

SOME NOTES ON THE TAXONOMY, BIOGEOGRAPHY AND ECOLOGY OF *DANAEA* (MARATTIACEAE)

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ABSTRACT

The neotropical genus *Danaea* is in revision and some notes on the genus are presented here. We find that the genus can be divided into three subgroups, based on morphological characters of the rhizome, stipe articulation and pinna margin serration. The tree groups are discussed and some taxonomic issues are addressed. The occurrence of bipinnate *D. nodosa* is reported from Jamaica, and trifoliate specimens of *D. simplicifolia* are reported from French Guiana. The identities of *D. alata*, *D. jamaicensis*, *D. jénmanii*, *D. mazeana*, *D. media*, *D. nodosa*, *D. trifoliata* and *D. ulei* and their synonyms are discussed. Further studies on the phylogeny, taxonomy and ecology of *Danaea* are needed.

INTRODUCTION

The genus *Danaea* Sm. is one of the few genera of ferns confined to the Western Hemisphere. It has been repeatedly observed that species limits within the genus are poorly understood, and that the genus is in great need of monographic study (e.g., Morton, 1951, Kramer, 1978). De Vriese & Harting (1853) monographed the Marattiaceae but excluded *Danaea*, which was at the time, placed in a separate family: the Danaeaceae. Underwood (1902) revised the North American species, and the Ecuadorian species were recently revised by Tuomisto and Moran (2001), but many taxonomic problems remain. In the recent monograph by Rolleri (2004) a large degree of synonymization was suggested, with which we do not agree.

In recent years, it has become obvious that information on characters such as plant habit, rhizome morphology and leaf colour are useful, and often necessary, in identifying *Danaea* specimens to the correct species (Tuomisto & Moran, 2001). Unfortunately, characters like habit and colour are not easily preserved through the process of pressing and drying, which complicates the identification of herbarium specimens of *Danaea*. Furthermore, the rhizome is cumbersome to collect and difficult to divide between several duplicates. Collecting the rhizome kills the plant in any case. Consequently, many herbarium specimens, especially those of the larger species, do not include enough rhizome to allow reconstructing its morphology. Especially historical specimens, many of which are types, do not include sufficient information about these characters, either on the specimen itself or on the accompanying label. This has made it difficult to establish the identity of various species with certainty.

To solve this problem, we have carried out field work in different parts of the neotropics. As many type localities as possible were visited to establish the identity of the type specimens. Observing the populations in the field also yields information about the natural variation in morphological characters, and hence helps in circumscribing the

species. So far, field work has been carried out in Colombia, Costa Rica, Ecuador, French Guiana, Jamaica, Peru, Puerto Rico, Suriname and the Lesser Antilles. Future phylogenetic and systematic studies will hopefully give a greater insight in the diversity and relationships between the species of *Danaea*.

DISTRIBUTION AND ECOLOGY OF *DANAEA*

Danaea occurs solely in the New World tropics. It can be found from Mexico, through all of Central and South America, south to Bolivia. It also occurs on all Greater Antilles, and the wetter, higher islands of the Lesser Antilles. There are isolated populations in Atlantic south-eastern Brazil, southern Paraguay and Cocos Island (Costa Rica). The biogeographical patterns of *Danaea* are presently being studied.

Danaea occurs mainly in permanently wet forests on well drained soils. Several species seem to prefer steep slopes or creek banks. *Danaea* is mostly found in undisturbed rainforests, although some species tolerate disturbance, and some species even seem to favour recently disturbed places like shady wet roadside banks. *Danaea* species can be found in lowland rainforests, up to an elevation of about 2000 m in montane cloud forest and elfin woodland, but most species are found between about 300 and 1000 m elevation. In Amazonian lowland rain forests, it has been found that different species grow on soils with different nutrient status (Tuomisto & Poulsen 1996).

THE THREE MAJOR GROUPS IN *DANAEA*

Based on morphological characters, we divide *Danaea* into three major groups. This division is still tentative, as the groups overlap in some of the characters, and some species cannot be unambiguously allocated to a group. This division does not follow any of the sections proposed by Presl (1845), and the phylogenetic relationships between the species are not yet known although they are being studied.

The first group consists of species that resemble *Danaea nodosa* and are often identified as such in herbaria. These are large-statured species whose adults often exceed 1.5 m in height. Most species are characterized by a creeping rhizome (except *D. erecta* Tuomisto & R.C.Moran), the absence of nodes on the stipes (except *D. media* Liebm.), and the presence of dentations at pinna apices (except *D. erecta* and *D. grandifolia* Underw.).

The second group consists of species supposedly related to *Danaea leprieurii* Kunze. This group of species has previously been united under the name *D. elliptica* (see below). These are species of intermediate stature, 0.4-1.5 m in height. This group is characterized by erect, radially symmetric rhizomes, stipes articulated with swollen nodes (nodes sometimes lacking in *D. bipinnata* Tuomisto) and entire pinna apices. The apical pinna is always present, never replaced by an apical bud.

The third group consists of species resembling *Danaea alata* Sm, *D. moritziana* C.Presl and *D. mazeana* Underw.. These are species of small to intermediate stature, 0.1-1.5 m in height, and are characterized by radially symmetric (rarely dorsiventral) rhizomes that can be erect, creeping or ascending. The stipes are nodose, the blade usually bares many crowded pinnae, and the pinna apices are (coarsely) serrate. Some of the smaller species have translucent pinnae (*D. trichomanoides* T.Moore ex Spruce, *D. imbricata* Tuomisto & R.C.Moran, *D. tenera* C.V.Morton), and many species have bicolorous fronds, with the abaxial side pale green or whitish. The apical pinna can be replaced by a proliferous bud, but this does not seem to be a distinguishing feature

between species. To distinguish species within this group, Underwood used mostly characters of the venation, which is, in most cases, also highly variable.

Notes on the *Danaea nodosa* group

Danaea nodosa, the type species of the genus, has always been considered to be widespread, occurring throughout the range of the genus. However, recent field studies and close study of herbarium material have revealed, that the name has been applied to several clearly separate species. Often these species have different ecological preferences.

The lectotype of *Danaea nodosa* is a plate in Plumier (1705), which is based on material either collected “between Morne Rouge and Saint Pierre, Martinique” or “Port-de-Paix, Haiti”. The latter locality was selected as the type locality by Underwood (1909). This was a fortunate choice, because the material we have seen from Haiti agrees with the type illustration very well: the plants have slender, dorsiventral rhizomes with two rows of leaf scars, and the pinnae are long and parallel-sided. In contrast, the plants that grow on Martinique do not match the type illustration: they have very bulky rhizomes with fronds arranged in several rows, and their pinnae are narrower and more tapering. It is obvious that the populations on the two islands represent two different species (Christenhusz, in press).

In Jamaica, most of the plants we have seen agree very well with the material from Haiti, and can thus be considered true *Danaea nodosa*. However, we found that leaf dissection in Jamaican plants varied from the normal once pinnate to fully bipinnate (Christenhusz & Tuomisto 3194 (IJ, TUR, UCWI). In some populations, the tendency to bipinnate fronds was stronger than in others, but in all populations where bipinnate fronds were found, once pinnate fronds were also present. No other differences were found between the once and twice pinnate fronds than the degree of leaf dissection. It seems obvious, therefore, that this is a case of within-species variation. An interesting question concerns the identity of the South American material. We have observed some differences in pinna shape between the Jamaican and South American populations, but their rhizomes and habit are similar. Even though we have never observed any tendency towards bipinnate leaf dissection in any South American population, for the time being we consider these as *D. nodosa*.

Field work in Western Amazonia has shown that *Danaea nodosa* grows on relatively nutrient-rich, clayey soils. Its juveniles have simple fronds only when very small, and the fronds become pinnate usually when they are still less than 10 cm long. A very similar plant but with cartilaginous pinna margins has been found on poorer, more loamy soils. This species has larger pinnae, especially at the juvenile stage when fronds often remain simple until they exceed 30 cm in length (Tuomisto & Groot, 1995, Tuomisto & Moran, 2001). On the basis of a photograph of one of the isotypes, the latter species was identified as *D. ulei* H.Christ. Unfortunately, other isotypes of *D. ulei* show clearly that the rhizomes in this species are erect, indicating that it belongs to the *D. leprieurii* group. Its pinna margins are not cartilaginous, either. Consequently, the poor-soil segregate of *D. nodosa* needs a new name (Christenhusz & Tuomisto, in press).

In Costa Rica, populations of supposed *Danaea nodosa* were found to be variable in whether the stipe is nodose or not. Juveniles usually had one or two nodes, but older fronds more often had none. The presence of nodes was variable even in fronds on the same rhizome, which shows that the two forms belong to the same species. These plants

have previously been identified either as *D. nodosa* or as *D. elliptica*, depending on whether nodes were present or not, as this has traditionally been the most important diagnostic character between the two species. Since true *D. nodosa* never has nodes, the names that can be applied to this species are *D. media* Liebm. and *D. elata* Liebm. *Danaea media* was described on the basis of small plants (with nodes) and *D. elata* on the basis of a large specimen (without nodes) from the same population in Mexico. These names have earlier been synonymized with *D. elliptica* and *D. nodosa*, respectively, but our observations indicate that they represent another taxon worthy of recognition at species level. We propose that the name *D. media* is used as the valid name for this species, because this epithet refers to the species having intermediate characters between the *D. nodosa* and *D. leprieurii* groups.

Notes on the *Danaea leprieurii* group

Most of the species in this group have at some stage been identified as *Danaea elliptica* Sm. in Rees, which has been considered a wide-spread and common species. The identity and typification of *D. elliptica* has however long been in turmoil. The lectotype designated by Proctor (1977) is: Jamaica, Mount Diablo, Herb. Sloane 1: 85 (BM-SL). It has been observed repeatedly that this specimen is actually a juvenile of *D. nodosa* (L.) Sm (e.g., Lellinger 2000, Tuomisto & Moran 2001). We have confirmed this by visiting Mount Diablo, where we only found individuals of *D. nodosa*. The issue of the synonymization of *D. elliptica* is discussed in more detail in Christenhusz & Tuomisto (in press).

As mentioned above, Underwood selected Haiti rather than Martinique as the type locality of *Danaea nodosa*. It is worth mentioning that since the two islands have different species of the *D. nodosa* group, the situation would now be very different had Underwood selected the other way round. If Martinique were the type locality, *D. nodosa* would be represented by a type illustration that matches the species occurring on that island rather poorly, and *D. elliptica* would become the valid name for the species that has so far been known as *D. nodosa* in the Greater Antilles and South America, which would be very confusing.

Due to the problems with the name *D. elliptica*, we call the present group of species the *D. leprieurii* group, as this is one of the oldest accepted names in this group. This group includes many apparently closely related species that are morphologically quite similar, but grow on different soil types and/or altitudes.

Danaea leprieurii was described from French Guiana, but recently also material from western Amazonia has been allocated to this species. (Tuomisto & Moran 2001). In western Amazonia, *D. leprieurii* grows on relatively poor substrates, whereas the recently described and morphologically rather similar *D. bipinnata* grows on richer soils. The two can be distinguished by size (*D. leprieurii* is smaller), the number of nodes on the stipes (2-3 in *D. leprieurii*, 0-1 in *D. bipinnata*), and usually the degree of lamina dissection. *Danaea bipinnata* was described from lowland Amazonia, but it is very similar to *D. elliptica* Sm. var. *crispula* Rosenst, which was described from lower montane elevations in the Peruvian Andes. However, *D. elliptica* var. *crispula* is never bipinnate, and it is usually larger than *D. bipinnata*.

Danaea simplicifolia Rudge is confined to the Guiana shield, and can easily be recognized by its simple fronds. The only other species with simple fronds is *D. carillensis* H.Christ, an endemic of Costa Rica, with a nodose stipe, creeping rhizome and apical dentations, and therefore belonging to the *D. alata* group. *D. simplicifolia*

only has a single node below its simple blade. From this node, sometimes one or two lateral pinnae are produced (French Guiana: *Christenhusz* 2325 (CAY, TUR), *Christenhusz* 2415 (CAY, TUR)). It then resembles *D. trifoliata* Rehb., a species that can be distinguished by its nodose stipe. Another character that distinguishes *D. simplicifolia* from juvenile *Danaea* that have not developed lateral pinnae yet, are the white abaxial surfaces of the blades, an uncommon feature in this group. It is only found in some representatives of the *D. alata* group and in the Ecuadorian *D. bicolor* Tuomisto & R.C.Moran.

Notes on the *Danaea alata* group

Danaea alata Sm. is a species confined to the Lesser Antilles (lectotype from Martinique, Plumier 1705). It is recognized by simple, widely spaced veins, nodose stipes, creeping, radial rhizomes and coarse apical dentations. Its synonyms are *D. fendleri* Underw. (Trinidad) and *D. stenophylla* Kunze (Guadeloupe).

At a first glance the closely related *Danaea mazeana* Underw. appears to be confined to Guadeloupe, but material from other Antilles is very variable. *D. mazeana* fits well within the variation of *D. jamaicensis* Underw., and cannot be consistently separated from it. However, *D. jamaicensis* sometimes has apical proliferations, which are never found in *D. mazeana*. This might be due to possible hybridization with *D. jenmanii* Underw. on Jamaica. *D. mazeana* differs in ecology from *D. alata*, as the former is confined to cloud forests above 600 m, whereas the latter is found only in rainforests at lower altitudes.

On present evidence, *Danaea jenmanii* and *D. wrightii* Underw. are conspecific. The type of *D. wrightii* is somewhat scallier, but all other characters overlap. Field work in Jamaica showed that the scalliness of *D. jenmanii* is variable. Because *D. jenmanii* has been applied more widely than *D. wrightii*, the first is proposed here for conservation over the latter. Both species were described in the same publication.

CONCLUSIONS

Field work and herbarium studies have shown that the diversity of *Danaea* is much greater than previously assumed. The first indication of this tendency was the Ecuadorian treatment (Tuomisto and Moran 2001) where 18 species were included, eight of which were described as new. The same tendency is continuing in other areas, and we now have several species in publication (Christenhusz, in press; Christenhusz & Tuomisto, in press). It seems obvious that the concepts of the geographical distribution ranges of the species will have to be changed once the taxonomy of the genus has been sorted out. More species than expected seem to have rather narrow ranges.

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