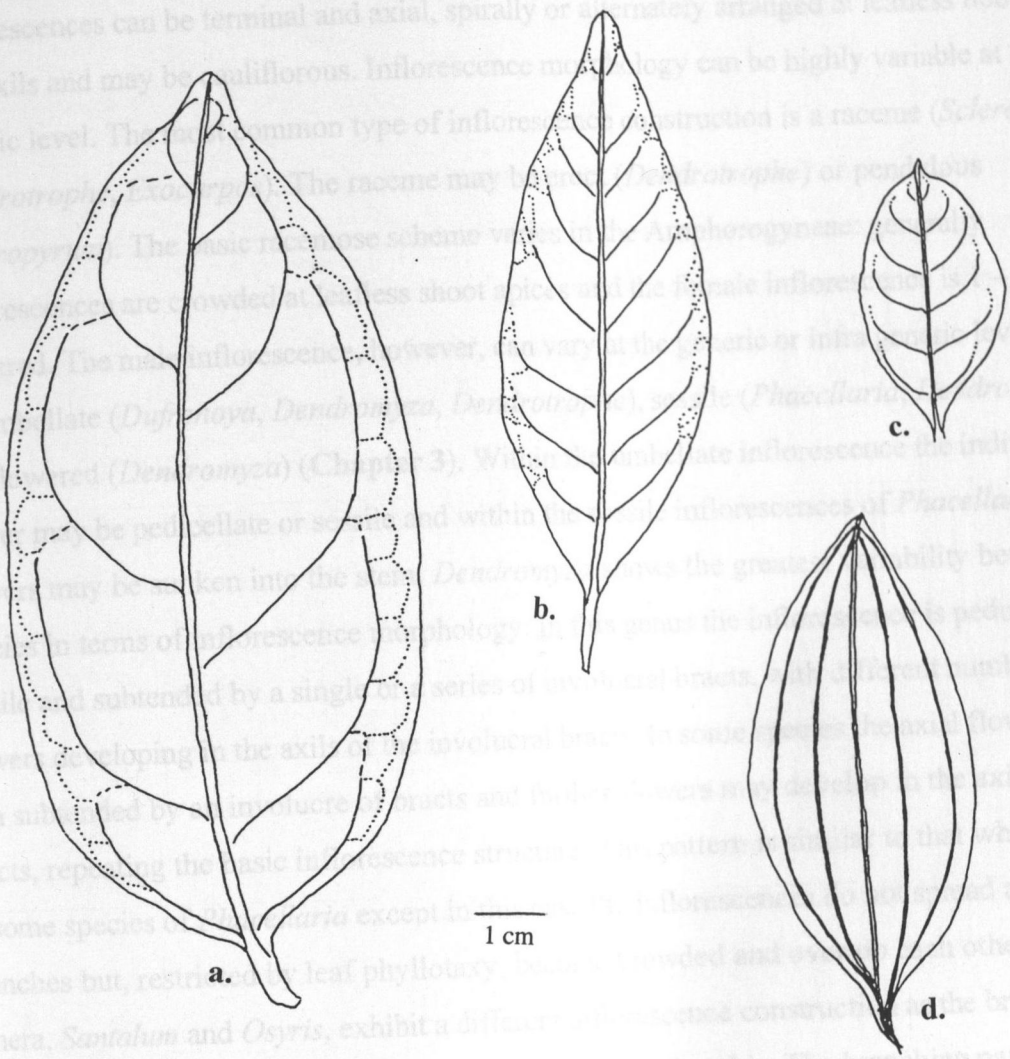


Fig. 39. Leaf primary venation patterns: **a.** Multi-arcuate (*Scleropyrum*), **b.** Compound rectipinnate (*Santalum*), **c.** curvipinnate (*Osyris*), **d.** Curvipalmate (Amphorogyneae, *Exocarpos*).

Phacellaria species generally have a dense, hirsute indument on the young shoots, which may be caducous so that the older branches appear papillate.

Inflorescence structure

Inflorescences can be terminal and axial, spirally or alternately arranged at leafless nodes or in leaf axils and may be cauliflorous. Inflorescence morphology can be highly variable at the generic level. The most common type of inflorescence construction is a raceme (*Scleropyrum*, *Dendrotrophe*, *Exocarpos*). The raceme may be erect (*Dendrotrophe*) or pendulous (*Scleropyrum*). The basic racemose scheme varies in the Amphorogyneae: generally inflorescences are crowded at leafless shoot apices and the female inflorescence is 1 – flowered. The male inflorescence, however, can vary at the generic or infra generic level and can be umbellate (*Dufrenoya*, *Dendromyza*, *Dendrotrophe*), sessile (*Phacellaria*, *Dendromyza)* or 1 – flowered (*Dendromyza*) (**Chapter 3**). Within the umbellate inflorescence the individual flower may be pedicellate or sessile and within the sessile inflorescences of *Phacellaria* the flowers may be sunken into the stem. *Dendromyza* shows the greatest variability between species in terms of inflorescence morphology. In this genus the inflorescence is pedunculate or sessile and subtended by a single or a series of involucral bracts, with different numbers of flowers developing in the axils of the involucral bracts. In some species the axial flowers are in turn subtended by an involucre of bracts and further flowers may develop in the axils of those bracts, repeating the basic inflorescence structure. This pattern is similar to that which occurs in some species of *Phacellaria* except in this case the inflorescences do not spread along the branches but, restricted by leaf phyllotaxy, become crowded and overtop each other. The other genera, *Santalum* and *Osyris*, exhibit a different inflorescence construction as the branching pattern within these genera is cymose *i.e.* with no central rachis. The branching pattern within *Osyris* is a compacted version of that found in *Santalum*.

Bracts

Bracts are confined to the inflorescence and the bases of young shoots. They are usually deltoid or ovate in shape, lanceolate in *Osyris*. The outer surface of the bracts are usually glabrous, tomentose in *Scleropyrum* and densely hirsute in *Phacellaria*. Bracts are generally fleshy but may be membranous in *Dendrotrophe* or papyraceus in some species of *Dufrenoya* where they are partially diagnostic. Bract margins are entire with the exception of *Dufrenoya*

and *Dendromyza* where they are ciliate to a greater or lesser degree. The bracts of the female inflorescence of *Dendrotrophe*, *Dufrenoya, Dendromyza* and *Phacellaria* form an involucre under the flower which may be persistent after flowering although they are usually caducous in species of *Dendrotrophe*. In *Phacellaria* bracts are generally persistent but occasionally withering.

Floral characteristics

Flowers may be hermaphrodite or dioecious, with staminodes or the rudiment of a style present in the female or male flower, either of which can be quite substantial. The perianth is undifferentiated and each perianth segment within the flower is termed a tepal. There are 3 - 6 tepals and the individual tepals are usually sepal like, green or pale yellow in colour. In the majority of the species the perianth and nectary change colour after flowering and become dark red or purple. The tepals are attached to the receptacle which is concave or flat in the male plants and elongated in the hermaphrodite and female flowers. There is usually a group of glandular hairs behind each stamen, emanating from the tepal, which is absent in *Phacellaria* and occasionally in species of *Dufrenoya*, *Dendromyza* and *Dendrotrophe*. The anthers have two thecae, each of which is bilocular. The shape of the anthers and their mode of dehiscence has previously been used to group genera or species (Pilger 1935) as follows:

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

Anthers bi-locular, locules divergent, dehiscence transverse: *Dufrenoya*, *Dendromyza*, *Dendrotrophe*, *Phacellaria*.

However, based on observations in this study, the situation is more variable than originally believed. In *Scleropyrum* the thecae are separated at the top of the filament and in *Osyris* the locules are unequal in size. Within the second group, the Amphorogyneae, the shape and mode of dehiscence of the anthers is generally a characteristic which can be used to group species within genera and can be used in conjunction with other characteristics in the diagnosis of species. Within this group the anther locules may be equal or unequal in size, in a single plane or with anterior and posterior locules and anther dehiscence can be transverse or longitudinal.

In all cases where the style is present in female and hermaphrodite flowers it is simple. The stigma may be lobed, entire or separate. The lobed condition is the most common stigma type and ocurs throughout all of the genera except in *Dendromyza* where the stigmas are separate. In just a few species of *Dufrenoya* the stigma is entire and very large, taking up the centre of the flower.

Pollen morphology

Within the Santalaceae the pollen structure is very variable and can be a diagnostic feature. Within the tribe Santaleae (*Santalum*, *Scleropyrum*, *Osyris*) the pollen grains are generally large, between 19 - 24 μm in polar length (**Chapter 2**). The exine sculpturing is microperforate or rugulate in *Scleropyrum* and perforate in species of *Osyris*. *Santalum* is unique in that the pollen grains of *S. album* are verrucate (wart-like) in the region of the intercolpium. Typically the genera in tribe Amphorogyneae (*Dendrotrophe*, *Dufrenoya*, *Phacellaria, Dendromyza*) have smaller pollen grains, 11 – 16 μm in polar length. Exine ornamentation is very variable within this tribe as a whole but is most useful at a specific rather than at a generic level with exception of *Phacellaria* where species have either rugulate or microperforate pollen grains. In *Dufrenoya* and *Dendrotrophe* pollen can be either rugulate or echinate. There are also differences in polar length between the species which can be used in combination with sculpturing patterns to differentiate between them. *Dendromyza* exhibits the most variability in exine ornamentation and pollen morphology can be used to identify most of the species.

Ovary position and topography

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

convex, 3 - locular and almost sessile in *Osyris*, sagittate and four lobed in *Santalum*. In Thesieae (*Thesium*) the ovary is 4 - locular, the placental column is short and the placental lobes are long and tortuous.

Fruit morphology

The fruit is an indehiscent nut or drupe, usually crowned by a persistent perianth. In *Santalum* and *Osyris* the fruits are globose and almost identical. The main difference between the two is in fruit size and there are also slight differences in the surface sculpturing of the endocarp. The fruits of *Scleropyrum* are pyriform and its species show variation in endocarp surface sculpture from punctate to scabrate. *Thesium* is the only genus in Southeast Asia where the fruit is a nut and the main attractant for dispersal may be the pedicel which is thought to act as an eliasome (Reid et al 1995). In *Exocarpos* (and all of the Anthoboleae) the pedicel becomes fleshy and swollen as the fruit develops. It is usually a contrasting colour to the exocarp of the fruit and is the main attractant for birds which act as dispersal agents. The greatest diversification in fruit morphology exists in the Amphorogyneae where fruit characteristics are used to delimit the genera. In **Chapter 3** the phylogenetic relationships of the aerial members of this tribe have been explored and the taxonomic treatment of this group is based on the findings in **Chapter 3**. In terms of morphology, in *Dendrotrophe* and *Dufrenoya* the fruits are chambered in the apex and the base, the mesocarp is fleshy in *Dendrotrophe* and membranous or sericeus in *Dufrenoya*. In *Phacellaria* the fruits are chambered in the apex only and the mesocarp is similar to *Dufrenoya*. In *Dendromyza* the scheme is quite elaborate: the endocarp may be unilocular or chambered in the base, the mesocarp is almost absent or sericeus, covering the entire endocarp or restricted to the apex and forming a 'beard'. In addition there are long fibres which emanate from the apex of the endocarp and lie along the internal surface of the exocarp. Theses structures have been termed 'tails' and they may be lax or fibrous, pilose or glabrous (**Fig. 15**, **Fig. 16**, **Fig. 40**). The mesocarp of *Dufrenoya* and the 'tails' of *Dendromyza* are probably important in the germination and establishment of young plants on the branches of trees and may have arisen in response to an aerial environment (**Chapter 3**).

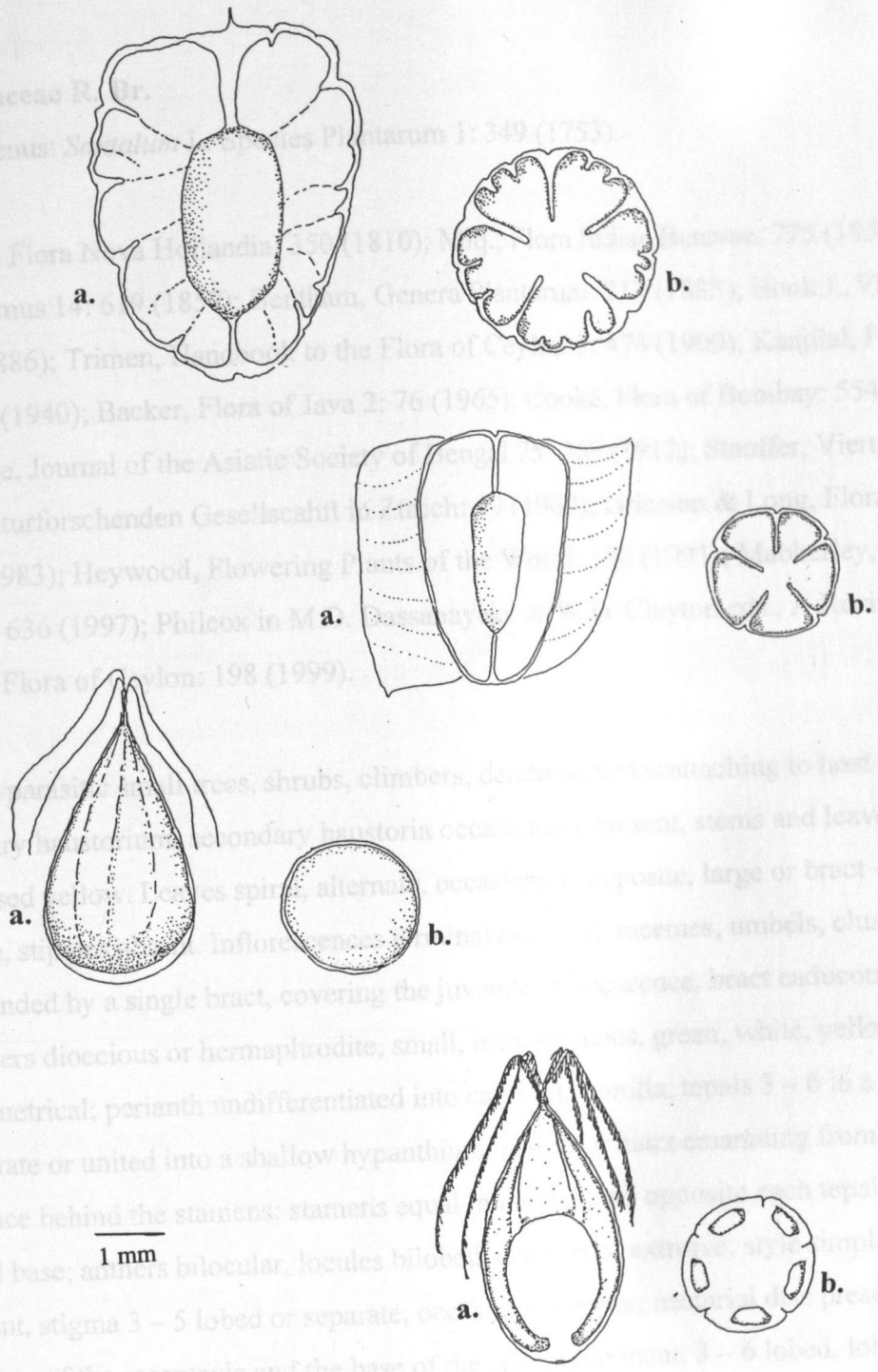


Fig. 40 Endocarp structure of the tribe Amphorogyneae. **1.** *Dendrotrophe*: **a.** the endocarp is chambered in the apex and the base and there are transverse chambers present throughout the endocarp, **b.** transverse section through the endocarp. **2.** *Dufrenoya*: a. the endocarp is chambered in the apex and the base and the mesocarp consists of long membranous strands, which wrap around the endocarp, **b.** transverse section through the endocarp. **3.** *Dendromyza*: **a.** the endocarp is unilocular and there are apical 'tails' emanating from the apex of the endocarp. **b.** transverse section through the endocarp. **4.** *Dendromyza*: **a.** in this case the endocarp is chambered from approximately the mid-point until the base and the apical tails on the endocarp are plumose, **b.** transverse section through the chambered endocarp.

Santalaceae R. Br.

Type genus: *Santalum* L. Species Plantarum 1: 349 (1753).

Brown, Flora Nova Hollandia: 350 (1810); Miq., Flora Indiae Batavae: 775 (1856); A.DC., Prodromus 14: 619 (1857); Bentham, Genera Plantarum: 217 (1883); Hook.f., Flora of India 5: 228 (1886); Trimen, Handbook to the Flora of Ceylon 3: 474 (1900); Kanjilal, Flora of Assam 4: 128 (1940); Backer, Flora of Java 2: 76 (1965); Cooke, Flora of Bombay: 554 (1906); Gamble, Journal of the Asiatic Society of Bengal 75: 269 (1912); Stauffer, Vierteljahrsschrift der Naturforschenden Gesellscahft in Zürich: 49 (1969); Grierson & Long, Flora of Bhutan 1.1: 140 (1983); Heywood, Flowering Plants of the World: 170 (1993); Mabberley, The Plant Book: 636 (1997); Philcox in M.D. Dassanayake & W.D. Clayton eds., A Revised Handbook to the Flora of Ceylon: 198 (1999).

Hemi-parasitic small trees, shrubs, climbers, dendroparasites attaching to host by means of a primary haustorium, secondary haustoria occasionally present, stems and leaves often suffused yellow. Leaves spiral, alternate, occasionally opposite, large or bract – like, margins entire, stipules absent. Inflorescences terminal and axial, racemes, umbels, clusters, cymes, subtended by a single bract, covering the juvenile inflorescence, bract caducous or persistent. Flowers dioecious or hermaphrodite, small, inconspicuous, green, white, yellow, radially symmetrical; perianth undifferentiated into calyx and corolla, tepals 3 – 6 in a single whorl, separate or united into a shallow hypanthium; glandular hairs emanating from inner tepal surface behind the stamens; stamens equal in number and opposite each tepal, adnate to the tepal base; anthers bilocular, locules bilobed; dehiscence extrorse; style simple, terete, or absent, stigma 3 – 5 lobed or separate, occasionally entire; nectarial disc present, covering the surface of the receptacle and the base of the style, prominent, 3 – 6 lobed, lobes short or long, alternating with the tepals; ovary basifixed, variable in position, 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 brightly coloured, mesocarp thin, fleshy, membranous or sericeus, endocarp hard or splitting easily, occasionally with

apical 'tails' at the apex; seed 1, fleshy or woody, entire or lobed, testa absent, endosperm copious.

Number of species: 400.

Distribution: Cosmopolitan, mainly Southern Hemisphere with greatest concentration in arid and semi arid tropics.

Notes: 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 2000). 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 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).

The glandular hairs behind the stamens produce a viscous, oily fluid, which is secreted onto the anthers. This may serve to attract pollinators and has been implicated in pollen maturation and germination in some species (Paliwal 1956, Bhaskar 1992). Certain tendencies have been identified within the family towards increased host specificity, leaflessness and predominantly red flowers (Stauffer 1969). In the group which contains *Thesium* there is also a tendency towards heteropolar pollen grains (Lobreau-Callen 1982).

Key to the Tribes

1. Perennial herbs; fruit a dry indehiscent nut.....**4. Thesieae**
   Woody trees, shrubs, climbers, dendroparasites; fruit a fleshy drupe.....(2)
2. Leaves and stems covered in a tufted indument; ovary superior; receptacle swollen below the fruit, often brightly coloured.....**3. Anthoboleae**

Leaves and stems without a tufted indument; ovary inferior or semi-inferior; receptacle not swollen below fruit.....(3)

3. Trees or shrubs; leaf venation pinnate; ovary semi inferior; placental column contorted or very short.....**2. Santaleae**

Scandent shrubs, climbers, dendroparasites; leaf venation curvipalmate or leaves absent; ovary inferior; placental column straight.....**1. Amphorogyneae**

Key to the Southeast Asian genera

1. Small trees.....(2)

Shrubs, climbers, dendroparasites, herbs.....(4)

2. Plants glabrous; leaves opposite; inflorescences cymose.....**6.** *Santalum*

Plants sparsely or densely hairy; leaves alternate; inflorescence catkin or spadix.....(3)

3. Leaf ventation palmate, indument tufted; infloresence a spadix, flowers hermaphrodite; fruit with a swollen, fleshy receptacle .....**8.** *Exocarpos*

Leaf venation pinnate, indument not tufted; inflorescence a catkin, flowers dioecious; fruit pyriform, receptacle not swollen.....**7.** *Scleropyrum*

4. Herbs; fruits nut-like.....**9.** *Thesium*

Shrubs, climbers dendroparasites; fruits drupes.....(5)

5. Shrub with pendant branches; leaf venation pinnate; inflorescences cymose.....**5.** *Osyris*

Scandent shrubs, climbers, dendroparasites; leaf venation palmate or leaves reduced to scales; inflorescence racemose, umbelate or forming sessile clusters.....(6)

6. Leafless hyperparasite on Loranthaceae and *Dufrenoya*; stems with a distinctly hirsute indument.....**4.** *Phacellaria*

Not hyperparasitic, stems glabrous.....(7)

7. Male inflorescences racemose; fruits spherical, elliptic, mesocarp fleshy, endocarp tuberculate, punctate.....**2.** *Dendrotrophe*

Male inflorescences umbels, sessile clusters or 1 – flowered; fruits, oblong, ovoid; mesocarp membranous sericeus, endocarp smooth.....(8)

8. Fruits with endocarp chambered at the apex; Southern India and China to Western Borneo.....**3.** *Dufrenoya*

Fruits with endocarp unilocular or chambered in the base, 'tails' present at the apex of the endocarp; Philippines, northeast Borneo to Australia.....**1.** *Dendromyza*

Note on keys and taxonomic descriptions

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; *Thesium* is herbaceous and within the dendroparasites *Dendromyza* is generally confined to eastern Malesia and *Dufrenoya* and *Phacellaria* to western Malesia. Within the latter group, species of *Phacellaria* all have leaves which are reduced to scales, whilst species of *Dufrenoya* all have an obvious leaf blade. All of the descritpitons in the following account are based on original observations and measurements. In the species descriptions three measurements have been made from the leaves: the leaf length, leaf width at the mid point and leaf width at the base. The leaf widths are indicated between brackets just after the leaf length. The fruits of members of the tribe Amphorogyneae are rather unusual and therefore an illustration has been provided to demonstrate the basic characteristics of the different fruit types encountered in this tribe (**Fig. 40, Fig. 15, 16**). **Chapter 3** furthermore discusses the relationships of the genera in this group and some of the taxonomic changes which are presented in this chapter are based on the findings in **Chapter 3**. In terms of the nomenclature at the beginning of each species description the notation n.v. (non vide) indicates that a particular specimen has not been seen; p.p. (pro parte) indicates that the original description was based on more than one species and square brackets are used in cases of synonomy where there was an error in the spelling of a genus or species rather than any nomenclatural change. The glossary at the end of the account explains further the terms which have been used in the descriptions.

1. Amphorogyneae Stauffer

Type genus: *Amphorogyne* Stauffer & Hürlmann, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich: 337 (1959).

Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 114: 49 (1969); Hewson & George, Flora of Australia 22: 43 (1984).

Shrubs, climbers, dendroparasites, leaves spiral, often scale – like, caducous, venation curvipalmate (**Fig. 39**). *Inflorescences* racemes, umbels, clustered or reduced to a single flower, female inflorescences always 1 - flowered. *Flowers* small, yellow, green or occasionally red; hermaphrodite or dioecious, glandular hairs often absent; anther locules isomerous or more commonly unequal in size, pollen 11 - 17 μm in length, oblate – prolate, exine surface ornamentation weakly rugulose, microperforate, echinate, style short or absent, stigma 5 – lobed or separate, nectary present, fleshy, shortly 4 – 6 lobed; *ovary* inferior, placenta 4 – 6 lobed, lobes short, placental column slender, short or long. *Fruit* a drupe, exocarp thin, smooth, coriaceous, perianth persistent, mesocarp fleshy, membranous, sericeus; seed entire or lobed.

Notes: Genera distributed from Southeast Asia to Australia, (**Fig. 41**) containing many dendroparasitic species and exhibiting the most variation within the family in terms of fruit and pollen morphology.

1. *Dendromyza* (Danser)

Type species: *Dendromyza reinwardtiana* Danser, Nova Guinea New Series 4: 134 (1940) — Type: Korthals (Holotypus *Henslowia reinwardtiana* L!; Isotypus P!), Sumatra.

Danser, Nova Guinea New Series 4: 133 (1940); Danser, Nova Guinea New Series 6: 262 (1955); Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 114: 59 (1969); *Thesium* p.p. Bl., Bijdragen tot de Flora van Nederlandsche Indië: 646 (1826); *Viscum* p.p. Bl., *l.c.*: 666 (1826); *Henslowia* p.p. Bl., Museum Lugduno Batavae 1: 242 (1850); *Dendrotrophe* p.p. Miq., Flora Indiae Batavae 1.1: 779 (1856); *Cladomyza* Danser, Nova Guinea New Series 4: 135 (1940); Danser, Nova Guinea New Series 6: 268 (1955); Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 114: 61 (1969) **syn. nov.**

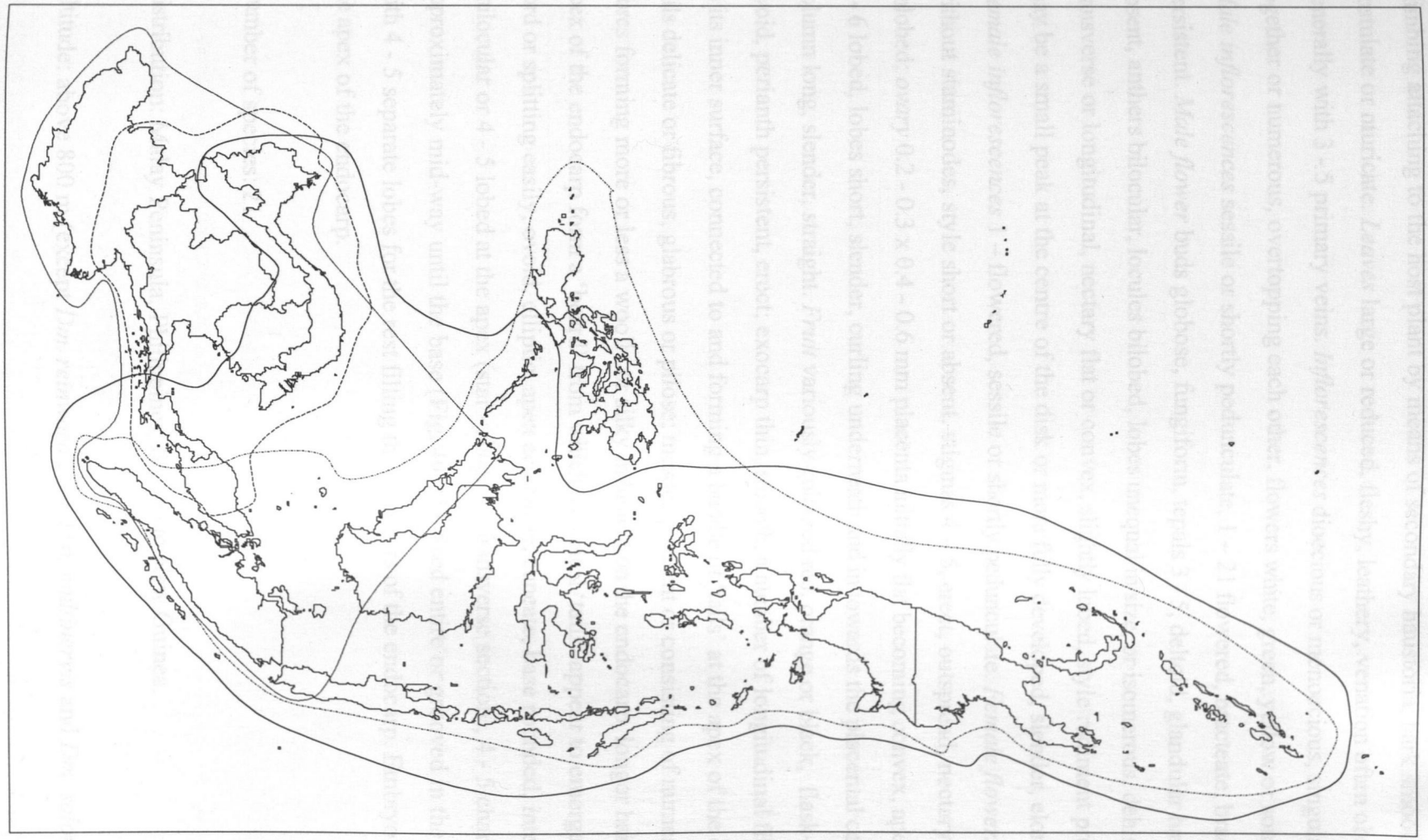


Fig.41 Geographic distribution of: —*Dendrotrophe*, ---*Dendromyza*, —— *Dufrenoya*, ---*Phacellaria*

Glabrous dendroparasitic shrubs or climbers, stems often suffused yellow, twining and when climbing attaching to the host plant by means of secondary haustoria; bark smooth, striate pustulate or muricate. *Leaves* large or reduced, fleshy, leathery, venation often obscure but generally with 3 - 5 primary veins. *Inflorescences* dioecious or monoecious, singular, several together or numerous, overtopping each other, flowers white, green, yellow or sometimes red. *Male inflorescences* sessile or shortly pedunculate, 1 – 21 flowered, bracteate, bracts persistent. *Male flower* buds globose, fungiform, tepals 3 - 5, deltoid, glandular hairs present or absent, anthers bilocular, locules bilobed, lobes unequal in size, or isomerous, dehiscence transverse or longitudinal, nectary flat or convex, slightly lobed, style rudiment present, which may be a small peak at the centre of the disk or more fully developed, slender, elongate. *Female inflorescences* 1 – flowered, sessile or shortly pedunculate. *Female flowers* with or without staminodes, style short or absent, stigmas 4 – 5, erect, outspread, nectary flat unlobed; *ovary* 0.2 - 0.3 x 0.4 - 0.6 mm placenta initially flat becoming convex, apex apiculate, 4 - 6 lobed, lobes short, slender, curling underneath and in towards the placental column, column long, slender, straight. *Fruit* variously coloured red, orange or black, flask-shaped, ovoid, perianth persistent, erect; exocarp thin, smooth, a number of longitudinal fibres attached to its inner surface, connected to and forming a bundle of 'tails' at the apex of the endocarp, tails delicate or fibrous, glabrous or pilose; mesocarp absent or consisting of numerous delicate fibres forming more or less a woolly or silky indument on the endocarp, longer hairs near the apex of the endocarp form a 'beard' from which the apical 'tails' appear to emerge; endocarp hard or splitting easily, ovoid, elliptic, apex acuminate, cuneate, base rounded, internally unilocular or 4 - 5 lobed at the apex (star - shaped in transverse section), 4 - 5 chambered from approximately mid-way until the base (**Fig. 40, 15**). Seed entire or grooved in the upper part with 4 - 5 separate lobes for the rest filling the chambers of the endocarp. Embryo located near the apex of the endocarp.

Number of species: 21

Distribution: Malay Peninsula, Philippines, Borneo to New Guinea.

Altitude: above 800 m (except *Dm. reinwardtiana*, *Dm. multinervis* and *Dm. salomonia*).

Habitat: Montane Fagaceae – Myrtaceae forests; margins of montane mossy forest or in open alpine and grassland shrubbery. In undisturbed areas or in secondary vegetation. Most commonly parasitic on species of Ericaceae: *Vaccinium, Rhododendron, Dimorphanthera.* Those species with straggling, scandent growth may have several hosts the most common of which are: *Homalanthus*, *Euphorbia*, *Glochidion*, *Macaranga* (Euphorbiaceae); *Drimys* (Winteraceae); *Eugenia* (Myrtaceae).

Notes: Name derived from *dendron* meaning tree or tree-like and *myzo*, to suck, referring to the parasitic habit. The most variable genus in terms of fruit structure and pollen morphology (**Chapter 2**) in the family, *Dendromyza* had been split into two separate genera, *Cladomyza* and *Dendromyza*, based on fruit structure. *Cladomyza* contained those species with chambered fruits, whilst in *Dendromyza* the fruits were unilocular. The distinction between these two fruit types is however not clear-cut as in some cases there are short chambers in *Dendromyza sensu stricto* and in *Cladomyza* the fruit is unilocular. In terms of habitat preferences, growth habit and floral structure there are no clearly distinguishing characteristics between the two groups. Based on phylogenetic analyses and inspection of variation in fruit, inflorescence and floral morphology *Dendromyza* is paraphyletic with *Cladomyza* and I have therefore subsumed *Cladomyza* into *Dendromyza* (**Chapter 3**). Species most abundant in the central mountain ranges of New Guinea with only a few spreading into the rest of Malesia. Some species are host specific and restricted to certain vegetation types at higher altitudes. Others, which have a more widespread distribution, may occur at lower elevations in association with a number of habitats and host plants. In particular, *Dm. reinwardtiana* is the most widespread species of *Dendromyza* in Southeast Asia, occurring from the Malay Peninsula to Australia.

Key to *Dendromyza*

1. Leaves bract-like, sheathing the stem.....**9.** *D. hiepkoiana*
   Leaves with an obvious blade.....(2)
2. Leaf apices with distinctly hooked (uncinate) tips.....(3)
   Leaf apices rounded, mucronate, attenuate.....(5)
3. Stems papillose.....**21.** *D. uncinata*
   Stems glabrous.....(4)

4. Erect climber, haustoria absent, bark rough, wrinkled with longitudinal fissures; male flowers with anther locules in a single plane, dehiscence transverse; female flowers without staminodes, apical 'tails' on the endocarp crisp.....**8.** *D. erecta*

   Scandent climber, haustoria present, bark smooth or weakly striated; male flowers with anthers with posterior and anterior lobes, dehiscence longitudinal; female flowers with staminodes; apical 'tails' on endocarp membranous.....**4.** *D. cucullata*

5. Young stems muricate, leaves lanceolate.....**2.** *D. angustifolia*

   Young stems not muricate, leaves elliptic, obovate, orbicular.....(6)

6. Leaves with a scleratomous, ovoid inclusion at the apex.....**1.** *D. acrosclera*

   Leaves without a scleratomous ovoid inclusion.....(7)

7. Mature leaves 3 – 11 mm in length.....(8)

   Mature leaves greater than 18 mm in length.....(11)

8. Leaves serpent-like, apex elongate – attenuate; male inflorescences 5 – 13 flowered, overtopping each other.....**5.** *D. cuneata*

   Leaves obovate, orbicular, apex rounded, shortly mucronate; male inflorescences 1 – 5 flowered not overtopping eachother.....(9)

9. Bark wrinkled, ridged; male flowers with glandular hairs behind the anthers, anther locules isomerous, dehiscence longitudinal; female fruits unilocular.....**3.** *D.crassifolia*

   Bark smooth or pustulate; male flowers without glandular hairs behind anthers, anther locules unequal in size, dehiscence transverse; female fruits chambered at the base.....(10)

10. Bark pustulate; mature leaves orbicular, leaves recurved; male inflorescences 5 – 6 flowered; fruits with lanate apical 'tails' on the endocarp, central column 1.0 – 1.5 mm long.....**12.** *D. microphylla*

    Bark smooth, striate; mature leaves obovate, curving upwards; male inflorescences 1 – flowered; fruits with glabrous 'apical' tails on the endocarp, central column short, 0.5 mm long.....**6.** *D. dendromyzoides*

11. Bark pustulate.....**14.** *D. pachydisca*

    Bark not pustulate.....(12)

12. Inflorescences pedunculate.....(13)

    Inflorescences sessile.....(17)

13. Stems papillose.....**15.** *D. puberula*

    Stems glabrous, striate.....(14)

14. Branches long, slender, twisted; leaves narrowly obovate, lanceolate, narrowly elliptic, fruits unilocular.....(15)
Climbing and non-climbing stems present; leaves broadly obovate, orbicular, venation not parallel; fruits chambered at the base.....(16)
15. Haustoria absent, primary veins not parallel, staminodes in female flower; Solomon Islands.....**17.** *D. salomonia*
Haustoria present; primary veins parallel; staminodes absent in female flower; Philippines, New Britain, Sulawesi, Moluccas, New Guinea.....**13.** *D. multinervis*
16. Leaves with irregular protruberances on the surface; male inflorescesces elongate pedunculate, 1.5 – 2.0 mm, 5 – flowered.....**10.** *D. kaniensis*
Leaves without irregular protruberances on the surface; male inflorescences shortly pedunculate, 0.5 mm, 4 – flowered.....**19.** *D. stellata*
17. Male inflorescences 5 – 21 flowered.....(18)
Male inflorescences 1 – flowered.....(20)
18. Stems papillate, haustoria absent; leaves 3 – nerved; inflorescences not overtopping each other, nectary thin.....**20.** *D. trinervia*
Stems glabrous, haustoria present; leaves 5 – nerved; inflorescences overtopping each other, nectary fleshy.....(19)
19. Bark granular; leaves elongate mucronate; apical 'tails' on endocarp delicate; endocarp 5 – locular.....**5.** *D. cuneata* var. *grandifolia*
Bark smooth or with longitudinal fissures; juvenile leaves shortly apiculate; apical 'tails' on endocarp robust; endocarp unilocular.....**11.** *D. ledermanii*
20. Anthers isomerous.....(21)
Anthers unequal.....**18.** *D. staufferia*
21. Erect shrub, haustoria absent; branches covered in a pale waxy deposit; inflorescences overtopping each other; fruits chambered at the base.....**7.** *D. densa*
Climber, haustoria present; branches pendulous, bark rough with longitudinal fissures, inflorescences not overtopping each other; fruits unilocular.....**16.** *D. reinwardtiana*

1. *Dendromyza acrosclera* (Danser) Macklin **comb. nov.**

Type: Brass 4749 (Holotypus B n.v. Isotypus L!), Central division, Murray Pass, Wharton range, Papua New Guinea.

Cladomyza acrosclera Danser, Nova Guinea New Series 4: 138 (1940); Danser, Nova Guinea New Series 6: 270 t.24 (1955); Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 114: 63 (1969) **syn. nov.**

Erect climber, much branched with some long twining shoots. *Juvenile stems* olive-yellow, angular, bracteate at the base, weakly striate and wrinkled; *older branches* terete, bark wrinkled with shallow longitudinal fissures which are lighter in colour than the surrounding stem. *Haustoria* usually present on all stems. *Juvenile leaves* with weakly ciliate margins; *mature leaves* confined to upper portion of the plant, yellow-green, darker underneath, orbicular to broadly spathulate, 6.5 - 18.0 (6.0 - 14.0 x 3.0 - 8.0) mm, apex weakly retuse with a distinctive ovoid, scleratomous inclusion, upper surface wrinkled, shiny, lower surface smooth, venation indistinct or primary veins 3; petiole short, decurrent, upper surface invaginated, lower surface angular. *Inflorescences* dioecious, sessile, in leaf axils on juvenile stems, crowded, overtopping each other. *Male inflorescences* 4 – 21 flowered, subtended by an imbricate involucre of 4 bracts, with 1 central and 3 - 4 axial flowers, each axillary flower subtended by an involucre of 4 smaller bracteoles, further flower buds developing in the axil of each bracteole, bracts ovate, 1.0 x 0.6 mm, cartilaginous, margins initially densely ciliate, later entire. *Male flowers* greenish yellow turning pink, buds conical, pedicellate, pedicel 0.8 - 1.5 x 0.4 - 0.6 mm, tepals 3 - 5, 1.1 - 1.5 x 0.8 - 1.5 mm, fleshy, ovate, apex acuminate, shortly apiculate on the inner surface, three parallel veins faintly visible on the inner surface, receptacle flat, glandular hairs present, filaments 0.2 - 0.3 x 0.2 mm, anthers basifixed, large, posterior lobes larger than the anterior, 0.3 - 0.4 x 0.4 - 0.5 mm, dehiscence transverse, nectary fleshy, faintly granular, apiculate in the centre. *Female inflorescences* subtended by 2 involucres of bracts. *Female flower* buds turbinate, receptacle long, slender 0.7 - 1.0 x 0.7 - 0.9 mm, tepals yellow turning deep red, 1.1 x 1.0 mm, deltoid, elongate-deltoid, apex acuminate, staminodes absent, style terete, broad 0.2 - 0.4 x 0.2 - 0.5 mm, stigma 5 - 6 lobed, lobes smooth, short, rounded, erect, nectary fleshy, unlobed, faintly granular. *Fruit* yellowish green maturing red and finally black, ovoid, relatively large, 8.5 - 10.0 x 3.5 - 5.0 mm, exocarp smooth, mesocarp confined to the apex of the

endocarp, sericeus, extending 1.5 - 2 mm beyond the apex, apical 'tails' robust, pilose, hairs sericeus, endocarp ovoid, splitting easily, 4.5 – 5.0 x 2.5 – 3.5 mm, weakly lobed, apex acuminate, internally 4 – 6 lobed at the apex, central chambers oblate or spherical, 0.4 - 0.6 x 0.3 - 0.4 mm; central column, ovoid, 1.5 - 2.5 x 1.1 x 1.2 mm.

Distribution: Central Papua New Guinea (**Fig. 42**).

Habitat: Sub - alpine shrubbery of *Papuacedrus - Decaspermum - Vaccinium* associations or forest margins near the summit of mountains in exposed areas and below the summit ridge. Usually found in associated with *Drimys* (Winteraceae) and Ericacous species such as *Vaccinium*.

Altitude: above 3000 m.

Notes: Name derived from the scleratomous thickening in the leaves. Characterised by leaves which are often yellowish to bronze in colour with a distinctive ovoid scleratomous thickening at the tips; flowers which change from yellowish green to deep red with maturity and ripe fruits which are generally larger than other species of *Dendromyza*. In terms of inflorescence structure similar to *Dm. uncinata* and *Dm. erecta*, distinguishable by its leaf structure, and larger fruits.

Additional material examined

Papua New Guinea: *Morobe district*:Womersley 17967 (BO, CANB), Mt. Amungwiwa, south of Wau, Morobe District; *Central highlands*: Brass 4587 (A, Z), Murray Pass, Wharton Range; Brass 4240a (A), Mt. Albert Edward; Brass 4240 (A), Mt. Albert Edward; van Royen 10919 (CANB), Mt. Victoria, track from Koma Creek to the Rock Pile, southeast of Mt. Service; Carr 13814 (CANB), Abour Mu Gap; Stevens & Coode 51393 (CANB, K), Tapini sub district; Hartley 12918 (A, CANB), Mt Dickson, Goilala subdistrict; Croft 61725 (CANB, L, K), southeast slopes of Mt. Victoria, Port Moresby sub district; Paijmans 671 (CANB), Mt. Albert Edward; van Royen 30089 (CANB, K), south slope of Mt. Albert Edward, West Dome, track to Mt. Biota; Croft 61469 (L, CANB), Mt. Albert Edward, west side, Goilala subdistrict; Ridsdale 36806 (CANB, L), Murray pass,

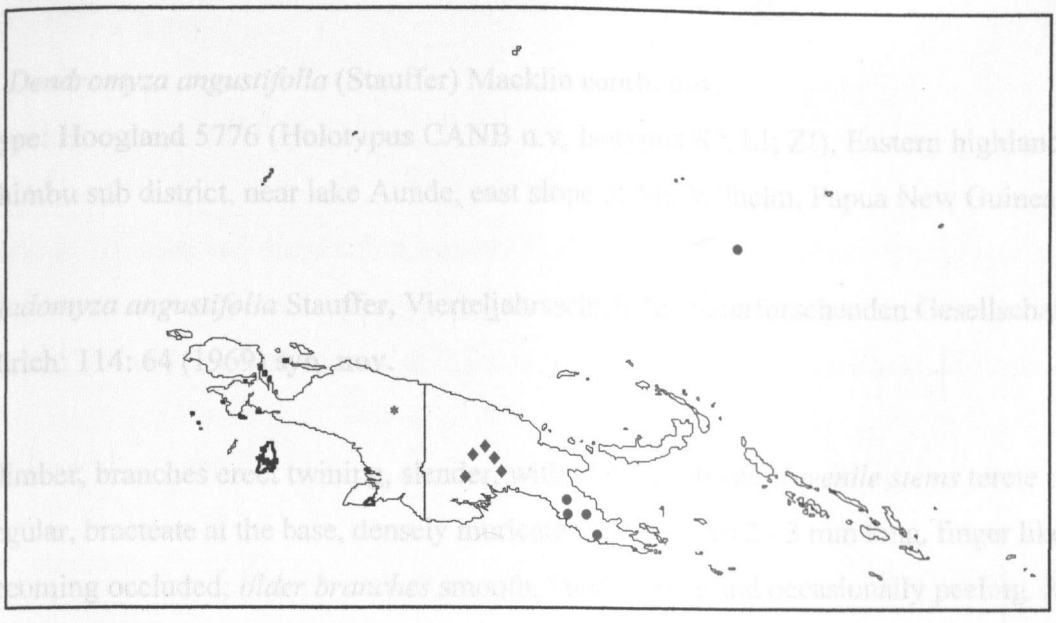


Fig. 42 Geographic distribution of: • *Dendromyza acrosclera*, ♦ *Dendromyza angustifolia* * *D. hiepkoiana.*

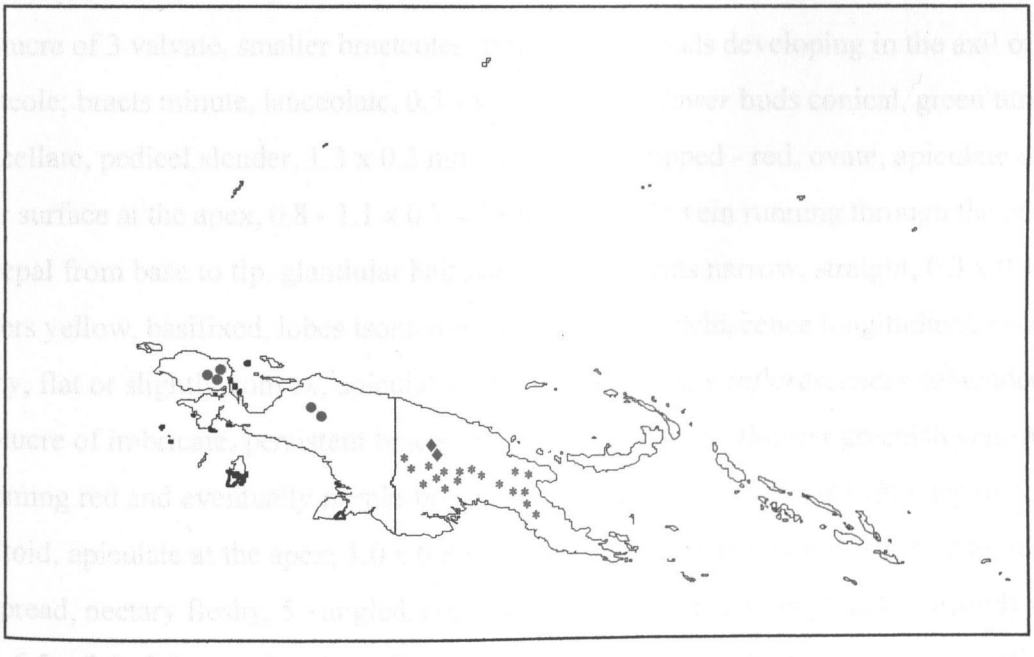


Fig. 43 Geographic distribution of: • *Dendromyza crassifolia*, ♦ *Dendromyza cucullata* * *Dendromyza cuneata.*

Goilala subdistrict; Coode & Stevens 46219 (CANB, K), Mt. Strong, Tapini subdistrict; Craven 2687 (CANB), northwest, Mt. Albert Edward, 8 23S 147 24E.

2. *Dendromyza angustifolia* (Stauffer) Macklin **comb. nov.**

Type: Hoogland 5776 (Holotypus CANB n.v, Isotypus K!; L!; Z!), Eastern highlands, Chimbu sub district, near lake Aunde, east slope of Mt. Wilhelm, Papua New Guinea.

Cladomyza angustifolia Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich: 114: 64 (1969) **syn. nov.**

Climber, branches erect twining, slender, with few side shoots. *Juvenile stems* terete or slightly angular, bracteate at the base, densely muricate, excrescences 2 - 3 mm long, finger like, later becoming occluded; *older branches* smooth, faintly striate and occasionally peeling. *Haustoria* extensive on all stems. *Juvenile leaves* with ciliate margins; *mature leaves* yellowish-green, lanceolate, 8.0 - 9.0 (2.0 - 3.0 x 2.0 - 3.0) mm, apex acute, acuminate, sharp tipped, base obtuse, margins flat or recurved, surfaces distinctly rugulate, venation indistinct; petiole short, narrow, invaginated. *Inflorescences* dioecious, sessile or slightly raised, 1 – 3 together in leaf axils on juvenile branches. *Male inflorescences* 5 - 17 flowered, subtended by valvate involucre of 4, membranous, bracts, with 1 central and 4 axial flowers, each axial flower subtended by an involucre of 3 valvate, smaller bracteoles, further flower buds developing in the axil of each bracteole; bracts minute, lanceolate, 0.5 x 0.3 mm. *Male flower* buds conical, green turning red, pedicellate, pedicel slender, 1.3 x 0.2 mm, tepals green tipped - red, ovate, apiculate on the inner surface at the apex, 0.8 - 1.1 x 0.7 - 0.8 mm, a single vein running through the centre of the tepal from base to tip, glandular hairs present, filaments narrow, straight, 0.3 x 0.1 mm, anthers yellow, basifixed, lobes isomerous, 0.2 x 0.4 mm, dehiscence longitudinal, nectary fleshy, flat or slightly convex, apiculate in the centre. *Female inflorescences* subtended by an involucre of imbricate, persistent bracts, bracts ciliate. *Female flowers* greenish yellow becoming red and eventually purple-brown, receptacle narrow, 0.9 x 0.5 mm, tepals 5, elongate - deltoid, apiculate at the apex, 1.0 x 0.8 mm, staminodes absent, stigmas 5, sessile, rounded, outspread, nectary fleshy, 5 - angled, convex. *Fruit* yellow becoming black, narrowly ovoid, 6.0 - 6.5 x 2.0 -3.0 mm, shortly pedicellate, exocarp thin, smooth, mesocarp fine, sericeus, not

extending beyond the apex of the endocarp, apical 'tails' delicate, long, pilose, hairs crisp, endocarp smooth, elliptic, splitting easily, 3.5 - 5.0 x 2.0 - 2.5 mm, weakly 5 - lobed, internally 5 lobed at the apex, central chambers 5, narrow, circular, 0.3 x 0.3 mm, central column elliptic, 1.3 x 0.7 - 0.9 mm.

Distribution: Eastern Papua New Guinea (**Fig. 42**).

Habitat: Of restricted distribution, usually found at the margins of montane mossy forests or in open alpine shrubbery. A straggling parasite which may have several simultaneous hosts but is usually found in association with Ericaceous species such as *Vaccinium* and *Rhododendron*.

Altitude: above 3000 m.

Notes: Name derived from the characteristic narrow, lanceolate leaves. This species is allied to *Dm. cuneata* but distinguished from it by narrow leaves and distinctly muricate bark. It also has flowers which turn from yellowish green to red, purple and then brown with maturity.

Vernacular name: Dendglponggi (Chimbu name, Western highlands).

Additional material examined

Papua New Guinea: *Southern highlands*: Vink 17283 (CANB), Tari sub district, Mt. Ambua 6S 143E. *Eastern highlands*: Sleumer 4159 (Z), east slope of Mt. Wilhelm; Womersley 8867 (A, CANB, K), Mt. Wilhelm; Brass 30105 (A, BO, CANB, K); Womersley 8925 (K), Near Lake Aunde, Mt. Wilhelm; Balgooy 21/4 (CANB), ridge of Lake Aunde, Mt. Wilhelm; Stevens 54590 (CANB, K), Goroka subdistrict, Mt. Kerigomna; Balgooy 105 (CANB), northeast of Lake Aunde, Mt. Wilhelm; Veldkamp 8607 (K), Mt. Otto, Repeater station;Went 179 (GH), Mt. Wilhelm, Lake Aunde *Western highlands*: Smith 15,174 (CANB), Northside of Pindannde Valley, Mt. Wilhelm; Kerenga & Umba 74328 (L), Chimbu district, Mt. Wilhelm, 5 47E 145 1S; Wade 7672 (CANB), Pindande Valley, Mt. Wilhelm; Vandenberg 39648 (CANB, K, L), Chimbu, Below Imbuka ridge, Kundiawa sub district; Stauffer 5659 (A, CANB, Z), Mt. Wilhelm; Stauffer 5658 (A, P) Mt. Wilhelm; Philipson 3451 (A), Mt. Wilhelm, 5 47S 145 2E.

3. *Dendromyza crassifolia* (Gibbs) Stauffer

Type: Gibbs 5620 (Holotypus BM n.v.; Isotypus L!), Arfak Mts., summit of Mt. Koebre.

Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 114: 61 (1969); *Henslowia crassifolia* Gibbs, Phytogeography and Flora of the Arfak Mountains: 132 (1917); *Cladomyza crassifolia* Danser, Nova Guinea New Series 4: 136 (1940); *Henslowia acutata* Pilger, Botanische Jahrbucher 59: 125 (1924) **syn. nov.** — Type: Lam 1649 (Isotypus U!) Mamberamo, Doormantop; Pilger in Engler & Harms, Natürliche Pflanzenfamilien 16b: 72 (1935); *Cladomyza acutata* Danser, Nova Guinea New Series 4: 136 (1940) **syn. nov.** *Cladomyza intricata* Danser, Nova Guinea New Series 6: 276 (1955) **syn. nov.** — Type: Lam 1986 (Holotypus L!) Mamberamo, Doorman; *Dendromyza intricata* Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 114: 61 (1969) **syn. nov.**

Climber, branches slender, long, tangled, shoots dimorphic with occasional non-climbing side shoots on climbing stems. *Juvenile branches* angular, striated, keeled at nodes; *older branches* striated, angular, bark wrinkled, ridged with shallow horizontal fissures. *Haustoria* present on all stems. Leaves sparse, generally confined to non-climbing shoots or at the base of climbing stems. *Juvenile leaves* fleshy with shortly mucronate apices, incurved, margins ciliate; *mature leaves* yellowish, obovate, 4.0 - 6.0 x 2.0 - 3.0 x 1.0 - 1.5 mm, surfaces, distinctly rugulate, upper surface weakly convex, margins revolute; petiole angular, dorsally flattened, decurrent. *Inflorescences* dioecious, sessile on juvenile branches and older stems, crowded together, overtopping each other, in leaf axils and at leafless nodes. *Male inflorescences* 1 - flowered, surrounded at the base by an involucre of 5, quincuncially arranged bracts, bracts, minute, lanceolate - deltoid, 0.3 x 0.1 mm, fleshy, withering. *Male flowers* yellow, pedicellate, pedicel angular, 1.1 - 1.6 x 0.5 - 0.6 mm, buds globose, tepals elongate-deltoid, fleshy, 0.8 x 0.6 mm, glandular hairs present, filaments short, broad, dilated at the base, 0.2 x 0.3 mm, anthers dorsifixed, 0.2 x 0.4 mm, posterior lobes larger than the anterior, dehiscence longitudinal, nectary fleshy, flat, lobed, style rudiment long, slender. *Female inflorescences* with the same arrangement of bracts as the male. *Female flowers* yellow, turning dark red, buds turbinate, receptacle long, broad, 1.0 x 0.9 mm, tepals fleshy, deltoid, not apiculate at the apex, 0.6 x 0.8 mm, style short, as broad as long, stigmas 5, delicate, outspread, rounded at the tip, nectary

flat, weakly lobed. *Fruit* purple, ovoid, 6.0 x 3.0 mm, exocarp smooth, mesocarp membranous, confined to the apex of the endocarp, apical 'tails' robust, pilose, hairs sericeus, endocarp ovoid, splitting easily, 3.8 x 2.3 – 2.6 mm, smooth, internally entirely unilocular.

Distribution: Irian Jaya (**Fig. 43**).

Habitat: At high elevations of *Nothofagus*-Myrtaceous forests, in summit heath vegetation. Parasitic on a variety of species associated with this vegetation type, particularly but not exclusively on Myrtaceae, other hosts include: *Rhododendron*, *Vaccinium* (Ericaceae); *Garcinia* (Guttiferae) and *Drimys* (Winteraceae).

Altitude: 2000 - 3500 m.

Notes: Name derived from the thick, fleshy leaves. This species has a rather restricted distribution, it may be confused with *Dm. microphylla* and their distributions overlap in Central Irian Jaya. It can be distinguished from *Dm. microphylla* by its 1 - flowered male inflorescence with glandular hairs behind the anthers and an unilocular endocarp in the fruit.

Additional material examined

Indonesia: *Irian Jaya*: Lam 1590 (L), Doorman; Lam 1696 (L), Doorman; Sleumer & Vink 4215 (L), Arfak Mts., Anggi Gita lake, Mt. Mesenuk; Sleumer & Vink 4296 (L, Z), Arfak Mts., Mt. Ukdehottammot; Kanehire & Hatusima 13526 (A), Vogelkop peninsula, Anggi, Arfak Mts., Mt. Koebre; van Royen & Sleumer 8173 (BO, L, Z), Vogelkop peninsula, north slope Mt. Nettoti, Wekari path, road at top of Mt. Nettoti; van Royen & Sleumer 7866 (L, Z), Vogelkop peninsula, summit of Mt. Nettoti.

4. *Dendromyza cucullata* (Danser) Stauffer

Type: Ledermann 12911 (Holotypus B!), Felsspitze.

Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 114: 61 (1969); *Cladomyza cucullata* Danser, Nova Guinea New Series 6: 274 t.12 (1955).

Climber, branches narrow twisted. *Juvenile stems* smooth, slightly angular; *older branches* terete, bark smooth or weakly striated. *Haustoria* present on all branches. *Juvenile leaves* elliptic, margins entire; *mature leaves* yellowish green, shining, obovate, 12.0 - 18.0 (6.0 - 10.0 x 2.0 - 3.0) mm, venation indistinct, apices obtuse, tips weakly mucronate, recurved, base attenuate, upper surfaces weakly convex, surfaces rugulate. *Inflorescences* dioecious, sessile in leaf axils and at leafless nodes on juvenile branches and on older stems, crowded, over topping each other, spreading outwards to girdle entire stem. *Male inflorescences* 5 – 21 flowered, 1 central and 4 axial flowers, subtended by an involucre of 4 valvate bracts, each axial flower subtended by an involucre of 3 smaller bracteoles, further flower buds developing in the axil of each bracteole; outer involucre valvate, bracts minute, 0.5 x 0.5 mm, leathery, margins ciliate. *Male flower* buds fungiform, reddish or orange-brown in colour, pedicellate, pedicel long, slender, tepals 5, elongate-deltoid, 0.8 - 0.9 x 0.6 - 0.8 mm, not apiculate at the tip, glandular hairs present, filaments straight, 0.2 x 0.2 mm, anthers dorsifixed, lobes isomerous, 0.2 x 0.3 mm, dehiscence longitudinal; nectary fleshy, flat, smooth, apiculate in the centre. *Female inflorescences* with the same arrangement of bracts as the male inflorescence. *Female flower* buds reddish green, obconical, receptacle narrow, 1.0 x 0.7 mm, tepals 5, ovate, 0.8 x 0.7 mm, nectary fleshy, weakly convex, unlobed, stigmas 5, sessile, delicate, erect. *Fruit* 6.0 - 7.0 x 3.5 - 4.0 mm, exocarp smooth, mesocarp sparse, membranous, covering the entire endocarp, apical 'tails' delicate, pilose, hairs membranous, endocarp ovoid, splitting easily, weakly 5 - lobed, apex attenuate, internally 5 - lobed at the apex, central chambers narrow, elliptic, 1.0 x 0.6 mm, central column slender, cylindrical, 1.5 - 2.0 x 0.6 mm.

Distribution: Eastern Papua New Guinea (**Fig. 43**).

Habitat: Ridge forest with *Araucaria*, parasitic on *Schizomeria* (Cunoniacae).

Altitude: 2000 - 2500 m.

Notes: Vegetatively very similar to *Dm. erecta*, distinguished by dorsifixed, longitudinally dehiscing anthers. Also closely related to *Dm. uncinata* but differs in terms of growth habit and glabrous stems.

Additional material examined

Papua New Guinea: *Sepik district*: Ledermann 12697 (B); Stevens & Veldkamp 55579 (CANB, L), Rabaraba subdistrict, on the south side of Guaru ridge near Mayu 2, 9 45S 149 04E.

5. *Dendromyza cuneata* (Danser) Macklin **comb. nov.**

Type: Carr 13092 (Holotypus *Cladomyza cuneata* B n.v.; Isotypus L!), southeast New Guinea, at 5000ft.

Cladomyza cuneata Danser, Nova Guinea New Series 4: 137 (1940) **syn. nov.**; Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 114: 64 (1969); *Cladomyza dubia* Stauffer *l.c.*: 65 — Type: Schodde 1746 (Holotypus CANB n.v.; Isotypus L!), west summit grasslands of Mt. Giluwe **syn. nov.**

Climber, branches slender, twining with long, lax, stems and occasional shrubby growth. *Juvenile stems* yellowish, smooth, angular, sulcate; *older branches* terete, slightly twisted, bark wrinkled, granular. *Haustoria* present on all stems. *Juvenile leaves* elliptic, obovate, tip apiculate, margins entire; *mature leaves* yellowish green - orange, 3.5 – 40.0 (2.0 – 14.0 x 1.5 - 3.0) mm, obovate, overall appearance serpent - like (leaf base angled close to the stem, then diverging abruptly at approximately the mid point and becoming almost perpendicular), apices acute, obtuse, tip elongate-mucronate, somewhat recurved, occasionally deciduous, base cuneate, upper surface rugulate, convex, thickened near the apex, lower surface granular, venation indistinct; petiole short, decurrent, flat or involuted on the upper surface, lower surface angular. *Inflorescences* dioecious, sessile on juvenile branches, in leaf axils, crowded, overtopping each other. *Male inflorescences* 5 - 21 flowered, with 1 central and 4 axial flowers, subtended by an involucre of 4, valvate, membranous, bracts, each axial flower subtended by an involucre of 3 valvate, smaller bracteoles, further flower buds developing in the axil of each bracteole, bracts elliptic - ovate, 0.5 x 0.3 mm, margins ciliate. *Male flower* buds yellow, fungiform, pedicellate, pedicel long, slender, 0.8 - 1.2 x 0.2 - 0.4 mm, tepals 0.8 - 1.3 x 0.7 – 1.0 mm, elongate-deltoid, apiculate on the inner surface at the apex, reflexed at the mid-point, forming a pseudo-hypanthium, glandular hairs present, filaments long, narrow, 0.3 - 0.4 x 0.1 - 0.2 mm, anthers light yellow, 0.2 - 0.3 x 0.5 - 0.6 mm, basifixed, bilocular, lobes isomerous,

dehiscence longitudinal, nectary flat, fleshy, granular, shortly apiculate in the centre. *Female inflorescences* singular, subtended by a single involucre of 3, valvate bracts. *Female flower* buds green - tinged pink, turbinate, receptacle short, broad, 1.1 x 0.9 mm, tepals 0.6 - 0.8 x 0.6 - 0.8 mm, ovate, thick, apiculate on the inner surface at the apex, style short, angular, 0.2 x 0.2 mm, stigma 5 - lobed, lobes short, rounded, outspread, nectary fleshy, punctate. *Fruit* green maturing yellow and then brown - black, ovoid, oblong, 5.0 - 5.5 x 2.5 - 3.5 mm, exocarp thick coriaceous, mesocarp sericeus, confined to the apex of the endocarp and extending up to 3 mm beyond it, apical 'tails' delicate, pilose, hairs sericeus, endocarp ovoid, not splitting easily, 2.5 - 3.0 x 2.0 - 2.5 mm, lobed, apex cuspidate, base apiculate, internally 5 – lobed at the apex, central chambers obovate, 0.3 - 0.4 x 0.3 - 0.4 mm, central column elliptic, 0.9 - 1.5 x 0.6 - 0.9 mm,

Distribution: Central and eastern Papua New Guinea (**Fig. 43**).

Habitat: Mountainous areas in undisturbed alpine and grassland shrubbery with Ericaceae and Myrtaceae at the edge of *Nothofagus* - *Quercus* forests; degraded and regrowth vegetation, between mossy forest and shrubby vegetation; swamp woodland, transition between forest and central grass swamp; secondary forest in fire induced shrubby vegetation. Parasitic on a number of species, often with several simultaneous hosts but generally associated with species of *Rhododendron*, *Vaccinium*, particularly *Dimorphanthera* (Ericaceae); *Homalanthus*, *Euphorbia*, *Glochidion*, *Macaranga* (Euphorbiaceae) Other hosts include *Polyosma* (Escalloniaceae), *Drimys* (Winteraceae), also once collected from Loranthaceae.

Altitude: 1800 – 4000 m.

Vernacular name: Mondidi (Mendi language, Southern highlands); Sanambo (Madang district); Korinala (Chimbu: Masul); Kuljaneh (Wahgi: Minj); Keringai (Hagen: Toboga); Omui-nairingkai (Mairi: Watabung).

Notes: One of the most widespread species in Papua New Guinea. Name derived from the shape of its leaves, which have cuneate or wedge shaped bases. Male and female plants have been collected from the same host. Characterised by a very distinctive leaf shape which is

often serpent-like with a distinctly elongated, attenuated tip. Taxonomically allied to *Dm. angustifolia*, distinguishable from it on the basis of leaf shape and bark which is granular rather than muricate.

Additional material examined

Papua New Guinea: *Sepik district*: Veldcamp 6803 (CANB), Star Mts., 5S 141 5E; Frodin 32131 (L), South of Nerenavip village in Hindenburg range 5 15S 141 40E; Craig 103 (CANB), Mt. Sirius, Telefomin subdistrict; Veldcamp 6443 (CANB), east ridge Mt. Capella, Star Mts., 5S 141 5 E; Veldkamp & Vinas 7446 (BO, CANB), Mt. Burgers, 5 9 S 143 18E; Croft 68048 (CANB, L), Telefomin sub district, southern slopes Mt. Scropion, Star Mts. *Southern highlands*: Schodde 1376 (L), Kubutu, Mendi valley 6 10S 143 40E; Stevens & Foreman 55780 (BO, CANB, K), Mt. Ialibu, near Repeater Station, Ialibu sub district; Stevens & Foreman 55856 (CANB, K, L), Mt. Ialibu, near Repeater Station, Ialibu sub district; Wiakabu & Veldcamp 73706 (CANB), northwest slopes of Mt. Kerewa, Tari subprovince, 5 20S 142 15E; Coode & Waring 32504 (CANB), slopes of Mt. Giluwe, Mendi sub district, 6 5S 143 52E; Wiakabu & Veldkamp 73682 (CANB, K), west slopes of Mt. Karoma, Tari sub province 5 20S 142 15E; Kalkman 4960 (CANB, L),Tari subdistrict, Mt. Ambua; Croft 60697 (CANB, L), Base of volcanic plug, Mt. Giluwe, Mendi subdistrict, 6 6 S 143 54E. Vink 17283 (L), Tari subdistrict, Mt. Ambua, 6S 143E; Wiakabu & Veldkamp 73729 (CANB, K), Tari sub province, western slopes of Mt. Kerewa, 5 20S 142 15E; Kalkman 4996 (CANB, L), Tari sub district, Mt. Ambua, 6S 143E; John 1574 (A, CANB, L), northeast side Mt. Giluwe; Croft 60744 (L), Mendi sub district, Mt. Giluwe, 6 7S 143 55E; Paijmans 1181 (CANB), Mt. Giluwe, 9 13S 149 13E. *Western highlands:* Hoogland & Schodde 7115 (CANB, L), Wabag subdistrict, Mt. Sugarloaf, 4 45S 141 39E; Stauffer 5630 (A, B, CANB, K), foot of Mt. Wilhelm, over Chimbu Tal; Stauffer 5643, 5644 (A, CANB, P), Pengagl creek, Mt. Wilhelm; Stauffer 5633 (A, B, CANB, K, Z), foot of Mt. Wilhelm, over Chimbu Tal; Stauffer 5631 (A, B, K, Z), foot of Mt. Wilhelm, over Chimbu Tal; Hoogland & Pullen 6183 (A, CANB), Komun-Pin divide, upper Wahgi valley; Stevens & Veldkamp 54951 (CANB, K, L), Mt. Hage sub district, below Klangan hill, Mt. Hagen, 5 35S 144 05E; Stauffer 5644 (CANB), Pengagl creek, Mt Wilhelm. *Madang*: Sayers 21273 (CANB, L, SING), Saidor subdistrict, Naho-Rawa divide, Finisterre Mts.; Sayers 21452 (L), Saidor subdistrict, Naho-Rawa divide, Lake Naho; *Eastern highlands*: van Royen 11483 (K), Mt. Giluwe; Brass 30561 (CANB), east slope Mt.

Wilhelm; Hoogland 5448 (A, CANB), near Daulo camp, Asaro-Mairi divide, Goroka sub district, 6 1S 145 11E; Brass 30896 (A, BO, CANB, K), south slope Mt. Otto; Stevens 51033 (CANB, K), Marafunga, extension area 1, Goroka sub district, 6 05S 145 15E; Millar & van Royen 18512 (CANB), Kerowagi, Kundiawa subdistrict, 5 50S 144 50E; Womersley 37382 (CANB, K, L), Goroka subdistrict, Kerigomma, slopes above Marafunga, 6S 145 05E; Womersley 14026 (CANB), Marafunga logging area, upper Asaro valley, near Goroka, 6 05S 145 15E.; van Royen 18264 (Z), Minj subdistrict, confluent of Warapuri and Warrangga rivers, Jimi divide, 6 10S 144 50E; Sands 1581 (CANB), Kainantu Sub province, Mt. Piora 6 43S 145 58E. *Morobe district*: Clemens' 4830 (B), Ogeramnang; Clemens' 9262 (B), Samanzing; Clemens' 6031 (A); Clemens' 7830 (A), Ogeramnang; van Royen 16134 (CANB), path from south of Merampi river to Mt. Sarawaket, Rawlinson range 6 27S 147E; Craven &Schodde 1299 (CANB), Aseki Patrol area, 7 2S 146 11E; Clemens 9106 (B), Samanzing. *Milne bay*: Brass 23343 (A, CANB, K), Milne Bay, north slopes Mt. Dayman, Maneau range. *Central district*: Brass 5013 (A, BO), Mt. Tafa; van Royen 20404 (CANB, K, L), Mt. Awormange, east of Woitape 8 34S 147 17E; van Royen 20369 (A), Mt. Awormange, east of Woitape 7S 147E; Paijmans 737 (CANB), north of Woitape, 8 27S 147 12E; van Royen 20333 (CANB, L), road from Woitape to Uriko, northwest of Woitape, 7S 147E.

Key to the Varieties

1. Climber; leaves spathulate, 20.0 – 40.0 mm long.....var. *grandifolia*
   Erect shrub; leaves orbicular, 5.5 – 7.8 mm long.....var. *fruticosa*

var. *grandifolia* (Stauffer) Macklin **comb. nov.**

Type: Womersley & Jones 8791 (Holotypus LAE n.v.), Western district.

Cladomyza cuneata var *grandifolia* Stauffer ,Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 114: 65 (1969) **syn. nov.**

Leaves spathulate, 20.0 – 40.0 (8.0 – 14.0 x 3.0 – 4.0) mm, apex obtuse, shortly mucronate, base attenuate. *Fruits* grey.

Distribution: Northeastern Papua New Guinea.

Habitat: Disturbed areas; *Castanopsis - Nothofagus* forest. Parasitic on *Glochidion* (Euphorbiaceae).

Altitude: 1000 - 2000 m.

Notes: Name derived from the characteristic large leaves.

Additional material examined

Papua New Guinea: *Morobe district*: Clemens 6810 (A, B), Sattelberg. *Eastern Highlands*: Millar & van Royen 18512 (A), Kundiawa sub district, Kerowagi, 5 50S 144 50E; Brass 31361 (A, CANB, K), northeast slopes Mt. Michael.

var. *fruticosa* Macklin **var. nov.**

Type: Balgooy 200 (Holotypus CANB, Isotypus SING designated here), Mt. Wilhelm, base of Pindunde valley, 145 5E 5 45S.

Frutex erectus. Folia obovata, orbiculata, apices rotundata brevi-mucronata, basi rotundata.

Shrub, erect growth habit. *Leaves* yellow, brownish, obovate, orbicular, 5.5 – 7.8 (4.5 – 6.5 x 3.0) mm, apex rounded, tip shortly mucronate, base rounded, margin undulate, upper surface weakly convex. *Male flowers* large, tepals 1.2 – 1.3 x 0.7 – 0.1 mm.

Distribution: Eastern Papua New Guinea.

Habitat: Alpine, mossy forest dominated by *Eugenia*, *Schizomeria*, *Pandanus*. Parasitic on Myrtaceae, *Eurya*, *Dimorphanthera*, (Ericaceae); *Symplocos* (Symplocaceae).

Altitude: above 3000 m.

Notes: Name derived from the erect shrubby growth habit of this mistletoe. Characterised by this and the rather broad, orbicular leaves with shortly mucronate apices. This variety of *Dm. cuneata* is ecologically distinct as it is found at high altitudes in alpine, mossy forests which are dominated by Ericaceae. In terms of floral morphology it is not distinct from *Dm. cuneata sensu stricto* and cannot therefore be named as a separate species. The distinctness of the variety is defined rather by vegetative morphology and growth habit.

Additional material examined

Papua New Guinea: *Western district*: Vink 16140 (CANB), Kubor range, Mt. Kantz, 6 06S 144 18E; Vink 16170 (A, CANB), Kubor range, Mt. Kinkain; Vink 16196 (A, CANB), Kubor range, Mt. Kinkain; Vink 16001 (A, CANB), Nona Minj divide, Kubor range, 6 6S 144 18E.

6. *Dendromyza dendromyzoides* (Stauffer) Macklin **comb. nov.**

Type: Sleumer & Vink 4484 (Holotypus L!; Isotypus K!), Vogelkop peninsula, Arfak Mts., Mt. Koebré, northeast of Mt. Tembrok, between Anggi lakes.

Cladomyza dendromyzoides Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 114: 62 (1969) **syn. nov.**

Climber with long slender twining branches, shoots dimorphic with short, erect non-climbing shoots inserted in fascicles on long, lax branches. *Juvenile stems* slightly angular, striate or smooth, bracteate; *older branches* distinctly angular, twisted, initially weakly pustulate, later rough with narrow horizontal fissures. *Haustoria* confined to climbing stems. Leaves confined to non climbing stems, curving upwards. *Juvenile leaves* elliptic, apices weakly mucronate, margins entire; *mature leaves* obovate, 5.0 - 9.0 (3.0 - 6.0 x 2.0 - 5.0) mm, apices rounded, retuse, base attenuate, upper surface convex, margins recurved, surfaces wrinkled, rugulate, venation indistinct or primary veins 3; petiole short, quite thick, angular. *Inflorescences* dioecious, in leaf axils or at leafless nodes, 1 – 3 together, on juvenile and mature stems. *Male inflorescences* 1 - flowered, very shortly pedunculate, peduncle 0.2 – 0.5 mm long, subtended by 3 whorls of 3 imbricate bracts, bracts broadly deltoid, 0.8 x 1.0 mm, leathery with pale dots on the inner surface, margins weakly ciliate. *Male flower* buds sessile, globose, tepals 3 - 5, deltoid, fleshy, 0.9 - 1.0 x 1.3 - 1.7 mm, not apiculate at the apex, inner surface with luminous

pale dots concentrated around the anther, glandular hairs absent, filaments short, distinctly dilate at the base, 0.3 - 0.4 x 0.6 mm, anthers basifixed, 0.6 x 1.0 mm, anterior lobes slightly smaller than the posterior, anther dehiscence transverse, nectary flat, slightly concave, very thin, wafer-like, smooth or faintly granular, style rudiment long and thin. *Female inflorescences* subtended by a single quincuncial involucre of 5 bracts. *Female flower* buds obconical, receptacle, 0.6 x 0.6 mm, tepals deltoid, fleshy, 0.5 x 0.5 mm, style short, broad, 0.2 x 0.2 mm, stigmas 4, delicate, erect, nectary flat, unlobed, thin. *Fruit* narrowly ovoid, 5.0 - 7.0 x 2.5 mm, exocarp thin, smooth, mesocarp restricted to the apex of the endocarp, sericeus, hardly extending beyond the apex, apical 'tails' not pilose, endocarp narrowly ovoid, splitting easily, 3.5 - 4.5 x 2.2 - 2.5 mm, slightly angular but unlobed, apex attenuate, internally 4 - lobed until nearly the base, basal chambers 4 - 5, very small, circular, 0.1 mm in diameter, central column oblate, 0.5 x 0.7 mm.

Distribution: Vogelkop of Irian Jaya (**Fig. 44**).

Habitat: In relict low *Nothofagus* - Myrtaceae forests, in summit scrub. Various hosts recorded: *Nepenthes* (Nepenthaceae), *Drimys* (Winteraceae) but mainly associated with species of Ericaceae *e.g. Vaccinium globosum.*

Altitude: 2000 – 3000 m.

Notes: Name derived from the fact that the endocarp of the fruit is almost unilocular. When generic boundaries were narrower this species was placed in *Cladomyza* because of its chambered fruits. The short basal chambers of *Dm. dendromyzoides* are however similar to the classical *Dendromyza* fruit which is unilocular. A straggling, scandent shrub, with a very limited distribution and represented by only four specimens in the herbaria consulted. Characterised by dimorphic shoots and upward curving leaves with retuse apices. The chambers in the endocarp are also very short and the seed probably does not extend into them. It is quite similar to *Dm. microphylla*, but distinguishable from it by the angular petiole, male flowers with a very thin, membranous nectarial disc and fruit structure.

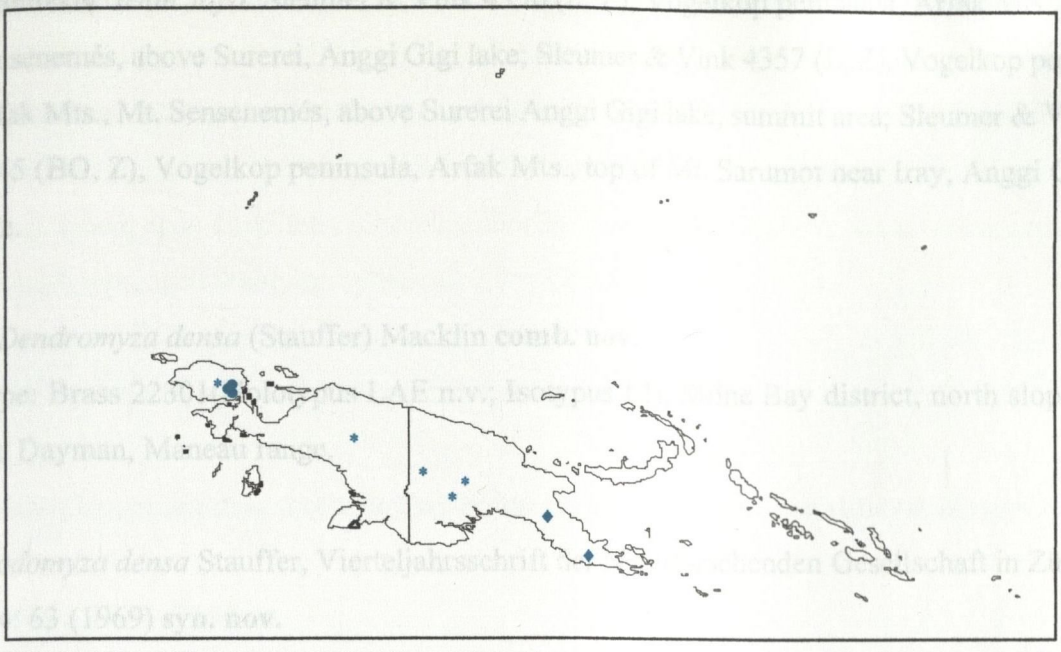


Fig. 44 Geographic distribution of: • *Dendromyza dendromyzoides*, ♦ *Dendromyza densa*, ▪ *Dendromyza erecta*.

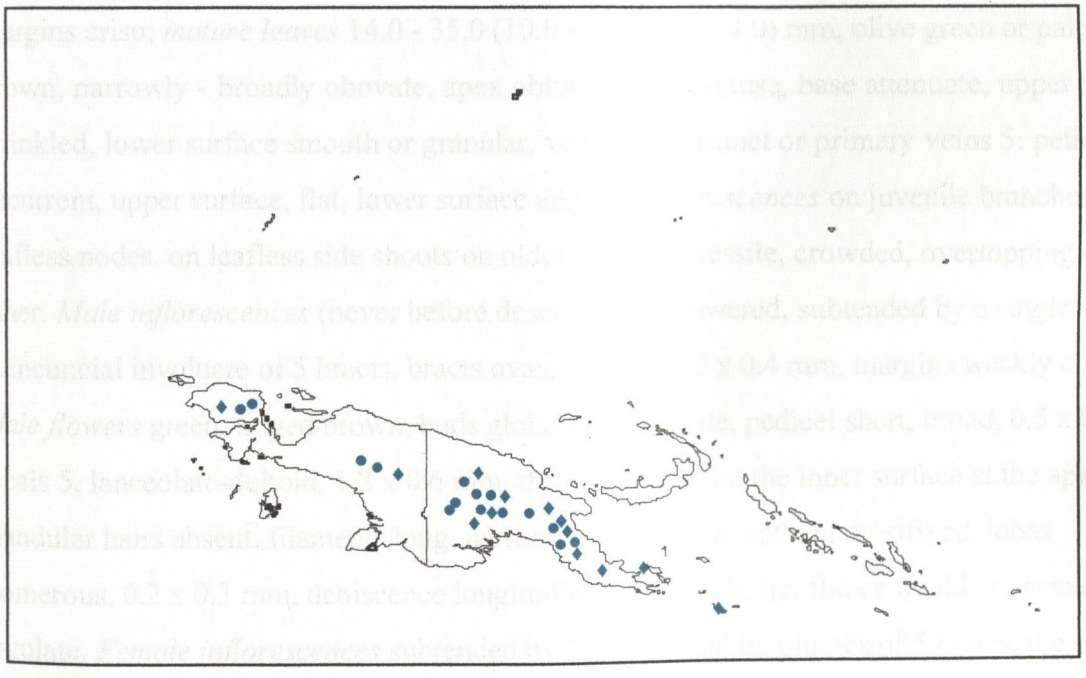


Fig. 46 Geographic distribution of: • *Dendromyza kaniensis*, ♦ *Dendromyza ledermanii*.

Additional material examined

Indonesia: *Irian Jaya*: Sleumer & Vink 4356 (L, Z), Vogelkop peninsula, Arfak Mts., Mt. Sensenemés, above Surerei, Anggi Gigi lake; Sleumer & Vink 4357 (L, Z), Vogelkop peninsula, Arfak Mts., Mt. Sensenemés, above Surerei Anggi Gigi lake, summit area; Sleumer & Vink 4445 (BO, Z), Vogelkop peninsula, Arfak Mts., top of Mt. Sarumot near Iray, Anggi Gigi lake.

7. *Dendromyza densa* (Stauffer) Macklin **comb. nov.**

Type: Brass 22301(Holotypus LAE n.v.; Isotypus L!), Milne Bay district, north slopes of Mt. Dayman, Maneau range.

Cladomyza densa Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 114: 63 (1969) **syn. nov.**

Erect shrub, forming dense clumps on trees. *Juvenile stems* angular, smooth or faintly striated, bracteate at the base, jointed; *older branches* terete with shallow, broad elliptic fissures, covered in a pale shiny, waxy deposit, distinctly different in appearance from the young stems. *Haustoria* absent. *Juvenile leaves* often involuted, tip apiculate, tinged red or brown, margins crisp; *mature leaves* 14.0 - 35.0 (10.0 - 19.0 x 3.0 - 4.0) mm, olive green or pale brown, narrowly - broadly obovate, apex obtuse, weakly retuse, base attenuate, upper surface wrinkled, lower surface smooth or granular, venation indistinct or primary veins 5; petiole decurrent, upper surface, flat, lower surface angular. *Inflorescences* on juvenile branches at leafless nodes, on leafless side shoots on older branches, sessile, crowded, overtopping each other. *Male inflorescences* (never before described) 1 - flowered, subtended by a single quincuncial involucre of 5 bracts, bracts ovate, minute, 0.5 x 0.4 mm, margins weakly ciliate. *Male flowers* green, tinged brown, buds globose, pedicellate, pedicel short, broad, 0.5 x 0.3 mm, tepals 5, lanceolate-deltoid, 1.2 x 0.6 mm, thick, apiculate on the inner surface at the apex, glandular hairs absent, filaments long, narrow, 0.3 x 0.1 mm, anthers dorsifixed, lobes isomerous, 0.2 x 0.3 mm, dehiscence longitudinal, nectary fleshy, flat or weakly concave, rugulate. *Female inflorescences* subtended by 2 quincuncial involucres of 5 bracts, the outer involucre directly opposite and smaller than the inner one, inner bracts large, 1.3 x 0.7 mm, ovate, fleshy with weakly ciliate margins. *Female flower* buds green, obconical, receptacle

short, broad, 0.6 x 1.6 mm, tepals fleshy, deltoid, not apiculate, 1.0 x 1.0 mm, style short, terete, twice as broad as long, 0.2 x 0.4 mm, widening at the base, stigmas 5, erect, fleshy, papillate. *Fruit* green, broadly ovoid, 6.6 x 4.0 mm, exocarp smooth, coriaceous, mesocarp delicate, sericeus confined to the apex of the endocarp and extending to 1 mm beyond it, apical 'tails' delicate, pilose, hairs long, filamentous, endocarp ovoid, splitting easily, 3.5 x 2.5 mm, deeply lobed, apex cuspidate, internally shortly 5 - lobed at the apex, central chambers circular, 0.6 x 0.6 mm, central column spherical, 2.0 x 1.8 mm.

Distribution: Northern and eastern Papua New Guinea (**Fig. 44**).

Habitat: Upper and mid montane Oak Forest, at forest margins, parasitic on Myrtaceae.

Altitude: 1000 - 2000 m.

Notes: Name derived from the erect, compact, growth habit. Represented by very few collections in the herbarium, this is the first time that the male plant has been described. This species is characterised by an erect growth habit and pale, waxy bark. It may be confused with *Dm. acrosclera* but can be distinguished from it by the absence of scleratomous inclusions in the leaves, the absence of glandular hairs in the male flowers and longitudinally dehiscing anthers. In terms of floral structure it is allied to *Dm. reinwardtiana* but is distinguished by a compact, erect growth habit and a chambered endocarp.

Additional material examined

Papua new Guinea: *Morobe district*: Sayers 21676 (CANB), Wagau; Hartley 12519 (A, CANB, K), Mt. Shungol, 5 miles southwest of Wagau, Maneau range.

8. *Dendromyza erecta* (Danser) Macklin **comb. nov.**

Type: Lam 1974 (Holotypus BO n.v.; Isotypus L!), Doorman.

Cladomyza erecta Danser, Nova Guinea New Series 6: 275 (1955); Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 114: 64 (1969) **syn. nov.**

Climber, branches erect, often with 2 - 3 branches from a single node. *Juvenile stems* smooth, terete or slightly angular towards the apex; *older branches* terete, twisted, bark rough, wrinkled with longitudinal fissures lighter in colour than the surrounding bark. *Haustoria* absent. *Juvenile leaves* elliptic, tips mucronate, margins entire; *mature leaves* pale, mid green or yellowish green, angled acutely to the stems, obovate, 14.0 - 23.0 (6.0 - 10.0 x 2.0 - 5.0) mm, apices obtuse, tips weakly recurved, base attenuate, surfaces rugulate when dry, venation indistinct; petiole involuted, slender, decurrent. *Inflorescences* dioecious, sessile in leaf axils on juvenile branches, crowded, overtopping each other. *Male inflorescences* 4 – 13 flowered, initially 1 - flowered, surrounded at the base by a valvate involucre of 3 membranous, withering bracts, a bud developing in the axil of each bract, each of which is subtended by an involucre of 3 valvate bracteoles, further flowers developing in the axils of the bracteoles. *Male flower* buds conical, shortly pedicellate, tepals 5, elongate-deltoid, 0.7 - 1.3 x 0.5 - 1.1 mm, fleshy, glandular hairs present, filaments long, narrow, base weakly dilated, 0.4 x 0.1 - 0.2 mm, anthers basifixed, lobes rounded, isomerous, locules in a single plane, 0.2 x 0.4 mm, dehiscence transverse, nectary fleshy, flat, style rudiment very much reduced or absent. *Female inflorescences* surrounded at the base by 2 - 3 involucres of imbricate bracts, bracts fleshy, ovate, margins ciliate; *Female flower* buds obconical, receptacle narrow, 1.0 x 1.0 mm, tepals 5, deltoid, fleshy, dull mid - green or yellow in colour, 0.7 - 0.8 x 0.6 - 0.7 mm, apices reflexed, staminodes absent, style terete, 0.2 x 0.2 mm, stigmas 5, fleshy, short, erect, nectary fleshy, unlobed, flat or slightly concave. *Fruit* green maturing purple, ovoid or elliptic, 5.5 - 6.0 x 3.0 - 2.5 mm, exocarp thin, smooth, mesocarp confined to the apex of the endocarp, sparse, sericeus, hardly extending beyond the apex, apical 'tails' delicate, not separating easily from the inner surface of the exocarp, pilose, hairs crisp, endocarp ovoid, not splitting easily, 3.0 - 3.5 x 2.0 - 3.0 mm, completely smooth and unlobed, apex cuspidate, internally 5-lobed at the apex, central chambers small, oblate, 0.2 x 0.4 mm, central column spheroidal, taking up almost the entire central portion of the endocarp, 1.9 - 2.0 x 1.2 - 1.5 mm.

Distribution: Irian Jaya and western Papua New Guinea (**Fig. 44**).

Habitat: Montane cloud forest and *Nothofagus - Phyllocladus* rainforest, in association with *Nothofagus* sp. (Fagaceae) and *Ilex* sp. (Aquifoliaceae).

Altitude: 2000 - 3000 m.

Vernacular name: Mondidi (Mendi language).

Notes: Name derived from erect growth habit with stems which lack haustoria. Leaf structure similar to *Dm. uncinata* with which it may be confused. Distinguishable from *Dm. uncinata* by the completely glabrous stems, anthers which are in a single plane and a smoother more rounded endocarp.

Additional material examined

Indonesia: *Irian Jaya*: Van Royen & Sleumer 7928 (L, Z), Vogelkop peninsula, south slope of Mt. Nettoti.

Papua New Guinea: *Sepik*: Vinas & Wikabu 59409 (CANB, L), Telefomin subdistrict, track to Busilmin. *Southern highlands*: Schodde 2111 (CANB, L), slope of Mt. Giluwe, above Klareg. *Western highlands*: Robbins 1062 (CANB), Tomba, Hagen subdistrict. *Morobe district*:Craven & Schodde 1135 (CANB), near Haumga, Aseki Patrol area.

9. *Dendromyza hiepkoiana* **sp. nov.**

Type: Hiepko 1200 (Holotypus B, designated here), Malingdam, West Irian Jaya.

Frutex erectus. Rami fasciculati, teretes, partim angulati. Folia squamosa. Inflorescentiae dioicae, sessiles, uniflorae. Flores femininae sessiles; tepala 4 – 5; staminodia nulla; stylus brevis; stigmata 4 – 5, subtili, recti. Endocarpium ovoideus; mesocarpium sericeum; apice filis plumosis coronatum.

Erect shrub, branches light brown, twisted, arising in fascicles from the host plant, curving upwards with several smaller side shoots arising spirally from the main stems often several from a single point. *Haustoria* absent. *Juvenile stems* smooth, waxy, striate, angular, flattened; *older branches* terete or slightly angular, bark with shallow longitudinal fissures and horizontal bands which have a powdery, waxy bloom. *Leaves* bract – like, percurrent with the stem, 1.0 –1.2 x 0.8 mm. *Inflorescences* dioecious, sessile or shortly pedunculate, on the side shoots crowded at tips of branches, later becoming separated into small groups of 2 – 3. *Male*

inflorescences unknown. *Female inflorescences* subtended by 2, valvate bracts and a single involucre of 3 – 5, imbricate bracteoles, bracts thin papyraceus 1.0 x 1.2 mm, margins ciliate. *Female flowers* brownish yellow, buds obconical, tepals 4 - 5, deltoid, fleshy, 1.2 x 1.0 mm, tips red, receptacle short, 0.7 – 1.0 x 1.4 - 1.5 mm, style twice as broad as long, dilated at the base, stigmas 4 – 5 sessile, delicate, erect, nectary fleshy, flat, angular. *Fruit* 5.0 x 2.5 mm ovoid, exocarp coriaceous, mesocarp sericeus covering the surface of the endocarp, apical 'tails' delicate, pilose, hairs sericeus, endocarp ovoid, not splitting easily, 3.0 x 1.5 mm, internally, 4 – lobed at the apex, central chambers elliptic, 0.5 x 0.2 mm, central column, elliptic, 1.5 x 1.0 mm. (**Fig. 45**)

Distribution: Western Irian Jaya (**Fig. 42**)

Habitat: Parasitic on *Homalanthus nervosus* (Euphorbiaceae).

Altitude: 2000 m.

Vernacular name: bon kubkubsina (bon = *Homolanthus nervosus*).

Notes: Name derived from the collector of the type specimen, Paul Hiepko, former director of the Berlin – Dahlem Museum. Characterised by seemingly leafless, fasciculate stems which are pale brown in colour. This species is locally abundant in the Eipomak valley. It has a similar vernacular name to *Dm. ledermanii* which is known as kubkubsina. The vegetative structure of this species is quite distinct. Its almost leafless stems are unique within *Dendromyza*. The spiral arrangement of the inflorescences along the shoots is also a distinctive characteristic and in many ways reminiscent of *Phacellaria*. In terms of reproductive morphology, the separate stigmas and chambered fruits which possess 'apical' tails on the endocarp, confirms the taxonomic position of this species as belonging to *Dendromyza*.

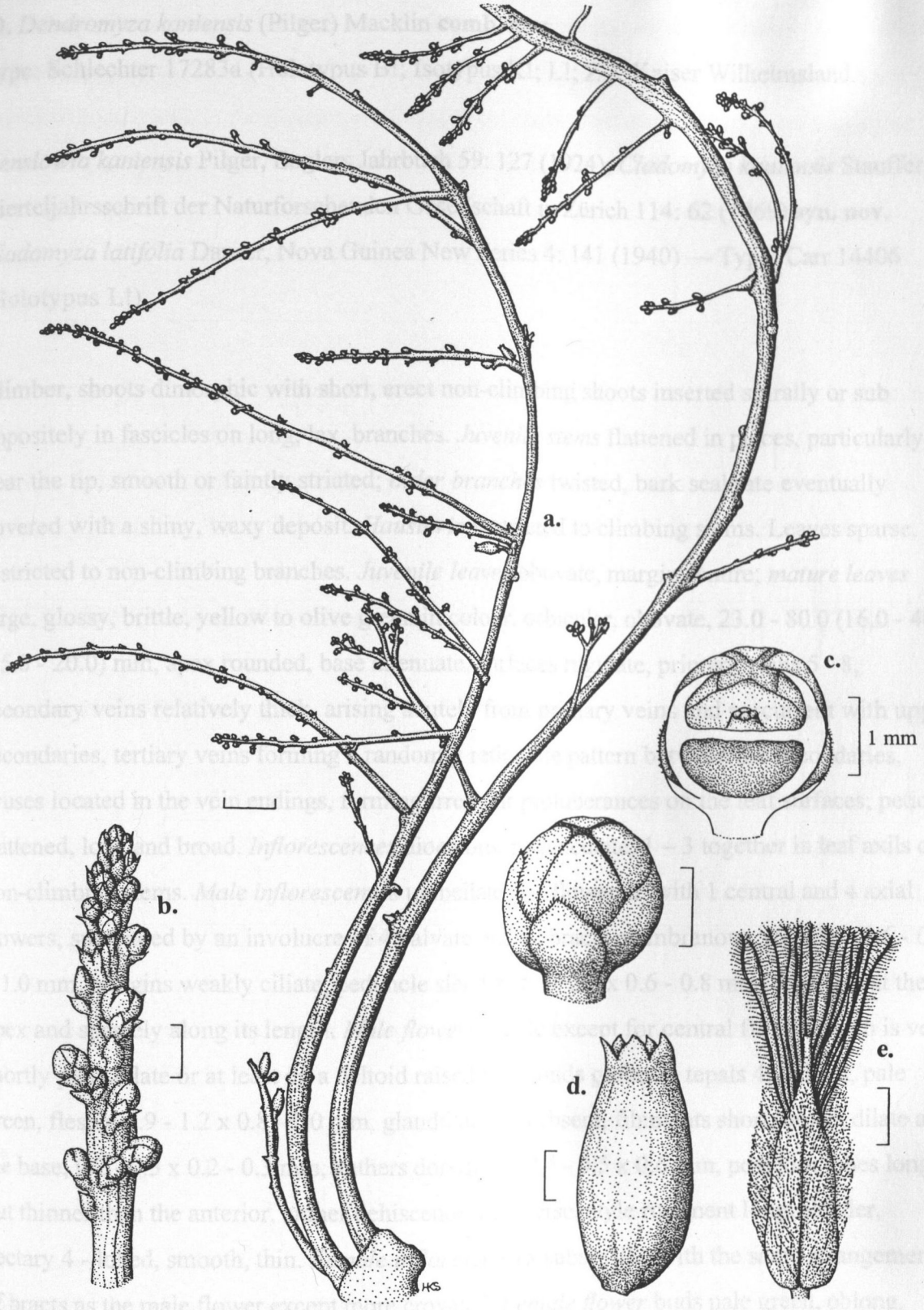


Fig. 45 Type specimen of *Dendromyza hiepkoiana*. **a.** habit, **b.** close up of inflorescence structure, **c.** close up of female flower bud, **d.** fruit, **e.** fruit when the exocarp is removed showing the sericeus mesocarp and the apical 'tails' at the apex of the endocarp.

10. *Dendromyza kaniensis* (Pilger) Macklin **comb. nov.**

Type: Schlechter 17283a (Holotypus B!; Isotypus K!; L!; Z!), Kaiser Wilhelmsland.

Henslowia kaniensis Pilger, Englers Jahrbuch 59: 127 (1924); *Cladomyza kaniensis* Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 114: 62 (1969) **syn. nov.** *Cladomyza latifolia* Danser, Nova Guinea New Series 4: 141 (1940) — Type: Carr 14406 (Holotypus L!).

Climber, shoots dimorphic with short, erect non-climbing shoots inserted spirally or sub oppositely in fascicles on long, lax, branches. *Juvenile stems* flattened in places, particularly near the tip, smooth or faintly striated; *older branches* twisted, bark scabrate eventually covered with a shiny, waxy deposit. *Haustoria* restricted to climbing stems. Leaves sparse, restricted to non-climbing branches. *Juvenile leaves* obovate, margins entire; *mature leaves* large, glossy, brittle, yellow to olive green in colour, orbicular, obovate, 23.0 - 80.0 (16.0 - 40.0 x 5.0 - 20.0) mm, apex rounded, base attenuate, surfaces rugulate, primary veins 5 - 8, secondary veins relatively thick, arising acutely from primary veins and percurrent with upper secondaries, tertiary veins forming a randomly reticulate pattern between the secondaries, druses located in the vein endings, forming irregular protuberances on the leaf surfaces; petiole flattened, long and broad. *Inflorescences* dioecious, pedunculate, 1 – 3 together in leaf axils on non-climbing stems. *Male inflorescences* umbellate, 5 – flowered, with 1 central and 4 axial flowers, subtended by an involucre of 4 valvate bracts, bracts membranous, rounded, 0.6 - 0.7 x 1.0 mm, margins weakly ciliate, peduncle slender, 1.5 - 2.0 x 0.6 - 0.8 mm, bracteate at the apex and sparsely along its length. *Male flowers* sessile except for central flower which is very shortly pedicellate or at least on a deltoid raised base, buds globose, tepals 4, deltoid, pale green, fleshy, 0.9 - 1.2 x 0.8 - 1.0 mm, glandular hairs absent, filaments short, broad, dilate at the base, 0.2 - 0.5 x 0.2 - 0.3 mm, anthers dorsifixed, 0.4 - 0.5 x 0.6 mm, posterior lobes longer but thinner than the anterior, anther dehiscence transverse, style rudiment long, slender, nectary 4 - lobed, smooth, thin. *Female inflorescences* subsessile, with the same arrangement of bracts as the male flower except more crowded. *Female flower* buds pale green, oblong, sessile on a raised, circular, cushion-like base, tepals 4, deltoid, fleshy, 0.9 - 1.0 x 1.0 mm. receptacle obconical, 0.8 - 1.5 x 1.1 - 1.5 mm, style short, terete, broadening towards the base, 0.3 x 0.3 mm, stigma 4 - 5 lobed, lobes pointed, erect, nectary unlobed, thin. Peduncle

extending after fruiting to 1.0 - 1.5 mm. *Fruit* yellow-green turning red, ovoid, 4.0 - 6.5 x 2.7 - 3.5 mm, nectary distinctly convex, protruding above the tepals so that stigma appears sessile, exocarp thick, leathery, mesocarp thin, sericeus covering the entire endocarp and extending to 4 mm above its apex, apical 'tails' delicate, not pilose, endocarp ovoid, not splitting easily, 3.5 x 2.5 mm, 5-angled, apex acuminate, internally 4 lobed at the apex, basal chambers elliptic, narrow, 0.6 - 0.8 x 0.2 - 0.3 mm, central column conical, 0.8 - 1.2 x 0.2 mm, broadening towards the base.

Distribution: Widespread in Papua New Guinea and Irian Jaya, eastern New Britain (**Fig. 46**).

Habitat: In hillside *Nothofagus* forests, mainly collected from forest margins. Parasitic on a variety of plants but primarily Melastomaceae and Fagaceae, other hosts include *Eurya* (Theaceae) *Polyosma* (Euphorbiaceae).

Altitude: 1000 – 3000 m.

Notes: Name derived from the location of the collection of the type specimen, Kaiser Wilhelmsland, *i.e.* Papua New Guinea. A widespread species, characterised by rather large leaves with distinct venation and a protruding, convex nectary in the fruit. Vegetatively it may be confused with *Dm. reinwardtiana* but is distinguishable by an umbellate male inflorescence and 4 – 5 chambered fruits. In terms of floral morphology it is similar to *Dm. dendromyzoides* but can be distinguished by longer pedunculate inflorescences and anthers where the posterior lobes are larger than the anterior. Also taxonomically close to *Dm. pachydisca* but differing in longer pedunculate inflorescences, a thinner nectarial disc in the male flower and a thick leathery exocarp. This species is newly recorded for New Britain.

Vernacular name: Walaloeka, Naserere (New Britain); Mandidi (Mendi language, Southern highlands, Papua New Guinea); Kumbiump (Enga language).

Additional material examined

Indonesia: *Irian Jaya*: Wally & Subari 6397 (BO), Uwosilimo; Mendum & Argent 92819 (E), near Namera and Mt. Trikora, track from Mulibaga to Mulalos village; Vink 15247 (Z), Vogelkop peninsula; Sleumer & Vink 4204 (K, Z), Vogelkop peninsula, Arfak Mts., in isolated forest patch near shore of Anggi Gita lake, base of Mt Mesenuk; Sleumer & Vink 4214 (Z), Vogelkop peninsula, Arfak Mts., Anggi Gita lake ascent to Mt. Mesenuk; Sleumer & Vink 4198 (Z), Vogelkop peninsula, Arfak Mts., Anggi Gita lake; van Royen & Sleumer 7482 (K), South slope of Mt. Nettoti, Vogelkop peninsula; Kostermans & Soegeng 594 (BO), Baliem valley near Wellesley.

Papua New Guinea: *Southern highlands*: Schodde 1508 (CANB), near Ebenda, Anga valley; Croft 60848 (CANB), Mendi sub-district, north Onim hill, southeast slope Mt. Giluwe; Schodde 1617 (CANB), Ebenda, Anga valley, 6 15S 143 42E. *Western highlands*: Henty & Galore 31948 (L), Western district, Ingembit, Kiunga subdistrict, 5 38S 141E; Henty & Streiman 38908 (L), below Dagarunga ridge, Jimi Valley; Henty & Galore 31956 (BO, CANB), Ingembit, Kiunga subdistrict; Womersley 55380 (BO, L), Mt. Hagen sub district, 5 50S 144 10E; Henty & Streimann 38908 (CANB), below Dagarunga ridge, Jimi valley, 5 28S 144 14E; Hoogland & Schodde 6967 (A, CANB, Z), Wabag sub district, Poio river. *Eastern highlands*: Stauffer & Sayer 5605 (A, B), Goroka, 6 miles from Kainantu; Stauffer & Sayers 5607 (A, B, CANB, Z), Numura, Goroka, near Okapa & Kainantu; Mc Kee & Floyd 6352 (BO, K), Goroka subdistrict, Daulo-Chauve road. *Morobe district*: Schodde & Craven 4975 (A, CANB, L), east slope of Spreader divide, northwest of Aseki, 7 15 S 146 10E; Streimann 24300 (L), Lae Subdistrict, southwest of Morobe, 7 48S 147 33E; Croft 68604 (CANB, K), Finschafen sub district, east of Mongi river, 6 40S 143 48E; Brass 11206 (CANB, K), Bele river, 18 km northeast of lake Habbema. *Central district*: Carr 10325 (CANB), Boridi, 9 05S 147 28E.

New Britain: Frodin 26905 (A, CANB, L), western slope of Mt. Tagis, Talasea; Croft & Katik 13174 (CANB), Eastern New Britain, Pomio, Mt. Sule, 25 miles northeast of Fulleborn harbour; Stevens & Lelean 58275 (CANB, L), lower slopes Mt. Lululua, 5 43S 151 02E.

Dendromyza kaniensis var *eymae* (Stauffer) Macklin **comb.nov.**

Type: Eyma 5180 (Holotypus L!), Wissel lake region, Barara.

Cladomyza kaniensis var *eymae* Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 114: 62 **syn. nov.**

Non-climbing parasitic shrub, strongly branched, often several branches from a single node. *Juvenile stems* angular, flattened, contracted at nodes, bracteate at the base; *older branches* granular, bark paler in colour and distinctly different from juvenile stems, initially with with continuous longitudinal fissures eventually entirely covered in a waxy, granular deposit. *Leaves* orbicular 12.5 - 13.5 x 12.0 - 12.5 mm, primary veins 7; petiole short upper surface weakly concave.

Distribution: Irian Jaya.

Habitat: In low and open *Nothofagus* forest in association with Ericaeous undergrowth, parasitic on *Garcinia* sp. (Guttiferae).

Altitude: 1950 - 2300 m.

Notes: Name derived from the collector of the type specimen, Eyma, a Dutch botanist and director of the Buitenzorg Botanic Gardens from 1940. A variety of *Dm. kaniensis* distinguished by erect growth habit and waxy, grey bark.

Additional material examined

Indonesia: *Irian Jaya*: Kanehira & Hatusima 14026 (A), Anggi, Arfak Mts., Vogelkop peninsula; Sleumer & Vink 4237 (K, Z), Vogelkop peninsula, Arfak Mts., Anggi Gita lake, ascent to Mt. Kongremottie; Sleumer & Vink 4458 (Z), Arfak Mts., Mt. Saru-mot near Anggi Gita lake, Vogelkop peninsula.

11. *Dendromyza ledermanii* (Pilger) Stauffer

Type: Ledermann 12211 (Holotypus *Henslowia ledermanii* B!), Schrauerberg.

Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 114: 60 (1969); *Henslowia ledermanii* p.p. Pilger, Botanische Jahrbucher: 59: 126 (1924); in Engler & Harms, Die Natürliche Pflanzenfamilien 16b: 72 (1935); *Cladomyza ledermanii* p.p. Danser, Nova Guinea New Series 6: 271 t.14 (1955); *Dendromyza apiculata* Danser *l.c.* p. 265 — Type: Clemens 199 (Holotypus B!, Isotypus L! Z!), Morobe district, Sattelberg; *Dendromyza mucronulata* Danser *l.c.*: 266 — Type: Carr 11918 (Holotypus B!, Isotypus L!), Koitaki; *Dendromyza papuana* Danser *l.c.*: 266 — Type: Brass 3800 (Isotypus L!), **syn. nov.**

Climber, stems slender, twining, with few side shoots, scarred with raised areas covered in bracts of previous seasons inflorescences. *Juvenile stems* generally twisted, angular, tangled together; *older branches* terete, smooth or with sparse longitudinal fissures. *Juvenile leaves* obtuse, mucronate, margins ciliate; *mature leaves* obovate, 20.0 – 36.0 (13.0 – 34.0 x 16.0 – 34.0) mm, apex obtuse, rounded, mucronate, may become weakly retuse, base rounded, primary veins 5, raised on the upper surface only, upper surface flattened or weakly convex, margins curling inwards; petiole slender, angular or completely flattened. *Inflorescences* dioecious, sessile on juvenile branches, or occasionally on older stems, crowded together in almost circular groups, over topping each other. *Male inflorescences* 6 - 31 flowered initially with 1 central and 5 axial flowers, subtended by an involucre of 5, valvate bracts, each axial flower subtended by an involucre of 5, minute bracteoles, further flowers developing in the axils of the bracteoles, bracts papyraceus, brittle, elongate-deltoid, 0.3 x 0.3 mm, margins finely ciliate, apex acuminate. *Male flowers* pedicellate, pedicel long, slender, buds conical, tepals elongate-deltoid 1.0 - 1.5 x 0.6 - 1.1 mm, glandular hairs present, filaments long slender, 0.3 x 0.2 mm, not dilated at the base, anthers dorsifixed, posterior lobes slightly larger than the anterior, dehiscence longitudinal, nectary fleshy, flat or slightly concave, 5 - lobed, style rudiment long, slender. *Female inflorescences* sessile subtended by a single involucre of valvate bracts. *Female flower* buds obconical, receptacle short, broad, 0.8 x 1.0 mm, tepals deltoid, not apiculate, 0.8 - 1.0 x 0.8 mm, style short, broad, 0.2 x 0.4 mm, stigmas 5, long, pointed, generally reflexed, papillate, nectary flat, fleshy, granular. *Fruit* 5.2 - 6.8 x 3.0 - 4.0 mm, exocarp smooth, coriaceous, mesocarp absent, apical 'tails' robust, pilose, hairs sericeus,

endocarp ovoid, splitting easily, 3.5 - 4.5 x 2.5 - 3.0 mm, completely smooth, unlobed, apex acute, base apiculate, internally completely unilocular.

Distribution: Irian Jaya, and Papua New Guinea (**Fig. 46**).

Habitat: Disturbed, secondary growth at forest margins and occasionally in grassland. Found in association with species from various families: *Mastixia* (Cornaceae); *Eugenia* (Myrtaceae); *Alphitonia* (Rhamnaceae); bamboo (Poaceae); *Wendtlandia* (Rubiaceae) but mainly parasitic on species of *Gymnacranthera* (Myristicaceae) and *Glochidion*, *Phyllanthus* (Euphorbiaceae).

Altitude:1000 - 2600 m.

Vernacular name: kubkubsina.

Notes: Name derived form the collector of the Type specimen, Carl Ledermann, a horticulturalist who made extensive collections in New Guinea between 1912 - 1914. Widespead in Papua New Guinea but particularly in the Morobe district. Characterised by slender climbing stems, apiculate leaf apices and crowded sessile male inflorescences. May be sometimes confused with *Dm. reinwardtiana* due to similarities in growth habit and superficial similarities in leaf shape, distinguished by shortly apiculate juvenile leaves, a multi-flowered male inflorescence, pilose apical 'tails' and an ovoid endocarp in the fruit.

Additional material examined

Indonesia: *Irian Jaya*: Johns 184 (L), northwest of Telefomin air strip; Hiepko 1115 (B, L), Eipomek – Tal, 4 25N 140 01E ; Vink 15228 (CANB), Vogelkop peninsula, Ajamaru

Papua New Guinea: *Sepik district*: Hoogland & Craven 11094 (CANB, L), Ambunti sub distirct, eastern ridge of Mt. Hunstein, 4 30S 142 41E. *Western highlands*: Schwabe 1987 (B), between Minj and Mt. Hagen; Sleumer 4179 (L, Z), upper Chimbu, Keglsugl; *Eastern highlands*: Stauffer & Sayers 5624 (A, B, CANB, L), Kainantu; Borgmann 356 (L), upper Chimbu valley; *Morobe district*: Stevens 54825 (CANB, K), track from Aseki to Hama, 7 20S 146 10E ; Hartley 10500 (CANB), 60 43S 146 47E; Stauffer, Pennington & Whitmore 5559 (A, L), near Bulolo; Stauffer, Pennington & Whitmore 5555 (A, CANB, L), near Bulolo;

Streimann & Kairo 47987 (L), Lae subdistrict, Saru river, 7 55S 147 14E; Lauterbach 583 (B), Sattelburg; Carr 14308 (CANB, L), Boridi, 9 05S 147 38E. *Central district*: Brass 5393 (A); Brass 3920 (A); Stauffer & Womersley 5690 (A, B, CANB, L, P), Port Moresby, near Sogeri; Stauffer & Womersley 5691 (A, B, CANB, L), Port Moresby near Sogeri ridge; Womersley 19132 (A, CANB, L), Sogeri near Surinumu, 99 25S 147 25E ; Schodde 2861 (CANB, L), Sogeri-Rouna divide. *Gulf district*: Craven & Schodde 777 (A, CANB, L, K), Ravikivau, Purari delta, 7 46S 145 10E. *Milne Bay district*: Brass 25059 (A, CANB, L), Goodenough island, 9 20S 150 14E ; Katik 70865 (L), Tagula island, Misima sub province, 11 30S 153 20E; Schodde 5549 (CANB, L), Mt. Simpson range, ridge between Agaun and Bonenau, 9 54S 149 23E.

12. *Dendromyza microphylla* (Lauterbach) Macklin **comb. nov.**

Type: von Roemer 1250 (Holotypus B, not found; Isotypus L!), Papua New Guinea.

Henslowia microphylla Lauterbach, Nova Guinea 8: 813 (1912); Pilger in Engler & Harms, Die Natürliche Pflanzenfamilien 16b: 72 (1935); *Cladomyza microphylla* Danser, Nova Guinea New Series 4: 136 (1940); Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 114: 63 (1969) **syn. nov.**; *Henslowia nivalis* Ridley, Transactions of the Linnean Society 9: 146 (1916) — Type: Boden Kloss (Holotypus L!, Isotypus K!); Pilger in Engler & Harms, Die Natürliche Pflanzenfamilien 16b: 72 (1935); *Cladomyza nivalis* Danser, Nova Guinea New Series 4: 136 (1940); Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 114: 63 (1969) **syn. nov.**; *Henslowia laevis* Pilger, Botanische Jahrbucher 59: 124 (1924) — Type: Pulle 1038 (Isotypus U!); *Cladomyza laevis* Danser, Nova Guinea New Series 4: 137 (1940); *H. acutata* Pilger, Botanische Jahrbucher 59: 125 (1924) — Type: Lam 1649 (Holotypus B n.v., Isotypus L!, U!); *Cladomyza acutata* Danser, Nova Guinea New Series 4: 136 (1940); Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 114: 65 (1969) **syn. nov.**; *Cladomyza robustior* Danser, Nova Guinea New Series 4: 137 (1940) — Type: Versteeg 2447 (Isotypus L!, U!), Summit of Mt. Hubrecht; *Cladomyza gracilis* Danser, Nova Guinea New Series 6: 275 (1955) — Type: Pulle 817 (Isotypus L!); Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 114: 62 (1969) **syn. nov.**

Climber, branches twining, dimorphic with short non-climbing side shoots inserted spirally on long lax branches. *Juvenile stems* terete or slightly angular, densely pustulate, bracteate at the base; *older branches* terete, bark rough, cracked with horizontal fissures. *Haustoria* present on climbing stems only. *Juvenile leaves* elliptic, margins entire; *mature leaves* recurved, fleshy, orbicular, leathery, apices rounded, tip mucronate, deciduous, base rounded, margins recurved, 3.0 – 11.0 (2.5 - 9.0 x 2.5 - 5.5) mm, surfaces rugulate, venation indistinct or primary veins 3 - 5; petiole short, upper surface invaginated. *Inflorescences* dioecious, sessile, slightly elevated or shortly pedunculate, 1 – 3 together in leaf axils on juvenile branches. *Male inflorescences* 5 - 6 flowered, with 1 central and 4 – 5 axial flowers, initially subtended by 2 involucres of 3 valvate bracts, the inflorescence expanding and arrangement becomes quincuncial, bracts 0.7 x 0.9 mm, fleshy, broadly ovate-deltoid, margins shortly ciliate. *Male flower* buds globose, sessile or very shortly pedicellate, tepals 4, broadly deltoid, 1.2 - 1.5 x 1.0 - 1.2 mm, fleshy, wrinkled, dull on outer surface, very shortly apiculate near the apex, glandular hairs absent, filaments long, narrow, 0.3 - 0.4 x 0.2 mm, anthers large, dorsifixed, posterior lobes slightly larger than the anterior, 0.3 - 0.4 x 0.5 - 0.6 mm, dehiscence transverse, a triangular elevation visible in the centre of the anther when dehisced, which consists of a cluster of druses, nectary fleshy, 4 - lobed, flat. *Female inflorescences* with the same arrangement of bracts as in the male plant. *Female flower* buds fungiform, receptacle narrow, 1.0 x 0.8 mm, tepals 4, fleshy, elongate - deltoid, 1.0 x 0.6 mm, stigmas 4, sessile, lobes rounded, outspread, nectary flat, convex underneath the stigma. *Fruit* 6.0 - 6.5 x 2.0 - 3.0 mm, exocarp leathery, mesocarp sericeus, covering the entire surface and hardly extending beyond the apex of the endocarp, apical 'tails' delicate, pilose, hairs crisp, endocarp elongate - ovoid, thin walled, splitting easily, 3.5 - 4.0 x 1.5 - 2.5 mm, weakly lobed, apex attenuate, internally 4- lobed at the apex, central chambers ovate, 0.4 x 0.2 mm; central column short, oblate, 1.0 - 1.5 x 0.7 - 0.8 mm.

Distribution: Central Papua New Guinea, western Irian Jaya (**Fig. 47**).

Habitat: Open forest margins and semi - alpine shrubbery. Parasitic on *Coprosma wollastonii*, *Rhododendron* (Ericaceae) and *Pittosporum* (Pittosporaceae).

Altitude: 2000 - 3500 m.

Notes: Name derived from the relatively small, orbicular leaves. Characterised by dimorphic stems and recurved, orbicular leaves which are often brown in colour. Allied to *Dm. dendromyzoides*, distinguishable by the generally smaller orbicular leaves transversally dehiscing anthers, crisp hairs on the apical 'tails' of the endocarp and a relatively short central column in the endocarp.

Additional material examined

Indonesia: *Irian Jaya*: Hope 16001 (CANB, L), Edge of Dayak, Carstensz Mts.; Mangen 210 (L), Mt. Trikora; Mangen 2405 (L), Valentijn Mts., trail from Koruppen to Angguruk camp, 4 20S 139 33E; Mangen 637 (L), Mt. Trikora; Mangen 1098 (L), Mt. Trikora, valley northeast of summit; Mangen 1835 (L), Valentijn Mts., south slope of main range, trail from base camp to Koruppen village 4 25S 139 43E.

Papua New Guinea: *Southern highlands*: Streimann 8591 (CANB, L), Mt. Giluwe, 6 04 S 143 55 E; Eyma 4423 (L), Wissel lake region at summit of Mt. Boebeira. *Eastern highlands*: Kalkmann 4485 (CANB), Mt. Antares; Brass & Meyer-Drees 9654 (L), Mt. Wilhelm.

13. *Dendromyza multinervis* (Danser) Macklin **comb. nov.**

Type: Brass 3430 (Holotypus *Cladomyza multinervis* B n.v.; Isotypus P!, L!), Isabel Island, Tatamba.

Cladomyza multinervis Danser, Nova Guinea New Series 6: 274 (1955) **syn. nov.**;
Dendromyza volubilis Danser *l.c.* — Type: Kostermans 1140 (Holotypus BO n.v.; Isotypus K!; L!), Morotai; Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 114: 61 **syn. nov.**

Climber, branches twining and erect, long, slender, twisted, often several from a single node. *Juvenile stems* distinctly flattened, angular; *older branches* terete, nodes distinctly swollen, bark smooth or with shallow, elliptic fissures. *Haustoria* present on twining stems. *Juvenile leaves* lanceolate, apices acuminate, becoming recurved, margin undulate; *mature leaves* green or yellowish green, elliptic, obovate, lanceolate, 25.0 - 30.0 (6.0 - 7.0 x 2.0 - 4.0) mm, primary veins 3 - 5 - 7, almost parallel, surfaces smooth or faintly rugulate; petiole decurrent, upper surface flat, lower surface angular. *Inflorescences* dioecious, pedunculate, singular on juvenile

branches and older stems, in leaf axils and at leafless nodes. *Male inflorescences* umbellate, 5 – flowered, with 1 central and 4 axial flowers, subtended by a valvate involucre of bracts, bracts unequal in shape and size but generally elongate-deltoid, 0.5 x 0.4 mm, margin sparsely ciliate, peduncle slender, angular, 1.5 – 1.8 x 0.7 mm, bracteate at the apex and along its length. *Male flowers* green, white, pedicellate, pedicel long, narrow, tepals 5, delicate, elongate-deltoid, 0.7 x 0.5 mm, apiculate on the inner surface at the apex, margin incurved, filaments slender 0.2 x 0.1 mm, anthers 0.2 x 0.4 mm, dorsifixed, bilocular, lobes isomerous, dehiscence longitudinal, nectary fleshy, weakly concave, 5 - lobed, style rudiment broad. *Female inflorescences* subsessile with the same arrangement of bracts as the male inflorescence but more crowded. *Female flower* buds turbinate, receptacle slender, angular, 1.5 x 0.8 mm, tepals yellow, 4 - 5, deltoid, thick, 0.6 x 0.6 mm, stigmas 4 - 5, erect, pointed, nectary flat, angular. Peduncle extending to 2.0 - 2.5 mm after flowering. *Fruit* green turning orange then red, elliptic, ovoid, 8.5 - 9.0 x 2.5 - 4.0 mm. Exocarp thin, smooth, mesocarp absent. Apical 'tails' robust, pilose, hairs sericeus, endocarp elliptic, splitting easily, 6.5 - 8.0 x 2.3 - 2.5 mm, internally unilocular.

Distribution: Philippines, western New Britain, Moluccas, eastern islands of New Guinea (**Fig. 48**).

Habitat: Primary rainforest, *Castanopsis* forests and at forest margins. Parasitic on a number of species but recorded from *Elaeocarpus* (Elaeocarpaceae), *Eugenia* (Myrtaceae) and *Mastixia* (Cornaceae).

Altitude: 500 - 1700 m.

Notes: Name derived from the numerous primary veins which appear closely packed and almost parallel on the narrow leaves. Characterised by long tangled, twining, branches and juvenile leaves with recurved tips. In this feature it is superficially similar to *Dm. uncinata* and *Dm. erecta* but can be differentiated from these two species by its pedunculate inflorescences, the absence of bracteoles in the male inflorescence and a unilocular endocarp. In term of fruit morphology allied to *Dm. reinwardtiana*, but distinguished by its narrow, multinerved leaves, pedunculate, multiflowered, delicate inflorescences.

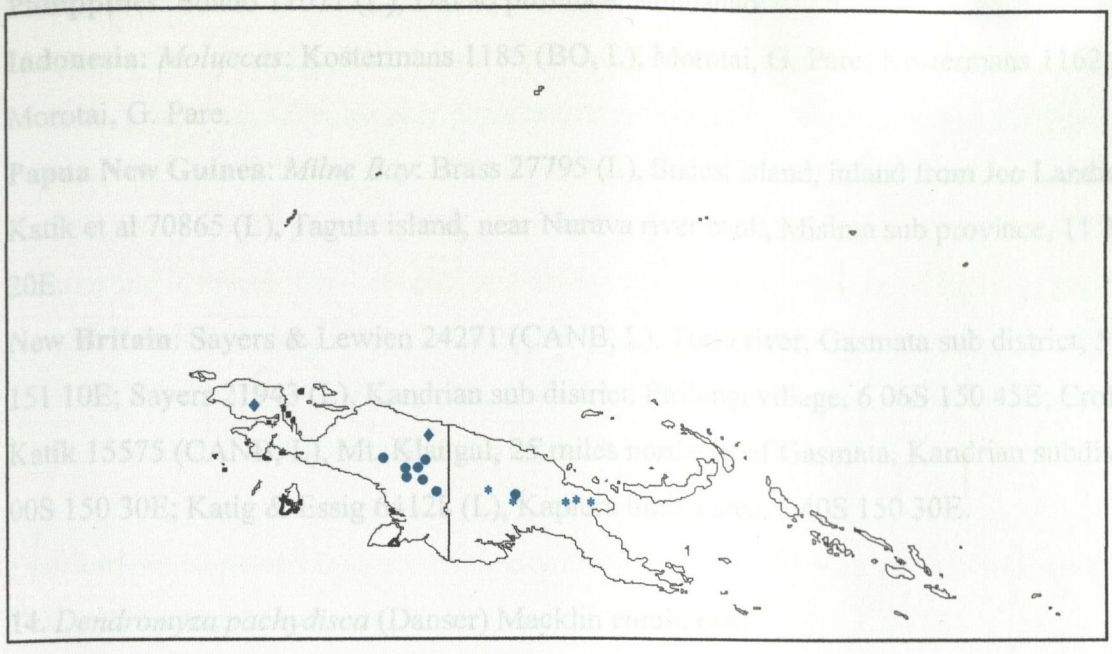


Fig. 47 Geographic distribution of: • *Dendromyza microphylla*, ♦ *Dendromyza puberula*, ⋆ *Dendromyza staufferia.*

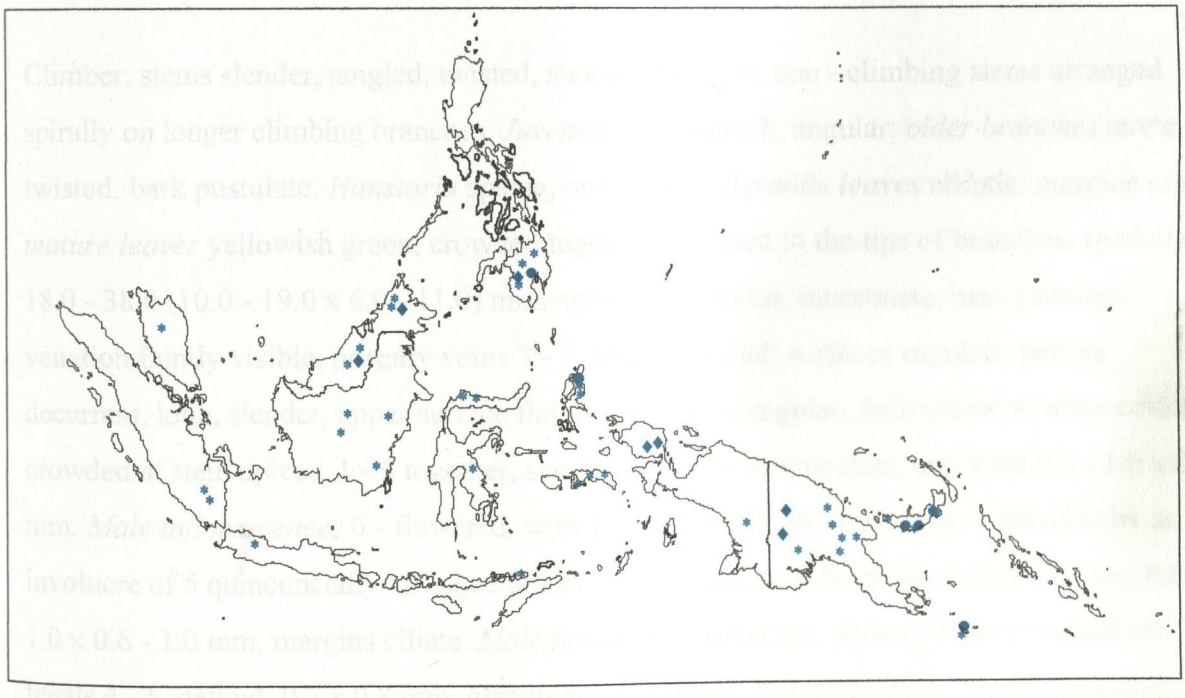


Fig. 48 Geographic distribution of: • *Dendromyza multinervis*, ♦ *Dendromyza pachydisca*, ⋆ *Dendromyza reinwardtiana*

Additional material examined

Philippines: Edano 11071 (L), Davao province, Mindanao.

Indonesia: *Moluccas*: Kostermans 1185 (BO, L), Morotai, G. Pare; Kostermans 1162 (L), Morotai, G. Pare.

Papua New Guinea: *Milne Bay*: Brass 27795 (L), Sudest island, inland from Joe Landing; Katik et al 70865 (L), Tagula island, near Nurava river bank, Misima sub province, 11 30S 153 20E.

New Britain: Sayers & Lewien 24271 (CANB, L), Torlu river, Gasmata sub district, 5 45S 151 10E; Sayers 21943 (L), Kandrian sub district, Pirilongi village, 6 06S 150 45E; Croft & Katik 15575 (CANB, L), Mt. Klangal, 25 miles northeast of Gasmata, Kandrian subdistrict, 6 00S 150 30E; Katig & Essig 64128 (L), Kapiura timber area, 5 40S 150 30E.

14. *Dendromyza pachydisca* (Danser) Macklin **comb. nov.**

Type: Clemens 27308 (Holotypus of *Cladomyza pachydisca* L!; Isotypus B!), Borneo, Mt. Kinabalu.

Cladomyza pachydisca p.p. Danser, Nova Guinea New Series 4: 140 (1940); Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 114: 61 (1969) **syn. nov.**

Climber, stems slender, tangled, twisted, shoots dimorphic, non - climbing stems arranged spirally on longer climbing branches. *Juvenile stems* smooth, angular; *older branches* terete, twisted, bark pustulate. *Haustoria* sparse, on all stems. *Juvenile leaves* elliptic, margins crisp; *mature leaves* yellowish green, crowded together, confined to the tips of branches, spathulate, 18.0 - 38.0 (10.0 - 19.0 x 6.0 - 11.0) mm, apex acute, obtuse, mucronate, base attenuate, venation faintly visible, primary veins 3 - 5, almost parallel, surfaces rugulate; petiole decurrent, long, slender, upper surface flat, lower surface angular. *Inflorescences* monoecious, crowded at stem apices, 1 - 3 together, sessile or shortly pedunculate, peduncle 0.5 - 1.0 x 0.5 mm. *Male inflorescences* 6 - flowered, with 1 central and 5 lateral flowers, subtended by an involucre of 5 quincuncially arranged bracts, bracts ovate, membranous, variable in size, 0.6 - 1.0 x 0.6 - 1.0 mm, margins ciliate. *Male flower* buds spherical, yellow, shortly pedicellate, tepals 4 - 5, deltoid, 0.7 x 0.8 mm, glandular hairs absent, filaments short, broad, diverging slightly at the base, 0.2 x 0.2 mm, anthers dorsifixed, posterior lobes larger than the anterior,

0.2 - 0.4 x 0.4 - 0.5 mm, dehiscence transverse, nectary lobed, very fleshy, style rudiment long, substantial, bulbous at the tip. *Female inflorescences* sessile. *Female flower* buds obconical, receptacle short, broad, 0.8 x 1.1 mm, tepals 4 - 6, deltoid, fleshy, 0.5 - 0.8 x 0.5 - 0.7 mm, stigmas 5, rounded, short, weakly papillate, nectary smooth, fleshy, unlobed, flat or slightly convex. *Fruit* green turning red and then purple, ovoid 4.5 - 7.5 x 2.5 - 4.0 mm, exocarp smooth, thin, mesocarp membranous, confined to the apex of the endocarp and extending to 1 mm beyond it, apical 'tails' delicate, not always detaching from inside of exocarp, pilose, hairs membranous, endocarp ovoid, 3.0 - 4.0 x 2.0 - 3.7 mm, distinctly 4 - 5 angled rather than lobed, thick but not robust, not splitting easily, apex cuspidate, internally 5 - lobed at the apex, central chambers narrow, elliptic, 0.7 x 0.2 mm, central column conical, 1.0 x 0.3 - 0.4 mm.

Distribution: Northeast Borneo, Philippines, Irian Jaya and Western district of Papua New Guinea (**Fig. 48**).

Habitat: In mountainous regions, at the edge of or in Primary *Nothofagus* (Fagaceae) forest with Myrtaceae and Podocarpaceae and an undergrowth of Ericaceae. Parasitic on *Symplocos* (Symplocaceae) and *Vaccinium* sp., (Ericaceae) exhibiting a variety of growth forms with partly climbing and pendant branches.

Altitude: 1000 – 2300 m.

Notes: Name derived from the fleshy nectarial disc of the male flower. One of the few species found outside New Guinea and the only one apart from *Dm. reinwardtiana* to extend into Borneo and the Philippines. Like *Dm. reinwardtiana*, the inflorescences are monoecious and the leaves are generally large, but distinguished from this species by the transversally dehiscing anthers and the 4 - 5 locular endocarp in the fruit. In New Guinea it may also be confused with *D. stellata* but can be differentiated from this species by the glandular hairs in the male flower, a fleshy nectary and again by 4 - 5 locular fruits.

Vernacular name: Djulediema (Huli language, New Guinea).

Additional material examined

Philippines: Edano 38947 (A, P), Mindanao, Bukidnon sub province.

Malaysia: *Sarawak*: Ilias 28530 (L), Bukit Tibang, Kapit district at the end of Balang ridge; *Sabah*: Clemens 26905 (L), Dallas, Mt. Kinabalu.

Indonesia: *Irian Jaya*: Sleumer & Vink 4410 (K, Z), Vogelkop peninsula, Arfak Mts., Mt. Disrebi, ridge near Iray, Anggi Gita lake; Sleumer & Vink 4459 (K, Z), Vogelkop peninsula, Arfak Mts., Mt. Saru-mot near Iray, Anggi Gita lake; Sleumer & Vink 4280 (SING, Z), Vogelkop peninsula, Arfak Mts., Anggi Gita lake ascent from Testega to Mt. Koebre; Sleumer & Vink 4294 (K, Z), Vogelkop peninsula, Arfak Mts., ascent to Mt. Koebre east slope from Testega, Anggi Gita lake; Burley & Ismail 4573 (L), Baliem valley, 39km north on Wamena Pass valley road, 3 40S 139E.

Papua New Guinea: *Southern highlands*: Ridsdale, Henty & Galore, 31948 (BO), Ingembit, Kiunga sub district; Vink 16867 (CANB), Tari subdistrict, Tigibi, 6S 143E. *Sepik region*: Ledermann 9387 (B), Etappenberg.

15. *Dendromyza puberula* Stauffer

Type: van Royen & Sleumer 7340 (Holotypus L!; Isotypus K!), Vogelkop peninsula, Kebar valley, above Suphur springs, path to Hatai.

Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 114: 60 (1969).

Erect shrub, several branches from a single node, contracted at the base. *Juvenile stems* slender, twisted, slightly angular; *older branches* terete, bark with longitudinal, elliptic fissures, all stems covered in a short papillose indument. *Haustoria* absent. *Juvenile leaves* reddish green, lanceolate, margins ragged; *mature leaves* 30.0 – 40.0 (14.0 – 15.0 x 7.0) mm, obovate, apex obtuse, tip mucronate, deciduous, base attenuate, margins undulate, primary veins 5, indistinct; petiole long, flat on upper surface, lower surface terete, decurrent. *Inflorescences* on juvenile branches at leafless nodes or on short leafless side shoots, pedunculate, peduncle long, slender, 1.0 - 2.5 x 0.6 mm. *Male inflorescences* 6 – flowered, umbellate with 1 central and 5 axial flowers subtended by a quincuncial involucre of 5 bracts, bracts broadly ovate thick, 0.6 x 0.8 mm. *Male flower* buds fungiform, tepals deltoid, 0.5 x 0.4 mm, stamens immature. *Female inflorescences* with the same arrangement of bracts as the male inflorescence. *Female flower*

buds yellowish, fungiform, tepals ovate, apex acuminate, 0.7 x 0.6 mm, receptacle long, slender, 1.0 x 0.7 mm, style short, as long as broad, 0.2 x 0.2 mm, stigmas 5, rounded, nectary convex, unlobed, smooth. *Fruit* yellow, narrowly ovoid, 7.0 x 2.8 mm, exocarp smooth, coriaceous, mesocarp absent, apical 'tails' robust, pilose, hairs membranous, endocarp ovoid, smooth, splitting easily, 5.0 x 2.0 - 2.5, internally unilocular.

Distribution: Irian Jaya (**Fig. 47**).

Habitat: Dense high forest, parasitic on *Quintinia* (Escalloniaceae) and Cunoniaceae.

Altitude: 850 - 1220 m.

Notes: Only two representatives were found in the herbaria consulted. Characterised by a papillose indumentum on shoots and a non - climbing growth habit. Allied to *Dm. multinervis*, distinguished by its shrubby growth habit, papillose stems, a shorter receptacle in the female flower and an ovoid endocarp.

Additional material examined

Indonesia: *Irian Jaya*: van Royen & Sleumer 6069 (L, Z), Hollandia district, Cyclops mountains, path from Ifar to Ormoe.

16. *Dendromyza reinwardtiana* (Bl.) Danser

Type: Reinwardt (Holotypus L!; Isotypus *Henslowia reinwardtiana* P!), Sumatra.

Danser, Nova Guinea New Series 4: 134 (1940); *Tupeia reinwardtiana* Bl., Flora Javae Loranthaceae (1838) — Type: Reinwardt (Isotypus L!, P!), Java ; *Tupeia racemosa* Korthals, Bulletin Neerlandica: 157 (1838) — Type: Korthals 1032 (Isotypus L!); *Henslowia reinwardtiana* Bl., Musuem Lugduno Batavae 1: 244 (1850); *Dendrotrophe reinwardtiana* Miq., Flora Indiae Batavae 1.1: 780 (1856); *Dendrotrophe plurinervia* Miq., *l.c.*: 1096 (1858) — Type: Blume 1075 (Holotypus U!), Java; *Henslowia plurinervis* Boerlage, Flora van Nederlandsch Indië: 181(1900); *Henslowia robinsonii* Merrill, Philippine Journal of Scientific Botany 11: 268 (1916) —Type: Robinson 1809 (Holotypus K!, Isotypus L!, P!), Amboina; *Dendromyza reinwardtiana* var. *aphylla* Stauffer, Vierteljahrsschrift der Naturforschenden

Gesellschaft in Zürich 114: 60 (1969) — Type: Elmer 14063 (Holotypus MAN n.v., Isotypus A!, L!, Z!), Philippines, Mindanao, Mt. Urdaneta **syn. nov.**

Climber, branches long, twining, often pendulous. *Juvenile stems* flattened or angular, weakly pustulate with several branches arising from a single node, contracted and bracteate at the base, *older branches* terete, bark rough, striated or with shallow longitudinal, elliptic fissures which are paler in colour than the surrounding wood. *Haustoria* present on all stems. *Juvenile leaves* fleshy, tinged red, margins entire; *mature leaves* dull green or yellowish green, narrowly - broadly obovate, spathulate, 21.0 – 80.0 (16.0 – 70.0 x 3.0 – 5.0) mm, apex obtuse, rounded, base attenuate, surfaces smooth, weakly rugulate, venation indistinct or primary veins 3 - 5, secondary veins absent or 2, parallel with primary veins; petiole angular, decurrent. *Inflorescences* dioecious or occasionally monoecious on juvenile branches, crowded at leafless shoot apices, 1 - 3 together, subsessile, pedunculate, peduncles 0.5 – 1.5 x 0.5 mm. *Male inflorescences* 1 - flowered, subtended by 3 involucres of 5, quincuncially arranged bracts, bracts large, fleshy, broadly deltoid, 0.8 - 1.0 x 0.8 - 1.0 mm, margins weakly ciliate. *Male flowers* green, buds globose, tepals deltoid, fleshy 1.0 - 1.2 x 1.0 - 1.1 mm, not apiculate, glandular hairs absent, filaments 0.3 - 0.5 x 0.1 - 0.3 mm, dilated at the base, anthers dorsifixed, lobes initially divergent, posterior lobes larger than the anterior, later isomerous, 0.3 - 0.5 x 0.5 - 0.6 mm, nectary fleshy, weakly pustulate, flat or weakly concave, apiculate in the centre. *Female inflorescences* subtended by a single quincuncial involucre of 5 bracts at the apex. *Female flowers* yellow, yellowish cream, buds obconical, tepals elongate - deltoid, 0.6 - 1.0 x 0.5 - 0.7 mm, receptacle broad 1.0 x 0.8 mm, stigmas 5 erect, papillose. *Fruit* green turning yellow and finally red, narrowly ovoid, elliptic, 7.0 - 9.0 x 2.5 - 3.0 mm, exocarp coriaceous, mesocarp absent, apical 'tails' robust, not pilose, endocarp elliptic, splitting easily, 4.5 - 6.0 x 2.5 - 3.5 mm, apex attenuate, internally unilocular.

Distribution: Philippines, Borneo, Java, Sumatra, Sulawesi, New Guinea, New Britain (**Fig. 48**).

Habitat: Generally in limestone regions on white sandy soil, in coastal areas and along riverbanks. Also recorded at higher elevations at the margins of primary lowland forests and in disturbed secondary vegetation. Found in association with several species but particularly

Saurauia (Sauriauiaceae) and *Ficus* (Moraceae) other hosts include: *Koordersiodendron* (Anacardiaceae), *Timonius*, *Wendlandia* (Rubiaceae); *Rhododendron* (Ericaceae) and *Alphitonia* (Rhamnaceae).

Altitude: 0 - 1700 m.

Vernacular name: Awamo (Kutubu name).

Notes: Name derived from collector of the type specimen, Reinwardt, a botanist who worked and collected in Malesia between 1816 and 1822. This species represents the most westerly extension of *Dendromyza* and is the only species of this genus to be collected in central Borneo, Java and Sumatra. It is very variable in terms of leaf shape, leaves may be very narrowly obovate, broadly spathulate or almost orbicular. The variation in leaf morphology is however continuous throughout the range of the species although the narrow leaf type is most common in the Philippines. Characterised by a twining growth habit, older branches with fissured bark, 1 – flowered male inflorescences, glabrous apical 'tails' on the endocarp and an elliptic endocarp. Allied with *Dm. ledermanii* and *Dm. staufferia*, distinguished from the former by generally larger obovoid leaves and a single flowered male inflorescence. It differs from the latter in terms of leaf shape, the absence of staminodes in the female flower and by an elliptic endocarp.

Additional material examined

Malaysia: *Malay Penninsula*: King 6203 (K), Perak. *Sarawak*: Sylvester 34848 (L), Dulit range, Ulu Tinjar, 4th division; Hallier 2190 (L), Soengri; Jacobs 5386 (K, L), Kapit district, Belaga sub district, 2 40S 113 50E; Endert 3843 (L); Primack 43333 (L), Gunong Api. *Sabah*: Clemens 30970 (A, L), Mt. Kinabalu; Clemens 32471 (A, L, Z), Dallas; Clemens 33039 (L), Mt. Kinabalu; Clemens 33155 (A, L), Mt. Kinabalu.

Philippines: Sands 3188 (L), Mindanao, Mt. Apo, 6km west of Todaya, 7S 125 15E; Elmer 11296 (A, L), Mindanao, Davao; Elmer 10106 (A, L), Negros; Wenzel 2553 (GH, L), Surigao.

Indonesia: *Kalimantan*: Kostermans 12883 (L), west Kutei, Mt. Palimasam near Tabang on Belayan river; Teysmann s.n. (L); Endert 5268 (L), central east Borneo; Buwalda 7817 (BO, L), Sampit; Kostermans 13742 (A, CANB, L), foot of Mt. Ilas Bungaan; *Sumatra*: si Boeea

9290 (A, L), east coast, Aek Moente; Borssum 1832 (L), west coast, Lubuk, Sikaping; Beccari 737 (K, L); Niniek 58 (L), Ketamba, Aceh Tenggara. Nooteboom 4444 (CANB, L, Z), Bukit Raya, 112 45E 0 45S. *Java*: Backer 4511 (L, U), Praengen; Bakhuizen & van den Brink 5244 (L, P); Bakhuizen & van den Brink 857 (U); van Steenis 11762 (L), Bogor; Backer 12462 (L), Gunong Samboeng; Backer 31508 (L), Banjoemas reserve; Indig 10 (BO, L, P), Tjibodas. *Sulawesi*: Eyma 3483 (BO, L, U), Menado; de Vogel 6361 (L), Luha island, on lake Towuti, 2 45S 121 33E ; de Vogel 5863 (L), Selantan, east side of lake Matano, 2 30S 121 21E; van Balgooy 3957 (K), near Soroaka 2 15S 121E. *Moluccas*: Teysmann (L), Seram; Buwalda 5623 (L), eastern Seram; Idjan & Moohtar 296 (L), Halmahera, Gunong Sembilan; Kuswata & Soepadmo 116 (L), Gemba, west Seram. Kostermans 939 (L), Morotai; Rant 323 (BO, L), Ambon; Rant 66 (BO), Ambon, Batoe Merah; Teysmann 5153 (L), Ambon; van Leeuwen 8674 (L), Ambon; Buwalda 6129 (L), Ambon. *Lesser Sunda Islands*: Kostermans 22148 (L), Flores, Ruteng, Pongkor; Kostermans & Wirawan 735 (L), Flores, slope of Mt. Ranaka. *Irian Jaya*: van Leeuwen 10687 (L), Nassau.

Papua New Guinea: *Southern highlands*: Schodde 2181 (CANB, L), lake Kutubu; Schodde 2163 (A, BO,CANB, L), near Tage, lake Kutubu; Conn 421 (A, L), Upper Baiune river, 7 S 146 50E; Carr 12060 (CANB, L), Koitaki. *Eastern highlands*: Stauffer & Sayers 5618 (CANB, L), Henganofi district, 6 17S 145 26E; Brass 31601 (A, CANB, L), Okapa area, 6 41S 145 32E. *Western highlands*: Croft & Lelean 65739 (L), Telefomin, Star Mts., 5S 141 05E. *Madang*: Sayers 21255 (CANB, L), Saidor, Finister Mts., 5 55S 145 58E. *Morobe district*: Streimann 24300 (CANB, L), Lae subdistrict, 7 48S 147 33E; Fryar 4009 (A, BO, CANB, L), Bulolo; Streimann 27786 (CANB), Bulolo 7S 146 40E; Stauffer 5559 (A, L), near Bulolo; Stauffer 5555 (A, CANB, L), near Bulolo; Womersley & Millar 8714 (BO, L), Wau-Salamaua road, 7 10S 147E. *Milne Bay*: Katik 70865 (K), Tagula island, 11 30S 153 20E.

New Britain: Sayers 21787 (A, CANB, K, L), Kandrian, Fullerborn village, 6 06S 150 40E; Henty & Frodin 27403 (A, CANB, L), Wariai, 5 47S 148 57E; Kairo 47660 (A, CANB, L); Sayers 24215 (BO, CANB), Torlu, Gasmata, 6S 151 02E; Paijmans 483 (CANB), Mt. Sago, 15 km southeast of Cape Hoskins; Croft & Katik 12975 (A, BO, CANB, L), road west of Fulleborn harbour, Pomio subdistrict, 6 10S 150 40E.

17. *Dendromyza salomonia* Danser

Type: Kajewski 1672 (Holotypus B n.v.; Isotypus P!), Bouganville island, Kupei gold fields.

Danser, Nova Guinea New Series 6: 267 (1955); Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 114: 61 t.4 (1969).

Climber, branches slender, jointed, twining, often several arising from a single node. *Juvenile branches* twisted, angular; *older branches* terete, bark smooth or with narrow longitudinal fissures, slightly paler in colour than the surrounding bark. *Haustoria* absent. *Juvenile leaves* obtuse, tip shortly apiculate, margins entire; *mature leaves* obovate, 22.0 - 27.0 (10.0 - 12.0 x 3.0 - 4.0) mm, apex obtuse, recurved, base attenuate, upper surface flat or weakly convex, texture smooth or faintly rugulate, primary veins 3 - 5; petiole short, decurrent. *Inflorescences* pedunculate, 1 – 3 together on juvenile stems and occasionally on older branches, in leaf axils and at leafless nodes. *Male inflorescences* umbellate, 5 – flowered, with 1 central and 4 axial flowers, subtended by an imbricate involucre of 4 bracts, bracts 1.0 x 0.7 mm, ovate, fleshy, margins basally ciliate, peduncles 0.6 – 3.2 x 0.4 – 0.6 mm, bracteate at the apex and the base, basal bracts minute. *Male flower* buds spherical, becoming conical, pedicellate, pedicel long, slender, tepals deltoid, fleshy, shortly apiculate on the inner surface at the apex, 1.0 x 1.1 mm, glandular hairs present, filaments tortuous, slender, 0.3 x 0.2 mm, anthers basifixed, 0.3 x 0.5 mm, lobes isomerous, dehiscence longitudinal, nectary lobed, fleshy, rugulate, flat or slightly concave, style rudiment long, slender. *Female inflorescence s* pedunculate as in the male inflorescence. *Female flower* buds conical, receptacle long, slender 1.5 x 1.0 mm, tepals deltoid, 0.7 x 0.7 mm, staminodes present, minute, style short, as long as broad, stigma 5 – lobed, lobes short, rounded, papillose, nectary unlobed, fleshy, weakly concave. *Fruit* slender, ovoid, 7.5 x 3.0 mm, mesocarp absent, apical 'tails' robust, minutely pilose, hairs membranous, endocarp ovoid, elliptic, splitting easily, 6.0 x 2.0 - 2.7 mm, internally unilocular.

Distribution: Solomon Islands.

Habitat: Primary rainforest, near stream. Parasitic on *Calophyllum* (Guttiferae).

Altitude: 30 - 950 m.

Vernacular name: Jong (Kwara'ae name).

Notes: Name derived from the geographic location from which the type specimen was collected. The only species of this genus to be found in the Solomon Islands. Characterised by staminodes in the female flower and an umbellate male inflorescence. Vegetatively similar to *Dm. reinwardtiana* and *Dm. ledermanii*, distinguished by geographic location, pedunculate male inflorescences, staminodes in the female flower and a 5 – lobed stigma.

Additional material examined

Solomon Islands: Corner 2781 (L),Tanabuli island; Whitmore 2999(L), southeast Choiseul island, across bay from Ruruvai.

18. *Dendromyza staufferia* Macklin **sp. nov.**

Type: Vink 16426 (Holotypus L, Isotypus CANB, designated here), Western highlands, Kubor range, Uinba, Nona Minj divide, 5 59S 144 37S.

Frutex scandens. Rami volubiles, graciles. Folia ovata, basi obtusa, apice acutata. Inflorescentiae monoicae, sessilae, uniflorae. Flores masculi sessiles; tepala 5, pilis postaminalibus destituta; antherae loculae inequale. Endocarpium ovoidum; apice filis plumosis coronatum.

Climber, branches long, slender, twisted with few side shoots. *Juvenile stems* angular, striate; *older branches* terete, bark smooth. *Haustoria* sparse, on mature shoots. *Juvenile leaves* purplish brown, fleshy, margins crisp, apex apiculate; *mature leaves* yellow to yellowish-green, leathery, ovate, 41.0 - 62.0 (22.0 - 38.0 x 12.0 - 21.0) mm, apex acute, base obtuse, rounded, primary veins 5, secondary veins, where visible, relatively thick, arising acutely, curving abruptly and percurrent with supra – secondaries; petiole short, flat on upper surface, lower surface angular. Inflorescences monoecious, sessile on juvenile branches and older branches, 3 - 5 together, 2 female inflorescences to a single male. *Male inflorescences* 1 - flowered, subtended by several involucres of bracts, inner involucre quincuncially arranged,

bracts large, 1.5 x 1.2 mm fleshy, ovate, margins ciliate. *Male flowers* greenish yellow, sessile, buds globose, tepals deltoid, fleshy, 0.9 - 1.1 x 0.7 - 0.8 mm, filaments long, slender, 0.3 x 0.2 mm, anthers dorsifixed, lobes unequal, anterior longer and narrower than the posterior, 0.5 x 0.6 mm, dehiscence longitudinal, nectary fleshy, granular, concave, unlobed, style rudiment short. *Female inflorescences* with the same arrangement of bracts as the male inflorescence. *Female flower* buds greenish yellow, obconical, tepals deltoid, fleshy, 0.8 - 0.9 x 0.8 mm, stigmas 5, pointed, papillate, nectary flat or weakly convex, granular. *Fruit* green turning red, ovoid, 6.0 - 6.5 x 3.0 - 4.3 mm, exocarp thick, coriaceous, mesocarp confined to the apex of the endocarp, short sericeus, apical 'tails' robust, outspreading, pilose, hairs sericeus, endocarp ovoid, splitting easily, 4.0 x 2.7 - 3.0 mm, apiculate at the base, internally unilocular (**Fig. 49**).

Distribution: Central and eastern Papua New Guinea (**Fig. 47**).

Habitat: Associated with disturbed habitats in depleted primary forest and open secondary growth. Parasitic on *Wendlandia*, *Mussaenda* (Rubiaceae), *Ficus* (Moraceae) *Piper* (Piperaceae).

Altitude: 1400 - 2000 m

Vernacular name: Toira (Yoowi dialect, Chimbu language); Urema (Southern highlands).

Uses: Painful joints "disjoints" may be rubbed with fresh leaves to provide relief.

Notes: Name derived from the Swiss botanist H.U. Stauffer who worked extensively on the Santalaceae. Characterised by ovate leaves and monoecious inflorescences with two female flowers to one male. Usually the female flowers develop first and produce fruits, a single smaller male flower bud then develops near the base of the fruits. Taxonomically allied to *Dm. reinwardtiana*, distinguishable by ovate leaves, unequal anther locules, pilose apical 'tails' and a distinctly ovoid endocarp. This species is also ecologically distinct from *Dm. Reinwardtiana* as it occurs at higher elevations. The geographic boundaries of the two species do overlap however, in central and eastern New Guinea but *Dm. Reinwardtiana* has a much broader distribution as it occurs as far west as the Malay peninsula. The habit preference of *D.*

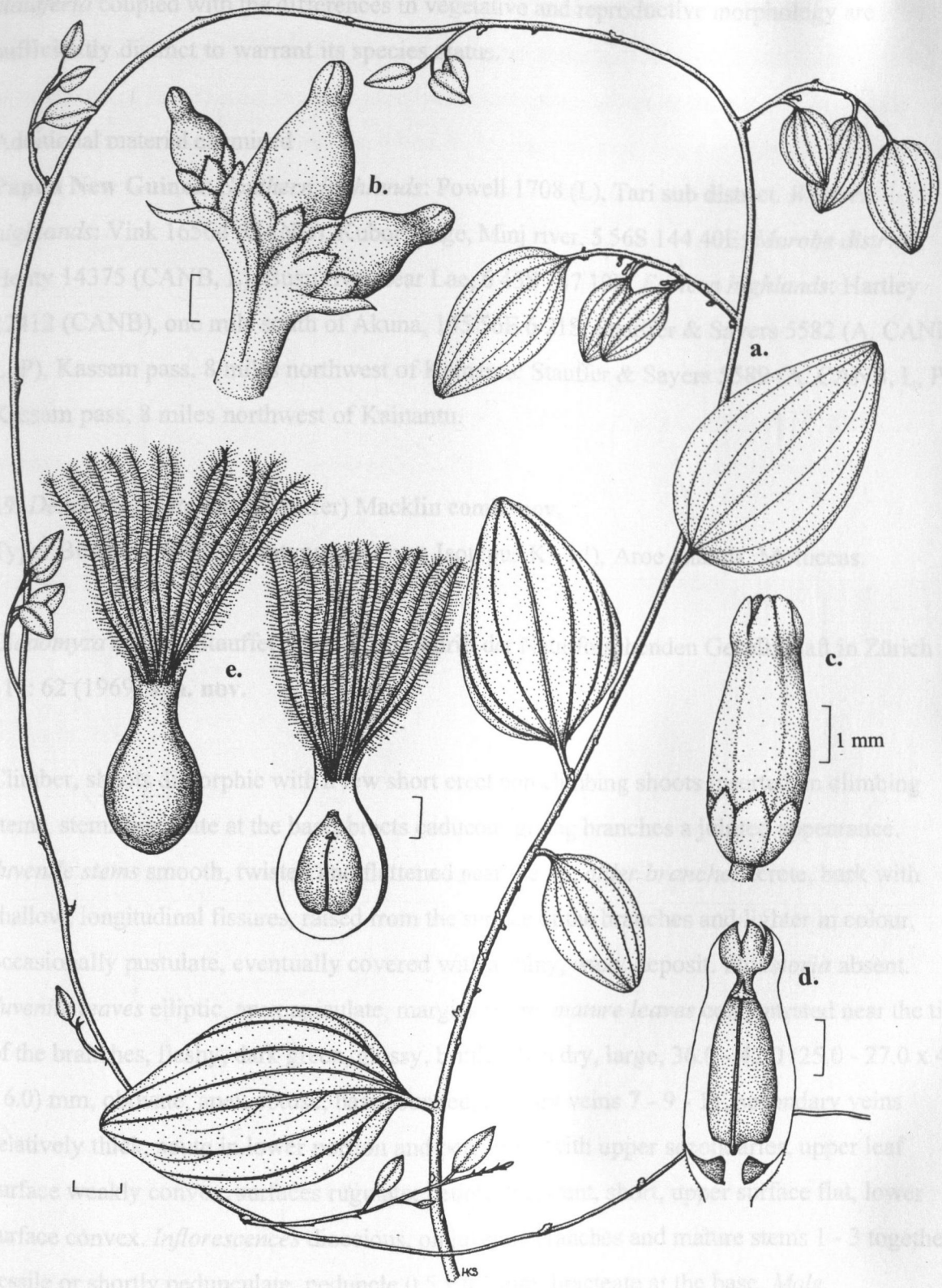


Fig. 49 Type specimen of *Dendromyza staufferia.* **a.** habit, **b.** close up of inflorescence, **c.** fruit, **d.** transverse section through fruit, **e.** fruit when the exocarp has been removed showing the apical 'tails' at the apex of the endocarp and transverse section through the endocarp showing the position and topology of the ovary.

staufferia coupled with the differences in vegetative and reproductive morphology are sufficiently distinct to warrant its species status.

Additional material examined

Papua New Guinea: *Southern highlands*: Powell 1708 (L), Tari sub district. *Western highlands*: Vink 16564 (CANB), Kubor range, Minj river, 5 56S 144 40E; *Morobe district*: Henty 14375 (CANB, L), Busu river near Lae, 6 45S 147 10E. *Eastern highlands*: Hartley 12412 (CANB), one mile south of Akuna, 145 56E 6 21S; Stauffer & Sayers 5582 (A, CANB, L, P), Kassam pass, 8 miles northwest of Kainantu; Stauffer & Sayers 5589 (A, CANB, L, P), Kassam pass, 8 miles northwest of Kainantu.

19. *Dendromyza stellata* (Stauffer) Macklin **comb. nov.**

Type: Buwalda 4992 (Holotypus BO n.v; Isotypus K!, L!), Aroe islands, Moluccas.

Cladomyza stellata Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 114: 62 (1969) **syn. nov.**

Climber, shoots dimorphic with a few short erect non climbing shoots inserted on climbing stems, stems bracteate at the base, bracts caducous giving branches a jointed appearance. *Juvenile stems* smooth, twisted and flattened near the tip; *older branches* terete, bark with shallow, longitudinal fissures, raised from the surface of the branches and lighter in colour, occasionally pustulate, eventually covered with a shiny, waxy deposit. *Haustoria* absent. *Juvenile leaves* elliptic, apex apiculate, margins entire; *mature leaves* concentrated near the tips of the branches, fleshy, dark green, glossy, brittle when dry, large, 36.0 - 42.0 (25.0 - 27.0 x 4.0 - 6.0) mm, obovate, apex obtuse, base rounded, primary veins 7 - 9 - 11, secondary veins relatively thick, acute in lower portion and percurrent with upper secondaries, upper leaf surface weakly convex, surfaces rugulate; petiole decurrent, short, upper surface flat, lower surface convex. *Inflorescences* dioecious, on juvenile branches and mature stems 1 - 3 together, sessile or shortly pedunculate, peduncle 0.5 x 0.7 mm, bracteate at the base. *Male inflorescences* 4 – flowered, with 1 central and 3 lateral flowers, subtended by an involucre of 3 imbricate bracts, bracts large ovate, 0.8 x 1.1 mm, margins entire. *Male flower* buds greenish yellow, sessile or shortly pedicellate, globose, central flower on a raised triangular, t-shaped

base, tepals broadly deltoid, leathery, 0.8 - 0.9 x 0.9 - 1.0 mm, stamens subsessile, glandular hairs absent, filaments 0.2 x 0.2 - 0.3 mm, divergent at the base, anthers dorsifixed, 0.3 x 0.5 mm, posterior lobes larger than the anterior, dehiscence transverse, nectary flat or weakly concave, thin, smooth, membranous, lobed, style rudiment long, slender. *Female inflorescences* sessile, bracts smaller, 0.6 x 0.9 mm. *Female flower* buds obconical, receptacle short, broad, 0.8 - 1.0 x 1.0 mm, tepals 5, fleshy, apiculate at the tip, 0.8 x 0.8 mm, stigmas 3 - 4, lobes, erect, pointed, nectary flat or weakly concave, smooth, fleshy. *Fruit* 3.0 x 2.5 mm, red, elliptic or narrowly ovoid, exocarp thick, leathery, mesocarp sparse, membranous, restricted to the apex of the endocarp, apical 'tails' delicate, not pilose, endocarp elliptic, smooth, thin – walled, splitting easily, 2.0 – 2.5 x 2.0 mm, shallowly 5 – lobed, internally entirely uni-locular, 5 - lobed.

Distribution: Moluccas, Irian Jaya.

Habitat: Primary oak forest on *Garcinia. sp.* (Guttiferae).

Altitude: 1000 m.

Notes: Name derived from the endocarp which is star - shaped in transverse section. Characterised by large obovate leaves and a unilocular, thin-walled, lobed endocarp. One of the few species of *Dendromyza* which occurs outside the island of New Guinea. Represented by only a small number of herbarium specimens. Allied to *Dm. pachydisca*, distinguished by broader leaves, a more shrubby growth habit, a thin, membranous nectarial disc and a unilocular endocarp.

Additional material examined

Indonesia: *Moluccas*: Buwalda 4204 (BO, L), Tenimbu islands; Buwalda 5421 (BO, L), Aroe islands; Buwalda 4992 (BO), Aroe islands. *Irian Jaya*: van Royen & Sleumer 7146 (BO, L, Z), Vogelkop peninsula, Aifat river valley.

20. *Dendromyza trinervia* (Stauffer) Macklin **comb. nov.**

Type: Brass 23305 (Holotypus A n.v.; Isotypus L!, K!), Milne Bay, north slopes of Mt. Dayman.

Cladomyza trinervia Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 114: 65 (1969) **syn. nov.**

Climber, branches slender, shoots dimorphic with a few short erect non-climbing shoots inserted on climbing stems. *Juvenile stems* flattened, angular, weakly papillose, becoming glabrous and smooth, covered in a pale, waxy deposit; *older branches* with shallow, longitudinal fissures, bark wrinkled. *Haustoria* absent. *Juvenile leaves* obovate, margins ciliate; *mature leaves* 30.0 - 35.0 (20.0 – 27.0 x 10.0 - 15.0) mm, obovate, orbicular, apex rounded or weakly retuse, base rounded, primary veins 3, secondary veins arising obtusely or almost parallel to the primary veins, percurrent; petiole very short, upper surface flat or angular, lower surface angular. *Inflorescences* sessile, 1 - 5 together, confined to juvenile stems. *Male inflorescences* 5 - flowered, with 1 central and 4 axial flowers, subtended by 2 involucres of 4 bracts, each involucre with two inner and two outer bracts, bracts minute, 0.5 x 0.5 mm, ovate, margins ciliate. *Male flower* buds green, fungiform, pedicellate, pedicel slender, 0.5 x 0.3 mm, tepals 4, elongate-deltoid, fleshy, 1.5 x 1.0 mm, reflexed at the midpoint to form a pseudo-hypanthium, glandular hairs present, filaments long, slender, divergent at the base, 0.5 x 0.3 mm, anthers dorsifixed, lobes isomerous, 0.4 x 0.5 mm, papillate at the apex, dehiscence longitudinal, nectary thin, smooth, weakly convex, apiculate in the centre. *Female* plant unknown.

Distribution: Papua New Guinea (**Fig. 50**).

Habitat: Montane forest.

Altitude: 1450 m.

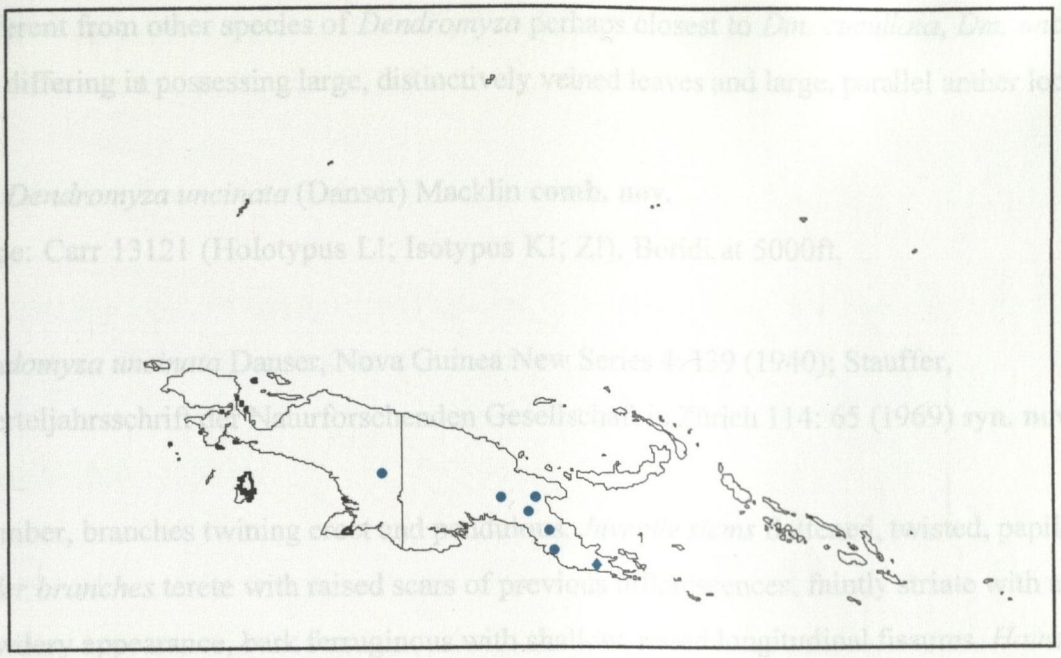


Fig. 50 Geographic distribution of: • *Dendromyza uncinata*, ♦ *Dendromyza trinervia*.

Notes: Name derived from the 3 primary veins. Only one representative collected, quite different from other species of *Dendromyza* perhaps closest to *Dm. cucullata*, *Dm. uncinata* but differing in possessing large, distinctively veined leaves and large, parallel anther locules.

21. *Dendromyza uncinata* (Danser) Macklin **comb. nov.**

Type: Carr 13121 (Holotypus L!; Isotypus K!; Z!), Boridi at 5000ft.

Cladomyza uncinata Danser, Nova Guinea New Series 4: 139 (1940); Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 114: 65 (1969) **syn. nov.**

Climber, branches twining erect and pendulous. *Juvenile stems* flattened, twisted, papillate; *older branches* terete with raised scars of previous inflorescences, faintly striate with a powdery appearance, bark ferruginous with shallow, raised longitudinal fissures. *Haustoria* confined to climbing stems. *Juvenile leaves* elliptic, margins ciliate, apices uncinate; *mature leaves* light yellowish green, fleshy, narrowly obovate, spathulate, 17 .0 - 35.0 (5.0 - 10.0 x 2.0 - 3.0) mm; apex attenuated, recurved, becoming obtuse, base attenuate, surfaces granular, primary veins indistinct or 3 - 5, almost parallel; petiole short, slender, decurrent. *Inflorescences* dioecious, sessile on juvenile branches and older stems, crowded, overtopping each other. *Male inflorescences* 4 – 13 flowered, initially 1 - flowered, subtended by a valvate involucre of 3 bracts, a bud developing in the axil of each bract, each of which is subtended by an involucre of 3, valvate bracteoles, further flowers developing in the axils of the bracteoles, bracts fleshy, 0.7 – 0.8 x 0.5 – 0.6 mm, ovate, margins ciliate. *Male flowers* yellowish green, shortly pedicellate, pedicel decurrent, tepals deltoid-ovate, faintly rugulate on the exterior surface, apiculate on the inner surface, 0.7 - 1.0 x 0.5 - 0.7 mm, glandular hairs present, filaments slender 0.4 x 0.2 mm, slightly dilate at the base, anthers whitish, basifixed, lobes isomerous, 0.2 x 0.4 mm, anther dehiscence transverse, nectary weakly concave, lobed, apiculate in the centre. *Female inflorescences* subtended at the base by 2 - 3 involucres of imbricate bracts. *Female flowers* sessile, buds turbinate, receptacle short broad, 0.6 x 1.0 mm, tepals deltoid, thick, 0.4 x 0.4 mm, staminodes absent, stigmas 5, sessile, erect, delicate, nectary concave. *Fruit* green maturing red to purple, ovoid or oblong, 6.0 - 7.0 x 3.0 - 4.0 mm, sessile, exocarp coriaceous, mesocarp sericeus, beginning midway on the surface of the endocarp, extending up to 2.0 mm beyond the apex of the endocarp, apical 'tails' delicate,

pilose, hairs sericeus, endocarp ovoid, thin, not splitting easily, 3.0 - 3.5 x 2.5 - 3.0 mm, deeply lobed, apex cuspidate, internally 5 - lobed at the apex, central chambers oblong 0.5 x 0.3 mm, central column elliptic 1.5 - 2.0 x 1.3 mm.

Distribution: Eastern Papua New Guinea (**Fig. 50**).

Habitat: Sub montane and montane Fagaceae - Coniferous forests in association with Fagaceae, particularly *Castanopsis*, *Pasania* (Ericaceae).

Altitude: 800 - 3000 m.

Notes: Name derived from leaves with recurved, hook-like tips. Male and female plants recorded from the same host. May be confused with *Dm. erecta* and *Dm. cucullata* due to similarities in leaf shape, distinguishable from both by papillate indumentum on young stems and inflorescences; differing additionally from *Dm. erecta* by its anthers which are not in a single plane, a more extensive indument on the endocarp and a shorter central column in the endocarp. Differing from *Dm. cucullata* by generally larger leaves and an umbellate male inflorescence.

Additional material examined

Indonesia: *Irian Jaya*: Brass 13409 (BO, L), Idenburg river; Womersley & Millar 8731 (L), Wau, 7 10S 147E.

Papua New Guinea: *Eastern Highlands*: Stauffer & Sayers 5561, 5562, (A, B, CANB, K, P, Z), Kassam Pass. *Morobe district*: Millar 23439 (CANB, L), Wangan; Henty 29103 (CANB, L), Lake Trist; Stauffer, Henty & Whitmore 5544, 5545 (A, BO, CANB, K, P, Z), Markham Pt.; Clemens 6396 (A, B). *Central district*: Croft & Lelean 34829 (L), Port Moresby subdistrict, southeast slope of Lake Myola, 9 9S 147 43E. *Milne Bay district*: Brass 23290 (A), north slopes of Mt. Dayman, Maneau range.

2. *Dendrotrophe* Miq.

Type species: *D. varians* var *umbellata* — Type: Korthals s.n. (Holotypus of *Thesium spathulatum* Bl., L!; Isotypus P!), Java.

Miq., Flora Indiae Batavae 1.1: 779 (1856); Danser, Nova Guinea New Series 4: 146 (1940); Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 114: 53 (1969); Hewson & George, Flora of Australia 22: 59 (1984); *Henslowia* p.p. Blume, Museum Lugduno Batavae 1: 243 (1850); non Wallich, Plantae Asiaticae Rariores: 14 t.221 (1832); A.DC., Prodromus 14: 630 (1857); Bentham, Genera Plantarum 3: 228 (1883); Gamble, Journal of the Asiatic Society of Bengal 75: 269 (1912); Pilger in Engler & Harms, Die Natürliche Pflanzenfamilien 16b: 71 (1935); Kanjilal, Flora of Assam 4: 129 (1940); [*Henslovia* Hook.f Flora of India 5: 232 (1886)].

Glabrous terrestrial shrub, climber or dendroparasite, often with twining stems but these never with secondary haustoria; bark smooth or with longitudinal fissures. *Leaves* variable in size but usually quite large, fleshy, primary veins 3 - 5 - 7. *Inflorescences* dioecious, or hermaphrodite, singular or 1 - 3 together, flowers yellow or green. *Male inflorescences* umbellate, racemose, paniculate, pedunculate, 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 transversal, nectary fleshy, flat or concave, lobed, style rudiment slender, capitate, ovary present, semi inferior, straight, abortive. *Hermaphrodite flowers* with short style, and enlarged receptacle. *Female inflorescences* 1 - flowered, shortly pedunculate, subtended by a series of involucral bracts. *Female flowers* with staminodes which are well developed but lack pollen, style short, stigma 5 – lobed; *ovary* 0.3 – 0.4 x 0.6 mm, placenta convex 4 – 6 lobed, lobes rounded, short, curling underneath and in towards the placental column, column long, straight. *Fruit* red or black, globose, elliptic, perianth persistent, erect or flat, exocarp thin, smooth or rugulose; mesocarp very thin, fleshy; endocarp hard, globose or elliptic, tuberculate, apex shortly apiculate, base rounded, attenuate, internally 4 - 5 chambered at the apex and the base, each chamber may be further lobed, 5 –10 lobed for the rest, transverse chambers present (**Fig.**

40, 16.1, 16.2). Seed ruminate, reminiscent of *Juglans*. Embryo situated in the centre of the endocarp.

Number of species: 4

Distribution: Southern China to Australia.

Habitat: 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* forests in montane regions and in disturbed areas in secondary vegetation.

Altitude: 0 – 3000 m.

Notes: Name derived from *dendron* meaning tree like and *trophe,* to nourish, referring to the parasitic habit. Contains one very widespread and variable species which occurs across the geographical range of the genus and three others with narrow distributions; one species is found in western Southeast Asia as far as Borneo and two others are endemic to New Guinea. Characterised by a tuberculate endocarp with transverse chambers. The species exhibit a variety of growth form from shrub to climber or dendroparasite, the growth habit can vary infraspecifically. In addition the species which occur in the Malay Peninsula and Borneo may be sparsely leafy or leafless. *Dendrotrophe* was originally described by Miquel to replace *Henslowia* of Blume. 8 species were originally described and a number of new species were subsequently described in isolation, all based on small numbers of specimens. To date 15 species have been described most of which are synonyms of *Dt. varians*.

Key to *Dendrotrophe*

1. Leaves large, broadly spathulate greater than 80 mm in length; male inflorescences umbellate.....**1.** *D. amorpha*
   Leaves lanceolate, obovate or narrowly spathulate, less than 75 mm in length; male and hermaphrodite inflorescences paniculate or racemose.....(2)

2. Leaves lanceolate, primary veins obscure, 2-3; inflorescences paniculate, flowers hermaphrodite .....**3.** *D. buxifolia*
   Leaves elliptic, obovate, primary veins usually obvious 3 – 5; inflorescences racemose, flowers dioecious.....(3)
3. Bark pustulate, leaves coriaceous; fruit with endocarp punctate, apex not apiculate, transverse chambers absent; endemic to Irian Jaya.....**2.** *D. arfakensis*
   Bark rough with transverse fissures, leaves thin or fleshy; fruit with endocarp rugulate, apex apiculate, transverse chambers present; widespead from S. China to Australia .....**4.** *D. varians*

1. *Dendrotrophe amorpha* Stauffer

Type: Clemens 3438 (Holotypus GH!), Papua New Guinea, Morobe district.

Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 114: 53 (1969).

Dendroparasitic climber. *Juvenile stems* smooth, occasionally pustulate, angular, flattened, bracteate at the base, older branches smooth or with broad longitudinal fissures. *Leaves* fleshy, elliptic, obovate, orbicular, 40.0 – 80.0 (35.0 –70.0 x 20.0 – 30.0) mm, apex rounded, base cuneate, attenuate, primary veins 7 – 9, raised on the upper surface; petiole long, angular, decurrent. *Inflorescences* 3 – 4 together, on older and juvenile branches, usually confined to short leafless side shoots. *Male inflorescences* umbellate, 5 - 6 flowered, pedunculate, peduncle 1.0 - 3.0 x 1.0 – 2.0 mm, an involucre of bracts at the apex and the base, occasionally a few bracts along the length; bracts membranous, broadly deltoid, 0.5 - 0.6 x 0.8 - 1.0 mm, margins ciliate. *Male flowers* subsessile, tepals 5, deltoid, valvate, membranous, 0.8 - 1.0 x 0.8 - 1.0 mm, glandular hairs present, anthers subsessile, 0.4 x 0.4 mm, nectary flat, scarcely lobed, style rudiment absent. *Female inflorescences* singular or 2 - 3 together, peduncle shorter than in male plant, 0.7 - 1.0 x 0.8 - 1.0 mm. *Female flowers* sessile, buds obconical, tepals 5, 0.6 x 0.5 mm, deltoid, swollen on inner surface near the apex, staminodes absent, stigma sessile, 5 - lobed, lobes outspread, papillate, nectary thin, concave, angular. *Fruit* red, globose, sub globose, 4.0 - 5.0 x 3.5 – 4.0 mm, persistent perianth flattened at the apex of the fruit, exocarp smooth, mesocarp thin, fleshy, apical 'tails' present at the apex of the endocarp, tails delicate, filamentous, endocarp robust tuberculate, globose, obovoid, 2.0 - 3.0 x 2.0 - 2.5 mm, apiculate

at the apex, internally 5 - chambered at the apex and the base, basal chambers prolonged, transverse chambers present.

Distribution: Central and Eastern Papua New Guinea (**Fig. 51**).

Habitat: Montane primary forest, forest regrowth. Parasitic on *Ficus* (Moraceae) and *Castanopsis* (Fagaceae).

Altitude: 1000 - 2000 m.

Vernacular name: Kumbabanai (Enga language).

Notes: Name derived from the fact that this species has a different form to other species of *Dendrotrophe*. It is characterised by very large leaves, male inflorescences which are clearly umbellate and echinate pollen grains. In New Guinea it may be confused with species of *Dendromyza* but is easily distinguished on the basis of leaf size and shape and fruit morphology. Within *Dendrotrophe* it is most similar to *Dt. buxifolia* in terms of fruit morphology but is distinguihed by apical 'tails' on the endocarp, umbellate male inflorescences and dioecious flowers.

Additional material examined

Papua New Guinea: *Morobe district*: Hoogland 8830 (CANB), Mongi valley, Huon Penn; Hoogland & Pullen 5956 (L), Wabag subdistrict, Yaki - Tal; Hoft 2818 (L), Mt. Kolorong, Kuper range, 7 31S 146 47E; *Central district*: Carr 13734 (CANB), Alola 8 59S 147 43E; Carr 15829 (CANB, L), Lala river; Hoogland & Schodde 2156 (CANB), Alola; Smith 1038 (L), Aiyura; Hoogland & Schodde 6969 (CANB, L), Aiyura; Hoogland & Schodde 6970 (L), Aiyura.

var. *falcata* Stauffer

Type: Brass 12788 (Holotypus A n.v., Isotypus L!), Idenburg river.

Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 114: 54 (1969).

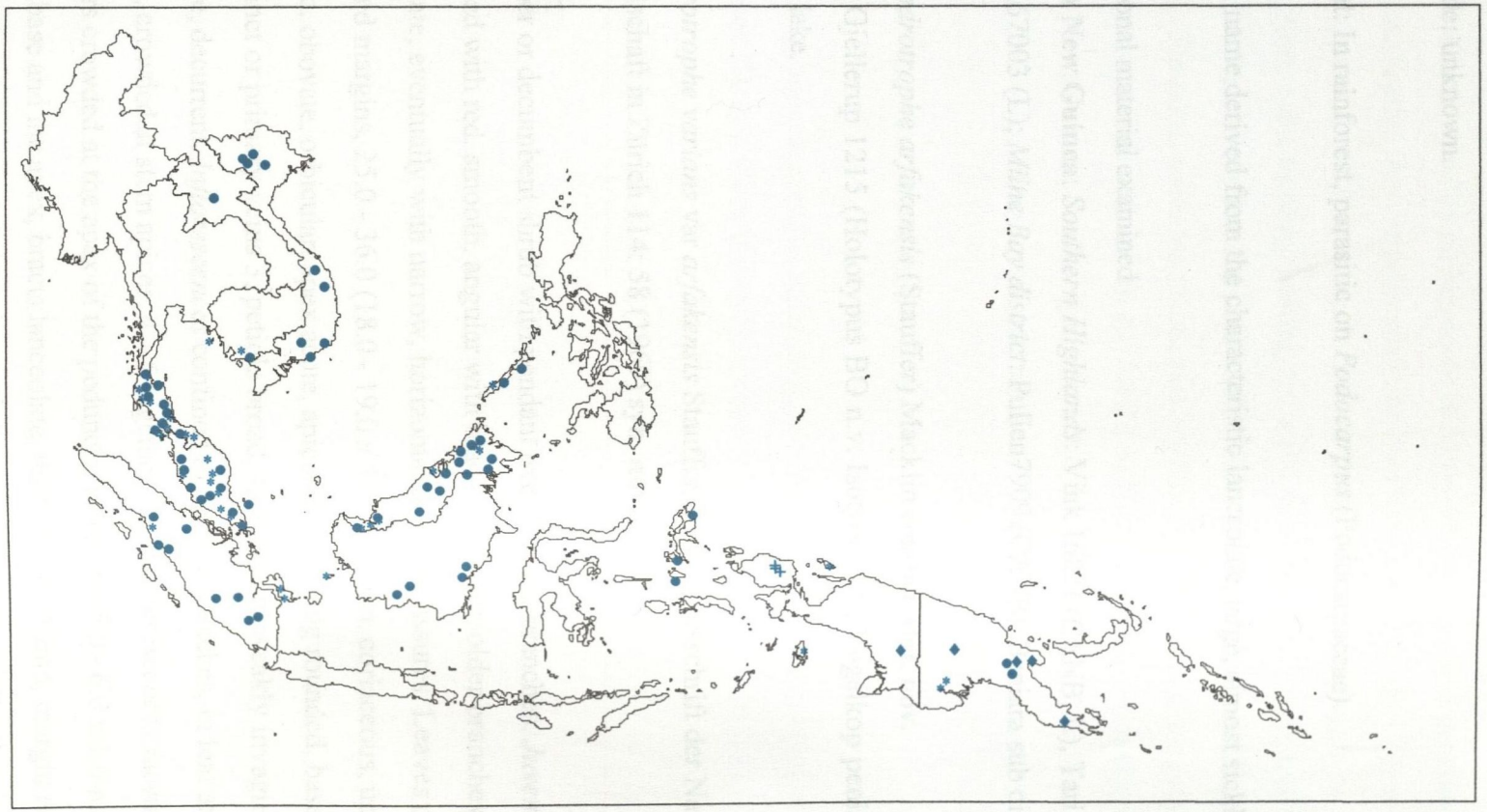


Fig. 51 Geographic distribution of: • *Dendrotrophe varians*, * *Dendrotrophe buxifolia*, ♦ *Dendrotrophe amorpha*, + *Dendrotrophe arfakensis*.

Leaves brownish green, shiny, lanceolate, curving outwards, 100 - 120 (40 - 50 x 20 - 25) mm.

Distribution: Southeast Papua New Guinea.

Altitude: unknown.

Habitat: In rainforest, parasitic on *Podocarpus* (Podocarpaceae).

Notes: name derived from the characteristic lanceolate, large, almost sickle-shape leaves.

Additional material examined

Papua New Guinea: *Southern Highlands*: Vink 16821 (CANB, L), Tari subdistrict, 6 S 143E; Vivas 67003 (L); *Milne Bay district*: Pullen7909 (CANB), Baniara sub district, 149 22E 9 54S.

2. *Dendrotrophe arfakensis* (Stauffer) Macklin **combet. stat. nov.**

Type: Gjellerup 1215 (Holotypus BO n.v. Isotypus L!), Vogelkop peninsula, Arfak Mts., Anggi lake.

Dendrotrophe varians var *arfakensis* Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 114: 58 (1969) **syn. nov.**

Climber or decumbent shrub with pendant over-hanging branches. *Juvenile stems* yellow suffused with red, smooth, angular with bract-like leaves, older branches terete, densely pustulate, eventually with narrow, horizontal cracks or fissures. Leaves olive or grayish green with red margins, 25.0 - 36.0 (18.0 - 19.0 x 5.0 - 6.0) mm, coriaceous, upper surface rugulate, elliptic, obovate, orbicular, apex acute, apiculate becoming rounded, base attenuate, venation indistinct or primary veins 3, petiole broad, short, flat or weakly invaginated on the upper surface, decurrent. *Inflorescences* confined to juvenile branches, in leaf axils and at leafless nodes, crowded at stem apices, 4 – 5 together. *Male inflorescences* racemose, 5 - 6 flowered, flowers crowded at the apex of the peduncle, peduncles 5.0 - 6.0 x 1.0 mm, angular, bracteate at the base and the apex, bracts lanceolate, thick, 1.0 x 0.5 mm, margin entire or weakly ciliate, caducous except at the base. *Male flowers* yellowish green, pedicellate, pedicel 1.0 - 1.5 x 0.6

mm, buds globose, tepals fleshy, deltoid, valvate, weakly apiculate on the inner surface at the apex, glandular hairs present, filaments short, dilate at the base, 0.2 x 0.4 mm, anthers, 0.3 x 0.5 mm, nectary concave, weakly 5-lobed, suberous, style rudiment short, 0.3 x 0.2 mm. *Female inflorescences* sub-sessile or very shortly pedunculate, peduncle 1.0 - 3.0 x 0.9 - 1.0 mm, subtended at the base by an involucre of 5, valvate bracts, bracts deltoid-ovate, 0.5 x 0.5 mm, caducous. *Female flowers* pedicellate, pedicel 1.0 - 2.0 x 0.8 mm, buds obconical, receptacle long, slender, 2.5 x 1.0 mm, tepals deltoid, thick, 1.2 x 0.9 mm, inner surface suberous, style terete, short, twice as broad as long, 0.2 x 0.4 mm, stigma 5 - lobed, lobes short, rounded, papillose. *Fruit* green turning purplish-black, spherical, 9.0 x 8.5 mm, apex flattened, persistent perianth flattened, nectary sunken, exocarp smooth, thick, mesocarp gelatinous, granular, endocarp hard, obovoid, 7.5 (6.8 - 7.0 x 3.5) mm, outer surface weakly punctate with 5 distinct, shallow, longitudinal grooves, apex flat, not apiculate, internally 5 - chambered at the apex and the base, chambers small, narrow, transverse chambers absent.

Distribution: Irian Jaya (**Fig. 51**).

Habitat: In summit areas of relict, low *Nothofagus* forests and open areas of *Nothofagus*-Myrtaceae forests. Parasitic on *Symplocos* (Symplocaceae).

Altitude: 2000 - 2500 m.

Notes: Name derived from the geographic location of the type specimen. This species has a restricted distribution, confined to the Arfak mountain ranges of the Vogelkop peninsula of Irian Jaya. It is characterised by densely pustulate bark and leathery leaves. Allied to *Dt. varians* but distinguished by leathery leaves, distinctly pustulate bark and also fruits with a punctate endocarp which lack transverse chambers.

Additional material examined

Indonesia: *Irian Jaya*: Sleumer & Vink 4268 (L, Z), Arfak Mts., Mt. Koebre, ridge above Testega, Anggi Gita lake; Sleumer & Vink 4203 (Z), Arfak Mts., Mt. Mesenuk, along path to Ransiki; Sleumer & Vink 4208 (L, Z), Arfak Mts., Mt. Mesenuk, along path to Ransiki; Sleumer & Vink 4217 (L, Z), Arfak Mts., Mt Mesenuk; Sleumer & Vink 4254 (L, Z), Arfak

Mts., Mt Kongremottie, Anggi Gita lake; Sleumer & Vink 4285 (Z), Arfak Mts., Mt. Koebre, towards Anggi Gita lake, Surerei; Sleumer & Vink 4413 (Z), Arfak Mts., Mt. Tidjei, near Anggi Gita lake; Sleumer & Vink 4353 (Z), Arfak Mts., Mt Sensenemes, above Surerei.

3. *Dendrotrophe buxifolia* (Bl.) Miq.

Type: Korthals s.n. (Holotypus *Dendrotrophe buxifolia* P!; Holotypus of *Henslowia buxifolia* L!).

Miq., Flora Indiae Batavae 1.1: 781 (1856); Miq., Sumatra Seine Planzenweit: 342 (1862); Danser, Nova Guinea New Series 4: 147 (1940); Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 114: 54 (1969); Wu & Tao, Flora Yunnanica 4: 293 (1986); Tam, Flora Reipublicae Popularis Sinicae: 72 (1988); Hô, Câyco Vietnam 2.1: 154 (1992); *Henslowia buxifolia* Bl., Museum Lugduno Batavae 1: 244 (1850); A.DC., Prodromus 14: 631 (1857); Hook.f., Flora of British India 5: 234 (1886); Ridley, The Flora of Singapore: 133 (1900); Boerlage, Flora van Nederlandsch Indie: 181 (1900); Gamble, Journal of the Asiatic Society of Bengal 75: 274 (1912); Lecomte, Bulletin du Muséum Histoire Naturelle Paris: 405 (1914); Lecomte, Flore Générale de l'Indo-Chine 5: 217 (1915); *Osyris rotundata* Griff., Notulae: 742 (1854).

Erect or prostrate shrub, occasional dendroparasite. *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, lanceolate, 15.0 – 45.0 (8.0 – 9.0 x 2.0 –3.0) mm, apex acute, obtuse, base attenuate, primary veins 2 - 3, inconspicuous; petiole short angular, decurrent. *Inflorescences* on mature and juvenile branches, often on raised scars, prolific, in clusters of more than 10 together, paniculate, 5 – 10 flowered, rachis 4.0 – 8.0 x 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 x 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 may be repeated several times. *Flowers* hermaphrodite yellowish green, buds obconical, sessile or very shortly pedicellate, pedicel 0.5 mm in length, tepals 5 - 6, valvate, deltoid, fleshy, 0.8 - 1.0 x 0.8 - 1.0, receptacle short, broad, 1.0 – 1.5 x 1.5 mm, filaments broad, short 0.1 - 0.2 x 0.2

mm, anthers 0.3 x 0.3 mm, style short, as broad as long, 0.2 - 0.3 x 0.2 - 0.3 mm, stigma 5 - lobed, lobes pointed, fleshy, papillate, nectary lobed, very shallowly concave, punctate, ridged, the ridges running into the nectarial lobes. *Fruit* ripening black, small, spherical, 3.0 - 3.5 x 2.5 - 3.5 mm, very shortly pedicellate, pedicel 0.3 - 0.5 x 0.5 mm, persistent perianth erect, exocarp thin, mesocarp thick, fleshy, endocarp spherical, 2.0 - 2.5 x 2.5 mm, tuberculate, 5 - armed, star - shaped scar at the apex which may be prolonged to the base, apex depressed, apiculate, internally 5 - 6 chambered at the apex and the base, transverse chambers present.

Distribution: Thailand, Philippines, Malay Peninsula, Borneo, Sumatra (**Fig. 51**).

Habitat: 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.

Altitude: 0 – 300 m.

Notes: Name derived from the small elliptic leaves. Characterised by small fleshy leaves and hermaphrodite flowers. It 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 most closely allied to *Dt. amorpha* in terms of fruit structure but vegetatively it is most similar to *Dt. varians*. The distributions of *Dt. buxifolia* and *Dt. varians* overlap, where the species co-occur *Dt. buxifolia* may be distinguished by smaller, globose fruits and a paniculate inflorescence with hermaphrodite flowers.

Additional material examined

China: Bodinier 124 (L), Hong Kong, Happy Valley.

Vietnam: Pierre 1409 (E, GH), Bhudue.

Cambodia: Kira et al 387 (KYO), Cheko, Koh Kong province.

Thailand: *South-Eastern*: Geesink 6655 (BKF, K), Trat, Koh Chang island, Koh Mai See; Hansen 12432 (BKF, L), Koh Boi Noi; *Peninsular*: Kerr 1889 (L), Chumphon, Tako

Langsuan; Kerr 18946 (L), Krabi, Ko Pu; Geesink 5259 (BKF), Krabi, Phang-nga, 8 25N 98 30E; Niyomdham 1734 (K), Narathiwat, Ban Sai; Sangkhachand 53357 (BKF), Narathiwat, Rangae; Chanby 1151 (BKF), Narathiwat, Tak Bai; Kerr 14106 (K), Satun, Adang; Kerr 13854 (K), Satun, Tola Satul; Kerr 15916 (L), Songkhla, Kampeng pet; Congdon 26 (AAU), Songkhla, Hat Yai; Maxwell 84/505 (A, BKF), Songkhla, Ton Nga Chang reserve, Hat Yai; Larsen 42184 (AAU), Songkhla, Ko Khlong, Hat Yai, 100 20E 7N; Maxwell 84/183 (A, BKF), Songkhla, Ko Khlong hill, Hat Yai; Geesink 7788 (BKF), Surat Thani, Ko Phangan, 9 55N 100 30E; Put 4177 (L), Surat Thani, Katuli; Put 750 (L), Surat Thani, Ko Phangan; Larsen 44004 (AAU), Trang.

Malaysia: *Malay Peninsula*: Sargent 27 (A); Ridley s.n. (K); Went s.n. (BO); Corner 29917 (BO), Penor (George Town), Penang; Balgooy 2200 (L), Penang; si Boeea 3615 (A), Batoe district, Penang; si Boeea 3364 (A), Laboehan, Penang; Burkill 2615 (L), Bukit Kroh forest reserve; Shah 2485 (SING), Kelantan, path to Gunong Rabong; Kingdom Ward 37469 (K); Maxwell 80-25 (L), Pahang; Corner 29917 (BO), Pahang; Poore 741 (K), north of Dunggun; Burkill 292 (L, SING), Pangkor island, Telok Gedong; Shah 2920 (SING), Johor; Corner & Henderson 36616 (SING, P), Johor; Burkill 4614 (L, SING), Terengganu. *Sarawak*: Chai 18009 (L), Bako national park, Telok Tajor; Chew 1411 (A, L, SING); Castro 9992 (A), Mt. Santubong; Dunselman 169 (L), summit of Santubong; Dan Bin & Bakar 3019 (L), Lambir hills; Dayang 50406 (L); Jacobs 5508 (L), northeast of Kuching, Bako national park; Sleumer 4677 (L), Bako national park, Kuching; Ashton 17969 (L, SING), Litang, path below Bukit Tambi, Bako national park; Ibrahim 183 (SING), Bukit Pantu, Lambir national park; Purseglove 5561 (L, SING), Telok Asam, Bako national park; Purseglove 4920 (L, SING), Telok Asam, Bako national park; Polak 253 (BO), Sungkawang. *Sabah*: Beaman 8407 (A, L), Sipitang; Carr 26951 (SING), Mt. Kinabalu, path to Ranau; Madani & Amin 86230 (L, SING), Sipitang; Hallier 1490 (L); Meijer 37869 (L), Karimata island; Mondi 186 (L, U), Karimata island, Poelau Seroetoe.

Brunei: Nangkat 23 (A), Belait district, near Labi road; Boyce 227 (L), Tutong district, Pasir Puteh, 4 42 N 114 31E.

Philippines: Edano 115 (A, SING), Palawan, Lapu lapu river.

Indonesia: *Sumatra*: Meijer 7593 (L), west coast, Tiku, north of Pariaman sand dunes; si Boeea 3623 (A); Teysmann 3460 (P, U), Bangka; Bunnemeijer 1473 (BO, L), Bangka;

Bunnemeijer 1621 (L), Bangka; Burger 25 (L), Bangka; Huitema 39 (L), Bangka; Kostermans & Anta 1353 (L, P), Bangka; Teysmann s.n. (U), Bangka.

4. *Dendrotrophe varians* (Bl.) Miq.

Type: Korthal s.n. (Holotypus *Henslowia varians* L!), Borneo.

Miq., Flora Indiae Batavae 1.1: 781(1856); Danser, Nova Guinea New Series 4: 147 (1940); Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 114: 56 (1969); *Henslowia varians* Bl., Museum Lugduno Batavae 1: 244 (1850); Hook.f., Flora of India 5: 233 (1886); Gamble, Journal of the Asiatic Society of Bengal 75: 271 (1912); *Henslowia cassiaefolia* Bl., Museum Lugduno Batavae 1: 244 (1850) — Type: Korthals s.n. (Holotypus L!), Borneo; *Dendrotrophe cassiaefolia* Miq., Flora Indiae Batavae 1.1: 781 (1856); *Henslowia spicata* Bl., Museum Lugduno Batavae 1: 244 (1850) — Type: Korthals s.n. (Holotypus L!), Borneo; *Dendrotrophe spicata* Miq., Flora Indiae Batavae 1.1: 781 (1856); *Henslowia retusa* Bl., Museum Lugduno Batavae 1: 213 (1850) — Type: Korthals s.n. (Holotypus P!) Java; *Henslowia frutescens* Champion, Hookers Journal of Botany 5: 194 (1853) — Type: Champion s.n. (Holotypus K!), Hong Kong; Lecomte, Flore Générale de l'Indo-Chine 5: 219 (1915); *Dendrotrophe frutescens* Danser, Nova Guinea New Series 4: 148 (1940); *Henslowia lobbiana* A.DC., Prodromus 14: 631 (1857) — Type: Lobb 334 (Isotypus TCD!), Penang; *Dendrotrophe lobbiana* Miq., Flora Indiae Batavae 1.1: 1096 (1858); Danser, Nova Guinea New series 4: 148 (1940); [*Henslovia lobbiana* Hook.f Flora of British India 5: 233 (1886)]; *Henslowia philippinensis* A.DC. Prodromus 14: 631 (1857) — Type: Cuming 2253 (Isotypus TCD!), Malay Peninsula; *Dendrotrophe philippinensis* Miq., Flora Indiae Batavae: 1096 (1858); *Henslowia erythrocarpa* Kurz, Journal of Botany 13: 329 (1879) — Type: Korthals s.n. (Holotypus L!); *Henslowia sessiliflora* Hemsley, Journal of the Linnean Society 26: 409 (1891) — Type: Playfair (Holotypus K!), Kwangtung; *Henslowia Ridleyi* Gamble, Kew Bulletin: 201 (1912) — Type: Ridley 15560 (Holotypus K!), Malay Peninsula; *Dendrotrophe ridleyi* Danser, Nova Guinea New Series 4: 148 (1940); *Henslowia wrayi* King ex Gamble, Journal of the Asiatic Society of Bengal 75: 201 (1912) — Type: King 10834 (Holotypus K!), Malay Peninsula; *Dendrotrophe wrayi* Danser, Nova Guinea New Series 4: 140 (1940); Tam, Flora Reipublicae Popularis Sinicae: 73 t.18 (1988); Hô, Câyco Vietnam 2.1: 154 (1992); *Henslowia umbellata var longifolia* Lecomte, Bulletin du Muséum Histoire Naturelle Paris:

405 (1914) — Type: Pierre 1267 (Holotypus P!), Cambodia; *Henslowia umbellata* var. *harmandii* Lecomte, *l.c.*: 405 (1914) — Type: Harmand 220 (Holotypus P!), Cambodia; *Henslowia tonkinensis* Lecomte, *l.c.*: 406 (1914) — Type: Bon 5117 (Holotypus P!), Tonkin; Lecomte, Flore Générale de l'Indo-Chine 5: 218 (1915); *Henslowia umbellata sensu* Lecomte, Flore Générale de l'Indo-Chine 5: 218 (1915); *Henslowia palawanensis* Elmer, Leaflets of Philippine Botany 5: 1834 (1913) — Type: Elmer 12752 (Holotypus U!), Palawan; *Dendrotrophe palawanensis* Danser, Nova Guinea New Series 4: 148 (1940); *Henslowia minor* Ridley, Journal of the Federal Malay States 7: 50 (1916) — Type Ridley s.n. (Holotypus K!), Malay Peninsula; *Dendrotrophe minor* Danser, Nova Guinea New Series 4: 148 (1940); *Exocarpos amboinensis* Merrill, Philippine Journal of Scientific Botany 11: 267 (1916) — Type Robinson 1810 (Holotypus L!), Ambon; *Henslowia schlechteri* Pilger, Botanische Jahrbucher 59: 127 (1924) — Type: Schlechter 19385 (Isotypus L!), Papua New Guinea; *Henslowia queenslandiae* Smith, Queensland Naturalist: 62 (1951) — Type Smith 3394 (Isotypus Z!); *Dendrotrophe varians* var *multinervis* Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich: 59 (1969) **syn. nov.** — Type: Wray 278 (Holotypus K!), Malaysia, Gunong Batu Patek, Kedah; *Dendrotrophe varians* var *minor* Stauffer, *l.c.*: 58 (1969) **syn. nov.**; *Henslowia frutescens* var *subquinquenervia* Tam, Bulletin of Botanical Research: 70 (1981) nom. illegit. — Type: Lee 6020228 (Holotypus n.v.); *Dendrotrophe punctata* C.Y. Wu ex D.D. Tao, Flora Yunnanica 4: 290 - 291 (1986) **syn. nov.** — Type: Wu 03707 (Holotypus KUN!); *Dendrotrophe umbellata* Tam, Flora Reipublicae Popularis Sinicae: 72 t.18 (1988); Hô, Câyco Vietnam 2.1: 155 (1992).

Climber, shrub, occasional dendroparasite. *Juvenile stems* smooth, slightly striated, angular, older stems terete, bark rough with transverse fissures. *Leaves* elliptic, obovate, orbicular, apex acute, obtuse, base attenuate, 13.0 – 75.0 x (6.5 – 50.0 x 2.0 – 12.0) mm, fleshy, thin, papyraceus, primary veins 3 – 5 - 7, petiole long, narrow, decurrent, upper surface flat, lower surface angular. *Inflorescences* dioecious, 1- 8 clustered together on juvenile branches. *Male inflorescences* racemose, rachis 1.0 - 10 x 0.2 - 1.0 mm, an involucre of imbricate bracts at the apex and the base, sparsely bracteate along its length, bracts membranous, deltoid, ovate, 0.5 - 1.0 x 0.3 - 0.8 mm, caducous except at the base; inflorescences 7 - 8 flowered, 4 - 5 crowded at the apex and 2 - 3 inserted spirally along the rachis. *Flower* buds globose, pedicellate, pedicel 0.8 - 2.0 x 0.5 - 0.8 mm, tepals 4 - 5, imbricate at the base, ovate, 0.8 - 1.3 x 0.5 - 1.0 mm,

apiculate on the inner surface at the apex, glandular hairs present, filaments broadening towards the base, 0.2 - 0.5 x 0.1 - 0.3 mm, anthers 0.2 - 0.4 x 0.2 - 0.4 mm, nectary slightly concave, angular, style rudiment 0.3 - 0.7 x 0.1 - 0.2 mm. *Female inflorescences* fewer in number, 1 - flowered, pedunculate, peduncle shorter, 2.0 - 6.0 x 0.8 - 1.4 mm. *Flower* buds obconical, sessile or shortly pedicellate, pedicel 0.5 - 2.0 x 0.5 mm, tepals 5, deltoid, 0.8 - 1.7 x 0.7 - 1.3 mm, receptacle 2.5 x 1.0 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 x 0.3 - 0.4 mm, stigma 5 - lobed lobes rounded, papillate. *Fruit* 4.0 – 14.0 x 3.0 – 11.0 mm, elliptic, obovoid, persistent perianth erect, exocarp coriaceous, mesocarp fleshy, thin, endocarp 5.0 – 12.0 x 4.0 – 8.0 mm, hard, globose, elliptic, smooth, rugulate, apiculate at the apex, a short 5 - 6 armed, star - shaped scar radiating from the apex, internally 5 - 6 chambered at the apex and the base, transverse chambers present.

Distribution: Southern China to Australia (**Fig. 51**).

Vernacular name: Iban name: Akar (Borneo); Marahugo (Philippines).

Habitat: On poor sandy, loamy soil in kerangas forest and coastal areas; in swamp forest and in montane regions in Fagaceae, *Quercus-Larix* or *Eugenia* forests; in upper montane mossy forests. In the Malay Peninsula it is particularly associated with dry, sclerophyllous vegetation and dwarf scrub. In Thailand it occurs predominantly in disturbed areas in secondary vegetation.

Altitude: 0 - 3000 m.

Notes: Name derived from the fact that this species exhibits a variety of leaf shape. Many new species have been named based on seemingly distinct vegetative and fruit morphological features. Like *Dt. buxifolia* it 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. *Dt. varians* is most closely allied to *Dt. arfakensis* in terms of inflorescence morphology and floral structure. It may be distinguished by bark which is fissured rather than pustulate and fruits which have a distinctly rugulate endocarp. 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 larger leaves and fruits.

Additional material examined

China: *Hainan*: Chow 78375 (E), Changjiang; How & Chun 70121 (E), Yacheng; Lau 6145 (E), Yeung Lam Shan, near Yeung Lam village,Yai-hsien district; Lau 5435 (E), Mt. Chim Fung, near Fong Ngau Po village, Kan-en district; Lau 20199 (L); Lei 374 (P), Lingshi; Henry 8527 (P); Liang 66469 (P); How 73951 (P); Chun 44326 (L), Mo San Leng; *Kwangtung*: Tung 5756 (L), Kwangtung, Luo-fu Shan; Yip 382 (L), Gaozhou, Guangdong; Tsang 22338 (P), Kwangtung border; Schindler 437 (P); *Hong Kong*: Hu & But 20103 (L), Ma On; Wright 400 (K); Wright 12 (P), Shan.

Laos: Harmand (P).

Vietnam: Tsang 30073 (A, E, K), Bac Phan, Sia Wong Mo Shan, Lung Wan village, Dam-ha; Petelot 2563 (A), Vinh Yen, road to Tom Dao; Petelot 2.561 (A), Bac Phan, Fan Si Pan; Petelot 6170 (A), Bac Phan, Santay, Hung Hoe; Petelot 6179 (A), Bac Phan, Fan Si Pan; Petelot 2.563 (A), Bac Phan, Vinh Yen; Petelot 6185 (A), Bac Phan, Fan Si Pan; Petelot 5703 (A); Chai 39734 (K); Eberhardt 3824 (P), Vinh Yen; Balansa 1565 (P), Bac Phan; Balansa 2320 (P), Bac Phan; Clemens (A); Pierre 1409 (A); Poilane 7132 (L); Squires 100 (A, E, K), Hue; Thorel 647 (K, E), Bien Hoa; Chevalier 40.447 (P), Nam Phan, Langbian; Clemens 3420 (K), Trung Phan, Da Nang; Pierre 326 (P); Chevalier 3800 (P), Nam Phan, Nha trang; Muller 1111 (P), Nam Phan; Poilane 27661 (P), Nam Phan, Hue; Poilane 32.771 (P, TCD), Nam Phan, Kontum; Poilane 32822 (P), Kontum; Eberhardt 2608 (P), Kontum; Thorel 9770 (P); Poilane 21945 (P), Nam Phan, Haut Donai; Chevalier 30819 (P), Nam Phan, Langbian; Poilane 32149 (P), Kontum; Poilane 30928 (P), Nam Phan; Poilane 3499 (P), Nam Phan.

Cambodia: Smitinand & Abbé 24672 (L), Kampot, Mt. Bokor; Pierre 1410 (P).

Thailand: *South-Eastern*: Put 1672 (L), Chumphon, Langsuan; Kerr 11853 (A, L), Chumphon, Na Sak, Langsuan; Kerr 11887 (L), Chumphon, Tako Langsuan. *Peninsular*: Kerr 14277 (K), Nakhon Si Thammarat, Ta Samet; Niyomdham 1454 (AAU, L), Narathiwat, Bang Nara river, Tak Bai; Kerr 18116 (K), Narathiwat, Ban Ko Sawat; Sangkhachand 29950 (K), Narathiwat; Larsen 33105 (BKF), Narathiwat; Kerr 16586 (K), Ranong, Ko Chang; Santisuk s.n. (BKF), Ranong; Niyomdham 1285 (K, L), Satun, Thung Wa; Maxwell 85/60 (BKF, A, L),

Songkhla, Khlong Ngae, Hat Yai; Maxwell 85/113 (A, BKF), Songkhla, Ko Hong hill; Maxwell 84/35 (A), Songkhla, Ko Hong hill, Hat Yai; Congdon 39 (A), Songkhla, Kuan Meed, south of Hat Yai; Kerr 14758 (L), Songkhla, Hat Yai; Geesink 7788 (AAU), Surat Thani, Koh Phangan; Haniff 3896 (K), Surat Thani, Koh Phangan; Put 789 (L), Surat Thani, Koh Phangan; Geesink 7750 (AAU, BKF, L, P), Surat Thani; Geesink 7776 (BKF), Surat Thani; Kerr 8262 (K), Surin; Put 3039 (L), Trat, Kao Kuap; Put 3030 (K), Trat, Kao Kuap; Kerr 17750 (K), Trat, Kao Kuap; Kerr 17873 (L), Trat; Put 3667 (L), Yala; Kerr 18949 (L), Krabi.

Philippines: Dransfield 1260 (L), Palawan, Mt. Victoria, Trident mine; Dransfield 1255 (L), Palawan, Mt. Victoria, Trident mine; Ridsdale 1039 (L), Palawan, Pulot, Massin river, 12km north of Brook point; Ridsdale 1111 (L), Palawan, forest north of Tagburos, 17 km north of Puerto Princessa; Ridsdale 1739 (L), Palawan, Narra, Mt. Victoria; Ebalo 429 (A, SING), Palawan, Mt. Sorgson; Edano 115 (A), Palawan, Lapu Lapu, Iwahig; Edano14242 (L), Palawan, Mt. Victoria; Elmer 12752 (BO, L), Palawan, Brook point; Elmer 12752 (U); Soejarto & Madulid 6168 (A, L) Palwan, Victoria range; Sulit 12326 (A, L), Palawan, Mt. Victoria.

Brunei: Ashton 285 (L), Tutong, Bukit Pasir Puteh; Ashton 5021 (L), Tutong, Bukit Pasir Puteh; Ashton 946 (L), Barakas; Ashton 5574 (L), Marundi; Ashton 970 (L); Jacobs 5671 (CANB, L), west Tutong district, near Telamba bridge; Wong 768 (A),Temburong district, north ridge of Bukit Retak.

Singapore: Sinclair 39243 (L), Singapore, Sungei Peropak, Jurong road; Sinclair s.n. (P) Singapore, Jurong road

Malaysia: *Malay Peninsula*: Cockburn 11032 (L), Selangor, Gunong Tapis; Chevallier 98112 (L), Kedah, Gunong Jerai forest reserve; Burkill 3317 (L, SING), Kedah, Gunong Jerai; Whitmore 12651 (K); Lo 86 (A), Gunong Jerai; Hardial 689 (SING), Penang; Maxwell 82-208 (L, SING), Penang, Penang hill; Kochummen 11470 (L), Penang, Frasers hill; Maingay 1315 (L), Penang, Government hill; Shimizu 13183 (KYO), Penang; Henderson 22939 (SING), Perlis, Bukit Ketri; Ridley 14933 (SING), Perlis; Shah 2483 (SING), Kelantan; Malvius s.n. (SING); Malvuis 773 (SING); Ridley 359 (SING); Burkill 3220 (SING); Holttum s.n. (SING); Hur & Kiah 7804 (SING); Kiah 31858 (BO, L, SING); Shah & Kadim 557 (BO, L), Kelantan, Kampong Gobek, Kerilla estate, Tamangan; Soepadmo 1077 (BO), Kelantan,Gunong Rabong; Soepadmo 974 (L), Gunong Thana; Moysey & Kiah 31067 (L, SING), Terengganu; Liew 366 (L), Terengganu; Nur 11286 (BO), Pahang, Fraser hill; Sinclair 39039 (BO, L, P, SING);

Kochummen 16255 (L), Fraser hill; Balgooy 2684 (CANB, L), Pahang, Cameron highlands; Burkill 2614 (L), Bukit Kroh forest reserve; Chew 943 (SING, L), Cameron highlands, Gunong Jasar 4 29N 101 22E; Cockburn 10996 (L), Pahang, Gunong Tapis; Curtis 2593 (SING), Kedah; Hardial & Samsuri 223 (L), Ayer Hitam dam reserve; Ismail 97808 (L), Pahang, Gunong Benom game reserve, Ulu Krau; Ng 20946 (L), Pahang, Gunong Tahan; Maxwell 80-24 (BKF, L), Pahang; Shah 1469 (A, L, SING), Pahang, path to Sungai Teku; Stone 11052 (L), Pahang, Genting highlands; Stone 9369 (L), Pahang, Fraser hill; Whitmore 15179 (L, SING), Pahang, Selangor, Fraser hill, Pine Tree Hill; Whitmore 20029 (A), northwest Pahang, Bukit Chergar; Haniff & Nur 7892 (SING), Pahang; Holttum 20721 (SING), Pahang; Ridley 89 (SING), Pahang; Ridley 1239 (SING), Pahang; Robinson 5484 (SING), Pahang; Samsuri 930 (SING), Pahang; Shah 2727 (SING), Pahang; Symington & Kiah 28842 (SING), Pahang, Gunong Tapis, Kuantan; Ridley 13 (SING); Maxwell 78/226 (L) Kota Tinggi; Awa 50867 (L), Bukit Lawi. *Sarawak*: Anderson 9835 (L), Sibu; Anderson 3044 (L), Lambir hills, Miri district; Chew 1392 (A, L), Mt. Santubong; Chew 1411 (A); Dyg et al 46864 (K), Bukit Dulit, Tinjar; Haron 21443 (L), Santubong; Ilias Azahari 35679 (L), Gunong Gaharu, 1st division; Jacobs 5508 (CANB, K, L), Kuching, Bako national park; Jawa 36623 (K), Kuching Pulau lakei; Jacobs 5503 (CANB, L), 30 km northeast of Kuching, Bako national park; Paie 46090 (L), Gunong Besi; Paul et al 37399 (L), Bukit Regu; Purseglove 5624 (L, SING), Bako national park; Purseglove 5626 (L), Telok Asam, Bako national park; Wiriadinata 870 (BO, L), Dalat; Yii Othma 46284 (L), Gunong Majar, Tebakang; Anderson 4742 (BO), Baram, Gunong Api; Anderson 30936 (L), Gunong Api, Ulu Melinau,Tutoh, Baram district; Anderson 4570 (L), Gunong Mulu, path from Melinau Paku; Awa & Lee 50867 (L); Brunig 10332 (L), Kuching; Chai 35925 (L), Barem district; Chai 37238 (L) Bukit Salong, Hose Mt., Melinau; Chai & Wright 29915 (L), Bako national park, Telok Asam; Chai 39906 (L), Gunong Buda, Gunong Mulu national park; Othman 37157 (L), Bako national park; Purseglove 5032 (L, SING), Pulau Lakei; Purseglove 5623 (L), Telok Asam, Bako national park; Sleumer 4676 (L), Bako national park, near Kuching, Litang path; Amin & Haya 102259 (L, SING), Limbang. *Sabah*: Beaman 8726 (A, L), Sipitang district, Bukit Sebuboh, 8 km southwest of Sipitang; Beaman 8407 (K, L), Sipitang, 5 02N 115 32E; Beaman 6947 (A, L), Mt. Kinabalu, Crocker range, 5 50N 116 20E; Beaman 9431 (A), Beaufort district, 1.5 km south of Weston; Clemens 34416 (A, L), Mt. Kinabalu, Olombon basin; Clemens 28620 (A, L), Mt. Kinabalu, Tenom; Clemens 29322 (A, L), Mt. Kinabalu; Clemens 50332 (A, L), Mt. Kinabalu, upper Penibukan west ridge; Clemens

9577 (A); Clemens s.n. (A), Penibukan; Clemens 31501 (L), Mt. Kinabalu; Clemens 29398 (L), Mt. Kinabalu, Tenom; Dewol & Karim 78036 (L), Mandahan forest reserve; Mondi 283 (L, SING, U), Pontianak, Kp. Mandor; Pingkun 10152 (BO, L), Banjaran forest district; Saikeh 72302 (L), Sipitang, Merintaman forest reserve; Smythies & Wood-Ashton 17143 (L), Temburong, summit of Bukit Patoi; Stevens 345 (L), Sandakan, Leila; Wood 3656 (L), Seguntor river, Sandakan; Husin 86192 (L), Mandahan, Papar; Meijer 57544 (L), Mt. Kinabalu national park near boundary pole 76; Meijer 48279 (L), Sandakan, Leila; Talib & Heya 80533 (L), Kimanis; Talib 50602 (L), Sipitang; Ampuria 41423 (L), Kimanis forest reserve; Bidin 80556 (K, L), Membakut; Chew 4634 (L), Mt. Kinabalu, Bembangan river; Dewol & Talib 80417 (L), Kepayan; Carr 26951 (SING), Mt. Kinanbalu; Stevens 345 (L), Sandakan.

Indonesia: *Kalimantan*: Endert 2011 (L), west Koetai; Giesen 160 (L), South Kalimantan; Giesen 161 (L), South Kalimantan; Hallier 318 (P); Hallier 1451 (L); Hallier 2351 (L); Koyama & Terao 31633 (A); Kuswata 1174 (L), East Kalimantan, north of Samarinda; Sidyasa 223 (E, SING), Kalimantan, Tengah; Sidyasa 223 (E), Kalimantan; Ambri & Arifin 126 (L), East Kalimantan, Samboja. *Sumatra*: de Raadt 95 (L), Palembang; de Wilde 20704 (L), south-southwest of Gunong Leuser National park, Belintang village, 2 43N 97 54E; Huitema 77 (L); Huitema 76 (L), Lintoeng, Dolok Sangoel; Lorzing 7983 (BO); Maradjo 397 (L), Halaban; Meijer 7369 (L), Mt. Sago near Payakumbuh; Meijer 7336 (L), west coast, near Tiku; Meijer 7072 (L), Taram, east of Payakumbuh, sandstone region of River Tyampo; Meijer 5377a (L), Mt. Sago near Payakumbuh; Meijer 7340 (L), Tiku sand dunes, west coast; Nagamasu 3814 (L), south of Mt. Sago, 0 22S 100 40E; de Raadt 93 (L), Palembang; si Boeea 4186 (A), Soengi Kanan; si Boeea 3465 (A, L), Langgapayung; si Boeea 3999 (A) Soengei Kanan, Laboehan Batoe; si Boeea 2220 (A), Rantau Parapat, Bila; si Boeea 4186 (A), Soengei Kanan, Laboehan Batoe; si Boeea 3318 (L), Kota Pinang; Blume 628 (L), Sibolga; Kjellberg 2078 (BO), Malili, Langea; Reinwardt 628 (L, U), Sibolga; Teysmann 3509 (U), Bangka, Teysmann 3323 (L, U), Bangka; Teysmann s.n. (U), Bangka; Teysmann 7560 (L, P), Bangka; Teysmann s.n. (U), Bangka; Huitema 14 (L), Bangka; Teysmann 3509 (U), Bangka; Huitema 76 (L); Kostermans 1553 (L), Bangka. *Moluccas*: De Haan 651 (BO, L), Halmahera, southern peninsula; de Vogel 4344 (CANB, L), Obi island, W. Jikodolong; Kostermans 1312 (L), Morotai, Gunong Pare.

Papua New Guinea: Henty 13684 (A, L), Markham point, near Lae; Stauffer & Henty 5546 (A, CANB), Morobe district, Markham point.

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

Key to the Varieties

1. Leaves small, elliptic 13 – 14 mm in length; female inflorescence 1 – 4 flowered; fruits unknown; endemic to south Vietnam.....var. *gracilor*
   Leaves spathulate, 18 – 32 mm in length; female inflorescence 1 – flowered; fruits small, spherical, 4 – 5 mm in length; Malay Penninsula, Sumatra, Java.....var. *umbellata*

var. *gracilor* Stauffer

Type: Poilane 6809 (Holotypus P!), Vietnam, Nam Phan, Nhatrang.

Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 114: 59 (1969).

Branches slender. *Leaves* small, elliptic, 13.0 – 14.0 (6.5 – 7.0 x 2.0 – 2.5) mm, thin, margins weakly involuted, primary veins 3, indistinct; petiole 5.0 – 6.0 x 0.6 mm. *Male inflorescences* unknown. *Female inflorescences* 1 – 4 flowered, pedunculate, peduncle 1.0 – 2.0 x 0.2 mm, slender, tortuous, bracts lanceolate, 0.8 x 0.4 mm, margins weakly ciliate, flowers crowded near the apex of the peduncle. *Female flowers* pedicellate, pedicel long, slender, 0.7 – 1.0 x 0.4 mm, tepals ovate, 0.8 – 0.7 mm. *Fruits* unknown.

Distribution: Southern Vietnam.

Habitat: Montane forest on marshy, poor soil.

Altitude: 1500 – 1700 m.

Notes: Name derived from the slender stems and delicate inflorescences. A variety of *Dt. varians* represented by a single collection. Characterised by small spathulate leaves. Vegetatively similar to *Dt. buxifolia*, distinguishable from it by racemose inflorescences, unisexual flowers and a smooth nectarial disc.

var. *umbellata* (Bl.) Macklin **stat. nov.**

Type: Korthals s.n. (Holotypus of *Thesium spathulatum* L! Isotypus P!), Java.

Thesium spathulatum Bl., Bijdragen tot de Flora van Nederlandsche Indië: 646 (1826); *Viscum umbellatum* Bl., *l.c.*: 666 (1826); *Tupeia umbellata* Bl., Flora Javae Loranthae t. 27 (1830); Korthals, Verhandling over de natuurlijke geschiedenis der Nederlandsche overzeesche Bezittingen: 195 (1839); *Henslowia umbellata* Bl., Museum Lugduno Batavae 1: 243 (1850); A.DC., Prodromus 14: 279 (1857) non Lecomte, Bulletin Muséum Histoire Naturelle Paris 20: 405 (1914), non Lecomte, Flora Générale de l'Indo-Chine 5: 218 t.23 (1915); *Henslowia pauciflora* Bl., Museum Lugduno Batavae 1: 244 — Type: Blume s.n. (Holotypus L!), Java; *Henslowia retusa* Bl., *l.c.*: 243 — Type: Blume s.n. (Holotypus L!, Isotypus P!), Java; *Henslowia monticola* Gamble, Kew Bulletin: 201 (1912) — Type: Wray 1536 (Holotypus K!), Malay Peninsula; *Dendrotrophe monticola* Danser, Nova Guinea New Series 4: 148 (1940); *Dendrotrophe umbellata* Miq., Flora Flora Indiae Batavae 1.1: 781(1856); Danser, Nova Guinea New Series 4: 147 (1940); Backer, Flora of Java 2: 78 (1965); Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich: 56 (1969) **syn. nov.**

Juvenile stems angular, flattened; *Leaves* spathulate, fleshy, 18.0 –32.0 (14.0 – 20.0 x 5.0 – 7.0) mm, margins weakly invlouted; Fruits small, spherical, 4.0 – 5.0 x 3.0 – 3.5 mm.

Distribution: Malay Peninsula, Sumatra and Java.

Habitat: Montane forest.

Altitude: 1000 – 1500 m.

Notes: Name derived from the spathulate leaves. This variety has been known as *Dt. umbellata* on account of its seemingly umbellate male inflorescences. In fact, it has a racemose male inflorescence with the flowers crowded near the apex of the peduncle and misinterpretation of the inflorescence structure led to it being assigned specific status. In his Flore Générale de l'Indo-Chine t.23 Lecomte (1915) showed the male inflorescence as umbellate and the fruits as large and ellipsoid. The plant which Lecomte described was actually *Dt. varians sensu stricto*

and his misidentification of the inflorescence and fruit structure persisted in later works. Confusion over the status of this taxon was probably exacerbated by the fact that there are also insect galls in the male flowers of the type specimen which makes them appear different to the standard *Dt. varians* flower. The variety is characterised by spathulate leaves and small spherical fruits. In terms of fruit structure it is similar to *Dt. buxifolia* but can be distinguished from it by racemose male inflorescences, unisexual flowers and a smooth nectarial disc.

Additional material examined

Indonesia: *Sumatra*: De Voogd 1153 (L), Lebong Pasir; Korthals s.n. (L). *Java*: De Voogd 2 (L), Mount Salak, west Java; Junghuhn s.n. (L); Koorders 3164a (L), Gunong Gedah; Went s.n. (L), Gunong Gedah.

3. *Dufrenoya* Chatin

Type species: *Df. platyphylla* Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 114: 53 (1969) —Type: Wallich 488 (Holotypus of *Viscum heteranthum* K!), India.

Chatin, Comptes Rendus Acadamie Paris 51: 657 (1860); Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 114: 66 (1969); Grierson & Long, Flora of Bhutan 1.1: 142 (1983); *Henslowia* p.p. A.DC., Prodromus 14: 630 (1857); Bentham, Genera Plantarum 3: 228 (1883); Hook.f., Flora of British India 5: 232 (1886); Pilger in Engler & Harms, Die Natürliche Pflanzenfamilien 16b: 71 (1935); *Hylomyza* Danser, Nova Guinea New Series 4: 141 (1940); Backer, Flora of Java 2: 77 (1965).

Glabrous dendroparasitic shrubs or climbers, stems without secondary haustoria; bark smooth, pustulate or with longitudinal fissures. *Leaves* varying in size but usually large, primary veins 3 - 11. Inflorescences dioecious, singular or 1 – 3 together, flowers yellow or green. *Male inflorescences* umbellate, 5 – 7 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 is not subtended by a bract and develops first. *Male flower* buds globose, fungiform, receptacle flat, tepals 5 - 6, deltoid, valvate, glandular hairs present, occasionally absent, anthers bilocular, locules bilobed, lobes isomerous or unequal in size with the posterior larger than the anterior, dehiscence transverse or longitudinal, nectary flat or

slightly concave, fleshy, smooth and scarcely 5 – lobed, style rudiment present which may be a small peak at the centre of the disk or occasionally more fully developed, slender, elongate. *Female inflorescences* 1- flowered, pedunculate. *Female flowers* with staminodes, style short, stigma 5 – lobed, papillose, nectary flat or convex, unlobed; *ovary* 0.2 – 0.4 x 0.5 – 0.6 mm, placenta convex 5 – 6 lobed, lobes short, curling underneath and in towards the placental column, column long, straight. *Fruit* green, red, elliptic, obovoid, perianth persistent, erect or flat; exocarp thin, smooth; mesocarp consisting of long 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 often at the base, 5 – 7 lobed for the rest (**Fig. 40, 16**). 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.

Number of Species: 11

Distribution: Southern China and India to Western Borneo.

Habitat: Restricted to mountainous regions in mostly open areas in sub montane and hill evergreen forests in Fagaceae - *Pinus* and Fagaceae - *Larix* associations. Parasitic on *Quercus* and *Lithocarpus* (Fagaceae); and *Eugenia* (Myrtaceae).

Altitude: above 1000 m.

Notes: 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. A number of species are 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. In Thailand the name Kaa Fak is attributed to one species, another is called Ainjeru in Nepal. 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. A feature of the majority of species is that there are often insect galls in the male flowers which causes the receptacle to become enlarged and may confuse identification.

Key to *Dufrenoya*

1. Stems pustulate.....(2)
   Stems smooth, rough, striated, fissured.....(5)
2. Inflorescence bracts small; anther locules unequal in male flower; staminodes present in female flower, stigma lobed.....**7.** *D. platyphylla*
   Inflorescence bracts large; anther locules isomerous in male flower ; staminodes absent in female flower, stigma entire.....(3)
3. Inflorescence bracts fleshy.....**9.** *D. robusta*
   Inflorescence bracts papyraceus.....(4)
4. Inflorescences shortly pedunculate; endocarp distinctly lobed at the apex, base apiculate.....**4.** *D. granulata*
   Inflorescences elongate pedunculate; endocarp obscurely lobed, not apiculate at the base.....**7.** *D. poilanei*
5. Bark faintly corrugated with short elliptic, transverse fissures; primary veins 9 – 11, almost parallel; male flowers pendulous.....**2.** *D. collettii*
   Bark smooth or with longitudinal fissures; primary veins obscure or 3 –5; male flowers not pendulous.....(6)
6. Stems papillose.....**6.** *D. papillosa*
   Stems not papillose.....(7)
7. Secondary veins visible; fruits chambered in the base.....(8)
   Secondary veins indistinct; fruits unilocular in the base.....(10)
8. Mesocarp membranous, long, wrapping around the endocarp; endocarp ovoid .....**10.** *D. sessilis*
   Mesocarp sericeus, short, randomly oriented; endocarp spherical, oblong.....(9)
9. Inflorescences on raised bract scars; endocarp oblong.....**3.** *D. euryphylla*

Inflorescences subtended by a single involucre of bracts;endocarp spherical .....**11.** *D. sphaerocarpa*

10. Leaves 12 – 20 mm in length, spathulate; Mesocarp short, randomly oriented, endocarp ovoid.....**5.** *D. oresitropha*

Leaves 25 –28 mm long, elliptic; Mesocarp long, wrapping around the endocarp, endocarp obovoid.....**1.** *D. aurantiaca*

1. *Dufrenoya aurantiaca* Stauffer

Type: Poilane 8118 (Holotypus P!; Isotypus Z!), South Vietnam, Trung Phan, near Tourane.

Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 114: 66 (1969).

Erect shrub. *Juvenile stems* angular, bracteate at the base, smooth, older branches distinctly different, pale in colour with a waxy sheen, bark rough and uneven with a dense network of longitudinal fissures. *Leaves* fleshy, coriaceous, elliptic, obovate, apex acute, obtuse, base cuneate, 25.0 - 28.0 (14.0 - 15.0 x 3.0) mm, upper surface weakly convex, shining, rugulate, lower surface dull, granular, primary veins 5, faintly discernible on the upper surface, secondary venation indistinct; petiole long, slender, 4.0 –7.0 x 1.0 – 1.5 mm. *Male inflorescences* unknown. *Female inflorescences* confined to stems of up to second years growth, and on short side shoots from older branches, up to 5 together, shortly pedunculate, peduncles 0.7 - 1.0 x 1.0 mm, with an involucre of 4 - 5 bracts at the base and the apex, apical involucre quincuncial, bracts also arranged alternately along the length of the peduncle, bracts minute, fleshy, broadly ovate, 0.5 x 0.8 mm, margins ciliate. *Female flower* buds (new description) obconical, tepals narrowly deltoid, 1.0 x 0.6 mm, shortly apiculate on the inner surface at the apex, staminodes present, glandular hairs present, filaments long, narrow, 0.3 x 0.2 mm, anthers 0.1 x 0.3 mm, thecae indistinct, style short, broad, 0.2 x 0.3 mm, stigma smooth, 5 - lobed, lobes rounded, nectary fleshy, flat or weakly concave, 5 - lobed. *Fruit* obovoid, 5.0 - 6.0 x 3.5 x 4.5 mm, persistent perianth erect, exocarp coriaceous, mesocarp long, membranous, wrapping around the endocarp, endocarp narrowly obovoid, 4.5 - 5.5 x 1.7 - 2.0 mm, unlobed, hard, depressed at the apex, apiculate at the base, internally 5 - chambered at the apex, incompletely so for the rest.

Distribution: South Vietnam (**Fig. 52**).

Habitat: Montane forest. Parasitic on Fagaceae.

Altitude: 1200 - 1800 m.

Notes: Name derived from the orange colour of the fruits in the dry state. Characterised by pale, waxy bark, erect growth habit and distinctly obovoid fruits. This species is known from only two collections from Southern Vietnam. It is most closely allied to the species in northern Thailand (*Df. collettii*, *Df. sessilis*) but can be distinguished by its coriaceous leaves and an endocarp which is unilocular in the base. In this respect it is similar to *Df. oresitropha* but may be easily distinguished by larger, elliptic leaves, a membranous mesocarp and an obovoid rather than ovoid endocarp.

Additional material examined

Vietnam: Averyanov et al 214 (P), South Vietnam, Kontum, northwest slopes Ngoc Linh.

2. *Dufrenoya collettii* (Gamble) Stauffer .

Type: Robertson 326 (Holotypus of *Henslowia collettii* K!), Burma, Southern Shan States.

Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 114: 69 (1969); *Henslowia heterantha* Wall. ex DC. var. *coriacea* Kurz, Forest Flora of British Burma 2: 328 (1877) — Type: Kurz 371 (Holotypus K!); *Henslowia collettii* Gamble, Kew Bulletin: 47 (1913).

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* spathulate, 70.0 - 95.0 (25.0 - 350 x 10.0 - 20.0) mm, apex obtuse, base attenuate, margins crisp, weakly undulate, upper surfaces smooth, shining, lower surfaces dull, granular, 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

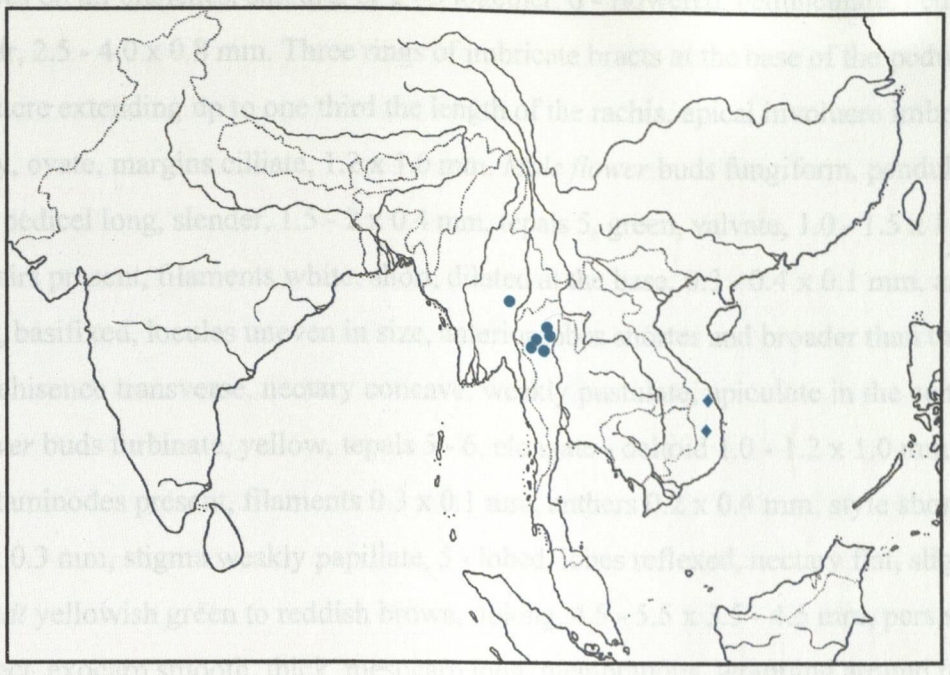


Fig. 52 Geographic distribution of: ♦ *Dufrenoya aurantiaca,* • *Dufrenoya collettii.*

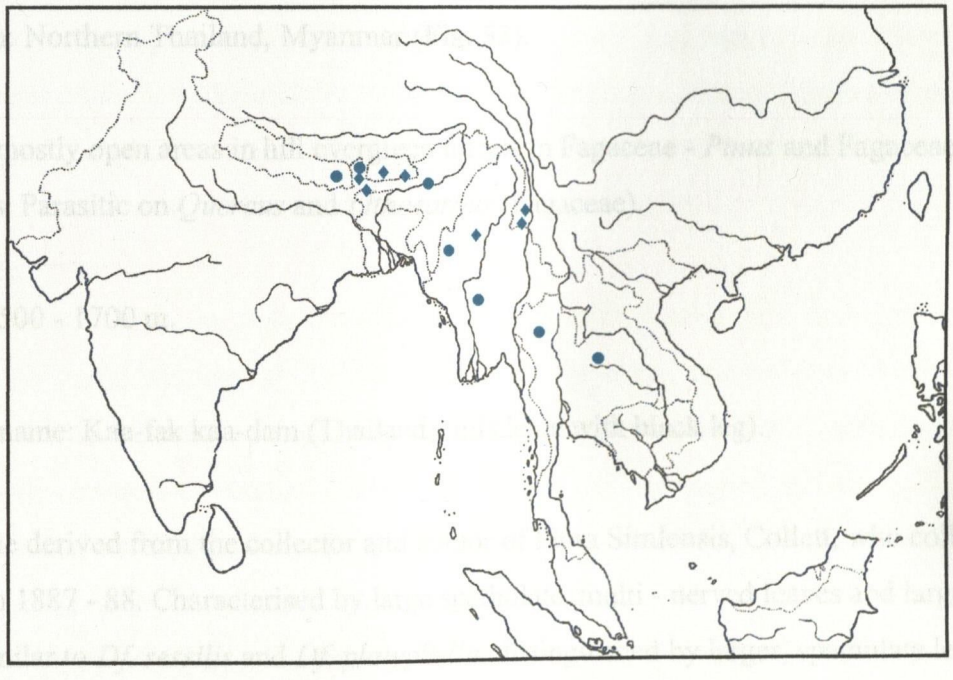


Fig. 53 Geographic distribution of: ♦ *Dufrenoya granulata,* • *Dufrenoya platyphylla.*

long, slender, 9.0 - 10.0 x 2.5 - 3.0 mm upper surface flat, lower surface convex. *Male inflorescences* on all branches, singular or 2 - 3 together, 6 - flowered, pedunculate, peduncles long, angular, 2.5 - 4.0 x 0.8 mm. Three 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 fleshy, ovate, margins cilliate, 1.2 x 1.0 mm. *Male flower* buds fungiform, pendulous, pedicellate, pedicel long, slender, 1.5 - 2 x 0.4 mm, tepals 5, green, valvate, 1.0 - 1.5 x 1.1 mm, glandular hairs present, filaments white, short, dilated at the base, 0.3 - 0.4 x 0.1 mm, anthers pale yellow, basifixed, locules uneven in size, anterior lobes shorter and broader than the posterior, dehisence transverse, nectary concave, weakly pustulate, apiculate in the centre. *Female flower* buds turbinate, yellow, tepals 5 - 6, elongate - deltoid 1.0 - 1.2 x 1.0 mm, apex apiculate, staminodes present, filaments 0.3 x 0.1 mm, anthers 0.2 x 0.4 mm, style short, broad, 0.2 x 0.3 mm, stigma weakly papillate, 5 - lobed, lobes reflexed, nectary flat, slightly angular. *Fruit* yellowish green to reddish brown, oblong, 4.5 - 5.5 x 3.5 - 4.5 mm, persistent perigone erect, exocarp smooth, thick, mesocarp long, membranous, wrapping around the endocarp; endocarp oblong, slightly obovoid, 3.5 - 4.0 x 2.0 - 2.5 mm, 5 - grooved, splitting easily, apex apiculate, internally 5 - chambered at the apex and the base, incompletely so for the rest.

Distribution: Northern Thailand, Myanmar (**Fig. 52**).

Habitat: In mostly open areas in hill evergreen forests in Fagaceae - *Pinus* and Fagaceae - *Larix* associations. Parasitic on *Quercus* and *Lithocarpus* (Fagaceae).

Altitude: 1500 - 1700 m.

Vernacular name: Kaa-fak kaa-dam (Thailand) (mistletoe with black leg).

Notes: Name derived from the collector and author of Flora Simlensis, Collett, who collected in Burma from 1887 - 88. Characterised by large spathulate, multi - nerved leaves and large male flowers. Similar to *Df. sessilis* and *Df. platyphylla*, distinguished by larger, spathulate leaves and larger, pendulous male flowers. The vernacular name in Thailand refers to the dendroparasitic growth habit and the dark brown-black stems.

Additional material examined

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

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

3. *Dufrenoya euryphylla* (Danser) Stauffer

Type: Junghuhn s.n. (Holotypus of *Hylomyza euryphylla* L!), Sumatra.

Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 114: 67 (1969); *Tupeia Reinwardtiana var angustifolia* Molkenboer ex Junghuhn, Plantae Junghuhnianae: 117 (1852) — Type: Junghuhn s.n. (Holotypus L!), Sumatra; *Hylomyza euryphylla* Danser, Nova Guinea New Series 4: 144 (1940); Backer, Flora of Java 2: 77 (1965).

Erect or pendulous shrub. *Juvenile stems* twisted flattened, angular, striate, branches keeled at nodes, sparsely leafy, bracteate at the base, older branches terete, covered in the bracts of previous seasons inflorescences, scars forming a distinct pattern on the stems and branches, bark irregularly fissured, sometimes with deep linear fissures, when twining fissures becoming short, elliptic. *Leaves* obovate, broadly spathulate, 35.0 - 50.0 (22.0 - 28.0 x 7.0 - 10.0) mm, apex obtuse, base attenuate, upper surface weakly convex, margins crisp, primary veins 5, distinct on the upper surface, secondary veins indistinct; petiole slender, 4.5 x 1.0 mm, upper surface flat, lower surface angular. *Male inflorescences* 1 - 3 together, on juvenile branches and older wood, on raised scars, pedunculate, peduncles terete, short 0.5 - 1.0 x 1.0 mm, two

involucres of bracts at the base, a single imbricate involucre at the apex, bracts minute, broadly ovate, 0.3 - 0.6 x 0.5 mm, margins sparsely ciliate. *Male flowers* greenish-yellow, buds globose, shortly pedicellate, pedicel 0.2 mm long, decurrent with the receptacle. Tepals 5, lanceolate, 1.0 x 0.5 - 0.7 mm, broadly apiculate on the inner surface at the apex, glandular hairs present, filaments short, dilated at the base, 0.2 x 0.1 mm, anthers, 0.2 x 0.3 mm, dorsifixed, lobes unequal in size, posterior longer than the anterior, nectary red, flat, five lobed, style rudiment absent. *Female flower* buds turbinate, receptacle 1.0 mm long, tepals 5, broadly deltoid, 0.6 x 0.5 mm, fleshy, shortly apiculate on the inner surface near the apex, staminodes present, filaments short, broad, 0.2 x 0.1 mm, anthers 0.1 x 0.3 mm, thecae indistinctly differentiated, style short, broad, 0.2 x 0.2 mm, stigma smooth, 5 - lobed, lobes long, pointed, outspread. *Fruit* shortly pedicellate, oblong, persistent perianth erect, exocarp thin, mesocarp short, sericeus, randomly oriented, endocarp 3.5 x 1.5 mm, oblong, 5 - 7 lobed, lobes splitting easily. Internally 5 chambered at the apex and the base, incompletely so for the rest, basal chambers short and narrow.

Distribution: Malay Peninsula, Java, Sumatra.

Habitat: Parasitic on *Quercus* (Fagaceae).

Altitude: unknown.

Notes: Name derived from large, well developed leaves. Represented by just a few rather ill preserved specimens in the herbarium, but as yet distinct enough to warrant specific status. Characterised by the large spathulate leaves, and narrow, oblong endocarp. Similar to *Df. collettii* and *Df. sessilis* from northern Thailand but distinguishable by geographic location, a short, sericeus mesocarp and an endocarp which is oblong with short basal chambers.

Additional material examined

Malaysia: *Malay Peninsula*: Batten Poole s.n.(SING).

Indonesia: *Java*: van Steenis 4072 (L); van Steenis 4872 (BO, L).

4. *Dufrenoya granulata* (Hook.f. & Th.) Stauffer

Type: Hook.f. (Holotypus *Henslowia granulata* K!; Isotypus TCD!; P!) India, Sikkim, Khasia.

Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich: 70 (1969); Grierson & Long, Flora of Bhutan 1.1: 142 (1983); *Henslowia granulata* Hook.f. ex A.DC., Prodromus 14: 632 (1857); Hook.f., Flora of British India 5: 232 (1886); Kanjilal, Flora of Assam 4: 129 (1940); [*Henslovia granulata sensu* Collett & Hemsley, Journal of the Linnean Society 28: 121 (1890)]; *Hylomyza granulata* Danser, Nova Guinea New Series 4: 145 (1940); *Dendrotrophe granulata* Tam, Flora Reipublicae Popularis Sinicae: 71 (1988) **syn. nov.**

Erect and pendant shrub. *Juvenile stems* angular, flattened, densely pustulate, bracteate at the base, bracts distinctive, large, papyraceus, older branches terete, bark scaly, pustules occluded. *Leaves* fleshy, elongate-obovate, 26.0 - 36.0 (14.0 - 20.0 x 4.0) mm, apex rounded, tip mucronate, deciduous, base attenuate, upper surfaces weakly convex, smooth, shining, lower surface rough, dull, margins thin, undulating, completely smooth and flattened, primary veins 5 - 9, raised on the upper surface, secondary veins indistinct; petiole long, 2.0 - 3.5 x 1.5 mm, upper surface flattened, lower surface angular. *Male inflorescences* on juvenile shoots and those of second years growth, usually 2 - 3 together, 6 - flowered, very shortly pedunculate, peduncles 0.5 - 0.6 x 1.0 - 1.2 mm, 2 - 3 involucres of bracts at the base and a single involucre of 5, quincuncially arranged bracts at the apex, bracts large, broadly ovate, 1.0 - 1.5 x 1.0 - 2.0 mm, papyraceus, clearly divided into two areas, inner region thick, hard, margin thin and entire or sparsely ciliate. *Male flower* buds turbinate, green, tinged red, pedicellate, pedicel long, broad, 0.8 - 1.5 x 0.8 mm, decurrent with receptacle, tepals 5, broadly ovate, 1.0 - 1.2 x 1.4 - 1.6 mm, fleshy, apiculate on the inner surface at the apex, glandular hairs present, filaments long, narrow, 0.3 x 0.2 mm, anthers dorsifixed, large, broad, 0.3 - 0.4 x 0.6 mm, bithecate, lobes isomerous, dehiscence longitudinal, nectary flat, distinctly 5 - lobed, lobes broad, pointed, style rudiment absent. *Female flower* unknown (description taken from fruiting specimen), tepals elongate - deltoid, 1.0 - 1.1 x 0.7 - 0.8 mm, apiculate on the inner surface at the apex, staminodes absent, stigma occupying the entire centre of the flower, sessile, large, entire, weakly papillose, slightly depressed in the centre, nectary flat or convex, angular. *Fruit* red to dark purple, globose, 4.5 - 5.0 x 4.5 - 5.0 mm, persistent perigone erect, exocarp smooth,

coriaceous, mesocarp short, membranous, randomly oriented, endocarp obovoid, 2.7 - 3.0 x 1.8 - 2.0 mm, splitting easily, distinctly 5 - lobed, apiculate at the base and the apex, internally 5 - chambered at the apex and the base.

Distribution: India, Bhutan and southern China (**Fig. 53**).

Habitat: Restricted to mountainous regions, in evergreen oak forests, associated with *Quercus* (Fagaceae).

Altitude: 2000 - 4000 m.

Vernacular name: Ainjeru (Nepali) (mistletoe).

Notes: Name derived from the granular, pustulate bark. Characterised by distinctly pustulate bark, thick, leathery leaves and sessile or sub-sessile, large male flowers. Taxonomically close to *Df. poilanei* and *Df. robusta* distinguishable by its sessile male inflorescences and lobed endocarp. The vernacular name in Nepal is also applied to members of the Loranthaceae (Grierson & Long 1983).

Additional material examined

India: Koelz 26135 (L), Takubama, Naga hills; Kingdom Ward 18244 (BM), Sirhoi; Hooker & Thompson (K); Griffiths 4389 (K), East Himalayas; Gamble 7887 (K), Bengal, Sikkim; Gamble 10082 (K), Bengal, Sikkim; Gamble 372A (K), Darjeeling.

China: T.T. Yü 17913 (E), Yunnan, Mienning, Poshang; Forrest 25759 (E, P), Yunnan, 27N 98 35E

Bhutan : Ludlow et al 18625 (E), South Bhutan, Kinga Rapden; Grierson & Long 3062 (E), Chhukha district, forest slope 2 km north of Jumudag, 26 55N 89 33E.

5. *Dufrenoya oresitropha* (Danser) Stauffer

Type: Clemens 29084 (Holotypus *Hylomyza oresitropha* L!; Isotypus B!), Upper Kinabalu, Borneo.

Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 114: 66 (1969); *Hylomyza oresitropha* Danser, Nova Guinea New Series 4: 143 (1940); *Hylomyza oocarpa* Danser *l.c.*: 143 (1940) — Type: Haniff & Nur 7918 (Holotypus B n.v., Isotypus L!), Pahang, Gunong Tahan; *Dufrenoya longicuneata* Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich: 67 (1969) — Type: Chevalier 40396 (Holotypus P!, Isotypus TCD!, Z!), Vietnam, **syn. nov.**

Erect shrub, branches long, slender, with few side shoots. *Juvenile stems* flattened, smooth, articulated at nodes, bracteate and slightly contracted at the base, often 3 - 4 arising from a single point, older branches terete, smooth or with a network of closely packed, pale, shallow, elliptic fissures. *Leaves* fleshy, olive or yellow, 12.0 - 20.0 (10.0 - 11.0 x 2.0 - 3.0) mm, obovate, spathulate, apex obtuse, base attenuate, upper surfaces weakly convex, margins crisp, primary veins 3 - 5, slightly raised on the upper surface, secondary venation indistinct; petiole short, 1.0 - 2.0 x 1.5 mm, upper surface flat, lower surface convex. *Male inflorescences* 3 - 5 together, confined to juvenile branches, rarely on older stems, 5 - flowered, pedunculate, peduncles long, slender, terete or slightly angular, 4.0 - 5.0 x 0.5 - 0.6 mm, a single valvate involucre at the base and the apex, sparsely bracteate along the length, bracts minute, broadly ovate, apex acuminate, base contracted, 0.5 - 0.6 x 0.5 - 0.6 mm, margins serrate. *Male flower* buds yellowish green, globose, pedicellate, pedicel slender 1.0 x 0.2 - 0.3 mm, decurrent with the receptacle, tepals yellowish green, 5, deltoid, 1.0 x 1.0 mm, weakly apiculate on the inner surface near the apex, glandular hairs present, filaments slender, 0.3 x 0.1 mm, anthers dorsifixed, 0.3 x 0.3 mm, bithecate, lobes unequal in size, posterior slightly longer and broader than the anterior, dehiscence longitudinal, nectary concave, fleshy, style rudiment, narrow, 0.3 mm long. *Female inflorescences* shortly pedunculate, peduncles 0.5 - 1.0 x 0.6 - 0.7 mm, apical bracts slightly imbricate at the base. *Female flower* buds turbinate, receptacle slender, 1.7 x 0.8 mm, tepals deltoid, 0.7 x 0.5 mm, staminodes present, filaments 0.1 x 0.1 mm, anthers 0.2 x 0.3 mm, style short, broad, 0.2 x 0.3 mm, stigma 5 - lobed, lobes pointed, outspread, minutely papillate, nectary flat, shallowly 5 – lobed. *Fruits* sessile or shortly pedicellate, green turning

purple, oblong, ovoid, 5.5 - 8.0 x 2.5 - 3.5 mm, persistent perianth erect, exocarp thin, smooth, mesocarp short, membranous, randomly oriented, endocarp elongate - ovoid, 4.0 - 6.0 x 2.0 - 2.5 mm, 5 - grooved, splitting easily, internally 5 - chambered at the apex, incompletely so for the rest, central cavity narrow and deeply lobed.

Distribution: South Vietnam, Cambodia, Malay Peninsula, Borneo (**Fig. 54**).

Habitat: In exposed areas, ridge tops in montane and sub - montane forests. Parasitic on *Eugenia* (Myrtaceae).

Altitude: 1000 - 2500 m.

Vernacular name: Kayu Alah (Iban).

Notes: Name derived from the fact that this species is found in montane habitats. Characterised by rather small, fleshy, obscurely nerved, spathulate leaves. Similar to *Df. sphaerocarpa* but distinguished by its narrow, obovate to spathulate leaves, echinate pollen grains and an oblong or ovoid endocarp which is unilocular in the base.

Additional material examined

Vietnam: Poilane 22351 (P, Z), Nam Phan, Blao, Haut Donai; Poilane 27661 (P), Trung Phan, Hue, Nai Bach Ma station; Lecomte & Finet 1459 (P), Da Lat; Evrard 2204 (L, P), Da Lat, around road to Phenh; Hayata (P), Da Lat.

Cambodia: Poilane 14943 (P).

Malaysia: *Malay Peninsula*: Holttum 20729 (BO, SING), Gunong Tahan, Pahang; Holttum 11386 (A, BO, SING), Fraser Hill, Pahang; Whitmore 3274 (K, L), main northeast ridge of Gunong Benom, Pahang; Whitmore 3420 (L, SING), Gunong Benom; Barnes 10908 (K), Kluang Terbang; Chew 792 (A, SING), Cameron highlands, 4 29N 101 23E ; Burkill & Holttum 7812 (SING), Fraser Hill, Selangor border; Whitmore 12651 (L), Terengganu. *Sarawak*: Martin 38921 (L), Gunong Mulu National Park. *Sabah*: Chew et al 830 (CANB, K), Mt. Kinabalu; Shah & Ali 3015 (SING), Genting highlands; Clemens 29084 (B), Upper Kinabalu.

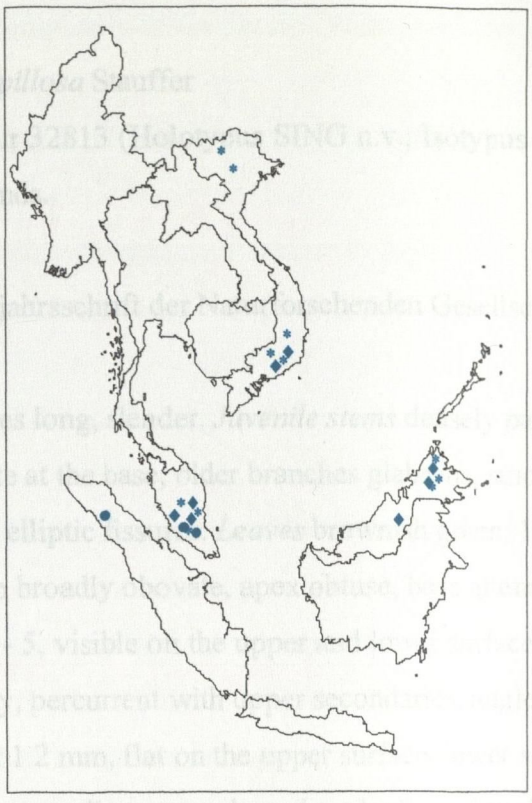


Fig. 54 Geographic distribution of: • *Dufrenoya papillosa*, ♦ *Dufrenoya oresitropha*, ▪ *Dufrenoya sphaerocarpa*

Brunei: Collett 21537 (K), south slopes of Mt. Kinabalu.

6. *Dufrenoya papillosa* Stauffer

Type: Mohd. Nur 32813 (Holotypus SING n.v.; Isotypus K!; L!), Malay Peninsula, Pahang, Cameron Highlands.

Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 114: 67 (1969).

Climber, branches long, slender. *Juvenile stems* densely papillose, twisted, twining, flattened, angular, bracteate at the base, older branches glabrous, smooth or wrinkled with long, closely - packed, shallow elliptic fissures. *Leaves* brownish green, 15.0 - 30.0 (8.0 - 20.0 x 2.0 - 7.0) mm, narrowly to broadly obovate, apex obtuse, base attenuate, upper surfaces weakly convex, primary veins 4 - 5, visible on the upper and lower surfaces, secondary veins moderately thick, diverging acutely, percurrent with upper secondaries, angle of convergence obtuse; petiole short, 1.5 - 2.0 x 1.2 mm, flat on the upper surface, lower surface angular. *Male inflorescences* papillose, profuse on all stems and on short leafless side shoots, on prominent, raised bract scars, solitary or up to 6 together, 6 - flowered, pedunculate, peduncles slender, 1.5 - 5.0 x 0.5 mm, subtended at the base and the apex by a single imbricate involucre of bracts, also arranged spirally along the length, bracts broadly elliptic, contracted at the base, acuminate at the apex, 0.8 - 1.0 x 0.6 - 0.7 mm, margins densely ciliate interspersed by a ferruginous tomentum. *Male flower* buds reddish green, globose, subsessile or shortly pedicellate, pedicel 0.3 x 0.3 mm, tepals 5 - 6, elongate - deltoid, weakly apiculate at the apex near the tip, 0.7 - 1.0 x 0.5 - 0.8 mm, glandular hairs present, filaments slender, 0.3 x 0.1 mm, dilated at the base, anthers 0.2 x 0.3 mm, dorsifixed, lobes isomerous or posterior slightly wider than the anterior, dehiscence longitudinal, incomplete at the base, nectary flat or shallowly concave, lobed, rugulate, apiculate in the centre. *Female flower* buds green, sub - globose, receptacle short, slender, 0.7 - 1.0 x 0.7 mm, tepals deltoid, 0.6 - 0.7 x 0.7 - 0.8 mm, weakly apiculate on the inner surface, staminodes present with the same dimensions as the male flower, style short, broad, 0.2 x 0.3 mm, stigma 5- lobed, lobes rounded, smooth, reflexed, slightly invaginated, nectary flat, angular. *Fruit* ovoid, oblong, 2.5 - 5.0 x 3.0 - 3.5 mm, persistent perianth erect, exocarp weakly papillose, mesocarp long, membranous, wrapping around the endocarp, endocarp 3.0 - 3.5 x

1.5 mm, oblong, shallowly 6 - 7 lobed, splitting easily, internally 6 - 7 chambered at the apex and the base, incompletely so for the rest, apical chambers prolonged.

Distribution: Malay Peninsula, Sumatra (**Fig. 54**).

Habitat: Restricted to mountainous regions in montane scrub, associated with *Lithocarpus* and *Quercus* (Fagaceae).

Altitude: 1400 - 2000 m.

Notes: Name derived from papillose tomentum on juvenile stems and inflorescences. Characterised by this feature and by prominent bract scars on older branches which occur because many seasons inflorescences arise repeatedly from the same point. Taxonomically close to *Df. oresitropha*, differentiated from this species by the papillose indumentum and obovate rather than spathulate leaves.

Additional material examined

Malaysia: *Malay Peninsula*: Abbe et al 9748 (A, L), Pahang, Mentigi Forest Reserve, 4 29 N 101 17E; Sleumer 4663 (L), Pahang, Cameron Highlands.

Indonesia: *Sumatra*: de Wilde & de Wilde-Duyfjes (L), northern Sumatra, Gunung Leuser reserve, Atjeh.

7. *Dufrenoya platyphylla* (Sprengel) Stauffer

Type: Wallich 488 (Holotypus of *Viscum heteranthum* K!; Isotypus P!; TCD!), India.

Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 114: 70 (1969); Grierson & Long, Flora of Bhutan 1.1: 143 (1983); *Viscum platyphyllum* Sprengel, Linnaeus Systema Vegetabilium XIV (1824), Curae Posteriores: 47 (1827); DC Prodromus 4: 279 (1830); *Viscum latifolium* Buch-Ham ex D. Don, Prodromus Flora Nepalensis: 142 (1825); *Viscum heteranthum* Wall ex DC, Prodromus 4: 279 (1830); *Henslowia hererantha* Hook.f. ex A.DC, Prodromus 14: 632 (1857); Kanjilal, Flora of Assam 4: 130 (1940); *Dufrenoya heterantha* Chatin, Comptes rendus Acadamie Paris 51: 657 (1860); *Hylomyza platyphylla*

Danser, Nova Guinea New Series 4: 145 (1940); *Dendrotrophe heterantha* Henry & Roy, Bulletin of the Botanical Survey of India 10: 274 (1969) **syn. nov.**

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, 40.0 - 75.0 (25.0 - 55.0 x 5.0 - 18.0) mm, elliptic, ovate, obovate, apex acute, obtuse, base obtuse, attenuate, upper surfaces shining, smooth, lower surfaces dull, primary veins 5 - 7, raised on the upper surface, secondary veins fine, arising at approximately right angles, opposite secondaries percurrent; petiole long, slender, angular, 8.0 - 10.0 x 1.5 mm. *Male inflorescences* profuse, singular or in groups of 3 - 4, on juvenile stems and on short shoots arising from the older stems, 6 - flowered, pedunculate, peduncles angular, 2.0 - 3.5 x 0.5 - 0.7 mm, 2 - 3 involucres of bracts at the base, a single quincuncially arranged involucre at the apex, bracts broadly ovate, minutely ciliate, 0.8 - 1.0 x 0.8 - 0.9 mm. *Male flower* buds globose, subsessile, yellowish green, tepals 5 - 6, lanceolate, 1.4 - 1.5 x 1.0 mm, weakly apiculate on the inner surface near the tip, glandular hairs present, filaments short, 0.2 - 0.3 x 0.1 - 0.2 mm, slightly dilated at the base, anthers basifixed, 0.2 - 0.3 x 0.4 - 0.5 mm, bithecate, lobes unequal in size, anterior shorter and broader than the posterior, dehiscence transverse, nectary 5- 6 lobed, flat, apiculate in the centre. *Female inflorescences* sessile or shortly pedunculate. *Female flowers* green, buds distinctly turbinate, tepals 5 - 6, elongate - ovate, apex acuminate, 1.0 x 0.6 mm, receptacle broad, 1.4 x 1.0 mm, staminodes present, filaments 0.2 x 0.2 mm, anthers 0.3 x 0.4 mm, style short, broad, 0.3 x 0.3 mm, stigma 3 - 5 lobed, lobes fleshy, weakly papillate. *Fruit* pale green ripening purple, 3.8 - 5.0 x 3.0 - 4.0 mm, globose or slightly obovoid, 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, apiculate at the base, distinctly 4 - 6 lobed, lobes rounded at the apex, internally 4 - 6 chambered at the apex and the base, incompletely so for the rest, basal chambers short.

Distribution: Southern India, Myanmar, northern Thailand (new record) (**Fig. 53**).

Habitat: In open areas in slightly disturbed evergreen forests. Parasitic on *Quercus*, *Castanopsis* (Fagaceae), *Dipterocarpus* (Dipterocarpaceae).

Altitude: 1500 - 2500 m.

Notes: 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 which may be functionally but are ontogenetically different to those found in species of *Dendromyza*. Taxonomically 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.

Additional material examined

India: Koelz 27552 (L), Assam, Hmuntha hills; Koelz 26626 A (L), Karong, Manipur; Koelz 27607 (L), Assam, Hmuntha hills; Long et al 939 (E), Sikkim, North district, north of Gangtok 27 24N, 88 36E; Stainton et al 5927 (Z), Nepal, Pasgam; Thakur Rup Chand 4462 (L), Assam, Hmuntha, Lushai hills; Gamble 27937 (K), Sikkim.

Myanmar: Haines 2017 (E), Tista valley; Dickinson 7303 (E), Yetagoni; Dickinson 7430 (L); Dickinson 7307 (L), Yetagoni; Dickinson 8573 (L), Kyautsit, Chaung, Chin hills; Kingdom Ward 21820 (BM, Z), Mindat, west central Myanmar.

Thailand: *Northern*: Maxwell 91/298 (GH), Doi Sutep, south side above Puping palace; Nankorn 91023 (AAU, BKF, GH), Chiang Mai, Doi Sutep. *North-Eastern*: Smitinand 2116 (GH, L), Loei, Phu Kradung.

8. *Dufrenoya poilanei* Stauffer

Type: Poilane 30716 (Holotypus P!; Isotypus Z!), Massif du Bi Doup, Haut Donai, Nam Phan.

Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 114: 68 (1969).

Climbing shrub, branches long, curving, occasionally pendulous. *Juvenile stems* 4 - 8 arising from a single node, angular, flattened, slightly striated, bracteate at the base, older branches

pustulate, bark rough, mottled with short generally elliptic raised, fissures. *Leaves* broadly spathulate to obovate, apex obtuse, mucronate, base attenuate, 32.0 - 36.0 (14.0 - 18.0 x 3.0 - 4.0) mm, upper surface weakly convex, margins undulate, involuted, primary veins 5 - 7, raised slightly on the upper surface, secondary veins indistinct; petiole long, 7.0 - 8.0 x 1.5 - 2.0 mm, flat on upper surface, lower surface angular. *Male inflorescences* 1 - 3 together on juvenile and mature shoots, 5 - 6 flowered, pedunculate, peduncles broad, angular, 1.5 - 2.0 x 1.3 mm with 3 involucres of alternating, valvate bracts at the base and a larger terminal, imbricate involucre, occasionally peduncle is entirely bracteate, bracts large in comparison to the rachis, papyraceus, broadly deltoid, outspread, shallowly involuted, 1.1 - 1.4 x 0.8 - 1.0 mm, margins torn, unevenly ciliate. *Male flowers* shortly pedicellate, pedicel 0.5 - 0.7 x 0.5 mm, decurrent with the receptacle, tepals 5, reflexed, 2.0 x 1.2 mm, narrowly ovate, apiculate on the inner surface near the tip, glandular hairs absent, filaments long, narrow, terete, 0.4 - 0.5 x 0.1 mm, anthers 0.5 x 0.8 mm, dorsifixed, lobes isomerous, dehiscence longitudinal, nectary flat, 5 - lobed, rugulate, style rudiment absent. *Female inflorescences* pedunculate, peduncles 2.0 - 3.0 x 0.7 - 0.8 mm, bracteate as in the male inflorescence. *Female flowers* yellow, tepals 5, broadly deltoid, fleshy, 0.7 x 1.0 mm, shortly apiculate on the inner surface, staminodes absent, stigma weakly papillate, sessile, fleshy, entire, occupying much of the centre of the flower, nectary flat, smooth, angular. *Fruit* greenish yellow, globose, ovoid, 3.0 - 4.0 x 2.5 - 3.2 mm, persistent perianth flattened, exocarp thick, smooth, mesocarp short, membranous, randomly oriented, endocarp obovoid, 2.0 - 2.5 x 2.0 mm, shortly apiculate at the apex, indistinctly 6 - lobed, splitting easily, internally 6 - chambered at the apex and the base, incompletely so for the rest.

Distribution: Southern China, Laos, Vietnam (**Fig. 55**).

Habitat: Mature montane forests. Parasitic on *Pasania* (Ericaceae) and *Castanopsis* (Fagaceae).

Altitude: 1500 - 2750 m.

Vernacular name: Tap dor, Etono (Southern Vietnam).

Notes: Name derived from the collector of the type specimen, Poilane who worked and collected extensively in Vietnam, Laos and Cambodia in the early part of the 20th century.

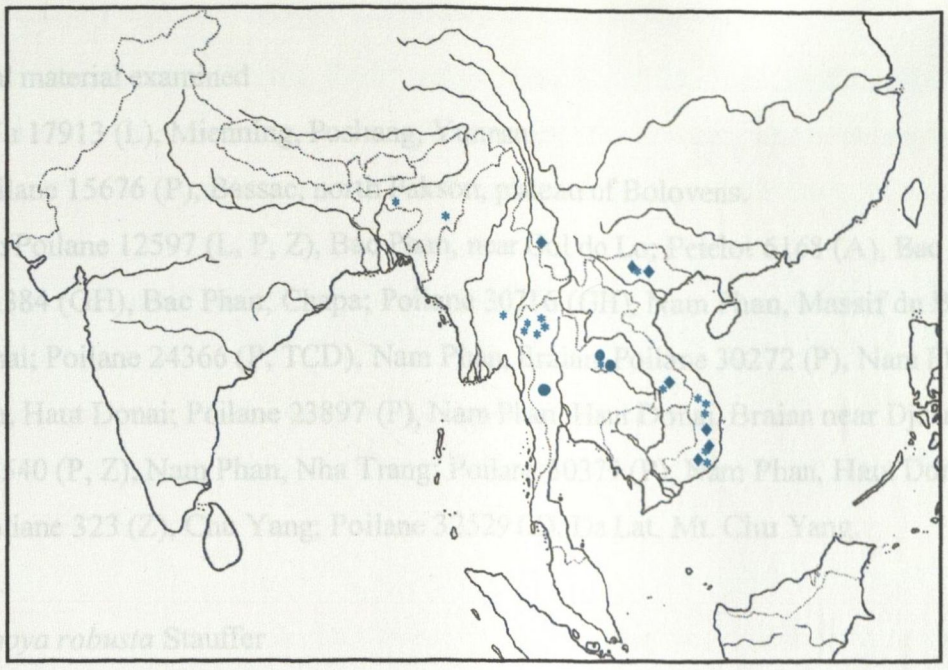


Fig. 55 Geographic distribution of: ♦ *Dufrenoya poilanei*, • *Dufrenoya robusta* ▪ *Dufrenoya sessilis*.

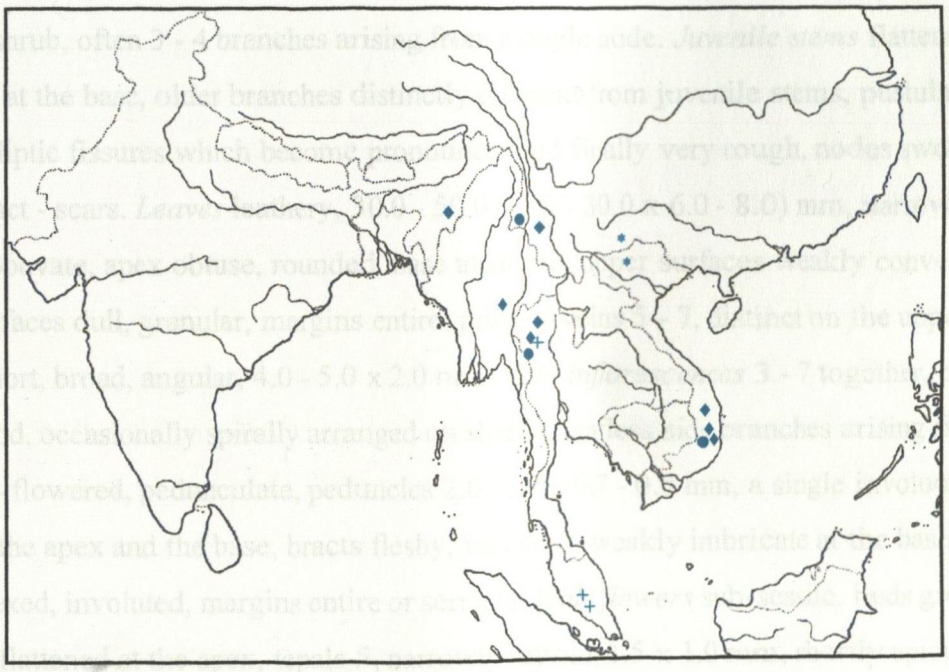


Fig. 56 Geographic distribution of: ♦ *Phacellaria compressa*, ▪ *Phacellaria fargesii*, + *Phacellaria malayana*, • *Phacellaria rigidula*.

Taxonomically close to *Df. robusta* and *Df. granulata*, differing from the former by mucronate leaves and distinguishable from the latter by pedunculate inflorescences.

Additional material examined

China: Yu 17913 (L), Mienning, Poshang, Yunnan.

Laos: Poilane 15676 (P), Bassac, north Pakson, plateau of Bolovens.

Vietnam: Poilane 12597 (L, P, Z), Bac Phan, near Col do Lo; Petelot 6168 (A), Bac Phan; Petelot 3.384 (GH), Bac Phan, Chapa; Poilane 30716 (GH), Nam Phan, Massif du Bi Doup, Haut Donai; Poilane 24366 (P, TCD), Nam Phan, Braian; Poilane 30272 (P), Nam Phan, north of Dankia, Haut Donai; Poilane 23897 (P), Nam Phan, Haut Donai, Braian near Djirung; Poilane 3540 (P, Z), Nam Phan, Nha Trang; Poilane 30379 (P), Nam Phan, Haut Donai, Bi Doup; Poliane 323 (Z), Chu Yang; Poilane 32529 (Z), Da Lat, Mt. Chu Yang.

9. *Dufrenoya robusta* Stauffer

Type: Kerr 10393 (Holotypus BM!; Isotypus K!; L!), Kao Ri Yai, Kanchanaburi, Thailand.

Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 114: 69 (1969).

Pendant shrub, often 3 - 4 branches arising from a single node. *Juvenile stems* flattened, striate, bracteate at the base, older branches distinctly different from juvenile stems, pustulate with raised, elliptic fissures which become pronounced and finally very rough, nodes swollen, with raised bract - scars. *Leaves* leathery, 30.0 - 50.0 (25.0 - 30.0 x 6.0 - 8.0) mm, narrowly - broadly obovate, apex obtuse, rounded, base attenuate, upper surfaces weakly convex, shining, lower surfaces dull, granular, margins entire, primary veins 5 - 7, distinct on the upper surface; petiole short, broad, angular, 4.0 - 5.0 x 2.0 mm. *Male inflorescences* 3 - 7 together, confined to older wood, occasionally spirally arranged on shorter, leafless side branches arising from older stems, 6 - flowered, pedunculate, peduncles 2.0 - 3.0 x 0.7 - 0.8 mm, a single involucre of bracts at the apex and the base, bracts fleshy, valvate or weakly imbricate at the base, 0.7 x 0.7 mm, reflexed, involuted, margins entire or serrated. *Male flowers* sub-sessile, buds green, globose, flattened at the apex, tepals 5, narrowly deltoid, 1.5 x 1.0 mm, shortly apiculate at the tip on the inner surface, glandular hairs absent, filaments long, narrow 0.5 x 0.2 mm, anthers large, dorsifixed, 0.5 x 0.5 mm, lobes isomerous dehiscence longitudinal, nectary 5 - lobed,

convex, warty, apiculate in the centre. *Female inflorescences* (never before described) fewer together and usually shorter pedunculate, peduncle 0.3 - 0.5 x 0.8 mm. *Female flower* buds turbinate, tepals 5, narrowly deltoid, ovate, apiculate on inner surface at the tip, 1.0 x 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.

Distribution: Northern Thailand, Myanmar (**Fig. 55**).

Habitat: Hill evergreen forest. Parasitic on *Quercus* (Fagaceae).

Altitude: 1000 - 1500 m.

Notes: 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 Burma. 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. In terms of floral morphology differing from other species of *Dufrenoya* found in Thailand with regard to its longitudinally dehiscing anthers and entire stigma. It has a greater affinity with *Df. poilanei* and *Df. granulata* but it can be distinguished from both of these species by the smooth young shoots and fleshy inflorescence bracts.

Additional material examined

Myanmar: Kurz 381 (K).

Thailand: *North-Eastern*: Koyama et al 31633 (A, BKF), Phu Luang; Niyomdham & Vidal 446 (AAU, BFK, P), Loei, Phu Luang; Smitinand 70389 (BKF), Loei, Phu Luang; Ogawa 21651 (KYO), Hoet That, Muong Khu.

10. *Dufrenoya sessilis* (Craib) Stauffer

Type: Kerr 1768 (Holotypus *Henslowia sessilis* K!; Isotypus BM!; TCD!), Thailand, Doi Sutep.

Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 114: 69 (1969); *Henslowia heterantha* var. *sessiliflora* Hook.f., Flora of British India 5: 233 (1886) — Type Hook.f. (Holotypus K!), India; *Henslowia sessilis* Craib, Kew Bulletin: 455 (1911); *Henslowia shanensis* Gamble, Kew Bulletin: 48 (1913) — Type: Robertson 295 (Holotypus K!), Southern Shan States.

Erect or pendulous shrub, branches twining, much interwoven. *Juvenile stems* slightly flattened and nodes keeled, older branches with shallow elliptic, vertical fissures, pale in colour. *Leaves* 35.0 - 85.0 (28.0 - 50.0 x 8.0 - 15.0) mm, elliptic to broadly obovate, apex obtuse, rounded, base attenuate, primary veins 5 - 9, raised on the upper surface only, 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 flat on upper surface, lower surface angular, 5.0 - 7.0 x 1.0 -1.5 mm. *Male inflorescences* confined to juvenile wood, singular or 2 - 3 together on shorter side branches, 6 - flowered, pedunculate, peduncles 1.5 - 2.0 x 0.5 - 0.6 mm, bracteate, 2 involucres of imbricate bracts at the base and 1 at the apex, bracts fleshy, broadly ovate 0.7 – 1.0 x 0.6 - 0.8 mm, margins ciliate. *Male flowers* buds yellowish green, globose, subsessile, shortly pedicellate, pedicel 0.6 x 0.6 mm, tepals 4 - 5, elongate - deltoid, fleshy, 1.0 - 1.2 x 0.6 mm, glandular hairs present, stamens subsessile, filaments 0.2 - 0.3 x 0.2 mm, dilate at the base, anthers dorsifixed, lobes unequal in size, posterior much larger than the anterior, dehiscence transverse, nectary flat, 4 - 5 lobed, fleshy, apiculate in the centre. *Female inflorescences* sessile or pedunculate, peduncles 0.2 - 1.0 x 0.8 mm. *Female flowers* yellowish, buds obconical, tepals 5 - 6, deltoid, thick, 1.0 x 1.0 mm, apiculate on the inner surface at the tip, staminodes present, quite large, filaments 0.2 x 0.1 mm, anthers 0.2 x 0.4 mm, style short, angular 0.3 x 0.3 mm, stigma 5 - lobed, lobes reflexed, smooth, nectary slightly concave, 5 - 6 lobed. *Fruit* yellowish green, oblong or ovoid, 4.5 x 3.5 - 4.0 mm, persistent perianth erect, exocarp quite thick, smooth, mesocarp long, membranous, wrapping around the endocarp, endocarp ovoid, 2.5 x 1.0 mm,

splitting easily, shallowly grooved, internally 5 - 6 chambered at the apex and the base, incompletely so for the rest.

Distribution: Northern Thailand, Laos, Vietnam (**Fig. 55**).

Habitat: At high elevations in hill evergreen and open grassy forests with *Quercus* and *Castanopsis*. Parasitic on *Lithocarpus, Quercus, Castanopsis* (Fagaceae), *Englehardtia* (Juglandaceae).

Altitude: 1500 – 2500 m.

Vernacular name: Kaa fak, Mai teen nok (Thailand) (mistletoe, sticking to the feet of birds).

Uses: Ingested to prevent food poisoning.

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

Additional material examined

India: Thakur Rup Chand 2771 (L), Assam, near Nokrek, Garo hills; Watt 6041 (E), Manipur, Myang Khong.

Laos: Poilane 26319 (L, P), between Nam Ma Oun and Nam Long, Haut Mekhong province; Poilane 20376 (P, Z).

Vietnam: Tsang 30272 (A, E, K), Sai Wong Mo Shan, Bac Phan; Averyanov et al 157 (P), Kontum, northwest slopes of Ngoc Linh; Chevalier 1053 (P), Tran; Poilane 7994 (P), Trung Phan, near Da Nang; Poilane 13411 (P), Trung Phan; Poilane 29068 (P), Trung Phan, Da Nang; Poliane 30928 (P); Poliane 32822 (P), Nam Phan, Nui Dai Ding near Dak; Poliane 32149 (P), Nam Phan, north of Kontum on summit of Ngoe Pong; Poliane 32567 (P), near Da Lat; Chevalier 20403 (P), Nam Phan, near Thu Dau Mot.

Thailand: *Northern*: Kerr 3240 (BM, K), Chiang Mai, Doi Sutep; Kerr 1768 (K), Chiang Mai, Doi Sutep; Larsen & Hansen 892 (BKF), Chiang Mai, Doi Sutep; Maxwell 92/249 (GH), Chiang Mai, Doi Sutep; Niyomdham & Kubat 1351 (AAU, BKF, E), Chiang Mai, Doi Sutep; Santisuk 1049 (BKF), Chiang Mai, Mae Taeng; Sorensen et al 6615 (A, Z), Chiang Mai, Doi Sutep; Bunchuai & Nimanong 1407 (BKF, L), Chiang Rai, Mae Suai; Sukkri 13 (BKF), Chiang Mai, Doi Sutep; Smitinand 8717 (K), north Chiang Mai, Pangboh hill; Nooteboom 670 (BKF), Chiang Mai, Doi Pui, 19 N 98 30 E; Phengklai & Koyama 39106 (A), Lampang, Doi Khun Tan, Mae Tha district; Larsen & Santisuk 2867 (BKF, E), Chiang Mai, Northern Pong Pho, near Doi Chiang Dao; *North-Eastern*: Kerr 20059 (BM), Loei, Phu Kradung; Smitinand 2105 (BKF), Loei, Phu Kradung; Smitinand 2533 (BKF, BK), Loei, Phu Kradung; Sorensen et al 6272 (E, SING), Loei, Phu Kradung; Smitinand 2205 (BKF), Loei, Phu Kradung; Abbe & Smitinand 9429 (A, BKF, L), Loei, Phu Kradung, 6 55N 101 47E.

11. *Dufrenoya sphaerocarpa* (Danser) Stauffer

Type: Clemens 31093 (Holotypus B!; Isotypus K!; Z!), Penibukan, Mt. Kinabalu, Borneo.

Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 114: 66 (1969); *Hylomyza sphaerocarpa* Danser, Nova Guinea New Series 4: 142 (1940); *Dufrenoya pruinosa* Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 114: 67 (1969) — Type: Poilane 32125 (Holotypus P!, Isotypus TCD!, Z!), **syn. nov.**

Shrub, with some pendulous branches, often 3 – 4 from a single node. *Juvenile stems* smooth, angular contracted and bracteate at the base, older stems with broad elliptic fissures. *Leaves* yellowish green, thin, 35.0 - 45.0 (18.0 – 28.0 x 5.0 - 7.0) mm, obovate to broadly spathulate, apex apiculate becoming obtuse, base attenuate, margins crisp, weakly undulate, primary veins 5, raised on the upper and lower surfaces, secondary veins indistinct or very fine, arising at acute angles, joining with supra - secondaries and percurrent with opposite secondaries; petiole 4.0 – 6.0 x 1.5 mm, flat on upper surface, lower surface angular. *Male inflorescences* confined to juvenile branches, singular or 3 - 4 together, 6 - flowered, pedunculate, peduncles slender, angular, 1.0 - 4.0 x 0.5 mm, subtended at the base and the apex by a single involucre of quincuncially arranged bracts, also sparsely bracteate along its length, bracts 0.5 x 0.5 mm, reflexed, broadly ovate, invaginated, margins minutely ciliate. *Male flower* buds globose,

pedicellate, pedicel 1.5 mm long, broad, angular, decurrent with the receptacle, tepals 5, narrowly deltoid, shortly apiculate on the inner surface at the apex, 1.3 x 0.7 mm, glandular hairs present, filaments short, broad, 0.1 – 0.2 x 0.1 – 0.2 mm, anthers basifixed, 0.2 x 0.4 mm, lobes unequal in size, posterior longer than the anterior, dehiscence transverse, nectary flat or weakly concave, 5 - lobed, apiculate in the centre. *Female inflorescences* shortly pedunculate, peduncle 1.0 - 1.2 x 0.5 – 0.6 mm. *Female flower* buds obconical, tepals narrowly deltoid, 0.5 - 0.6 x 0.4 mm, fleshy, apiculate on the inner surface at the apex, staminodes present, filaments narrow 0.2 x 0.1 mm, anthers 0.1 x 0.3 mm, locules parallel, style short, broad, 0.2 x 0.3 mm, stigma 4 - 5 lobed, lobes long slender, smooth, reflexed, nectary distinctly 5 – lobed. *Fruit* sessile, globose, 2.0 - 3.0 x 1.5 - 2.5 mm, persistent perianth erect, mesocarp short, membranous, randomly oriented, endocarp sub - globose 2.5 x 2.0 mm, apiculate at the apex, distinctly 5 - lobed, splitting easily, internally 5 - chambered at the apex and the base, apical chambers prolonged.

Distribution: Vietnam, Malay Peninsula, Sumatra, northern Borneo (**Fig. 54**).

Habitat: A variety of habitats from juvenile forest and heath woodland to upper montane forest and montane oak forest. Parasitic on a variety of species, *Eugenia* (Myrtaceae), *Eubucklandia* (Hamamelidaceae) and *Loranthus* (Loranthaceae).

Altitude: 700 - 2000 m.

Vernacular name: Tap Joo (South Vietnam).

Notes: Name derived from the spherical endocarp of the fruit. Characterised by this feature, the reflexed bracts of the male inflorescence and the pedicellate male flowers. Taxonomically close to *Df. oresitropha* but distinguishable by larger leaves with distinct venation, spherical fruits and an endocarp with basal locules. *Df. pruinosa* was proposed as a separate species based on the glaucous appearance of the male flowers in the type specimen. However, this is not a reliable feature as it is present within many species of *Dufrenoya*.

Additional material examined

Vietnam: Poilane 6170 (A), Bac Phan, Hung Hoa, road to Santay; Poilane 6180 (A), Bac Phan, Fan Si Pan; Poilane 21767 (L, P, TCD), Nam Phan, Haut Donai, Blao; Poilane 21783 (P), Nam Phan, Blao, Haut Donai; Poilane 29404 (P), Nam Phan, Guang Nam; Poilane 30872 (P, SING, TCD), Nam Phan, Bi Doup near Haut Donai.

Malaysia: *Malay Penninsula*: Purseglove 4920 (SING), Telok Assam, Bako National Park; Henderson 23578 (BM), Cameron highlands, Pahang; Whitmore 12651 (K), Trengganu; *Sabah*: Clemens 31117 (A, B, SING), Penibukan; Clemens 40831 (A, B), Penibukan, Kinabalu; Clemens 30857 (B), Penibukan, Kinabalu; Carr 27556 (SING), below Kamborangah, Kinabalu; Carr 27847 (SING), above Thamis, Kinabalu; Carr 26574 (SING), Kinataki river, Kinabalu; Hallier 373 (P), Soengei Kenepri; Smith & Rant 493 (BO).

Indonesia: *Sumatra*: van Steenis 6440 (BO).

4. *Phacellaria* (Bentham)

Type species: *Phacellaria rigidula* Bentham, Genera Plantarum 3: 229 (1883) — Type: Griffith 2745 (Holotypus K!).

Bentham, Genera Plantarum 3: 229 (1883); Hook.f., Flora of India 5: 235 (1886); Pilger in Engler & Harms, Die Natürliche Pflanzenfamilien 16b: 71 (1935); Danser, Blumea 3: 212 (1939); Danser, Nova Guinea New Series 4: 145 (1940).

Erect shrubs, with some endophytic growth, stems originating in bundles from the branches of the host plant through lenticels, seldom branching, never climbing, glabrous or with a hirsute indument, juvenile stems always at least papillose; secondary haustoria absent. *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 involucres of bracts, bracts persistent or withering. *Male flower* buds globose, receptacle flat, tepals 4 – 6, valvate, glandular hairs absent, anthers 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 x 0.3 – 0.4 mm, placenta sessile, convex, 4 - 6 lobed, lobes

short. *Fruit* green, oblong, ovoid, perianth persistent, erect; exocarp thin, smooth, mesocarp consisting of long or short membranous, sericeus strands which are attached to the endocarp and wrap around it, finally lying against the inner surface of the exocarp; endocarp splitting easily, ovoid, oblong or obovoid, apex obtuse or acuminate, base rounded; internally 5 - 7 chambered at the apex, 5 – 7 lobed for the rest (**Fig. 15**). Seed with separate lobes at the apex. Embryo located near the apex of the endocarp between the apical lobes.

Number of species: 4

Distribution: Southern China to the Malay Peninsula.

Habitat: In hill evergreen forest, ridge forest and open forest of *Pinus khasya* and *Dipterocarpus tuberculatus*. Hyperparasite on species of *Scurrula*, *Macrosolen*, *Taxillus* and *Loranthus* (Loranthaceae); *Viscum* (Viscaceae); *Dufrenoya* (Santalaceae).

Altitude: above 1000 m.

Notes: Name refers to the fasciculate nature of the stems and possibly to the origination 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, that is they are parasitic on other parasitic plants. *Phacellaria* is the only genus in the family where endophytic growth has been observed, and it follows closely the distribution of *Dufrenoya* but with a more contracted geographic range. The fruits are dispersed in a similar manner to *Dufrenoya*. The genera occupy similar habitats and parallel evolution may have resulted in the similar fruit types of the two genera, which in other respects are very different.

Key to *Phacellaria*

1. Inflorescence subtended by 2 axillary bracts.....**2.** *P. fargesii*
   Inflorescence subtended by an involucre of bracts.....(2)

2. Inflorescence 5 – 6 flowered, bracts withering.....**4.** *P. rigidula*
   Inflorescence 1 – flowered, bracts not withering.....(3)

3. Flowers sunken, dioecious; stigma lobed; endocarp distinctly lobed.....**1.** *P.compressa*
   Flowers not sunken, inflorescences monoecious; stigma capitate; endocarp with dark, longitudinal grooves.....**3.** *P. malayana*

1. *Phacellaria compressa* Bentham

Type: Parish s.n. (Holotypus K!), China, Yunnan, Tali range.

Bentham, Genera Plantarum 3: 229 (1883); Hook.f., Flora of British India 5: 235 (1886); Hieronymus, Die Natürliche Pflanzenfamilien 3: 216 (1889); Collett & Hemsley, Journal of the Linnean Society 28: 122 (1890); Boerlage, Flora van Nederlandsch Indie: 181 (1900); Brandis, Indian Trees: 554 (1906); Pilger in Engler and Harms, Die Natürliche Pflanzenfamilien 16b: 71 (1935); Danser, Blumea 3: 227 (1939); Wu & Tao, Flora Yunnanica 4: 288 (1986); Hô, Câyco Vietnam 2.1: 152 (1992); *Phacellaria wattii* Hook.f., Flora of British India 5: 236 (1886) — Type: Watt 6154 (Holotypus K!), India; *Phacellaria ferruginea* W. W. Smith, Notes of the Botanical Garden of Edinburgh, 10: 49 - 50 (1918) — Type: Forrest 11585 (Isotypus K!), China Tali range; *Phacellaria caulescens* Collett & Hemsley, Journal of the Linnean Society 28: 122 t. 17 (1890) **syn. nov.** — Type: Collett 736 (Holotypus K!), Shan hills, Burma; *Phacellaria tonkinensis* Lecomte, Bulletin Muséum Histoire Naturelle Paris 20: 399 (1914) **syn. nov.** — Type: Balansa (Holotypus P!), Annam, Dalat; Lecomte, Flore Générale de l'Indo-Chine 5: 213 (1915); Wu & Tao, Flora Yunnanica 4: 287 (1986); Hô, Câyco Vietnam 2.1: 153 (1992); Tam, Flora Reipublicae Popularis Sinicae: 69 (1988); *Phacellaria glomerata* Wu & Tao, Flora Yunnanica 4: 288 (1986) **syn. nov.** — Type: Li 2653 (Holotypus KUN!) Yunnan.

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 diameter, thickening to 2.0 – 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 covered in the same tomentum as the stems, later becoming papillose, tepals light green, 4 - 5, deltoid, 0.7 - 1.0 x 0.7 - 1.0 mm, slightly contracted at the base, tips slightly inflexed and shortly apiculate on the inner surface, stamens 4 - 5, filaments long, dilated at the base, 0.3 x 0.1mm, anthers cream, dorsifixed, 0.2 x 0.5 mm, nectary, green, fragrant, flat, style rudiment 0.5 mm long, slender. *Female flowers* sessile, buds turbinate, tepals green, 4 - 5, 0.4 x 0.6 mm, deltoid, thick, apiculate on the inner surface at the tip, externally papillose, receptacle 0.5 x 0.5 mm, staminodes absent or occasionally 1 - 2, stigma subsessile, 4 - lobed, lobes rounded, nectary flat, angular, unlobed. *Fruit* oblong, 5.0 - 6.0 x 3.0 mm, exocarp smooth, thick, mesocarp short, sericeus, abundant at the apex of the endocarp extending 0.5 mm beyond it, endocarp oblong or slightly ovoid, 4.0 x 2.5 mm, distinctly 4 - 6 lobed, apiculate at the base.

Distribution: Southern China, southern India, Myanmar, Thailand, Vietnam (**Fig. 56**).

Habitat: Primary evergreen, mixed evergreen forest. Hyperparasite on *Viscum* (Viscaceae) *Loranthus*; *Macrosolen* (Loranthaceae) and *Dufrenoya* (Santalaceae).

Altitude: 800 – 1200 m

Notes: 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 sericeus rather than membranous mesocarp.

Additional material examined

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

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

Burma: Robertson 2110 (K), Taunggi crags, Southern Shan States; Collett 331 (K), Shan hills.

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

Thailand: *Northern*: Santisuk 10603 (BKF), northern Chiang Mai, Doi Saket; Kerr 5796 (BM, L), Dan Sai, Kao Keo; Maxwell 91-242 (GH), Chiang Mai, Mae Soi ridge.

2. ***Phacellaria fargesii*** Lecomte

Type: Farges 1511 (Holotypus P!; Isotypus L!), Southern China, Tchen-Keou-Tin.

Lecomte, Bulletin Muséum Histoire Naturelle Paris 20: 401 (1914); Pilger in Engler & Harms, Die Natürliche Pflanzenfamilien 16b: 71 (1935); Danser, Blumea 3: 218 (1939).

Branches tortuous, seldom branching, covered in a villous, ferruginous tomentum. *Juvenile stems* 1.0 mm in diameter, thickening at the base to approximately 2.5 mm on maturity. Plants dioecious. *Inflorescences* crowded at the tips of the branches and arranged spirally along stems, singular, 1 - flowered, subtended by one large, deltoid and two smaller axillary ovate bracts, outer bract. 1.0 x 1.0 mm, outer surface with the same indument as the other plant parts, axillary bracts 2, 0.7 x 0.6 mm, persistent, fleshy, papillose on the outer surface, margins sparsely ciliate. *Male* plant unknown. *Female flowers* green, obconical in bud, receptacle short, broad, 1.0 x 1.0 mm, tepals 4 - 5, deltoid, elongate-deltoid, fleshy, 0.7 x 0.6 mm, tips curved in towards the centre of the flower, staminodes present, filaments long slender, 0.3 x 0.2 mm, anthers minute, rounded, 0.2 x 0.2 mm, style short, terete, 0.2 x 0.2 mm, stigma 4 - 5 lobed, lobes short, pointed, out-spread, nectary smooth, fleshy, flat or weakly concave, unlobed, 4 - 5 angled. *Fruit* green, ovoid, 5.5 x 3.5 mm, exocarp smooth, thin, mesocarp short, membranous, endocarp ovate, 4.5 x 2.5 mm, thin with 5 shallow longitudinal grooves, obscured by the

mesocarp.

Distribution: Southern China, Vietnam (**Fig. 56**).

Habitat: Parasitic on *Taxillus* and *Loranthus* (Loranthaceae).

Altitude: 1400 m.

Notes: Name derived from the collector of the type specimen, Farges. Restricted to southern China and northern Vietnam. Characterised by slender juvenile branches, the two axillary inflorescence bracts and staminodes in the female flower. Taxonomically close to *P. rigidula*, differentiated by 1 – flowered inflorescences and persistent bracts.

Additional material examined

China: Farges 1511 (P), Southern China, Tchen-Keou-Tin.

Vietnam: Petelot 171 (BO), Bac Phan, Chapa.

3. *Phacellaria malayana* Ridley

Type: Robinson s.n. (Holotypus K!), Selangor, at 5000ft.

Ridley, Journal of the Asiatic Society of Bengal 82: 193 (1920); Flora of the Malay Penninsula 3: 170 (1924); Danser, Blumea 3: 222 (1939).

Branches tortuous, erect, stems flattened. *Juvenile stems* 1.5 mm in diameter, ridged, covered in a sparse ferruginous, villous, matted indument, not thickening considerably with age, very seldom branching. Plants dioecious or a few male flowers on the female plant. *Inflorescences* concentrated near the tips of the branches, separating and arranged spirally along the ridges of the branches, singular or 2 - 3 together, 1 - flowered, sessile but not sunken into the stem, surrounded at the base by an involucre of 5 bracts, bracts ovate, fleshy, 0.4 x 0.4 mm, margins ciliate. *Male flowers* greenish yellow, globose, receptacle short, tepals 1.1 x 0.8 mm, elongate-deltoid, shortly apiculate on the inner surface at the apex, outer surface weakly papillose, reflexed half way to form a pseudo-hypanthium, filaments long, slender, dilated at the base, 0.5

x 0.2 mm, anthers dorsifixed, 0.2 x 0.5 mm, nectary 5 - lobed, flat, style rudiment slender, long. *Female flower* buds greenish yellow, globose, becoming oblong, sessile, receptacle long, broad, 1.0 x 1.2 mm, tepals deltoid 0.6 x 0.6 mm, staminodes absent, style short, broad, 0.2 x 0.2 mm, stigma capitate, unlobed, faintly papillose, nectary flat or convex, 5 – angled. *Fruit* red, oblong, 5.5 - 6.0 x 2.0 - 3.0 mm, exocarp thick, granular, mesocarp short, sericeus, extending 1.5 mm beyond the apex of the endocarp, wavy in this region, endocarp oblong, ovoid, 5.0 x 1.2 mm, thin, with 5 - 6, distinct, dark coloured, longitudinal grooves.

Distribution: Malay Peninsula, Thailand (new record) (**Fig. 56**).

Habitat: In ridge forest and open forest of *Pinus khasya* and *Dipterocarpus tuberculatus*. Hyperparasite on species of *Macrosolen* (Loranthaceae).

Altitude: 1200 - 1500 m.

Notes: Name derived from the geographic location of the type specimen. Characterised by 1 – flowered male inflorescences, a capitate stigma in the female flower and a long, sericeus mesocarp. Taxonomically similar to *P. compressa*, but differentiated by sessile but not sunken male flowers which are subtended by a single involucre of bracts.

Additional material examined

Thailand: *North-Eastern*: van Beusekom & Phengklai 1185 (L), Ob Luang table land along road from Bo Luang to Om Koi.

Malaysia: *Malay Peninsula*: Henderson 23444 (BO, SING), Pahang, Cameron highlands; van Steenis 18530 (L), Selangor, Fraser Hill.

4. *Phacellaria rigidula* Bentham

Type: Griffith 2745 (Holotypus K!).

Bentham, Genera Plantarum 3: 229 (1883); Hook.f., Flora of British India 5: 235 (1886); Hieronymus, Die Natürliche Pflanzenfamilien 3.1: 216 (1889); Boerlage, Flora van Nederlandsch Indie: 181 (1900); Brandis, Indian Trees: 554 (1906); Pilger in Engler & Harms,

Die Natürliche Pflanzenfamilien 16b: 71 (1935); Wu & Tao, Flora Yunnanica 4: 288 (1986); Tam, Flora Reipublicae Popularis Sinicae: 69 (1988); *Phacellaria gracilis* Danser, Blumea 3: 225 (1939) **syn. nov.** — Type: Poilane 25403 (Holotypus P! Isotypus L!), Nam Phan; Hô, Câyco Vietnam 2.1: 153 (1992).

Branches terete, slender, tortuous, not at all branching, faintly striate and ridged. *Juvenile stems* entirely papillose or weakly hirsute, less than 1 mm in diameter, thickening to 1.5 – 2.0 mm, glabrous. *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 in shape. *Male flowers* green, tepals 5 - 6, glabrous, elongate - deltoid, 1.0 x 0.5 mm, filaments 0.2 x 0.1 mm, dilated at the base, anthers 0.3 x 0.4 mm with the same structure as *P .compressa*, nectary 5 - lobed, slightly angular, apiculate in the centre. *Female flower* buds turbinate, tepals 5, deltoid, 0.5 x 0.5 mm, glabrous, inflexed at the tips and shortly apiculate on the inner surface, receptacle narrow, elongate, 0.8 x 0.5 mm, staminodes absent, stigma subsessile 4 - lobed, lobes rounded weakly papillose, nectary flat, 5 - lobed, lobes rounded. *Fruit* yellowish, 6.0 - 7.0 x 3.5 – 4.0 mm, oblong, ovoid, exocarp smooth, thick, mesocarp long, silky, membranous, endocarp smooth oblong, ovoid, 5 - 6 lobed.

Distribution: Southern China, Thailand (new record) (**Fig. 56**).

Habitat: Secondary and dry Dipterocarp forest. Parasitic on *Loranthus* and *Scurrula* (Loranthaceae).

Altitude: 500 - 2500 m.

Notes: 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.

Additional material examined

China: Bartholomew et al 207 (E), Yangbajain, west side of Diancang, Shan montain range, 25 43N 100 02E; Henry 11085 (K),Yunnan.

Thailand: *Northern*: Beusekom & Phengklai 2546 (AAU, BKF, E, KYO, L), Chiang Mai, Bo Luang, road to Omkoi.

2. Santaleae A.DC.

Type genus: *Santalum* L. Species Plantarum 1: 349 (1753).

A.DC., Prodromus 14: 624 (1857); Hewson & George, Flora of Australia 22: 60 (1984); Osyrideae Reichenbach, Conspectus regni Vegetabilis: 80 (1828); Bentham, Genera Plantarum 3: 222 (1883); Pilger in Engler & Harms, Die Natürliche Pflanzenfamilien 16b: 69 (1935); Buckleyeae Torr., American Journal of Science 45: 170 (1843); A.DC., Prodromus 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, anther locules isomerous, occasionally unequal in size, pollen 19 –24 μm in length, prolate, exine surface ornamentation rugulate, perforate, verrucate, 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, lobes long, slender, contorted, placenta long or short, placental column contorted or straight. *Fruit* a drupe, exocarp thin, perianth persistent or caducous, mesocarp fleshy, thin, endocarp hard, smooth or rugulate, seed entire.

Notes: Distribution cosmopolitan but generally Southern hemisphere, containing mainly shrubby and tree species. Several monotypic genera in South America. Variable in terms of ovary construction. Pollen and fruit construction varying at generic level only.

5. *Osyris* L.

Type species: *Osyris alba* L., Systema Naturae (1735) — Type Linneaus (Holotypus BM).

L., Systema Naturae: 1101 (1735); Species Plantarum 2: 1022 (1753); Systema Vegetabilium 14: 881 (1774); A.DC., Prodromus 14: 632 (1857); Hook.f., Flora of British India 5: 232 (1886); Trimen, Handbook to the Flora of Ceylon 3: 474 (1895); Cooke, Flora of Bombay 2: 555 (1906); Bentham, Genera Plantarum 3: 227 (1883); Stauffer, Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 106: 388 –399 (1961); Grierson & Long, Flora of Bhutan 1.1: 142 (1983).

Glabrous terrestrial shrubs, branches pendulous, bark smooth or faintly striate. *Leaves* large, rounded or elliptic, fleshy, glaucous, venation curvipinnate (**Fig. 39**), 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, receptacle flat, anthers bilocular, locule bilobed, lobes unequal in size, posterior smaller than the anterior, glandular hairs present, nectary flat, lobed, apiculate in the centre. *Female inflorescences* 1 - flowered, pedunculate as before, peduncle slightly shorter than the male. *Female flowers* pedicellate, receptacle enlarged and elongated, staminodes present, style short, stigma 3 – lobed; *ovary* inferior, 0.3 x 0.3 mm, sub - sessile, placenta shallowly convex, 3 - lobed, lobes rounded short, curling under the placenta, placental column short, broad. *Fruit* red, black, globose, perianth caducous, leaving a faint scar; exocarp thin, smooth; mesocarp thin, fleshy; endocarp hard, thin, completely smooth, globose, slightly obovate, internally unilocular. Seed fleshy, entire; embryo located at the centre of the endocarp.
Number of species: 1 (2 worldwide).

Distribution: Southern Europe, Africa, India, Myanmar, northern Thailand, Vietnam.

Habitat: In disturbed and exposed, dry areas on limestone. Associated with bamboo in Thailand.

Altitude: above 1000 m.

Notes: Name derived from the goddess Osiris. Southeast Asia is the most southerly extent of the geographic range of this genus which is most common in Africa. It is characterised by shrubby growth and 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. & Steudel

Type: Schimper s.n. 1832 (Holotypus *Osyris lanceolata* K!), Portugal, Algarve.

A.DC., Prodromus 14: 633 (1857); Grierson & Long, Flora of Bhutan 1.1: 142 (1983); Hô, Câyco Vietnam 2.1: 154 (1992); *Osyris arborea* Wallich, Catalogue 4035 (1831); Hook.f., Flora of British India 5: 232 (1886); Trimen, Handbook to the Flora of Ceylon 3: 474 (1895); Cooke, Flora of Bombay 2: 555 (1906); Collett, Simla Flora: 441 (1902); Burkill, Botanical Survey of India 4: 129 (1910); Lecomte, Flora Générale de l'Indo-Chine 5: 215 (1915); Kanjilal, Flora of Assam 4: 130 (1940); *Osyris arborea* var. *tipitata* — Lecomte, Bulletin du Muséum Histoire Naturelle Paris 10: 404 (1914) **syn. nov.** — Type: Wilson 4443 (Holotypus P!); *Osyris nepalensis* Griffith, Notulae 4: 376; *Osyris wightiana* Wallich, Catalogue 4036 (1831); Wallich ex Wight, Icone Plantae Indica Orientale 5: 17 (1852) — Type: Wight 5 (Holotypus K!), India, Madras; Botanical Survey of India 16: 269 (1953); Baehni, Candollea 16: 215 (1958); Hara, Flora of the Eastern Himalayas 2: 20 (1971); Wu & Tao, Flora Yunnanica 4: 293 (1986); Philcox in M.D. Dassanayake & W.D. Clayton eds., Revised Handbook to the Flora of Ceylon 13: 199 (1999); *Osyris quadrifida* Bentham, Genera Plantarum 3: 227 (1883) — Type: Gay s.n. (Holotypus K!); *Osyris arborea* var. *rotundifolia* Tam, Bulletin of the Botanical Reservation of the North East Forest Institute 1.3: 71 (1981) **syn. nov.** — Type: Pan 60 – 1145 (Holotypus SZ n.v.); Tam, Flora Reipublicae Popularis Sinicae: 24: 64 (1988).

Shrub with pendulous branches, 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*

fleshy, elliptic, lanceolate, 22.0 - 44 .0 (11.0 - 28.0 x 7.0 - 12.0) 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 6.0 – 10.0 x 0.5 mm, angular, unevenly dilated at the apex, usually 8-10 flowered, flowers crowded at the apex of the peduncle, many caducous, only 4 - 5 reaching maturity, each flower subtended by a single tortuous, lanceolate bract, bract 1.0 x 0.2 mm flowers grouped in triads with 1 central and 2 lateral flowers, the central flower reaching maturity first. *Male flowers* pedicellate, pedicel approximately 1.0 mm long, tapering towards the base, tepals fleshy, broadly ovate, 1.0 - 2.0 x 1.2 - 1.5 mm, leaf-like with one central veinlet, apiculate at the tip on the inner surface, margins slightly involuted, papillose, filaments long, narrow, slightly dilated at the base, 0.4 x 0.1 mm, anthers 0.2 x 0.3 mm. *Female inflorescences* 1 - flowered, pedunculate, peduncle 3.0 – 4.0 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, 1.0 - 2.0 x 1.2 - 1.5 mm, shortly apiculate on the inner surface, papillose along the inner margins, style long, angular, 0.5 x 0.3 mm, stigma 3 - lobed, lobes fleshy, pointed, smooth, nectary flat or slightly concave. *Fruit* green ripening orange, globose, 5.0 – 6.0 x 5.0 – 5.5 mm, smooth, a circular scar at the apex, perianth caducous, nectary and style may be persistent, exocarp thin, smooth, mesocarp thin, fleshy, endocarp thin, hard, completely smooth, globose or slightly obovate.

Distribution: China, India, northern Thailand, Vietnam.

Habitat: Often associated with bamboo in exposed areas on limestone.

Altitude: 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.

Notes: Name derived from the lanceolate leaves. Characterised by shrubby pendulous growth habit, lanceolate leaves and typically trimerous, unisexual flowers. This species is similar to *S.*

album, but distinguished by its smaller, inconspicuous, unisexual flowers and shorter nectarial lobes.

Additional material examined

India: Nicolson 2232 (BO), Nepal, Bagmati zone, Lalitpur district.

China: Tsai 56195 (P), Peiping, Hsien Lan ling; Wilson 4443 (P), west China; Simeon (P), Yunnan.

Laos: Melville 37.11 (P), Traminh, near Xiengkhouang; Poilane 2201 (P), Tranminh; Poilane 20096 (P), Tranminh, Muong Soni; Poilane 20023 (P, Z), Muong Soui, Tranminh.

Vietnam: Abbé Bon 5006 (P), Bac Phan, Ke Dua; Bon 3346 (P), Bac Phan, Luang Xa mountain; Chevalier 30708 (P), Nam Phan, Langbian, Da Lat; Balansa 1010 (P); Poilane 32470 (P), Nam Phan; Pierre 3077 (P).

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

Africa: Schliessen 4606 (Z), East Africa; Lewalle 2476 (Z), Burundi.

Europe: Daveau s.n. (Z), Lagos, Algarve, Portugal; Kramer 8785 (Z), Lagos, Algarve, Portugal.

6. *Santalum* L.

Type species: *Santalum album* Breynius, Prodromus fasciculi rariorum plantarum 1: t5 (1680) (Holotypus BM!), Timor; Kuswata Kartawinata 1738 (Epitype BO, designated here), Timor, 5 km from Soe.

L., Species Plantarum 1: 349 (1753); Genera Plantarum: 165 (1754); Brown, Flora Nova Hollandia: 355 (1810); Miq., Flora Indiae Batavae 1.1: 77 (1856); A.DC., Prodromus 14: 681

(1857); Cooke, Flora of Bombay: 554 (1906); Roxburgh, Flora Indica 1: 462 (1820); Bentham, Genera Plantarum 3: 224 (1883); Hook.f., Flora of British India 5: 231 (1886); Pilger in Engler & Harms, Die Natürliche Pflanzenfamilien 16b: 81 (1935); Backer, Flora of Java 2: 78 (1965); Hewson & George, Flora of Australia 22: 61 (1984); Philcox in M.D. Dassanayake & W.D. Clayton ed.s, Revised Handbook to the Flora of Ceylon 13: 201 (1999); *Fusanus* Brown, Prodromus Flora Nova Hollandia: 355 (1810); A.DC., Prodromus 14: 684 (1857); Bentham, Flora of Australia 3: 215 (1895); *Sirium* L., Systema Vegetabilium 14: 160 (1784); *Sandalum* Rumphius, Herbarium Amboinensis 2: 42, 47 t.11 (1741); *Eucarya* Mitchell, Three expeditions to Australia 2: 100 (1839); Sprague & Summerhayes, Kew Bulletin 11: 196 (1927).

Small glabrous tree to 6 m; bark smooth or rough, brown or dark gray. *Leaves* opposite, alternate, large, elliptic, thin, venation compound rectipinnate (**Fig. 39**), 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, receptacle elongated, tepals cream, white, 4 - 5, reflexed, fused into a deep hypanthium, glandular hairs present, profuse, anthers bilocular, locules separated by a relatively thick connective, diverging near the apex, bilobed, posterior lobes slightly shorter than the anterior, dehiscence longitudinal, stamens flexed into the centre of the flower at anthesis, nectary bright red, lobes short or long and protruding between the perianth segments, style long, slender, stigma 2 - 4 – lobed, lobes erect; ovary 1.3 - 1.5 mm long, semi inferior, the apex of the placenta protruding into the base of the style, placenta saggitate, 3 - 4 lobed, lobes very short not curling in towards the placental column, column short, broad. *Fruit* pedicellate, red, black, globose, perianth caducous, leaving a circular depression at the apex of the fruit; exocarp smooth, thin; mesocarp thin, fleshy; endocarp smooth, hard with a tri-radiate scar running from the apex to the base. Seed fleshy, entire; embryo located at the centre of the endocarp.

Number of species: 1 (25 world – wide).

Distribution: Java to Pacific Islands, one species cultivated in Southeast Asia.

Habitat: Coastal areas, behind beaches; on rocky, free draining soil in lowland forests; in secondary woodland and savannah.

Altitude: 0 – 300 m.

Notes: 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 fertilization, 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. The wood is a source of sandalwood oil which is widely used in perfumery and traditional medicine, the active constituent of which 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 overexploitation. *S. album* which is cultivated in Southeast Asia is currently the most commercially valuable, containing the highest concentrations and the best quality sandalwood oil.

Santalum album L.

Type: Breynius Prodromus fasciculi rariorum plantarum 1: t.5 (1680) (Holotypus BM!), Timor; Kuswata Kartawinata 1738 (Epitype BO, designated here), Timor, 5km from Soe.

L., Species Plantarum 1: 349 (1753); Species Plantarum 2: 497 (1762); L., Systema Vegetabilium 14: 164 (1784); Loureiro, Flora Cochinchinensis 2: 87 (1790); Roxburgh, Flora Indica 1: 462 (1820); Miq., Flora Indiae Batavae 1.1: 776 (1856); Beddome, Flora Sylvaticus t.256 (1873); Kurz, Forest Flora of British Burma 2: 329 (1877); Boerlage, Flora van Nederlandsch Indie: 180 (1900); Cooke, Flora of Bombay: 555 (1906); Pilger in Engler & Harms, Die Natürilche Pflanzenfamilien 16b: 81 (1935); Engler, Syllabus der Pflanzenfamilien: 186 t.184 (1964); Kanjilal, Flora of Assam 4: 129 (1940); Backer, Flora of Java 2: 78 (1965); Philcox in M.D. Dassanayake & W.D. Clayton ed.s, Revised Handbook to the Flora of Ceylon

13: 201 (1999); George, Flora of Australia 22: 61 (1984); *S. myrtifolium* Roxb., Flora Indica 1: 443 (1820) **syn. nov.** — Type: Roxburgh s.n. (Holotypus K!), India; *Sirium myrtifolium* L., Systema Vegetabilium 14: 160 (1784); *Santalum ovata* Brown, Prodromus Florae Novae Hollandiae: 355 (1810) — Type: Brown s.n. Melville bay (Holotypus BM!); Bl., Bijdragen tot de Flora van Nederlandsche Indiae: 645 (1825); *Santalum ovatum* Miq., Flora Indiae Batavae 1.1: 777 (1856); [*Sandalum album* Rumphius, Herbarium Amboinensis 2: 42, 47 t.11 (1741)].

Juvenile stems smooth, angular, bracteate at the base, appearing jointed, older branches terete, bark rough, cracked, with narrow horizontal fissures. *Leaves* opposite or sub - opposite, coriaceous, brittle, elliptic, ovate, 50.0 - 70.0 (22.0 - 31.0 x 7.0 - 11.0) 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, 8.0 - 9.0 x 1.1 - 1.2 mm, upper surface involuted, lower surface angular. *Inflorescences* terminal and axial, cauliflorous and on young shoots, pedunculate, peduncles slender, 10.0 - 13.0 x 0.6 - 0.7 mm, tortuous, angular, sulcate, each flower on a very short stalk, 0.3 - 0.5 mm long. *Flowers* scented, creamy white turning red and purple, buds turbinate, shortly pedicellate, pedicel slender, angular, 1.0 - 1.5 x 0.5 mm, receptacle short broad, 1.0 - 1.5 x 2.0 mm, tepals large, narrowly deltoid, 3.0 - 3.5 x 1.0 - 1.5 mm, reflexed, filaments long, narrow, 1.4 - 1.5 x 0.3 mm, weakly dilated at the base, anthers dorsifixed, style long slender, extending beyond the hypanthium, 2.5 - 2.7 x 0.3 mm, angular, broadening towards the base, stigma 3 - lobed, lobes out-spread, weakly papillate, nectary concave, deeply 5 - lobed, lobes tongue - shaped, up to 1.0 mm long, protruding between the perianth segments. *Fruit* red, dark purple, globose, 8.0 - 10.0 x 8.0 - 9.0 mm, crowned by a circular raised scar and style remnant, exocarp smooth, endocarp globose, 7.5 - 8.5 x 7.5 - 8.5 mm.

Distribution: Native from Java to the Timor Islands. Cultivated in India and Thailand.

Habitat: Cultivated at roadsides or beside villages. In secondary woodland and savannah.

Altitude: 30 - 100 m.

Vernacular name: Safed chandan, Sandal (Hindi); Chandanah, Taliaparnam (Sanskrit); Chandana (Bengal).

Notes: 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 distributed in Australia and the Pacific islands. Characterised by relatively large flowers, with petal – like perianth segments which are fused into a sort of hypanthium and a large, distinctive, brightly coloured nectary. Allied to *Osyris lanceolata* but distinguishable by larger, hermaphrodite, more showy flowers. The detail on Breynius's plate is insufficient as it shows just the vegetative structure of this species and therefore an epitype for *Santalum album* has been designated here to avoid confusion with other species.

Additional material examined

India: Nicolson 232 (E), Mysore, Hassan district; Royle s.n. (TCD); Sundara Raghavan 69577 (K), Nalur Agumbe, Mysore; Gandhi 2106 (K), Mysore; Perrotet s.n. (K), Pondichery; Gamble 10762 (K), Madras; Wight 2496 (K), Madras; Matthew et al 19326 (K), Madras; Ridsdale 47 (K), Courtallum, Tamilnadu; van der Maesen 3441 (K), Tamilnadu; van der Maesen 3520 (K), Tamilnadu; Haines 2136 (K), Dehra Dun.

Bhutan: Grierson & Long 3511 (E), Samchi district, 26 54S 89 06E.

Thailand: *Central*: Smitinand 89/48 (BKF), Phu Khae Botanic Gardens; Santisuk 6874 (BKF), Phu Khae Botanic Garden.

Philippines: Sulit 7028 (A), Luzon, Laguna province, Makiling national park.

Indonesia: *Java*: Zollinger 2804 (A); Groenhart 92 (U), East Java; Altona s.n. (BO), Pasoeroean, Malang. *Timor*: Darnaaedi 649 (K), Kapan, Soe.

Papua New Guinea: *Central district*: Zieck 36143 (CANB), Port Moresby, north end Palli Palla hills, 8 10S 146 17E; Zieck 36121 (BO), Rigo sub district.

7. *Scleropyrum* Arnott

Type species: *Scleropyrum pentandrum* (Dennst.) Mabberley, Taxon 26: 533 (1977) — Type: Rheede (Isotypus *Tirri Itti Canni* Hortus Indicus Malabaricus 7: 57 t.30. (1688), TCD!), India.

Arn., Magazine of Zoology & Botany 2: 549 (1838); Miq., Flora Indiae Batavae 1.1: 778 (1856); Hook.f., Flora of British India 5: 234 (1886); Trimen, Handbook to the Flora of Ceylon 3: 475 (1895); Gamble, Journal of the Asiatic Society of Bengal 75: 275 (1912); Cooke, Flora of Bombay 2: 556 (1906); Pilger, Englers Jahrbuch 59: 122 (1924); Pilger in Engler & Harms, Die Natürliche Pflanzenfamilien 16b: 72 (1935); *Pyrularia* p.p. A.DC., Prodromus 14: 628 (1857); *Scleromelum* Lauterbach & Schumann, Flora der Deutschen Schutzgebiete in der Sudsee: 300 t.5 (1900); [*Scleropyron* Bentham, Genera Plantarum 3: 228 (1883)].

Small trees, 4 – 6 m, occasionally with spines on the trunk, branches weakly or densely pubescent, bark white or brown, smooth. *Leaves* large, glabrous or more or less tomentose beneath, venation multi-arcuate (**Fig. 39**), veins raised on the lower surface, secondary veins 3 – 10, basal veins placed opposite each other, others arranged alternately, forming a co - arcuate infra - marginal vein and breaking up into a series of small arching loops, forming a zone between the infra - marginal vein and the leaf margin. *Inflorescences* dioecious, pubescent, catkins, singular or several together, cauliflorous and in leaf axils. *Male inflorescences* many flowered (up to 100 per inflorescence), long, rachis slender, ridged, flowers placed along the ridges. *Male flowers* sessile, shortly pedicellate, receptacle flat - deeply concave, tepals 4 - 6, valvate, lightly imbricate at the base, green, or pale yellow, glandular hairs present, profuse, anthers bilocular, locules bilobed, lobes unequal in size, the posterior longer and broader than the anterior, dehiscence longitudinal, incomplete at the base, stamens flexed into the centre of the flower at anthesis. Pollen grains large 23 - 24 μm long, prolate, exine sculpturing rugulate or microperforate, nectary fleshy, 4 - 6 lobed, rudimentary style short, slender, capitate; ovary present, superior, slender, saggitate, abortive. *Female inflorescences* fewer flowered than the male, rachis broader, flowers larger. *Female flowers* sub-sessile, pedicel extending considerably at fruiting, staminodes present, curving under the stigma, receptacle enlarged, elongated, 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 or globose, perianth persistent, erect, pedicel decurrent with the base of the fruit; exocarp thin, smooth or

slightly tuberculate; mesocarp thin, fleshy, endocarp hard, sulcate or scabrate on the exterior, a circular depression at the apex. Seed entire, globose, woody. Embryo located at the centre of the endocarp.

Number of species: 4

Distribution: Southern China and India to New Guinea.

Habitat: Generally associated with disturbed habitats. 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 collected from coastal areas from vegetation behind beaches.

Altitude: 0 - 1500 m.

Notes: 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 puberulous stems and inflorescences. Contains one very widespread species which occurs across the range of the genus and two species are endemic to New Guinea. The species are all morphologically very similar but can be distinguished on the size and aestivation of the male flowers and the shape of the fruits. The fruits are generally poisonous but in New Guinea the flowers are sometimes eaten after being cooked.

Key to *Scleropyrum*

1. Older branches and juvenile stems with spines.....**4.** *S. pentandrum*
   Older branches and juvenile stems without spines.....(2)
2. Stems and leaves glabrous or weakly hairy; Malay Penninsula and southern Thailand.....**3.** *S. maingayi*
   Stems and undersurfaces of leaves hirsute; New Guinea.....(3)
3. Leaf apices tapering for 10 mm; Inflorescences less than 10 mm long....**2.** *S. brevistachyum*

Leaf apices short, terminating in a sharp point, inflorescences greater than 15 mm long.....**1.** *S. aurantiacum*

1. *Scleropyrum aurantiacum* (Lauterb. & K.Schum.) Pilger

Type: Lauterbach 2849 (Holotypus of *Scleromelum aurantiacum* B!), Papua New Guinea.

Pilger, Englers Jahrbuch 59: 123 (1924); Pilger in Engler & Harms, Die Natürliche Pflanzenfamilien 16b: 72 (1935); *Scleropyrum leptostachyum* Pilger, Englers Jahrbuch 59: 123 (1924) — Type Ledermann 12845 (Holotypus B n.v . Isotypus K!); Pilger in Engler & Harms, Die Natürliche Pflanzenfamilien 16b: 72 (1935) **syn. nov.**; [*Scleromelum aurantiacum* Lauterbach & Schumann, Flora der Deutschen Schutzgebiete in der Sudsee: 300 t.5 (1900)]; *Lepionurus pubescens* Ridley, Transactions of the Linnean Society of Botany 9: 27 (1916) — Type: Boden Kloss s.n. (Isotypus K!) **syn. nov.**

Juvenile stems angular, covered in an indument of short, appressed, waxy hairs, older branches slender, terete, covered in a granular, waxy deposit, bark pale gray, smooth, spines absent. *Leaves* narrowly ovate, 120.0 – 150.0 (40.0 – 50.0 x 15.0 – 24.0) mm, apex acuminate, tapering gradually to a sharp point, base attenuate, upper surface weakly convex, totally glabrous or with a few hairs along the mid vein, lower surface sparsely to densely hairy, secondary veins 5 – 6, tertiary veins placed perpendicularly to the mid vein and joining with opposite tertiaries arising from the secondary veins, higher order venation forming a orthoreticulate pattern; petiole slender, 5.0 x 2.0 mm. *Male inflorescences* greater than 15.0 mm long, in leaf axils, tortuous, covered in an indument of sparse, appressed hairs, bracts ovate-lanceolate, 1.0 x 0.7 mm, reflexed against the rachis, outer surface densely pubescent. *Male flowers* cream or pale yellow, sub sessile, buds fungiform, tepals 5, valvate, 1.2 - 1.8 x 1.0 - 1.6 mm, elongate - deltoid, sparsely hairy on the outer surface, filaments short, not dilate at the base, 0.2 - 0.4 x 0.2 - 0.3 mm, anthers dorsifixed, 0.2 x 0.5 - 0.6 mm, locules isomerous, separated by a narrow connective, nectary flat or slightly convex, lobes pointed, style rudiment slender, 0.6 x 0.3 mm, stigma indistinctly lobed. *Female flowers* yellow or cream, maturing to orange or dark red, sessile, buds obconical, receptacle cuneate, tepals 5, deltoid, valvate, weakly pubescent, 1.1 x 0.9 mm, style short, broad, 0.3 x 0.6 mm, terete, stigma large, 3 - lobed, lobes outspread, luminous, smooth, margins undulate, nectary smooth, concave,

shallowly 5 – lobed. *Fruit* green, turning pink or red, globose, sessile, 17.0 - 20.0 x 17.0 mm, apex blunt, nectary becoming convex at fruiting, perianth caducous, eventually other floral parts may also be shed, exocarp coriaceous, sparsely hairy, rugulate or more or less smooth when dry, mesocarp thin, endocarp pyriform, apex rounded, smooth, with a faint circular scar, densely scabrate for the rest.

Distribution: Moluccas, Irian Jaya, Papua New Guinea (**Fig. 57**).

Habitat: Generally associated with disturbed habitats. Locally common on limestone in lowland hillside forest, in the undergrowth of *Castanopsis-Quercus* (Fagaceae) forest and in *Eurya* (Theaceae) dominate secondary forest.

Altitude: 0 - 1600 m.

Vernacular name: Amies (Male plant), Lolloh (Female plant) (Maibrat language, Irian Jaya); Mameagam (East Sepik); Boeing (Hattam language, Irian Jaya); Manua (West Sepik).

Uses: Fruits and flowers are edible, the flowers are placed in hot ashes before consumption.

Notes: Name derived from the fact that the flowers change from pale cream or yellow to dark orange/red with age. Characterised by narrowly ovate leaves which terminate in an abrupt point. Taxonomically similar to *S. pentandrum*, distinguished by subsessile flowers with valvate aestivation, a very broad, luminous stigma and a distinctly scabrate endocarp. *Scleropyrum aurantiacum* and *S. leptostachyum* were originally described as separate species based on leaf shape and the absence of a pistillode in the male flower of *S. leptostachyum*. The variation in leaf shape is such however that it is not possible to distinguish between the two species based on this characteristic. In terms of the pistillode in the male flower, on closer examination of the type specimen it seems that it was not originally absent and may have fallen off or been eaten by an insect.

Additional material examined

Indonesia: *Moluccas*: Balgooy & Hidayat 6416 (BO), Pulau Kobroor, 6 30S 134 35E.

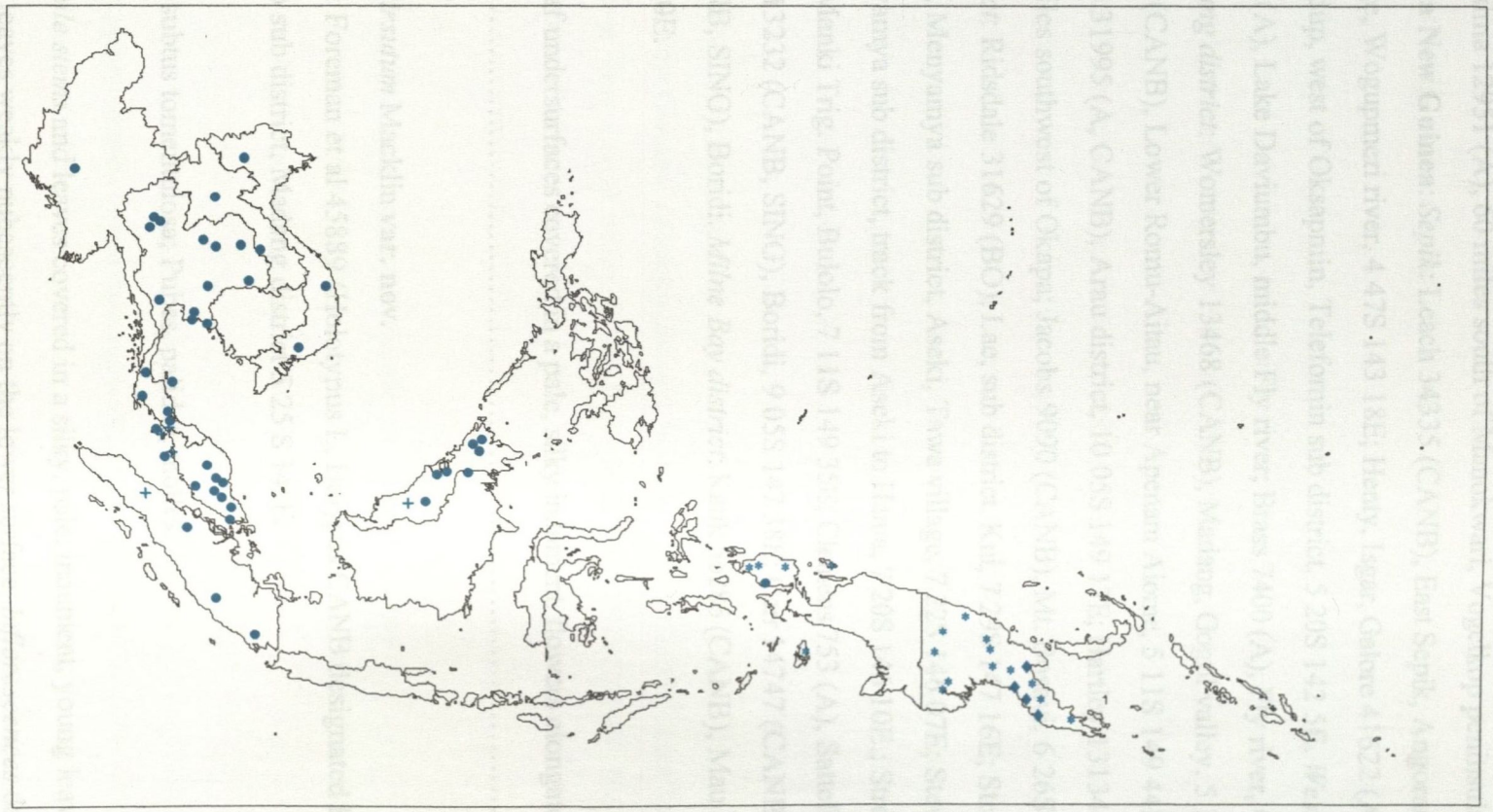


Fig. 57 Geographic distribution of: • *Scleropyrum pentandrum*, * *Scleropyrum aurantiacum*, ♦ *Scleropyrum brevistachyum*, + *Scleropyrum maingayi*.

Irian Jaya: Vink 15213 (CANB, K), Vogelkop peninsula, Ajamaru; Vink 15274 (CANB), Vogelkop peninsula, Segior, northwest side of lake Ajamaru; Vink 11298 (CANB), Pulau Yapen, 1 47S 136 44E; Versteegh 4991 (CANB), Vogelkop peninsula, Ajamaroe, 1 18S 132 13E; Versteegh 12631 (CANB), Arfak Mts., Mt. Nerimbau, near Minjambau; Kanehira & Hatusima 12951 (A), 60 miles south of Manokwari, Vogelkop peninsula.

Papua New Guinea: *Sepik*: Leach 34335 (CANB), East Sepik, Angoram sub district, Latoma village, Wogupmeri river, 4 47S 143 18E; Henty, Isgar, Galore 41622 (A), West Sepik, Bilindup, west of Oksapmin, Telefomin sub district, 5 20S 142 5E. *Western district*: Brass 7902 (A), Lake Daviumbu, middle Fly river; Brass 7400 (A), Fly river, Oroville camp. *Madang district*: Womersley 13468 (CANB), Madang, Gogol valley, 5 10S 145 15E; Robbins 1439 (CANB), Lower Romu-Aitau, near Apenam Aiome, 5 11S 149 44E. *Eastern highlands*: Brass 31995 (A, CANB), Arau district, 10 05S 149 17E; Hartley 13134 (A), near Wanatabi, 15 miles southwest of Okapa; Jacobs 9090 (CANB), Mt. Bosavi, 6 26S 142 50E. *Morobe district*: Ridsdale 31629 (BO), Lae, sub district, Kui, 7 29S 147 16E; Streimann & Kairo 27616 (BO), Menyamya sub district, Aseki, Tawa village, 7 22S 146 07E; Stevens 54824 (CANB), Menyamya sub district, track from Aseki to Hama, 7 20S 146 10E.; Streimann & Kairo 27939 (A), Manki Trig. Point, Bulolo, 7 11S 149 35E; Clemens 753 (A), Sattelberg. *Central district*: Carr 13232 (CANB, SING), Boridi, 9 05S 147 38E; Carr 14747 (CANB), Boridi; Carr 14873 (CANB, SING), Boridi. *Milne Bay district*: Katik 56286 (CANB), Mau river, Rabaraba, 9 37S 149 10E.

1. Leaf undersurfaces covered in a pale, silky indument, flowers elongate pedicellate .....var. *hirsutum*

var. *hirsutum* Macklin **var. nov.**

Type: Foreman et al 45889 (Holotypus L, Isotypus CANB designated here), Amiaba river, Usino sub district, Madang district 5 25 S 145E.

Folia subtus tomentulosa; Pubes, palidae, molles.

Juvenile stems and leaves covered in a silky, pale, indument, young leaves densely pubescent, older leaves weakly pubescently on the lower surface. *Inflorescences* densely tomentose,

flowers on a raised, wedge - shaped base which is up to 0.5 mm long, pedicellate, pedicel 1.2 x 0.7 mm.

Distribution: Papua New Guinea.

Habitat: Ridge forest on alluvial terrace.

Altitude: 200 - 300 m.

Vernacular name: Bumasis (Kaigorin), Waweh (Rawa, Madang).

Notes: Name derived from densely pubescent leaves and inflorescences. Characterised by a silky pale indument on the inflorescences and undersurfaces of the leaves. This variety is not geographically distinct from *S. aurantiacum sensu stricto* but ecologically it has different requirements. *Scleropyrum aurantiacum sensu stricto* is found in association with locally disturbed habitats in Fagaceae and Theaceae dominated secondary forests whilst the variety *hirsutum* is found in ridge top forests.

Additional material examined

Papua New Guinea: *Madang district*: Hoogland 5001 (CANB), near Jal village, half way to Bamesos, Gogol river valley, 5 19S 145 30E; Pullen 1097 (CANB), lower Ramu-Atitau, half mile north of Josephstaal, 4 44S 145E; Foremann, Farley & Noble 45889 (CANB, L), Amiaba river, Usino sub district, 5 25S 145E.

2. *Scleropyrum brevistachyum* Stauffer ex Macklin **sp. nov.**

Type: Schodde 2988 (Holotypus L; Isotypus CANB, designated here), Central district, 3 miles south of Sogeri, Sirinumu region, 9 29 S 147 30E.

Folia ovata, apice longi-acuminata, subtus densus, velutinus tomentosa. Inflorescentiae rectae, brevae, pauci-florae. Flores masculi sessiles; filis graciles; antherae, 0.3 x 0.3 mm, basifixae, isomerae. Flores femininae ignotae.

Branches spreading, horizontal, angular. *Juvenile stems* flattened, longitudinally grooved, covered in a dense indument of velutinous, pale, hairs, spines absent. *Leaves* 151.0 (80.0 - 85.0 x 23.0 - 25.0) mm, elliptic, apex acuminate, narrowing abruptly and tapering for approximately 10 mm, base obtuse-attenuate, upper surface glossy, shining, smooth, lower surface densely pubescent, indument brownish yellow, velvety, secondary veins 5 - 6, tertiary veins diverging obtusely from the secondary veins and joining with tertiaries from the opposite secondaries, forming an S - shaped curve, where veins meet they become forked and give rise to fourth order ramifications, ultimate vein endings free, branching twice dichotomously; petiole involuted on the upper surface, 10.0 x 3.0 mm. *Male inflorescences* singular or 4 - 5 together in leaf axils, short and delicate, less than 10.0 mm long, few flowered, flowers crowded near the apex of the rachis, densely pubescent, bracts lanceolate-ovate, 1.0 - 1.5 x 0.6 - 0.7 mm, tomentose on the outer surface. *Male flower* buds sessile, creamy white, globose, tepals lanceolate, elongate-deltoid, 1.5 - 1.8 x 1.0 - 1.2 mm, reflexed at approximately half way, forming a shallow hypanthium, filaments long, slender, 0.5 x 0.2 mm, anthers 0.3 x 0.3 mm, basifixed, separated by a narrow connective, nectary shallowly concave, lobed, style rudiment long, angular, 0.5 x 0.3 mm. *Female plant* unknown (**Fig. 58**).

Distribution: Papua New Guinea (**Fig. 57**).

Habitat: Under storey shrub in gallery and ridge top rainforest.

Altitude: 150 - 500 m.

Notes: Name derived from the short, delicate male inflorescences. Characterised by broadly ovate leaves with elongated acuminate tips, which are densely pubescent on the lower surfaces. Taxonomically close to *S. aurantiacum* but distinguished from this species by its broader more velutinous leaves, and short, few - flowered male inflorescences. Geographically *S. brevistachyum* occurs in the same area as *S. aurantiacum* and the habitat is similar to that occupied by *S. aurantiacum var. hirsutum*. The geographic ranges of this variety of *S. aurantiacum* and *S. brevistachyium* do not, however, overlap. In terms of reproductive morphology *S. brevistachyum* is quite distinct as it has short, few-flowered, delicate male inflorescences and palynologically the pollen grains of this species are almost spherical and

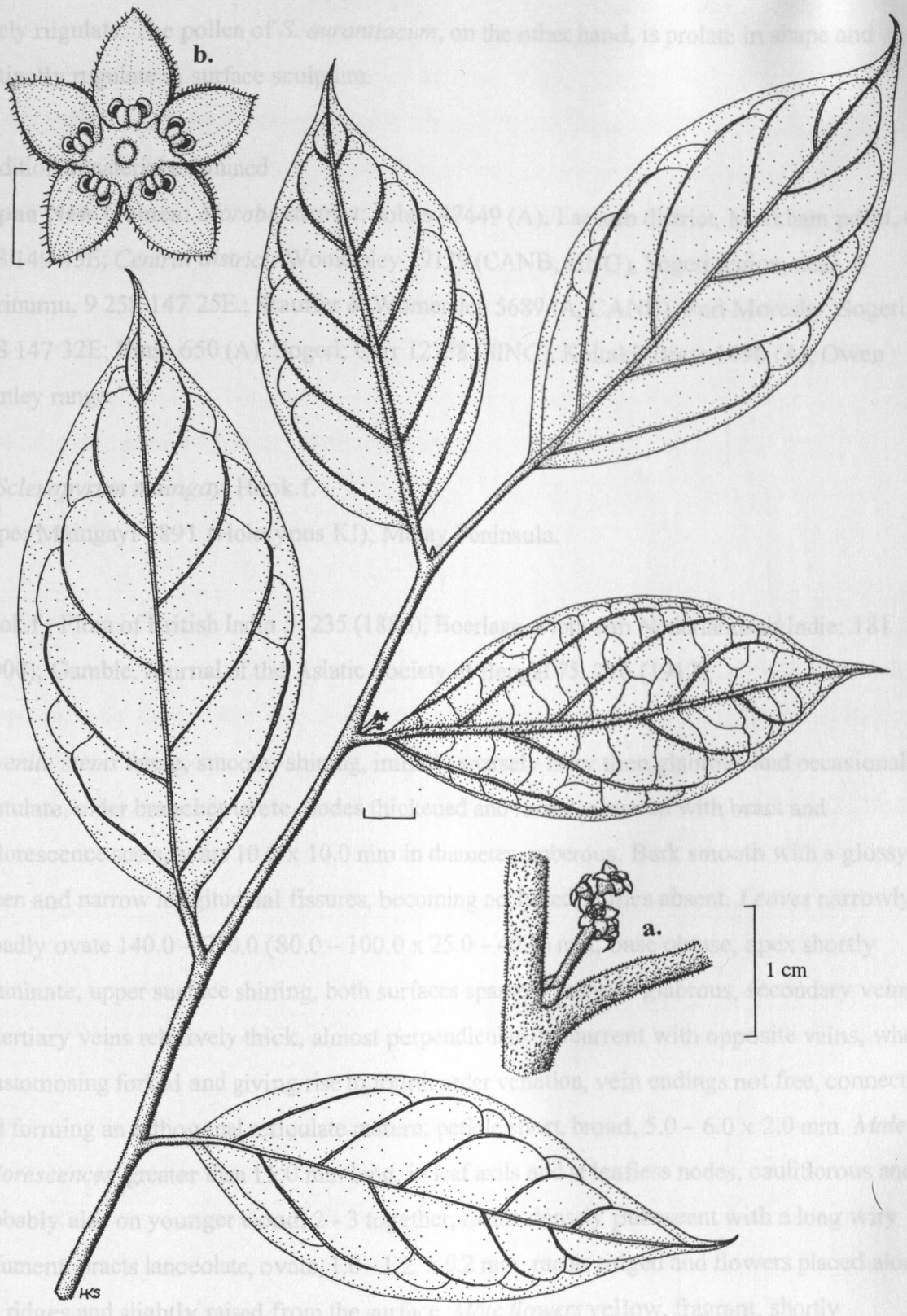


Fig 58. Type specimen of *Scleropyrum brevistachyum*. **a.** close up of inflorescence, **b.** close up of male flower showing the arrangement of the stamens and their mode of dehiscence.

finely rugulate. The pollen of *S. aurantiacum*, on the other hand, is prolate in shape and distinctly rugulate in surface sculpture.

Additional material examined

Papua New Guinea: *Morobe district*: Johns 47449 (A), Lae sub district, Markham point, 6 35S 149 45E; *Central district*: Womersley 19129 (CANB, SING), Sogeri region, near Surinumu, 9 25S 147 25E.; Stauffer & Womersley 5689 (A, CANB), Port Moresby, Sogeri, 9 25S 147 32E; Brass 650 (A), Sogeri; Carr 12758 (SING), Koitaki. Brass 1498 (A), Owen Stanley range.

3. *Scleropyrum maingayi* Hook.f.

Type: Maingayi 1891 (Holotypus K!), Malay Peninsula.

Hook.f., Flora of British India 5: 235 (1886); Boerlage, Flora van Nederlandsch Indie: 181 (1900); Gamble, Journal of the Asiatic Society of Bengal 75: 276 (1912).

Juvenile stems terete, smooth, shining, initially sparsely hairy then glabrous and occasionally pustulate, older branches terete, nodes thickened and raised, covered with bract and inflorescence scars, scars 10.0 x 10.0 mm in diameter, suberous. Bark smooth with a glossy sheen and narrow longitudinal fissures, becoming occluded, spines absent. *Leaves* narrowly – broadly ovate 140.0 – 270.0 (80.0 – 100.0 x 25.0 – 40.0) mm, base obtuse, apex shortly acuminate, upper surface shining, both surfaces sparsely hairy or glabrous, secondary veins 3 - 4, tertiary veins relatively thick, almost perpendicular, percurrent with opposite veins, where anastomosing forked and giving rise to fourth order venation, vein endings not free, connecting and forming an orthogonal reticulate pattern; petiole short, broad, 5.0 – 6.0 x 2.0 mm. *Male inflorescences* greater than 15.0 mm long, in leaf axils and at leafless nodes, cauliflorous and probably also on younger wood, 2 - 3 together, rachis densely pubescent with a long wiry indument, bracts lanceolate, ovate, 1.0 - 1.2 x 0.2 mm, rachis ridged and flowers placed along the ridges and slightly raised from the surface. *Male flowers* yellow, fragrant, shortly pedicellate, pedicel 0.7 - 1.0 x 0.4 - 0.5 mm, buds initially globose, later broadly campanulate, tepals valvate, 4 - 5, 1.7 - 2.2 x 1.5 mm, ovate, sparsely hairy, outspreading and reflexed forming a shallow hypanthium, tip recurved and shortly apiculate, filaments short, broad 0.3 -

0.5 x 0.3 - 0.5 mm, anthers basifixed, twice as broad as long, 0.3 - 0.4 x 0.7 - 1.0 mm, locules completely separate from each other, style rudiment short, thick, 0.3 - 0.5 x 0.3 - 0.5 mm, stigma indistinctly lobed, nectary concave. *Female flower* unknown. *Fruit* yellow, large, 20.0 – 35.0 x 20.0 – 30.0 mm, pyriform, perianth persistent, pedicellate, pedicel extending to 15 mm, exocarp thin, smooth, waxy, mesocarp thin, endocarp with a circular scar at the apex, surface entirely weakly punctate.

Distribution: Thailand (new record), Malay Peninsula, Sumatra, Java, Borneo (**Fig. 57**).

Habitat: Open areas in primary evergreen forest.

Altitude: 100 - 1400 m.

Notes: 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 glabrous leaves; small, fragrant male flowers and large yellow fruits. This species is taxonomically similar to *S. pentandrum*, differentiated by its large ovate, glabrous leaves, smaller male flowers with valvate tepals, and shorter filaments. The species is newly recorded for Peninsular Thailand here.

Additional material examined

Thailand: *Peninsular*: Congdon 1003 (A), Rawi Island; Kerr 14116 (K), Adang, Satun; Kerr 5012 (L), Ban Tin; Kerr 19061 (L), Kaw Libong; Phusomsaeng & Smitinand 180 (L), Khao Chong.

Malaysia: *Malay Peninsula*: Chan 6849 (SING), Langkwai, north Kedah. *Sarawak*: Ashton 16764 (BO, L), Lambir hills.

Indonesia: *Sumatra*: de Wilde & de Wilde Duyfjes 14387 (K), Ketambe, Lau Alas valley, Gunong Setan. *Java*: Koorders 10045 (BO).

4. *Scleropyrum pentandrum* (Dennst.) Mabberley

Type: Rheede (Isotypus *Tirri Itti Canni* TCD!), India.

Mabberley, Taxon 26: 533 (1977); *Tirri Itti Canni* Rheede, Hortus Indicus Malabaricus 7: 57 t.30. (1688); *Idou – Moulli* Rheede *l.c.* 4: 41 t.18 (1683); *Pothos pentandrus* Dennstedt, Schlüssel zum Hortus Indicus Malabaricus: 16, 24, 33 (1818); Fortsetzung Allegemeinen Teutschen Garten Magazins 3: 34, 42, 82 (1818); Dillwyn, Review: 33 (1839); *Sphaerocarya wallichiana* Wight & Arn., Edinburgh Philosophical Journal 15:180 (1833) — Type Wight 948 (Holotypus E!), India; Roxb., Flora Indica ed. 1: 371 (1824); *Sphaerocarya moschifera* Bl., Museum Lugduno Batavae 1: 245 (1850) — Type Korthals s.n. (Holotypus L!), Sumatra, **syn. nov.**; *Pyrularia ceylanica* A.DC., Prodromus 14: 629 (1857); *Pyrularia wallichiana* A.DC., *l.c.* (1857); Beddome, Flora Sylvatica: t.304 (1873); *Scleropyrum wallichianum* Arn., Magazine of Zoology and Botany 2: 550 (1838); Hook.f., Flora of British India 5: 234 (1886); Collett & Hemsley, Journal of the Linnean Society 28: 121 (1890); Trimen, Handbook to the Flora of Ceylon 3: 475 (1895); Cooke, Flora of Bombay 2: 556 (1906); Lecomte, Flore Générale de l'Indo-Chine 5: 221 (1915); Philcox in M.D. Dassanayake & W.D. Clayton eds., Revised Handbook to the Flora of Ceylon 13: 200 (1999); *Scleropyrum mekongense* Gagnep. in H. Lecomte, Notulae Systematicae: 196 (1909) — Type: Spire 743 (Holotypus P!) Laos; *Scleropyrum wallichianum* var *siamensis* Lecomte, Bulletin Muséum Histoire Naturelle Paris 20: 404 (1914) **syn. nov.** —Type: Kerr 1701(Holotypus P!, Isotypus AAU!, K!); *Scleropyrum wallichianum* var *mekongense* Lecomte, *l.c.* p. 404 **syn. nov.**; Wu & Tao, Flora Yunnanica 4: 294 t.82 (1986); *Scleropyrum ridleyi* Gamble, Kew Bulletin: 202 (1912) — Type: Ridley 4761 (Holotypus K!), Singapore; Gamble, Journal of the Asiatic Society of Bengal 75: 276 (1912), **syn. nov.**

Juvenile stems striate, covered in a light waxy sheen, slightly flattened, becoming terete, initially densely pubescent becoming glabrous, older branches covered in the remnants of bracts and inflorescence scars, scars 10.0 x 10.0 mm in diameter, suberous. Bark smooth, gray, 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 – broadly elliptic, ovate, 100.0 – 180.0 (35.0 –

58.0 x 15.0 – 25.0) 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 long, slender, 6.0 - 10.0 x 2.0 mm. *Male inflorescences* greater than 15.0 mm long, at leafless nodes of at least the second years growth, solitary or 2 - 3 together, tortuous, densely pubescent, bracts ovate- lanceolate, 1.3 - 1.5 x 0.3 – 0.5 mm, apex acuminate, base rounded. *Male flowers* smelling unpleasant, yellow, greenish-yellow, subsessile or pedicellate, pedicel 0.5 – 1.5 x 0.3 mm, buds initially globose, later broadly campanulate, tepals weakly imbricate at the base, 4 - 5, ovate, 2.0 - 3.0 x 1.3 - 1.6 mm, reflexed half way, forming a shallow hypanthium, tips recurved but not apiculate, sparsely hairy, filaments long, narrow, 0.7 - 1.0 x 0.2 - 0.4 mm, anthers basifixed, separated by a narrow connective, 0.4 - 0.5 x 0.6 - 0.8 mm, nectary concave, lobed, smooth, style rudiment slender, 0.4 - 0.9 x 0.2 - 0.4 mm. *Female flowers* sessile, obconical in bud, densely pubescent, tepals imbricate, 2.0 - 2.5 x 1.0 - 1.5 mm, ovate, apiculate on the inner surface at the apex, receptacle 2.5 mm long, nectary smooth, concave, style short, broad, 0.5 - 0.6 x 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, pyriform, variable in size 18.0 – 33.0 x 13.0 – 26.0 mm, perianth persistent, pedicel extending to 17.0 mm, exocarp thin, smooth, initially sparsely hairy, later waxy, mesocarp thin, endocarp globose, broadly elliptic, robust, a circular scar at the apex, surface perforate or sulcate, particularly near the apex (**Fig. 59**).

Distribution: India to Irian Jaya (**Fig. 57**).

Habitat: Generally associated with disturbed habitats on sandy soil. Common by streams in open areas of evergreen forests, dry evergreen forests, lowland dipterocarp forests. Also collected in coastal areas from vegetation behind beaches.

Altitude: 0 - 1000 m.

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



Fig. 59 Type illustration of *Scleropyrum pentandrum* (Dennst.) Mabberley (Idou Mulli Rheede). Taken from Rheede's Hortus Malabaricus Volume 7 t. 18.

Notes: Name derived from the pendulous inflorescences. In Rheede's Hortus Malabaricus (1688) *Tirri* refers to the racemose inflorescence and *itticanni* means parasite. Flowers may have a slightly foetid smell and the fruits are poisonous. Characterised by spines on the trunk and young branches, pubescent leaves and quite large pyriform fruit. *Scleropyrum ridleyi* was described as 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. *wallichianum* 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 sub glabrous leaves. It has been found that 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 however, seems to vary continuously within *S. pentandrum* from subsessile to distinctly pedicellate. *Scleropyrum pentandrum* may be confused with *S. maingayi* but can be distinguished by 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.

Additional material examined

India: Huber 546 (E), Ceylon, Ratna hura district; Lawson s.n. (K); Bourdillon 517 (K), Madras; Walker 48 (E), Ceylon.

Myanmar: English 46 (K), Mandalay.

China: *Hainan*: How 73290 (P), Po ting; Fleury 32036 (P); Lau 1346 (P), Changjiang district, Ue lung ling; Lau 3086 (P), Changjiang district; Lau 1188 (P), Tan district, I Kap Shan; Poilane 13472 (P), Telephon; How 73290 (P); Lau 1346 (P), Ue lung ling; Lau 3086 (P), Ka Chik Shan.

Laos: Vidal 1466 (P), Sa Phan Menk; Spire 743 (P), Luangprabang; Pierre 5040 (P); Harmand 247 (P) Se Moun; Poilane 11921 (A, P), Savannakhet.

Vietnam: Petelot 3.785 (P), Chapa, Bac Phan; Petelot 3.765 (P), Chapa; Tsang 30317 (A, BO, E, P), Sai Wong Mo Shan, Bac Phan; Tsang 30021 (A, E), Sai Wong Mo Shan, Bac Phan; Pierre 1427 (P), Phu Luoc; Fleury 32036 (P), Nam Phan, Bienhoa.

Cambodia: Pierre 856 (P); Chevalier 176 (P).

Thailand: *Northern*: Vidal 5336 (P), Chiang Mai, Ban Ta Fang; Kerr 16 (K), Me Tsung; Kerr 1026 (K, TCD) Ban Sun, Doi Saket; Kerr 1701 (AAU, K), Doi Sutep; Kerr 1711 (K, TCD), Doi Sutep; Larsen Hansen 6882 (BKF), Doi Sutep; Maxwell 88/354 (AAU, L), Chiang Mai; Maxwell 88/225 (L), Chiang Mai; Maxwell 88/533 (A), Chiang Mai; Native 410 (A), Doi Sutep; Smitinand 3307 (BKF), Doi Sutep; Sukkri 2 (BKF), Doi Sutep; Sorenson *et al* 3415 (BKF), Doi Sutep; Sorenson, Larsen & Hansen 6894 (BKF), Doi Sutep; Suvarnakoses 68 (BK), Doi Sutep; Worawot 3 (BKF), Doi Inthanon. *North-Eastern*: van Beusekom & Santisuk 2912 (AAU, BKF, L), Udon Thani; Suvarnakoses Smitinand 2037 (L), Phu Phan; Suddee *et al* 1007 (BKF, TCD), Phu Phan National park, 17 03N, 103 58E, trail north of park headquarters; Sangkadrand 3080 (L), Phetchbun; Smitinand 11295 (E, K, L), Phu Phan; Suoatabandhn 75 (BKF, K), Phu Kradung. *Eastern*: Suvarnakoses 1502 (BKF, L), East Si Sa Ket; Put 2212 (K), Hui Taleng, Nakhon Ratchasima; *South-Eastern*:Kerr 9428 (L), Kao Saming, Trat; Koyama *et al* 33012 (A, L), southwest Pranchin Buri; Niyomdhan Kubat 1306 (AAU, E, L), Ban Phe, Rayong; Phengklai 4009 (A), Rayong; Put 39 (BKF), Prachin Buri, Tapaya. *South-Western*: Phengklai 362 (BKF, E, L), Kanchanaburi. *Peninsular*: Congdon 387 (AAU), Tarutao national park, northeast from Adang HQ; Geesink & Hattink 7320 (L), Satun, east side of Koh Tarutao, 6 30N, 99 45E; Hansen 11162 (E, K), Phu Muang, Phangnga; Hansen Smitinand 12497 (K), Tarutao; Kerr 9791 (K), Sakeo, Krabi; Kerr 16865 (K), Kampang, Ranong; Kerr 20184 (K), Kuan San; Kerr 14567 (E, L, TCD), Satal, Kao Keo range; Maxwell 85/290 (A, AAU, E), Songkhla, Hat Yai, Dton Nga Chang reserve; Maxwell 85/336 (BKF, L), Songkhla; Sangkhahun 618 (BKF, L), southeast Chon Buri; Santisuk 6685 (BKF), Ubol, Pho Sai, Pong Ta Wang; Smitinand 387 (A), Tarutao; Smitinand 2685 (BK); Smitinand 7320 (AAU), Satun, 6 30N 99 45E; Smitinand 10239 (L), Tat Noi; Smitinand 85-290 (A, L), Songkhla; Smitinand *et al* 6039 (L), Rayong, 12 037N 101 10E; Suoatabandhn 7824 (L), Rayong.

Malaysia: *Malay Peninsula*: Rogstad 528 (A), Pasoh reserve, Negri Sembilan, 2 58N 102 19E; Panti 1683 (A), Kepong, Selangor; Kochummen 23009 (L), Selangor, Kepong ridge; Kiah 35071 (SING), Kedah; Kiah 35374 (SING), Gunong Baling Kedah; Henderson 22652 (A,

SING), Kelantan; Whitmore 4011 (A), Kepong, south Kelantan, Gunong Musang; Liew 285 (A), Pulau Redang, Terengganu; Henderson 22278 (BO), Pahang; Kamarudin 28381 (A), Lesong, Pahang; Corner 29348 (BO), Johor; Forbes 3227 (L); Curtis 3082 (SING), Penang. *Sarawak*: George 43059 (K), Ulu Medamit; Alston 13327 (A), Permantang, south of Kwajan; Suib 23467 (SING), Long Dam, Ulu Dapoi, 4th division; Othman et al 43533 (K), Belaga. *Sabah*: Clemens 32836 (A), Mt. Nunkok; Elmer 21735 (A), north Borneo; de Vogel 8551 (L), Pa Sia on Sarawak border, 4 20N 115 39E; de Vogel 8061 (L), west coast, Crocker range, 5 29N 116 01E; Carr 27848 (SING), above Thamis; Sigin et al 112265 (K), Kampung Nalumad, Ranau; Clemens 32836 (A), Mt. Kinabalu.

Brunei: Wong 1468 (A), Temburong, Bukit Belalong; Dransfield 7140 (K), Bukit Belalong, 429N 115 11E.

Indonesia: *Sumatra*: Soepadmo 217 (A), Upper Riauw; Teysmann 3833 (BO), Palembang; Djunaedi 1636 (K, L), Bukit Batu, south Sumatra; Meijer 33 (L), central Sumatra, Taluk region. *Irian Jaya*: Carr 14812 (CANB), Boridi; van Royen & Sleumer 7248 (L), Vogelkop peninsula, Aifat river valley.

3. Anthoboleae Dumortier

Type genus: Anthobolus R. Br., Flora Nova Hollandia: 357 (1810).

Dumortier, Analyse des Familles des Plantes: 15 (1829); Bartling, Ordines Naturales Plantarum (1830); A.DC., Prodromus 14: 687 (1857); Bentham, Genera Plantarum 3: 219 (1883); Pilger in Engler & Harms, Die Natürliche Pflanzenfamilien 16b: 65 (1935); Stauffer, Revisio Anthobolearum, Mitteilungen Botanische Museum University of Zürich: 213 (1959); George, Flora of Australia 22: (1984).

Shrubs to 2 – 3 m, leaves alternate, persistent or frequently leafless. *Inflorescences* racemes, spikes, sometimes reduced to a single flower. *Flowers* small, yellow or green, hermaphrodite, dioecious, glandular hairs absent, occasionally present, anther locules isomerous, pollen 19 μm in length, prolate, exine surface ornamentation striate, echinate, style short or absent, stigma 3 – 5 – lobed or entire, nectary present, fleshy, shortly 3 – 5 – lobed; *ovary* superior, almost indiscernible, placental column absent. *Fruit* a drupe, exocarp thin, perianth caducous, mesocarp very thin, fleshy, receptacle enlarged and fleshy below fruit; seed entire.

Notes: Genera distributed from Southeast Asia to Australia and the Pacific islands, most species found in Australia with 2 genera endemic. Tribe distinctive in terms of superior ovary and fleshy, enlarged receptacle under the fruit. A number of species have very small leaves or are completely leafless, in addition the ovary is highly reduced and simplified.

8. *Exocarpos* Labill.

Type species: *Exocarpos cupressiformis* Labill., Relation du Voyage à la recherche de la Perouse 1: 156 t.14 — Type: Labillardiere s.n. (Holotypus FI n.v.).

Labill., Relation du Voyage à la recherche de la Perouse 1: 155 (1798); Brown, Flora Nova Hollandia: 356 (1810); A.DC., Prodromus 14: 688 (1857); Stauffer, Revisio Anthobolearum, Mitteilung Botanische Museum, University of Zürich: 213 (1959); Backer, Flora of Java: 76 (1965); George, Flora of Australia 22: 34 (1984); [*Exocarpus* Miq., Flora Indiae Batavae 1.1: 781 (1856); Bentham, Genera Plantarum 3: 230 (1883); Pilger, Botanische Jahrbucher 59: 121 (1924); Pilger in Engler & Harms, Die Natürliche Pflanzenfamilien 16b: 69 (1935)]; *Xylophyllos* Rumphius, Herbarium Amboinensis 7: 19 t.12 (1755).

Small trees or large shrubs, branches erect or pendulous, terete or flattened angular, faintly striate, sparsely to densely pubescent, indument tufted; bark gray brown, shallowly fissured, peeling. *Leaves* coriaceous, often caducous or reduced to scales or phylloclades. In Southeast Asia leaves large, ovate, tomentose, venation curvipalmate (**Fig. 39**), primary veins 7 – 9. *Inflorescences* a spadix, erect or pendulous, singular or several together on a short peduncle. *Flowers* sunken, small, hermaphrodite, tepals 4 - 5, fleshy, densely papillate on the inner and outer surface, receptacle flat, weakly concave, glandular hairs present, anthers subsessile, bilocular, locules bilobed, lobes isomerous, stamens flexed into the centre of the flower at anthesis, style sub-sessile, stigma 3 – 5 - lobed, nectary fleshy, concave, 5 – lobed; *ovary* superior, minute, unilocular. *Fruit* obovoidal, ellipsoid, perianth caducous, stigma may be persistent, receptacle swollen, often brightly coloured, may be almost the same size as the drupe; exocarp papillate or shining, mesocarp very thin, fleshy, endocarp hard, smooth, globose. Seed fleshy, entire.

Number of species: 1 (26 worldwide).

Distribution: Philippines to Australia.

Habitat: Coastal dunes, riverbanks, in sandy soil in forests, often in association with *Eucalyptus* (Myrtaceae).

Altitude: 0 – 300 m.

Notes: Name derived from *Exo-* outside and *carpos* seed, name refers to the unusual fruit structure where the swollen receptacle is fleshy and the fruit is borne above it. Characterised by a stellate indument on the stems and leaves, a spadix inflorescence, very small, hermaphrodite flowers and the brightly coloured swollen receptacle of the fruit. Only one species, *E. latifolius*, is widespread in Southeast Asia, the majority of species occur in Australia and the Pacific islands, many of which are endemics.

Exocarpos latifolius R.Br.

Type: Brown 3208 (Holotypus BM!), Keppel Bay, East coast, Australia.

Boerlage, Flora van Nederlandsch Indie: 181 (1900); Pilger, Englers Jahrbuch 59: 122 (1924); Backer, Flora of Java 2: 77 (1965); George, Flora of Australia 22: 36 (1984); *Exocarpos latifolia* Brown, Prodromus Florae Novae Hollandiae: 356 (1810); A.DC., Prodromus 14: 688 (1857); *Exocarpus ovata* Bl., Museum Lugduno Batavae I.: 181 (1850); [*Exocarpus latifolia sensu auctorum* Miq., Flora Indiae Batavae: 781 (1856); Bentham, Flora of Australia 6: 228 (1873); *Exocarpus latifolius* Pilger in Engler & Harms, Die Natürliche Pflanzenfamilien 16b: 69 (1935)]; *Exocarpos luzonensis* A.DC., Prodromus 14: 688 (1857) — Type: Cuming 1195 (Isotypus K!, TCD!), Luzon, Philippines; Miq., Flora Indiae Batavae: 1096 (1856); *Xylophyllos latifolius* Kuntze Revisio Genera Plantarum: 589 (1891).

Branches pendulous. *Juvenile stems* angular not bracteate at the base, densely pubescent, older stems terete, glabrous or weakly papillate, bark pale grey, brown, striate with short, broad, elliptic fissures. *Juvenile leaves* in-folded, covered in a dense indument of tufted, papillate hairs, mature leaves coriaceous, sparsely hairy, broadly elliptic, ovate, apex acute, occasionally apiculate, base obtuse, attenuate 38.0 - 52.0 (25.0 - 40.0 x 10.0 - 20.0) mm, secondary veins

absent or indistinct, texture weakly rugulate, upper surface weakly convex, margin entire; petiole short, decurrent, 6.0 - 8.0 x 2.0 mm, upper surface flat, lower surface angular. *Inflorescences* in leaf axils of juvenile shoots, spadix, up to 30 mm long, densely papillate, flowers spirally inserted along the rachis, crowded at the apex, up to 100 flowers per inflorescence, opening from the base towards the apex. *Flowers* yellowish-green, buds globose, tepals deltoid, 0.5 x 0.5 mm, reflexed, receptacle approximately 0.2 mm long, anthers dorsifixed, 0.2 x 0.3 mm, style 0.2 x 0.2 mm, stigma shallowly 3 - lobed, papillate, centre depressed. Only 1 - 2 fruits developing per inflorescence. *Fruits* green, obovoid, 6.0 - 8.0 x 7.0 - 8.0 mm, apex smooth, rounded, a faint 3 - lobed scar visible, receptacle red, 6.0 - 7. 5 x 4.0 mm, densely papillate, exocarp thin, papillate.

Distribution: Philippines to Australia.

Habitat: Coastal areas in scrub woodland, stunted open forest and savannah woodland on limestone. Found in association with *Eucalyptus* and *Melaleuca* (Myrtaceae).

Altitude: 0 - 300 m.

Notes: Name derived from the large, broad leaves which are quite atypical for this genus. The only species of *Exocarpos* found in western Malesia, characterised by large 7 - 9 nerved leaves, a tufted indument on the leaves and inflorescences and a distinctive fruit with a brightly coloured, enlarged, fleshy receptacle.

Additional material examined

Philippines: Podzorski 2128 (A, CANB), Palawan, Mt. Victoria; Ridsdale 1610 (A, CANB), St. Pauls Bay, Mt. Bloomfield; Ramos 41202 (A), Busuanga island; Mendoza 91307 (A, CANB), Tamlangon island, Palawan; Merrill 613 (GH), Cluion island; Herre 1239 (A), Sibutu island; Ramos & Edano 44630 (A), Luzon; Ramos 27291 (A), north Luzon; Vidal 1803 (A). **Indonesia**: *Kalimantan*: Wood & Wyatt-Smith 4286 (SING), Tabawan island, central ridge. *Java*: Backer 17868 (U); Iboet 433 (U); Backer 29555 (U). *Timor*: Teysmann 8845 (U); Boschproefstation 12437 (U), Koepang; Teysmann 16396 (U); Korthals 2736 (U). *Celebes*:

Curran 3440 (A), Donggala; van Leeuwen 1928 (U). *Moluccas*: Kosterman & Wirawan 68 (A, CANB), west Flores. *Irian Jaya*: van Royen 5360 (A, CANB), Waigeo island, 0 14S 130 34E. **Papua New Guinea**: *Western district*: Zieck 36262 (A, CANB), Daru sub district, 8 50S 142 54E; Henty & Katik 38741 (A, CANB), Morehead sub district, 8 57S 141 59E; Zieck 36169 (A, CANB), Morehead sub district, 8 37S 141 45E; Zieck 36170 (A, CANB), Morehead sub district, 8 37S 141 45E; Paijmans 1483 (A, CANB), Daru sub district, 8 33S 142 41E; Brass 5729 (A), Oriomo river, Wuroi; Brass 5758 (A), Oriomo river, Wuroi; Brass 8412 (A), Tarara, Wassai, Kussa. *Morobe district*: Streimann 44310 (A, CANB), Lasanga island, Lae, 7 25S 147 15E; Streimann 39418 (BO), Buso sub district, Lae, 7 30S 147 15E. *Central district*: Carr 11834 (CANB), Port Moresby, 9 29S 147 09E; Pullen 6876 (A, CANB), Tavai creek area, Port Moresby, 9 43S 147 27E; Brass 6529 (CANB), Mabaduan, 9 17S 142 44E; Pullen 6901 (A, CANB), Tavai creek area, Port Moresby, 9 43S 147 27E; Hayligers 1195 (A, CANB), Tovobada hills, Port Moresby, 9 16S 147 15E; Pullen 3387 (A, CANB), Port Moresby, 9 25S 147 03E; Zieck 36134 (A, CANB), Port Moresby, 9 25S 147 11E; Stauffer 5679 (A, CANB), Port Moresby, 9 25S 147 16E; Brass 862 (A), Port Moresby; Brass 3714 (A), Baroka, Nakeo district; Schodde 2724 (CANB), Kapa kapa, 9 44S 147 28E; Brass 25920 (A, CANB), Normanby island, 10 01S 150 59E; Darbyshire 755 (CANB), Yule island, Kairuka sub district, 8 48S 146 31E; Pullen 3263 (A, CANB), Rigo sub district, near Kapa Kapa, 9 50S 147 30E.

4. Thesieae Reichb.

Reichenbach, Handbuch des Natürlichen Pflanzensystems: 167 (1737); Bentham, Genera Plantarum 3: 218 (1883); Pilger in Engler & Harms, Die Natürliche Pflanzenfamilien 16b: 84 (1935).

Glabrous herbs, small shrubs, leaves alternate, spiral, large or reduced to phylloclades. *Inflorescences* reduced to a single flower, solitary. *Flowers* small, yellow or green, hermaphrodite, glandular hairs present, profuse, anther locules isomerous, pollen heteropolar, exine surface ornamentation smooth, perforate, 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.

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

9. *Thesium* L.

Type species: *Thesium linophyllum* L., Genera Plantarum: 60 (1737) — Type L. (Holotypus BM n.v.).

L., Hortus Cliffortianus: 41 (1737); Genera Plantarum: 60 (1737); Species Plantarum: 207 (1753); Brown, Flora Nova Holandia: 352 (1810); A.DC., Prodromus 14: 637 (1857); Hook.f., Flora of British India 5: 229 (1886); Bentham, Genera Plantarum 3: 221 (1883); Hill, Flora Capensis 5.2: 136 – 200 (1915); Pilger in Engler & Harms, Die Natürliche Pflanzenfamilien 16b: 67 (1935); Grierson & Long, Flora of Bhutan 1.1: 140 (1983); George, Flora of Australia 22: 67 (1984).

Slender, glabrous herbs, erect or prostrate, branches angular, sulcate. *Leaves* small, often bract – like, decurrent, crowded near shoot apices. *Inflorescences* solitary, 1 - flowered, sessile or pedunculate. *Flowers* hermaphrodite, receptacle slender, elongate, tepals valvate, sometimes united into a short hypanthium, receptacle elongate, glandular hairs present, anthers bilocular, locules bilobed, lobes isomerous, dehiscence longitudinal, nectary membranous or absent, style short or absent, 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 thin, ribbed; mesocarp absent, endocarp globose, apex apiculate, outer surface sulcate, rugulate.

Number of species: 1 (325 world – wide).

Distribution: Cosmopolitan.

Habitat: grassland.

Altitude: above 1000 m.

Notes: Name derived from Theseus of Greek mythology. Characterised by herbaceous, often prostrate growth, small, scale – like leaves and a nut – like drupe. 1 species found in Southeast Asia, the majority of species occur in South Africa.

Thesium psilotoides Hance

Type: Hance 13749 (Holotypus BM!).

Hance, Journal of Botany: 48 (1886); Forbes, Chinese Botany 1.6: 409 (1888); Lecomte, Bulletin du Muséum Histoire Naturelle Paris: 403 (1914); Lecomte, Flore Générale de l'Indo-Chine 5: 214 (1915).

Herb, stems long, angular, sulcate, side shoots concentrated at shoot apices, spirally inserted. *Leaves* reduced to scales. *Juvenile shoots* bracteate at the apex, bracts crowded, spirally inserted, 1.0 - 1.5 x 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, 1.5 - 2.0 x 0.7 mm, ovate, lanceolate, apex acuminate, outer surfaces convex, inner surface flat. *Flowers* hermaphrodite, receptacle slender 1.0 x 0.8 - 1.0 mm, tepals deltoid 0.5 - 0.6 x 0.5 mm, fleshy, outer surface convex, inner surface flat with a distinctive lip or edge at the tepal margin, filaments slender, tortuous, 0.3 x 0.1 mm, anthers dorsifixed, 0.4 x 0.3 mm, nectary membranous, concave, smooth, 5-lobed, stigma sessile. *Fruit* 4.0 - 4.5 x 3.0 - 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 - 3.0 x 3.0 - 3.5 mm.

Distribution: Laos, northeast Thailand.

Habitat: Open areas in marshy grassland and grassy areas of *Quercus* - *Pinus* forests.

Altitude: 1200 - 1300 m.

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

Additional material examined

Laos: Pierre 5506 (P), Phu Luoc.

Thailand: *North-Eastern*: Pooma 67 (BKF), Loei, Phu Kradung; Smitinand 5872 (BKF), Loei, Phu Kradung; Smitinand 437 (BKF), Loei, Phu Kradung; Smitinand 1116 (BKF), Loei, Phu Kradung; Hance 7570 (BKF), Loei, Phu Kradung.

Glossary

General terms

Adnate: adhering to the surface of an object

Central column: Internal structure in the lower portion of the endocarp which is attached basally. When the endocarp is viewed in longitudinal section it does not appear to be attached to the walls of the endocarp.

Central chambers: in transverse section, circular or elliptic chambers which are arranged around the circumference of the central column of the endocarp.

Cushioned: convex or rather flattened

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)

Endophytic: a portion of haustorium which extends into the host tissue; shoots may then emerge on different parts of the host plant

Extrorse: turned outwards, away from the axis to which it appertains

Fascicled: numerous similar objects proceeding from a common point

Haustorium: a modified root which physically connects the parasite to the host; primary haustorium if the radicle apex is directly transformed into a haustorium; secondary haustorium if formed from tissue other than the radicle apex such as aerial roots on stems.

Hemiparasite: a parasitic plant which relies on its host for water and nutrients but possesses chlorophyll and retains photosynthetic activity.

Hyperparasite: a parasitic plant which is attached to another parasite

Petaloid: petal-like

Pendulous: hanging downward as a consequence of weakness of support

Procumbent: spread over the surface of the ground

Prostrate: lying flat on the ground

Staminodes: sterile, non-functioning stamens

Tepal: undifferentiated perianth segment

Tortuous: irregularly bending and turning

Twining: the property of twisting around an object

Duration

Caducous: falling off very early

Persistent: neither falling nor withering

Withering: not falling but fading and disintegrating with time

Aestivation

Imbricate: parts overlapping at the margin

Valvate: applied to each other by the margin only

Quincuncial: pieces five in number, two exterior, two interior and the fifth covers the interior with one margin and has its other margin covered by the exterior

Hair covering and superficial processes

Bearded: having a tuft of long weak hairs growing from the apex of an object

Ciliate: fringed with a row of short hairs

Glabrous: devoid of all vestiture

Crisp-hairy: bearing long kinky hairs

Filiformis: thread-shaped, slender like a thread

Hirsute: covered in coarse hairs

Pilose: with soft, long, hairs

Sericeus: covered with very fine silky hairs

Spine: bearing one or more modified stems or leaves reduced to spines which are hard, sharp and needle like

Tomentose: covered with dense rather rigid short hairs, perceptible to touch

Villous: moderately dense, soft, often curly hairs more or less erect but not necessarily straight

Velutinous (velvety): like hirsute but denser resembling velvet

Markings, Consistency

Coriaceous: leathery and thick

Cartilaginous: hard tough and thin

Fleshy: firm, juicy, and easily cut

Gelatinous: the texture and appearance of jelly

Glaucous: covered in a fine bloom, like a cabbage leaf

Granular: divided into little knobs and knots

Membranous: thin and semi-transparent

Muricate: furnished with numerous short, hard excrescences

Papillose: covered with minute capitate hairs or excrescences of unequal size and rather soft

Papyraceus: with the consistency of writing paper and quite opaque

Punctate: marked by minute impressions, like the point of a pin

Pustulate: covered with little excrescences or warts

Rugulose: covered with randomly reticulate lines, the spaces in between are concave

Ruminate: A seed which has numerous rounded, irregular-shaped lobes which point in various directions

Scarred: marked by the scars left by bodies which have fallen off

Squamose: covered by minute scales

Striate: marked (often by colour differences) by longitudinal lines

Suberous: corky

Sulcate: marked by longitudinal channels

Torn: irregularly divided by deep incisions

Wrinkled: parts folded irregularly in every direction

Shapes

Angular: with projecting longitudinal angles

Conical: shaped like a cone

Deltoid: an object which is triangular in outline

Fungiform: (mushroom-like) cylindrical with rounded convex, overhanging extremities

Keeled: formed in the manner of the keel of a boat, i.e. with sharp projecting ridges arising from a flat or concave central rib.

Obconical: inversely conical

Oblong: an object with parallel sides and rounded ends

Obovoidal: inversely egg shaped

Ovoid: egg shaped

Pyriform: pear shaped, like turbinate but more elongated

Turbinate: inversely conical and contracted at the apex

Leaves

Acuminate: tapering gradually into a point at the apex

Apiculate: terminating abruptly in a point, not hard and continuous with the rest of the leaf

Attenuate: tapering towards the base

Cuneate: (wedge-shaped) inversely triangular with rounded angles, straight sided, converging at the base

Cordate: heart -shaped

Decurrent: running into the body to which it is attached without any clear delineation

Elliptic: oval shaped with a narrow apex and base

Involuted: edges rolled inwards

Mucronate: abruptly terminated by a sharp hard point

Ovate: oval shape with a narrow apex and a rounded base

Obovate: inversely ovate

Obtuse: tapering gradually into a rounded end

Orbicular: perfectly circular

Lanceolate: narrow elliptic, tapering

Reflexed: suddenly bent backwards

Retuse: terminating in a rounded end, the centre of which is depressed

Revoluted: edges rolled backwards

Rounded: shaped like the arc of a circle

Spathulate: similar to obovate but with an elongated, narrow base.

Undulate: having uneven convex and concave margins

Uncinate: (hooked) curved suddenly back at the apex

Leaf venation

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

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

Curvipinnate: similar to compound rectipinnate but the secondary veins curve gradually towards the margin of the leaf not supplying it directly

Multi- arcuate: 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

Inflorescence

Catkin: a pendulous racemose inflorescence where the flowers are unisexual

Cymose: lacking a homogenous main axis which dominates the lateral branches, constructed with a sequence of axes which terminate in a flower

Cauliflorous: inflorescence produced from resting buds on well developed buds or major limbs

Panicle: a branched racemose inflorescence

Racemose: inflorescence characterised by a continuous main axis with stalked flowers arising from lateral nodes

Spike: sessile flowers placed on a main axis

Umbel: a racemose inflorescence with nodes crowded so that the flowers or flower stalks arise from one point

The ovary

Free central placentation: unilocular ovary where the ovules are arranged at the top of a central column

Placenta: the zone within the ovary occupied by the ovules

Placental column: stalk to which the placenta is attached

Placentation: mode of arrangement of the ovules within an ovary

(Based on: Nickrent 2000, Heywood 1997, Stearn 1996, Melville, 1976)

This study has provided a revision of the Santalaceae in Southeast Asia which comprises 48 species. Species delimitations were determined by examination of herbarium material gathered from all of the major European herbaria and from several Southeast Asian and Australian institutes. Additional information, which aided in the understanding of specific boundaries, was obtained by a palynological study of the Southeast Asian species. Ecological information described on herbarium collections has led to an understanding of the habitat preferences of the species and of current geographical distributions. A phylogenetic study of the Santalacean dendroparasites, which are the dominant group of Santalaceae in Southeast Asia, has elucidated the evolutionary relationships of these genera and has suggested that this group was part of the Gondwanan element, which migrated into Southeast Asia after the collision of India with Laurasia. Migration, tectonic activity and climatic fluctuations have resulted in the current geographical distributions of these genera. The selective environment of the aerial environment has also meant that this group displays the most variability in terms of fruit and pollen morphology in the Santalaceae.

Dendrotrophe

This genus contains just four species and occurs from southern China to northern Australia making it the most widespread Santalacean genus in Southeast Asia. Due to the effect of climatic influence it does not however occur above the peninsular region of Thailand and in Cambodia and Vietnam it is found only in areas which have climatic affinities with the Malay Peninsula. It is therefore confined to regions where there is a degree of unseasonality and high precipitation. Of the four species one, *Dt. varians*, is very widespread and occurs throughout the geographical range of the genus. It has been demonstrated in **Chapter 4** that this species is very variable in terms of ecological requirements and growth form. Certain tendencies have however been identified in that populations which occur in Indochina have generally larger fruits and narrower leaves than those which occur elsewhere. These differences are however not clear cut and past changes in sea level and climate has contributed to the variability of this species. Of the other species, *Dt. buxifolia* follows closely the distribution of *Dt. varians* but with a much contracted distribution and the other two species are narrow endemics in New Guinea. Generally the species occur on poor sandy, loamy soil, in kerangas and in peat

swamps at a variety of elevations, although the New Guinean species are always found at higher elevations in association with northern temperate taxa. One of the species in New Guinea is always a dendroparasite and differs from the other taxa in having umbellate male inflorescences, echinate pollen grains and apical 'tails' on the endocarp. In this respect it is similar to the other dendroparasitic genus, *Dendromyza*. Investigation of pollen morphology and fruit structure has however revealed that this pollen type and appendages on the endocarp are as a result of convergent evolution with *Dendromyza*, which may indicate that there are strong selective forces in operation for this particular pollen and fruit type.

All species of *Dendrotrophe* are characterised by the fact that they lack secondary haustoria on the stems and apart from *Dt. amorpha* they are terrestrial climbers or scandent shrubs. In terms of fruit structure they are characterised by a fleshy mesocarp, an endocarp which is chambered in the apex and the base and the presence of transverse chambers in the endocarp. Pollen morphology is generally rugulate and the pollen grains of these species are generally small with simple endomorphology (**Chapter 2**). The species are distinguished on the basis of inflorescence and fruit morphology and leaf shape. In the taxonomic revision of this genus *Dt. arfakensis*, which was originally named as a variety of *Dt. varians*, has now been raised to species status on the basis of fruit structure and vegetative morphology. Phylogenetic analysis has indicated that *Dendrotrophe* is sister to all of the other dendroparasites and it was probably an ancestor of *Dt. varians*, which migrated with the Gondwanan flora into Southeast Asia (**Chapter 3**).

Dendromyza

Dendromyza is now the largest Santalacean genus in Southeast Asia with some 21 species. Originally it was described as two separate genera, *Dendromyza* and *Cladomyza* by Danser (1940) based on fruit morphology. The separation of the genera was based on the internal construction of the endocarp: *Cladomyza* was said to have a chambered endocarp whilst the fruits of *Dendromyza* were said to be unilocular. Phylogenetic analysis of morphological characters has indicated, however, that the genera were artificial constructs and it now seems appropriate to subsume *Cladomyza* into *Dendromyza* (**Chapter 3**).

The species of *Dendromyza* are all dendroparasites and are characterised by female flowers which usually have separate stigmas, an endocarp which is crowned by a bundle of apical 'tails' and the majority of the species have secondary haustoria on their branches. In addition the majority of the species are confined to eastern Malesia with the greatest species diversity in New Guinea. There is one widespread species, *Dm. reinwardtiana*, which occurs from the Malay Peninsula to northern Australia and two others, *Dm. pachydisca* and *Dm. multinervis* are occasionally found in the Philippines (both species) and northeast Borneo (*Dm. pachydisca*). The species are distinguished on the basis of leaf shape, the presence or absence of secondary haustoria, the number of flowers and their arrangement in the male inflorescence and whether the fruits are chambered or not.

Dendromyza as well as being the largest is also the most variable Santalacean genus in Southeast Asia in terms of fruit and pollen morphology. Palynological analysis has revealed that the pollen of this genus can be rugulate, echinate, microechinate or striate (**Chapter 2**). In addition species with echinate pollen also have a particular floral morphology. In these species the glandular hairs which are a common feature of many Santalacean flowers are absent and anther dehiscence is transverse. Molecular phylogenetic analysis has indicated that this group is very divergent from the western Southeast Asian genera and it was not possible to resolve the relationship of *Dendromyza* to the other Santalacean dendroparasites based on this evidence. Analysis of morphological characters, however, indicated that this group may have a derived position within the aerial parasites as a whole with the closest affinity to *Phacellaria* (**Chapter 3**).

In terms of ecology species of *Dendromyza* are generally found above 1000 m in sub alpine and alpine vegetation and they parasitise species of Ericaceae and Euphorbiaceae which are associated with vegetation types at high elevations. They are often found in disturbed habitats in these areas and again are parasitic on species such as *Macaranga* and *Homolanthus* which are indicative of disturbed conditions. In many instances male and female plants have been collected from the same host tree which may indicate certain chemical cues are operating to control sexual determination in individual plants. This strategy may also ensure the continuation of generations in fragmented populations and increase the likelihood of species differentiation within smaller gene pools. A similar strategy, of the co-occurrence of male and

female plants on the same host tree, has been observed in the other dendroparasitic genera *Phacellaria* and *Dufrenoya*.

In the taxonomic treatment of *Dendromyza* two new species have been described, *Dm. hiepkoiana* and *Dm. staufferia*. The former species is very distinctive and is characterised by small bract-like leaves, an erect growth habit, the absence of secondary haustoria and an inflorescence structure which is very similar to that seen in *Phacellaria*. The latter species is close to *Dm. reinwardtiana* but is distinguished from it by ovate leaves, echinate pollen grains and pilose apical 'tails' on the endocarp. A new variety of *Dm. cuneata*, *Dm. cuneata* var. *fruticosa*, has also been described and it is characterised by a shrubby, non climbing growth habit and broad leaves (**Chapter 5**).

Dufrenoya

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. They are also generally parasitic on temperate taxa such as Fagaceae and occasionally Myrtaceae and Junglandaceae and may be tracking the distribution of those species in Southeast Asia. In contrast to *Dendrotrophe*, which is found in warm tropical, unseasonal climates, species in this genus are restricted to cooler montane climatic conditions.

The genus is characterised by the absence of secondary haustoria on the stems, umbellate male inflorescences and a membranous or sericeus indument on the endocarp. The species are all very similar and often they are represented by sparse herbarium collections, which may mean that they are rare or that they have been overlooked. It is certainly possible that *Df. euryphylla* which occurs in Java is now extinct due to the widespread forest clearance in this region and the fact that it is represented by such a small number of herbarium sheets. The species can be differentiated on the basis of bark morphology, the morphology of the inflorescence bracts and the shape of the endocarp (**Chapter 5**). Palynological investigation has revealed that the majority of the species have rugulate pollen grains but echinate pollen is a feature of certain species (**Chapter 2**). As with *Dendromyza* this pollen type is associated with a particular floral morphology. All of the species with echinate pollen have longitudinally dehiscing anthers and like *Dendromyza* they lack glandular hairs.

Phylogenetic analysis of morphological and molecular characters has indicated that *Dufrenoya* is a sister to *Dendrotrophe* and *Phacellaria* (**Chapter 3**). It is possible that an ancestral species of *Dendrotrophe* was a progenitor to *Dufrenoya* in the mountain ranges of Southeast Asia. The species migrated from the north and only extended as far as northern Borneo. In the taxonomic treatment of this genus no major changes were made but some species were combined based on the lack of insufficient evidence for maintaining them separately. In addition, one species, *Df. platyphylla*, has been recorded as new to Thailand.

Phacellaria

Species of *Phacellaria* are characterised by having bract-like leaves, an indument on the stems, the absence of secondary haustoria and an erect growth habit. Like *Dufrenoya* they also have a sericeus or membranous mesocarp and the fruits of some species of *Dufrenoya* are strikingly similar to *Phacellaria* in that they lack basal chambers in the endocarp. There are now 4 species in *Phacellaria*, which occurs from southern China as far as the Malay Peninsula, and the geographical range of this genus does not extend eastward of this area. Like *Dufrenoya*, species of *Phacellaria* are confined to montane regions and they are more host specific, being hyperparasites on Loranthaceae and occasionally *Dufrenoya*. The species are also under collected which may be due to their inconspicuous flowers and fruits and slender almost leafless stems which render them practically invisible in the canopy. The species are also all morphologically very similar, the reduction in terms of floral morphology and uniformity in terms of pollen morphology in this genus means that species delimitation is quite difficult. The species are, however, distinguished on the basis of inflorescence structure, the distribution of male and female flowers and the shape of the stigma. Two species, *P. malayana* and *P. rigidula* have been newly recorded for Thailand and generally in the taxonomic treatment the number of species in this genus has been reduced (**Chapter 5**). Phylogenetic analysis of morphological and molecular characters indicated that *Phacellaria* may be a sister to *Dufrenoya* and derived from an element within that genus (**Chapter 3**). There were however very long branch lengths associated with this genus in both sets of phylogenetic analyses, indicating that this genus has accumulated a lot of genetic and morphological differences to the other dendroparasites. Considering the reduction in terms of vegetative and floral morphology in *Phacellaria* it is not surprising that in particular the molecular analysis was inclusive.

Osyris

There is just one species of *Osyris* in Southeast Asia, and northern Thailand and Vietnam represent the most southerly distribution of *O. lanceolata*, which occurs as far north as southern Europe. Unlike the preceding genera this species is a terrestrial root parasite and is characterised by pendulous branches, cymose inflorescences and trimerous flowers. In Southeast Asia it is found above 1000 m and is associated with open, disturbed habitats where there is a preponderance of bamboo (**Chapter 5**). The flowers of this species change colour with age, which is thought to increase pollinator efficiency, as the darker older flowers may be invisible to prospective pollinators. The pollen of this species is also larger than the preceding genera and this may be correlated with plant nutrition (**Chapter 2**). Phylogenetic analysis of molecular characters has indicted that *Osyris* is a sister to *Santalum*. This corresponds to morphology as both genera have cymose inflorescences and occasionally the oil obtained from the heart wood of *O. lanceolata* has been used as an inferior substitute to that obtained from *Santalum album*.

Santalum

Santalum contains approximately 25 species but only one, *S. album* occurs in Southeast Asia. This species is native to Timor but is widely cultivated in India for its valuable aromatic oil and fragrant timber. The species is very distinctive, like *Osyris* it is a terrestrial root parasite and may only depend on a host plant in the early stages of development. The species is characterised by cymose inflorescences, large creamy white, hermaphrodite flowers and an extensive nectarial disc (**Chapter 5**). Like *O. lanceolata* the flowers change colour with age but this change is more dramatic in the larger flowers of *S. album*. The species generally occurs at low elevations, in coastal areas behind beaches, and in lowland forests. It has also been recorded from areas where there is evidence of disturbance and in cultivated areas along roadsides and near villages in India. Linnaeus first described the species in 1753 from the Prodromus of Breynius (1680) but the type specimen was a simple drawing which lacked detail. An epitype has therefore been designated to complement the drawing by Breynius. Palynologically *S. album* is very distinctive, the pollen of this species is very large and the exine sculpturing is uniquely verrucate compared to the other Southeast Asian species of Santalaceae. The sculpturing pattern of the exine is also dimorphic in that the poles and the area of the colpi are completely psilate. The internal construction of the pollen grain of this

species is also more complicated in that the pores are defined by a wedge-shaped thickening and the endoaperture is distinctly rectangular. The complexity of the pollen of this species is possibly related to its size as larger grains require greater internal support to counteract the desiccating influences of the external environment once they are released from the anther.

Scleropyrum

Scleropyrum contains 4 species and its geographical range does not extend beyond Southeast Asia. It has one very widespread species, *S. pentandrum*, which occurs from southern India and China to western New Guinea and three others with much narrower geographical ranges. *S. maingayi* is confined to the Malay Peninsula and peninsular Thailand and is a new record for this region. The other two species are located in New Guinea and one of them *S. brevistachyum* is a new species (**Chapter 5**). In respect to geographic distribution *Scleropyrum* is quite similar to *Dendrotrophe* which also has one widespread species and the rest are either confined to eastern or western Southeast Asia. All of the species of *Scleropyrum* are small trees and the genus is characterised by pubescent juvenile stems and leaves, catkin-like inflorescences and pyriform fruits. The species are all quite similar but they may be differentiated by the presence or absence of spines on the stems and trunk, inflorescence length, leaf shape and geographic distribution. Species of *Scleropyrum* are generally associated with disturbed vegetation and they are common beside streams in lowland forests. They can occur up to 1500 m but they have a preference for lower altitudes. Palynologically all of the species are very similar in that they have either a rugulate or punctate exine ornamentation (**Chapter 2**). Like *Osyris* and *Santalum*, the pollen of *Scleropyrum* is quite large and this may again be associated with growth habit. In general pollen morphology is a good defining characteristic for these three genera.

Exocarpos

There is just one species of *Exocarpos* in Southeast Asia and the remaining 26 species are confined to Australia. *Exocarpos* is thought to be the most derived genus in the Santalaceae due to its very small superior ovary which is reduced to a mamelon. *Exocarpos latifolius* occurs from the Philippines to Australia and is a terrestrial root parasite which is usually found in coastal areas, on sandy soil behind beaches, in association with *Eucalyptus*. The species is characterised by leaves and stems which have a tufted indument, a spadiform inflorescence,

small hermaphrodite flowers and fruits which have an enlarged brightly coloured receptacle (**Chapter 5**). The exine ornamentation of the pollen of this species is striate and like species of *Dendromyza* this sculpturing pattern is associated with an elongated polar axis (**Chapter 2**). The internal construction of the pollen of this species is also quite elaborate as the pores are thickened and the endoaperture forms a girdle around the mid point of the pollen grain.

Thesium

Thesium is the largest genus in the Santalaceae, the majority of the 325 or so species are found in South Africa and just one species is present in Southeast Asia. *Thesium psilotoides* is characterised by a herbaceous growth habit and the leaves are reduced to phylloclades, the inflorescence is one flowered and the fruit is a dry indehiscent nut (**Chapter 5**). This species is confined to northeast Thailand and Laos in grassy areas of *Pinus* - *Quercus* forests which may be indicative of disturbed conditions. The pollen of this species is heteropolar and distinctly different from the other Southeast Asian species. Recent molecular evidence has suggested that *Thesium* and some South American Santalaceae may form a separate monophyletic group to the Southeast Asian Santalaceae and Eremolepidaceae, a small family of dendroparasites from South America (Nickrent 1998).

Biogeographical implications

This study has revealed some important findings on the biogeography of the Santalaceae in Southeast Asia, and in particular the aerial parasites. It seems likely that the progenitor of *Dendrotrophe* was part of the Gondwanan flora which migrated from Australia along the southern shores of the Tethys sea. This species rafted to Sundaland on the Indian microcontinent and then, due to favourable climatic conditions, migrated into Southeast Asia and the islands of the Malay Archipelago. The present day distribution of *Dendrotrophe*, from India and southern China to as far east as northern Australia, is indicative of this type of migration pattern. The presence of *Dt. arfakensis* in New Guinea, which may be a relictual species, also points to a Gondwanan origin for *Dendrotrophe* followed by migration into Southeast Asia via India. *Phacellaria*, *Dufrenoya*, *Osyris* and *Scleropyrum* appear to belong to a Southeast Asian element. *Phacellaria*, *Osyris* and *Dufrenoya* possibly evolved in the montane areas of the region and spread eastwards along mountain ranges in concert with northern temperate taxa from Asia.

Dendromyza, *Exocarpos* and *Santalum*, on the other hand, belong to an eastern, Sahul or Australian element which diversified on the Australian plate prior to the late Tertiary contact with Sundaland. These genera later made minor incursions into western Malesia following the collision of New Guinea with the leading edge of the Philippines, Halmahera Arc system. The presence of *Dendromyza* and *Exocarpos* in western Malesia can therefore be ascribed migration following this collision. Malesia is therefore a crossroads for the Santalaceae. Some genera have a western Southeast Asian origin, whilst others are probably of eastern Malesian and Australian origin and the mixing of these two elements reflects the tectonic instability of the region. Isolation and contact via collision events has led to the evolution of distinct groups which have occasionally come together again from opposite directions in Southeast Asia and have, to some extent, overlapped in distribution.

Conclusions

The uniformity and reduction of floral characteristics in the Santalaceae have often posed problems for species delimitation and the investigation of specific and generic relationships. This study has provided a revision of the 48 species in Southeast Asia using a combination of macromorphological, pollen morphological and molecular data to gain insight into generic and specific relationships. Ecologically many of the genera are confined to particular vegetation types in either lowland or montane regions and the majority are found in association with disturbed habitats. Phylogenetic analysis has indicated that the dendroparasitic Santalaceae form a monophyletic group. *Dendrotrophe* is sister to all of the other dendroparasites and morphological phylogenetic analysis has indicated that *Dufrenoya* is sister to *Phacellaria* and the other genera. *Dendromyza* appears to be the most derived member of the aerial Santalaceae. Molecular analysis has provided a similar picture but in this case the lack of sufficient material for sequencing meant that the positions of *Dendromyza* and *Phacellaria* are still uncertain. The inclusion of further taxa in this analysis would help to resolve this problem by breaking up the lineages. Further molecular work is also required to determine the relationship between the Santalaceae and the Viscaceae. Molecular analysis would also help to resolve the boundaries of the Santalaceae *sensu stricto*. Palynological investigation of the Southeast Asian species has proved to be a useful tool for assisting in generic delimitation and has been more useful at the specific level in the tribe Amphorogyneae. This latter tribe is also

the most variable in terms of pollen morphology and certain floral morphological features are associated with pollen morphology in *Dendromyza* and *Dufrenoya*. The use of phylogenetic analysis and pollen morphological characters assisted in the delimitation of species and genera in the taxonomic account of the Southeast Asian species. In this last section *Cladomyza* has been subsumed into *Dendromyza* and 3 new species and 2 varieties of Santalaceae have been described.

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Appendix 1. Character matix of morphological characters for phylogenetic analysis (**Chapter 3**)

D_varians	1 0 0 0 1 0 0 0 1 0 0 0 0 1 0 1 0 1 1 0 0 0 0 1 0 0 1 0 0 1 0 0 0 0 0 0 0 1 0 1 1 1 0 0 1 0 0 1 0 0 1 1
D_buxifolia	1 0 0 0 1 0 0 0 1 0 0 0 0 1 0 1 0 1 1 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 1 ? 0 0 0 1 0 0 0 0 0
D_amorpha	1 0 0 0 1 0 0 0 1 0 0 0 0 1 0 1 0 1 1 0 0 0 0 0 1 0 0 0 1 0 0 1 0 0 1 0 0 0 0 0 1 0 1 1 1 0 0 0 1 0 0 1 0 0 0
D_arfakensis	1 0 0 0 1 0 0 0 0 1 0 0 0 1 0 1 0 1 0 0 0 0 0 0 1 0 0 1 0 0 1 0 0 1 0 0 1 0 0 0 1 0 1 1 1 1 0 0 ? ? 0 0 0 0 1 1
D_aurantiaca	0 1 0 0 0 0 0 0 1 1 0 0 0 0 1 0 1 1 0 0 0 0 1 0 1 0 0 0 1 0 0 1 0 1 0 0 0 0 0 ? ? 1 0 ? ? ? ? ? ? 0 ? ?
D_poilanei	0 1 0 0 0 0 0 0 1 1 1 0 0 0 1 0 1 0 1 0 1 0 1 1 1 0 0 0 1 0 0 1 0 1 0 0 0 1 0 0 0 0 1 0 0 1 0 0 1 0 0 0
D_granulata	0 1 0 0 0 0 0 0 1 1 0 0 1 0 1 0 1 1 0 0 0 0 1 1 1 0 1 0 1 0 0 1 0 0 0 0 1 0 0 0 1 0 1 0 1 2 1 0 0 0 0 0
D_robusta	0 1 0 0 0 0 0 0 1 ? 0 0 ? 0 1 0 1 0 1 0 1 0 1 1 1 0 0 0 1 0 0 1 0 1 0 0 0 1 1 0 0 0 1 0 0 1 0 0 1 0 0 0
D_papillosa	0 1 0 0 0 0 0 0 1 0 0 0 0 1 0 1 0 1 0 1 0 1 0 1 1 1 0 1 0 1 0 0 1 0 0 0 1 0 0 0 0 1 1 0 0 0 1 0 1 0 0 1 1
D_sphaerocarpa	0 1 0 0 1 0 0 1 1 0 0 1 0 1 0 1 0 1 0 1 0 1 1 1 0 1 0 1 0 0 1 0 0 0 1 0 1 0 0 0 1 0 1 1 1 0 1 1 0 0 1 0 0 0 0
D_oresitropha	0 1 0 0 0 0 1 0 1 0 0 0 0 1 0 1 1 0 0 1 0 1 1 1 0 1 0 1 0 0 1 0 1 0 0 0 0 0 0 1 1 0 0 0 1 0 0 1 0 0 0
D_euryphylla	0 1 0 0 0 0 0 1 0 0 0 1 0 1 0 1 0 1 0 1 1 1 0 0 0 1 0 0 1 0 1 0 0 0 0 0 1 1 1 0 0 0 0 0 1 0 0 0 0
D_collettii	0 1 0 0 0 0 0 1 1 0 0 0 0 1 0 1 0 1 0 1 0 1 1 1 0 0 0 1 0 0 1 0 1 0 0 0 0 0 1 1 1 0 0 1 0 0 1 0 0 1 1
D_sessilis	0 1 0 0 0 0 0 1 0 1 0 0 0 1 0 1 0 1 0 1 0 1 1 1 0 1 0 1 0 0 1 0 1 0 0 0 1 0 1 1 1 0 0 1 0 0 1 0 0 0 0
D_platyphylla	0 1 0 0 0 0 0 1 0 0 0 1 0 1 0 1 0 1 0 0 0 1 1 1 0 0 0 1 0 0 1 0 0 0 0 1 1 0 1 1 1 0 1 1 0 0 1 0 0 1 1
P_rigidula	0 1 0 0 0 0 1 0 0 0 0 1 0 1 0 1 1 0 0 1 1 0 0 0 1 0 0 0 1 0 1 1 0 0 1 0 0 1 1 0 1 0 1 1 0 0 1 0 0 0 0
P_malayana	0 1 0 0 0 1 0 1 0 0 0 0 0 0 1 0 1 1 0 0 1 1 0 1 0 1 0 0 0 1 0 1 1 0 0 1 0 0 1 1 1 1 1 1 1 0 0 1 0 0 0 0
C_densa	0 1 1 1 0 0 1 0 0 0 1 1 0 0 1 1 0 1 0 1 1 1 1 1 1 0 1 0 0 1 0 1 0 1 0 1 0 0 0 1 1 0 1 2 1 0 0 0 0 1 0 0 0 0
C_microphylla	0 1 0 1 0 0 1 0 0 0 0 0 1 0 0 1 1 0 1 0 1 1 1 1 1 1 0 1 0 1 0 0 1 0 1 0 0 0 0 1 1 1 2 1 0 0 0 0 0 0 1 0 0
C_dendromyzoides	0 1 1 1 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 0 1 1 1 0 1 0 0 1 0 1 0 0 0 0 1 0 1 1 1 2 1 0 0 0 0 0 1 0 0 0
C_kaniensis	0 1 0 1 0 0 1 0 0 0 0 0 1 0 1 1 0 1 0 0 0 1 1 1 0 1 0 1 0 0 1 0 0 0 0 1 1 1 1 1 2 1 0 0 0 0 0 0 1 0 0
C_pachydisca	0 1 1 1 0 0 1 0 0 0 1 0 1 0 1 1 0 1 0 0 0 1 1 0 1 0 0 1 0 0 1 0 0 1 0 0 0 0 1 0 1 1 1 2 1 0 0 0 0 0 1 0 0 0
C_angustifolia	0 1 0 1 0 0 1 0 0 0 0 1 0 0 1 1 0 1 0 1 1 1 1 1 1 0 1 0 0 1 0 1 0 1 0 0 1 0 0 1 1 0 0 2 1 1 0 1 0 1 0 0 1 1
C_trinervia	0 1 ? 1 0 0 1 0 0 0 ? ? ? 0 1 1 0 ? 0 ? 1 1 1 1 0 1 0 0 1 0 1 0 1 0 0 0 1 0 1 1 0 0 2 1 0 0 0 0 0 0 1 0 0
C_cuneata	0 1 1 1 0 0 1 0 0 0 1 1 0 0 1 1 0 1 0 0 1 1 1 1 1 0 1 0 0 1 0 1 0 1 0 0 0 0 1 1 0 0 0 2 1 0 0 0 0 1 0 0 0 0
C_stellata	0 1 1 1 0 0 1 0 0 0 0 1 0 0 1 1 1 0 0 1 0 1 1 1 1 0 0 0 1 0 0 1 0 1 0 0 0 1 1 1 1 2 1 0 0 1 0 0 1 0 0 0
C_acrosclera	0 1 1 1 0 0 1 0 0 0 0 1 0 0 1 1 0 1 0 1 1 1 1 1 1 0 1 0 0 1 0 1 0 1 0 0 0 0 0 1 1 2 1 0 0 0 0 1 0 0 0 0
C_erecta	0 1 1 1 0 0 1 0 0 0 1 0 0 0 1 1 0 1 0 0 1 1 1 1 1 0 1 0 0 1 0 1 0 1 0 0 0 0 0 1 1 2 1 0 0 1 0 0 1 0 0 0
C_uncinata	0 1 1 1 0 0 1 0 0 0 1 1 0 0 1 1 0 1 0 0 0 1 1 1 0 0 0 1 0 0 1 0 1 0 0 0 0 0 1 1 2 1 0 0 0 0 0 1 0 0 0
D_crassifolia	0 1 1 1 0 0 1 0 0 0 0 0 0 0 0 1 1 1 0 0 1 1 1 1 1 1 0 1 0 0 1 0 1 0 1 0 0 0 0 0 1 0 0 0 2 1 1 0 1 0 1 0 0 1 1
D_hiepkoiana	0 1 0 1 0 0 1 0 0 0 0 0 0 1 0 1 1 0 1 0 0 1 1 1 1 0 0 0 0 1 0 1 1 1 0 0 0 0 ? ? ? 2 1 ? ? ? ? ? ? 0 ? ?
D_cucullata	0 0 ? 1 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 0 0 0 0 1 0 1 0 0 0 0 0 0 0 0 0 0 2 1 0 0 1 0 1 0 0 0 0
D_reinwardtiana	0 0 ? 1 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 1 0 1 0 0 0 1 0 1 0 1 0 0 0 0 1 0 0 2 1 0 1 0 0 1 0 0 1 1
D_ledermanii	0 0 ? 1 0 0 1 0 0 1 0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 0 1 0 0 1 0 1 0 1 0 0 0 0 0 0 0 0 2 1 0 1 0 0 1 0 0 1 1
D_puberula	0 0 ? 1 0 0 1 0 0 0 0 1 0 0 0 0 0 0 0 0 1 0 1 1 1 0 1 0 1 0 0 1 0 0 0 1 0 0 ? ? ? 2 1 ? ? ? ? ? ? ? ? ?
D_salomonia	0 0 ? 1 0 0 1 0 0 0 0 1 0 0 0 0 0 0 0 0 1 0 1 1 1 0 1 0 1 0 0 1 0 1 0 0 0 1 0 0 0 2 0 ? ? ? ? ? ? ? ? ?
D_multinervis	0 0 ? 1 0 1 0 0 0 0 0 1 0 0 0 0 0 0 0 0 1 1 1 1 1 0 1 0 1 0 0 1 0 0 0 0 0 1 0 0 0 2 1 1 1 0 0 1 0 0 0 0
D_staufferia	0 1 ? 1 0 0 1 0 0 1 1 0 0 0 0 0 0 0 0 0 1 1 1 1 0 1 0 0 0 1 0 1 0 0 0 0 0 0 0 0 0 0 1 2 1 0 0 0 0 0 1 0 0 0
S_pentandrum	0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 1 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 1 0 0 0 1 0 1 0 0 1 1
O_lanceolata	0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 1 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 1 1 1 0 0 1 1 0 0 0 0
S_album	0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 1 0 0 0 1 0 0 0 1 ? 1 0 1 ? ? ? ? 1 1

Appendix 2. Character matrix for ITS2 sequence data for phylogenetic analysis (**Chapter 3**)

```
O_lanceolata ------------------------------------------------------------CTACGCTTATTGATATGCTTAAACTCAGCGGGTAACCCCACCGTG?CCCGGGGTCGCCA--
-----AATG?GTTCCATTCTCAC--------------TGTGTTAA--GAGTCCCACCAGTCTT-ATATCTCCTCACC-TGGTAACACGACTACCAACGC-------TGTTA-----TC-
ACATACTCGTCATG--AGGCTTG-TCACC-ATGGT-ACTATTATATTTCGGCTATCCGCGC-ACCTTA---TTGG-ACGGGAAACCAACC-TTCGCTCCTAG-
GACCTTCACCCATCATAAAATATGGAAGACATGAGGAGCAGCACTATGCG--TGACGCCCAGGCAGGCGTGCCCTTGGCCTAATGGCTTTGGGCGCCCCTTGCGTTCAAAGACCTTGATGCATTAC

S_album      -GAATTCCCCGGTTCGCTCGCCG---TTACTAAGGGAATCCTTGT-AAGTTTCTTTTCCTCCGCTTATTGATATGCTTAAACTCAGCGGGTAGCCCCACC-TGACCTGGGGTCGCAA--
-----AGGGACCTCTATTTTCAT--------------CATGTAAACAAAGTCCCACGAATCTTTATAGTTTGTCGTG-TGGCGACCCGAAGAA-GACGT-------TGTTA-----TCCACA-
ACTCGTCATG--AGACGCG-TCGCC-AAGG--ACTATAGTATTTCAGCTAACCGCGC-CATTGT---TTGC-ACGGGAAGCCAGCA-TTCGTTCCCAAAGGTCCCCGCCCAT--TAAAA---GGGGGT--
TAGGGAGCAGCACGGTGCG--TGACACCCAGGCAGGCGTGCCCTTAACCTAATGGCTTCGGGCGCACCTTGCGTTCCAAAGACTCGATG-ATTC?

S_pentandrum ---TTTCCCCGGTTCGCTCGCCG---TTATCTAGGGGATCCTTGT-AAGTTTCTTTTCCTCCGCTTATTGATATGCTTAAACTCAGCGGGTAGCCCCGCC-TGACCTGGGATCGCAA--
-----AGGAAAATG-ATTC-CAT------------------------GGGTCATACGAGTA------------CACA-TGATGGCACGAGA---GACA--------TGTTA-----CC-ACA-
GGTCGTCGTG--AAACGTG-TCACC-AGTG--ACT-CCGAATTTCGATCAACCGC---ACTGT?---TCGT-ACGGGAG?CC?ACA-TCCAC-CCCAATACTC?CC?TCTCT--TA------GGAGG---
TTAGGGGCGACGC?ATGCA--TGATGCCCAGGC???CGTGCCCTCAGCCAAAAGGCTTTGGGCGCAACTTGCGTTCAAAAA-CTCGATG-ATTCA

D_buxifolia  ----CCCCGGTTCGCTCG--CCGTTACTAGGG--GAATCCTTGT--AAGTTTCTTTTCCTCCGCTTATTGATATGCTTAAACTCGGCGGGTAGCCCCGCC-TGACCTGGGGTCGCACT-
-GGTGAGCTCCGTCTCCCCCGAGAAGGAGAC------GAGATTAGAAGGTCCCGGGAGTTT------------CGCACGGCGACACGGAGTCGGA-CGC-------AGTCG----TCCAAAA-
CTCGTCCCG---CGACGCG-TCGCCGAGAAAACCATAT--TTCGGG-CCAGCCGCGCAGCAGTAAACATGC-ACGGGAGGCCA-ACGTTCGCGCCC-----CCAACGC----CCGAGAG---
GGGAGCTTTGGGGGGCGACTCGATGCG--TGACGCCCAGGCAGGCGTGCCCTCGACCTACTGGTTTCGGGCGCAACTTGCGTTCAAAGA-CTCGATG-GTTCA

D_varians    CATTCCCCGGTTCGCTCG--CCGTTACTAGGG--GAATCCTCGT--AAGTTTCTTTTCCTCCGCTTATTGATATGCTTAAACTCAGCGGGTAGCCCCGCC-TGACCTGGGGTCGCATT-
-GGTGAGCCCCGTCTCCCCCGAGAAGGAGAC------GAAATTCGAGGGTCCTGGGAGTTT------------CGCACGGCGACACGGAGTCGGA-CGC-------AGTCG----TCCAGAA-
CTCGTCCCG---CGACGCG-TCGCCGAGGAAACCGTAAAGTTTAGG-CCAGCCGCGCAATAGT---CGCGC-ACGGGAGGCCA-GCGTTCGCGCCC-----CCGACCCGTCCCCGAGAG---GGGAG-
TCCGGGGGGCGACTCGATGCG--TGACGCCCAGGCAGGCGTGCCCTCGACCTAATGGTTTCGGGCGCAACTTGCGTTCAAAGA-CTCGATG-GTTCA

D_robusta    -ATTCACCGGATCCCTCGC-CAGTTTTTAGGTC---AATCCTTGT-AAGTTTCTTCTCCTCCGCTTATTTATATGCTTAAACTCAGCGGGTAGTCCCGCC-TGACCTGGGGTCG-GG--
-TCCGAACGA------------------------TGG-GTCCTTCGGGCCCTC--ACGCC-------CGCTGCGAGCCGAGGCACGGCACCTAGA--ACAACTTGTGTCG-----CCCACC-
ATGTGCTGTGCCCGGCACGGTACGCCGGCA--GCCCCAAC-TTCGGCCCACCGCGCCCTGCG-------GCGCGGGGAG-CCAAACACCGCGTCCCG-----ACCCG---ACCCGAGG----AGGGG--
TTCGGGAGCGACTTTTGGCG--TGACGCCCAGGCAGGCGTGCCCTCGGCCAGAAGGCCTCGGGCGCAACTTGCGTTCAAAAA-CTCGATG-GTTGG

D_sessilis   ---ATTCCTCGG-TCTCGCGTCTCCGTTAGTATCGGAATCATTGTTAAGTTTCTTCTCCTCCGCTTATTTATATGCTTAAACTCAGCGGGTAGTCCCGCC-TGACCTGGGGTCGCGG--
-TCCGAGCGGCGTGCCC----TGCGGTCGG----TTGG-GTCCTTATGGCC?CT--GCGCC-------GGTTGCGCGCC-GGGGCGCTGCAC-AGACAACAACTAGTGTCG-----CCCACC-
ATGTGCTGGGCCCGGCACGGAACGCCGGCA--GCCCCAAC-TTCGGTCCACCCCTCCCTGCT-------GCAGGGGGGG-CCAGACACAGATTCC-------ATCCG-----C-CAGGG---GGTGGT----
GGGAG?GTCTTTTGGCG--TGACGCCCAGGCAGGCGTGCCCTCGGCCAGAAGGCCTCGGGCGCAACTTGCGTTCAAAAA-CT-GATG-GTTCC

D_ledermanii AATTCCCCGGTTCGCTCG--CCGTTATTAGGG--GAATCCTCGT--AAGTTTCTTTTCCTCCGCTTATTGATATGCTTAAACTCAGCGGGTAGCCCCGCC-TGACCTGGGGTCGCACT-
-GGTGAG--------------------------------GGGTCCCGGGTGTTT------------CGCACGGCAACGCGGAGTCGGACGC---------AGTTA----TCCAGAA-CTCGTCCCG----
CGACGCG-TCGCCGAGAGAACCGTGT--TTTCGGCCAGCCGCGCGATAGCCC--TGCGC-ACGGGAGACCA-?CGTTCGCGCCC-------CCGGCGT--CCGAGAG---GGGAG-
CTCGGGGGGCGACTCGATGCG--TGACGCCCAGGCAGGCGTGCCCTCGACCTAGTGGTTTCGGGCGCAACTTGCGTTCAAAGA-CTCGATG---------GTTCA

P_rigidula   ----------------CTCG--------------------------AACTTTCTTCTCCTCCGCTTAATTATATGCTTAAACTCAGCGGGTGGCCCCGCC-TGACCTGGGGTCTTGG--
-TCCGAG-GA--TGC------CGTTCGGCAT------------CCGTGCGTCCGGGGTGACACGA--GGCTTCCCGCTCGGGGGCACGACGGGCGACGTACGGCTCGCGTGAGCAATCCACC-
```

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ACTCGCCACTGCCGGCCCCAATCGGCA--A--GCCACATGCTTCGGCCCGCCGAGCCCGAGG-------GCAAGGATGG-CCATGCTCCGCATCCCG-----CCACG-------TAAAA---GATGGGC--
AAGGAGCGTTAGTGGGCAACTGACGCCCAGGCAGGCGTGCCCTCAGCCGAATGGCCTCGGGCGCAACTTGCGTTCAAAAA-CTCGATG-GTTCA
```

Appendix 3. Character Matrix of ITS2 sequence data for Santalaceae and Viscaceae (**Chapter 3**).

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K_japonicum TTGAA-----------GCTTT-----------TGCCCAATGTGGATG--------ACCTGAGAACA-TGTT-G-------AACATGATGGCGAGG-------
TGAACGGACATGGGATGGCC----------TAGCTTCTGCCGC----GTAGCGGTTA--GATGCGTGCT-GGCCATTCCTTGTCCAC---CTCGGTGTGG-------
GATAAATGACTGGCGCGGGATGTGCCAAGTGATACTTTTGGTT-------CGGGGATGGATGGCCTTCTGGC--------GTGCCGCGCATTGCGGTTACGGCTT--------
GAGGGCCCCTCCCTTTCTATAATCATAGAATGACTCTTGACAACGGATATCTTGGCTCTCGCATCGATGAAGA-
GCGCAGCGAAATGCGATACTTGGTGTGAATTGCAGAATCCCGTGAATCATCGAGTTCTTGAACGCAAG-----TTGC

V_cruciatum --GAAT----------GCTCGTA-------------GAATG-------CCGTTGGACATGTGGAC--TGGTTGG------AACAT--AGGC-AGC-----GGGGTGCACGGG-
ATCTCCCCCGCGTGACCCCTTTTGGT-CGTTGGCGG---CATGCCTCGGGGGGC-GTGTGA--GCACT--TTGATCTAC--CTCTTACATCGGCACG--GGAAGTGCCAA---GGCAAAAAA----
CGGATTGGAAGAGCTCCTGG--------TGGCCCCGTGCGGTGTGCGCCTTTGAGGCGCTCGCGGGATCCACGAAGGTGACTTTTGAAATCAT--
GCTAAAACGACTCTCGGCAATGGATATCTCGGCTCCCGTGTCGAT-------------GAAGAACGCAGCGAAATGCGATACATGGTGTGAATTGCAGAATCTCGTGAATCATTGA-
GTTTTTGAACGCAAG---TTGC

O_lanceolata------------------------------------------------------------CTACGCTT-ATTGATATGCTTAAACTCAGCGGGTAACCCCACCGTG?CCCGGGGTCGCCA--
-----AATG?GTTCC--ATTCTCAC--------------TGTGTTAA--GAGTCCCACCAGTCTT-ATATCTCCTCACC-TGGTAACACGACTACCAACGC-----------TGTTA-----TC-
ACATACTCGTCATG--AGGCTTG-TCACC-ATGGT-ACTATTATATTTCGGCTATCCGCGC-ACCTTA---TTGG-ACGGGAAACCAACC-TTCGCTCCTAG-
GACCTTCACCCATCATAAAATATGGAAGACATGAGGAGCAGCACTATGCG--TGACGCCCAGGCAGGCGTGCCCTTGGCCTAATGGCTTTGGGCGCCCCTTGCGTTCAAAGACCTTGATGCATTA

S_album     --GAATTCCCCGGTTCGCTCGCCG---TTACTAAGGGAATCCTTGT-AAGTTTCTTTTCCTCCGCTTATTGATATGCTTAAACTCAGCGGGTAGCCCCACC-TGACCTGGGGTCGCAA--
-----AGGGACCTCTATTTTCAT--------------CATGTAAACAAAG--TCCCACGAATCTTTATAGTTTGTCGTG-TGGCGACCCGAAGAA-----GACGT-------TGTTA-----TCCACA-
ACTCGTCATG--AGACGCG-TCGCC-AAGG--ACTATAGTATTTCAGCTAACCGCGC-CATTGT---TTGC-ACGGGAAGCCAGCA-TTCGTTCCCAAAGGTCCCCGCCCAT--TAAAA---GGGGGT--
TAGGGAGCAGCACGGTGCG--TGACACCCAGGCAGGCGTGCCCTTAACCTAATGGCTTCGGGCGCACCTTGCGTTCCAAAGACTCGATGATTC?
s_pentandrum----TTTCCCCGGTTCGCTCGCCG---TTATCTAGGGGATCCTTGT-AAGTTTCTTTTCCTCCGCTTATTGATATGCTTAAACTCAGCGGGTAGCCCCGCC-TGACCTGGGATCGCAA--
-----AGGAAAATG-ATTC-CAT------------------------GGG--TCATACGAGTA------------CACA-TGATGGCACGAGA-------GACA--------TGTTA-----CC-ACA-
GGTCGTCGTG--AAACGTG-TCACC-AGTG--ACT-CCGAATTTCGATCAACCGC---ACTGT?---TCGT-ACGGGAG?CC?ACA-TCCAC-CCCAATACTC?CC?TCTCT--TA------GGAGG---
TTAGGGGCGACGC?ATGCA--TGATGCCCAGGC???CGTGCCCTCAGCCAAAAGGCTTTGGGCGCAACTTGCGTTCAAAAA-CTCGATGATTCA

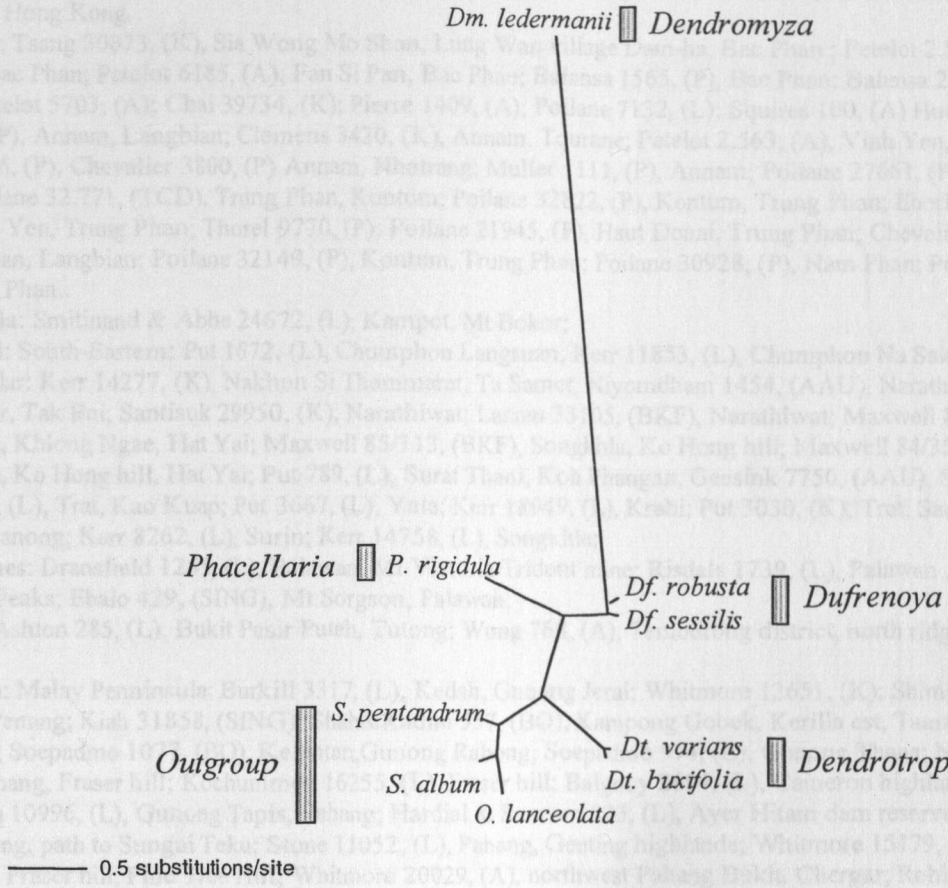
D_buxifolia -----CCCCGGTTCGCTCG--CCGTTACTAGGG--GAATCCTTGT--AAGTTTCTTTTCCTCCGCTTATTGATATGCTTAAACTCGGCGGGTAGCCCCGCC-TGACCTGGGGTCGCACT-
-GGTGAGCTCCGTCTCCCCCGAGAAGGAGAC------GAGATTAGAAGGT--CCCGGGAGTTT------------CGCACGGCGACACGGAGTCGGA-----CGC-------AGTCG----TCCAAAA-
CTCGTCCCG---CGACGCG-TCGCCGAGAAAACCATAT--TTCGGG-CCAGCCGCGCAGCAGTAAACATGC-ACGGGAGGCCA-ACGTTCGCGCCC-----CCAACGC----CCGAGAG---
GGGAGCTTTGGGGGGCGACTCGATGCG--TGACGCCCAGGCAGGCGTGCCCTCGACCTACTGGTTTCGGGCGCAACTTGCGTTCAAAGA-CTCGATGGTTCA
D_varians   -CATTCCCCGGTTCGCTCG--CCGTTACTAGGG--GAATCCTCGT--AAGTTTCTTTTCCTCCGCTTATTGATATGCTTAAACTCAGCGGGTAGCCCCGCC-TGACCTGGGGTCGCATT-
-GGTGAGCCCCGTCTCCCCCGAGAAGGAGAC------GAAATTCGAGGGT--CCTGGGAGTTT------------CGCACGGCGACACGGAGTCGGA-----CGC-------AGTCG----TCCAGAA-
CTCGTCCCG---CGACGCG-TCGCCGAGGAAACCGTAAAGTTTAGG-CCAGCCGCGCAATAGT---CGCGC-ACGGGAGGCCA-GCGTTCGCGCCC-----CCGACCCGTCCCCGAGAG---GGGAG-
TCCGGGGGGCGACTCGATGCG--TGACGCCCAGGCAGGCGTGCCCTCGACCTAATGGTTTCGGGCGCAACTTGCGTTCAAAGA-CTCGATGGTTCA

D_robusta   --ATTCACCGGATCCCTCGC-CAGTTTTTAGGTC---AATCCTTGT-AAGTTTCTTCTCCTCCGCTTATTTATATGCTTAAACTCAGCGGGTAGTCCCGCC-TGACCTGGGGTCG-GG--
-TCCGAACGA------------------------TGG-GTCCTTCGGGC--CCTC--ACGCC-------CGCTGCGAGCCGAGGCACGGCACCTAGA------ACAACTTGTGTCG-----CCCACC-
ATGTGCTGTGCCCGGCACGGTACGCCGGCA--GCCCCAAC-TTCGGCCCACCGCGCCCTGCG-------GCGCGGGGAG-CCAAACACCGCGTCCCG-----ACCCG---ACCCGAGG----AGGGG--
TTCGGGAGCGACTTTTGGCG--TGACGCCCAGGCAGGCGTGCCCTCGGCCAGAAGGCCTCGGGCGCAACTTGCGTTCAAAAA-CTCGATGGTTGG
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D_sessilis  ----ATTCCTCGG-TCTCGCGTCTCCGTTAGTATCGGAATCATTGTTAAGTTTCTTCTCCTCCGCTTATTTATATGCTTAAACTCAGCGGGTAGTCCCGCC-TGACCTGGGGTCGCGG--
-TCCGAGCGGCGTGCCC----TGCGGTCGG----TTGG-GTCCTTATGGCC?--CT--GCGCC-------GGTTGCGCGCC-GGGGCGCTGCAC-AGACAACA-ACTAGTGTCG--------CCCACC-
ATGTGCTGGGCCCGGCACGGAACGCCGGCA--GCCCCAAC-TTCGGTCCACCCCTCCCTGCT-------GCAGGGGGGG-CCAGACACAGATTCC-------ATCCG-----C-CAGGG---GGTGGT----
GGGAG?GTCTTTTGGCG--TGACGCCCAGGCAGGCGTGCCCTCGGCCAGAAGGCCTCGGGCGCAACTTGCGTTCAAAAA-CT-GATGGTTCC

D_ledermanii-AATTCCCCGGTTCGCTCG--CCGTTATTAGGG--GAATCCTCGT--AAGTTTCTTTTCCTCCGCTTATTGATATGCTTAAACTCAGCGGGTAGCCCCGCC-TGACCTGGGGTCGCACT-
-GGTGAG-----------------------------GGGTCCCGGGTGTTT-----------CGCACGGCAACGCGGAGTCGGACGC--------AGTTA----TCCAGAACTCGTCCCG------
CGACGCG-TCGCCGAGAGAACCGTGT--TTTCGGCCAGCCGCGCGATAGCCC--TGCGC-ACGGGAGACCA-?CGTTCGCGCCC-------CCGGCGT--CCGAGAG---GGGAG-
CTCGGGGGGCGACTCGATGCG--TGACGCCCAGGCAGGCGTGCCCTCGACCTAGTGGTTTCGGGCGCAACTTGCGTTCAAAGA-CTCGAT-------------GGTTCA

P_rigidula  ---------------CTCG----------------------------AACTTTCTTCTCCTCCGCTTAATTATATGCTTAAACTCAGCGGGTGGCCCCGCC-TGACCTGGGGTCTTGG--
-TCCGAG-GA--TGC------CGTTCGGCAT------------CCGTGCGTCCGGGGTGACACGA--GGCTTCCCGCTCGGGGGCACGACGGGCGACGTACGGCTCGCGTGAGCAATCCACC---
ACTCGCCACTGCCGGCCCCAATCGGCA--A--GCCACATGCTTCGGCCCGCCGAGCCCGAGG-------GCAAGGATGG-CCATGCTCCGCATCCCG-----CCACG-------TAAAA---GATGGGC--
AAGGAGCGTTAGTGGGCAACTGACGCCCAGGCAGGCGTGCCCTCAGCCGAATGGCCTCGGGCGCAACTTGCGTTCAAAAA-CTCGAT----GGTTCA
```



Appendix 3.1 Maximum Likelihood tree of ITS sequence data for Santalacean dendroparasites and outgroup taxa.

Maximum Likelihood tree generated using the heuristic search option with NNI branch swapping. Substitution rates were alowed to follow a gamma distribution with a shape parameter = 0.5. Base frequencies were estimated using the HKY '85 model which allows for unequal substitution rates. *Dendrotrophe* is a sister to the other dendroparasites; *Phacellaria* is a sister to *Dendromyza* and *Dufrenoya*. There are long branch lengths associated with *Dendromyza* and *Phacellaria*.

Appendix 4: List of Field numbers and locations of herbarium specimens from which measurements were taken for morphometric analysis **(Chapter 4).**

China: Hainan: Chow 78375, (E), Changjiang; How & Chun 70121, (E), Yacheng; Lau 5435, (E), Chim Fung Mt near Fong Ngau Po village Kan-en district; Fung 20209, (P) Chim Shan, Fan maan Ts'uen; Lei 374, (P), Pak Shik Ling; Henry 8527, (P); Liang 66469, (P); How 73951, (P); Chun 44326, (L), Mo San Len; Kwangtung: Tsang 22338, (P), Kwangtung border; Schindler 437, (P); Hong Kong: Hu & But 20103, (L), Ma On; Wright 400, (K), Hong Kong.
Vietnam: Tsang 30073, (K), Sia Wong Mo Shan, Lung Wan village Dam-ha, Bac Phan ; Petelot 2.561, (A), Fan Si Pan, Bac Phan; Petelot 6185, (A), Fan Si Pan, Bac Phan; Balansa 1565, (P), Bac Phan; Balansa 2320, (P) Bac Phan; Petelot 5703, (A); Chai 39734, (K); Pierre 1409, (A); Poilane 7132, (L); Squires 100, (A) Hue; Chevalier 40.447, (P), Annam, Langbian; Clemens 3420, (K), Annam, Tourane; Petelot 2.563, (A), Vinh Yen, Bac Phan; Pierre 326, (P); Chevalier 3800, (P) Annam, Nhatrang; Muller 1111, (P), Annam; Poilane 27661, (P), Annam, Hue; Poilane 32.771, (TCD), Trung Phan, Kontum; Poilane 32822, (P), Kontum, Trung Phan; Eberhardt 3824, (P), Vinh Yen, Trung Phan; Thorel 9770, (P); Poilane 21945, (P), Haut Donai, Trung Phan; Chevalier 30819, (P), Trung Phan, Langbian; Poilane 32149, (P), Kontum, Trung Phan; Poilane 30928, (P), Nam Phan; Poilane 3499, (P), Nam Phan..
Cambodia: Smitinand & Abbe 24672, (L), Kampot, Mt Bokor;
Thailand: South-Eastern: Put 1672, (L), Chumphon Langsuan; Kerr 11853, (L), Chumphon Na Sak, Langsuan. Penninsular: Kerr 14277, (K), Nakhon Si Thammarat, Ta Samet; Niyomdham 1454, (AAU), Narathiwat, Bang Nara river, Tak Bai; Santisuk 29950, (K), Narathiwat; Larsen 33105, (BKF), Narathiwat; Maxwell 85/60, (L), Songkhla, Khlong Ngae, Hat Yai; Maxwell 85/113, (BKF), Songkhla, Ko Hong hill; Maxwell 84/35, (A), Songkhla, Ko Hong hill, Hat Yai; Put 789, (L), Surat Thani, Koh Phangan; Geesink 7750, (AAU), Surat Thani; Put 3039, (L), Trat, Kao Kuap; Put 3667, (L), Yala; Kerr 18949, (L), Krabi; Put 3030, (K), Trat; Santisuk s.n., (BKF), Ranong; Kerr 8262, (L), Surin; Kerr 14758, (L), Songkhla;
Philippines: Dransfield 1255, (L), Palawan, Mt Victoria Trident mine; Risdale 1739, (L), Palawan , Narra Victoria Peaks; Ebalo 429, (SING), Mt Sorgson, Palawan;
Brunei: Ashton 285, (L), Bukit Pasir Puteh, Tutong; Wong 768, (A), Temburong district, north ridge of Bukit Retak.
Malaysia: Malay Penninsula: Burkill 3317, (L), Kedah, Gunong Jerai; Whitmore 12651, (K); Shimizu 13183, (KYO), Penang; Kiah 31858, (SING); Shah&Kadim 557, (BO), Kampong Gobek, Kerilla est, Tamangan Kelantan; Soepadmo 1077, (BO), Kelantan,Gunong Rabong; Soepadmo 974, (L), Gunong Thana; Nur 11286, (BO), Pahang, Fraser hill; Kochummen 16255, (L), Fraser hill; Balgooy 2684, (L), Cameron highlands, Pahang; Cockburn 10996, (L), Gunong Tapis, Pahang; Hardial & Samsuri 223, (L), Ayer Hitam dam reserve; Shah 1469, (A), Pahang, path to Sungai Teku; Stone 11052, (L), Pahang, Genting highlands; Whitmore 15179, (L), Pahang, Selangor, Fraser hill, Pine Tree Hill; Whitmore 20029, (A), northwest Pahang Bukit. Chergar; Robinson 5484, (SING), Pahang; Shah 2727, (SING), Pahang; Cockburn 11032, (L), Gunong Tapis, Selangor; Sarawak: Dyg et al 46864, (K), Bukit Dulit, Tinjar; Haron 21443, (L), Santubong; Ilias; Jawa 36623, (K), Pulau lakei, Kuching; Paie 46090, (L), Gunong Besi; Anderson 4742, (BO), Baram, Gunong Api; Anderson 30936, (L), Gunong Api, Ulu Melinau,Tutoh,Baram district, northeast flank of mountain; Brunig 10332, (L), Kuching; Chai & Wright 29915, (L), Bako national park, Telok Asam; Chai 39906, (L), Gunong Buda, Gunong Mulu national park; Purseglove 5032 (L, SING) Pulau Lakei; Awa 50867, (L), Bukit Lawi; Sabah: Beaman 8726, (A), Sipitang district Bukit Sebuboh 8km southwest of Sipitang; Beaman 9431, (A), Beaufort district 1.5km south of Weston; Clemens 28620, (A), Mt Kinabalu, Tenom; Clemens 29322, (L), Mt Kinabalu; Clemens 50332, (L), Mt Kinabalu, upper Penibukan west ridge; Clemens 31501, (L), Mt. Kinibalku; Pingkun 10152, (BO, L), Banjaran, forest district; Husin 86192, (L), Mandahan,Papar; Meijer 57544, (L), Kinabalu national park near boundary pole 76; Talib & Heya 80533, (L), Kimanis; Talib 50602, (L), Sipitang; Dewol & Talib 80417, (L), Kepayan; Castro 9992, (A); Carr 26951, (SING), Mt Kinanbalu; Stevens 345, (L), Sandakan;
Indonesia
Borneo: Giesen 160, (L), South Kalimantan; Giesen 161, (L), South Kalimantan; Koyama & Terao 31633, (A); Kuswata 1174, (L), East Kalimantan, north of Samarinda; Sidyasa 223, (E), Kalimantan Tengah;
Sumatra: de Wilde 20704, (L), S. ,SW of Gunong Leuser National park, Belintang village, 2 43N 97 54E; si Boeea 3465, (A), Langga Pajoeng; si Boeea 3318, (L), Kota Pinang; Teysmann 3509, (U), Bangka; Huitema 76 (L);
New Guinea: Henty 13684, (L), Markham Pt. near Lae
Australia: Smith 3752, (L), Mt. Edith Lamb, Queensland

Appendix 5: Transformed character matrix for female individuals of *Dendrotrophe varians* (**Chapter 4**)

field no.	country	leaf length	leaf width 1	leaf width 2	√petiolel	Logpeduncle 1	1/pedunclew	distance 1 - 2	Logtepal 1	√tepalw
12752	Philippines	60.00	41.00	24.00	2.83	0.60	1.00	11.00	0.11	1.05
16127	Malaysia	28.00	12.00	6.00	2.00	0.98	1.25	4.00	0.18	1.22
1267	Cambodia	70.00	22.00	10.00	3.16	0.40	0.77	8.00	0.00	1.22
1536	Malaysia	28.00	25.00	8.00	2.24	0.60	1.25	5.00	-0.10	0.84
	Borneo	57.00	25.00	9.00	0.95	0.54	1.43	5.00	0.08	1.05
1810	Philippines	74.00	31.00	11.00	2.65	0.88	0.67	7.00	0.00	1.05
	Java	27.00	14.00	5.00	2.00	0.30	1.67	3.00	-0.22	0.84
	Bangka	30.00	20.00	10.00	2.83	0.18	1.67	9.00	-0.10	0.84
400	Hong Kong	52.00	28.00	12.00	3.32	0.18	1.67	7.00	0.11	1.05
7132	Indochina	67.00	30.00	15.00	3.46	0.78	1.25	9.00	0.08	1.18
2.561	Vietnam	70.00	58.00	38.00	2.45	0.74	1.00	11.00	0.08	1.10
30073	Vietnam	75.00	32.00	15.00	3.16	0.40	1.00	8.00	-0.05	0.95
3509	Bangka	38.00	21.00	11.00	2.83	0.11	1.43	6.00	0.04	1.22
789	Thailand	68.00	31.00	14.00	2.83	0.48	1.00	8.00	0.15	1.18
18949	Thailand	32.00	25.00	10.00	2.24	0.18	1.00	5.00	-0.10	1.00
1672	Thailand	35.00	25.00	10.00	2.83	0.30	1.00	6.00	0.04	1.22
3039	Thailand	70.00	25.00	12.00	2.65	0.00	0.00	7.00	0.11	1.26
33105	Thailand	50.00	34.00	13.00	3.32	0.30	1.43	8.00	0.08	1.10
1255	Philippines	51.00	30.00	11.00	2.65	0.54	1.00	6.00	0.08	1.14
1739	Philippines	31.00	22.00	8.00	2.83	0.40	1.00	5.00	0.08	1.10
429	Philippines	65.00	40.00	20.00	2.83	0.40	1.00	8.00	0.00	1.00
2684	Malaysia	34.00	26.00	15.00	3.32	0.74	1.00	5.00	0.00	1.05
31657	Malaysia	42.00	21.00	10.00	2.45	0.81	1.00	5.00	0.08	1.10
11286	Malaysia	74.00	65.00	40.00	3.16	0.88	0.67	11.00	-0.05	0.95
11052	Malaysia	33.00	23.00	15.00	2.24	0.65	0.67	5.00	0.00	1.00
5484	Malaysia	48.00	29.00	14.00	2.00	0.60	1.25	6.00	0.00	1.10
223	Borneo	45.00	36.00	23.00	2.45	0.40	0.67	8.00	0.00	1.05
80417	Borneo	48.00	18.00	11.00	3.16	0.08	1.43	4.00	0.04	1.00
39906	Borneo	21.00	10.00	3.00	2.45	0.08	1.25	3.00	-0.10	0.89
768	Brunei	45.00	28.00	8.00	3.16	0.18	1.67	8.00	0.00	1.18
57544	Borneo	47.00	14.00	5.00	2.83	0.78	1.00	3.00	0.04	1.10
29322	Borneo	48.00	18.00	10.00	3.16	0.81	1.00	5.00	-0.05	0.95
10332	Borneo	60.00	30.00	18.00	3.16	0.30	1.00	6.00	0.00	1.00
10152	Borneo	58.00	28.00	11.00	3.16	1.00	1.00	7.00	0.08	1.00

9431	Borneo	71.00	48.00	20.00	3.16	0.30	1.00	10.00	0.00	1.00
80533	Borneo	48.00	29.00	12.00	2.65	0.54	1.25	8.00	0.00	1.00
10996	Malaya	56.00	3.00	15.00	2.45	1.26	0.67	6.00	-0.05	1.00
15179	Malaya	45.00	47.00	25.00	3.16	0.70	0.67	10.00	0.00	1.10
26951	Borneo	40.00	17.00	7.00	3.00	0.65	1.00	4.00		

field no.	country	leaf length	leaf width 1	leaf width 2	√petiolel	Logpeduncle 1	1/pedunclew	distance 1 - 2	Logtepal 1	√tepalw
26951	Borneo	40.00	17.00	7.00	3.00	0.65	1.00	4.00	0.00	1.10
5032	Borneo	71.00	28.00	15.00	2.65	-0.30	0.91	6.00	0.00	1.05
9992	Borneo	46.00	25.00	12.00	2.45	0.48	1.25	5.00	0.00	1.10
28620	Borneo	50.00	37.00	15.00	2.83	0.78	1.00	5.00	0.00	0.89
11623	Malaysia	39.00	25.00	11.00	2.83	1.08	1.00	4.00	-0.10	0.84
3465	Sumatra	50.00	39.00	15.00	2.65	0.54	1.00	8.00	0.00	1.10
557	Malaysia	45.00	28.00	14.00	3.87	0.40	1.25	10.00	0.04	1.05
85-113	Thailand	87.00	51.00	26.00	3.74	0.70	1.67	10.00	0.04	0.95
3030	Thailand	55.00	22.00	13.00	2.83	0.40	1.00	6.00	0.08	1.22
6.185	Vietnam	35.00	15.00	8.00	2.24	0.40	0.67	4.00	0.11	1.22
283	Borneo	33.00	19.00	6.00	2.45	0.30	1.00	3.00	0.00	1.05
76	Sumatra	35.00	18.00	10.00	2.24	0.60	1.00	5.00	-0.10	1.10
7750	Thailand	72.00	39.00	20.00	2.83	0.40	1.00	10.00	0.18	1.14
1454	Thailand	38.00	25.00	11.00	2.83	0.70	1.43	8.00	0.00	1.05
	Malaysia	61.00	34.00	21.00	2.24	0.78	1.00	3.00	0.04	1.14
3420	Vietnam	50.00	33.00	13.00	2.65	0.40	1.00	10.00	0.04	1.14
31858	Malaysia	65.00	51.00	28.00	3.16	0.08	1.43	6.00	-0.05	0.95
50652	Borneo	50.00	32.00	16.00	2.24	0.00	1.43	8.00	0.08	1.10
943	Malaysia	60.00	34.00	21.00	4.24	0.90	1.25	13.00	0.04	1.05
14277	Thailand	53.00	18.00	8.00	2.83	0.38	1.67	5.00	0.00	0.89
22731	Vietnam	62.00	27.00	6.00	2.45	0.40	1.00	8.00	0.04	1.05
3778	Vietnam	40.00	14.00	9.00	3.00	0.70	1.00	4.00	0.26	1.34
362	Vietnam	50.00	20.00	6.00	3.00	0.51	1.25	5.00	0.08	1.18
30.689	Vietnam	68.00	32.00	15.00	3.74	0.60	1.00	8.00	0.15	1.22
32.771	Vietnam	65.00	34.00	12.00	2.65	0.78	0.71	10.00	0.23	1.30
32567	Vietnam	44.00	22.00	11.00	3.61	0.54	1.00	6.50	0.18	1.22
7132	Vietnam	62.00	34.00	10.00	2.65	0.58	1.00	8.30	0.08	1.05
22338	China	42.00	22.00	8.00	3.16	0.30	0.67	9.00	0.04	1.10
27661	Vietnam	51.00	22.00	8.00	3.16	0.30	0.77	6.00	0.23	1.10
40.447	Vietnam	47.00	24.00	7.00	2.83	-0.40	1.25	7.00	0.18	1.26
20209		65.00	25.00	8.00	3.32	0.48	1.25	7.00	0.04	1.05
1111	Vietnam	55.00	24.00	15.00	2.45	0.60	1.00	6.50	0.20	1.18
3800	Vietnam	40.00	13.00	6.00	2.65	0.70	0.59	4.00	0.08	0.95
374	Hainan	40.00	16.00	5.00	2.83	0.18	1.25	4.00	0.04	1.05

2.563	Vietnam	56.00	30.00	11.00	2.83	0.40	1.43	9.00	0.04	1.10
16255	Malaysia	45.00	40.00	7.00	3.32	1.13	0.91	9.00	0.08	1.10
29915	Borneo	46.00	24.00	11.00	2.45	0.00	1.00	6.00	-0.10	0.95
46590	Borneo	75.00	20.00	5.00	2.45	0.11	1.11	5.00	0.04	1
161	Borneo	43.00	30.00	8.00	2.45	0.08	1.67	9.00	0.00	1
974	Malaysia	43.00	0.50	15.00	1.73	0.18	0.77	0.00	0.08	1.05

√tepalw	1/√filament length	Logstyle 1	fruit length	√fruit w	√endocarp 1	endocarp width2	endocarp width 3	Log apical chamber
1.05	1.58	0.00	9.00	2.74	2.45	6.00	4.00	0.00
1.22	1.41	-0.52	11.00	2.45	3.00	5.00	4.30	0.40
1.22	1.58	0.00	11.00	2.92	2.83	6.50	4.50	0.40
0.84	1.83	0.00	3.80	1.82	1.73	3.00	2.00	-0.15
1.05	1.83	0.00	7.00	2.35	2.24	4.00	2.50	0.00
1.05	1.58	0.00	10.00	2.74	2.65	5.50	4.00	0.00
0.84	2.24	0.00	6.00	2.00	2.24	3.50	2.50	0.18
0.84	1.83	0.00	7.50	2.24	2.12	4.00	3.50	-0.15
1.05	2.24	-0.52	12.00	2.65	3.00	6.00	4.50	0.40
1.18	1.83	-0.52	11.50	2.65	2.83	6.50	5.50	0.40
1.10	1.83	-0.30	12.50	2.83	3.32	6.50	4.50	0.48
0.95	1.83	-0.70	11.50	2.65	2.92	5.50	3.50	0.40
1.22	2.24	-0.52	8.00	2.45	2.35	4.00	3.00	0.00
1.18	2.24	-0.52	9.50	2.12	2.45	4.50	3.50	0.00
1.00	2.24	-0.70	9.00	2.74	2.55	5.50	4.50	0.11
1.22	1.58	0.00	6.50	2.45	2.55	5.50	4.50	0.11
1.26	1.41	-0.52	10.00	2.74	2.55	5.50	3.20	0.00
1.10	1.83	-0.40	8.50	2.45	2.55	5.50	3.50	0.11
1.14	1.83	0.00	10.50	3.08	2.74	7.00	3.50	0.18
1.10	1.58	0.00	9.00	2.83	2.45	5.50	4.00	0.11
1.00	2.24	0.00	8.00	2.55	2.45	6.00	4.00	0.08
1.05	2.24	-0.70	10.00	2.74	2.86	7.00	4.50	0.34
1.10	1.58	-0.40	9.50	2.45	2.65	4.00	2.50	0.38
0.95	1.41	-0.30	15.00	3.16	3.46	8.50	5.50	0.48
1.00	1.83	-1.00	9.00	2.74	2.68	6.50	4.50	0.40
1.10	2.24	0.00	9.50	2.45	2.74	4.00	3.00	0.38
1.05	2.24	-0.70	13.00	3.00	3.08	8.00	5.50	0.30
1.00	1.83	-0.70	5.00	2.00	1.73	3.50	2.50	0.00
0.89	1.83	0.00	6.00	2.24	2.17	3.80	3.00	0.08

1.18	1.83	0.00	13.00	2.55	2.92	5.00	3.50	0.40
1.10	1.83	-0.70	10.00	2.83	2.92	6.50	4.50	0.08
0.95	1.83	-0.70	10.00	2.83	2.65	6.00	3.50	-0.15
1.00	1.58	0.00	9.00	2.65	2.65	5.50	4.00	0.30
1.00	1.83	0.00	6.50	2.35	2.12	4.30	3.00	-0.30
1.00	2.24	0.00	8.00	2.74	2.35	5.50	4.00	0.18
1.00	1.83	0.00	7.00	2.45	2.35	4.50	3.50	0.00
1.00	2.24	0.00	8.00	2.74	2.55	5.20	3.00	0.18
1.10	1.83	-0.70	15.00	3.00	3.00	7.00	5.50	0.30

√tepalw	1/√filament length	Logstyle l	fruit length	√fruit w	√endocarp l	endocarp width2	endocarp width 3	Log apical chamber
1.10	1.83	-0.70	12.00	3.08	2.92	7.00	4.50	-0.30
1.05	1.83	0.00	6.00	2.24	2.00	3.50	3.00	0.00
1.10	1.83	0.00	6.00	2.35	2.00	4.50	3.50	-0.22
0.89	1.83	-0.52	9.50	2.65	2.65	5.00	3.00	0.00
0.84	1.83	0.00	8.00	2.65	2.45	6.50	5.50	0.18
1.10	1.83	0.00	9.00	2.45	2.35	5.00	3.00	0.00
1.05	1.83	0.00	8.00	2.35	2.45	5.00	3.00	0.00
0.95	1.83	0.00	10.50	2.55	2.65	5.50	3.00	0.18
1.22	1.83	-0.30	13.00	2.83	3.16	6.50	4.00	0.30
1.22	1.41	-0.30	14.00	3.00	3.00	6.00	5.00	0.30
1.05	1.83	-0.70	8.50	2.12	2.12	5.50	4.00	0.00
1.10	2.24	0.00	6.00	2.45	2.24	4.00	3.00	0.18
1.14	1.83	0.00	9.00	2.65	2.45	5.00	3.00	0.08
1.05	2.24	0.00	7.50	2.35	2.24	5.00	3.00	0.00
1.14	2.24	0.00	9.50	2.83	2.74	6.50	5.50	0.00
1.14	1.58	-0.70	10.50	2.92	3.00	6.50	4.00	0.40
0.95	2.24	0.00	7.00	2.35	2.55	5.50	4.50	0.18
1.10	1.83	0.00	6.50	2.35	2.24	4.50	3.50	0.00
1.05	1.58	-0.52	13.00	3.46	2.92	7.00	5.00	0.48
0.89	1.58	0.00	7.00	2.05	2.12	3.60	2.50	0.00
1.05	1.58	-0.52	10.60	2.74	2.74	5.50	3.00	0.34
1.34	1.20	0.00	17.00	3.05	3.61	8.00	4.50	0.54
1.18	1.58	-0.52	9.50	2.49	2.47	5.00	4.00	0.04
1.22	1.29	-0.52	13.50	3.16	2.92	7.50	5.00	0.43
1.30	1.20	-0.22	16.00	3.08	3.39	7.30	4.00	0.48
1.22	1.41	-0.15	12.50	2.83	3.08	7.00	4.50	0.48
1.05	1.83	-0.70	13.00	3.00	2.88	6.00	3.50	0.30

1.10	1.83	0.00	9.50	2.45	2.83	6.00	3.50	0.18
1.10	1.05	-0.30	14.50	3.16	3.16	8.00	5.00	0.40
1.26	1.58	-0.30	10.50	2.65	2.74	6.00	3.50	0.30
1.05	1.58	0.00	9.50	2.83	2.57	5.50	3.00	0.18
1.18	1.29	-0.30	12.00	2.45	2.83	5.00	3.20	0.30
0.95	1.58	-0.30	13.00	2.49	3.24	6.00	2.50	0.40
1.05	1.58	0.00	8.50	2.61	2.35	5.20	3.50	0.18
1.10	1.41	0.00	10.00	2.65	2.65	5.40	3.50	0.30
1.10	1.41	0.00	13.50	3.32	3.39	8.50	2.00	0.54
0.95	1.83	-0.22	6.50	2.35	2.12	4.70	2.00	0.18
1.00	2.24	0.00	8.20	2.41	2.24	4.50	1.50	0.00
1.00	2.24	0.00	7.50	2.45	2.12	4.00	3.00	-0.10
1.05	2.24	0.00	9.00	2.55	2.55	6.00	2.00	0.36

Appendix 6. Transformed character matrix for male individuals of *Dendrotrophe varians* (**Chapter 4**)

Field no.	Country	√Leaf length	√Leaf w2	√Leaf w1	√distance 1-2	√Petiole l	Pedicel length	width	√bract l	√bract w	√bract w base	Rece widt
1315	Malaysia	5.48	2.24	4.24	1.73	2.45	1.50	0.60	0.95	0.84	0.84	
1469	Malaysia	5.29	2.65	4.36	2.24	2.24	1.60	0.40	0.84	0.71	0.71	
8726	Malaysia	7.14	3.00	5.39	2.45	2.65	2.00	0.50	0.84	0.71	0.77	
8262	Thailand	7.75	3.16	5.48	2.45	2.45	1.60	0.60	0.84	0.77	0.84	
86192	Malaysia	7.81	2.45	5.00	2.45	2.83	1.60	0.40	0.84	0.71	0.77	
5503	Malaysia	6.56	3.16	5.00	2.24	2.24	1.00	0.40	0.63	0.55	0.55	
Teysmann	Bangka	5.57	2.45	3.87	2.24	2.24	1.00	0.60	1.00	0.55	0.71	
36623	Malaysia	6.78	3.16	4.69	2.45	2.00	1.20	0.70	0.84	0.71	0.71	
3317	Malaysia	6.56	3.74	6.00	3.00	2.65	0.60	0.30	0.95	0.71	0.55	
4742	Malaysia	4.69	2.00	3.32	2.00	2.24	0.70	0.40	0.84	0.63	0.55	
50867	Malaysia	5.20	2.45	3.74	2.00	2.45	1.50	0.50	0.89	0.77	0.63	
J&M Clemens	Malaysia	9.22	3.00	5.39	2.65	3.16	1.00	0.50				
20946	Malaysia	5.00	2.24	4.00	2.24	1.73	0.40	0.30	0.71	0.55	0.45	
13183	Malaysia	6.32	3.16	6.24	3.00	2.45	1.00	0.50	0.95	0.71	0.71	
1174	Borneo	5.83	2.45	4.69	2.24	2.65	1.20	0.40	0.77	0.71	0.63	
30936	Borneo	5.92	2.24	4.00	2.24	2.00	1.10	0.40				
285	Borneo	6.08	2.83	4.69	2.45	2.65	1.10	0.50	0.95	0.77	0.71	
78375	Hainan	8.12	3.16	5.10	2.65	2.65	2.50	0.70	0.89	0.89	1.00	
11853	Thailand	6.71	2.65	4.58	2.45	2.45	2.00	0.40	1.05	0.84	0.84	
84-35	Thailand	6.32	4.24	5.74	2.45	2.65	1.00	0.40	0.89	0.63	0.63	
85-60	Thailand	7.75	3.00	6.40	3.32	2.45	1.20	0.30	0.95	0.95	1.05	
13684	New Guinea	6.78	3.46	5.00	2.65	2.65	1.50	0.60	1.10	0.55	0.55	
23838	Vietnam	8.37	3.46	5.29	2.83	3.32	2.00	0.30	0.71	0.71	0.84	
3499	Vietnam	4.90	2.00	3.32	1.73	2.24	1.50	0.30	0.77	0.55	0.55	
437	China	4.58	2.24	3.46	1.41	2.24	2.70	0.70	0.89	0.84	0.77	
30928	Vietnam	5.66	3.46	3.16	2.65	1.00	4.00	0.60	0.89	0.77	0.95	
32149	Vietnam	7.55	3.00	5.48	2.83	2.65	2.50	0.70	0.84	0.77	0.89	
30819	Vietnam	4.69	2.00	3.46	2.00	2.45	3.20	0.70	0.71	0.77	0.84	
1565	Vietnam	6.00	2.24	3.74	1.73	2.00	2.00	0.40	0.71	0.77	0.84	
220	Cambodia	6.56	2.83	5.29	2.45	2.65	2.50	0.50	0.63	0.63	0.71	
2320	Vietnam	5.66	2.65	3.61	2.00	1.73	1.00	0.40	0.95	0.63	0.63	
9117	Vietnam	4.69	2.00	3.32	1.73	2.24	1.20	0.40	0.89	0.55	0.55	
66469	Hainan	5.48	2.24	3.61	1.73	2.45	1.80	0.50	0.71	0.63	0.71	

Tepal length	Log tepal width1	Log tepal w base	Log filament 1	√anther 1	style length
1.10	-0.70	-0.70	-0.52	0.55	0.10
0.90	-0.70	-0.40	-0.40	0.45	0.20
1.00	-0.70	-0.40	-0.70	0.55	0.50
1.40	-0.70	-0.52	-0.40	0.55	0.00
0.60	-0.70	-0.70	-1.00	0.45	0.20
0.80	-0.70	-0.52	-1.00	0.55	0.30
0.70	-0.70	-0.70	-0.70	0.55	0.30
0.60	-1.00	-0.70	-1.00	0.45	0.20
0.50	-1.00	-1.00	-1.00	0.45	0.20
0.40	-0.70	-0.70	-1.00	0.45	0.20
1.00	-0.70	-0.70	-0.70	0.45	0.30
0.60	-0.52	-0.52	-0.70	0.55	0.30
0.50	-0.70	-0.70	-0.52	0.45	0.30
0.70	-0.70	-0.70	-0.70	0.55	0.30
0.90	-0.70	-0.70	-0.70	0.55	0.30
0.60	-0.70	-0.52	-1.00	0.55	0.20
0.90	-0.70	-0.70	-0.70	0.55	0.30
1.30	-0.70	-0.70	-0.40	0.55	0.20
0.80	-0.70	-0.70	-0.70	0.45	0.30
0.80	-0.70	-0.70	-1.00	0.45	0.30
1.00	-0.70	-0.52	-0.70	0.55	0.20
0.80	-0.70	-0.70	-1.00	0.55	0.40
1.00	-0.70	-0.70	-0.70	0.63	0.20
0.80	-0.70	-0.70	-0.70	0.45	0.30
1.30	-0.52	-0.40	-0.52	0.55	0.30
1.00	-0.70	-0.70	-0.70	0.63	0.20
1.50	-0.70	-0.70	-0.40	0.55	0.00
1.40	-0.70	-0.52	-0.40	0.55	0.20
0.90	-0.70	-0.70	-0.70	0.45	0.10
1.10	-0.40	-0.22	-0.40	0.63	0.10
0.90	-0.70	-0.70	-0.70	0.55	0.20
0.80	-0.70	-0.70	-0.70	0.55	0.30
0.70	-1.00	-0.70	-0.52	0.55	0.20

Field no.	Country	√Leaf length	√Leaf w2	√Leaf w1	√distance 1-2	√Petiole 1	Pedicel length	width	√bract 1	√bract w	√bract w base	Rece widt
73951	Hainan	6.71	2.45	4.69	2.24	2.45	2.50	0.80	0.84	0.63	0.63	
8527		4.12	2.00	3.16	1.41	1.73	1.60	0.60	1.05	0.77	0.77	
3824	Vietnam	5.57	2.45	3.74	1.73	2.24	1.10	0.70	0.77	0.71	0.63	
Emweiss	Hong Kong	5.74	3.00	4.36	2.00	2.65	2.20	0.50	0.77	0.77	0.71	
5435	Hainan	7.07	2.45	4.58	2.45	3.32	3.00	0.45	0.71	0.77	0.55	
5.703	Vietnam	5.92	2.45	4.12	2.00	2.24	3.00	0.60	0.89	0.84	1.05	
44326	Hainan	6.08	3.32	5.10	2.24	2.83	2.00	0.70	0.84	0.84	0.77	
14758	Thailand	7.87	3.00	5.66	3.00	2.24	0.80	0.50	0.89	0.63	0.55	
Santisuk	Thailand	7.21	2.45	5.48	3.00	2.00	1.50	0.40	0.71	0.77	0.77	
1353	Bangka	6.40	3.00	4.58	2.65	2.24	1.30	0.40	0.89	0.77	0.71	
20704	Sumatra	7.21	2.83	5.74	3.00	2.65	0.90	0.40	0.63	0.71	0.77	
20103	Hong Kong	5.92	2.24	4.12	2.00	2.45	1.80	0.60	0.95	0.95	0.89	
11032	Borneo	6.00	2.00	4.24	1.73	1.73	2.00	0.30	0.77	0.63	0.55	
345	Borneo	5.74	2.24	4.24	2.24	2.00	0.60	0.30	0.77	0.71	0.71	
160	Borneo	7.42	2.45	4.36	2.24	2.65	1.30	0.40	0.71	0.77	0.71	
3752	Queensland	6.78	3.00	5.20	2.45	3.00	0.70	0.30	0.77	0.77	0.71	
29950	Thailand	7.75	3.46	6.08	3.00	3.16	1.50	0.30	0.95	0.89	0.84	
72302	Borneo	6.16	3.00	4.36	2.00	2.45	1.40	0.30	0.84	0.63	0.63	

Tepal length	Log tepal width1	Log tepal w base	Log filament 1	√anther 1	style length
1.20	-0.70	-0.70	-0.40	0.55	0.30
0.90	-0.70	-0.52	-0.70	0.55	0.40
1.00	-0.52	-0.52	-0.52	0.55	0.30
0.90	-0.70	-0.52	-0.52	0.45	0.20
1.10	-0.70	-0.52	-0.30	0.55	0.20
0.80	-0.70	-0.70	-0.52	0.63	0.20
0.80	-0.70	-0.70	-0.70	0.55	0.20
0.60	-0.70	-0.52	-0.70	0.55	0.20
0.80	-1.00	-0.70	-0.52	0.45	0.20
0.70	-0.70	-0.52	-0.70	0.45	0.40
0.70	-0.70	-0.52	-0.70	0.55	0.20
1.30	-0.70	-0.52	-0.40	0.55	0.20
0.60	-0.70	-0.70	-0.70	0.55	0.20
0.90	-0.70	-0.70	-0.70	0.55	0.20
1.00	-0.70	-0.52	-0.52	0.55	0.40
1.10	-0.70	-0.52	-0.70	0.55	0.10
0.90	-0.70	-0.70	-0.70	0.45	0.20
0.70	-0.70	-0.52	-0.70	0.45	0.20

Appendix 7. Canonical Discriminant Analysis for female individuals of *Dendrotrophe varians* (**Chapter 4**).

CDA including vegetative and inflorescence characters

Group means

GROUP	ANT.L	D.F.APEX	DIST.BET	ENDO.L
1	1.05878	.16872	6.16667	2.60595
2	1.13813	.35058	7.56190	2.95476
3	1.01152	.00290	6.15000	2.28180
Total	1.06853	.17551	6.55811	2.61733

GROUP	ENDO.W	ENDO.W2	ENDO.W3	FIL.L
1	2.62570	5.61515	3.69697	.60055
2	3.00108	6.77619	4.35714	.64811
3	2.19394	4.14500	2.85000	.55885
Total	2.61554	5.54730	3.65541	.60278

GROUP	FRUIT.L	FRUIT.W	LEAF.LEN	LEAF.W1
1	-.25635	9.43939	48.66667	25.80303
2	-.35183	12.62381	56.04762	29.47619
3	-.09825	7.00000	45.35000	24.05000
Total	-.24072	9.68378	49.86486	26.37162

GROUP	PEDUN.L	PEDUN.W	PET.L	STYLE.L
1	.49415	1.07505	2.85754	1.77249
2	.57969	.95215	2.98879	1.64507
3	.37072	1.30853	2.48313	1.97764
Total	.48507	1.10327	2.79359	1.79178

GROUP	TEPAL.L	TEPAL.W
1	.80909	.04004
2	1.03333	.08486
3	.68500	-.00993
Total	.83919	.03926

Group standard deviations

WAR.ALL	ANT.L	D.F.APEX	DIST.BET	ENDO.L
1	.09784	.16624	2.51454	.18517
2	.09941	.14688	2.32712	.21875
3	.11162	.15233	1.87153	.18751
Total	.11169	.20264	2.36046	.31773

WAR.ALL	ENDO.W	ENDO.W2	ENDO.W3	FIL.L
1	.22273	.63744	.74895	.05535
2	.24123	.88142	.92389	.06289
3	.22155	.51858	.56429	.05313

Total	.37679	1.19843	.93956	.06544

GROUP	FRUIT.L	FRUIT.W	LEAF.LEN	LEAF.W1
1	.31482	1.51429	13.81274	12.04674
2	.27887	1.98794	11.50424	7.90961
3	.21662	1.42681	13.56961	6.84009
Total	.29358	2.66546	13.60331	9.86556

GROUP	PEDUN.L	PEDUN.W	PET.L	STYLE.L
1	.32507	.26132	.45200	.30567
2	.23627	.24106	.52008	.33936
3	.27925	.24248	.49106	.22305
Total	.29683	.28219	.51540	.31825

GROUP	TEPAL.L	TEPAL.W
1	.34493	.07313
2	.35402	.08330
3	.22542	.08569
Total	.34276	.08613

Pooled within-groups correlation matrix

	ANT.L	D.F.APEX	DIST.BET	ENDO.L	ENDO.W	ENDO.W2
ANT.L	1.00000					
D.F.APEX	.18218	1.00000				
DIST.BET	.02566	-.00689	1.00000			
ENDO.L	.15174	.01569	.17189	1.00000		
ENDO.W	.36733	.49802	-.03020	.35812	1.00000	
ENDO.W2	.14228	.06662	.00908	.60532	.44835	1.00000
ENDO.W3	.12598	-.19225	-.00400	.12861	-.02225	.28957
FIL.L	.07458	-.14866	.01659	-.05117	-.04058	.06863
FRUIT.L	.03247	.02074	.12884	.00902	-.06222	-.04270
FRUIT.W	.39045	.35306	.07029	.38536	.80176	.38861
LEAF.LEN	-.02411	-.14176	.44846	.00586	-.16492	-.14052
LEAF.W1	-.13285	-.14796	.68159	.06237	-.14123	.05335
PEDUN.L	-.11845	-.09018	-.00895	.23107	.19219	.14408
PEDUN.W	-.05165	.04001	.21174	-.21797	-.12277	-.29553
PET.L	-.05693	-.08183	.49941	.10193	-.04799	.16282
STYLE.L	-.16098	-.13721	.00245	-.07828	-.12814	-.06061
TEPAL.L	.14937	-.15119	-.03413	.23410	-.05773	.13390
TEPAL.W	.67923	.15346	.08503	.09543	.35156	.15513

	ENDO.W3	FIL.L	FRUIT.L	FRUIT.W	LEAF.LEN	LEAF.W1
ENDO.W3	1.00000					
FIL.L	.13555	1.00000				
FRUIT.L	-.20409	-.02755	1.00000			
FRUIT.W	-.00321	.11850	-.15254	1.00000		
LEAF.LEN	-.19700	.12225	.20672	-.06228	1.00000	
LEAF.W1	.12126	.07822	.10733	-.08702	.51566	1.00000
PEDUN.L	.02571	-.14092	.00857	.10559	.02420	-.01998
PEDUN.W	.02249	.09199	.08063	-.06751	.09626	.20373
PET.L	.10572	.15893	.00973	.06144	.25726	.31959
STYLE.L	.02747	-.00138	-.16487	-.24383	.12187	.17369
TEPAL.L	.13220	.19627	-.15918	.09522	.03942	.03731
TEPAL.W	-.09144	.16808	.06163	.47381	.17219	-.04378

	PEDUN.L	PEDUN.W	PET.L	STYLE.L	TEPAL.L	TEPAL.W
PEDUN.L	1.00000					
PEDUN.W	-.28120	1.00000				
PET.L	-.00459	.32297	1.00000			
STYLE.L	-.14409	.03119	-.09072	1.00000		
TEPAL.L	.10220	-.18479	-.08435	.02306	1.00000	
TEPAL.W	-.03957	-.01033	.02116	-.38068	.18996	1.00000

Standardized canonical discriminant function coefficients

	Func 1	Func 2
ANT.L	-.03489	.44019
D.F.APEX	.36545	.18605
DIST.BET	-.09148	.60766
ENDO.L	.28481	-.01754
ENDO.W	.38636	-1.13644
ENDO.W2	.21313	.16641
ENDO.W3	.33564	-.08886
FIL.L	.25570	.07055
FRUIT.L	-.14395	.15526
FRUIT.W	-.01273	1.24940
LEAF.LEN	.45413	.16077
LEAF.W1	-.00574	-.27417
PEDUN.L	-.09295	.18184
PEDUN.W	-.16546	.37618
PET.L	.06467	-.69699
STYLE.L	-.23606	.14449
TEPAL.L	.06725	.09654
TEPAL.W	-.19787	-.60805

Structure matrix:

Pooled within-groups correlations between discriminating variables and canonical discriminant functions.
(Variables ordered by size of correlation within function)

	Func 1	Func 2
ENDO.W2	.66777*	-.14102
ENDO.W	.61883*	-.04438
ENDO.L	.59960*	.14428
FRUIT.W	.59752*	.31207
D.F.APEX	.38559*	.10356
ENDO.W3	.34624*	-.07967
FIL.L	.27307*	.08892
PEDUN.W	-.24876*	.19271
ANT.L	.21584*	.18959
TEPAL.W	.20802*	-.00552
STYLE.L	-.19624*	.10816
TEPAL.L	.18935*	.18536
FRUIT.L	-.15769*	.09300
PEDUN.L	.12589*	-.05009
DIST.BET	.10593	.32036*
PET.L	.18373	-.23360*
LEAF.LEN	.14163	.17729*
LEAF.W1	.09656	.11344*

* denotes largest absolute correlation between each variable and any discriminant function.

Canonical discriminant functions evaluated at group means (group centroids)

Group	Func 1	Func 2
1	.03332	-.54114
2	2.76702	.44448
3	-2.96035	.42618

Case Number	Mis Val	Actual Group		Highest Group	P(D/G)	P(G/D)	2nd Highest Group	P(G/D)	Discrim Scores
1		1		1	.6597	.9501	2	.0328	.0177
									.3709
2		1		1	.9765	.9780	3	.0137	-.1811
									-.5012
3		2		2	.7023	.9979	1	.0021	3.2268
									1.1483
4		3		3	.0113	1.0000	1	.0000	-5.8572
									-.3351
5		3		3	.2952	.9990	1	.0010	-3.1058
									1.9814
6		2		2	.3571	.5609	1	.4390	1.3331
									.3862
7		3		3	.6032	.9997	1	.0003	-3.8881
									.8138
8		3		3	.5648	.9993	1	.0007	-3.4098
									1.3960
9		2		2	.6902	.8618	1	.1382	2.0787
									-.0730
10		2		2	.8883	.9807	1	.0193	2.5103
									.8581
11		2		2	.6511	.9042	1	.0958	2.3401
									-.3777
12		3		3	.9867	.9885	1	.0115	-2.8229
									.3380
13		3		3	.5557	.8301	1	.1698	-1.8874
									.2711
14		1		1	.7028	.9390	2	.0529	.2318
									.2749
15		1		1	.0923	.9822	3	.0177	-.9129
									-2.5083
16		1		1	.7504	.9699	3	.0284	-.5830
									-.9822
17		2		2	.3129	.5112	1	.4885	1.2426
									.4348
18		1		1	.9159	.9763	3	.0194	-.3591
									-.6883
19		1		1	.9576	.9728	2	.0167	-.0132
									-.2505
20		1		1	.1134	.5535	2	.4465	1.8617
									-1.5464
21		1		1	.2992	.5896	3	.4102	-1.5189
									-.6040
22		1	**	2	.1980	.5053	1	.4946	1.7707
									-1.0544
23		3		3	.1877	.6179	1	.3812	-1.2549
									1.0874
24		2		2	.9457	.9939	1	.0061	2.9980
									.6858
25		3		3	.1929	.9984	1	.0016	-3.9554
									-1.0908
26		3		3	.2055	.9963	1	.0037	-3.6993
									-1.1920
27		1		1	.0111	.6639	2	.2816	.1834

							2.4562
28	1		1	.1475	.9131	2 .0869	1.2653
							-2.0609
29	1		1	.9075	.9767	2 .0211	.3013
							-.8909
30	1		1	.2730	.7859	2 .2141	1.4063
							-1.3848
31	3		3	.2081	.9521	1 .0479	-2.8778
							-1.3437
32	1		1	.8162	.9601	2 .0282	.0584
							.0957
33	3		3	.4984	.8105	1 .1894	-2.0256
							-.2943
34	1		1	.4338	.8866	3 .1046	-.5300
							.6220
35	2		2	.1817	.9997	1 .0003	3.5775
							2.1040
36	1		1	.7346	.9208	2 .0786	.7729
							-.8053
37	3		3	.9955	.9913	1 .0087	-2.8756
							.4680
38	1		1	.4351	.9927	3 .0056	-.2919
							-1.7897
39	1		1	.2466	.6460	2 .3540	1.5843
							-1.1693
40	3		3	.2614	.8238	1 .1760	-1.5523
							1.2631
41	1	**	3	.1711	.6931	1 .3069	-2.1228
							-1.2558
42	1		1	.5906	.8960	2 .0992	.4315
							.4048
43	2		2	.9865	.9771	1 .0229	2.6031
							.4248
44	2		2	.7472	.9925	1 .0075	2.7350
							1.2073
45	1	**	3	.6681	.9224	1 .0776	-2.0788
							.5975
46	3		3	.9964	.9941	1 .0059	-3.0339
							.3833
47	1		1	.6445	.9193	3 .0749	-.5437
							.1975
48	3		3	.6404	.9988	1 .0012	-3.2619
							1.3209
49	2	**	1	.4717	.6932	2 .3067	1.2577
							-.4805
50	2		2	.8273	.9525	1 .0475	2.5230
							-.1209
51	1		1	.1824	.9965	3 .0020	-.1327
							-2.3785
52	3		3	.8719	.9674	1 .0326	-2.5401
							.1140
53	2		2	.5986	.9991	1 .0009	3.5706
							1.0615
54	3		3	.8081	.9972	1 .0028	-3.4179
							-.0393
55	2		2	.3382	.6833	1 .3166	1.3543
							.8595
56	2		2	.5073	.9991	1 .0009	3.9017
							.1799
57	1		1	.8430	.9650	3 .0193	-.1319
							.0194
58	2		2	.2146	.9999	1 .0001	4.5140
							.6058
59	2		2	.1912	.9999	1 .0001	4.0027
							1.7795
60	2		2	.2541	.9779	1 .0221	3.1856

							-1.1570
61		2	2	.4777	.9422	1 .0578	1.9270
							1.3230
62		1	1	.5354	.9929	2 .0046	.0136
							-1.6587
63		2	2	.0880	.9990	1 .0010	4.3083
							-1.1319
64		1	1	.8205	.9158	2 .0827	.5985
							-.2649
65		1	1	.7838	.9071	2 .0910	.5802
							-.1075
66		1	1	.6382	.9194	2 .0743	.3333
							.3578
67		1	1	.1988	.9808	2 .0190	.7328
							-2.1968
68		1	1	.4434	.7551	3 .2446	-1.2420
							-.5373
69		1	1	.2361	.8916	2 .0804	.0853
							1.1572
70		2	2	.7019	.9785	1 .0215	2.9172
							-.3835
71		3	3	.6313	.8960	1 .1040	-2.0038
							.4965
72		3	3	.5525	.9268	1 .0732	-1.9932
							.9273
73		3	3	.2276	.9998	1 .0002	-3.7440
							1.9578
74		1	1	.6514	.9275	3 .0656	-.4876
							.2243

Classification results

Actual Group	No. of Cases	Predicted Group Membership 1	2	3
Group 1	33	30	1	2
		90.9%	3.0%	6.1%
Group 2	21	1	20	0
		4.8%	95.2%	.0%
Group 3	20	0	0	20
		.0%	.0%	100.0%

Percent of "grouped" cases correctly classified: 94.59%

CDA for female individuals of *Dendrotrophe varians*. Analysis based on inflorescence charactersistics only.

Standardized canonical discriminant function coefficients

	Func 1	Func 2
ANT.L	.16362	-.29638
D.F.APEX	.04833	-.13641
ENDO.L	.04281	.25446
ENDO.W	.33611	.32965
ENDO.W2	.20025	-.36796
ENDO.W3	.25588	.05035
FIL.L	.12602	.21471
FRUIT.L	-.21554	.28597

FRUIT.W	.60526	-.38723
PEDUN.L	.18073	-.40681
PEDUN.W	.14361	-.68016
PET.L	.07098	.71448
STYLE.L	.35499	.56957
TEPAL.L	-.20626	.21676
TEPAL.W	-.00986	.46316

Structure matrix:

Pooled within-groups correlations between discriminating variables and canonical discriminant functions
(Variables ordered by size of correlation within function)

	Func 1	Func 2
FRUIT.W	.77564*	-.11694
ENDO.W	.75937*	-.05997
ENDO.W2	.55097*	.20235
ENDO.L	.47887*	.19245
D.F.APEX	.34820*	-.18033
ENDO.W3	.30501*	.06096
ANT.L	.26508*	-.00905
TEPAL.W	.23334*	.09103
FRUIT.L	-.19190*	.13069
PET.L	.16375	.44639*
FIL.L	.22932	.34063*
STYLE.L	-.12548	.32422*
PEDUN.W	-.17340	-.26412*
TEPAL.L	.13365	.24134*
PEDUN.L	.13091	-.20007*

* denotes largest absolute correlation between each variable and any discriminant function.

Canonical discriminant functions evaluated at group means (group centroids)

Group	Func 1	Func 2
1	-.76825	.31773
2	2.67415	-.19422
3	-3.48924	-.53238

Case Number	Mis Val	Actual Group		Highest Group	Probability P(D/G)	P(G/D)	2nd Highest Group	P(G/D)	Discrim Scores
1		1		1	.9088	.9828	3	.0160	-.8799
									.7406
2		2		2	.0135	.9743	1	.0257	1.5665
									-2.9127
3		2	**	1	.1727	.5248	2	.4751	1.0370
									.8208
4		3		3	.0417	1.0000	1	.0000	-5.9793
									-.9227
5		3		3	.0894	.9902	1	.0098	-3.0204
									-2.6791
6		1		1	.8387	.9904	3	.0060	-.5549
									.8711
7		3		3	.1830	.9807	1	.0193	-2.8952
									-2.2771
8		1	**	3	.6690	.8322	1	.1678	-2.5930
									-.5050
9		2		2	.2163	.9982	1	.0018	3.0016
									1.5248

10	2	2	.8281	.9994	1	.0006	2.9992
							-.7155
11	2	2	.8375	.9824	1	.0176	2.0793
							-.2237
12	1	1	.9093	.9498	3	.0497	-1.1990
							.3863
13	1	1	.7275	.9857	2	.0120	-.2046
							.8823
14	1	1	.5876	.9208	2	.0781	.2537
							.1800
15	1	1	.8313	.9179	3	.0816	-1.2610
							-.0384
16	1	1	.9234	.9887	3	.0066	-.5167
							.6277
17	2 **	1	.2546	.5894	2	.4105	.8859
							.3172
18	1	1	.8078	.9802	3	.0191	-1.0043
							.9270
19	1	1	.5171	.9936	3	.0035	-.5353
							1.4423
20	2	2	.4718	.9906	1	.0094	2.4461
							1.0101
21	1	1	.3082	.8386	3	.1605	-1.1932
							-1.1566
22	1	1	.2171	.6236	2	.3760	.7040
							-.6243
23	1	1	.5486	.9628	2	.0306	-.1446
							-.5832
24	2	2	.4520	1.0000	1	.0000	3.9290
25	3	3	.5370	.9982	1	.0018	-4.4799
							-.0202
26	3	3	.8340	.9951	1	.0049	-4.0321
							-.2710
27	2	2	.5155	.9959	1	.0041	2.3484
							-1.2983
28	2	2	.5299	.9075	1	.0925	1.5566
							-.3398
29	1	1	.4013	.7981	2	.2016	.5815
							.2517
30	1	1	.5954	.9908	3	.0080	-.8066
							1.3354
31	3	3	.0783	.6339	1	.3661	-2.8764
							1.6401
32	1	1	.1472	.9882	3	.0116	-1.2229
							2.2216
33	3	3	.4108	.5886	1	.4114	-2.3382
							.1418
34	1	1	.8608	.9811	3	.0180	-.9527
							.8332
35	2	2	.2142	1.0000	1	.0000	4.3516
							.3234
36	2	2	.9664	.9957	1	.0043	2.4705
							-.3582
37	3	3	.9253	.9546	1	.0454	-3.1984
							-.2664
38	1	1	.8614	.9881	2	.0078	-.3617
							.6826
39	1	1	.1017	.6623	3	.3372	-1.3727
							-1.7332
40	1	1	.8294	.9243	3	.0752	-1.2058
							-.1096
41	1	1	.1874	.9424	3	.0576	-1.7222
							1.8794
42	1	1	.3664	.7566	2	.2431	.6160
							.0142
43	2	2	.7303	.9995	1	.0005	3.2321

								.3691
44	2		2	.9613	.9962	1	.0038	2.5724
								.0675
45	1		1	.1334	.6174	3	.3823	-1.5016
								-1.5508
46	3		3	.7610	.8786	1	.1214	-2.7591
								-.4184
47	1		1	.3014	.9859	3	.0139	-1.1621
								1.8155
48	1		1	.5637	.7785	3	.2214	-1.5819
								-.3783
49	2		2	.4682	.8712	1	.1288	1.5428
								.2934
50	2		2	.5201	.9238	1	.0762	1.5870
								-.5483
51	1		1	.5755	.9848	3	.0146	-1.0327
								1.3352
52	3		3	.7764	.8882	1	.1118	-2.8634
								-.1940
53	2		2	.7086	.9998	1	.0002	3.4809
								.0011
54	3		3	.8203	.9915	1	.0085	-3.5486
								-1.1590
55	1		1	.4064	.8969	2	.1008	.2214
								-.5887
56	2		2	.0042	1.0000	1	.0000	5.7876
								-1.3209
57	1		1	.4949	.9302	2	.0669	.1076
								-.4821
58	2		2	.6886	.9999	1	.0001	3.5323
								-.0955
59	2		2	.2003	1.0000	1	.0000	4.3199
								-.9064
60	2		2	.4251	.9989	1	.0011	3.0892
								1.0461
61	2		2	.9280	.9977	1	.0023	2.6176
								-.5766
62	1		1	.1676	.9163	2	.0835	.5032
								1.7161
63	2		2	.6615	.9992	1	.0008	3.1087
								.6043
64	1		1	.4861	.8818	2	.1177	.4257
								.4498
65	1		1	.9367	.9884	3	.0077	-.5733
								.6222
66	2	**	1	.1616	.5970	2	.4024	.6938
								-.9100
67	2		2	.8818	.9883	1	.0117	2.1871
								-.3139
68	1		1	.5269	.8502	3	.1493	-1.3119
								-.6752
69	1		1	.1702	.9509	2	.0252	-.3363
								-1.5140
70	2		2	.7448	.9996	1	.0004	3.1049
								-.8296
71	3		3	.7876	.9905	1	.0095	-3.8801
								.0376
72	1		1	.2075	.7034	3	.2966	-2.2491
								1.2938
73	1	**	3	.4736	.6406	1	.3594	-2.3234
								-.1642
74	1		1	.6833	.9647	3	.0350	-1.2669
								1.0339

Classification results

Actual Group	No. of Cases	Predicted Group Membership 1	2	3
Group 1	36	34	0	2
		94.4%	.0%	5.6%
Group 2	26	3	23	0
		11.5%	88.5%	.0%
Group 3	12	0	0	12
		.0%	.0%	100.0%

Percent of "grouped" cases correctly classified: 93.24%

Appendix 8: Principal Components Analysis for female individuals of *Dendrotrophe varians*.

PCA including vegetative and inflorescence characteristics

Variable	Communality	*	Factor	Eigenvalue	Pct of Var	Cum Pct
ANT.L	1.00000	*	1	6.53399	34.4	34.4
D.F.APEX	1.00000	*	2	2.82324	14.9	49.2
DIST.BET	1.00000	*	3	1.59039	8.4	57.6
ENDO.L	1.00000	*	4	1.21465	6.4	64.0
ENDO.W	1.00000	*	5	1.14670	6.0	70.0
ENDO.W2	1.00000	*	6	.94383	5.0	75.0
ENDO.W3	1.00000	*	7	.73148	3.8	78.9
FIL.L	1.00000	*	8	.70585	3.7	82.6
FRUIT.L	1.00000	*	9	.56378	3.0	85.5
FRUIT.W	1.00000	*	10	.53702	2.8	88.4
LEAF.LEN	1.00000	*	11	.51457	2.7	91.1
LEAF.W1	1.00000	*	12	.41155	2.2	93.2
LEAFW.2	1.00000	*	13	.37197	2.0	95.2
PEDUN.L	1.00000	*	14	.30055	1.6	96.8
PEDUN.W	1.00000	*	15	.18571	1.0	97.8
PET.L	1.00000	*	16	.16844	.9	98.7
STYLE.L	1.00000	*	17	.12714	.7	99.3
TEPAL.L	1.00000	*	18	.07970	.4	99.7
TEPAL.W	1.00000	*	19	.04944	.3	100.0

PCA scores for first five principal axes:

	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5
FRUIT.W	.90398	-.16908	.09066	-.01290	-.08972
ENDO.W2	.88842	-.07442	-.18138	-.05669	-.12194
ENDO.W	.88184	-.21887	.03104	-.10966	-.12794
ENDO.L	.86354	-.03232	-.14638	-.13469	-.04254
D.F.APEX	.65579	-.19781	.16847	-.10382	-.21469
ENDO.W3	.63105	.04308	-.34490	.25072	-.21274
TEPAL.W	.62427	-.14704	.52795	.14175	.34010
ANT.L	.60434	-.23487	.41039	.26880	.25926
FIL.L	.55295	.09200	.01547	.41370	.01606
PEDUN.W	-.50341	.29091	.40851	.25045	-.33515
TEPAL.L	.48923	-.00743	-.27902	.29466	.48066
STYLE.L	-.46835	.30065	-.39351	.30924	.08697
LEAF.W1	.27771	.84733	-.02601	-.01859	.02102
LEAFW.2	.27899	.74547	-.30333	.04406	.17146
DIST.BET	.34562	.72251	.24454	-.12757	-.11271
LEAF.LEN	.32709	.64030	.19089	-.09619	.32455
FRUIT.L	-.33610	.18295	.43956	-.39269	.26850

PEDUN.L	.33832	-.05921	-.35425	-.64486	.16361
PET.L	.44075	.44295	.15788	-.03045	-.48317

PCA including inflorescence characteristics only.

Variable	Communality	*	Factor	Eigenvalue	Pct of Var	Cum Pct
ANT.L	1.00000	*	1	6.17717	44.1	44.1
D.F.APEX	1.00000	*	2	1.46414	10.5	54.6
ENDO.L	1.00000	*	3	1.21745	8.7	63.3
ENDO.W	1.00000	*	4	1.00931	7.2	70.5
ENDO.W2	1.00000	*	5	.80800	5.8	76.3
ENDO.W3	1.00000	*	6	.70340	5.0	81.3
FIL.L	1.00000	*	7	.62337	4.5	85.7
FRUIT.L	1.00000	*	8	.57487	4.1	89.8
FRUIT.W	1.00000	*	9	.52516	3.8	93.6
PEDUN.L	1.00000	*	10	.36206	2.6	96.2
PEDUN.W	1.00000	*	11	.20367	1.5	97.6
STYLE.L	1.00000	*	12	.17486	1.2	98.9
TEPAL.L	1.00000	*	13	.10534	.8	99.6
TEPAL.W	1.00000	*	14	.05120	.4	100.0

PCA scores for first five principal axes:

	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5
FRUIT.W	.91799	.08755	-.02496	-.16173	-.01398
ENDO.W	.90671	.04400	-.13583	-.26199	-.03024
ENDO.W2	.88870	-.18143	-.03131	-.10422	.14319
ENDO.L	.85674	-.18361	-.08584	-.03608	.09984
D.F.APEX	.67810	.20404	-.16355	-.47456	-.07807
ANT.L	.63564	.49430	.17839	.14504	-.28023
TEPAL.W	.63498	.58230	.06387	.28495	-.20114
ENDO.W3	.62067	-.30061	.29077	-.04709	.30009
PEDUN.W	-.55449	.36918	.26677	-.19928	.26458
FIL.L	.53090	.01803	.46689	.15222	.47345
STYLE.L	-.50170	-.34496	.36758	-.20506	-.25445
FRUIT.L	-.36498	.42961	-.40055	.24460	.41807
PEDUN.L	.34368	-.42462	-.58906	.31269	.00660
TEPAL.L	.49388	-.22807	.33336	.55693	-.16602

Appendix 9. Canonical Discriminant Analysis for male individuals of *Dendrotrophe varians* (**Chapter 4**).
Analysis including vegetative and inflorescence characteristics

Group means

GROUP	PL	RL	SL	TL
1	2.27294	1.40909	.23182	.76364
2	2.47214	2.11538	.25385	1.13846
3	2.67573	1.38182	.23636	.80909
Total	2.42555	1.60217	.23913	.88043

GROUP	TW1	TW2	AL	BL
1	-.74002	-.66127	.48833	.83413
2	-.64872	-.52114	.56076	.82455
3	-.72634	-.64629	.52801	.85688
Total	-.71095	-.61809	.51829	.83686

GROUP	BW1	BW2	DBT	FL
1	.69135	.67372	2.16002	-.69432
2	.77450	.78209	2.11356	-.47524
3	.70968	.70312	2.81144	-.80844
Total	.71923	.71138	2.30266	-.65969

GROUP	LFL	LW1	LW2	PC.W
1	5.86520	4.22236	2.51983	.43182
2	6.27387	4.38178	2.52866	.60385
3	7.11566	5.66950	3.32087	.39091
Total	6.27972	4.61347	2.71388	.47065

GROUP	PCL
1	1.40000
2	2.21538
3	1.10909
Total	1.56087

Group standard deviations

GROUP	PL	RL	SL	TL
1	.33399	.28604	.08386	.15289
2	.35948	.40176	.13301	.19381
3	.35287	.27502	.08090	.18141
Total	.37617	.45190	.09770	.23534

GROUP	TW1	TW2	AL	BL
1	.10574	.08518	.05058	.09588
2	.09992	.13380	.03182	.11603
3	.09076	.14668	.05763	.14946

Total	.10630	.12947	.05643	.11397

GROUP	BW1	BW2	DBT	FL
1	.09384	.10099	.33489	.15213
2	.09214	.14385	.40073	.12090
3	.12644	.16183	.32462	.15188
Total	.10588	.13510	.44959	.18881

GROUP	LFL	LW1	LW2	PC.W
1	.79247	.60855	.39700	.11705
2	1.26822	.78528	.39544	.11630
3	.70998	.49237	.41109	.10445
Total	1.04347	.86835	.52076	.14086

GROUP	PCL
1	.48892
2	.69143
3	.41341
Total	.68068

Standardized canonical discriminant function coefficients

	Func 1	Func 2
PL	-.12667	.17945
RL	.17040	.56015
SL	.30127	.20360
TL	.00978	.32216
TW1	.04456	-.03665
TW2	.15809	.19093
AL	-.09807	.62631
BL	.03920	.17103
BW1	.18115	-.05108
BW2	-.09375	-.28616
DBT	-.75633	-.03065
FL	.56170	-.38518
LFL	.72413	-.05323
LW1	-.07696	.72704
LW2	-.36192	.06336
PC.W	.53471	-.04039
PCL	.15306	-.10654

Structure matrix:

Pooled within-groups correlations between discriminating variables and canonical discriminant functions
(Variables ordered by size of correlation within function)

	Func 1	Func 2
RL	.48813*	.36167
FL	.46654*	.08935
PCL	.42051*	.14321
PC.W	.38715*	.18184
BL	-.05246*	.02858
LW1	-.34689	.53671*
LW2	-.34982	.44106*
AL	.17736	.44063*

TL	.42096	.43371*
DBT	-.35560	.38092*
LFL	-.14307	.36761*
PL	-.08261	.35372*
TW2	.23556	.23575*
BW2	.13904	.19342*
TW1	.17027	.18580*
BW1	.14320	.17997*
SL	.03942	.04815*

* denotes largest absolute correlation between each variable and any discriminant function.

Canonical discriminant functions evaluated at group means (group centroids)

Group	Func 1	Func 2
1	-.26441	-1.30990
2	2.55758	.97834
3	-2.49377	1.46358

Case Number	Mis Val	Actual Group		Highest Group	Probability P(D/G)	P(G/D)	2nd Highest Group	P(G/D)	Discrim Scores
1		1		1	.6640	.9961	2	.0038	.4986
									-1.7965
2		2		2	.0481	.9934	3	.0061	1.2150
									3.0434
3		2		2	.2366	.9994	1	.0003	1.8065
									2.5011
4		1		1	.6339	.9893	3	.0107	-1.2125
									-1.4229
5		3		3	.8818	.9961	1	.0039	-2.0047
									1.5745
6		1		1	.8814	.9991	3	.0006	-.3811
									-1.7986
7		1		1	.8038	.9870	3	.0127	-.8920
									-1.1026
8		3		3	.0039	1.0000	1	.0000	-5.6343
									.3487
9		1		1	.0353	.9994	3	.0006	-2.0754
									-3.1567
10		1		1	.7363	.9876	2	.0121	.5180
									-1.3137
11		1		1	.1985	.9999	3	.0001	-.8538
									-3.0089
12		3		3	.5744	.9998	1	.0002	-2.1675
									2.4648
13		1		1	.2182	.6338	3	.3567	-.7682
									.3607
14		1	**	3	.1562	.7394	1	.2282	-.5960
									1.1301
15		2		2	.8273	.9998	1	.0002	2.8519
									1.5192
16		1		1	.9456	.9958	2	.0034	.0698
									-1.3191
17		3		3	.3722	.9997	1	.0003	-3.8232
									1.0063
18		3		3	.8822	.9995	1	.0005	-2.4691
									1.9637
19		3		3	.9033	.9958	1	.0042	-2.0459
									1.5160
20		3		3	.7411	.9993	1	.0007	-2.0867

							2.1221
21	1	1	.4983	.9998	2	.0002	-.0391
							-2.4685
22	2	2	.1979	1.0000	1	.0000	4.3555
							1.0658
23	2	2	.6722	.9999	1	.0001	3.4489
							.9832
24	1	1	.2312	.9925	2	.0075	1.1379
							-2.2907
25	2	2	.0942	.9885	3	.0093	1.0853
							2.5778
26	1	1	.8679	.9870	3	.0104	-.4357
							-.8060
27	1	1	.8169	.9844	2	.0119	.0712
							-.7697
28	1	1	.2832	.9634	2	.0365	1.2644
							-1.7410
29	2	2	.4959	.9994	1	.0006	3.4679
							.2207
30	2	2	.3467	.9643	1	.0357	2.5677
							-.4772
31	2	2	.6293	.9984	1	.0016	3.1344
							.2078
32	1	1	.3755	.9110	2	.0889	1.1270
							-1.1587
33	2	2	.9459	.9955	1	.0045	2.2785
							.7958
34	2	2	.4083	.9070	1	.0929	2.0200
							-.2474
35	1	1	.1408	.6561	2	.2470	.1599
							.6241
36	3	3	.2703	.9551	1	.0373	-.8860
							1.6420
37	1	1	.9483	.9972	3	.0023	-.5600
							-1.4468
38	1	1	.7883	.9791	3	.0180	-.5088
							-.6649
39	3	3	.7067	.9687	1	.0313	-2.1194
							.7192
40	2	2	.6630	.9981	1	.0019	3.0508
							.2176
41	1	1	.7024	.9910	2	.0088	.5544
							-1.4999
42	1	1	.4824	.9349	3	.0650	-1.4010
							-.9023
43	2	2	.6718	.9678	1	.0322	1.9662
							.3106
44	3	3	.8953	.9954	1	.0046	-2.0248
							1.4989
45	3	3	.9262	.9933	1	.0067	-2.1699
							1.2433
46	1	1	.2973	.9980	3	.0019	-1.4946
							-2.2652

Classification results

Actual Group		No. of Cases	Predicted Group Membership 1	2	3
Group	1	22	21	0	1
			95.5%	.0%	4.5%
Group	2	13	0	13	0

			.0%	100.0%	.0%
Group	3	11	0	0	11
			.0%	.0%	100.0%

Percent of "grouped" cases correctly classified: 97.83%

CDA for male individuals of *Dendrotrophe varians*. Analysis based on inflorescence charactersistics only.

Standardized canonical discriminant function coefficients

	Func 1	Func 2
RL	.44396	.28393
SL	.11115	.45339
TL	-.07262	-.06679
TW1	.35188	-.23924
TW2	-.39844	.09878
AL	.20208	-.23258
BL	.19891	.47337
BW1	.07239	.12577
BW2	-.21446	.22807
FL	.65352	.49549
PC.W	-.19648	-.82435
PCL	.89929	-.17765

Structure matrix:

Pooled within-groups correlations between discriminating variables and canonical discriminant functions
(Variables ordered by size of correlation within function)

	Func 1	Func 2
PCL	.66264*	-.29582
RL	.43811*	.11971
FL	.42567*	.29177
TL	.33425*	.04437
TW2	.13215*	.00086
PC.W	.19964	-.47319*
BW1	.16945	.41753*
AL	.16491	-.29225*
BW2	.16822	.23296*
BL	-.04022	.22175*
SL	-.02784	.15313*
TW1	.13965	-.14078*

* denotes largest absolute correlation between each variable and any discriminant function.

Canonical discriminant functions evaluated at group means (group centroids)

Group	Func 1	Func 2
1	.19164	.49690
2	-3.00459	-.59033
3	4.86814	-.74930

Case Number	Mis Val	Sel	Actual Group	Highest Group	Probability P(D/G)	P(G/D)	2nd Highest Group	P(G/D)	Discrim Scores
1			1	1	.5291	.9995	2	.0005	.4001
									1.6058
2			1	1	.5956	.9997	3	.0002	1.0385

3	1	1	.2574	.9779	3	.0220	1.0619 1.7230
4	2	2	.7066	.9879	1	.0121	-.1105 -2.4032
5	2	2	.2975	.9999	1	.0001	-1.1673 -3.7313
6	2	2	.7364	.9770	1	.0230	-1.9675 -2.2878
7	2	2	.1719	1.0000	1	.0000	-.9035 -4.2452
8	2	2	.2482	.9996	1	.0004	-1.9983 -4.1231
9	2	2	.3712	1.0000	1	.0000	.6489 -4.2978
10	1	1	.9458	.9902	2	.0098	-1.1468 -.0830
11	2	2	.1327	.7809	1	.2191	.3071 -2.2534
12	1	1	.6113	.9334	2	.0666	1.2739 -.7963
13	1	1	.4196	.7896	2	.2104	.5881 -.9589
14	1	1	.7475	.9653	2	.0347	-.1460 -.5693
15	3	3	.5732	.9999	1	.0001	.5520 4.6043
16	1	1	.2483	.9997	3	.0002	.2722 1.2556
17	2	2	.8914	.9992	1	.0008	1.7832 -3.4763
18	1	1	.0683	.9027	2	.0973	-.5044 -1.4504
19	2	2	.2875	.9638	1	.0362	2.1317 -1.8736
20	1	1	.3557	.9958	3	.0038	-1.6922 1.2472
21	1	1	.9196	.9891	2	.0109	-.4794 -.2097
22	3	3	.9347	1.0000	1	.0000	.5786 4.5894
23	3	3	.3157	1.0000	1	.0000	-.5099 6.3867
24	1	1	.5328	.9984	3	.0012	-.7394 1.0786
25	3	3	.3096	.9998	1	.0002	-.1906 3.8623
26	1	1	.4551	.8214	2	.1786	-1.9039 -1.0481
27	1	1	.8067	.9708	2	.0292	.3033 -.3969
28	1	1	.8342	.9965	2	.0035	.2085 .3732
29	3	3	.2182	.9994	1	.0006	-.0772 3.6256
30	1	1	.9302	.9984	2	.0016	-1.9744 .3087
31	1	1	.2924	.9835	2	.0164	.8589 .2221
32	1	1	.2122	.9613	3	.0386	-1.0711 1.9224
33	3	3	.4172	1.0000	1	.0000	.1730 5.9221
34	3	3	.9304	1.0000	1	.0000	.0490 5.0866
35	1	1	.0335	.9894	3	.0060	-.4387 .9405

								-1.9991
36	2		2	.5563	.8857	1	.1143	-1.9630
								-.2937
37	1		1	.4141	.9681	2	.0319	-.8174
								1.3600
38	1		1	.2044	.9775	2	.0225	-.8927
								1.9111
39	2		2	.9804	.9936	1	.0064	-2.8071
								-.5665
40	1		1	.1656	.9814	3	.0186	2.0003
								1.0668
41	1		1	.3378	.9961	3	.0035	1.1990
								-.5783
42	2		2	.5849	.9761	1	.0239	-2.7216
								.4060
43	1		1	.7245	.9967	2	.0033	-.0600
								1.2592
44	2		2	.7043	.9877	1	.0123	-2.8764
								.2371
45	1		1	.2556	.9996	2	.0004	.2856
								2.1461
46	1	**	2	.4280	.7914	1	.2086	-1.7293
								-.3238

Classification results

Actual Group		No. of Cases	Predicted Group Membership 1	2	3
Group	1	26	25	1	0
			96.2%	3.8%	.0%
Group	2	13	0	13	0
			.0%	100.0%	.0%
Group	3	7	0	0	7
			.0%	.0%	100.0%

Percent of "grouped" cases correctly classified: 97.83%

Appendix 10 : Principal Components Analysis for male individuals of *Dendrotrophe varians*.

PCA including vegetative and inflorescence characters

Variable	Communality	*	Factor	Eigenvalue	Pct of Var	Cum Pct
AL	1.00000	*	1	4.74723	27.9	27.9
BL	1.00000	*	2	3.93966	23.2	51.1
BW1	1.00000	*	3	1.70874	10.1	61.2
BW2	1.00000	*	4	1.42969	8.4	69.6
DBT	1.00000	*	5	.93282	5.5	75.0
FL	1.00000	*	6	.75689	4.5	79.5
LFL	1.00000	*	7	.69214	4.1	83.6
LW1	1.00000	*	8	.67156	4.0	87.5
LW2	1.00000	*	9	.47082	2.8	90.3
PC.W	1.00000	*	10	.38174	2.2	92.5
PCL	1.00000	*	11	.28431	1.7	94.2
PL	1.00000	*	12	.26423	1.6	95.8
RL	1.00000	*	13	.24435	1.4	97.2
SL	1.00000	*	14	.16878	1.0	98.2
TL	1.00000	*	15	.13725	.8	99.0
TW1	1.00000	*	16	.11584	.7	99.7
TW2	1.00000	*	17	.05391	.3	100.0

PCA scores for first five principal axes:

	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5
RL	.88145	.03952	.11408	-.09570	-.03845
TL	.86099	.13796	-.00278	.07094	.00222
FL	.79044	-.08305	-.16663	-.21227	-.04499
PCL	.77948	-.00399	.09865	-.07369	-.28847
TW2	.57902	-.02816	-.48056	.22834	.37312
BW2	.57853	.43654	.40027	-.20406	.21629
PC.W	.55811	-.12907	.38683	.31299	-.41052
BW1	.54766	.43964	.44975	-.26110	.33820
AL	.50546	.09607	-.24350	.38778	-.29045
LW1	-.18086	.91838	-.10968	.09619	.02123
LFL	-.01326	.88263	-.14056	-.02070	-.10729
DBT	-.26697	.86918	-.04824	.03576	.02129
LW2	-.26141	.77393	.02729	.25748	-.06305
PL	.17280	.66959	-.18666	.12692	-.18271
BL	-.14683	.06574	.74533	.40777	.25058
SL	-.14093	-.22955	.27593	.66684	-.03847
TW1	.46471	-.13914	-.39306	.50042	.42283

PCA including inflorescence characteristics only.

Variable	Communality	*	Factor	Eigenvalue	Pct of Var	Cum Pct
AL	1.00000	*	1	3.88701	35.3	35.3
BL	1.00000	*	2	1.89942	17.3	52.6
BW1	1.00000	*	3	1.25218	11.4	64.0
BW2	1.00000	*	4	1.03276	9.4	73.4
DBT	1.00000	*	5	.84273	7.7	81.0
FL	1.00000	*	6	.54534	5.0	86.0
PC.W	1.00000	*	7	.45550	4.1	90.1
PCL	1.00000	*	8	.38221	3.5	93.6
TL	1.00000	*	9	.30198	2.7	96.4
TW1	1.00000	*	10	.24235	2.2	98.6
TW2	1.00000	*	11	.15850	1.4	100.0

PCA scores for first five principal axes:

	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5
TL	.86281	.03527	.01820	-.00635	-.02618
FL	.76909	-.13794	.12467	-.30942	-.00874
PCL	.76439	.02879	-.20303	-.31869	.03045
TW2	.60654	-.41900	.33566	.22030	-.25511
BW1	.55431	.69446	.17389	-.04935	-.26997
BW2	.60858	.64781	.15303	.02697	-.01267
PC.W	.55981	.05969	-.62241	.00968	.24590
DBT	-.20112	.50992	.59245	.24273	.32506
TW1	.49950	-.47159	.07111	.56646	-.27345
BL	-.11032	.52552	-.53242	.54083	-.17635
AL	.55294	-.19663	.04309	.33367	.65644