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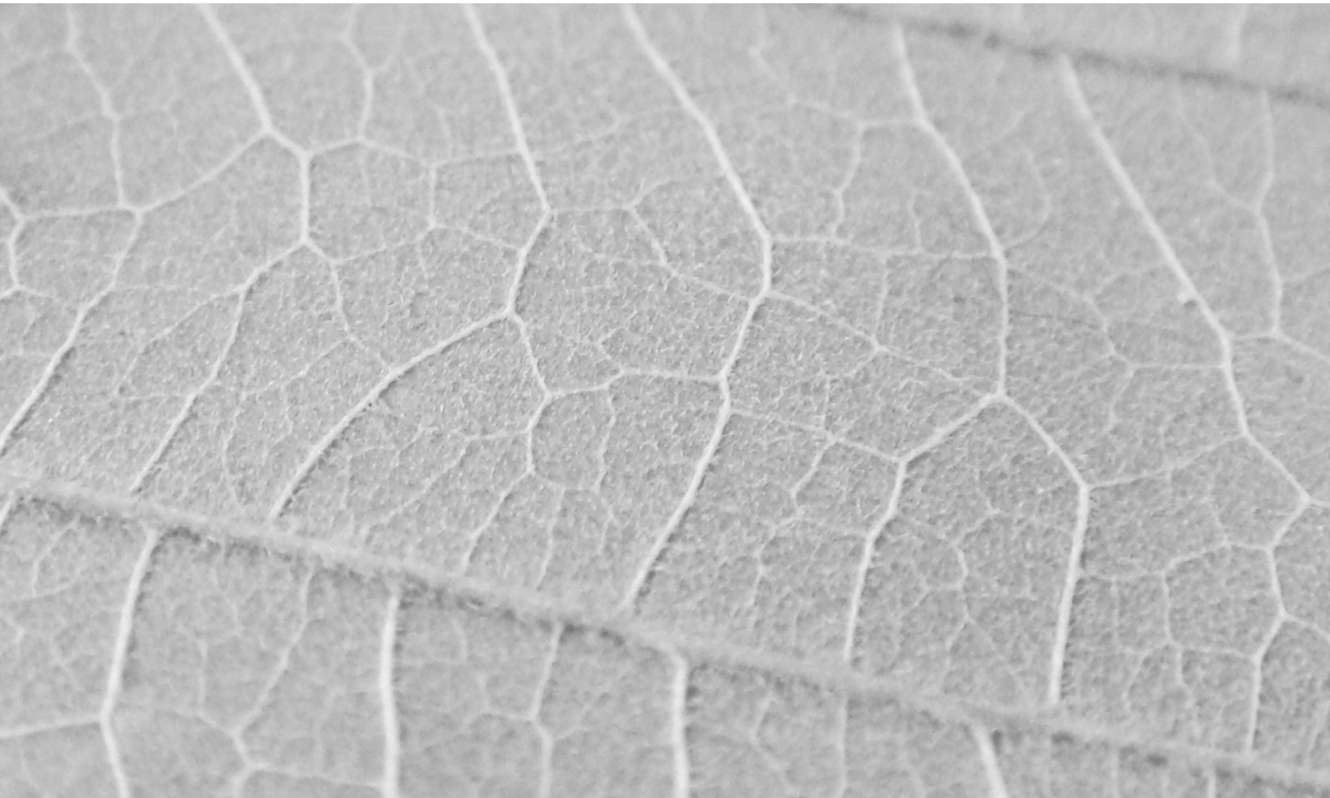
Summary & Conclusions



Summary and Conclusions

Derris Lour. (family Fabaceae/tribe Millettieae) is a quite well-known legume genus as many species are a source of Rotenone toxin, a commercial organic insecticide and fish poison used in many countries. Because of the toxicity, species are also used as traditional medicine for many purposes in some SE Asian countries. The genus is characterized mainly by its indehiscent, flat, thin but leathery pods with usually wing(s) along the suture(s). In the tribe Millettieae, however, there are several plants in the tropical areas of the old and new world which have similar pods and other morphological characters comparable to *Derris*. They all are called *Derris*-like taxa (or *Derris*-like plants) in this thesis and divided into two groups: the palaeotropic and neotropic *Derris*-like taxa. In the course of time, different generic circumscriptions of these plants were proposed by various taxonomists. For example, because of their morphological similarities Bentham (1860) united most of them into a large genus called *Derris* in the wider sense (sensu lato: s.l.) and placed them in several sections. Geesink (1984) and Adema (2000) accepted *Derris* in a more strict sense (sensu stricto: s.s.) by raising most of Bentham's sections to generic level. Geesink and Adema differed in their concept of *Brachypterum* (Wight & Arn.) Benth., which was recognized as a distinct genus by Geesink (1984) but synonymised with *Derris* s.s. by Adema (2000). Molecular phylogenetic studies of the tribe Millettieae (Hu et al., 2000, 2002) indicated that *Derris* s.l. is inappropriate, because it is polyphyletic, but *Derris* s.s. seems to be more acceptable. However, those studies are generally not comprehensive enough to draw final conclusions with regard to the generic circumscription of the genera, especially for the old world taxa, because of insufficient sampling. *Derris* s.s. is morphologically quite variable, which often hinders species-level identifications. The main objectives of this thesis are to clarify the relationships between species and genera within this complex group of *Derris*-like taxa (mainly focused on the old-world Asian genera) and to provide a new classification which reflects the evolutionary and biogeographic relationships of these plants.

How many and which species of Derris-like taxa occur in Thailand? How do they differ morphologically and ecologically? What are their diagnostic morphological characters?

The revision of *Derris*-like taxa in Thailand (Sirichamorn et al., 2012a, see chapter 2) showed that *Aganope* Miq. contains three species, *Paraderris* (Miq.) Geesink four species and *Derris* (including *Brachypterum*) comprises 16 species. Following the new

circumscription proposed in chapters 3 and 4, then *Aganope* remains the same, but the reinstated *Brachypterum* will have four species in Thailand and and *Derris* (now including *Paraderris*) will comprise 16 species in Thailand. Two *Derris* s.s. species were newly described, but recently another new, but still unnamed species was found in a limestone area in central Thailand. The genus *Aganope* can be recognized by its true panicles, flowers usually with shorter pedicels than *Brachypterum* and *Derris* s.s., free wing petals, 10-free finger-shaped nectary glands and diadelphous stamens. Dried specimens usually turn black. Typical for *Derris* (not including *Brachypterum* or *Paraderris*) are the pseudoracemes/pseudopanicles (intermediate forms and true panicles also occasionally occur), brachyblasts usually bearing flowers throughout, wing petals adhering to the keel petals and monadelphous stamens. *Paraderris* is slightly different from *Derris* by its slightly larger flowers present only apically on the brachyblasts and usually by standard petals with basal callosities. Species belonging to the *Brachypterum* group have more leaflets per leaf, stipellae often present, disks tubular and lobed, only one wing along the upper suture of the pods and distinct seed chambers in dry pods. *Derris* and *Paraderris* species are probably water preferring plants as they usually occur along waterways. They also seem to be dispersed by water because of their light, buoyant pods. The presence of wings along the pods may also be indicative of wind dispersal, but the light weight and thinness of pods seems to be a more influent character to facilitate wind dispersal than the pods' wings which are relatively small and narrow. Only a few *Derris* species inhabit areas like limestone, where free water is limited. *Aganope* species, like *Derris* species, also prefer humid, but exposed, sunny areas. *Brachypterum* species, in contrast, seem to be more drought tolerant as they grow in wider range of habitats, even in very disturbed areas far away from waterways. Pollination of Thai *Derris*-like species is usually done by bees.

Is the most recent generic concept of Derris, Derris *sensu Adema, monophyletic? If not, how about the monophyly of* Derris *sensu Geesink or other previous generic concepts?*

As mentioned above, *Derris* in broad sense (s.l.) was already rejected by the molecular phylogenic studies of Hu et al. (2000, 2002). In this thesis, the molecular phylogenetic studies based on chloroplast (*trnK-matK*, *psbA-trnH* IGS and *trnL-F* IGS) and nuclear (ITS/5.8S) markers using maximum parsimony and Bayesian inference indicate that the most recent concept of *Derris* proposed by Adema, which includes *Brachypterum*, represents a polyphyletic taxon, because *Brachypterum* is phylogenetically a distinct group, but morphologically rather similar to *Derris* s.s.. *Derris* sensu Geesink, in which *Brachypterum* is recognized as a genus, is paraphyletic, because *Paraderris* is not included. *Paraderris* [without *P. laotica* (Gagnep.) Adema] is a monophyletic group nested within paraphyletic *Derris* sensu Geesink. In order to make *Derris* s.s. monophyletic, *Paraderris* should be synonymized with it.

How are the three genera: *Brachypterum, Derris s.s. and Paraderris, related to each other and to other genera of Millettieae, particularly Derris-like taxa such as Aganope, Deguelia, Leptoderris, Lonchocarpus, Ostryocarpus and Philenoptera?*

The molecular phylogeny in this thesis indicates that *Aganope* is monophyletic and sister to the African genus *Ostryocarpus* Hook.f. Both genera are considered as basal taxa in the Millettieae, which is congruent with the previous molecular phylogenetic studies of Hu et al. (2000; 2002). The *Aganope* clade can be divided into two subclades characterised by some apomorphies and different geographic distribution. One is an Asian subclade containing three species that mainly occur from India through much of in SE Asia. The other is an African subclade, also including the former genera *Ostryoderris* Dunn and *Xeroderris* Roberty. Similar to *Aganope*, the African genus *Leptoderris* Dunn was considered as a "Basal Millettioid and Phaseoloid Group" (Gasson et al., 2004), however, my results show that the genus is unrelated to *Aganope*, but sister to the African *Derris*-like genus *Philenoptera* Fenzl ex A. Rich. (Bayesian inference) or even the "American *Derris*" genus *Deguelia* Aublet (parsimony). Within the "core Millettieae" both *Deguelia* and *Philenoptera* are monophyletic and they are phylogenetically not related to the neotropical genus *Lonchocarpus* Kunth. Therefore, the concept of *Lonchocarpus* sensu lato, which sometimes includes *Deguelia* and *Philenoptera*, is not correct. This result is also congruent with the phylogeny of *Lonchocarpus* s.l. (Da Silva et al., 2012). All previously mentioned genera form their own clades, all with high statistical supports, and they are clearly separated from the Asian genera *Brachypterum*, *Derris* and *Paraderris*. The genus *Brachypterum* is a closer relative of *Derris*. It forms a highly supported clade within the core Millettieae in parsimony analyses, and appears as sister to the clade formed by *Fordia* Hemsl. + *Millettia pinnata* (L.) Panigrahi in Bayesian analyses. *Derris* (incl. *Paraderris*) is monophyletic and consists of two clades, one clade contains *Derris* (according to Geesink) species and *P. laotica* (morphologically intermediate between *Derris* and *Paraderris*), the other clade comprises the monophyletic, recognizable *Paraderris* and two species of *Derris* s.s. [*D. amoena* Benth. and *D. monticola* (Kurz) Prain]. The latter two species are morphologically typically *Derris*. Therefore, it is no option to recognize the second clade as *Paraderris* (the other clade then being *Derris*). This will render both groups morphologically unrecognizable, therefore, *Paraderris* is synonymised with *Derris*.

How are the infrageneric groups previously proposed for the genus related to each other? Are those groups monophyletic and does the molecular phylogeny corroborate these or other infrageneric groups?

Five sections of *Derris* previously proposed by Bentham (1860) and followed by some legume taxomomists, e.g. Thothathri (1961, 1982) are considered inappropriate. Section *Aganope* (Miq.) Benth. and *Brachypterum* Wight & Arn. are now recognized as genera. The other three remaining sections (*Eu*)*Derris* Benth., *Dipteroderris* Benth. and *Paraderris* Miq. form the genus *Derris*. As indicated in the former section, *Paraderris*, recognizable by its apomorphies, may be given an infrageneric rank, but this means that both *D. amoena* and *D. monticola* should also become taxa with the same rank. The latter two will be monotypic and are only recognizable by their specific typical characters. This is considered as undesirable. Sections *Derris* (*Euderris*) and *Dipteroderris* differ mainly in the number of pod wings, *Derris* has pods with a single wing, only along the upper suture, whereas *Dipteroderris* pods are winged along both sutures. The first section consists only of *D. trifoliata* and *D. elegans* Graham ex Benth. (Thothathri, 1961), while most species of *Derris* belong to section *Dipteroderris*. Unfortunately, those two sections are phylogenetically not recognizable. One possible subgeneric division is to recognize a subclade containing species with true panicles or intermediate inflorescence types, but this clade is weakly supported. Therefore, no infrageneric classification of *Derris* s.s. is proposed in this thesis.

Can the clades be classified as genera or infrageneric taxa? Are they recognizable morphologically and how can we explain the trends in morphological evolution of Derris*-like taxa?*

Twenty nine qualitative morphological characters are analyzed together with the molecular data of the earlier studies. Chapter 4 shows that all genera have several typical apomorphic characters. Only with *Derris* s.s. (incl. *Paraderris*) the two apomorphies (liana habit and 2-winged pods) have to be used in combination with plesiomorphies to characterize the genus.

The morphological characters were mapped onto the molecular phylogeny in chapter 4. Some of the more interesting developments are summarized here. The liana habit is seemingly derived from a tree-like habit that is found in more basal genera of the "core Millettieae", e.g. *Lonchocarpus*, *Piscidia* L., *Pongamiopsis* R. Viguier and *Neodunnia* R. Viguier. Only with *Brachypterum* it is indecisive, because it is part of an unresolved trichotomy, though the liana habit is probably the derived state, because the tree-like condition is present in the local outgroup for *Brachypterum*, the *Millettia pinnata*-

Fordia clade. A paniculate inflorescence is the most primitive type of inflorescence in the Dalbergieae-Millettieae group, whereas pseudoracemes-pseudopanicles form the derived state. Intermediate forms are supposed to be transitions between these two types of inflorescence. Character optimization also reveals that reversals to true panicles occurred quite often during the evolution of the tribe. Wart- or knob-like brachyblasts with more flowers scattered throughout are the commonly found plesiomorphy, while the elongated cylindrical brachyblasts with few (2 or 3) apical flowers are the derived condition. Wing petals show a general tendency to change from free or irregularly adherent to distinctly adnate to the keel petals. Adhesion between wings and keels is not correlated with the presence of lateral pockets on the wings and keels, because the lateral pockets are present in all sampled taxa, even in *Aganope* and *Ostryocarpus*, which have free or irregularly adnate wings. Revolute wing petals can be found in some species of only *Derris*. This typical apomorphy evolved more than once. A fused androecium is considered as derived from the free state. Several forms of floral disk are found in various genera of Millettieae and they are derived condition from an indistinct or annular disk. Winged pods are derived from a wingless condition. The presence of only one wing along the upper suture is a synapomorphy for *Brachypterum, Deguelia* and *Leptoderris*. The presence of two wings along both sutures is a synapomorphy for *Aganope* and *Derris*, however, reduction to one wing has evolved several times in the *Derris* major clade. The seed chambers obviously visible in dry pods is derived condition, synapomorphy not only for *Brachypterum*, but also for *Deguelia* and *Philenoptera*. The position of the seed hilum changes from a distinctly eccentric hilum, to slightly eccentric or central hilum.

Where and when did major diversification events occur in the Derris-like taxa? How can we explain the paleotropical intercontinental disjunctions (PIDs) of Aganope and some species of Brachypterum and Derris?

Molecular dating analyses (chapter 6) suggest an origin of three palaeotropic *Derris*-like genera in early Miocene (*Brachypterum* originated slightly later: the transition between early and mid-Miocene). A wide ancestral distribution in Africa and Asia was inferred for the *Aganope* stem and crown groups, and vicariance between Africa and Asia in the early Miocene was supported. The PID in *Aganope* is likely the result of vicariance, possibly caused by climate deterioration subsequent to the Middle Miocene Climatic Optimum. *Brachypterum* and *Derris* have the continental SE Asia mainland as ancestral areas. Numerous dispersal events both westward to India, and eastward throughout Malesia and across Wallace’s Line to New Guinea were indicated starting from the middle Miocene, when collision between the Sunda and Australian plates occurred and created a chain of islands allowing eastward migrations of Sundanian taxa (Hall, 2009), and onwards. The inferred temporal origins of PIDs in *Derris* and *Brachypetrum* (e.g. the widespread *D. trifoliata* and *B. scandens*) in the Plio-Pleistocene are most consistent with long-distance dispersal. The dispersal patterns of *Brachypterum* and *Derris* are similar to patterns identified in several other SE Asian plant taxa, and highly congruent with geological events in SE Asia from the early Miocene until present. Preadaptation to a spectrum of environmental conditions and habitats including mangrove swamps, and high dispersal capabilities by hydrochory may explain wide distributions of some species, and frequent dispersal across oceanic water bodies separating western and eastern Malesia.

Future Studies

The studies presented in this thesis provide us with a better understanding of the evolution of the palaeotropic *Derris*-like taxa, satisfy our knowledge of the tribe Millettieae and they even help to distinguish new species of this plant group. Although the phylogenies at generic level of *Aganope*, *Brachypterum* and *Derris* are resolved and strongly supported, the phylogeny at species level of some taxa, especially for *Derris* (including *Paraderris*), is still problematic. Species pairs that resemble each other morphologically, like *D. cuneifolia* Benth. and *D. montana* Benth., *D. ferruginea* (Roxb.) Benth. and *D. pubipetala* Miq., for example,were shown to be unrelated in the molecular phylogeny. However, only one representative of each species was analyzed due to difficulties with the DNA extraction from herbarium material. Obviously, *D. elliptica* (Wall.) Benth. is a morphologically variable species and possibly contains several cryptic lineages that need further investigation. Only four samples (three morphological variations) of *D. elliptica* were included in the analyses, but they do not form a monophyletic group, even not the two samples collected from the same locality, with an almost identical morphology. Cytological or population genetic studies with more samples may possibly clarify the complexity of this species and provide an improved species delimitation of these morphologically variable taxa. All in all, the phylogenies were based on rather good sampling, in *Aganope* and *Brachypterum* almost all taxa were covered, in *Derris* (including *Paraderris*) somewhat less. Still, a more complete sampling, more species and more specimens per species, will improve our insight in the phylogeny and historical biogeography and advance the infrageneric classifications of the genera.

The results of this thesis show that *Derris* sensu Sirichamorn et al. only has a few synapomorphies. This is partly due to the fact that usually only qualitative macroscopic morphological characters are considered, because they are most convenient to classify and identify the plants. Microscopic characters from anatomical or palynological studies can provide more characters and possibly including additional apomorphies of *Derris*.

In addition, as the palaeotropic *Derris*-like plants contain chemical compounds used for various purposes, the chemotaxonomy of these plants might generate a new tool to improve the classification and also to provide essential information on plant biochemical compounds, which might be commercially or medically important for humans in the future.