

CHAPTER 10

Conclusions

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General discussion

Phyllanthus L. sensu lato (s.l.) is known as a diverse clade with often difficult to distinguish species due to the small flowers and the often high resemblance in leaf shapes and sizes. In this thesis I explored the evolution of this group while also proposing an alternative classification as a solution to the apparent paraphyly (not all descendents of an ancestral species included). Initial work by Linneaus (1753, 1778) and De Jussieu (1803) already indicated a diversity of characters that were used to place the species in different genera. After Müller (11863, 1865, 1866) defined *Phyllanthus* as one genus with over 40 different sections, the biggest update to this system was implemented by Webster (1956, 1957, 1958 and thereafter). Webster focused on the West Indian and American species of *Phyllanthus*, but treatments for other floristic regions were scattered and a global inventory of the number of accepted species was overdue. The systematic history was summarised in chapter 3 in the form of a list, which included all accepted species and their infrageneric placement to that point. While Webster published many treatments for the Neotropical flora, the Palaeotropics remained understudied. The first of these groups to be treated was *Phyllanthus* subgenus *Macraea* (Wight) Jean F. Brunel (Chapter 4). Follow-up revisions that focus on other groups are now also being progressed (Wibowo et al. unpublished; Hinloopen et al. unpublished).

By increasing our understanding of the relationship between groups in tribe Phyllantheae while revising various groups to look for synapomorphies, this thesis presents another option to the apparent paraphyly of *Phyllanthus*, which has been under discussion already for several years. Also an investigation in the metabolites of several species was included as this field keeps growing and the interest in *Phyllanthus*, already substantial in traditional medicines, is increasing.

How large is the diversity of Phyllanthus and tribe Phyllantheae and how is it structured?

Our initial review of the long taxonomic history of *Phyllanthus* resulted in a list containing 880 species, which could be classified into 18 subgenera and 70 accepted sections (chapter 3). A few overlooked issues were found that needed to be addressed. *Phyllanthus* subsections *Callidisci* Jean F. Brunel and *Odontadenii* Jean F. Brunel & Jacq. Roux had been placed in a large concept of *Phyllanthus* subgenus *Phyllanthus* by Brunel (1987). However, the phylogenetic study of Kathriarachchi et al. (2006) had already shown that this subgenus was polyphyletic and a new subgenus was subsequently created with the goal of housing the African and Malagasy species in the revision work by Ralimanana & Hoffmann (2011, 2014). Their work did not take into account the subsections defined by Brunel (1987). In chapter 3 we transferred these subsections, but also specifically listed all species that we hypothesized to be included in subgenus *Afroswartziani* Ralim. & Petra Hoffm.

Other changes, in *Phyllanthus* subgenus *Gomphidium* (Baill.) G.L.Webster, were also included based on recommendations in Webster's manuscripts that were never completed or published.

Additional changes to the number of species in *Phyllanthus* came with the revision of one of the understudied subgenera (chapter 4) and the study of some poorly known species from Sulawesi (chapter 5). The revision of *Phyllanthus* subgenus *Macraea* included 24 species with indications that there might be a few more in India. It is a Palaeotropical group with the majority of its diversity in Asia and previously species of this group were only treated separately for local floras. This group of species is characterized by non-phyllanthoid branching, 3-merous flowers with three free stamens and clypeate pollen. The constituent species were expanded to include species from the Philippines and the Pacific, indicating that *P.* subgenus *Macraea* is distributed from Africa all the way to Hawai'i.

Koorders (1898) published two species of *Phyllanthus* for the island of Sulawesi, but only included a concise description, which precluded assignment to any subgenus. After studying the specimens collected by him, we lectotypified these species and also concluded that they should be placed in *Phyllanthus* subgenus *Eriococcus* (chapter 5). They are most likely related to similar looking species from the Philippines of which one appeared to be synonymous. These species likely belong to a lineage that might have originated on the mainland and dispersed through the Philippines to Sulawesi and ultimately reached the Lesser Sunda islands.

The infrageneric framework outlined in chapters 2–5 provided the best hypothesis to test for monophyletic groups as potential candidates to be integrated in a re-classification of *Phyllanthus* s.l. A phylogenetic study of five molecular markers found several problems with the previous system, most commonly due to monospecific taxa or small sections, which were found to be embedded in other groups (chapter 7). Some subgenera like *Phyllanthus* subgenus *Gomphidium* and *Kirganelia* were found to be polyphyletic and the paraphyly of *Phyllanthus* was again confirmed. *Phyllanthus* s.l. appeared to consist of eight separate clades with *Glochidion* closely related to a paraphyletic *Phyllanthus* subgenus *Phyllanthodendron*. A new classification has to correct for these findings, but could focus on these clades as potentially separate genera.

Medicinal properties of Phyllanthus

Species of *Phyllanthus* s.l. are used in various traditional medicines. Plant metabolomics using Proton nuclear magnetic resonance (HNMR) combined with anti-bacterial and anti-fungal testing provided a strong method to study these effects and potentially find bioactive compounds, which could be targets for future studies. Unfortunately our results were minimal as only a few extracts of species were found to possess antibacterial effects. Most likely due to concentration issues we could not determine which compounds were responsible for these effects. A

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survey across the literature showed that more and more compounds are discovered in tribe Phyllanthae every year and potentially a study of the related species suggested by our phylogenetic work, can identify new candidates for future work.

Monophyletic or monophyletic, large versus small genera

The paraphyletic nature of *Phyllanthus* s.l. was one of the main focuses of this thesis. After indications from Wurdack et al. (2004) and confirmation by Kathriarachchi et al. (2006), a new classification of tribe Phyllanthae sought to combine *Phyllanthus* with *Breynia*, *Sauropus* and *Glochidion* (Hoffmann et al. 2006). *Phyllanthus* would be monophyletic when combining all embedded groups, but also by creating a new classification by dividing the genus into smaller genera based on clades and recognisability. However, creating one giant genus would temporarily solve the problem and identifications issues would just be pushed to subgeneric levels. A broader treatment of *Phyllanthus* would still result in a few hundred species needing to be transferred, while *Phyllanthus* becomes a giant genus with no apparent synapomorphies. Christenhusz (2020) advocated for a conservative approach in naming with increasingly larger genera on the basis that it would be more stable as it would be easier to maintain monophyly. As long-standing genera have large bodies of literature attached to them, dividing genera into new groups would ignore the relations between clades and their evolutionary history. Then what to do with paraphyletic groups? Christenhusz (2020) indicated that these should not be accepted, but instead create larger groups and look for similarities between the clades (giving an example of birds and reptiles). Applying this to *Phyllanthus*, would result in a group with no distinct synapomorphy and the characters that differ between clades are equal or larger than the difference between *Phyllanthus* s.l. and *Flueggea* Willd., *Margaritaria* L.f. and the rest of tribe Phyllanthae. The alternative approach presented here, might not work in other genera, but actively avoiding one side of the argument is not good science.

In chapter 9 we present our classification of tribe Phyllanthae with 18 genera based on the results from our phylogenetic and morphological work. A new phylogeny is presented by combining the contemporaneous studies of Chapter 7 and Falcón et al. (2020). *Phyllanthus* s.s. is restricted to mostly the Neotropics while the genera *Cathetus* Lour., *Cicca* L., *Dendrophyllanthus* F.Muell., *Embllica* Gaertner, *Kirganelia* A.Juss, *Moeroris* Raf., *Nellica* Raf. and *Nymphanthus* Lour. are reinstated and *Lysiandra* (F.Muell.) R.W.Bouman, I.Telford & J.J.Bruhl is raised to the level of genus. Each genus is (re-)described while taking into account all previously defined subgroupings of which not all are retained. Especially a number of monospecific sections are subsumed in larger groups. While we present a more conservative approach in the number of subgenera and (sub)sections of the various genera, we feel that this classification

Morphological evolution

The large morphological diversity found in *Phyllanthus* s.l. could already be seen in the large number of subgenera and sections. The flowers show large differences between taxa while there are also some interesting oddities. While studying the phylogeny of tribe Phyllanthae, it became apparent that some morphological features thought to be indicative of common ancestry, were actually the result of convergent evolution (chapter 7).

The specific type of branching found in the majority of species of tribe Phyllanthae, the so called phyllanthoid branching, sets it apart of other members of the Phyllanthaceae. It is likely that this branching system is involved with energy management and maximizing photosynthetic potential. How this system exactly works and whether nutrients flows are reversed is not known. The ability to shed whole branchlets and have leaves on the main stem reduced to scales provides the plants with a great system for energy management and to prevent light competition between its own branchlets while keeping a slim habit.

Staminate flowers usually show little difference between species in a particular clade, but they are invaluable for distinguishing genera. Early diverged clades in *Phyllanthus* s.l. have trimerous flowers with two perianth whorls and this trait seems to be conserved in parts throughout the phylogeny. Pentamerous flowers originated independently at least six times. In contrast pistillate flowers show more differences in the shape of the style and stigmas related to different pollination systems and these can be used to differentiate species.

Capsules are common fruits in the Phyllanthaceae family, but several instances are found in tribe Phyllanthae, where berries have evolved.

Dispersal history

The reconstruction of *Phyllanthus* showed that it likely originated somewhere in the Early Eocene and possibly in the boreotropics. Early dispersals to North America, Africa and Asia have lead to the present day distribution of the reinstated *Nellica*, a clade sister to the rest of *Phyllanthus* s.l. The diversification of *Flueggea* and *Margaritaria* is of a more recent date, which suggests that their pantropical distribution is also an effect of more recent long-distance dispersals than a boreotropical origin. Initial results indicated that boreotropical dispersal might have influenced the distribution of several clades, with *Nellica* present in North America, Africa and Asia, while some clades only show major distribution centers in Asia and Africa (*Cathetus* and *Moeroris*). Subsequent dispersal out of Africa to the Neotropics are inferred to have occurred during the Oligocene, which lead to *Phyllanthus* sensu stricto (s.s.; here the only clade retained as *Phyllanthus*, chapter 9). Within *Phyllanthus* s.s. several independent diserspals northwards are found to Mexico, but also to the West Indies. From Africa, one clade also dispersed to Australia, which lead to *Cicca* and the very diverse *Dendrophyllanthus*. *Cicca* has a wide distribution with a few species in Asia to more diverse clades in Madagascar, Africa and again some species in the Neotropics, which seems to be the result of

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more recent dispersals. In mainland Asia, several groups diverged to form *Emblica*, *Glochidion*, *Breynia* (more explored in van Welzen et al. 2015) and with one dispersal event, which lead to *Synostemon* in mainly Australia.

Diversification of tribe Phyllanthae

Species diversity within *Phyllanthus* s.l. shows an uneven pattern, with some highly speciose clades seeming to be very young, while others that diverged earlier do not include as many species. A diversification analysis on the dated tree of chapter 8 showed two possible shifts in speciation. One was for the clade comprising the reinstated genera *Cicca* and *Dendrophyllanthus*, while the other occurred for the genus *Glochidion*. A high rate of speciation of tribe Phyllanthae had previously been related to a pollination mutualism with parasitic moths, but this pattern was not observed in all clades where this system has been inferred. Other factors such as dispersal strategy are proposed to have affected potential speciation rates, but a larger ecological study is necessary to understand this. As the pollination system is also found to vary between genera and also species, subtle nuances could also still have an effect. Highest speciation rates and the strongest shift was still found for *Glochidion* subgenus *Glochidion* and not as much in the former *Phyllanthodendron* attributed species. Species placed here in *G.* subgenus *Pseudoactephila* and *G.* subg. *Phyllanthodendron* were hypothesized to be pollinated perhaps by flies and some characters like the inflated fruits have previously been attributed as a defense against herbivory and seed predation (Kato & Kawakita 2017). The pollination mutualism with moths is hypothesized to have evolved from an original parasitic system (Kato & Kawakita 2017) and perhaps parasitism is present in more clades in the tribe, with some species evolving defences against this.

Future perspectives

This thesis investigated the global evolutionary patterns of *Phyllanthus* and how to translate these in a monophyletic classification at generic level. Studying other factors such as flower development and differences in ecology, could provide more insight in the evolution of the diverse tribe Phyllanthae. Especially ecological information on many species is lacking and as in many plant families, the life histories of the plants have barely been studied.

The pollination mutualism with parasitic moths has, since its first publication (Kato 2003), garnered much attention as an ideal study system for co-evolution and co-diversification of two groups. While the diversification rates for tribe Phyllanthae were studied here in relation to this mutualism, the amount of data on other ecological factors and variations in this system is very limited. Other ecological factors such as dispersal mechanics are also a field that presents interesting opportunities within tribe Phyllanthae. The phylogeny showed several shifts in fruit type, which probably indicate differences in dispersal vectors, but which vectors or how this is associated with speciation has not been studied. An

interesting system could be in the genus *Cicca* where the fruits are capsules in the Malagasy clades, while in *C.* subgenus *Cicca* different types are found from small berries to apple-like fruits and inflated capsules that are a contender for the biggest fruits in the tribe.

As the speed and data originating from molecular tools is rapidly increasing, future studies might implement a much broader sampling of the genome of the various genera in tribe Phyllanthae. Initial studies have already sequenced the plastid genome of species of *Breynia* (Cai et al. 2019; Zhou et al. 2020), *Glochidion* (Cheon et al. 2019) and *Flueggea* (Wang et al. 2020) and as more information becomes available, it will be possible to study other aspects then phylogenetics such as genome duplication patterns or the evolution of gene function and composition. Indications of whole genome duplications in Phyllanthaceae have been found by Cai et al. (2019), but they only included two species of this family. Chromosome counts from Miller & Webster (1966) found that the base number in Phyllanthaceae (then Euphorbiaceae subfamily Phyllanthoideae) was $x = 13$ (also in Webster & Ellis 1962). The same base number has been found in species of *Flueggea*, *Margaritaria*, *Kirganelia*, *Nellica*, *Cathetus* (Webster & Ellis 1962; Hans 1973), while higher chromosome numbers are found in *Moeroris*, *Phyllanthus* s.s., *Breynia* and *Synostemon* (Webster & Ellis 1962; Miller & Webster 1966). This indicates at least one possible duplication or hybridisation event within tribe Phyllanthae with possibly more since some clades have species that are tetraploids (Hans 1973).

New taxonomic studies will continue on tribe Phyllanthae, however to prevent overlooked species, revision work should focus on separate taxa instead of local floras. Some taxa are in dire need of an updated treatment, like the reinstated genus *Emblica*, where its constituent species have always been scattered over several subgeneric groups. By understanding more of the phylogenetic context of each genus, it will be easier to make comparisons between groups of species to find more diagnostic characters between them. Following our new classification of tribe Phyllanthae, several genera are already geographically separated and once the genus is known, species identification becomes more narrow in this framework. Hopefully this will aid future taxonomists with their understanding of these awesome plants.

Final remarks

My journey with *Phyllanthus* has been long and interesting. Not all experiments succeeded and naturally not all species could be exhaustively treated. Still, I hope that the work presented in this thesis has demonstrated how wonderful the plants that made up *Phyllanthus* s.l. are. The species in the tribe Phyllanthae display an enormous variation in habit, flowers and fruit morphology, which is only indicative of a long and intricate evolutionary history and likely partly due to the moth pollination. I have attempted to redefine *Phyllanthus* s.l. and create a classification

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that shows this history, with reinstated genera that show where clades diverged, but which sometimes also showed convergent evolution. A new view on *Phyllanthus* and its related genera creates the way to actively compare clades and study how these evolved to lead to the diversity we see today.

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SUMMARY

In the past 50 years, plant systematics has undergone a revolution with the advent and rapid accessibility of molecular techniques, which greatly influenced how we study and classify taxa. While many organism groups and theories have been proven accurate, some appeared to be more complex than previously thought. The plant genus *Phyllanthus* (Phyllanthaceae tribe Phyllantheae) is a good example of a group of species with varying views on its taxonomy and it has always been treated as closely related to the genera *Glochidion*, *Breynia* (including *Sauropus*) and *Synostemon*. Previous studies found the latter genera to have developed within *Phyllanthus* and a proposal was made to merge all, thereby creating one giant genus with over 1200 species with an enormous variation in morphological features. To study the evolutionary history and possibilities in classification, we explored this genus in greater detail. A number of species of *Phyllanthus* are also used in traditional medicine and two well-known examples (*P. emblica* and *P. acidus*) are species grown for their their edible fruits that contain high numbers of vitamin C.

The genus *Phyllanthus* was first described by Linnaeus in 1753 and with subsequent publications over the past 250 years, this group has grown to include over 800 species. Some have been treated as separate genera by some authors, but in the 19th century clusters of similar species were united in one *Phyllanthus* and grouped in a classification below the genus level consisting of over 40 sections. From the 1950s onwards, the relation between these sections was organized in several subgenera. This classification was based on anatomy, which was expanded with the incorporation of various morphological features including habit, branching system and pollen morphology. However, taxon recognition often focused on specific regions instead of complete (sub) groups and in chapter 3 we compiled a checklist that incorporated all the subgroups that have been defined and placed almost all species in this framework. Almost all 800 species were in the framework, based on morphological features and past classifications, and it resulted in the recognition of 18 subgenera, 70 sections and 14 subsections. The various subgenera presented strong candidates for a new classification on genus level of *Phyllanthus* and the related genera. We followed up the checklist with the publication of a new species (chapter 2), a study on *P.* subgenus *Macraea* (chapter 4) which included species never placed in that group before and a study of the species described by Koorders for the island of Sulawesi (chapter 5).

The results from previous phylogenetic studies had included around 10% of the species of *Phyllanthus*. In our phylogenetic study based on five markers (chapter 6), we included species from all subgenera and 53 of the 70 sections, while discussing patterns of morphological evolution and several instances of convergent

evolution. Characters such as the specialized branching system present in the majority of species, has been lost in several clades independently. Other features such as the loss of the nectar disk, or the simplified style and stigma morphology that is associated with a specific pollination system involving mutualistic moths is also indicated to have evolved several times. By comparing the phylogeny with the framework outlined in the checklist of chapter 3, we found multiple instances of paraphyletic subgroups often related to small (usually monospecific) taxa nested in other groups. However, the backbone phylogeny showed good support between major clades that are often morphologically distinct.

In addition to their diversity and evolution, *Phyllanthus* is also an interesting group with regards to the medicinal usage of several species. Species of *Phyllanthus* are used in various ways and extractions are also sold as tablets with vitamin supplements, to help kidney and liver function or to combat inflammation. A few species are grown in botanical gardens throughout Europe, which provided a great opportunity to study their antimicrobial and antifungal effects. In chapter 6 we sampled several species from the living collections of the Hortus botanicus Leiden and we used Proton Nuclear Magnetic Resonance (^1H NMR) to study their metabolite profiles. This was correlated with the results from a screening for bioactivity against *Escherichia coli* and *Staphylococcus aureus* and followed by a targeted approach using High Performance Thin Layer Chromatography (HPTLC). Indications were found for significant activity against gram-negative bacteria for *P. arbuscula*, *P. muellerianus*, *P. tenellus* and *P. urinaria*, but we were unable to identify the compounds that underly this. Future studies would need a larger sample set, but our results indicate that their focus could be especially on the phenolics produced by these species.

Following the results from our phylogenetic work, it was necessary to create a new classification for *Phyllanthus* and its related genera. While previous studies had proposed to merge everything, we decided to divide *Phyllanthus* into smaller segregates (Chapter 8). We reinstated the genera *Cathetus*, *Cicca*, *Dendrophyllanthus*, *Emblica*, *Kirganelia*, *Moeroris*, *Nellica* and *Nymphanthus* while *Lysiandra* was raised to the generic level. This retained the genera *Glochidion*, *Breynia* and *Synostemon* while creating a classification based on recognisable monophyletic groups. More than 600 species were transferred to another genus in this new classification. Several paraphyletic sections and subgenera are expanded to include the species nested within them. Both solutions to the paraphyly of *Phyllanthus* are valid, union of all or separation, but by dividing *Phyllanthus* into smaller groups as proposed here, the evolutionary history of the group is reflected in a much better way.

Using the phylogeny from chapter 5 we had previously looked at various morphological evolutionary patterns, but barely touched on the subject of how the whole tribe became so diverse and how it dispersed through time. While a broad treatment of *Phyllanthus*, considered it to be a pantropical genus, the reinstated

segregate genera are often restricted to one or two continents. In chapter 9 we explain how the current distribution came to be and whether there have been shifts in its diversification. Traditionally the pantropical distribution of the clade has been attributed to a Gondwanan origin, but we found that tribe Phyllanthae probably originated during the Late Palaeocene close to the Palaeocene-Eocene Thermal Maximum (PETM). The genera *Nellica* and *Cathetus* indicate early dispersals between Africa and Asia, with the former genus also being present in North America. This distribution is consistent with a possible boreotropical origin followed by subsequent extinction in Europe. Fossil pollen findings in Europe also indicate that *Flueggea* or a related genus was present there at the time. Within clades/genera we found that their distribution is often the result of a limited number of dispersal events. While studying diversification rate shifts in the tribe, we found that the pollination mutualism present in several clades is not always consistent with an increase in diversification. In some clades, this did not lead to a higher rate of diversification and this is possibly caused but not fully explained by a difference in dispersal vectors/mechanisms.

The evolution of tribe Phyllanthae is explored here in relation to its systematics and dispersal history, but as outlined in chapter 10, many questions remain to be answered. Future studies can explore the evolution of specific clades and how the species diverged and adapted to different conditions. Especially the pollination mutualism with moths present in several clades provides a great opportunity to study how both pollinator and plant are locked in an evolutionary struggle and how they adapt to each other. In this thesis I have expanded upon our knowledge of the phylogeny of *Phyllanthus* and its related genera while trying to provide a system for all species that were attributed to it. While this classification may change again in the future, the tribe remains an interesting study group.

SAMENVATTING

De afgelopen 50 jaar was er een revolutie in de plantensystematiek met de komst en snelle en relatief goedkope toegankelijkheid van moleculaire technieken. Deze hebben een enorme invloed gehad op hoe taxa bestudeerd en geclassificeerd worden. Hoewel veel groeperingen van organismen en theorieën werden bewezen, is ook gebleken dat sommige complexer zijn dan eerder werd gedacht. Het plantengeslacht *Phyllanthus* (Phyllanthaceae-tribus (= stam) Phyllanthaeae) is een goed voorbeeld van een groep soorten waarbij vorige auteurs verschillende opvattingen hadden. Deze groep is altijd beschouwd als nauw verwant aan de geslachten *Glochidion*, *Breynia* (inclusief *Sauropus*) en *Synostemon*. Eerdere studies vonden dat de laatst genoemden ontstaan zijn binnen *Phyllanthus* en dat resulteerde in een voorstel om alles samen te voegen. Dit zou uitmonden in één gigantisch geslacht met meer dan 1200 soorten met een enorme variatie in morfologische kenmerken. Om de evolutionaire geschiedenis en mogelijkheden in classificatie te bestuderen, hebben we dit geslacht in detail onderzocht. Verscheidene soorten van *Phyllanthus* worden ook gebruikt in de traditionele geneeskunde en twee bekende voorbeelden zijn soorten die worden gekweekt voor hun eetbare vruchten die een hoog gehalte aan vitamine C bevatten.

Het geslacht *Phyllanthus* werd voor het eerst beschreven door Linnaeus in 1753 en door de daaropvolgende publicaties in de afgelopen 250 jaar is de groep gegroeid en bevat het meer dan 800 soorten. Sommige zijn door sommige auteurs als afzonderlijke geslachten behandeld, maar in de 19e eeuw werden clusters van vergelijkbare soorten gegroepeerd in een classificatie van meer dan 40 secties onder het geslachtsniveau. Vanaf de jaren vijftig van de 20^{ste} eeuw werd de relatie tussen deze secties georganiseerd in verschillende ondergeslachten. Dit was een op anatomie gebaseerde classificatie die werd uitgebreid met de opname van verschillende morfologische kenmerken, waaronder groeivorm, vertakkingsstelsel en pollenmorfologie. Floristische werken zijn meestal gericht op specifieke regio's in plaats van op (sub)groepen zodat een overzicht van alle soorten per groep ontbrak, daarom hebben we in hoofdstuk 3 een checklist samengesteld waarin alle gedefinieerde subgroepen zijn opgenomen met bijna alle soorten erin geplaatst. De verschillende ondergeslachten waren sterke kandidaten voor een nieuwe indeling van het geslacht *Phyllanthus* en de gerelateerde groepen in meerdere geslachten. We volgden de checklist op met de publicatie van een nieuwe soort (hoofdstuk 2), een studie over het ondergeslacht *Macraea* (hoofdstuk 4) met soorten die nog nooit eerder in die groep waren geplaatst en een studie van de soorten beschreven door Koorders voor het eiland Sulawesi (hoofdstuk 5). Bijna alle soorten waren in dit systeem geplaatst, gebaseerd op morfologische kenmerken en classificaties uit het

verleden en het resulteerde in een indeling met 18 ondergeslachten, 70 secties en 14 subsecties.

De resultaten van eerdere fylogenetische studies waren gebaseerd op ongeveer 10% van het aantal soorten binnen *Phyllanthus* waarbij niet alle ondergeslachten waren bemonsterd. In onze fylogenetische studie, gebaseerd op vijf markers (hoofdstuk 6), hebben we soorten uit alle subgenera en 53/70 secties opgenomen terwijl we patronen van morfologische evolutie en verschillende gevallen van convergente evolutie bespraken. Een kenmerk zoals het gespecialiseerde vertakkingssysteem dat in de meeste soorten aanwezig is, is in verschillende takken van de stamboom onafhankelijk van elkaar verloren gegaan. Er is ook een specialistisch bestuivingssysteem met mutualistische motten en in dit systeem hebben de bloemen vaak geen nectarschijf meer en zijn de stijl en stempel simpeler of geslotener dan bij andere systemen. Deze kenmerken lijken een aantal keren onafhankelijk te zijn geëvolueerd. Door de fylogenie te vergelijken met de groepenindeling van de soortenlijst van hoofdstuk 3, vonden we meerdere gevallen van parafyletische subgroepen (niet alle soorten die afstammen van een voorouder verenigd). Vaak werd dit veroorzaakt doordat kleinere taxa met meestal maar één soort genesteld waren in grotere groepen. De stamboom toonde een sterke ondersteuning voor de grotere groepen die vaak ook morfologisch verschillend zijn.

Naast hun diversiteit en evolutie is *Phyllanthus* ook een interessante groep met betrekking tot het medicinaal gebruik van verschillende soorten. Verscheiden soorten worden gebruikt tegen verschillende kwaaltjes en sommige worden ook verkocht als vitaminesupplementen of om de nier- en leverfunctie te ondersteunen. Een paar soorten komen voor in botanische tuinen in Europa, wat een geweldige kans bood om hun antimicrobiële en antischimmeleffecten te bestuderen. In hoofdstuk 6 hebben we verschillende soorten uit de levende collecties van de Hortus botanicus Leiden bemonsterd en hebben we Proton Nuclear Magnetic Resonance (1H NMR) gebruikt om hun metabolietprofielen in kaart te brengen. Dit werd vergeleken met de resultaten van een screening op bioactiviteit tegen *Escherichia coli* en *Staphylococcus aureus* en vervolgens gebruikten we High Performance Thin Layer Chromatography (HPTLC). Voor *P. arbuscula*, *P. muellerianus*, *P. tenellus* en *P. urinaria* werden aanwijzingen gevonden voor significante activiteit tegen gramnegatieve bacteriën, maar de onderliggende stoffen konden we helaas niet identificeren. Toekomstige studies zouden een grotere steekproefset nodig hebben, maar onze resultaten geven aan dat hun focus zou kunnen liggen op de fenolen die door deze soorten worden geproduceerd.

Na de resultaten van ons fylogenetische werk was het noodzakelijk om een nieuwe classificatie voor *Phyllanthus* en de nauw gerelateerde geslachten te creëren. Terwijl eerdere studies hadden voorgesteld om alles samen te voegen, besloten we *Phyllanthus* op te delen in kleinere groepen (hoofdstuk 8). Hiervoor werden de groepen *Cathetus*, *Cicca*, *Dendrophyllanthus*, *Emblica Kirganelia*, *Moeroris*, *Nellica* en *Nymphanthus* weer als aparte geslachten beschouwd en het ondergeslacht

Lysiandra werd ook als een aparte groep beschreven. Met deze indeling worden de geslachten *Glochidion*, *Breynia* en *Synostemon* behouden, terwijl er een classificatie wordt gecreëerd op basis van monofyletische groepen. Meer dan 600 soorten werden in deze nieuwe classificatie verplaatst van *Phyllanthus* naar een andere groep. Als *Glochidion* en de andere geslachten in *Phyllanthus* werden opgenomen, dan zou dit ook hebben geleid naar de overzetting voor 400 verschillende soorten. Verschillende parafyletische secties en ondergeslachten werden uitgebreid met de soorten die erin genesteld zijn. Beide oplossingen voor de parafylie van *Phyllanthus* zijn mogelijk, maar door het geslacht op te delen in kleinere groepen zoals hier voorgesteld, vinden we dat dit de evolutionaire geschiedenis van de groep beter weerspiegelt. In plaats van een gigantische groep met meer dan 1200 soorten, wordt er zo een onderscheid gemaakt tussen kleinere geslachten met een variabel aantal soorten van 20 tot 210 soorten.

Met behulp van de fylogenie uit hoofdstuk 5 hadden we eerder gekeken naar verschillende morfologische evolutionaire patronen, maar we wilden verder kijken hoe de hele stam Phyllantheae zo divers werd en hoe deze zich in de loop van de tijd verspreidde. Terwijl een breed gedefinieerd geslacht *Phyllanthus* voor zou komen in alle tropische gebieden op aarde, zijn de hier afgesplitste groepen vaak alleen aanwezig op een of twee continenten. In hoofdstuk 9 duiken we in de verspreidingsgeschiedenis en hoe de huidige distributie van verschillende groepen tot stand is gekomen. Hierbij wilden we ook kijken naar de diversificatie van verschillende groepen, omdat deze niet allemaal even soortenrijk. De verspreiding die we zien bij de Phyllantheae wordt meestal toegedragen aan een oorsprong ten tijde van het zuidelijke continent Gondwana. Onze resultaten toonden aan dat de Phyllantheae-stam waarschijnlijk is ontstaan tijdens het Laat-Paleoceen dichtbij het Paleoceen-Eocene Thermal Maximum (PETM). De geslachten *Nellica* en *Cathetus* duiden op een vroege uitwisseling van soorten tussen Afrika en Azië. *Nellica* is een kleinere groep soorten die op de stamboom zuster is van de rest van de soorten vroeger toegedragen aan *Phyllanthus*. Deze groep komt voor in Afrika, Azië en Noord-Amerika. Deze verdeling ten tijde van het PETM komt overeen met een mogelijke oorsprong in wat bekend staat als de boreale tropen. Dit was een tropisch regenwoud hoog op het noordelijk halfrond aan het eind van het Paleoceen dat zorgde voor een verbinding en makkelijkere uitwisseling tussen Europa en Noord-Amerika en toen het na het PETM afkoelde, verspreidden veel planten zich naar het zuiden richting Afrika en zuidelijk Azië. Veel tropische groepen waaronder wellicht *Nellica* stierven daarna uit in Europa. Vondsten van fossiel pollen in Europa wijzen er ook op dat *Flueggea* uit de stam Phyllantheae (zustergroep van *Nellica* en de andere groepen) of een verwant geslacht daar destijds aanwezig was. Binnen clades/genera vonden we dat hun verspreiding vaak het resultaat is van een beperkt aantal verspreidingsgebeurtenissen. Vaak werd het grote aantal soorten voor sommige groepen verklaard door een bestuivingsmutualisme met kleine motjes. Zowel de plant als bestuiver zouden een co-diversificatie zijn ondergaan. Bij het bestuderen

van verschuivingen in de diversificatiesnelheid binnen de stam, ontdekten we dat het onderlinge bestuivingsmutualisme in verschillende clades niet altijd gelijk staat met een toename in de soortsvorming. In sommige clades heeft dit niet geleid tot een hogere mate van diversificatie en dit wordt mogelijk (maar niet volledig) verklaard door een verschil in verspreidingsvectoren/mechanismen.

De evolutie van de stam Phyllanthae werd hier onderzocht in relatie tot zijn systematiek en verspreidingsgeschiedenis, maar zoals uiteengezet in hoofdstuk 10, zijn er nog genoeg onderwerpen om verder te onderzoeken. Toekomstige studies kunnen de evolutie van specifieke clades proberen te ontrafelen en hoe de verschillende soorten zich hebben aangepast aan verschillende omstandigheden en zo van elkaar zijn gaan verschillen. Vooral het bestuivingsmutualisme met motten die in verschillende clades aanwezig zijn, biedt een geweldige kans om te bestuderen hoe zowel bestuiver als plant opgesloten zitten in een evolutionaire strijd en hoe ze zich aan elkaar aanpassen. In dit proefschrift heb ik onze kennis van de fylogenie van *Phyllanthus* en zijn verwante geslachten uitgebreid. Daarbij probeerden we de taxonomie weer te baseren op monofylie met groepen die nog steeds morfologisch van elkaar te onderscheiden zijn. Hoewel deze classificatie in de toekomst weer kan veranderen, blijft de stam een interessante studiegroep.

Curriculum Vitae

Roderick Bouman was born on October 31st, 1991, in Hilversum, the Netherlands. He obtained his bachelor degree in Biology at the University of Utrecht in 2013 and worked for his thesis on the fluctuations in CO₂ levels during the Dark Ages based on lake core samples from Germany. From 2013 to 2015 he studied in Leiden and graduated cum laude for his Masters in Biology with



a specialization in Evolution, Biodiversity and Conservation. While studying for his masters degree, he pursued several of his research interests during two major research internship, one on fossil crinoids and the other on pollination of heathers (*Erica*) in South Africa. After his masters, he worked for a brief research project on the evolution of *Erica* at Naturalis and the University of Mainz supervised by Timo van der Niet and Mike Pirie.

Since 2015 he has been working on his PhD at the Hortus botanicus Leiden in collaboration with Naturalis Biodiversity Center under the supervision of Prof. Paul Keßler and Prof. Peter van Welzen. The focus of this project was the evolution, systematics and bioactivity of the plant genus *Phyllanthus*. The preliminary results of this study and the new classification of *Phyllanthus* were presented to several research groups and at the Flora Malesiana XI conference in Brunei in 2019. While finishing his thesis, he started in 2019 as a taxonomist for cultivated varieties of bulbiferous plants at the Royal General Bulbgrowers Association (KAVB) in Hillegom where he worked for 2.5 years and in November 2021 he has been appointed scientific collection manager at the Hortus botanicus Leiden.

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Acknowledgements

With working at so many different departments in Leiden, there are also so many people I wish to thank. Naturally I would like to thank everyone at the Hortus botanicus Leiden for welcoming me and making my time there so great. I especially want to thank my promoters Paul Keßler and Peter van Welzen for their guidance and long support with my PhD. From the botanical garden I would also like to express my gratitude to Hanneke who always invited me to all sorts of projects and activities at the garden and to Gerda for her critical questions.

Both at Naturalis Biodiversity Center and at the Institute Biology of Leiden I had so many people supporting me. The lab staff was always willing to help me and I would like to thank Arjen, Bertie-Joan, Elza, Frank, Marcel and Roland. Thanks also goes out to Young Choi and Kim and all the students at the Natural Products lab for introducing me to the world of metabolites. Esmee Winkel is gratefully acknowledged for the beautiful illustrations of the new species in this thesis.

A heartfelt thanks goes out to everyone who helped me while gathering material and data. The fieldwork was only made possible through the funding from the Alberta Mennega foundation and the help I received from Richard Saunders in Hong Kong, Richard Corlett in Xishuangbanna and Joeri Strijk in Guangxi.

When I first started, the National herbarium was still located in that isolated little corner of the city near the station of Leiden Lammenschans, but it was never boring due to the people there. I would like to thank Nicolien, Roxali, Marnel, Ron, Jan, Paul and Hiltje, Pieter, and Brigitta, Frits, Sylvia, Michael, the late Jan-Frits, Willem, Max and my office roommate the late Peter Hovenkamp for making my time there so enjoyable.

My thanks also goes out to my fellow friends and fellow PhD students Andres, Kevin, Panos, Werner, Lizzie, Hector, Vicky, Dewi, Nienke, Ryan, Le Qin, Deyi, Marcel, Mehrdad, Leon my old “herbarium crew” of Mega, Izu, Dul, Saroj, Renyong and Richa and everyone else. I also want to thank my wonderful students Janna, Gerry and Aninda for their valuable help with tackling these tiny-flowered plants.

To my dear friends from my hometown, Raymond, Emma, Darius and Rogier, thank you for listening to my ramblings and all your support. A special thanks goes to my girlfriend Eka Iskandar who always stood by me during happy and sad moments and who I could always invite to go out for a walk to distract ourselves. Finally, I would like to thank my parents and the rest of my family for their love and support while I was finishing my studies.



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