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Evolutionary History and Taxonomy of Neotropical Marattioid Ferns:

Studies of an Ancient Lineage of Plants

by

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They arrived at an inconvenient time
I was hiding in a room in my mind
They made me look at myself, I saw it well
I'd shut the people out of my life

So now I take the opportunities
Wonderful teachers ready to teach me
I must work on my mind, for now I realise
Every one of us has a heaven inside

They open doorways that I thought were shut for good
They read me Gurdjieff and Jesu
They build up my body, break me emotionally
It's nearly killing me, but what a lovely feeling!

I love the whirling of the dervishes
I love the beauty of rare innocence
You don't need no crystal ball
Don't fall for a magic wand
We humans got it all, we perform the miracles

Them heavy people hit me in a soft spot
Them heavy people help me
Them heavy people hit me in a soft spot
Rolling the ball, rolling the ball, rolling the ball to me

Kate Bush ❧ The Kick Inside, 1978

This dissertation is based on the following studies, which are referred to by their Roman numerals in the text:

I Christenhusz, M. J. M. 2006. Three new species of *Danaea* (Marattiaceae) from French Guiana and the Lesser Antilles. *Annales Botanici Fennici* 43: 212-219.

II Christenhusz, M. J. M. and Tuomisto, H. 2006. Five new species of *Danaea* (Marattiaceae) from Peru and a new status for *D. elliptica*. *Kew Bulletin* 61: 17-30.

III Christenhusz, M. J. M. and Cremers, G., in review. Two new epitypes in *Danaea* (Marattiaceae, Pteridophyta) selected from original historical collections in Paris. Manuscript submitted to *Candollea.*

IV Christenhusz, M. J. M., Tuomisto, H., Metzgar, J. and Pryer, K. M., in press. Evolutionary relationships within the Neotropical, eusporangiate fern genus *Danaea* (Marattiaceae). *Molecular Phylogenetics and Evolution.*

V Christenhusz, M. J. M. and Toivonen, T. K., in review. Giants invading the tropics: The Oriental vessel fern, *Angiopteris evecta* (Marattiaceae). Manuscript submitted to *Biological Invasions*.

CONTENTS


Maarten Christenhusz

1. INTRODUCTION

1.1. Importance and history of giving names

> 'Is it you, Moonchild?' Bastian asked. She laughed in a strangely lilting way. 'Who else would I be? Why, you've just given me my lovely name. Thank you for it. Welcome my saviour and my hero.'... 'Look, Moonchild,' he whispered 'It's glowing and glittering. And there - look! A little flame is coming out of it. No, it's not a grain of sand, it's a seed. It's a luminous seed and it's starting to sprout!' 'Well done, my Bastian!' he heard her say. 'You see how easy it is for you.' ... The seed sprouted so quickly that one could see it grow. It put forth leaves and a stem and buds that burst into many-coloured, phosphorescent flowers. Little fruits formed, ripened, and exploded like miniature rockets, spraying new seeds all around them.
> From the new seeds grew other plants, but these had different shapes. Some were like ferns or small palms, others like cacti, horsetails, bulrushes or gnarled trees. Each glowed in a different colour. ... 'You must give all this a name,' Moonchild whispered. Bastian nodded. 'Perilin, the Night Forest,' he said.

In this passage from *The Neverending Story* (Ende 1979 [1983]) Bastian realises that everything needs a name; thus he becomes a taxonomist. The power of name-giving makes him the creator and saviour of a vast land with all its creatures, who need names to exist. It is easy for Bastian, as a human, to assign new names; since early history humans have named and classified the organisms that surround them. The basic semantic function of words is that of naming (Lyons 1977). In the human mind nothing really exists without a name, because it is difficult to communicate about nameless subjects. Names are therefore vital for the recognition and acceptance of a species, for example to enact legislation for protection and trade. Taxonomy, and the names it provides, has for a long time formed the backbone of biology. Nevertheless its importance is sometimes ignored, and in the 21st century it has evolved in a highly specialised sub-discipline of evolutionary science. For the biologist, however, it is vitally important that data on a species are communicated by its correct name, so that the information is verifiable. Few people realise that even at present not all organisms have been named. Chapman (2006) has estimated that only about 19% (1.8 million) of the world's species have been described. The majority of undescribed taxa are to be found in fungi, bacteria and beetles, but almost 20% of seed plants are also presumed to be unknown to science. Pteridophytes (which consist of two lineages of vascular spore-bearing plants: ferns or Monilophyta and clubmosses or Lycophyta; Fig. 1) are estimated to represent about 15,000 species worldwide, of which only about 85% have been described (Chapman 2006). Taxonomy is therefore greatly needed to identify, describe and classify the remaining unknown species.

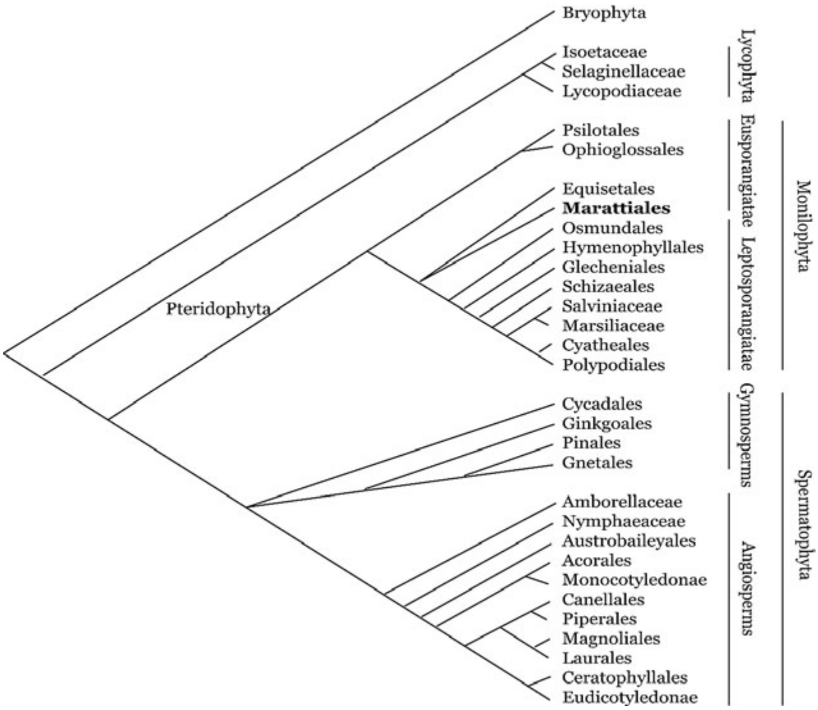

Figure 1. Cladogram of extant lineages of vascular plants; based on Pryer et al. (2001, 2004), Smith et al. (2006) and Qiu et al. (2006).

Plant taxonomy deals not only with the naming of plants, but also with their identification, description, delineation and classification. In ancient times Greek philosophers classified plants according to their growth form and habit (Lawrence 1951). These works were copied during the Middle Ages, but it was naturalists such as Lobelius, Dodoens (Dodonaeus) and Clusius who, in the 16th century Renaissance, first based descriptions and illustrations on direct observations of plants and animals (Egmond 2005). Dodoens (1554), who studied the plants in his large herbal garden, decided to classify plants according to their medicinal uses. The technique of preserving plants by drying them under pressure resulted in herbals, *horti sicci* and herbaria, in which plants were organized according to these medicinal classifications (Christenhusz 2004).

At that time species names were usually written as polynomials: a descriptive phrase consisting of several words, acceptable in various languages. This became confusing when the number of newly discovered species increased, and the polynomials were therefore listed by Bauhin (1623). Later Linnaeus (1753) assigned them binomial names.

Linnaeus (1753) sorted his species in a deliberately artificial classification (i.e. the Linnaean sexual system), serving the sole purpose of identification. An increased knowledge on the anatomy, morphology, and life cycles led to the realization that there are more natural affinities between plants than was indicated by these artificial classifications (Lawrence 1951). Several systems based on morphological relationships were hence proposed (e.g. Adanson 1763, Lamarck 1778, Jussieu 1789, Candolle 1813, Bentham and Hooker 1862-1883). The application of the theory of natural selection as a mechanism for evolution (Darwin 1859) required major changes in the traditional systems. Eichler (1875-1878) was first to propose a system implementing genetic relationships between plants. Other classifications with Darwin's evolutionary theory in mind soon followed (e.g. Engler and Prantl 1887-1915, Wettstein 1901, Hutchinson 1926-1934).

More recently, molecular techniques have found increased use in phylogenetic studies, which are resulting in redefinition of many (mostly higher) taxa to describe monophyletic groupings of species and genera. The fern classification by Smith et al. (2006) is a good example of a recent classification system based on a combination of molecular and morphological characters.

1.2. Focus

In this dissertation, I am studying and revising the taxonomy of fern species from tropical America, an area with extraordinarily high species richness (Gentry 1988). Recent ecological studies in Amazonia have revealed that plant diversity correlates well with, among other factors, edaphic gradients in the forest (Ruokolainen et al. 1997, Tuomisto et al. 2002, 2003, Tuomisto 2006). In Amazonia several fern species appear to have a narrow ecological range and a clear preference for certain soil types (Tuomisto and Poulsen 1996). Thus, ferns can be used as indicators of different forest types. However, many fern genera in South America are poorly taxonomically understood; they cannot be used as indicators until their taxonomy is clarified.

This is especially evident in the tropical fern family Marattiaceae. When observed fresh, some species are clearly distinguishable from related ones by colour, texture or habital characters, which often appear to be correlated with different soil preferences. Once dried in the herbarium, however, it is often far more difficult to separate species on the basis of these field characters, because these are seldom preserved when the specimen is dried. The approach best suited to arrive at a resolved taxonomy, and to better understand the biogeographical, ecological and evolutionary patterns of Neotropical ferns, is therefore a combination of field studies, herbarium studies and laboratory work. I apply both classical and molecular taxonomy to gain a better insight into relationships within the Marattiaceae.

In this family, the Neotropical genus *Danaea* (Marattiaceae) is of particular evolutionary interest because morphologically similar species pairs have been found to be ecologically different (Tuomisto and Poulsen 1996). Some species groups are poorly differentiated and may be undergoing speciation. Phylogenetic and taxonomic studies of this fern family can thus shed light on relationships between speciation, ecology and biogeography.

In this dissertation I provide a general overview of the extant and fossil members of the Marattiaceae, and discuss the studies carried out on the three genera found in the American tropics: *Angiopteris, Danaea* and *Marattia*.

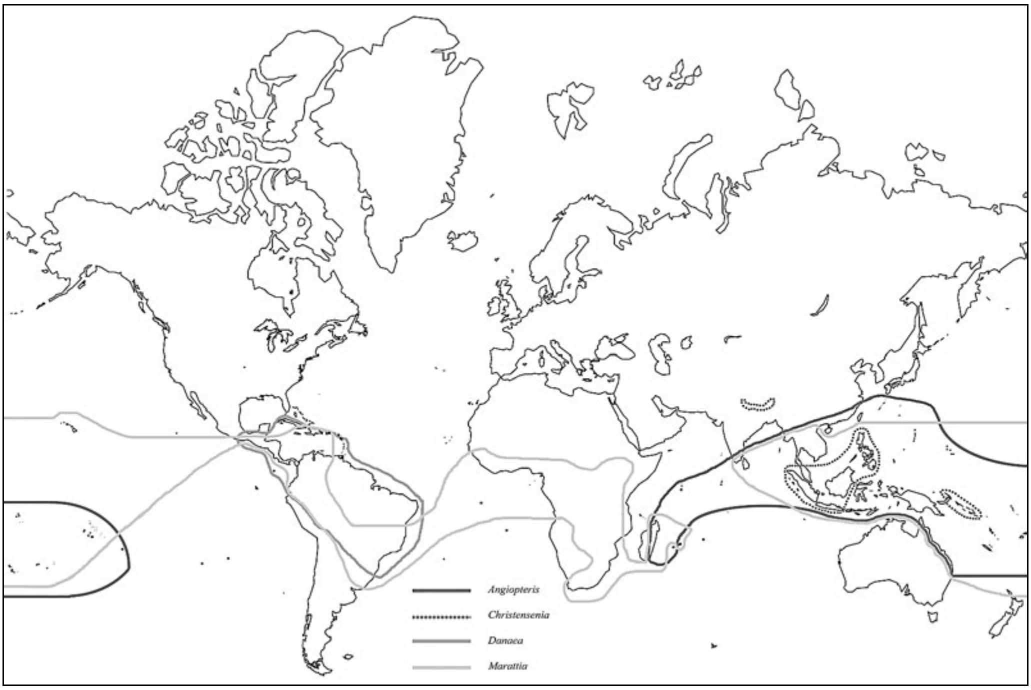

Figure 2. Global distribution of four genera of Marattiaceae.

1.3. The family Marattiaceae

1.3.1. Description and geographic distribution

The fern family Marattiaceae (Kaulfuss 1824; *nom. cons. prop.*, Murdock et al., 2006), is one of the oldest lineages of vascular plants, with extant members that have changed little over periods of millions of years. Together with another ancient family, the horsetails (Equisetaceae), it forms one of the basal lineages of ferns (Monilophyta, Fig. 1). Despite the unique evolutionary position of this family, it has received scant attention from taxonomists. The diversity of the genera is poorly known, and species are often poorly delimited. The large plant size of many representatives of the Marattiaceae makes it difficult to preserve complete specimens, greatly hampering herbarium studies. The phenotypic plasticity displayed by many taxa also makes it often difficult to establish species boundaries on morphological grounds.

The family Marattiaceae is one of four extant eusporangiate fern families (Fig. 1). Eusporangiate ferns have sporangia that arise from several epidermal cells, in contrast with leptosporangiate ferns, where the sporangium is formed from a single initial cell. While the leptosporangium is an apomorphic character, the eusporangium is a plesiomorphic character state and can be found also in seed plants and bryophytes. Therefore leptosporangiate ferns form a monophyletic clade, whereas eusporangate ferns are polyphyletic (Pryer et al. 2004).

Figure 3. Habital sketches of marattioid fern genera. From left to right: *Danaea polymorpha, Christensenia aesculifolia, Marattia alata, Psaronius sp.* (reconstruction)*, Angiopteris evecta, Archangiopteris itoi.*

Table 1. Overview of morphological characters of extant genera of Marattiaceae.

genus	rhizome	indument	blade division	venation	sporangia
Angiopteris Hoffm.	erect	hairs	2(-3) pinnate	free, 1-2 forked	almost free
Archangiopteris H.Christ & Gies.	creeping	hairs	1 pinnate	free, 1-2 forked	almost free
Christensenia Maxon	creeping	scales	palmate	reticulate	fused, radial
Danaea Sm.	creeping/ erect	scales	simple 1(-2) pinnate	free, 0-1 forked	fused, linear, sunken
Macroglossum Copel.	erect	hairs	1 pinnate	free, 1-2 forked	almost free
Marattia Sw.	erect	hairs	(1-)2-4 pinnate	free, (0-)1-2 forked	fused, bilabiate

There are six extant genera in the Marattiaceae, none of which have been thoroughly taxonomically monographed. Three genera of Marattiaceae occur in tropical America: *Marattia* Sw., a pantropical genus, of which the Neotropical species have been revised by Lavalle (2003); *Danaea* Sm.*,* a Neotropical genus, in great need of monographic study because the variability and distinctness of several species are insufficiently known (Kramer 1978); and *Angiopteris* Hoffm., an Old-World genus that has become naturalised in some Neotropical countries. The other genera, *Archangiopteris* H.Christ & Gies., *Christensenia* Maxon, and *Macroglossum* Copel. only occur in tropical Asia. The genera of Marattiaceae are depicted in Figure 3, and their characters are summarised in Table 1.

The Marattiaceae are a distinct group of (almost always) terrestrial ferns with large, fleshy, erect or creeping rhizomes, with a polycyclic dictyostele, and mucilage canals in the roots, rhizomes and leaves (Sporne 1962, Smith et al. 2006). Young plants usually contain a mycorrhizal fungus - the oomycete *Stigeosporium marattiacearum* C.West - within the cortex (West 1916, Sporne 1962). Other notable features are the starchy, leathery or papery, stipule-like, paired auricles at the base of each petiole, which are unique among ferns. Many species produce proliferous buds on the stipules or on the leaves (Uffelen 1994). The leaves are generally large and leathery (except in some “filmy” *Danaea*), and 1-3 times pinnate (simple in some *Danaea*, or palmate in *Christensenia*). The petioles and rachises have polycyclic xylem and swollen pulvinae at the base of each internode. The sporangia are usually fused in round or elongate synangia, where a thin part of the sporangium dries and shrinks to form a pore through which the spores fall, except in *Angiopteris, Archangiopteris* and *Macroglossum*, where the sporangia are almost free. Each sporangium encloses very large numbers of spores (from about 1000 in *Angiopteris* to 7000 in *Christensenia*); these are usually monolete, bilateral or ellipsoid, and echinate (Sporne 1962, Smith et al. 2006).

The spores germinate rapidly, within a few days of being shed, and develop into large, monoecious, dark-green, mycorrhizal prothalli that can live for several years. An old prothallus may be several centimetres long and may closely resemble a large thalloid liverwort (Sporne 1962).

The young parts of *Angiopteris, Archangiopteris*, *Macroglossum* and *Marattia* are covered with short simple hairs, while those of *Christensenia* and *Danaea* bear peltate scales (Sporne 1962). Microscopic characters, such as hairs, scales and indusia, which are of great taxonomic importance in other fern groups, are absent or vary little within marattioid genera.

Vegetative reproduction appears to be an important way of dispersal. Reproduction by means of stipule cuttings is also the easiest way of propagation in cultivation for *Marattia* and *Angiopteris* (Uffelen 1994, Chiou et al. 2006), but *Christensenia* and *Danaea* are difficult to cultivate because their requirements are unknown (Schneider 1893). Some *Danaea* species reproduce vegetatively, by means of apical buds on the leaves, where the terminal pinna is replaced or aborted; the bud can grow into a new plant when the leaf arches and the tip reaches the substrate. In this way, large uniform populations are sometimes formed.

The Marattiaceae are found in tropical or subtropical forests where the temperature and air humidity remain high throughout the year. While *Angiopteris, Archangiopteris, Christensenia* and *Macroglossum* prefer lowland rain forest and grow in partly open habitats, *Marattia* has a preference for high elevation cloud forest and semi-deciduous forest in the subtropics. *Danaea* grows mostly in closed canopy, lowland and mountain rain forest and other shady, humid places, along stream banks, in ravines, and in sinkholes or near waterfalls, often on rather steep slopes.

1.3.2. The genera **Angiopteris, Archangiopteris** *and* **Macroglossum**

In this dissertation I treat *Angiopteris* in its traditional sense, including the segregate genera *Protangiopteris* and *Protomarattia*. The generic delimitation of *Angiopteris* has been in turmoil; in their recent fern classification, Smith et al. (2006) additionally included the commonly used genera *Archangiopteris* and *Macroglossum* in

Angiopteris. Even though their genetic distinctness from *Angiopteris* is yet to be proven, I apply these generic names here, because they are morphologically easily distinguishable (Table 1).

Archangiopteris differs from *Angiopteris* by its creeping rhizomes and once-pinnate blades, and has been taxonomically revised by Mengascini (2002).

Macroglossum smithii (Rac.) Campbell, the single species in this genus, resembles *Archangiopteris* in its once-pinnate blades, but differs in the spirally arranged rhizomes, which are ascending to erect.

Angiopteris has been revised by Rolleri (2002, 2003), who recognised only ten species; she diverted over half of the 200 described taxa to dubious names, and placed the rest in synonymy. Ching (1999) listed 37 species for China alone, and authored a total of 64 species in *Angiopteris* and six in *Archangiopteris* (Zhang 1999), many of which are based on minor characters and fragmentary specimens. Mabberley (1997) considered the genus to consist of approximately 200 poorly defined microspecies. In light of this fluctuation in species numbers, it is obvious that *Angiopteris* is in great need of a modern taxonomic revision. For these studies, fieldwork, cultivation experiments and molecular studies are indispensable, because type material is often difficult to interpret. The enormous size of the leaves of many species means that most herbarium specimens are highly incomplete. Often, only parts of pinnae or a single pinnule are represented in a specimen, making it difficult to reconstruct the whole leaf or plant.

Angiopteris species are large to giant ferns with rhizomes that are globular and radial. The leaves are usually bipinnate (rarely once pinnate or tri-pinnate) and can be gigantic, measuring up to 9 m in length in *A. teysmanniana* from Java. The pinnae and pinnules are (usually) placed alternately. Veins are free and forked once or twice. The sporangia are almost free, attached only at the base, and are surrounded by a crude annulus of thickened cells; the contractions of which pull the sides of the sporangium apart along a line of dehiscence on the inner face (Sporne 1962).

Angiopteris is confined to the Old World tropics, occurring from Japan and Polynesia to Australia, India and Madagascar (Fig. 2). Species of *Angiopteris* are used in the Pacific to perfume coconut oil, and in India the starch from the rhizome is eaten and used to brew an intoxicating drink (Mabberley 1997). *Angiopteris evecta* is documented as naturalised in Hawaii (Wilson 1996) and Jamaica (Proctor 1985).

1.3.3. The genus **Christensenia**

Christensenia, with one or two variable species, is confined to the Indo-Malaysian region (Sporne 1962, Fig. 2). They have creeping, dorsiventral rhizomes, palmately arranged blades with reticulate venation and radially arranged synangia (Rolleri 1993). Vriese and Harting (1853) described four species (as *Kaulfussia*); in the revision by Rolleri (1993) these were reduced to two species and one variety. Two cytotypes (diploid, n = 40, and tetraploid, n = 80) are known, and their distribution would be of interest (Camus 1990). In the future field studies and molecular evidence will be needed to assess the diversity of this genus.

Because of its radial synangia, an archaic character that is also found in fossil Asterothecaceae, *Christensenia* has been considered to be an ancient lineage, despite the lack of fossil evidence. The reticulate venation, on the other hand, is often considered to be a more derived character, and it has therefore been placed in a family of its own, the Christenseniaceae (Ching 1940). I prefer, however, to treat the family Marattiaceae as all extant members of marattioid ferns, following Camus (1990) and Smith et al. (2006), because they represent a clearly defined, isolated evolutionary lineage.

1.3.4. The genus **Danaea**

Danaea is restricted to the Neotropics (Fig. 2) and I estimate it to consist of about 50 species. These species have creeping to erect, radially or dorsiventrally arranged rhizomes, simple (*D. carillensis* and *D. simplicifolia*) or (bi-)pinnate leaves with opposite pinnae, and free, simple, paired or once-forked venation. The pinna margins can be entire or denticulate, which is an important character in species determination. Some species produce proliferous buds - aborting the terminal pinna - that can grow into a new plant when the leaf bends down and touches the ground. The leaves are dimorphic; the fertile pinnae are narrower and *acrostichoid*, i.e. completely covered below with synangia that are sunken into the lamina. For this reason, Linnaeus (1753) initially placed them in the genus *Acrostichum*.

Danaea is found in various primary and secondary forest types, such as lowland or montane rain forest, cloud forest and elfin woodland, and it even occurs in semi-deciduous subtropical forests. *Danaea* requires a more or less constant high humidity, and most species prefer shady or dark habitats, such as forested ravines or steep mountain slopes, along the steep banks of creeks and rivers, along trails, near waterfalls, or on the clayey bottom of shaded sinkholes in karsted limestone hills. Apart from a few species that grow in swamps, most specimens have been collected on well-drained soils and steep slopes.

Danaea spores are wind-dispersed, but in enclosed stream valleys and on the rain forest floor the wind velocity is generally low, which may result in a limited distribution. Combined with the narrow ecological range of many species, a preference for certain soil types (Tuomisto and Poulsen 1996), and the tendency of some species to reproduce vegetatively, populations can sometimes appear quite uniform locally, but large morphological plasticity within species can be observed when a species is examined over its full geographic range.

A study of growth rates showed, that the leaves of *Danaea wendlandii* are very long-lived; the plants measured were at least 23 years old. *Danaea* species are thus one of the slowest-growing ferns, with a relatively long life expectancy (Sharpe 1993).

1.3.5. The genus **Marattia**

Marattia is a pantropical genus of about 60 species (Mabberley 1997), occurring northward to Hawaii and southern Mexico, and southward to New Zealand (Fig. 2). Their rhizomes are radially arranged and usually globular. The leaves are usually two or three times pinnate, except for *M. rolandi-principis* (Rosenstock 1911) from New Caledonia, where they are once pinnate. The ultimate pinnules are generally alternately arranged, but the pinnae are often opposed, especially in 3-pinnate species with deltate blades. The synangia are sessile or stalked. When ripe, the synangium splits into halves, which are slowly pulled apart so as to expose the spores in each sporangium (Sporne 1962).

In recent molecular phylogenetic studies on Marattiaceae (Murdock, *unpublished*), *Marattia* is divided into two clades by the placement of *Christensenia*. In the future, *Marattia* may therefore have to be divided into two genera (*Marattia* and *Eupodium*).

The American species of *Marattia* were revised by Lavalle (2003), but the genus is in need of worldwide taxonomic revision because many species are still poorly defined and type specimens are sometimes fragmentary. In this dissertation, I revise Lavalle's work and provide a key and taxonomic history of the Neotropical species.

1.3.6. Conservation

Conservation plans have been proposed for *Marattia purpurascens* (Vriese & Harting 1853), an endemic of the isolated Ascension Island in the South Atlantic, where a single population remains. This population is now believed to be more stable than previously feared, but long-term threats to its survival do exist in the form of competition with introduced plant species and grazing by sheep (Gray et al. 2005).

In addition, *Angiopteris chauliodonta*, an endemic of Pitcairn Island in the Southeast Pacific, is critically endangered by forest clearing, erosion and the threat of overgrowth by introduced plant species such as *Syzygium jambos* and *Lantana camara*. Both *in* and *ex situ* conservation actions are now underway (Kingston et al. 2004) to prevent this species from becoming extinct. In Australia a recovery programme has been initiated for threatened populations of *A. evecta* (NSW National Parks and Wildlife Service 2001).

In situ conservation of the endangered *Archangiopteris somai* (= *Angiopteris henryi*) has been opted for in China (Cheng and Huang 1999). An *ex situ* conservation programme (Chiou et al. 2006) has been started in Taiwan for *A. itoi* (Fig. 3) and *A. somai*.

1.4. Palaeohistory of marattioid ferns

The order Marattiales dates back to the Carboniferous Period, with the oldest fossils being about 345 million years old. They have a more or less continuous fossil record down to the present, and have undergone little major structural changes (Mapes and Schabilion 1979). The origin of these early ferns is not certain. Numerous fossils from the Palaeozoic and Mesozoic attest to the great diversity and abundance of these ferns in the past (Taylor and Taylor 1993). In this section I will shortly discuss the better known marattioid fossils, and place them in an evolutionary perspective. Fig. 4 provides a possible hypothesis of the evolutionary palaeohistory of marattioid ferns.

1.4.1. Palaeozoic Period (345-248 Ma)

Hill and Camus (1986) divided the order Marattiales into two families: the Marattiaceae and the Psaroniaceae. For the latter, however, the name Asterothecaceae (Sporne 1962) is preferable, because it has priority and is based on fertile structures. The family Asterothecaceae, comprising of form genera with radially symmetrical synangia (e.g. *Asterotheca*, *Scolecopteris*, *Zhutheca*), was numerically and taxonomically dominant during the Palaeozoic Period, but became extinct during the mid Triassic (Liu et al 2000). Marattiaceae includes all modern taxa, and many fossil lineages with elongate and/or bilaterally arranged synangia.

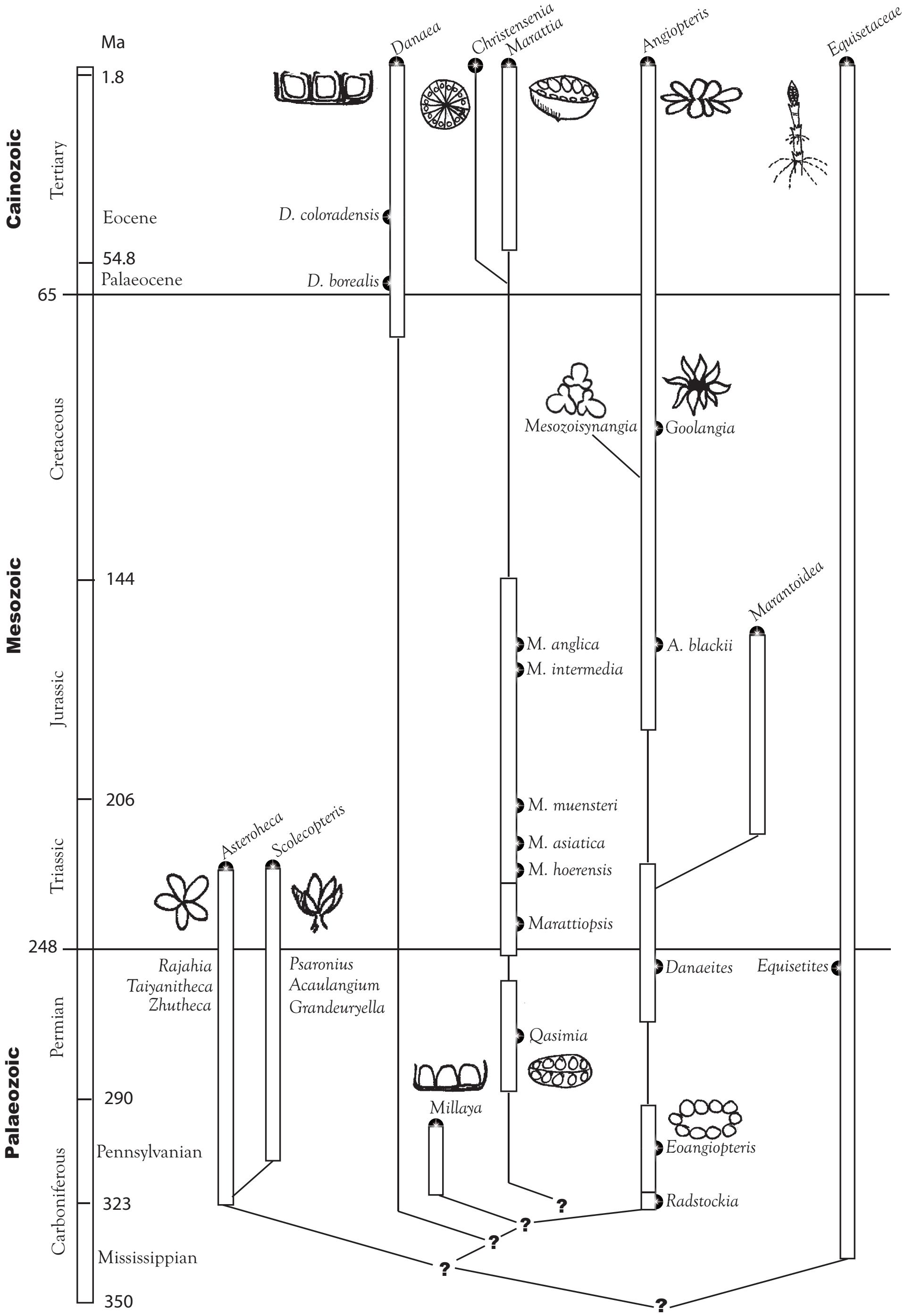

Figure 4. Hypothesis of marattioid fern evolution; freely composed from Hill and Camus (1986), **IV**, Murdock (unpublished), and fossil literature (Millay 1978, Mapes and Schabilion 1979, Hill et al. 1985, Wan and Basinger 1992, Liu et al. 2000, Hu et al. 2006). Bars refer to known fossil evidence, single lines represent tentative lineages. Time in million years before present.

The most commonly encountered marattioid fossils from the late Palaeozoic and early Mesozoic belong to the genus *Psaronius*. Originally this name was applied only to stem fossils, but when fossils were found with *Psaronius* stems attached to fertile *Scolecopteris* leaves, the name *Psaronius* was eventually applied to the whole plant. These giant ferns grew a stem up to about 10 m tall, bearing a crown of large, multiple pinnate leaves (Fig. 3), with which they could exploit light efficiently in the *Lepidodendron* swamp forests, where they occupied the non-inundated areas (Willis and McElwain 2002). The stem was covered in adventitious roots, growing downward from below the apex of the stem, forming a thick root mantle which kept the trunk upright (Taylor and Taylor 1993), much like the trunks of some modern species of *Danaea* and *Cyathea*.

Asterotheca is the name given to pecopterid fossils bearing sessile sori made up of four or five sporangia fused at the base into a radial synangium (Sporne 1962). Several other genera with an *Asterotheca* type synangium are known, e.g. *Acitheca, Fascipteris, Rajahia, Taiyanitheca* and *Zhutheca* (Liu et al. 2000). The commonly encountered fossils of the *Scolecopteris* type are similar, but the radially arranged synangium was elevated on a short receptacle (Sporne 1962).

The fertile compression fossil *Radstockia kidstonii* appears to be based on not fully developed unpaired synangia. They were probably more similar to *Eoangiopteris* than they were to the bivalve synangia of *Marattia* (Millay 1978), as previously suggested.

The genus *Eoangiopteris* with two species, *E. andrewsii* (Mamay 1950) and *E. goodii* (Millay 1978), during the Pennsylvanian Period had similar synangial structures as extant *Angiopteris*. *Eoangiopteris* may be an early representative of the Marattiaceae with nearly free sporangia (Millay 1978). The pecopterid compression genus *Danaeites* was also covered in linear synangia, and were very similar to *Eoangiopteris*, in which anatomical structures were preserved (Millay 1978). The recently described *Sydneia manleyi* (Pšenicka et al. 2003) also appears to be closely related to *Eoangiopteris*, and may be congeneric.

The evolutionary relationships of *Millaya tularosana* (Mapes and Schabilion 1979), a fossil with elongated, basally fused, sunken synangia, are not clear. The sunken synangia were most similar to *Danaea*, but it may also be that *Millaya* can serve best as a link between Palaeozoic scolecopterids and more advanced Mesozoic forms (Mapes and Schabilion 1979).

Qasimia schyfsmae (Hill et al. 1985) from the Upper-Permian of Saudi Arabia had bilaterally fused synangia and is therefore considered to be an ancestor of *Marattia*.

1.4.2. Mesozoic Period (248-65 Ma)

The Mesozoic was a period with a warm global climate. During the early Triassic, marattioid ferns already formed a significant element of the Laurasian flora, but were only a minor component of the flora of Mesozoic Gondwana. Occurrences in the southern hemisphere became more common during the late Triassic, but always remained a small element of that flora (Webb 2001). It can therefore be concluded that the marattioid ferns originated in Laurasia and later migrated into Gondwana.

The presently widespread (sub-)tropical genus *Marattia* has fossils from the Jurassic of Europe (England, Germany, Denmark, Sweden and Poland), and the Rhaeto-Liassic of Iran, suggesting a Eurasian origin of the genus. Triassic fossils are often called *Marattiopsis*, but differ little from extant *Marattia*. The approximately ten known *Marattia* or *Marattiopsis* species from the Mesozoic show a transition from the Palaeozoic representatives (e.g. *Qasimia*) to the extant members of *Marattia*, and are important in understanding the evolutionary trends of marattiaceous ferns (Wang et al. 2001). The bivalved synangia of *Marattia* are hard and often preserve well. Therefore, numerous fossils of *M. anglica, M. angustifolia, M. crenulatus, M. curvinervis, M. intermedia, M. hoerensis, M. muensteri*, and especially *M. asiatica* (Wang et al. 2001) are known, forming an important part of the flora during the Lower Jurassic in Eurasia (Wang 2002). Konijnenburg-Van Cittert (1975a) found that the fossil spores of *M. anglica* and other Jurassic *Marattia* species agree in all aspects with modern *Marattia* species. Further study is however needed on the evolution of this genus, and its relationship with extant *Eupodium* and *Christensenia,* and fossil *Qasimia*.

Modern representatives of the genus *Angiopteris* are found in Madagascar and the Indo-Pacific region, but fossils of *Angiopteris blackii* van Cittert are recorded from the Jurassic of Yorkshire, England, which suggests a much wider range of the genus during the Mesozoic (Konijnenburg-van Cittert 1975b). *Angiopteris blackii* was similar to extant species of *Angiopteris*, but differs in the more elongate and pointed sporangia, giving the synangium a star-shaped appearance (Hill 1987). There are very few other fossils attributed to *Angiopteris*. From the Upper Trias in China, four species are known, of which only *Angiopteris antiqua* was based on fertile material, but may be an immature or abortive specimen (Hill 1987). In comparison with extant species, *A. blackii* most closely resembles *A. pruinosa* (Hill 1987), a species from the Philippines.

In the palaeobotanic literature, the extant genus *Danaea* is sometimes confused with compression fossils named *Marantoidea* because of superficial similarity in fertile structures. *Marantoidea* has often been erroneously referred to as *Danaeopsis* (Heer 1864), but this name is illegitimate because of the extant genus *Danaeopsis* (Presl 1845, = *Bolbitis*), which has priority (Webb 2001). A name like *Danaeopsis* also implies a relationship with *Danaea*, but the elongate synangia found in *Marantoidea* are formed of nearly free sporangia, and are not fused and sunken into the lamina as in *Danaea.* Moreover, it has alternate pinnae (Mamay 1950) and may therefore not be so closely related to *Danaea* as initially assumed.

Even though fossils of the extant genera *Marattia* and *Angiopteris* are known from the Jurassic, no marattialean fossils where previously known from the Cretaceous with certainty. Hu et al. (2006) described two genera based on mesofossil synangia from the mid-Cretaceous of central North America, proving the existence of the Marattiaceae during the late Mesozoic. The first, *Goolangia minnesotensis* (Hu et al. 2006), had sessile sporangia, which were half-fused laterally into an elongated synangium. It is most closely related to *Angiopteris*, and in the future may be found to belong to it. The second, *Mesozoisynangia trilobus* (Hu et al. 2006), was very odd in having synangia consisting of three sporangia, which are each three-lobed. This species is without a doubt also related to *Angiopteris*, but represents its own, now extinct lineage.

1.4.3. Cainozoic Period (65-1.8 Ma)

Recent molecular studies (Pryer et al. 2004, Schuettpelz et al. 2006, Murdock *unpublished*), suggest *Danaea* to be the basal lineage in the extant Marattiaceae. However, the placement of *Danaea* (and *Christensenia* which has no fossil record) may be tentative, because the branches are long and convergent evolution in protein-coding genes may have possibly occured. Further phylogenetic study, based on conserved genes and morphological characters of both extant and extinct members, is required to study the true relationships between the genera of Marattiaceae. *Danaea* is usually considered to be the most advanced of the extant marattioid genera (Mapes and Schabilion 1979). The earliest *Danaea* fossils are known from Cainozoic sediments of the USA (*D. coloradensis* Knowlton (1922): Eocene of Colorado, and *D. borealis* Pabst (1968): Lower Tertiary of Washington).

The difference between totally fused synangia (as in *Danaea*), and apparently free sporangia (as in *Millaya, Eoangiopteris* and *Angiopteris*) is directly attributable to differential growth of the intersporangial tissue, a relatively small ontogenetic factor (Mapes and Schabilion 1979). It may additionally be assumed that the present-day exclusively Neotropical distribution is due to extinction elsewhere. It has been suggested (Moran 2004) that the ancient Guiana Shield formation could have functioned as a refuge, from which several genera radiated. This may also have been the case for *Danaea*.

1.4.4. Evolutionary trends

The evolution of marattioid ferns displays several morphological trends. These trends, however, are not linear and reversals can also be assumed.

It was suggested (Mamay 1950, Sporne 1962) that evolution from a sporangial organisation in which the sporangia are almost free - basally held together by a common zone of tissue (as can be observed in *Angiopteris*) - could have evolved towards complete bivalvate synangia. It is however more likely that a sorus was elongated laterally across a pinnule, which was increasing in width (Millay 1978). Most Palaeozoic taxa have small, incurved, narrow pinnae in blades that were at least four times pinnate, whereas most Post-Palaeozoic marattioid taxa have a lower degree of leaf division, simple or once or twice pinnate in *Angiopteris* and *Danaea*, and up to three times pinnate in *Marattia*. An exception amongst the Palaeozoic species is *Qasimia schyfsmae*, which had broad pinnules (Taylor and Taylor 1993). It is not certain what triggered this general change of foliar morphology, although Asama (1960) demonstrated that when *Angiopteris* is cultivated in cooler climates its foliage becomes less complex. Climatic variability during the Permian and Triassic may therefore have been responsible for these evolutionary trends.

1.5. Aims

This dissertation has three aims: 1) to clarify the current taxonomic confusion in *Danaea* (**I, II, III**), 2) to study the ecology, evolutionary relationships and biogeography of *Danaea* species (**IV**), and 3) to address conservation issues surrounding the invasive species *Angiopteris evecta* (**V**).

All species names mentioned in my dissertation are based on study of the original type specimens, images of which are provided in the Appendix. The studies concerning *Danaea* are additionally built upon revision of the genus for the *Flora of Ecuador* (Tuomisto and Moran 2001), which is revised and expanded to all Neotropics.

The ultimate goal of these PhD studies was to complete a full monograph of the Marattiaceae for the *Flora Neotropica* (Christenhusz and Tuomisto, *unpublished*), but it was not possible to solve all taxonomic problems within the timeframe of the dissertation. The monograph will therefore be completed at a later stage.

2. MATERIAL AND METHODS

2.1. Data collection

2.1.1. Field studies

The present dissertation is based on extensive field studies in tropical America (Fig. 5, Fig. 6), covering various forest types and geological formations.

Many of the original type specimens of *Danaea* are fragmentary. I have therefore sought to visit as many type localities as possible within the timeframe of this dissertation. Additional habital characters of these species were noted, especially those that could not be preserved in herbarium specimens. Many of the older collections were labelled with scant locality information, but in many cases I was able to find these collection sites by questioning local people.

Fieldwork was carried out during four separate expeditions (Fig. 5). My first trip (July-August 2002) took me to Peruvian Amazonia, where I visited the lowland rain forests of Loreto and the mid-elevation forests of San Martín. The second expedition coincided with the Flora of the Guianas meeting in Cayenne (February 2003), whence I made trips to various sites in French Guiana, to the Brownsberg Reserve in Suriname (March 2003) and to the Lesser Antillean islands of Martinique, Guadeloupe and Dominica (March-April 2003). The third expedition took me to Jamaica (January-February 2004), and to Puerto Rico (March 2004). The fourth journey took me to Guadeloupe and Puerto Rico (March 2005) to study the diverse pteridophyte floras of these islands in more detail.

During specimen collection, special attention was paid to characters that disappear during the drying process. I therefore made field notes describing posture, and took measurements of leaves and rhizomes. In most cases I took habital photographs before collecting the plant. Most of my specimens consist of multiple sheets and a separately dried rhizome, to preserve as much of the plant as possible. The material collected was usually first preserved with alcohol (± 60-70% ethanol) in the field to prevent the specimens from moulding. Later, the specimens were dried in the herbarium. However, all the collections from Suriname could be dried directly in the field, and part of the collections from Jamaica, Puerto Rico and French Guiana were dried in the local herbarium. These specimens did not first have to be preserved in alcohol. Leaf samples intended for molecular study (**IV**) were dried separately on silica.

In total, I collected 160 specimens of *Danaea* (22 species, Fig. 5), three specimens of *Marattia* (2 species, Fig. 6), and five specimens of *Angiopteris evecta*, most of which were duplicated. The first set was deposited in TUR; duplicates were deposited in local herbaria (e.g. AMAZ, BBS, CAY, GUAD, IJ, MAPR, UPR, UPRRP, USM; herbarium acronyms according to Holmgren and Holmgren 1998). Additional duplicates will be distributed after completion of the study.

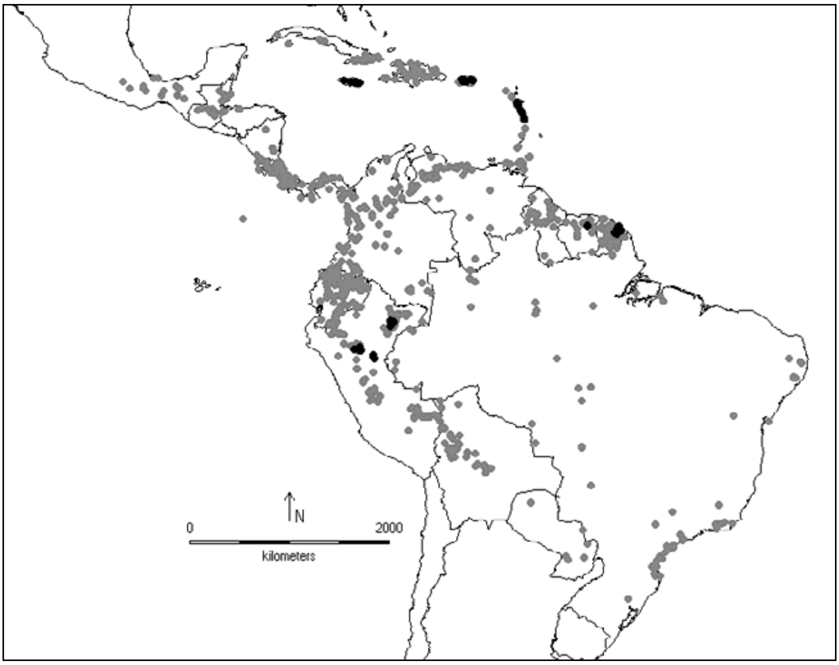

Figure 5. Distribution of *Danaea* based on 2383 georeferenced voucher specimens from various herbaria (gray dots). Black dots indicate locations of field collections for this study.

Figure 6. Distribution of *Marattia* in the Neotropics based on 355 georeferenced voucher specimens from various herbaria (gray dots). Black dots indicate localities where *Marattia* was collected for this study.

2.1.2. Herbarium studies

In order to taxonomically revise the genera *Danaea* and *Marattia*, I studied a total of 3077 Neotropical specimens from 52 herbaria (A, AAU, AMAZ, B, BBS, BM, BR, C, CAY, DUKE, E, F, FBG, FI, G, GB, GH, GOET, GUAD, H, IJ, K, L, LINN, LZ, M, MAPR, MO, MT, NY, P, PE, PMA, PR, PRC, S, SJ, SP, TUB, TUR, U, UC, UCWI, UPR, UPRRP, UPS, US, USM, W, WU, YU, Z; herbarium acronyms according to Holmgren and Holmgren 1998). I compared all specimens to the original type specimens of the species.

Study **V** is based on 141 georeferenced voucher specimens from 15 herbaria and 17 field observations of *Angiopteris evecta*. Specimens were studied in P and TUR, and the dataset was supplemented with digitised specimens from NY (http://www.nybg.org/) and with records from various digital databases (http://www.GBIF.org/, http://www.HEAR.org/).

2.2. Molecular phylogenetics

2.2.1. Taxon sampling

The importance of adequate taxon sampling in phylogenetic studies is well known (Hillis 1998). I examined various floristic treatments and species descriptions carefully, in order to include a wide geographic range and cover the broad morphological variability of the genus.

In study **IV**, I followed the taxonomy of Tuomisto and Moran (2001) for Western Amazonian species, Kramer (1978) for the Guianas, Proctor (1977, 1985, 1989) for the Antilles, and Camus (1995) for Central America, with corrections and additions to these floras provided in **I** and **II** and based on studies of the original type specimens. Whenever possible I chose material collected from or close to a type locality. In several cases, material of the original type specimen of recently described species (Tuomisto and Moran 2001, **I, II**) was available for DNA extraction. When available, I included several specimens from various parts of the geographic range of a species.

Despite my extensive field studies, I was unable to sample all species of *Danaea* myself. Fortunately, I was able to supplement my data with material collected by colleagues studying ferns in other Neotropical countries. Hanna Tuomisto provided material from Peru, Ecuador, Costa Rica and Panama, Mirkka Jones from Costa Rica, Marcus Lehnert from Ecuador, Michael Kessler from Tobago and Bolivia, and Michel Boudrie from French Guiana. Andrew Murdock kindly exchanged samples of several outgroup taxa (*Archangiopteris, Christensenia, Macroglossum*) for samples of *Danaea*.

Silica-dried leaf samples of some 220 *Danaea* specimens by various collectors and some 250 specimens of other ferns (the majority collected in 2005 on Guadeloupe) were deposited in the fern DNA database at the laboratory of Kathleen Pryer (http://www.pryerlab.net/), to be available for future molecular studies and phylogenetic analyses.

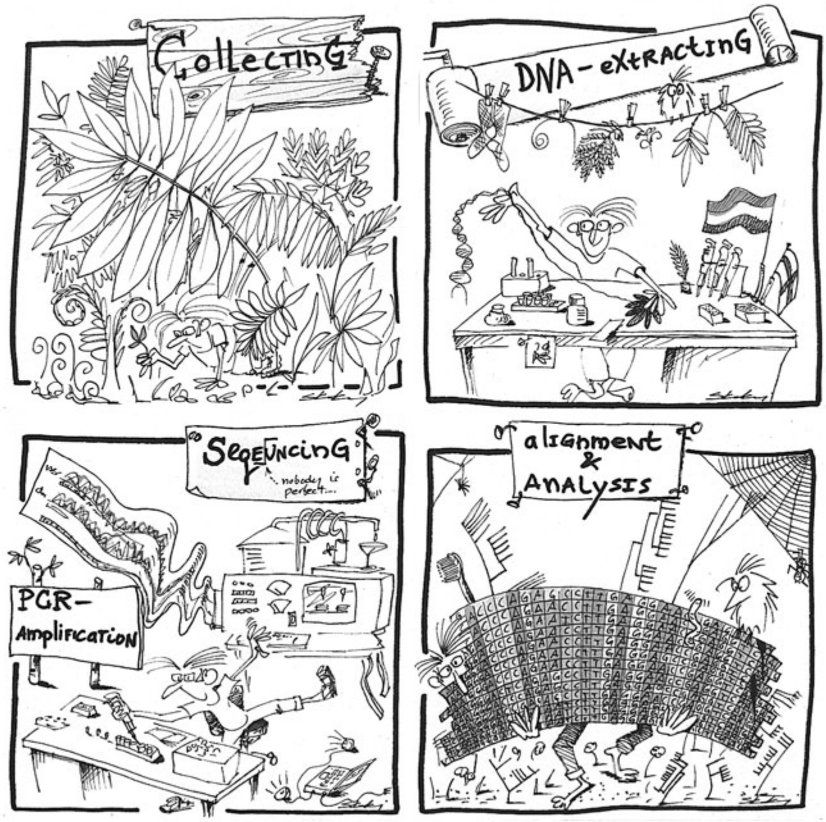

Figure 7. Cartoon illustrating the steps necessary to arrive at a molecular phylogeny of *Danaea*. Drawn by Michal Skakuj and reproduced with permission.

2.2.2. Laboratory work

I carried out the extraction, amplification, sequencing and analyses for the molecular phylogeny study (**IV**) in the laboratory of Kathleen Pryer at Duke University, North Carolina, who studies the deeper phylogenetic relationships of ferns (http://www.pryerlab.net). Here, I isolated DNA of 3 chloroplast regions (*rbcL, atpB* and *trnL-trnF*) from silica-dried leaf samples. Chromatograms were produced for both strands of these regions; these were then combined into double-stranded sequences, to check for possible sequencing errors. Figure 7 illustrates the steps from the living plant to molecular phylogeny.

2.2.3. Alignment and analyses

I evaluated the sequences for possible contamination and aligned them manually in order to check for ambiguous regions. I did not code gaps as a fifth character state, as is done in some studies, but coded these as missing data. Gaps are not actually observed data, but are constructs of the alignment representing implied insertions or deletions (Phillips et al. 2000).

There are several methods for estimating a phylogeny based on DNA sequences, including parsimony, maximum likelihood and the Bayesian approach. The merits and shortcomings of these methods have been debated, and a discussion of methodology is not within the scope of this dissertation, especially because I found that the methods mentioned above gave concordant results. Bayesian statistics use prior knowledge (an evolutionary model) to test the hypothesis, and are strongly allied to maximum likelihood (Holder and Lewis 2003). The Bayesian approach is commonly used in molecular phylogenetics, and is the method preferred by Dr. Pryer, who is co-author of study **IV**.

2.3. Species distribution modelling

Predicting the distributions of *Danaea* species by modelling their climatic niche became problematic; some species are still not well defined, and the patterns obtained in preliminary analyses thus did not appear to reflect the reality.

To obtain a rough idea of the range of the genus *Danaea*, I analysed the data points with a simple Bioclim model in DIVA-GIS (http://www.diva-gis.org/), based on WorldClim data (Hijmans et al. 2005) and the available herbarium specimens (Fig. 5). This is presented in Figure 10.

After observing naturalised populations of *Angiopteris evecta* in Jamaica, I decided to focus on modelling the potential distribution of this species in the Neotropics. This species from the southern Pacific was long ago introduced to, and naturalised in, Jamaica, Hawaii and Costa Rica (**V**).

The first step in this study was to carry out a historical survey, based on interviews, herbarium specimens and the literature, to identify the speed of naturalisation and the geographical spread.

Herbarium specimens from the native range were studied and georeferenced. It was sometimes difficult to distinguish between *A. evecta* and related taxa, as some specimens were quite fragmentary or incomplete. I therefore excluded all doubtful specimens.

Desktop GARP (Genetic Algorithm for Rule-set Production, http://nhm.ku.edu/desktopgarp/index.html) is a software package that can create ecological niche models representing the environmental conditions (such as climate) where a species would be able to maintain populations. The input consists of a set of geographical point localities from observations, or from labels on herbarium specimens, and a set of geographic layers representing the ecological parameters. The output is a set of prediction maps, which are overlaid and viewed in a Geographic Information System (GIS). Unfortunately the GARP method is not very transparent, and it can therefore be difficult to explain the patterns found. The GARP maps were therefore compared to a simple climatic envelope model, to see which environmental layers most influence our results.

Most of the samples were collected on small islands, which typically have a small-scale variation of climatic conditions; this variation was not represented in our climatic layers. There are substantially fewer weather stations in the tropics than there are in temperate regions, and the WorldClim dataset (Hijmans et al. 2005) therefore has a lot of extrapolated values. Nevertheless WorldClim is the best climatic dataset available, and should function relatively well for our purpose of extrapolation on a global scale.

Since all data points were found in close proximity to the sea, we decided to include the euclidean distance to the sea as an additional variable. This factor acts as a surrogate for the climatic variability between island climates and continents, allowing extrapolation to continents.

3. RESULTS AND DISCUSSION

3.1. Study of the genus *Angiopteris*

3.1.1. Potential distribution modelling

In the Neotropics, *Angiopteris evecta* is known to be cultivated in Florida, Mexico, Cuba, Jamaica and Costa Rica (**V**). In the last two countries and in Hawaii the species has become naturalised. It was first introduced from Tahiti into Jamaica in the 18th century and has spread steadily in that country. It can now be found throughout the eastern half of the island. In the 1960s a cutting from a Jamaican plant was taken to Costa Rica, where it is now also becoming naturalised and is slowly spreading.

The GARP species distribution model provided us with the possibility of assessing the potential spread of this species based on climatic data. The potential distribution map indicated that, based on climate data, the species may spread to many parts of tropical America and mainland Africa. In these continents there are no native *Angiopteris* species, and an invasion of *A. evecta* in these regions may result in a lower local biodiversity. Intriguingly, the species is endangered in parts of its natural range (i.e. NSW National Parks and Wildlife Service 2001). Thus the conservation concern with regard to *A. evecta* is two-sided.

3.2. Study of the genus *Danaea*

3.2.1. Species delineation and synonyms

I recognise a greater diversity of *Danaea* species than was estimated previously. This is partly because most recent field studies on ferns by the Turku University Amazon Research Team yielded new *Danaea* species. Additionally, the many new records of *Danaea* species resulted in an expansion of the known geographic ranges.

Mabberley (1997) stated that *Danaea* consists of about 30 poorly defined species. My taxonomic studies resulted in the acceptance of 38 published species, of which eight are newly described (**I, II**). Previous to this study 62 species have been described in *Danaea*; 27 of these were found to be synonymous and 2 were found to belong to other genera. An additional 11 new species have been discovered and await description, resulting in a total of 49 species in *Danaea*. This is still an estimate, since several species complexes have not been completely resolved.

I have observed large phenotypic differences within species and even within the same population or individual. Species circumscription based solely on a few quantitative morphological characters can therefore be difficult. In *Danaea,* the species are always defined by combinations of characters. Rhizome habit, leaf texture and colour are very important characters in identifying fresh material, but are often difficult to assess on herbarium specimens. The petiole nodes, serration of pinna apices, pinna number, shape and size, and venation are easier to observe in herbarium specimens, but are not always sufficiently discriminative between species.

The taxonomic revision of *Danaea* resulted in redefinition of many species. For example, the names *D. sellowiana, D. nigrescens, D. media*, and *D. grandifolia* were previously all considered synonyms of *D. nodosa* (Mickel and Beitel 1988, Lellinger 1989, Tryon and Stolze 1989, Camus 1995, Rolleri 2004). I have epitypified *D. nodosa*

(**III**), which I treat here in a strict sense. I restored *D. media* and *D. grandifolia* to the species level, because they are morphologically distinct from typical *D. nodosa* in having rhizomes with multiple rows of leaves and entire pinna apices. *Danaea sellowiana* and *D. nigrescens* together form a species complex, which is difficult to separate from typical *D. nodosa* on morphological grounds, even though Amazonian and Guianan specimens of the *D. sellowiana/nigrescens* complex appear to be genetically isolated from *D. nodosa* (**IV**).

The name *D. elliptica* has, since its description, been variously applied. Most authors (i.e. Proctor 1977, 1985, 1989, Mickel and Beitel 1988, Tuomisto & Moran 2001, Rolleri 2004) considered this species to have nodose petioles, entire pinna apices and erect rhizomes. Hence *D. bipinnata, D. geniculata, D. leprieurii, D. polymorpha, D. simplicifolia,* and *D. trifoliata* have all been suggested as synonyms of *D. elliptica*. I do not believe that this is a single polymorphic species; rather, I consider it to be a complex of closely related species. The molecular study (**IV**) separated *D. simplicifolia, D. antillensis* and *D. trifoliata* from other *Danaea*'s, but unfortunately did not provide further insights into the evolutionary relationships of other species in this group.

The lectotype of *D. elliptica*, as designated by Proctor (1977), is a juvenile specimen of *D. nodosa,* and the name *D. elliptica* is therefore synonymous with *D. nodosa* (**II**). Since *D. elliptica* is a widely applied name, Lellinger (2000) designated a different lectotype, without a valid reason for rejecting the lectotype of Proctor (1977). Moreover, the specimen selected as lectotype by Lellinger (2000) is ambiguous in origin, and complicates the taxonomy of the *D. leprieurii* group even further (**II**). It is therefore preferable to let the name *D. elliptica* evanesce into synonymy, and to redefine the species and complexes of the *D. leprieurii* group. Based on a careful study of type material of this group, I found differences in habit and pinna shape, allowing the separation of *D. leprieurii, D. bipinnata*, *D. polymorpha, D. trifoliata, D. ulei* and three new species: *D. antillensis* (**I**), *D. arbuscula* and *D. lingua-cervina* (**II**). The remainder of this group, which I here refer to as the *D. geniculata* complex, is polymorphic and not yet well resolved. Further study is still needed to clarify the morphological boundaries between the species in this complex.

The name *Danaea ulei* was first applied to the largest species in the genus, having nodeless petioles and creeping rhizomes (Tuomisto and Groot 1995, Tuomisto and Poulsen 1996, Tuomisto and Moran 2001). Closer study of the type of *D. ulei*, however, revealed that this name should be applied to a species with an erect rhizome and nodose petioles. Tuomisto and Groot (1995) mentioned that the rhizome habit was not evident in the photograph of the type, and they already anticipated that this name might not apply to their material. The species referred to *Danaea ulei* in recent papers (and fully circumscribed in Tuomisto and Moran 2001), therefore needed a new name: *D. cartilaginea* (**II**). The true *D. ulei* of Christ (1905) is known only from the type collection from Acre (Brazil), although some specimens from Bolivia are morphologically close.

The type specimen study has led to the acceptance of several names that have not previously been commonly applied. Some established names were clearly synonyms of others. All names published in *Danaea,* and my current interpretation, are listed in Table 2.

Table 2. List of published names of *Danaea*. Names accepted in this dissertation are in boldface. New synonyms that emerged during this work are indicated with an asterisk after their current name.

Published name	Publication	Current name
Acrostichum nodosum	Linnaeus 1753: 1070	= *D. nodosa*
Asplenium nodosum	Linnaeus 1763: 1539	= *D. nodosa*
Danaea nodosa	Smith 1793: 420	
Danaea alata	Smith 1793: 420	
Danaea evecta	Sprengel 1800: 272	= *Angiopteris evecta*
Danaea simplicifolia	Rudge 1805: 24	
Danaea elliptica	Smith in Rees 1808	= *D. nodosa**
Danaea longifolia	Desvaux 1811: 307	= *D. nodosa*
Danaea geniculata	Raddi 1825: 75	= *D. geniculata* complex
Danaea paleacea	Raddi 1825: 76	= *Bolbitis serratifolia*
Danaea trifoliata	Reichenbach in Kunze 1837: 4	
Danaea stenophylla	Kunze 1840: 55	= *D. alata**
Danaea leprieurii	Kunze 1843: 137	
Danaea intermedia	Smith 1843: 393	= *D. sellowiana/nigrescens* complex
Danaea angustifolia	Presl 1845: 35	= *D. nodosa*
Danaea moritziana	Presl 1845: 35	= *D. moritziana* complex
Danaea dubia	Presl 1845: 36	= *D. sellowiana/nigrescens* complex
Danaea sellowiana	Presl 1845: 37	= *D. sellowiana/nigrescens* complex
Heterodanaea stenophylla	Presl 1845: 38	= *D. alata**
Danaeopsis paleacea	Presl 1845: 39	= *Bolbitis serratifolia*
Danaea augusti	Karsten in Kunze 1847: 2	= *D. geniculata/D. leprieurii* ?
Danaea cuspidata	Liebmann 1849: 306	= *D. moritziana* complex
Danaea media	Liebmann 1849: 306	
Danaea elata	Liebmann 1849: 306	= *D. media**
Danaea alata var. *moritziana*	Moore 1861: 285	= *D. moritziana* complex
Danaea trichomanoides	Spruce in Moore 1861: 285	
Danaea humilis	Moore 1861: 286	
Danaea nodosa var. *angustifolia*	Moore 1861: 287	= *D. nodosa*
Danaea simplicifolia var. *trifoliata*	Moore 1861: 287	= *D. trifoliata*
Danaea cordata	Fée 1869: 216	= *D. sellowiana/nigrescens* complex
Danaea crispa	Endrés in Reichenbach 1872: 489	
Danaea wendlandii	Reichenbach 1872: 490	
Danaea serrulata	Baker 1881: 208	= *D. humilis**
Danaea polymorpha	Leprieur in Baker 1891: 116	
Danaea oligosora	Fournier in Baker 1891: 116	= *D. polymorpha**
Danaea elliptica var. *major*	Jenman 1898a: 208	= *D. nodosa*
Danaea elliptica var. *repens*	Jenman 1898a: 209	= *D. nodosa*
Danaea nigrescens	Jenman 1898b: 413	= *D. sellowiana/nigrescens* complex
Danaea fendleri	Underwood 1902: 673	= *D. alata*
Danaea jamaicensis	Underwood 1902: 675	= *D. mazeana**
Danaea mazeana	Underwood 1902: 676	
Danaea wrightii	Underwood 1902: 676	= *D. jenmanii**

Published name	Publication	Current name
Danaea jenmanii	Underwood 1902: 677	
Danaea ulei	Christ 1905: 368	
Danaea paraguariensis	Christ 1907: 927	= *D. moritziana* complex
Danaea moritziana var. *brasiliensis*	Rosenstock 1907: 162	= *D. moritziana* complex
Danaea muelleriana	Rosenstock 1907: 162	= *D. moritziana* complex
Danaea excurrens	Rosenstock 1907: 163	
Danaea carillensis	Christ 1909: 234	
Danaea pterorachis	Christ 1909: 235	= *D. media**
Danaea elliptica var. *crispula*	Rosenstock 1909: 310	= *D. geniculata* complex*
Danaea grandifolia	Underwood 1909: 18	
Danaea plicata	Christ 1910: 19	
Danaea urbanii	Maxon 1924: 195	
Danaea muenchii	Rosenstock 1925: 23	= *D. moritziana* complex
Danaea nodosa var. *intermedia*	Hassler 1928: 89	= *D. sellowiana/nigrescens* complex
Danaea tenera	Morton 1951: 276	
Danaea oblanceolata	Stolze 1987: 33	
Danaea acuminata	Tuomisto & Moran 2001: 27	
Danaea bicolor	Tuomisto & Moran 2001: 29	
Danaea bipinnata	Tuomisto in Tuomisto & Moran 2001: 31	
Danaea erecta	Tuomisto & Moran 2001: 37	
Danaea falcata	Tuomisto & Moran 2001: 40	
Danaea imbricata	Tuomisto & Moran 2001: 44	
Danaea latipinna	Tuomisto & Moran 2001: 46	
Danaea longicaudata	Tuomisto in Tuomisto & Moran 2001: 50	
Danaea ulei	Tuomisto & Moran 2001: 62	= *D. cartilaginea**
Danaea antillensis	**I**: 212	
Danaea kalevala	**I**: 215	
Danaea ushana	**I**: 217	
Danaea arbuscula	**II**: 18	
Danaea cartilaginea	**II**: 18	
Danaea lingua-cervina	**II**: 23	
Danaea riparia	**II**: 25	
Danaea vivax	**II**: 25	

3.2.2. Taxonomic history

The first description of a species currently classified in the genus *Danaea* is *Acrostichum nodosum* by Linnaeus (1753: 1070), who based his description on a plate in Plumier (1705). In the second edition of *Species Plantarum*, Linnaeus (1763) reconsidered the placement of this species and transferred it to *Asplenium*.

James Edward Smith (1793) formally established the genus *Danaea*. He based it on Linnaeus' *Asplenium nodosum*, and in addition he described Plumier's other plate (1705) as *Danaea alata*. The two plates of Plumier are discussed in III. Soon thereafter J. E. Smith revised his genus for the *Cyclopaedia* of Rees (1808).

Seven new species were added to the genus in the following years (Desvaux 1811, Raddi 1825, Kunze 1837, 1840, 1843, J. Smith 1843), until Presl (1845) made a classification of the Marattiaceae (Table 3). He described an additional four species in *Danaea* and segregated two genera: *Danaeopsis* and *Heterodanaea*. The remaining genus *Danaea* was divided into three sections: *Eudanaea*, *Arthrodanaea* and *Holodanaea* (Table 3). Presl's (1845) classification and descriptions of genera and species are inconsistent, but species identities could be resolved by studying Presl's collections in Prague (PRC).

Presl's genus *Danaeopsis* (1845) was based on *D. paleacea*, but the type specimen of that species (*Raddi s.n.*, Brazil, PI) is *Bolbitis serratifolia* (Mertens ex Kaulf.) Schott, Dryopteridaceae (Pichi Sermolli 2005). Later, the name *Danaeopsis* (Heer 1864) was incorrectly applied to fossils correctly named *Marantoidea* (Webb 2001).

Table 3. The classification of Presl (1845) compared to the molecular phylogeny (**IV**). The type species of the section or genus is indicated with an asterisk (*). Clades are based on the definitions of groups given in Christenhusz and Tuomisto (2005, see also *3.2.3.*), and the clades in study **IV**.

genus	Section	classification	current name	clade/group
Danaea	*Eudanaea*	*D. simplicifolia*	*D. simplicifolia*	"leprieurii"
	(= *Danaea*)	*D. trifoliata*	*D. trifoliata*	"leprieurii"
		*D. nodosa**	*D. nodosa*	"nodosa"
		D. longifolia	*D. nodosa* ?	"nodosa"
		D. angustifolia	*D. nodosa*	"nodosa"
		D. elliptica	*D. nodosa*	"nodosa"
		D. moritziana	*D. moritziana*	"alata"
		D. dubia	*D. sellowiana*	"nodosa"
	Arthrodanaea	*D. leprieurii**	*D. leprieurii*	"leprieurii"
	Holodanaea	*D. alata**	*D. alata*	"alata"
		D. sellowiana	*D. sellowiana*	"nodosa"
Heterodanaea	--	*H. stenophylla* *	*Danaea alata*	"alata"
Danaeopsis	--	*D. paleacea* *	*Bolbitis serratifolia*	--

Even though Presl's classification (1845) does not agree with our molecular phylogeny (IV), the sectional names can be applied by basing them on the type species alone (indicated with * in Table 3), but not on Presl's diagnoses. When subgeneric groups are accepted within *Danaea* these names should be applied, but in that case should be redefined. Christenhusz and Tuomisto (2005) recognised three groups based on morphology, to which Presl's sections could in principle be applied.

After Presl's classification, little taxonomic attention was given to *Danaea* during the following 57 years, apart from listings in various '*indices*' (Moore 1861, Hooker and Baker 1874, Hooker 1887), and the occasional addition of species (Liebmann 1849, Fée 1869, Reichenbach 1872, Baker 1881, 1891, Jenman 1898b).

Underwood (1902) provided a review of the genus with descriptions and a key to twelve species, of which five were newly described. This review was used as a model for his treatment of the family in the *North American Flora*, for which Underwood (1909) also gives descriptions of a dozen species; this, however, is a different set of species from those in his 1902 revision. Underwood utilized type of venation to a considerable extent, which can be a highly variable character even in the same plant, and is best used in conjunction with other characters. Considering the limited number of specimens available to him at the time, his two *Danaea* studies provide a fairly complete overview of the genus.

Meanwhile several new species were described (Christ 1905, 1907, 1909, 1910, Rosenstock 1907, 1909), and Christensen (1906, 1913) listed a total of 32 species.

It took nearly a century, during which only a few additional new species were described (Maxon 1924, Rosenstock 1925, Morton 1951, Stolze 1987), before Tuomisto and Moran (2001) revised the challenging genus *Danaea* for the *Flora of Ecuador*. They recognised 18 species for Ecuador alone, of which eight were newly described. Their study was based on extensive field and herbarium work and ecological studies, and many taxonomic problems were addressed or resolved.

Rolleri (2004) revised the genus based on somewhat non-discriminative microscopic anatomy. Her study did not include field observations, and the revision was based on relatively few herbarium specimens. Moreover, several commonly recognised species were synonymised, only few original type specimens were studied and these were often cited erratically. Thus I believe that *Danaea* remains in need of an adequate taxonomic monograph.

3.2.3. Classification

Based on morphological characters, I recognise three major groups within *Danaea* (Christenhusz and Tuomisto 2005). These are:

1) The *D. leprieurii*-group (sect. *Arthrodanaea*): Species with always erect, radially arranged rhizomes, usually nodose petioles, and few, entire pinnae (at most sinuate at apex); terminal pinnae never replaced by proliferous buds.
2) The *D. nodosa*-group (sect. *Danaea*): Generally tall species with mostly creeping (rarely erect) rhizomes, often lacking petiole nodes, and having leaves with many elongate pinnae; generally without apical proliferations.
3) The *D. alata*-group (sect. *Holodanaea*): Generally intermediate to small species with radially arranged, creeping, ascending or erect rhizomes, nodose petioles, and leaves with many pinnae that usually have denticulate apices; often with apical proliferations. This group includes species with leathery, bicolorous leaves and species with leaves of a membranaceous translucent texture.

The phylogenetic hypothesis (**IV**) resulted in three well-supported clades within *Danaea* that correlated well with the morphological sections described above. The three clades of *Danaea* all have a wide distribution, spanning the entire geographical range of the genus. Within these clades ecological and geographical patterns could be identified that provided a better insight into the evolution and speciation of *Danaea*. In the following sections (3.2.4-6), I address the taxonomy and species complexes of these three groups.

3.2.4. The **Danaea leprieurii** *group*

Danaea elliptica, as previously applied by many authors, comprises several species that I collectively call the *D. leprieurii* group (Christenhusz & Tuomisto 2005). I segregate several morphologically different entities, and match these to type material of names that in earlier works were often listed as synonyms of *D. elliptica* (e.g. Lellinger 1989, Rolleri 2004).

Even after distinguishing *D. antillensis*, *D. arbuscula*, *D. bipinnata*, *D. leprieurii*, *D. lingua-cervina*, *D. polymorpha*, *D. simplicifolia*, *D. trifoliata*, and *D. ulei*, there remain samples that are difficult to place. At the population level there were certainly differences observable between species, but in studying the genus over a larger geographical range it became more and more difficult to distinguish between some of these species on morphological grounds. Unfortunately the molecular phylogeny (**IV**) gave little resolution in this group. These populations mostly form a complex of species surrounding *D. geniculata*, a name I tentatively apply to this complex for lack of a better alternative. If *D. geniculata*, a species described from the Atlantic forests in Brazil, is distinct from other South American populations, the next available name is *D. augusti*. The type of that species from Venezuela has not been found, however, and the original description suggests a close affinity to *D. leprieurii*. If *D. augusti* is a synonym of *D. leprieurii*, the next available name will be *D. elliptica* var. *crispula*, which will then need to be raised to species level. Further study on the *D. geniculata* complex is thus needed, in order to ascertain which names are to be applied in the future.

The holotype of *D. leprieurii* had been extant in Leipzig (LZ), but was regrettably destroyed during the Second World War. A lectotype therefore had to be chosen from among existing Leprieur specimens. This was quite complicated, since the isotypes listed in Tuomisto and Moran (2001) were not all collected prior to the publication date of the species (Kunze 1843). Apparently only two specimens of *D. leprieurii* from French Guiana (*Leprieur s.n., anno 1839;* BR!, E!) had been collected before the publication of the species, and would be good candidates for lectotypification.

The typification of all species has been revised, and several other species need to be lectotypified in both *Danaea* and *Marattia*. These results will be published in the *Flora Neotropica* treatment of the family (Christenhusz and Tuomisto, *in preparation*).

In Guadeloupe, I found two species that both keyed to *D. elliptica* in Proctor (1977). Specimens with few (3-5) pinnae and a dull green colour closely fitted the type of *D. polymorpha*. The other species had many (up to 8) pairs of glossy pinnae, and could not be matched with any existing taxon. I therefore described these as *D. antillensis* (**I**). The distinction of these two species was corroborated by the phylogeny (**IV**), where the two resolved to different subclades. These species most likely reached the island by independent migration events. In a similar fashion, I was able to distinguish several other new species, of which *D. arbuscula* and *D. lingua-cervina* are described in **II**. Several other species are recognised in this group (*sp. B, sp. C, sp. D, sp. G, sp. H*), but remain to be described.

3.2.5. The **Danaea nodosa** *group*

Danaea nodosa has always been a widely applied name, but the material identified as such is highly variable; I therefore doubted that it consisted of a single species. This conclusion is consolidated by the molecular data (**IV**), which renders *D. nodosa* s.l. as polyphyletic. The Greater Antillean specimens belong to a different clade than those from continental South America.

Since the lectotype locality is in Haiti (Underwood 1909), the name *D. nodosa* has to be applied to specimens from the Greater Antilles. Thus, the South American clade needs a different name. This clade is quite polymorphic and includes the newly described *D. cartilaginea*, making the South Amercian clade paraphyletic. I tentatively refer to this group of morphologically similar species as the *D. sellowiana/nigrescens* complex. *Danaea sellowiana* is a species described from the Atlantic rain forests in southern Brazil, and resembles *D. nigrescens*, described from Guyana. If the two species are conspecific, *D. sellowiana* has priority; if they are not, *D. nigrescens* applies to the Guianan and most likely also to the Amazonian specimens, whereas the specimens from coastal Brazil remain under *D. sellowiana*. The Atlantic rain forests are geographically disjunct from the Amazonian rain forests (Fig. 8). Since the 'Mata Atlântica' is also known to be a region with a high rate of endemism (Morellato and Haddad 2000), there may be a possibility that *D. sellowiana* and *D. nigrescens* are not the same species. Additional field observations and molecular evidence, however, will be needed to resolve the taxonomy of this complex.

While the complex could not be fully resolved in this dissertation, there are several species previously called *D. nodosa* that are morphologically quite distinct from that species and from the *D. sellowiana/nigrescens* complex. For instance, several species in the *D. nodosa* group were found to lack apical dentations in the pinnae. Central American specimens with entire, caudate pinna apices match well to the type of *D. elata*. Juveniles of this species sometimes bear a node on the petiole, which is why many of these specimens were erroneously labelled as *D. elliptica*. These juveniles closely matched the type specimen of *D. media*, which was published simultaneously with *D. elata* (Liebmann 1849). To prevent confusion with the name *D. alata*, I prefer the name *D. media* for this species over *D. elata*, since neither name has priority over the other.

The type of *D. grandifolia* has entire pinna apices as well. This species was described from northern Colombia (Underwood 1909), but the name was rarely used after that, even though isotypes were distributed to many herbaria. I found no morphological differences between the type specimen and material from Puerto Rico, where it replaces *D. nodosa* (sensu stricto) at higher elevations. The type specimen, however, does not include a rhizome, and there thus remains a minor possibility that *D. grandifolia* is not conspecific with the Greater Antillean material.

Likewise in French Guiana there are specimens of the *D. nodosa* group without pinna teeth. These plants have a much smaller stature; since no species of this kind was known, I described *D. ushana* as new (**I**).

After studying the specimens of the Lesser Antilles, I was certain that these were not typical *D. nodosa*. These specimens had much larger rhizomes with several rows of leaves, making the rhizome appear almost radial, whereas *D. nodosa* has only two rows of leaves on strictly dorsiventral rhizomes. This gave the plants a completely different posture, even though there were no apparent differences between the leaves of the two in herbarium specimens. I described the species as new (**I**), and named it after the Finnish heroic epic, the *Kalevala*, in gratitude for the hospitality of my host country. This species is supported by the molecular phylogeny (**IV**).

Based on historical collections it is known that *D. kalevala* was once widespread in the Lesser Antilles, but recently collected specimens are uncommon. When I discovered the species in 2003 (**I**), I encountered only six individuals in the entire population at the type locality in Martinique. In 2005, a larger population was encountered on Guadeloupe below Bains Jaunes. Studies are needed on the conservation status and methods of preserving this slow-growing species.

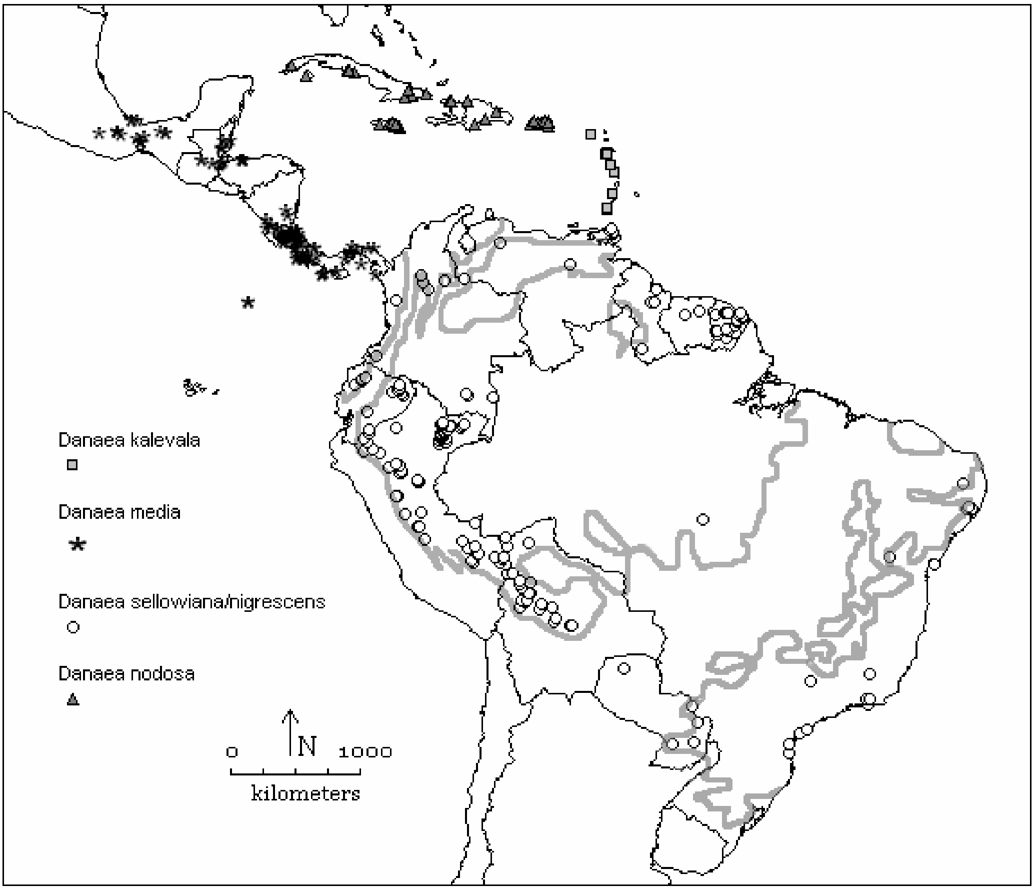

Figure 8. Distribution map showing selected species from the *D. nodosa* group based on georeferenced herbarium specimens. Thick gray lines roughly indicate the original extent of the rain forests, adapted from Morellato and Haddad (2000) and Mongabay.com (http://news.mongabay.com/2005/0424-rhett_butler.html).

3.2.6. The **Danaea alata** *group*

In addition to a few species, such as *D. crispa, D. trichomanoides* and *D. carillensis*, which are readily distinguishable, the *D. alata* group was initially thought to consist of two highly variable species, *D. alata* and *D. moritziana*, their major difference being in the posture of the rhizome. The molecular phylogeny (**IV**), shows that the relationships in this group are more complex. Selecting an epitype for *D. alata* (**III**) made it easier to distinguish this species from similar ones such as *D. mazeana* and *D. urbanii*, based on characters of pinna shape and venation. The type of *D. stenophylla* (Kunze 1840), on which Presl (1845) based his genus *Heterodanaea*, is clearly conspecific with *D. alata* (**III**), and that genus is thus synonymous with *Danaea*. Proctor (1977) erroneously applied *D. stenophylla* to specimens of *D. mazeana*, creating some confusion.

Species in the *D. alata* group with erect rhizomes have often been referred to as *D. cuspidata* in Central America and as *D. moritziana* in South America. The types of *D. moritziana* from Venezuela are highly variable and most likely consist of material from several plants. The type has leaves with short and wide pinnae, appearing similar to specimens from Paraguay (*D. paraguariensis*), but it also includes leaves with narrow elongate pinnae typical of many Central American populations (*D. cuspidata*). Between these extremes many intermediate forms are present in herbaria, and it was therefore impossible to divide this complex. What remains is a polymorphic species with a very wide geographical and elevational range. I have not been able to study this complex in the field, and the species are difficult to distinguish on the basis of the often incomplete herbarium material. The *D. moritziana* complex cannot be resolved as long as morphological observations on variability within populations in the field are lacking.

3.2.7. Species diversity

The greatest diversity of *Danaea* (Fig. 9, Tab. 4) can be found in Loreto (Peru) with twelve species, Napo and Morona-Santiago (Ecuador) with eleven and ten species, respectively, and Costa Rica, French Guiana and Puerto Rico, each with nine species. In the Lesser Antilles the greatest diversity is found in Trinidad and Guadeloupe, which harbour eight and seven species, respectively. This might be related to the fact that these are all areas with high precipitation. Moreover, the fern flora of these areas is relatively well collected compared to other areas such as Estado Amazonas in Brazil, a vast area, where only six species of *Danaea* are known to occur (Table 4). There were 40 more samples available for study from Costa Rica than from Brazil, which is more than 165 times larger in area. Regions with the highest *Danaea* diversity (Fig. 9) correspond to the collecting density map of South America, provided by Schulman et al. (2007). This sampling bias has certainly influenced the local species diversity. Also my fieldwork has contributed to the local knowledge of *Danaea* diversity. It is therefore not surprising, that many of my collection sites (Fig. 5) are found in areas of high *Danaea* diversity (Fig. 9).

While I know there is a collection bias in my data, I think some patterns can be observed. By calculating the minimum and maximum values of the WorldClim dataset (Hijmans et al. 2005) of all collecting sites of *Danaea* (Fig. 5, Fig. 10), I found that 91% of the samples are in areas with temperature values between 7 and 35ºC and an annual temperature range of 9-20 degrees. Additionally, *Danaea* occurs in areas with an annual precipitation of 750-4500 (-7500) mm and little seasonality in rainfall.

Figure 10 shows the potential distribution of *Danaea*, based on climatic variables. This figure demonstrates the existence of a large number of areas where *Danaea* has not yet been sampled. A closer study of the predicted areas will result in range expansions of many species, and new species may also be discovered.

In the present study, field characters facilitated the recognition of species that were otherwise difficult to separate based on herbarium samples. Field studies also made the interpretation of herbarium samples less contentious, and helped to distinguish between similar species.

This allowed me to redefine known species and to identify new species for the areas where fieldwork was carried out. I am therefore confident that future expeditions focussing on ferns will likely increase the knowledge of local *Danaea* diversity. I especially expect range expansions of known species, and possibly the encountering of new *Danaea* species, in parts of Colombia, the Darien, Nicaragua, northern Venezuela, northern Brazil (Amazonas, Pará, Roraima), and the slopes of table mountains in Guyana, regions that have not been botanically well explored.

Table 4. Numbers of *Danaea* species per political division and their respective surface area.

Country	Division	No of species	Area (km^2)
Peru	Reg. Loreto	12	368 852
Ecuador	Prov. Napo	11	12 426
Ecuador	Prov. Morona-Santiago	10	23 875
France	D.O.M. Guiane Française	9	90 000
Costa Rica	--	9	51 100
Puerto Rico	--	9	8 875
Ecuador	Prov. Zamora-Chinchipe	8	10 556
Ecuador	Prov. Pastaza	8	29 086
Peru	Reg. Pasco	8	25 320
Peru	Reg. San Martín	8	51 253
Colombia	Dept. Chocó	8	46 530
Trinidad & Tobago	Trinidad island	8	4 769
France	D.O.M. Guadeloupe	7	1 705
Dominican Republic	--	7	48 671
Peru	Reg. Madre de Dios	7	58 301
Brazil	Estado Amazonas	6	1 570 947
Guyana	--	6	214 969
Brazil	Estado Santa Catarina	4	95 443
Mexico	Estado Oaxaca	3	93 952

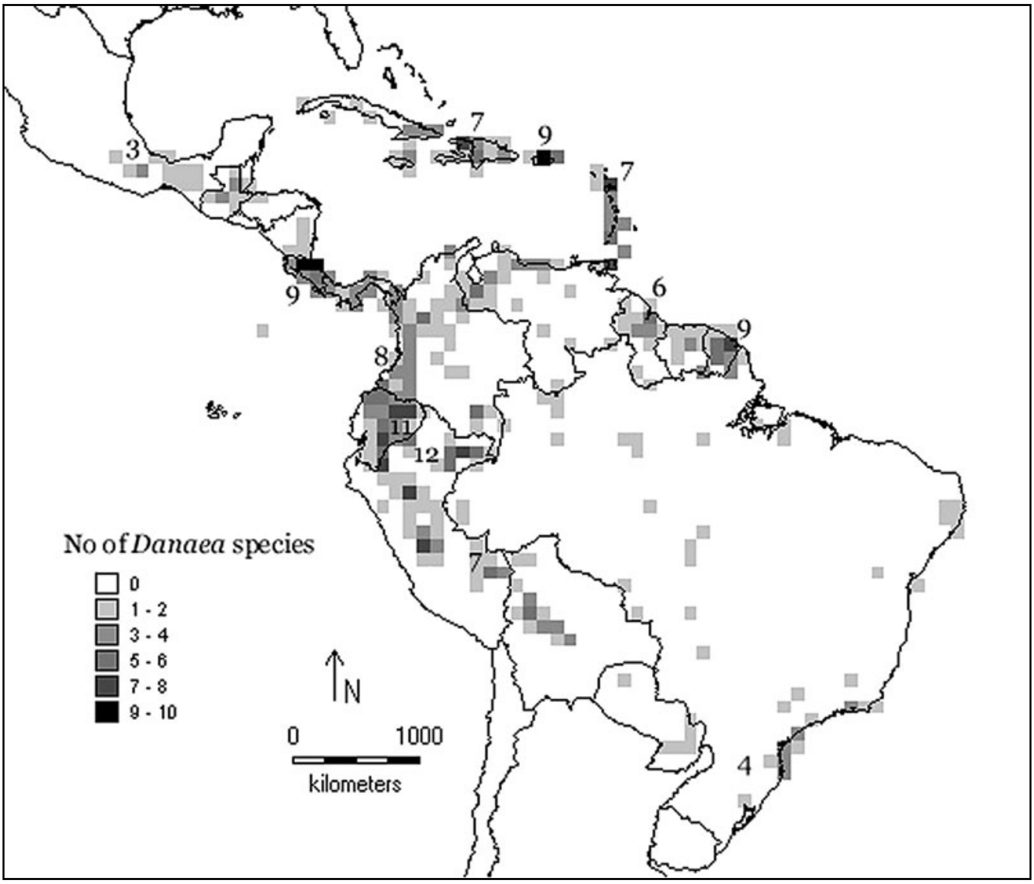

Figure 9. Diversity of *Danaea* in a 2 degree grid, based on the voucher data presented in Fig. 6 and Fig. 11. A selection of species numbers per political division according to Table 4 is also given.

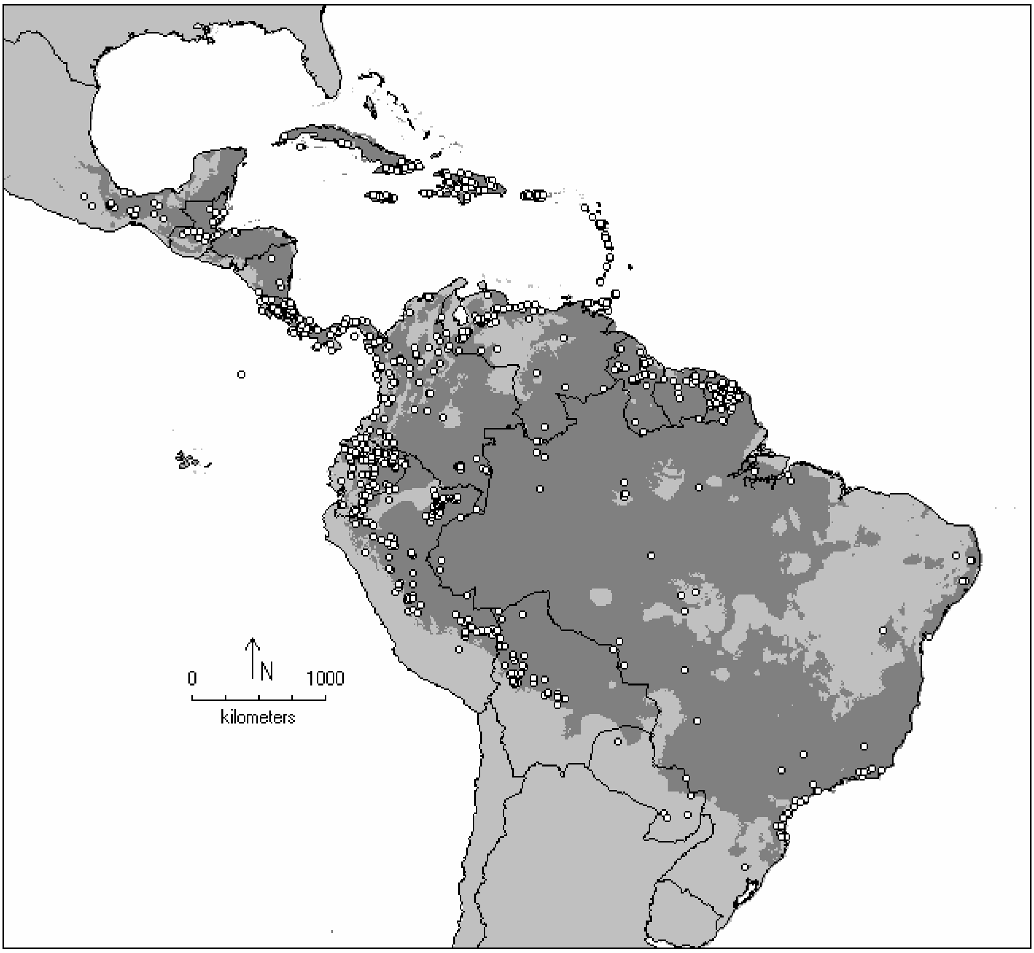

Figure 10. Potential distribution of *Danaea* (dark gray), based on climatic data and all herbarium samples studied (white dots). The potential distribution was estimated using climate data from WorldClim (Heijmans et al. 2005), and the Bioclim model (percentile = 0.005) provided by DIVA-GIS (http://www.diva-gis.org/).

3.2.8. New **Danaea** *species*

Eleven new species have been recognised from among herbarium specimens. These are included in Figure 11, Table 5 and in the identification key (3.8.2.). *Danaea sp. D* and *sp. H* occur in Trinidad and belong to the *D. leprieurii* group; *Danaea sp. B, sp. C* and *sp. G* also belong to this group. These new species all differ in pinna size, shape and texture. *Danaea sp. E* and *sp. K* are close to *D. moritziana*, but come from isolated populations in French Guiana and Colombia and differ in pinna shape and size. *Danaea sp. F* of the Chocó (Colombia) resembles *D. humilis*, but has larger leaves, more pinnae and is concolorous. Blue iridescent adult plants resembling *D. nodosa* were collected in Costa Rica by Mirkka Jones and are included in the key as *sp. A*. *Danaea sp. I* is remarkable in being the only known epiphytic member of the Marattiaceae; *Danaea sp. J* somewhat resembles *D. bicolor* but is not bicolorous. The distributions of the new species are given in Table 5. An article describing these new *Danaea* species is in preparation.

Table 5. Species occurrence of Marattiaceae in all Neotropical countries.

	Argentina	Belize	Bolivia	Brazil	Colombia	Costa Rica	Cuba	Dominica	Dominica Rep.	Ecuador	El Salvador	French Guiana	Grenada	Guadeloupe	Guatemala	Guyana	Haiti	Honduras	Jamaica	Martinique	Mexico	Montserrat	Nicaragua	Panama	Paraguay	Peru	Puerto Rico	Saint Kitts & Nevis	Saint Lucia	Saint Vincent	Suriname	Trinidad & Tobago	Venezuela
Angiopteris evecta						X	X												X		X												
Danaea acuminata										X																X							
Danaea alata								X					X	X						X		X							X	X		X	X
Danaea antillensis								X						X															X	X			
Danaea arbuscula			X	X	X					X				X												X							X
Danaea bicolor										X																							
Danaea bipinnata				X						X																X							
Danaea carillensis						X																											
Danaea cartilaginea				X	X					X																X							X
Danaea crispa						X																		X									
Danaea erecta					X					X																							X
Danaea excurrens				X																													
Danaea falcata					X					X																							
Danaea geniculata		?	?	X	X	?	X		?	X		X		X	?	X	X	?	X		?		?	?	X	X	X				X		X
Danaea grandifolia					X				X								X										X						X
Danaea humilis					X					X														X									X
Danaea imbricata										X																							
Danaea jenmanii							X		X								X		X								X						
Danaea kalevala									X				X	X						X								X		X		X	
Danaea latipinna										X																							
Danaea leprieurii				X						X		X														X							
Danaea lingua-cervina					X																					X							
Danaea longicaudata					X					X																							
Danaea mazeana							X		X					X			X		X								X						
Danaea media		X		X		X									X			X			X		X	X									
Danaea moritziana			X	X	X	X				X					X						X				X	X							X
Danaea nodosa							X		X								X		X								X						
Danaea oblanceolata					X					X																X							
Danaea plicata						X																											
Danaea polymorpha									X				X	X																		X	
Danaea riparia																										X							
Danaea sellowiana/nigrescens			X	X	X					X		X				X									X	X					X	X	X
Danaea simplicifolia				X								X				X															X	X	?
Danaea tenera					X					X																							
Danaea trichomanoides										X																X							
Danaea trifoliata				X								X				X															X	X	?
Danaea ulei			?	X																													
Danaea urbanii									X								X										X						
Danaea ushana												X																					
Danaea vivax					X																					X							
Danaea wendlandii					X	X				X														X									
Danaea sp. A						X																											
Danaea sp. B			X			X				X							X									X	X						
Danaea sp. C				X								X				X															X		
Danaea sp. D																																X	
Danaea sp. E												X																					
Danaea sp. F					X																												
Danaea sp. G						X																		X									
Danaea sp. H																																X	
Danaea sp. I					X					X																							
Danaea sp. J					X																					X							
Danaea sp. K					X																												
Marattia alata							X		X										X		?												
Marattia chiricana																								X									
Marattia cicutifolia				X																													
Marattia excavata						X					X				X			X			X		X										
Marattia interposita						X												X			X			X									
Marattia laevis	X		X	X	X	X	X		X	X														X		X	X						X
Marattia laxa						X												X			X			X									
Marattia weinmanniifolia															X						X												

3.2.9. Species distribution patterns

The changes in taxonomy resulted in a change of chorological patterns. Ranges of many species were expanded due to the inclusion of additional specimens. Table 5 lists all species and their distribution in the Neotropical countries, based on my current studies. Species of *Danaea* are widely distributed from Oaxaca in southern Mexico to Santa Catarina in southern Brazil. The genus is also found on all humid Caribbean Islands and on Cocos Island in the Pacific (Fig. 5). The elevational range is from sea level up to 2300 m, but the species are most abundant and most diverse between 100 and 1000 m elevation (Fig. 12).

Most *Danaea* species appear to have a restricted geographical range, whereas only a few are widespread. For instance, *D. carillensis, D. crispa* and *D. plicata* can be found in a small area of the highlands of Costa Rica and Panama, whereas *D. media* has a much wider range throughout Central America (Fig. 8). The Cocos Island population also matches *D. media* and is therefore likely of Central American origin.

On either side of the Andes we find a different set of species (Fig. 11). Few species are found on both sides. On the Pacific side of the Andes and in Central America, for instance, we find *D. wendlandii*, but on the Amazonian side of the Andes this species is replaced by the morphologically similar and closely related *D. oblanceolata*.

In some Andean valleys we find several species with highly restricted geographical ranges, e.g. *D. tenera, D. imbricata* and *D. trichomanoides*. This can be explained by elevational fragmentation of suitable habitats. This topographical isolation, however, is not a general pattern; in Western Amazonia, an area with little elevational variation, few species are widespread. Here several species, such as *D. lingua-cervina, D. falcata, D. ulei* and *D. sp. J*, have a limited distribution. This is probably related to the poor sampling in large parts of lowland Amazonia, but local ecological or edaphic conditions will be of importance as well.

Since the main division in the *D. nodosa* clade (**IV**) is geographical, the distribution of the previously widely applied name *D. nodosa* and related species of the same clade had to be reconsidered. My taxonomic studies suggest a more restricted range for *D. nodosa* to the Greater Antilles. The Central American specimens previously referred to *D. nodosa* belong to *D. media*. In the Lesser Antilles, *D. nodosa* is replaced by *D. kalevala*, and D. nodosa-like specimens in mainland South America mostly belong to the *D. sellowiana/nigrescens* complex (Fig. 8).

Danaea leprieurii, a common species in French Guiana, has also been reported from Amazonian Ecuador and Peru (Tuomisto & Moran 2001). My studies resulted in a range expansion to Colombian Amazonia and to Central-Amazonian Brazil, making its distribution area contiguous. Future field studies in Brazil may result in an expansion towards other areas of Brazilian Amazonia, an area where *Danaea* has been relatively poorly collected.

Soon after *D. arbuscula* was described for Peru (**II**), I noted that populations found on Guadeloupe also belong to this new species, even though the colour of the plants was slightly different. Additional specimens from Bolivia, Brazil (Mato Grosso), Colombia and Venezuela were found among herbarium specimens, substantially expanding the range of this species.

Several species, such as *D. geniculata, D. moritziana* and *D. sellowiana/nigrescens*, appear to have a more general distribution; these species complexes, however, are taxonomically not well resolved, and probably include geographically restricted species that are difficult to distinguish solely on the basis of morphology.

Figure 11. Global distribution of *Danaea* species per biogeographic region. Names in italics are species restricted to a given region.

3.2.10. Ecology and speciation

The revised chorological and ecological patterns, together with my new phylogenetic hypothesis (**IV**), allows a better understanding of speciation in *Danaea*. I illustrate this here with some examples.

Closely related species belonging to the same clade in study **IV** have been found to replace each other along an elevational gradient. This is best illustrated by *D. nodosa* and *D. grandifolia* in Puerto Rico. The former species occurs in lowland forests, and is replaced by the latter with increasing elevation. A similar pattern was observed for *D. alata* (lower elevation) and *D. mazeana* (high elevation) in Guadeloupe.

The same pattern was also found in the sub-Andean zone of San Martín, Peru, where *D. vivax* occurs between 600 and 1000 m (II). Its most closely related species, *D. acuminata* and *D. falcata*, are both found between 100-300 m in Amazonian Peru and Ecuador.

In the highlands of Costa Rica, occur three closely related (**IV**) but morphologically quite different species: *D. carillensis, D. crispa* and *D. plicata.* These have a very restricted range; they occur in similar places at similar elevations. *Danaea crispa* is somewhat more widespread. Although sympatric speciation of these species may have occurred, little is known about their ecology; other ecological factors (e.g. edaphic) may be involved. Moreover, *D. plicata* is morphologically intermediate between *D. carillensis* and *D. crispa*, and it is therefore possible that this is a species of hybrid origin.

Since many species have rather restricted ranges that are probably closely linked to local ecological factors (Tuomisto and Poulsen 1996), they may be excellent indicators for certain forest types in combination with other ferns (Salovaara et al. 2004).

Several closely related species show obvious differences in ecological distribution. For example, *D. cartilaginea* grows on poor loamy soils in western Amazonia (Tuomisto and Poulsen 1996; as *D. ulei*), whereas in the same region the *D. sellowiana/nigrescens*-complex usually occurs on richer clayey soils (Salovaara 2004, Tuomisto and Poulsen 1996; as *D. nodosa*). Similarly, we find *D. leprieurii* (sometimes together with *D. cartilaginea*) on loamy fertile soils, whereas the closely related *D. bipinnata* is found on intermediately rich substrates (H. Tuomisto, pers. comm.). Similar differences in edaphic distribution between closely related species have also been found in other Amazonian plants, such as *Clidemia* of the Melastomataceae (Schulman et al. 2004) and the fern genus *Polybotrya* (Tuomisto 2006).

Morphological intermediates between *D. jenmanii* and *D. mazeana* were observed in Jamaica (pers. obs.), and Proctor (1985) considered these to be hybrids. Hybrids intermediate between *D. mazeana* and *D. urbanii* have also been reported (Proctor 1989). Further cytological studies on ploidy levels will be necessary to confirm if hybridisation is in fact occurring in the Marattiaceae. The presence of collapsed spores might give an indication, although sterile hybrids can become fertile through allopolyploidy. This is well known to occur in many temperate fern genera, such as *Asplenium* (e.g. Reichstein 1981), *Cystopteris* (Haufler et al. 1985), *Dryopteris* (e.g. Gibby and Fraser-Jenkins 1985), *Gymnocarpium* (Pryer and Haufler 1993, Haufler and Windham 1991), *Hypolepis* (Brownsey 1983), *Isoëtes* (Taylor et al. 1985), *Polypodium* (Haufler and Windham 1991) and *Polystichum* (Wagner 1973). Because it is uncertain if allopolyploidy plays a role in the speciation within *Danaea,* further study is needed on hybridisation, polyploidy, and speciation in this genus.

3.3. Study of the genus *Marattia*

3.3.1. Redefined species and new synonyms

The taxonomic study of Neotropical *Marattia* did not result in many novelties, apart from some additional synonyms (Table 6). The main difference from the treatment by Lavalle (2003) is that I accept *M. chiricana* as a species separate from *M. interposita*. *Marattia chiricana* differs consistently in having the terminal pinnulets about as large as the largest lateral pinnulet of the same leaf, whereas *M. interposita* has terminal pinnulets that are much larger than the largest lateral pinnulets.

The variable and widespread *M. laevis* constitutes a complex of probably four closely related species that needs further taxonomic revision, but this will require additional fieldwork. Recent molecular studies strongly suggest that the *M. laevis* complex should be placed in a different genus: *Eupodium* (Andrew Murdock, pers comm.).

Elevation appears to influence species diversity in Marattiaceae, as illustrated in Figure 12. The diversity of *Marattia* is greatest between 1500 and 2100 m, whereas the greatest species diversity of *Danaea* occurs below 1500 m, with peaks between 200 and 1000 m. The *Marattia* species occurring at lower elevations were all collected at higher latitudes in Mexico (*M. laxa*) and Brazil (*M. cicutifolia*). Both are species with a lesser blade division (bipinnate) than other Neotropical *Marattia*'s. The cooler climatic conditions may have resulted in a selection for individuals with less complex leaves (Asama 1960).

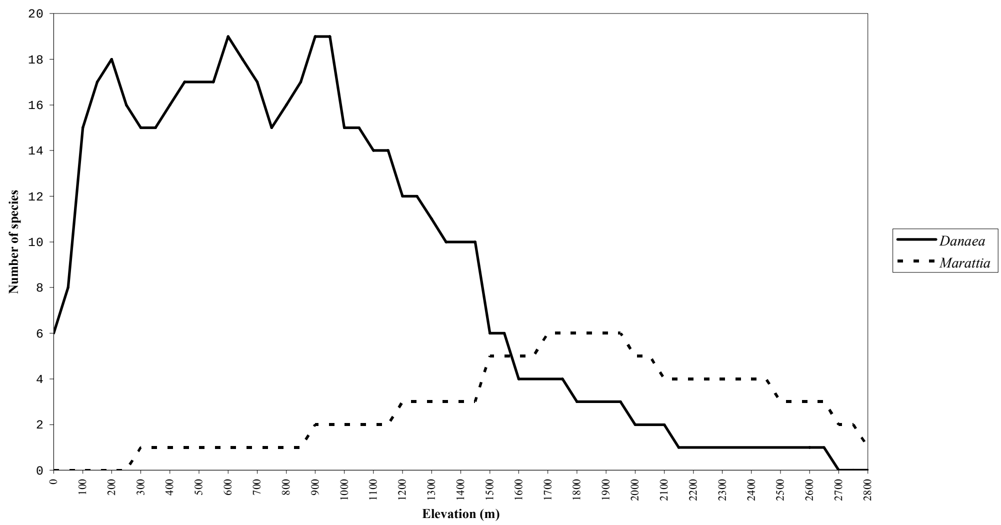

Figure 12. Relationship between elevation and species diversity of Neotropical Marattiaceae, based on elevational data taken from herbarium specimens.

3.3.2. Taxonomic history

Marattia was first described by Swartz (1788), but the diagnosis was minimal. Fortunately the original Swartz specimen of *M. alata* is preserved in S, typifying the genus. Smith (1790) then described *M. laevis*, and both species were subsequently placed in *Myriotheca* (Lamarck & Poiret 1797). An illustration of *Marattia kaulfussii* was published (Hooker 1838), and this name has since been widely applied. It is part of the *M. laevis* complex. Hooker (1842) later placed his species in *Eupodium*, based on the stalked synangia.

As he did for *Danaea*, Presl (1845) revised the genus *Marattia*; he created several new genera, such as *Discostegia* (which includes *M. alata*, the type of *Marattia*), *Gymnotheca* (based on *M. cicutifolia*), and *Stibasia* (based on *M. douglasii* from Hawaii).

In their monograph on the Marattiaceae, de Vriese and Harting (1853) followed Presl's classification. Fée (1857, 1869) also adopted Presl's genera. Martius (1859), Christ (1906), Underwood (1909) and Maxon (1914) included all genera in *Marattia*, as is done in this dissertation.

Table 6. List of published names of *Marattia*. Names accepted in this dissertation are in boldface. Names differently applied or not listed by Lavalle (2003) are indicated with an asterisk.

Published name	Publication	Current name
Marattia alata	Swartz 1788: 128	
Marattia laevis	Smith 1790	
Myriotheca alata	Lamarck & Poiret 1797: 403	= *M. alata*
Myriotheca laevis	Lamarck & Poiret 1797: 403	= *M. laevis* complex
Marattia cicutifolia	Kaulfuss 1824: 32	
Marattia raddiana	Schott 1834: t.5	= *M. laevis* complex*
Marattia kaulfussii	Hooker 1838: t.26	= *M. laevis* complex
Eupodium kaulfussii	Hooker 1842: t.118	= *M. laevis* complex
Marattia laxa	Kunze 1844: 306	
Discostegia alata	Presl 1845: 12	= *M. alata*
Discostegia laevis	Presl 1845: 12	= *M. laevis* complex
Gymnotheca cicutifolia	Presl 1845: 13	= *M. cicutifolia*
Gymnotheca raddiana	Presl 1845: 13	= *M. laevis* complex*
Gymnotheca polyodon	Presl 1845: 14	= *M. cicutifolia*
Gymnotheca obtusidens	Presl 1845: 15	= *M. cicutifolia*
Gymnotheca laxa	Presl 1845: 15	= *M. laxa*
Marattia weinmanniifolia	Liebmann 1849: 308	
Gymnotheca podolepis	Vriese & Harting 1853: 10	= *M. cicutifolia*
Gymnotheca verschaffeltiana	Vriese & Harting 1853: 10	= *M. cicutifolia*
Gymnotheca weinmaniifolia	Vriese & Harting 1853: 11	= *M. weinmanniifolia*
Discostegia microphylla	Fée 1857: 43	= *M. weinmanniifolia**
Marattia laucheana	Blass 1858: 233	= *M. weinmanniifolia*
Marattia polyodon	Sturm in Martius 1859: 150	= *M. cicutifolia*
Marattia obtusidens	Sturm in Martius 1859: 151	= *M. cicutifolia*
Marattia podolepis	Sturm in Martius 1859: 151	= *M. cicutifolia*
Marattia verschaffeltiana	Sturm in Martius 1859: 153	= *M. cicutifolia*
Gymnotheca cicutifolia var. *stipulacea*	Fée 1869: 214	= *M. cicutifolia**
Eupodium kaulfussii var. *acuminatum*	Fée 1869: 215	= *M. laevis* complex*
Eupodium kaulfussii var. *macropteron*	Fée 1869: 215	= *M. laevis* complex*
Marattia microphylla	Fournier 1872: 136	= *M. weinmanniifolia**
Marattia juergensii	Rosenstock 1905: 68	= *M. cicutifolia*
Marattia interposita	Christ 1906: 285	
Marattia raddii var. *juergensii*	Rosenstock 1907: 161	= *M. cicutifolia*
Marattia excavata	Underwood 1909: 22	
Marattia chiricana	Maxon 1914: 421	*
Marattia pittieri	Maxon 1914: 421	= *M. laevis* complex
Marattia alata var. *laevis*	Farwell 1931: 308	= *M. laevis* complex

3.4. Diagnostic keys to Neotropical Marattiaceae

Below, I provide keys to identify 58 species of Neotropical Marattiaceae. These keys are primarily useful to identify adult plants, since juvenile specimens differ greatly from adult ones, especially in blade division, size and numbers of pinnae. I consider plants bearing fertile leaves adult; many herbarium specimens of *Danaea*, apparently adult, are represented only by sterile specimens. Some species may have simple blades when adult (*D. carillensis, D. lingua-cervina, D. simplicifolia, D. trifoliata*) and some have very large juveniles with simple blades (i.e. *D. cartilaginea, D. ulei*). These species made the construction of this key contentious, and hence may complicate the identification of these plants.

Most characters can be observed in well-preserved herbarium specimens, but sometimes it was impossible to separate specimens solely by herbarium characters. For this reason the keys also include certain field characters, such as colour, texture and rhizome posture. For correct identification it is thus important that collectors note these important field characters on labels, as these characters disappear when the specimen is dried. Additionally, plants should be collected in their entirety, and well-marked multiple sheets should be made of large species. When a rhizome is collected a description of the plants habit should also be included. If killing the plant is of conservation concern, a photograph of the rhizome will suffice. Habit photographs can be a helpful additional aid for species identification.

Some of the names in these keys are tentative because the taxonomy is not fully resolved. Most notably, the species complexes surrounding *Danaea geniculata, D. moritziana, D. sellowiana/nigrescens* and *Marattia laevis* need further study.

3.8.1. Key to genera of Neotropical Marattiaceae

1.a. Leaves (normally) fully dimorphic, the fertile leaves contracted, with the lower sides of the fertile pinnae (almost) completely covered by the synangia; synangia sunken into the laminae; adult leaves once pinnate, in some species simple or trifoliate or irregularly bipinnate; rhizomes slender, erect or creeping; stipules small, delicate ***Danaea***

1.b. Leaves monomorphic, the fertile leaves similar to the sterile leaves; adult leaves normally 2 to 4 times pinnate; rhizomes massive, spherical to erect; stipules large, leathery or hard **2.**

2.a. Sporangia almost free, attached only at the base in a dense double row; leaves to 5(-7) m long, fully bipinnate; largest pinnae up to 150 cm long, with up to 50 pinnules; [naturalised] ***Angiopteris evecta***

2.b. Sporangia fused in 8-16 locular synangia, these spaced on the lower side of the leaves; leaves to 2 (-3) m long, 2-4 times pinnate, if bipinnate then the largest (basal) pinnae usually much shorter than 100 cm long, with up to 20 pinnules ***Marattia***

3.8.2. Key to species of Danaea

1.a. Leaves of adult plants simple (Fig. 13 O) or trifoliate (juvenile plants of other species can also be simple or trifoliate, but this key concerns only adult specimens) **2.**

2.a. Pinna apices denticulate; petioles with 2-4 nodes; rhizomes creeping-ascending; blades (almost always) simple; (Costa Rica) ***Danaea carillensis***

2.b. Pinna apices entire; petioles with 1-2 nodes; rhizomes erect; blades simple or trifoliate; (South America) **3.**

3.a. Leaves white below, bicolorous, mostly simple, but when trifoliate, the pinnae sprouting from the single node below the blade, then leaving the petioles without nodes (Fig. 13 O) ***Danaea simplicifolia***

3.b. Leaves concolorous, not white below, mostly trifoliate or more divided, occasionally simple, but then the petiole with 1-2 nodes **4.**

4.a. Largest lateral pinnae elliptic-oblong, 2-3 times longer than wide; apices acute to short-acuminate; terminal pinnae large 24-36 x 6.4-9.4 cm; (Guianas, N Brazil, tierra firme forests) ***Danaea trifoliata***

4.b. Largest lateral pinnae oblong-elliptic to lanceolate-elliptic, about 3 times longer than wide; apices abruptly acuminate, with slightly sinuate margins; terminal pinnae smaller (12.4-)15.5-25 x (2.8-)4.7-6.8 cm; (Western Amazonia, swamp forests) ***Danaea lingua-cervina***

Figure 13. Pinnae and illustrations of *Danaea* species. A. *D. acuminata* (pinna); B. *D. falcata* (pinna); C. *D. moritziana* (pinna); D-E. *D. crispa* (pinna and habit); F. *D. jenmanii* (habit); G. *D. excurrens* (pinna); H. *D. longicaudata* (pinna); I. *D. plicata* (habit); J. *D. media* (pinna); K. *D. leprieurii* (pinna); L. *D. sp. H* (pinna); M. *D. bipinnata* (habit); N. *D. nodosa* (pinna bases of bipinnate leaf); O. *D. simplicifolia* (habit).

1.b. Leaves of adult plants pinnate (Fig. 13 E, F, I) or bipinnate (Fig. 13 M), with at least 2 pairs of pinnae **5.**
5.a. Pinna margins erose throughout, crispate-undulate, irregularly biserrate throughout; blades transparent, always terminated by a bud (Fig. 13 D, E) ***Danaea crispa***
5.b. Pinna margins entire, entire or denticulate to serrate at apices; blades leathery or transparent, with or without terminal buds **6**.
6.a. Pinna margins dentate, denticulate, serrate serrulate, or crenulate at apices 7.
7.a. Blades strongly bicolorous, dark green above, white below; largest lateral pinnae 3.2-4.2 cm wide ***Danaea bicolor***
7.b. Blades mostly concolorous, sometimes lighter green (not white) below; if (slightly) bicolorous, then the largest lateral pinnae less than 3 cm wide **8.**
8.a. Pinnae apices abruptly acute-acuminate with caudate-spathulate, sharply serrated tips; pinnae linear-oblanceolate; (Fig. 13 G); S Brazil ***Danaea excurrens***
8.b. Pinnae apices obtuse to caudate, without spathulate tips; pinnae variously ovate to lanceolate **9.**
9.a. Rhizomes erect with roots on all sides; leaves radially arranged **10**.
10.a. Pinna apices sharply denticulate to serrulate (Fig. 13 C); petioles with (0-)1-3(-4) nodes ***Danaea moritziana***
10.b. Pinna apices sinuate to crenulate; petioles without nodes ***Danaea erecta***
9.b. Rhizomes creeping, sometimes with the tips ascending, dorsiventrally arranged, with all roots on the lower side and leaves in two or more rows **11**.
11.a. Blades transparent or thin and opaque, up to 30 cm long, usually terminated by a proliferous bud **12**.
12.a. Pinnae biserrate throughout (Fig. 13 D, E) ***Danaea crispa***
12.b. Pinnae once denticulate at apex **13**.
13.a. Blades with 3-6 pinna pairs; terminal pinnae much longer than the lateral pinnae of the same leaf; terminal pinnae usually midway aborted by proliferous buds (Fig. 13 I) ***Danaea plicata***
13.b. Blades with 10 or more pinna pairs; terminal pinnae, when present, as long as or shorter than the largest lateral of the same leaf; blades with or without proliferous buds **14**.
14.a. Pinna apices acute to acuminate; petioles 11-26 cm long with 2-4 nodes ***Danaea tenera***
14.b. Pinna apices obtuse; petioles to 11 cm long with 0-2 indistinct nodes **15**.
15.a. Pinnae crowded, often overlapping at the base, margins coarsely serrulate to crenulate; veins forked well above the base ***Danaea imbricata***
15.b. Pinnae well spaced, not (or rarely) overlapping; veins mostly simple, but occasionally a few forked ones **16.**
16.a. Pinnae ovate to obovate, 1.3-3.2 x 0.6 -1(-1.3) cm; margins sinuate to widely denticulate at pinna apices; veins 8-11 per cm ***Danaea trichomanoides***
16.b. Pinnae linear-oblong to lanceolate, 2-5.1 x 0.6-1.3 cm; margins denticulate at pinna apices; veins 11-22 per cm ***Danaea wendlandii***
11.b. Blades thick, leathery, longer than 30 cm, terminated by pinnae or buds **17**.
17.a. Petioles without nodes; blades abrupt at the base, without reduced pinnae protruding from the lowest nodes **18**.
18.a. Rhizomes dorsiventral, distichous, with two rows of leaves **19**.
19.a. Pinnae elliptic-lanceolate, widest at the middle, with a darker zone around the midvein; margins cartilaginous; apical teeth not incising the green part of the lamina ***Danaea cartilaginea***
19.b. Pinnae oblanceolate, usually widest above the middle, concolorous; margins usually not cartilaginous; apical teeth incising the green lamina **20.**
20.a. Pinnae often cordulate to auriculate at base, sometimes bipinnate; Greater Antilles, usually on clay in karsted limestone hills (differs genetically from the next, see **IV**) ***Danaea nodosa***
20.b. Pinnae acute to obtuse-truncate at base, never with extra pinnae; continental South America (differs genetically from the previous) ***Danaea sellowiana/nigrescens***
18.b. Rhizomes dorsiventral, with several rows of leaves on the upper sides **21**.
21.a. Pinna apices finely serrulate-sinuate to minutely serrulate-denticulate; Lesser Antilles ***Danaea kalevala***
21.b. Pinna apices entire to sinuate(-denticulate), Fig 13 J; Central America ***Danaea media***
17.b. Petioles with (0-)1-4 nodes; when nodes absent, than blades gradually tapering towards very reduced, small, almost rotund pinnae at the blade bases **22**.
22.a. Largest lateral pinnae (2.7-) 3-5 cm wide **23.**
23.a. Pinnae strongly bicolorous, white below ***Danaea bicolor***
23.b. Pinnae concolorous, light green below ***Danaea sp. J***
22.b. Largest lateral pinnae 0.4-2.9 cm wide **24.**
24.a. Rhizomes clearly dorsiventral; leaves up to 2 m long ***Danaea media***
24.b. Rhizomes usually radially arranged; when dorsiventral in appearance, then leaves shorter than 1 m **25**.

25.a. Terminal pinnae more than twice the length of the largest lateral of the same leaf; terminal pinnae always present, often with a but at the pinna apices (Fig. 13 I) ***Danaea plicata***
25.b. Terminal pinnae absent and replaced by buds, or present with or without a bud at the apices; when terminal pinnae bearing buds, than much shorter than the lateral pinnae of the same leaf (Fig. 13 F) **26.**
26.a. Largest lateral pinnae 2-5.1 cm long **27**.
27.a. Terminal pinnae replaced (or aborted) by proliferous buds **28**.
28.a. Leaves with 5-11 lateral pinna pairs; veins usually forked; terminal pinnae aborted by or completely replaced by buds (Fig. 13 F) ***Danaea jenmanii***
28.b. Leaves with 10-26 lateral pinna pairs; veins simple or paired at base; when pinnae 10-12 pairs, then veins paired at the base; terminal pinnae completely replaced, but may be present on some leaves of the plant **29**.
29.a. Lateral pinnae acute-acuminate, somewhat falcate; blades bicolorous, parallel-sided ***Danaea humilis***
29.b. Lateral pinnae acute, not falcate; blades concolorous, lanceolate ***Danaea wendlandii***
27.b. Terminal pinnae present, never replaced or aborted by buds **30**.
30.a. Blades lanceolate with 8-15 pinna pairs; veins 11-17 per cm **31**.
31.a. Sterile leaves all in an appressed rosette; veins mostly paired at base; (western Amazonia) ***Danaea acuminata***
31.b. Sterile leaves upright, arching; veins mostly forked; (Greater Antilles) ***Danaea urbanii***
30.b. Blades parallel-sided with 12-24 pinna pairs; veins 14-36 per cm **32**.
32(56).a. Blades bicolorous; veins 14-18 per cm, mostly forked; largest lateral pinnae 2.2-3.7 cm long ***Danaea humilis***
32.b. Blades concolorous; veins dense, 21-36 per cm, mostly simple and paired at base; largest lateral pinnae 3.4-5.1 cm long ***Danaea sp. F***
26.b. Largest lateral pinnae 5.3-21 cm long **33**.
33.a. Sterile leaves in a prostrate rosette or pendent; fertile leaves erect **34**.
34.a. Pinnae 2.3-6.2 cm long, 3-5 times longer than wide; pinna apices abruptly acute to acuminate (Fig. 13 A) ***Danaea acuminata***
34.b. Pinnae 7.5-8.5 cm long, 7-8 times longer than wide; pinna apices gradually acute to long-acuminate ***Danaea riparia***
33.b. Sterile leaves erect or arching, held similarly as the fertile leaves **35**.
35.a. Blades (usually) terminated by proliferous buds, sometimes terminal pinnae present on leaves of the same plant **36.**
36.a. Pinna apices abruptly acute to short acuminate **37.**
37.a. Veins mostly forked; leaves with 5-11 pinna pairs (Fig 13 F); (Greater Antilles) ***Danaea jenmanii***
37.b. Veins mostly simple; leaves with 10-20 pinna pairs; (South America) **38.**
38.a. Blades slightly bicolorous, lighter below; apices sharply serrulate; veins dense, 13-20 per cm; (French Guiana) ***Danaea sp. E***
38.b. Blades concolorous, apices denticulate; veins 11-16 per cm; (Western Amazonia) ***Danaea oblanceolata***
36.b. Pinna apices gradually (long-)acuminate to caudate **39.**
39.a. Pinna apices acuminate ; veins simple ***Danaea sp. E***
39.b. Pinna apices long-acuminate to caudate, falcate; veins usually forked or paired at base . **40.**
40.a. Pinnae clearly stalked, longer than 1 mm; pinna apices coarsely denticulate (Fig. 13 B); lowland ***Danaea falcata***
40.b. Pinnae (sub-)sessile; pinna apices sharply serrulate; mid- to higher elevation **41.**
41.a. Veins about 16 per cm; fertile pinnae narrow, about 0.6 cm wide ***Danaea vivax***
41.b. Veins usually 17-21 per cm; fertile pinnae broad, 1.2-1.4 cm wide ***Danaea sp. K***
35.b. Blades terminated by normal well-developed pinnae, never terminated by buds **42.**
42.a. Veins mostly simple or paired at base, rarely a few forked ones **43.**
43.a. Blades with 6-8 pinna pairs, concolorous; lateral pinnae oblanceolate, 8 times longer than wide (Fig. 13 G) ***Danaea excurrens***
43.b. Blades with 8-16 pinna pairs, lighter green below, dark glossy green above lateral pinnae 4-8.2 times longer than wide **44.**
44.a. Pinna apices sinuate to denticulate, acuminate to cuspidate; (Lesser Antilles, N Venezuela) ***Danaea alata***
44.b. Pinna apices sharply serrulate, acute to acuminate; (French Guiana)

Danaea sp. E

42.b. Veins mostly forked, sometimes paired at base or a few simple ones **45.**

45.a. Pinnae abruptly acuminate to cuspidate; Antilles **46.**

45.b. Pinnae gradually long-acuminate to caudate; South America *D. falcata, D. vivax, D. sp. 11*: **40.**

46.a. Pinnae rather narrow 1-1.5 cm wide, 5-9 cm long ***Danaea urbanii***

46.b. Pinnae wider, 1.1-2.4 cm wide, 6.8-15 cm long ***Danaea mazeana***

6.b. Pinna margins entire, sometimes slightly sinuate at apices **47**.

47.a. Rhizomes creeping, sometimes with the tip ascending, dorsiventrally arranged, with all roots on the lower side and leaves in two or more rows **48.**

48.a. Pinnae with cuspidate or abrupty caudate apices; blades usually terminated by a proliferous bud, replacing the terminal pinnae ***Danaea latipinna***

48.b. Pinnae with acute to acuminate-attenuate apices; blades always with well- developed terminal pinnae, never replaced by buds **49**.

49.a. Rhizomes strictly dorsiventral, with two rows of leaves, placed alternately on the rhizomes **50**.

50.a. Pinna apex acuminate-attenuate; pinnae 27-49 cm long; leaves large, up to 3 m long ***Danaea cartilaginea***

50.b. Pinna apex acute; pinnae 23-28 cm long; leaves much shorter, up to 1 m long (French Guiana) ***Danaea ushana***

49.b. Rhizomes dorsiventral, but with several rows of radially placed leaves; roots all on the lower side **51.**

51.a. Pinna apices acute; veins simple; blades iridescent blue-green when plants adult ***D. sp. A***

51.b. Pinna apices acuminate to caudate; veins paired at base or forked; blades only iridescent when plants juvenile **52**.

52.a. Pinna apices acuminate; pinnae lanceolate, parallel-sided, widest at the middle ***Danaea grandifolia***

52.b. Pinna apices acuminate-cuspidate to caudate; pinnae oblanceolate, widest above the middle (Fig. 13 J) ***Danaea media***

47.b. Rhizomes erect; leaves radially arranged, with roots on all sides **53**.

53.a. Petioles always without nodes; leaves mostly terminated by a proliferous bud (except in plants from a population in the eastern Andean slopes in Ecuador) ***Danaea erecta***

53.b. Petioles usually nodose (1-4 nodes); when nodes absent, then there are always nodes present on other leaves of the same plant; leaves never terminated with buds **54**.

54.a. Pinnae more than 11 pairs; pinna apices abruptly acute-acuminate with a caudate-spathulate tips (Fig. 13 H) ***Danaea longicaudata***

54.b. Pinnae less than 8 pairs, pinna apices not caudate-spathulate **55**.

55.a. Largest lateral pinnae 1-3(-4) cm wide **56**.

56.a. Pinnae abruptly tapering into an acuminate to cuspidate, somewhat falcate apex **57.**

57.a. Pinna margins strongly sinuate at apex; pinnae elliptic to (ob-)lanceolate (Fig. 13 L); (Trinidad) ***Danaea sp. H***

57.b. Pinna margins not to very weakly sinuate at apex; pinnae parallel-sided, oblong-lanceolate to oblanceolate (Fig. 13 K); (continental South America) ***Danaea leprieurii***

56.b. Pinnae gradually tapering into a acute to acuminate apex **58.**

58.a. Pinnae ovate elliptic to oblong (rarely oblanceolate), widest at the middle; blades sometimes bipinnate (Fig. 13 M) ***Danaea bipinnata***

58.b. Pinnae elliptic-oblong to oblanceolate, widest at or above the middle ***Danaea geniculata***

55.b. Largest lateral pinnae 3-6 cm wide **59**.

59.a. Terminal pinnae equal or smaller than the largest lateral pinnae of the same leaf **60.**

60.a. Rhizomes 5-8 cm thick, the leaves crowded at the tip; pinnae 5-8 pairs per leaf, ovate-elliptic to ovate-lanceolate, gradually tapering to (long-) acuminate apices ***Danaea antillensis***

60.b. Rhizomes 1-3 cm thick, the leaves (usually) well spaced along the rhizome; pinnae 2-8 pairs per leaf, but when more than 5 pairs, the pinnae oblanceolate and/or abruptly tapering at apex **61**.

61.a. Lateral pinnae 4-6.5 times longer than wide **62.**

62.a. Rhizomes tall and slender, up to 110 cm long; leaves well-spaced; lateral pinnae dull above, abruptly acuminate ***Danaea arbuscula***

62.b. Rhizomes shorter and stout, up to 50 cm long; leaves more crowded; lateral pinnae usually glossy above, gradually acute to long-acuminate ***Danaea geniculata***

61.b. Lateral pinnae 2-3.5 times longer than wide **63.**

63(19).a. Leaves well-spaced on slender rhizomes; lateral pinnae elliptic-oblong to oblanceolate, lighter along the midrib above when fresh, thick and leathery; margin cartilaginous; pinna apices abruptly acute; 3-4 pinna pairs per leaf; (Panama) ***Danaea sp. G***

63.b. Leaves crowded on stout rhizomes; pinnae oblong to lanceolate, concolorous, leathery, but margin not cartilaginous; pinna apices abruptly (long-) acuminate; 2-5 pinna pairs per leaf; (Guianas) ***Danaea sp. C***

59.b. Terminal pinnae much larger than largest lateral pinnae of the same leaf **64.**

64.a. Largest lateral pinnae broad-lanceolate, 5.5-7 cm wide **65**.

65.a. Largest lateral pinnae 3-4 times longer than wide, 17-22 x 4.8-6 cm ***Danaea ulei***
65.b. Largest lateral pinnae 2-3 times longer than wide, 7-18 x 2.6-7 cm **66**.
66.a. Terminal pinnae 2-3.4 times longer than the largest lateral of the same leaf; lateral pinnae elliptic-oblong ***Danaea trifoliata***
66.b. Terminal pinnae 1.5-2 times longer than the largest lateral of the same leaf; lateral pinnae broad-lanceolate ***Danaea sp. B***
64.b. Largest lateral pinnae oblong to (broad)-lanceolate, 2.6-5.4 cm wide **67**.
67.a. Pinna apices abruptly acute to abruptly short-acuminate; pinnae dull above; (Antilles) ***Danaea polymorpha***
67.b. Pinna apices gradually acute to acuminate; pinnae dull or glossy; (South America, Trinidad) **68**.
68.a. Pinna apices (slightly) sinuate; terminal pinnae (12.4-) 15.5-27.2 cm long **69**.
69.a. Lateral pinnae oblong-elliptic to lanceolate-elliptic, widest at the middle, 11-15 cm long; (swamp forests of Western Amazonia) ***Danaea lingua-cervina***
69.b. Lateral pinnae oblong to broad-oblancelate widest at or above the middle, 13-21 cm long; (mountain forests of Trinidad) ***Danaea sp. D***
68.b. Pinna apices entire, not sinuate; terminal pinnae (19-) 24-36 cm long **70**.
70.a. Lateral pinnae 7-17 cm long, elliptic-oblong; blades 21-36 cm long ***Danaea trifoliata***
70.b. Lateral pinnae 17-22 cm long, broadly lanceolate; blades 30-49 cm long ***Danaea ulei***

3.8.3. Key to Neotropical species of Marattia

1.a. Blades 2-pinnate; internodes of similar and constant length **2**.
2.a. Terminal pinnules much longer than the largest lateral; lateral pinnules widened at base; margins irregularly serrate, biserrate or triserrate; veins mostly twice bifurcating; synangia marginal, sessile; (C America) ***Marattia laxa***
2.b. Terminal pinnules about the same length as the lateral; lateral pinnules not widened at base; margins serrate, regular or irregular; veins mostly paired at base, or branched, rarely branched twice; synangia supramedial or nearly marginal; (Brazil) ***Marattia cicutifolia***
1. b. Blades 3-4-pinnate; internodes becoming shorter towards the leaf apices **3**.
3.a. Veins simple or rarely with some bifurcated ones in the apical pinnules; basal pinnulets small, the largest usually to 1 cm long **4**.
4.a. Pinnules 15-20 pairs; pinnulets lanceolate-elliptic with acute apex; veins mostly simple, rarely with a bifurcated one; synangia intramarginal ***Marattia alata***
4.b. Pinnules 23-28 pairs; pinnulets elliptic-oblong with an obtuse apex; veins always simple; synangia supramedial ***Marattia weinmanniifolia***
3.b. Veins mostly bifurcated; largest pinnulets longer than 1 cm **5**.
5.b. Synangia stalked (overdeveloped receptacles), supramedial; spinules often present on the abaxial side of the costules; pinnulets with lobed margins; trichomes absent ***Marattia laevis***
5.a. Synangia sessile, (normal, plain receptacle), intramarginal; spinules absent; pinnulets with serrate margins; trichomes fimbriate **6**.
6.a. Pinnulets oblanceolate-elliptic with obtuse to rounded apices; pinnule apices tapering to lobed segments ***Marattia excavata***
6.b. Pinnulets lanceolate-elliptic or falcate with acute attenuate apices; pinnule apices terminating in entire pinnulets, which are lobed at the bases **7**.
7.a. All pinnulets about the same size; terminal pinnulets not much larger than the largest lateral pinnulets; lateral pinnae large, 2.5-7 x 1-2 cm ***Marattia chiricana***
7.b. Terminal pinnulets much larger than largest lateral pinnulets of the same leaf; lateral pinnae short and narrow, up to 4.6 x 1.3 cm ***Marattia interposita***

4. CONCLUSIONS

The results of the studies comprising this dissertation provide further evidence that the fern diversity of the Neotropics is greater than previously assumed. The estimate of thirty species for *Danaea* (Mabberley 1997) has been revised to be closer to fifty. Eight new species are described in the studies forming this dissertation, and eleven will be published elsewhere. In the Neotropics, the genus *Marattia* is much less diverse, with only eight species – one more than listed in the revision by Lavalle (2003).

The greatest diversity of *Danaea* can be found in western Amazonia, in the Pacific forests of northern Ecuador to Costa Rica, in the eastern part of the Guianas, and on the Caribbean islands of Hispaniola, Puerto Rico, Guadeloupe and Trinidad. All of these areas, however, have been very well studied, and there is a certain collection bias in diversity and distribution patterns. I predict that the genus will be found to be much more widespread throughout Amazonia, but there is as yet little data available for the Brazilian part of the distribution area.

This study resulted in the redefining of many species, which may complicate the interpretation of previously published species lists. Previously widely applied names, such as *D. alata*, and *D. nodosa* have been redefined, and should be applied more strictly. Many species of the genus have been found to have a much more restricted range than previously assumed. To facilitate revision of these lists, the geographic distribution of all species is shown in Table 6.

Danaea elliptica was found to be synonymous with *D. nodosa*, thus that name should no longer be applied. Instead, the correct name for taxa previously called *D. elliptica* should be chosen from among species of the *D. leprieurii* group. Several taxa in this group remain undescribed, especially in the *D. geniculata* complex, and can be more accurately circumscribed when the taxonomy of this group is further clarified. The diagnostic keys provided in this dissertation may help to find the correct names for the species of Neotropical Marattiaceae.

The restricted geographic range of many *Danaea* species is probably closely related to local ecology, soil gradients and elevation, which may make *Danaea* species useful forest type indicators. However, for that purpose the taxonomy needs to be further unravelled and the edaphic and climatic preferences of all species individually revised.

Even after redefining and circumscribing many species, some complexes remain that could not be unravelled. Specifically, the species complexes surrounding *Danaea geniculata, D. moritziana, D. sellowiana/nigrescens*, and *Marattia laevis* are still in need of further taxonomic revision. A combination of molecular (DNA) and morphological data in phylogenetic analyses may be a good aid to resolving these problematic complexes; to obtain good resolution, however, populations need to be sampled throughout their range, and molecular markers need to be identified that provide better resolution at species or population levels. This requires additional field and laboratory work, which could not be included in this dissertation.

This dissertation also provides evidence of the importance, whenever possible, of studying a species at or close to its type locality. That way one can be more certain of the species identity. The inclusion of material from or near to the type locality in a phylogenetic analysis, in combination with other populations, will make it possible to test whether a species is monophyletic, and, if not, to determine which of the populations should carry the name. In molecular phylogenies, widespread species should be tested for monophyly. Additional field characters, not preserved in the type material, can be studied, that can help in distinguishing between otherwise similar species. I have noted that species that were clearly separate in the field resembled each other once dried in the herbarium.

My phylogeny resulted in a few new insights into the taxonomy of *Danaea*; it provided me with a framework in which several evolutionary patterns can be studied. Based on the ecology of closely related species, study **IV** provided hints at some speciation patterns in *Danaea*. In addition to detailed distribution maps and ecological data, a fully resolved phylogeny with larger species sampling may provide sufficient information to resolve the remaining taxonomic issues and species complexes, and will be necessary to obtain an overall perspective of the biogeography and evolution of this genus.

To study the complete evolutionary history and present a data-based phylogeny of the Marattiales, a different approach will be needed. DNA sequences and morphological characters of extant taxa, should be combined with morphological data from fossils. This may provide deeper insights into the evolutionary relationships of the Marattiales, and may give us a better understanding of the morphological evolution of basal ferns and early land plants. Before such an exercise can be undertaken, all Marattiales, both fossil and extant, need further taxonomic revision.

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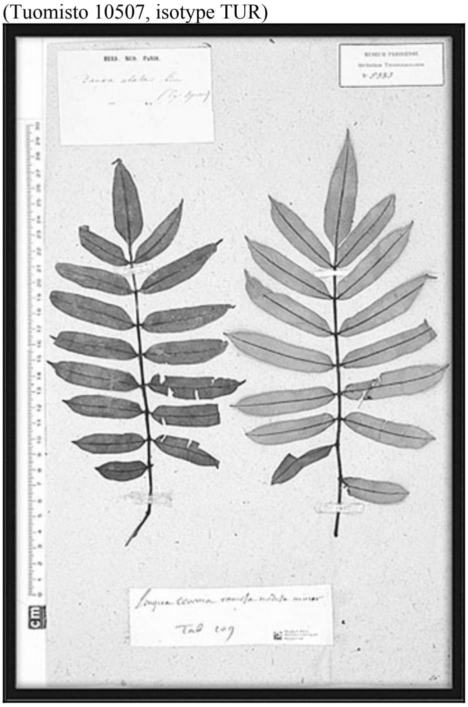
Appendix: Type specimens of Neotropical Marattiaceae

Danaea acuminata Tuomisto & R.C.Moran
(Tuomisto 10507, isotype TUR)

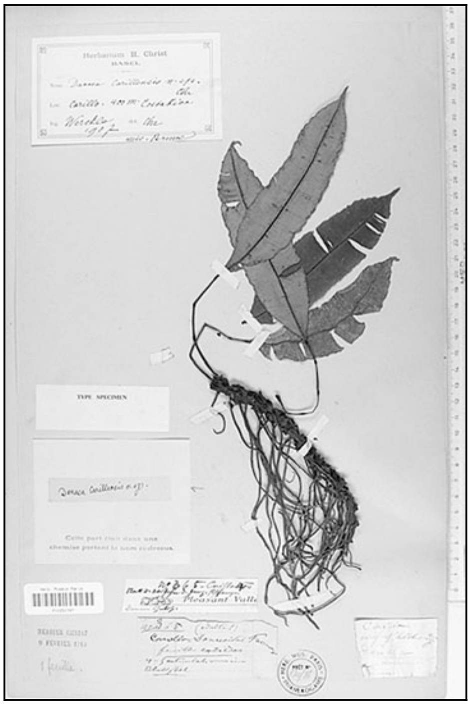
Danaea antillensis Christenh.
(Christenhusz 2747, part of holotype TUR)



Danaea alata Sm.
(Tournefort 5377, P-TRF)

Danaea arbuscula Christenh. & Tuomisto
(Christenhusz 2074, isotype TUR)

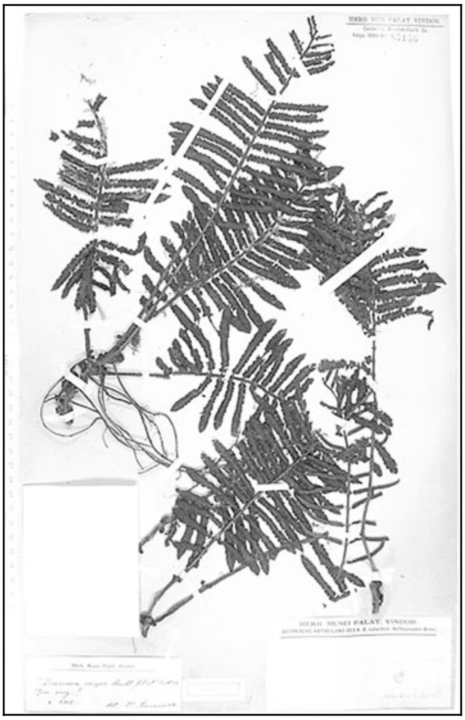
Danaea bicolor Tuomisto & R.C.Moran
(Øllgaard 99719, isotype TUR)



Danaea carillensis H.Christ
(Wercklé 365, holotype P)

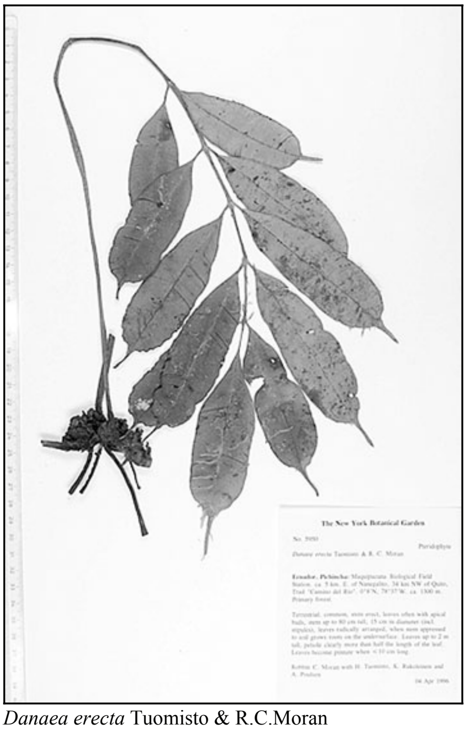
Danaea bipinnata Tuomisto
(Tuomisto 10643, isotype TUR)

Danaea cartilaginea Christenh. & Tuomisto
(Tuomisto 10081, isotype TUR)



Danaea crispa Endrés
(Endrés s.n., lectotype W)

Danaea excurrens Rosenst.
(Hansch 11, lectotype S)

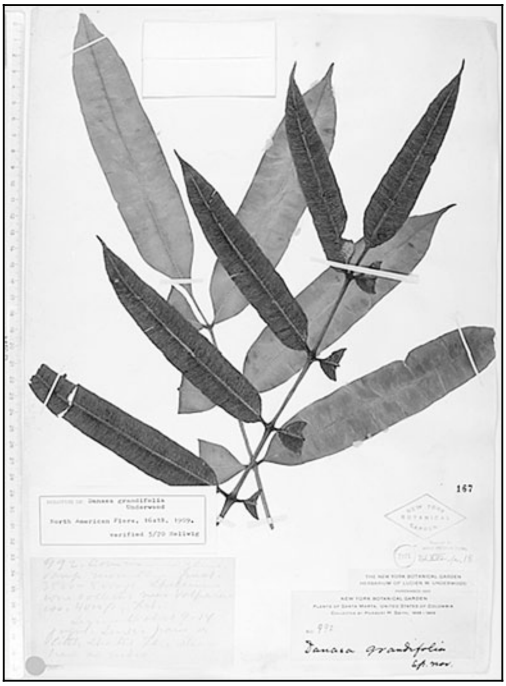


Danaea erecta Tuomisto & R.C.Moran
(Moran 5950, isotype TUR)

Danaea falcata Tuomisto & R.C.Moran
(Tuomisto 10832, isotype TUR)

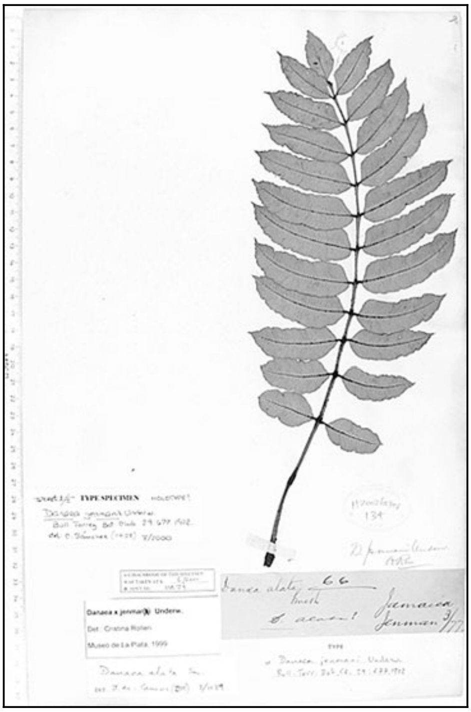
Danaea geniculata Raddi
(Raddi s.n., isolectotype PRC)

Danaea humilis T.Moore
(Spruce 4769, lectotype K)



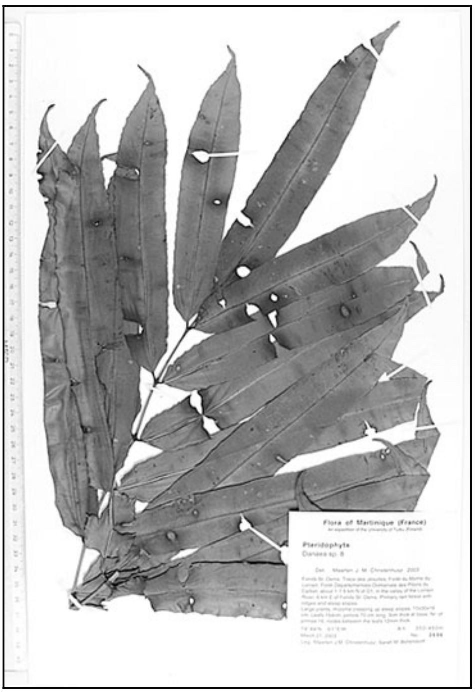
Danaea grandifolia Underw.
(H.H.Smith 992, holotype NY)

Danaea imbricata Tuomisto & R.C.Moran
(Øllgaard 99600, isotype TUR)

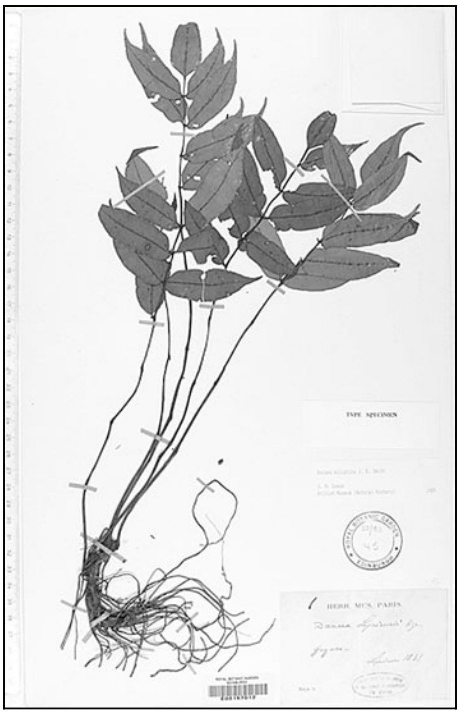


Danaea jenmanii Underw.
(Jenman 66, holotype K)

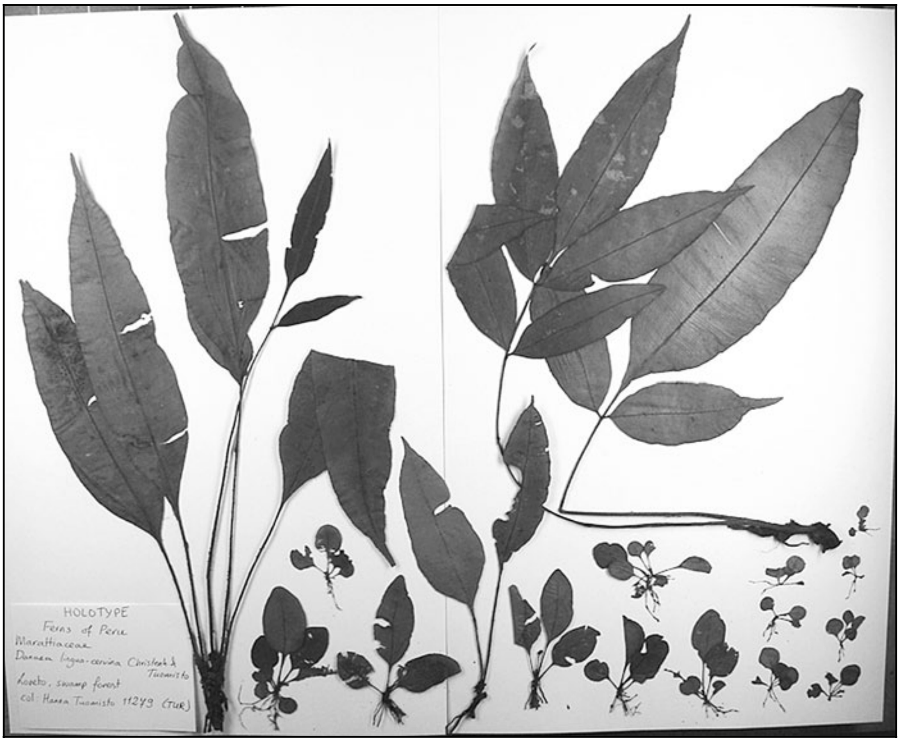
Danaea latipinna Tuomisto & R.C.Moran
(Moran 6023, isotype TUR)



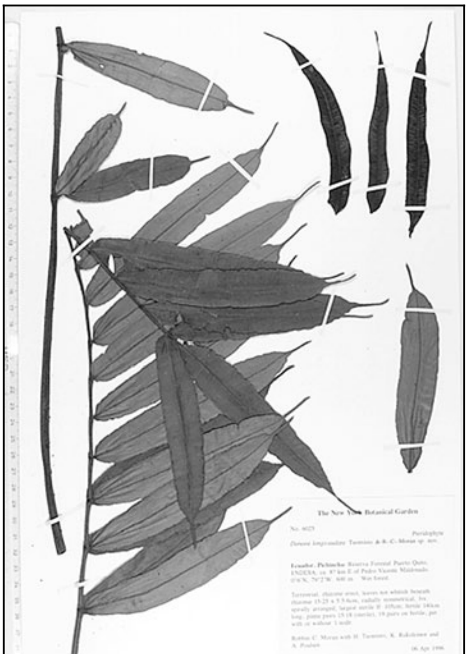
Danaea kalevala Christenh.
(Christenhusz 2696, part of holotype TUR)



Danaea leprieurii Kunze
(Leprieur s.n., type E)



Danaea lingua-cervina Christenh. & Tuomisto (Tuomisto 11279, isotype TUR)



Danaea longicaudata Tuomisto
(Moran 6025, isotype TUR)

Danaea mazeana Underw.
(Mazé 11.143.485, holotype K)

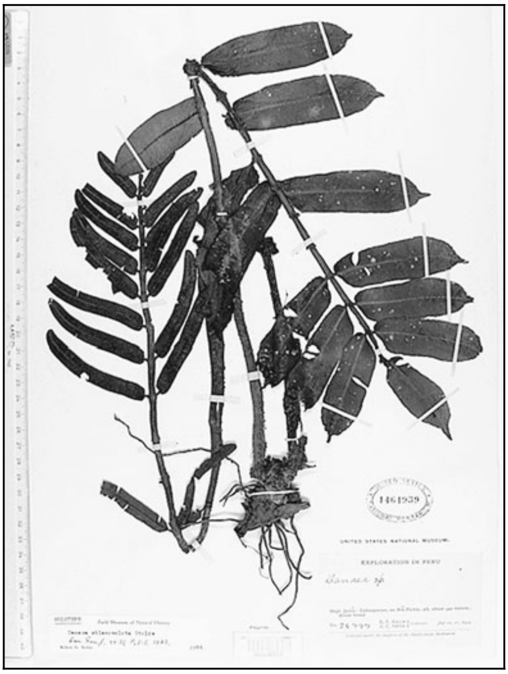
Danaea media Liebm.
(Liebmann s.n. Pl. Mex. 2185, Fl. Mex. 849, type C)

Danaea moritziana C.Presl
(Mortiz 257, type W)

Danaea nodosa Sm.
(Tournefort 5383, P-TRF)

Danaea cuspidata Liebm. = *D. moritziana*
(Liebmann s.n., Pl. Mex. 2184, Fl. Mex. 656, type C)

Danaea elliptica Sm. in Rees = *D. nodosa*
(Herb. Sloane 1: 85, lectotype BM-SL)



Danaea oblanceolata Stolze
(Killip 26777, holotype US)

Danaea polymorpha Lepr. ex Baker
(Mazé 483.1028, lectotype K)

Danaea plicata H.Christ
(Brade 327, type S)

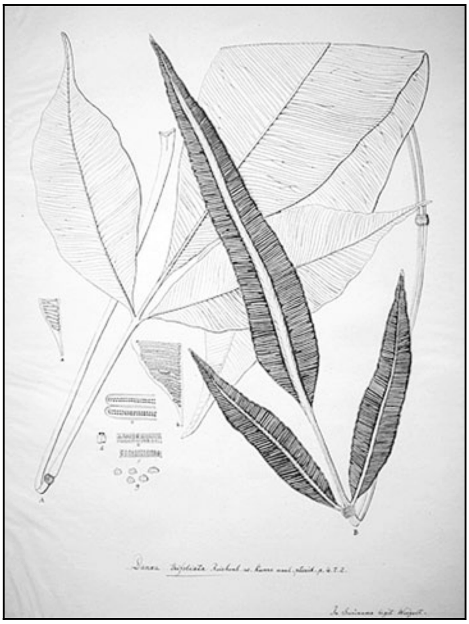
Danaea riparia Christenh. & Tuomisto
(Tuomisto 10060, isotype TUR)

Danaea sellowiana C.Presl
(Sello s.n., type PRC)

Danaea tenera C.V.Morton
(Von Sneidern 1578, holotype US)

Danaea simplicifolia Rudge
(Martin s.n. ex herb. Rudge, holotype BM)

Danaea trichomanoides Spruce ex T.Moore
(Spruce 4710, lectotype K)

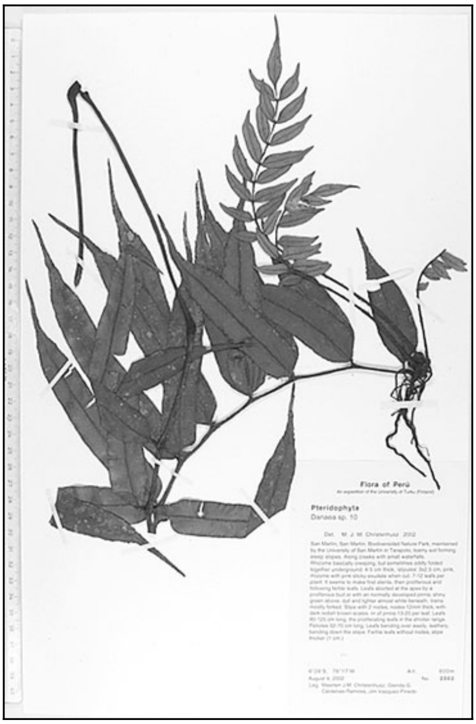


Danaea trifoliata Reichenb.
(original illustration in PRC,
published in: Kunze, Analecta Pteridogr.: t. 2. 1837)

Danaea ulei H.Christ
(Ule 5758, lectotype L)

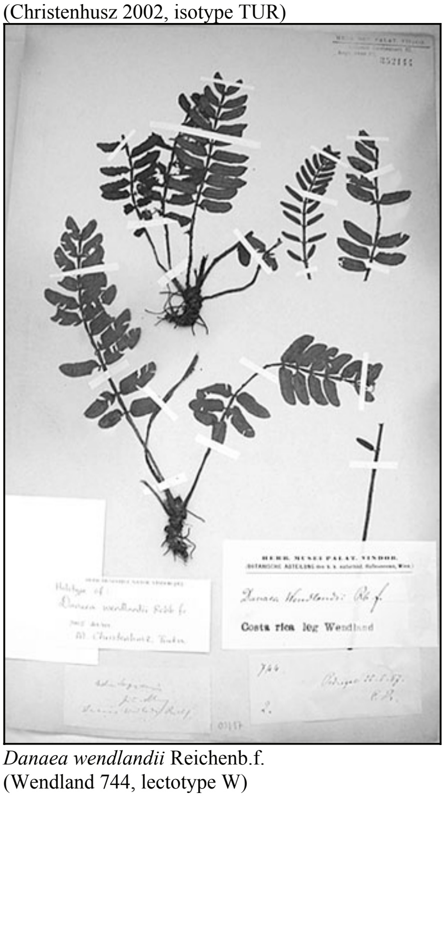
Danaea urbanii Maxon
(Fuertes 942, isotype S)

Danaea ushana Christenh.
(Christenhusz 2519, part of holotype TUR)



Danaea vivax Christenh. & Tuomisto
(Christenhusz 2002, isotype TUR)

Danaea sp. A
(Jones 484, TUR)



Danaea wendlandii Reichenb.f.
(Wendland 744, lectotype W)

Danaea sp. B
(Christenhusz 2005, TUR)

Danaea sp. C
(Christenhusz & Bollendorff 2619, TUR)

Danaea sp. E
(Cremers et al. 9089, Z)

Danaea sp. D
(Jermy 11025, BM)

Danaea sp. F
(Killip 35263, BM)

Danaea sp. G
(Tuomisto 15163, TUR)

Danaea sp. H
(Broadway 5939, BM)

Danaea sp. I (Øllgaard 57448, AAU)

Danaea sp. J (Higgins 1266, TUR)

Danaea sp. K
(Alverson et al. 336, NY)

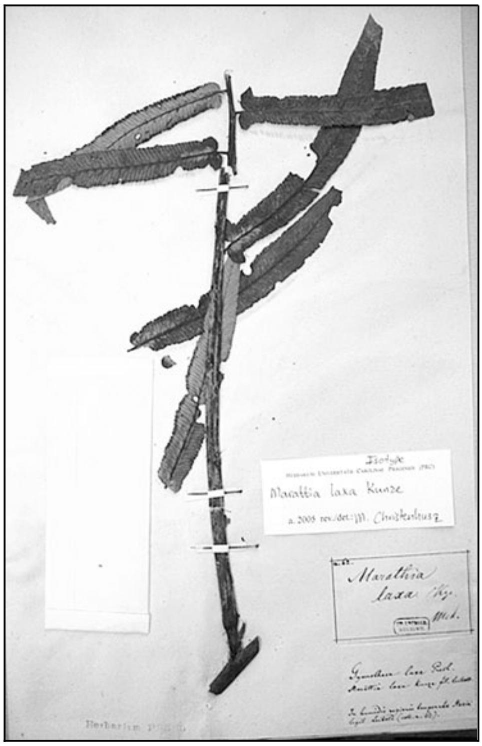
Marattia alata Sw.
(Swartz s.n., holotype S)

Marattia cicutifolia Kaulf.
(Sello s.n., syntype PRC)

Marattia chiricana Maxon
(Maxon 5525, part of holotype US)

Marattia excavata Underw.
(Maxon 272, holotype US)

Marattia interposita H.Christ
(Wercklé s.n., part of holotype P)



Marattia laxa Kunze
(Leibold 62, type PRC)

Marattia laevis Sm.
(Thierry 90, holotype Smith Herbarium 1644.5 LINN)

Marattia weinmanniifolia Liebm.
(Liebmann Fl. Mex. 651, isotype US)

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