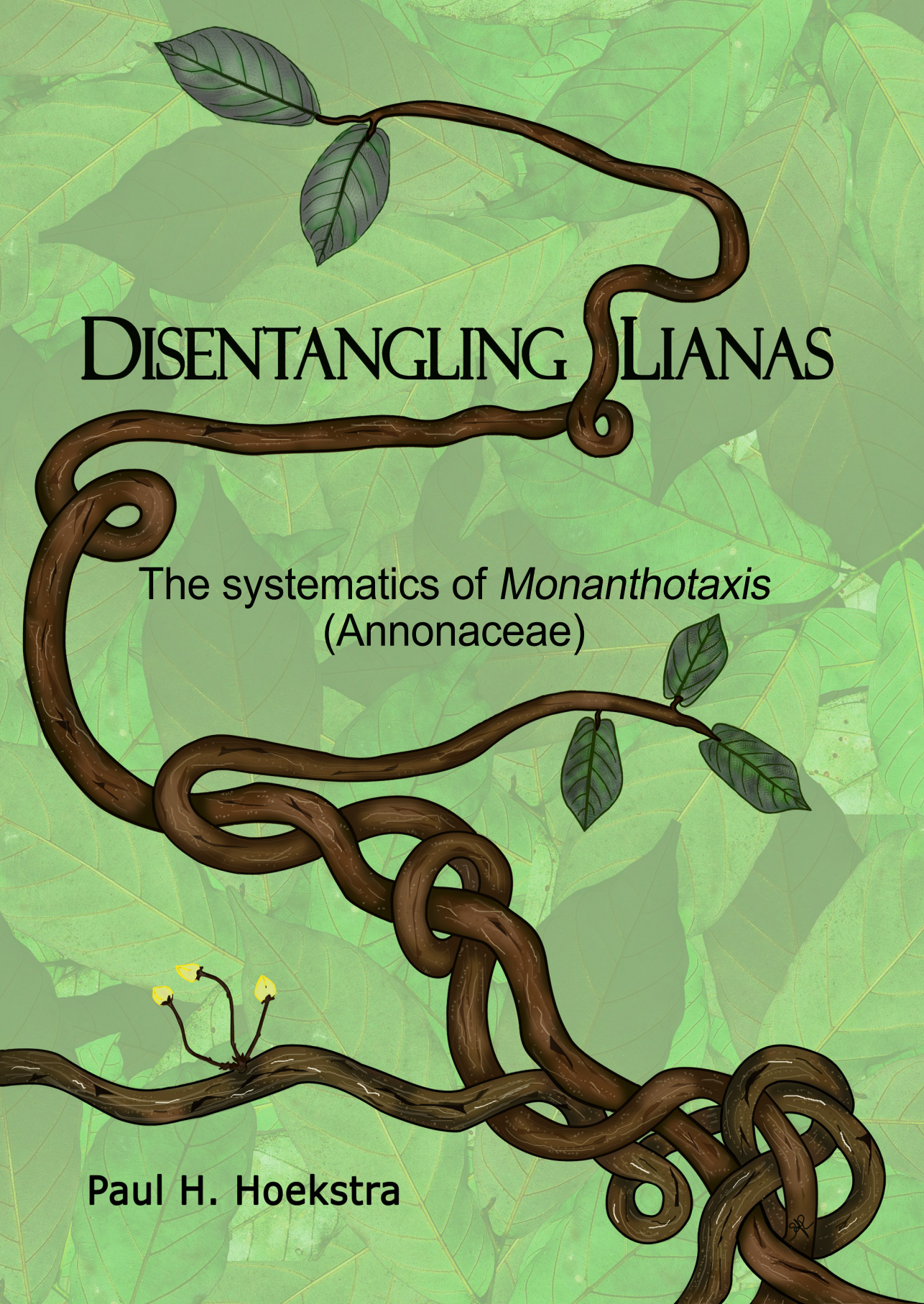
DISENTANGLING LIANAS
The systematics of *Monanthotaxis* (Annonaceae)
Paul H. Hoekstra

Propositions

1. Dividing the genus *Monanthotaxis* into subgenera will create taxonomic instability.
   (this thesis)

2. Shifts in pollination syndromes are the most likely explanation of the diverse floral morphology in *Monanthotaxis*.
   (this thesis)

3. The shift of funding from fundamental sciences to applied sciences is detrimental for long term scientific progress.

4. It is necessary for scientists to change the pressure to publish into pressure to communicate to a general public.

5. Long living woody lianas are barely protected by current FSC certifications.

6. Reducing consumption is essential to battle climate change.

Propositions belonging to the thesis, entitled

Disentangling lianas: the systematics of *Monanthotaxis* (Annonaceae)

Paul H. Hoekstra
Wageningen, 6 April 2022

Disentangling lianas: the systematics of *Monanthotaxis* (Annonaceae)

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Disentangling lianas: the systematics of *Monanthotaxis* (Annonaceae)

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Chapter 1

Introduction

1.1 Biodiversity

The importance of biodiversity is paramount. The enormous variety of life forms on our planet are intertwined in a dynamic network. The higher the diversity of organisms in an ecosystem, the more complex is the web of interactions between them, producing ecosystems more resilient to a variety of disasters. A high diversity improves also the quality of human lives by providing ecosystem services, such as food, medicines, water quality regulation and nutrient cycling (Duraiappah et al. 2005). Biodiversity is thus key in sustaining the different life forms on earth. Despite its importance, the current decline of biodiversity is immense, and species extinction rates over the last hundred years have been much higher than would be expected on the basis of the geological record (Ceballos et al. 2015, Dirzo & Raven 2003). The urgency of battling biodiversity loss is widely recognized and because of this, the Convention on Biological Diversity was adopted in 1992, and nowadays has been ratified by almost 200 countries. However, there still exists a huge hole in the knowledge of the more essential information about species. In herbaria's around of the world, there are yet numerous unidentified specimens, including a lot of undescribed species for science (Bebber et al. 2010). To be able to protect the unknown diversity of species and to minimize the current loss of biodiversity, it is urgent to resolve first two basic and fundamental questions: what species exist and where do they occur. The solution of these basic but essential questions will permit us to deepen into more complex processes, such as the way in which species evolve.

Tropical Africa belongs to one of the most species diverse regions of the world, but the plant diversity and distributions are still very poorly known (Sosef et al. 2017). One third of the known flora is potentially threatened by extinction (Stévart et al. 2019). This percentage shall probably rise as still many species are undescribed (Pimm & Joppa 2015) and most recently described species are threatened (Hoekstra et al. 2016, Hoekstra et al. 2021, Johnson et al. 2017), which makes it likely that this also counts for the undescribed species. Large parts of the ecosystems of Africa are under pressure because of human needs. In West and East Africa more than 80% of the tropical forests have disappeared since 1900 (Aleman et al. 2018). In Central Africa the decline of forests is less severe and even the total amount of tropical forest has slightly increased at the expense of savannahs in the same period (Aleman et al. 2018). In large parts of Central Africa, such as in Gabon, only commercial trees are removed from the forest. This selective logging is less detrimental for the forest than clear-cutting. One of the plant groups which still are severely affected by this type of logging are thick woody lianas. Lianas are normally cut prior to logging to prevent felled trees from tearing down other trees. Therefore, the abundance of thick woody lianas in forests with selected logging is much lower compared to intact primary rain forests (Gerwing & Vidal 2002).

1.2 Annonaceae

One of the more abundant and diverse tree families in tropical rain forests is the family Annonaceae (Kenfack et al. 2007, Phillips & Miller 2002, Sonké & Couvreur 2014, van Gemerden et al. 2003). In tropical African rainforests this family also belongs to the top ten of most diverse and abundant liana families (Ewango et al. 2015, Tchouto et al. 2006). The family Annonaceae belongs to the order Magnoliales and are woody plants with simple, alternate, exstipulate leaves which are distichously arranged in almost all genera (except *Tetrameranthus*) and the flowers generally are trimerous. Annonaceae are distinguished from similar families of the Magnoliales by the presence of sepals and petals (excludes Eupomatiaceae), ruminate endosperm (excludes Magnoliaceae) and meso- or endotestal seeds (excludes Myristicaceae) (Keßler 1993). The family contains 109 genera and around 2500 species (Chatrou et al. 2018, Rainer & Chatrou 2006). It occurs worldwide in the tropics and only the genus *Asimina* occurs in subtropical to temperate areas.



Fig. 1. Flowers of *Asimina pygmaea* of the family Annonaceae

Although the family Annonaceae is clearly defined and monophyletic (Sauquet et al. 2003), the infrafamilial relationships have long been unclear and have changed many times since the description of the family in the end of the 18th century (Jussieu 1789). The first infrafamilial

classifications used characters of the fruits, while later classifications included flower characters (Chatrou et al. 2012). With the use of molecular phylogenetic analyses it became clear that the Annonaceae consists of 4 main clades (Couvreur et al. 2011, Richardson et al. 2004). With the increase of sampled genera and molecular markers the deeper nodes of the Annonaceae phylogenetic tree attained high support. The major clades of the Annonaceae have been given the rank of subfamilies, the Anaxagoreoideae, Ambavioideae, Malmeoideae and Annonoideae (Chatrou et al. 2012). Of these, the Malmeoideae has been further subdivided in nine tribes and the Annonoideae in seven tribes (Chatrou et al. 2012, Couvreur et al. 2019, Guo et al. 2017).

One of the tribes in the Annonoideae is the Uvarieae. This tribe includes about 475 species in Africa and Asia (Chatrou et al. 2018, Rainer & Chatrou 2006). Almost all species of this tribe are lianas, a feature which is rare in the rest of the Annonaceae family and only occurs in the African-Asian genus *Artabotrys* (tribe Xylopieae), the African genera *Letestudoxa* and *Pseudartabotrys* of the tribe Duguetieae and rarely in a few species of the Neotropical genera *Guatteria* (Maas et al. 2015) and *Annona* (Lundell 1974).

The generic delimitation within the tribe Uvarieae has long been unclear. At the beginning of this PhD project it was clear that the genera *Dasymaschalon*, *Friesodielsia* and *Monanthotaxis* were polyphyletic. Some African *Friesodielsia* and the genus *Exellia* were nested within the genus *Monanthotaxis* rendering that genus also polyphyletic (van 't Padje 2013) and the African *Friesodielsia* species clearly belonged to a different clade than the Asian *Friesodielsia* species (Wang et al. 2012). Verdcourt (1971b) already indicated that the African and Asian *Friesodielsia* species could belong to different genera noting that the Asian *Friesodielsia* species have outer petals that are much longer than the inner petals and monocarps with one or two seeds, while the African *Friesodielsia* species have less marked differences between the outer and inner petals and monocarps with mostly more than one seed. One of the objectives of this thesis was to provide clear generic boundaries for the genus *Monanthotaxis* and allied genera.

The genus *Monanthotaxis* is a highly diverse and interesting genus. In the family Annonaceae, flowers normally contain two whorls of petals, many stamens, and rarely contain staminodes. Some species of *Monanthotaxis* also show these characteristics, but the majority deviates from this pattern. *M. bidaultii*, for example, has tiny flowers with only three petals in a single whorl and three stamens. Also, flowers of several species have staminodes, while this is absent in other species. All these characters make it an interesting group to study trait evolution and one of the goals of my thesis is to elucidate the possible mechanisms which could have caused the diversity in floral traits. The genus *Monanthotaxis* is also an interesting genus in the search for medicines against cancer and malaria as an unidentified *Monanthotaxis* from Ghana and *Monanthotaxis heterantha* from Madagascar are locally used against malaria and other diseases (Asase et al. 2005, Rasoanaivo et al. 1992). Furthermore a wide array of different

chemical compounds have been identified on different species of *Monanthotaxis* (Liang et al. 1988, Mulholland et al. 2000, Waterman & Pootakahm 1979b)). Some compounds have antimicrobial or antifungal activities and the compound Crotepoxide has antiproliferative activity against cancer cells (Starks et al. 2012).

A limitation in the study of *Monanthotaxis* is the lack of ecological data of the genus. Most species occur in tropical rainforest where they climb up in the trees and have small flowers high in the canopy, which is often more than 40 meter high. As a result the flowers are rarely encountered and nothing is known about pollination. Most interesting collections in herbaria of *Monanthotaxis* have been collected on fallen trees or rarely from flowering specimens at lower heights, such as next to rivers, at roadsides or at Inselbergs. Furthermore, it is quite a species-rich genus with variability in leaf shape and sizes within species and even within single plants. All identification keys for the species were confined to local floras (Le Thomas 1969, Verdcourt 1971a) and the species currently in *Monanthotaxis* were scattered over multiple genera making it difficult to identify the species with those keys. At the start of my PhD almost half of all specimens of *Monanthotaxis* in herbaria where not identified to species level, and many of the identified specimens where wrongly identified. An objective of my thesis was to revise the genus *Monanthotaxis* and resolve the taxonomic problems and to infer its phylogeny.



Fig. 2. *Monanthotaxis diclina*.

1.3 Phylogenetics

A great help in resolving phylogenies have been the surge of next-generation sequencing (NGS) methods. During the last thirty years the nucleotide sequences of DNA have mostly been inferred using chain-termination methods (Sanger et al. 1977), commonly referred to as Sanger sequencing. Although several improvements of the method have been made (e.g. Smith et al. 1986) it still costs around 1500 dollar to sequence one million base pairs (Glenn 2011). With the development of NGS methods, this cost has been reduced to only 1 dollar for sequencing one million base pairs. The most commonly used NGS methods are pyrosequencing (Roche/454), sequencing by synthesis (Illumina/Solexa, Helicos, Pacific BioSciences) and sequencing by ligation (Life/APG). These methods have in common that different DNA fragments are separated in space making it possible to sequence thousands to billions of DNA fragments in the same run (Metzker 2010).

The availability and vast amount of data generated by NGS techniques generated new possibilities and challenges in phylogenetic analyses. A difference between Sanger sequencing and most NGS techniques such as Illumina HiSeq is that in Sanger sequencing the quality of each sequenced base is checked manually by verifying the chromatograms, however the vast amount of data generated with NGS techniques makes this an undoable task. Instead of chromatograms, quality scores are being used and bad reads are discarded based on a threshold (McCormack et al. 2013). There will still be some error in the data, therefore enough coverage of each nucleotide position is needed to have certainty about the identity of the nucleotide and to separate sequencing errors from real polymorphisms. High copy markers, such as organellar DNA and rDNA have a higher coverage with NGS sequencing than low copy markers. In phylogenetics the most commonly used markers are from the organelles and the rDNA. Therefore, a deep coverage of low nuclear copy markers is not essential for phylogenetics as skimming the data for high copy markers still delivers loads of information (Straub et al. 2012). As the reading fragments with most NGS techniques are short, this skimming of the data can also be used on specimens with degraded DNA, such as herbarium collections (Bakker et al. 2016, Dodsworth et al. 2018). It is possible to multiplex several organisms and sequence them in one lane. In this way multiple species can be included in a phylogenetic study for the same cost. The techniques for multiplexing are still advancing. New techniques are being implemented to generate DNA barcodes for many different specimens at the same time (Krehenwinkel et al. 2018).

A recurrent problem in phylogenetics are paralogous genes. With sanger sequencing they can be detected by the presence of multiple alleles when using targeted primer pairs. In NGS techniques only a single strand is sequenced and therefore any paralogy remains undetected until after alignment (McCormack et al. 2013). When viewing the raw NGS data it is often

obvious that too much variation occurs within the putative paralogous loci. Generally loci with different paralogous copies have a higher coverage in NGS data, therefore in some research the alignments with the highest coverage are being deleted (Emerson et al. 2010). When several species are being multiplexed in one lane for NGS sequencing the sequencing depth is insufficient to assemble most of the nuclear genome. In such cases the sequencing depth is mostly only sufficient to assemble the organellar genomes and rDNA, which are also the regions most often used in phylogenetic studies (Straub et al. 2012). In these genomic regions paralogy is assumed to be less of a problem as no genome duplications and recombination occur in the organellar genomes (Schrempf & Szöllősi 2020) and the multiple copies of rDNA are generally homogenized by concerted evolution (Buckler et al. 1997, Poczai & Hyvönen 2010).

There are many statistical methods to infer phylogenies. In this thesis three methods are used, maximum parsimony, maximum likelihood and Bayesian inference. The last two are model-based, while maximum parsimony is "non-model" based. Maximum parsimony searches for the phylogenetic tree which minimizes the total number of character changes, the minimal amount of evolution (Felsenstein 2004). The advantages of maximum parsimony analyses are that the methods are straightforward, easy to understand and it is not necessary to make any assumptions about a model of evolution. Also the principle that the best tree is the one with the least amount of evolution follows "Ockham's razor", delete all things that are unnecessary. One of the greatest possible pitfalls of parsimony analyses is the problem of long-branch attraction. This is the case when two taxa are erroneously inferred as sister taxa based on convergent evolution caused by long branches. With increasing branch length, the chance of random mutations occurring simultaneously twice in unrelated taxa becomes higher (Felsenstein 2004).

The problem of long-branch attraction mainly affects maximum parsimony methods, however it can also distort Maximum likelihood and Bayesian inferred phylogenies (Kück et al. 2012, Susko 2014). In maximum likelihood the likelihood is calculated of the observed data for any given tree and model of evolution. The tree with the highest maximum likelihood value is considered the best tree. Advantages of this method is that it is statistically consistent, the maximum likelihood tree inference will converge to the true tree with more data and maximum likelihood is robust to most model violations (Felsenstein 2004, Kück et al. 2012, Swofford et al. 2001). The most common critic of maximum likelihood inference is that it heavily relies on the chosen model of evolution. Therefore, testing the validity of the chosen model is highly important (Brooks et al. 2007, Felsenstein 2004).

In Bayesian inference the prior probability of a tree is combined with the likelihood of the data to create a posterior probability distribution of the tree. Bayesian Inference also uses likelihood functions, but the parameters of the model are allowed to vary freely over a prior distribution. A big advantage of Bayesian Inference is that the posterior probabilities of the

tree are easily interpretable. If all assumptions are not violated, the posterior probabilities indicate the probability that the tree is correct given the data (Brooks et al. 2007). Another advantage of Bayesian Inference is that it can present and compare easily multiple hypotheses, while Maximum likelihood converges to a single hypothesis and maximum Parsimony shows the shortest topology. In maximum likelihood and maximum parsimony analyses therefore normally bootstrapping or jack-knifing are applied to have indications of the robustness of the results (Felsenstein 2004). Bayesian Inference receives similar criticism as Maximum Likelihood in that it relies on the chosen model of evolution, but furthermore it relies on the chosen prior values (Brooks et al. 2007, Felsenstein 2004).

There have been many debates about the differences between maximum parsimony, maximum likelihood or Bayesian inference and which method should be preferred (Huelsenbeck & Hillis 1993, Philippe et al. 2005, Svennblad et al. 2006, Swofford et al. 2001). If the different methods lead to different results then one or multiple assumptions have been violated. All phylogenetic methods have the same assumptions about the evolutionary process, i.e. evolution occurs in a branching pattern and the evolution is independent in each lineage (Swofford et al. 1996). When using maximum likelihood it is assumed the model of evolution correctly represents the evolution and in Bayesian inference the priors should be within the range of the priors. Simulations have shown that the methods are more or less robust against small violations of these assumptions (e.g. Sullivan & Swofford 2001). If there is sufficient data with enough phylogenetic signal and the models are correct then all these methods would converge to the same results.

1.4 Rate of evolution

One of the assumption in model-based phylogenetic inference is that the same stochastic process of variation in substitution rates applies to all lineages of the tree (Felsenstein 1981). However, non-stochastic lineage heterogeneity of substitution rates often occurs between lineages, but also different substitution rates occur within different parts of the genome of a single lineage. This raises the following questions: what is the effect of heterogeneity for phylogenetic inference and what is the cause of this heterogeneity?

Heterogeneity of substitution rates has great effects on phylogenetic inferences. Zhong et al. (2011) state that lineage heterogeneity and heterotachy are one of the problems in the variability in the reconstruction of the origin of gnetophytes. In maximum parsimony the lineage heterogeneity can cause the problem of long-branch attraction, while in Maximum Likelihood and Bayesian Inference this heterogeneity can bias and distort phylogenetic trees. Several relaxed clock-models have been developed to accommodate this variation in evolutionary rates (Huelsenbeck et al. 2000, Mayrose et al. 2005, Thorne et al. 1998). In the

strict clock models only one rate of evolution is accommodated over a phylogenetic tree, while in relaxed clock-models the rates are allowed to vary over different branches in a tree . Drummond and Suchard (2010) used a Bayesian local random clocks which allows for different rates of evolution over different parts of the phylogeny. These models however have been shown to be biased when strong rate-heterogeneity is present (Dornburg et al. 2012, Wertheim et al. 2012).

In phylogenetic trees the branch lengths represent the time multiplied by the rate of evolution. As two sister lineages have the same ancestor, the absolute time towards that ancestor should be equal. Thus any variation in branch length between sister lineages should be caused by differences in the rate of evolution. This rate of evolution can be increased by several processes, such as an increase in substitution rates or shorter generation times. A higher rate of evolution with shorter generation times has been shown in mammals (Ohta 1993) and also annual plants show longer branch lengths than perennial plants (Andreasen & Baldwin 2001). Relaxation in purifying selection can also increase the rate of evolution, such as an increase in the substitution rates in the plastomes of carnivorous plants (Wicke et al. 2014), mycoheterotrophic and parasitic plants (Bromham et al. 2013, Lemaire et al. 2011). Besides these, there are many more causes that can effect substitution rates, such as different DNA repair mechanisms (Britt 1996), population size (Woolfit & Bromham 2005), genome duplication (Mower et al. 2004) and so on.

In the family Annonaceae the two most species-rich subfamilies, the Annonoideae and the Malmeoideae, show a remarkable lineage-specific rate heterogeneity in phylogenetic trees (Chatrou et al. 2014, Richardson et al. 2004). The Annonoideae have a much wider variation in branch lengths than the Malmeoideae and these two sister subfamilies account together to almost 95% of the species of Annonaceae. No obvious differences in generation time or in life traits are visible between those two subfamilies, which could explain this heterogeneity. All previous studies on this group only focused on a few chloroplast markers (Chatrou et al. 2014, Pirie & Doyle 2012, Richardson et al. 2004), leaving the question open if this heterogeneity is only confined to the chloroplast or the entire genome. Therefore there is a huge number of possibilities which could explain the rate heterogeneity in the two major subfamilies of the Annonaceae.

1.5 Thesis outline

The goal of this thesis was to better understand the evolution of Annonaceae with a special focus on *Monanthotaxis*. This thesis consists of two parts; the first part focuses on the evolution of Annonaceae and consists of chapter two. The second part consists of chapter three to five and focuses on the systematics and the evolution of *Monanthotaxis*.

In the first part the differences in the molecular rate of evolution between the two major subfamilies of Annonaceae are studied. There are many different causes and correlates with

differences in the rate of evolution. The number of hypotheses explaining the different molecular rates of evolution greatly reduces by evaluating in which parts of the genomes of Annonaceae these different rates exist. For this the chloroplast and nuclear ribosomal sequences were assembled from Next-Gen sequencing data and subsequently the relative molecular rates of evolution were compared between the different subfamilies.

In the second part the taxonomy, phylogeny and evolution of *Monanthotaxis* are being studied. The generic delimitation of *Monanthotaxis* and related genera was obscure and taxonomically problematic before this thesis. To resolve this, in chapter 3 a phylogeny consisting of seven DNA regions and 101 taxa was created. Using strict monophyly in combination with morphological characters the generic delimitation of *Monanthotaxis* and related genera is resolved.

In chapter four the continental species of *Monanthotaxis* are revised following the generic delimitation of chapter 3. It contains a detailed description of the biology of *Monanthotaxis*, a dichotomous and synoptic key to the species and detailed descriptions of each species. Further preliminary assessments of the IUCN red list status are given for each species.

Finally, with the taxonomic revision as a basis, the floral evolution of *Monanthotaxis* is being studied in chapter 5 using a phylogeny and character mapping of six morphological traits. Support for a general pattern towards a reduction in flowers in *Monanthotaxis* has been shown and several hypotheses are being postulated which could explain this evolutionary trend.

Chapter 2

Correlated evolutionary rates across genomic compartments in Annonaceae

This chapter is based on:

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Abstract

The molecular clock hypothesis is an important concept in biology. Deviations from a constant rate of nucleotide substitution have been found widely among lineages, genomes, genes and individual sites. Phylogenetic research can accommodate for these differences in applying specific models of evolution. Lineage-specific rate heterogeneity however can generate bi- or multimodal distributions of substitution rates across the branches of a tree and this may mislead phylogenetic inferences with currently available models. The plant family Annonaceae is an excellent case to study lineage-specific rate heterogeneity. The two major sister subfamilies, Annonoideae and Malmeoideae, have shown great discrepancies in branch lengths. We used high-throughput sequencing data of 72 genes, 99 spacers and 16 introns from 24 chloroplast genomes and nuclear ribosomal DNA of 23 species to study the molecular rate of evolution in Annonaceae. In all analyses, longer branch lengths and/or higher substitution rates were found for the Annonoideae compared to the Malmeoideae. The Annonaceae had wide variability in chloroplast length, ranging from minimal 175,684 bp to 201,723 for Annonoideae and minimal 152,357 to 170,985 bp in Malmeoideae, mostly reflecting variation in inverted-repeat length. The Annonoideae showed a higher GC-content in the conserved parts of the chloroplast genome and higher omega (d_N/d_S)-ratios than the Malmeoideae, which could indicate less stringent purifying selection, a pattern that has been found in groups with small population sizes. This study generates new insights into the processes causing lineage-specific rate heterogeneity, which could lead to improved phylogenetic methods.

2.1 Introduction

Since Zuckerkandl & Pauling (1965) postulated the molecular clock, the concept of a constant rate of molecular evolution has been an important tool in biology. Soon after the molecular clock hypothesis was proposed, it was linked to Darwinian evolution by demonstrating that a constant substitution rate over evolutionary time is predicted by the neutral theory (Kimura & Ohta 1971). Nonetheless, over the years evidence has accumulated demonstrating non-clock-like heterogeneity of substation rates (Britten 1986, Lemey et al. 2009). These deviations from a constant rate of substitution can be explained by evolutionary mechanisms, notably lineage-specific changes in mutation rate, the effect of population sizes, and the effects of natural selection (Bromham & Penny 2003, Ho 2014). The literature indicating that substitution rates vary among evolutionary lineages (Britten 1986, Li et al. 1996), genomes (Drouin et al. 2008, Wolfe et al. 1987), genes (Dickerson 1971, Zhu et al. 2014), and individual sites (e.g. codon positions, Bofkin & Goldman 2007, Simmons et al. 2006) is ever increasing.

There is general awareness that substitution rates differ among genomes, genes and individual sites (e.g. Drummond & Suchard 2010). These differences can be accommodated, e.g. by applying models of molecular evolution that incorporate higher substitution rates of third codon positions (Shapiro et al. 2006). Moreover, substitution rate differences among genes and genomes may be utilized in a sampling strategy to optimize the phylogenetic informativeness of the data for a given evolutionary time scale (López-Giráldez & Townsend 2011). However, lineage-specific differences in substitution rates are rarely addressed. Lineage-specific rate heterogeneity will lead to a continuous distribution of rates with two or more modes, and the number of well-designed analyses of empirical data and simulation studies indicating the phenomenon is increasing (Dornburg et al. 2012, Drummond & Suchard 2010, Wertheim et al. 2012). However, commonly used relaxed-clock models instead assume a unimodal distribution of substitution rates across all branches in a tree (Mayrose et al. 2005), an assumption which in such cases is clearly violated. The Bayesian Random Local Clock (Drummond & Suchard 2010) was therefore designed to accommodate lineage-specific rate heterogeneity, however it was shown that this model does not fit the data well when strong rate-heterogeneity is present (e.g. Dornburg et al. 2012, Wertheim et al. 2012).

A better understanding of patterns of rate heterogeneity, and of the underlying mechanisms, is important for the advance of phylogenetic methods, as this will allow the integration of more accurate models. The plant family Annonaceae provides a good example of a clade that is appropriate for exploring lineage-specific rate heterogeneity. The Annonaceae consist of c. 2,350 species of woody plants occurring throughout the tropics (Rainer & Chatrou 2006). Four subfamilies are currently recognized in the Annonaceae, two of which (Anaxagoroideae, Ambavioideae) are species-poor and form the first two basal branches of the family. The remaining two subfamilies, Annonoideae (1,500 spp.) and Malmeoideae (800 spp.), are sister clades that together include more than 95% of the species diversity of the family (Chatrou et

al. 2012). Already in the first phylogenetic analyses of the family it was noted that these two major clades differ markedly in branch lengths (Richardson et al. 2004). These analyses, and all subsequent family-wide analyses, have been based on a number of chloroplast markers. A better understanding of the distribution of substitution rates across lineages of Annonaceae could improve the inference of phylogenetic relationships, of branch lengths and clade ages. Additionally, it could provide insight into factors associated with substitution rate differences that may be of wider relevance to angiosperms in general.

One of these factors is generation time, which has been shown to influence substitution rates in mammals (Li et al. 1987, Ohta 1993). In plants, clear rate differences, related to differences in generation time, have been found between annuals and perennials (Andreasen & Baldwin 2001) and between woody plants and herbs (Kay et al. 2006, Smith & Donoghue 2008, Yang et al. 2015). In contrast, a clear correlation between substitution rates and generation time in plants was not demonstrated in other studies (e.g. Jobson & Albert 2002, Whittle & Johnston 2003), suggesting that other factors than mere generation time could explain the relationship between functional traits and molecular rate of evolution, such as a decrease in the rate of mitotic cell divisions (Lanfear et al. 2013).

So far, the available data on substitution rates in Annonaceae are limited. Studies which shown and/or further analysed the molecular rate heterogeneity in Annonaceae only used a small number of chloroplast markers (e.g. Chatrou et al. 2014, Pirie & Doyle 2012, Richardson et al. 2004), leaving open the question as to whether lineage-specific rate differences run in parallel across the three plant genomes. In this study, we use next-generation sequence data to investigate the molecular rate of evolution in Annonaceae. We test whether the rate heterogeneity between the subfamilies Malmeoideae and Annonoideae is confined to the chloroplast genes or if it occurs across the chloroplast genome and nuclear ribosomal DNA to reduce the number of possible hypotheses explaining the discrepancy in rates in Annonaceae. Further, we explore correlations between the rate heterogeneity and several sequence metrics, viz. chloroplast genome size and GC-content. Finally, we discuss the remaining hypothesis and possibilities for follow-up studies to disentangle the molecular rate of evolution in Annonaceae or more generally, in any other plant family.

2.2 Materials and methods

2.2.1 Plant material and sequencing

Twenty-four species were selected initially for skimming the high copy fraction of the genome: ten from the Annonaceae subfamily Annonoideae, ten from the sister subfamily Malmeoideae, and four from outgroups, which included representatives of the two remaining Annonaceae subfamilies (Anaxagoroideae and Ambavioideae) and two Magnoliaceae. The

data of *Liriodendron tulipifera* were extracted from GenBank (Supplementary Table S1). During the analyses the chloroplast genome of *Annona cherimola* (subfam. Annonoideae) became available (Blazier et al. 2016) which was subsequently added to the chloroplast analyses.

One cm^2 or 20 mg of leaf tissue dried in silica gel, from herbarium material or fresh material from the Botanical Garden of Utrecht University, the Netherlands, was used for DNA extraction. DNA was extracted using a modified CTAB protocol and the Wizard DNA Cleanup System from Promega as described in Staats et al. (2011). Four of the samples were submitted to the Centre for Geogenetics in Copenhagen, Denmark for library preparation as described in Bakker et al. (2016) and were subsequently sequenced on four lanes on an Illumina HiSeq 2000 platform using paired end chemistry at the Danish National High-throughput Sequencing Centre. Library preparation and sequencing, according to the same protocols, was done for four more samples at Macrogen, Seoul, Korea. The library preparation of the other samples was done with minor modifications to the protocol in Bakker et al. (2016). Nine of these samples were sent to Beijing Genomics Institute, Hong Kong, China and paired-end sequenced on an Illumina HiSeq 2500 platform and paired-end libraries for the remaining six samples were prepared and sequenced in one flow cell of an Illumina NextSeq sequencer by the Maastricht University group. Sequence data are deposited at NCBI SRA under BioProject accession numbers PRJNA377337 and PRJNA388015. Sequence platform information and statistics are given in Supplementary Table S2.

2.2.2 Assembly

Reads were assembled using the Iterative Organelle Genome Assembly (IOGA) pipeline (Bakker et al. 2016) for all newly sequenced specimens. Plastid genome sequences of *Liriodendron tulipifera* and *Annona cherimola* were extracted from GenBank. The IOGA-pipeline is described in detail in Bakker et al. (2016). In brief, first the low-quality, adapter and Illumina-specific sequences were trimmed from the data with Trimmomatic (Bolger et al. 2014), then the read pool was aligned to a reference genome with Bowtie2 (Langmead & Salzberg 2012) to filter out the desired reads. The chloroplast genome of *Liriodendron tulipifera* (Magnoliaceae, Cai et al. 2006) was used as reference genome to filter out the chloroplast data. For a few specimens the same set of reference genomes as used in Bakker et al. (2016) were applied, but this did not significantly improve the assemblies. For the assembly of nuclear ribosomal DNA a set of reference sequences was used from different species of Annonaceae and Magnoliaceae (Supplementary Table S3). Next, the filtered reads were assembled using SOAPdenovo2 (Luo et al. 2012) with k-mer values ranging from 37 to 97. Subsequently, the best assembly was chosen using the N50 criterion and that assembly was used to find target-specific reads from the pool using the reference genomes and this new set of reads was again assembled with SOAPdenovo2. These steps were repeated until no

extra reads could be filtered from the pool. This final set of reads was assembled with SPAdes3.0 (Bankevich et al. 2012) with eight different k-mer settings. Finally, the likelihood of the assemblies with SOAPdenovo2 and SPAdes3.0 were calculated with ALE (Clark et al. 2013). We attempted to assemble parts of the mitochondrial genomes using several reference sequences of mitochondrial genes (e.g. *matR* and *atp1*), but failed to produce good sequences for the majority of species. Therefore, we have excluded the mitochondrial genome from further analyses.

From the IOGA output the assembly with the highest likelihood score was selected as the best assembly. However, in three cases the assembly with the second-highest likelihood score was selected, as the highest score was given to a significantly shorter total assembly with a lower N50 value. Contigs and scaffolds shorter than 500bp were deleted from each assembly or were discarded when they did not blast against chloroplast or nuclear ribosomal DNA. Total IR length was inferred based on the double coverage of reads compared to the single copy regions of the chloroplast as both IRs were assembled as one contig. Furthermore, the boundaries of the IRs were often assembled multiple times in two or three different contigs, making it possible to infer their relative position. Most remaining gaps between contigs were parts of microsatellites or short repeats. The IOGA-reads were remapped onto the assemblies to check for polymorphisms. Nucleotide positions were marked as polymorphisms when at least 20% of the mapped reads contained a different nucleotide than the consensus assembly. The chloroplast assemblies were annotated in DOGMA (Wyman et al. 2004). The 18S and 28S regions of the nuclear ribosomal DNA assemblies were annotated using the RNAmmer 1.2 Server (Lagesen et al. 2007) and the ITS and 5.8S regions with ITSx version 1.0.11 (Bengtsson-Palme et al. 2013). All annotations were manually verified and compared to other annotated sequences in GenBank.

2.2.3 Alignment and data partitioning

One of the IR copies in the two chloroplast sequences obtained from GenBank were deleted to match our assemblies. Subsequently, the assemblies were aligned with progressiveMAUVE (Darling et al. 2010). Furthermore, the annotations were double-checked with the alignment. The alignment dataset of the chloroplast genomes was partitioned into each individual gene, intron and spacer. The ten spacers which spanned the boundaries of the contiguous blocks of the MAUVE-alignment were excluded from further analyses. Each gene alignment was verified manually and poorly aligned or highly divergent genes were removed from further analyses. Poorly aligned or highly divergent regions in the introns and spacers, in both the chloroplast and nuclear data sets, were removed using the program GBlocks (Castresana 2000, Talavera & Castresana 2007) with a minimum of 20 sequences for conserved positions and flank positions, a minimum block length of 8, and the allowed Gap positions parameter set to

'none'. As most of the ITS and ETS regions of the nuclear ribosomal DNA alignment were removed using these specified settings of GBlocks, the original nuclear Ribosomal DNA alignment of MAUVE was realigned with the L-INS-i option in MAFFT v7.304 (Katoh & Standley 2013) and manually edited without using GBlocks.

2.2.4 Tree inference

All phylogenetic analyses were run on six datasets; 1. all chloroplast data, 2. chloroplast protein-coding genes, 3. chloroplast introns, 4. chloroplast spacers, 5. Non-coding chloroplast regions (introns and spacers together), 6. the nuclear ribosomal alignment. Trees were inferred with maximum parsimony in the program PAUP version 4.0a150 (Swofford 2002), Bayesian analyses with MrBayes v3.2.5 (Ronquist & Huelsenbeck 2003) and Maximum likelihood analyses with RaxML v8 (Stamatakis 2014). In all analyses, the Magnoliaceae served as outgroup taxa.

For the maximum parsimony analyses, all characters of the different datasets were treated as unordered and of equal weight (Fitch parsimony) with gaps excluded from the analyses. A heuristic search with tree bisection-reconnection branch swapping and 1,000 random addition sequence replicates saving 50 trees per replicate was performed. Clade support was assessed with non-parametric bootstrap analyses with 1,000 replicates and 100 random addition sequence replicates saving 50 trees per replicate.

After initial Bayesian analyses in MrBayes, it appeared that the parameters TL, LnPr and m did not converge without partitioning the data. Therefore and to better fit the different patterns of molecular evolution at different sites, all datasets were broken up into their different loci and the best partitioning scheme was assessed with Partitionfinder v1.1.1 (Lanfear et al. 2012). The best partitioning scheme for the intron and nuclear ribosomal datasets was inferred using the greedy algorithm allowing all nucleotide models available in MrBayes and an additional run allowing only the two models available in RAxML. For the other datasets, containing a much higher number of loci the relaxed hierarchical clustering algorithm was used, which only allows the GTR+G+I and GTR+G substitution models. Finally, all different partition schemes were compared using the Bayesian Information Criterion and the best fitting were used in the subsequent analyses.

The Bayesian analyses were performed with the best partitioning schemes from PartitionFinder (Supplementary Table S4). For most partitions this was the general time-reversible nucleotide substitution model (nst = 6 in MrBayes) with gamma distributed rates and a proportion of invariable sites. Each analysis was run for 100 million generations with two parallel runs and each four independent Metropolis-Coupled Markov Chain Monte Carlo chains and the default temperature parameter on the CIPRES Gateway server (Miller et al. 2010). The first 25% of the trees were discarded as burn-in. The standard deviation of split

frequencies was checked to be close to zero and the potential scale reduction factor (PSRF) and the convergence of posterior probabilities of splits were verified to be close to 1.0 with the sump command in MrBayes. The effective sample size (ESS) for each parameter was verified to be higher than 200 with the program Tracer v1.6 (Drummond & Rambaut 2007).

The maximum likelihood analyses were performed on the CIPRES Gateway server with the GTR-gamma model of substitutions and the partitions as defined with PartitionFinder (Supplementary Table S4). Subsequently a rapid bootstrap analysis was performed on the best-scoring tree with 1,000 bootstrap iterations.

2.2.5 Substitution rate analyses

The branching pattern of the single shortest tree resulting from the maximum parsimony analysis was used as input in the program baseml, part of the Paml 4.8 package (Yang 2007), to calculate the relative substitution rates of the noncoding regions and the nuclear ribosomal DNA. Each analysis was run with the GTR + G model assuming no clock leaving the rates free to vary from branch to branch. This model was run against a null model with a global clock, i.e. the same rate for all branches. Likelihood ratio tests were performed on the likelihood values of the model with no clock compared to the global clock model to test for differences in branch rates.

The program codeml, part of the PAML4.8 package (Yang 2007), was used to calculate nonsynonymous and synonymous substitution rates for coding regions. The genes were trimmed at the 5'or 3' end when at least one of the species had different start and/or stopcodon positions. All models were run with the F3x4 codon frequency model and no molecular clock assumed. First a branch model with three branch types was set to allow different omega (ω) ratios for the Annonoideae and the Malmeoideae and a background rate for the remaining species. Next, the free-ratios model was run which assumes independent ω ratios for each branch. Each of the analyses was run 15 times with various difference approximation of derivates values to check for convergence. Subsequent statistics were calculated on each of these runs to show the robustness of the results. The resulting likelihoods of the branch models were compared to a null model in which all branches had a fixed ω using likelihood ratio tests, while the likelihood of the free-ratios models were tested against the branch models.

The branch site model of positive selection (Yang et al. 2005) was applied on each gene to test if positive selection had taken place for the branch leading to the Annonoideae. These tests were compared with the null model which has ω fixed. The likelihood ratio test was computed of the log-likelihood values of the two models and the corresponding p-values were Bonferroni corrected to adjust for multiple comparisons.

2.2.6 Statistical analyses

GC-content of each dataset was calculated in R with the package APE v3.5 (Paradis et al. 2004). Additionally, the GC-contents were calculated separately for the ETS, ITS and rRNA-regions of the nuclear ribosomal DNA and for the entire chloroplast genome and for all spacers including the highly divergent regions. The GC-contents were compared between the Annonoideae and Malmeoideae for significant differences using a two-sided Wilcoxon rank sum test.

The branch lengths of the Annonoideae and the Malmeoideae were extracted for each dataset in R using the packages APE v3.5 (Paradis et al. 2004) and Geiger v2.0.6 (Harmon et al. 2008) for the following trees: 1) (one of) the most parsimonious tree from PAUP, 2) 50% Bayesian majority rule consensus tree and Bayesian maximum clade credibility tree, 3) the best scoring maximum likelihood tree from RAxML, 4) the baseml output-tree, and the 5) d_N, 6) d_S and 7) ω-ratios labeled tree from the codeml-analyses. We are aware that branch lengths of parsimonious trees may not be accurate as that method does not allow for multiple substitutions on the same site (Lanfear et al. 2010). Even so, we include the parsimonious trees in the analyses to see whether parsimony branch lengths generate different patterns. One-sided Wilcoxon rank sum tests were performed on these sets of branch lengths to test if the values of Annonoideae were higher than for Malmeoideae.

As the plastome DNA sequences of *Liriodendron tulipifera* and *Annona cherimola* were obtained from GenBank, these species were missing from the nuclear ribosomal datasets. In addition, as the assembly of the chloroplast sequence of the outgroup *Tetrameranthus duckei* was unreliable due to low coverage and therefore excluded, the datasets of the chloroplast DNA and nuclear ribosomal DNA slightly differed in number of terminals. Furthermore, because by adding *Annona cherimola*, the Annonoideae were represented with 11 specimens instead of 10, which could introduce a slight node-density effect (Hugall & Lee 2007). To test if this affected the results, these three species were deleted from the datasets and all tree inferences and subsequent analyses were repeated for all datasets.

2.3 Results

2.3.1 Assemblies

The final dataset consisted of 24 chloroplast genomes and 23 nuclear ribosomal DNA sequences with both subsets containing at least 10 species of Annonoideae and Malmeoideae. The chloroplast assembly length varied from 114,827 to 143,355 (excluding the second copy of the inverted-repeat) and consisted of 1 to 36 contigs, with an average median N50 of 49,480. The assemblies had a coverage ranging from 22 in *Stenanona costaricensis* to 990 in *Pseudoxandra bahiensis*. Estimated inverted repeat (IR) length was c. 26,000 bp for the

Malmeoideae and outgroup species, but c. 38,000 bp for the genus *Oxandra* and ranged from 39,000 to 64,000 for the species of Annonoideae (Table 1). The chloroplast DNA assembly of *Tetrameranthus duckei* was removed from all further analyses as only 20,000 bp were assembled with an average coverage of five.

Nuclear ribosomal DNA assembly length varied from 4,810 bp in *Tetrameranthus duckei* to 12,215 bp in *Mosannona discolor* and consisted of one to five contigs. Almost all of the variation in length was attributable to the non-transcribed spacers. Coverage of the nuclear ribosomal DNA assemblies was as high as 1,769 in *Monanthotaxis buchananii*, and at least 100 for all other specimens with the exception of *Stenanona costaricensis*, which had an average coverage of 46.

The number of polymorphisms ranged from 0.2 to 7 per 1,000 bp in the nuclear ribosomal DNA assemblies and from 0 to 1.1 per 1,000 bp in the chloroplast assemblies except for *Duguetia hadrantha* with an average of two polymorphisms per 1,000 bp, concentrated in regions with a coverage lower than 20. Although these polymorphisms may add some noise to the analyses, we interpret the effect to be negligible due to concerted evolution (Feliner & Rosselló 2007, Hillis et al. 1991). Furthermore, most of the polymorphisms were found either in regions with low coverage or near contig breaks, and therefore can be expected to be false positives. The polymorphisms found in the chloroplast assemblies are probably caused by plastid DNA transferred to the mitochondrial and nuclear genome (Scarcelli et al. 2016). Given the lower coverage of these polymorphisms we assume to have retrieved the correct chloroplast assembly and used these assemblies in further analyses.

The concatenated chloroplast alignment contained 8,939 parsimony informative characters (PICs). The chloroplast gene-coding dataset 5,181 PICs, the spacers 2,573 PICs, and the introns 1,185 PICs. The nuclear ribosomal DNA alignment contained 683 PICs. Gene order was highly conserved with only one inversion of six genes (*ycf4-atpE*) in the large single copy region in all Annonaceae compared to other Magnoliids (Cai et al. 2006). Of the 79 protein coding genes, 72 were included in the final gene-coding dataset consisting of 52,635. Of the seven excluded genes, *psbM* and *rpl32* were not assembled for all species, while the genes *accD*, *rpoA*, *rps18*, *ycf1* and *ycf2* were so highly divergent that only small parts of the genes could be aligned. Most of these genes could only be aligned between closely related species or between both the Malmeoideae and the Magnoliaceae, not with the more divergent species of Annonoideae. The spacer alignment consisted of 99 (partial) spacers and contained 16,712 characters. The intron alignment consisted of 16 introns with a total length of 11,269 characters. The nuclear ribosomal DNA dataset contained 6,436 characters. The 5.8S ribosomal region was not assembled for the outgroups *Anaxagorea phaeocarpa* and *Tetrameranthus duckei* and not for the ingroup species *Xylopia peruviana.* Parts of the ITS1 and/or ITS2 regions were missing for 11 species.

Table 1. Assembly statistics for the chloroplast and nuclear ribosomal DNA

	Chloroplast						nrDNA		
Species	Cov	AL	Con	N50	CHL	IR	Cov	AL	Con
Liriodendron tulipifera (O)	X	X	X	X	159,886	26,385[a]	X	X	X
Magnolia kobus (O)	336	133,627	5	47,368	160,258	26,611	673	8,315	2
Anaxagorea phaeocarpa (O)	275	114,827	36	9,840	142,363	27,536	236	6,399	3
Tetrameranthus duckei (O)	X	X	X	X	X	X	102	4,810	2
Annona cherimola (A)	X	X	X	X	201,723	64,493[a]	X	X	X
Annona muricata (A)	593	137,441	3	69,457	196,848	58,903	814	6,210	3
Annona sp. (A)	201	133,707	14	14,344	180,234	46,527	1,401	8,203	1
Duguetia hadrantha (A)	50	133,510	11	45,924	175,684	42,174	382	8,662	1
Mkilua fragrans (A)	243	143,355	2	139,617	182,355	39,000[b]	112	9,610	3
Monanthotaxis buchananii (A)	177	126,135	35	10,655	174,443	48,308	935	5,870	2
Monanthotaxis cf.laurentii (A)	354	131,240	22	10,359	179,659	48,508	572	7,591	1
Monodora myristica (A)	83	137,220	2	123,339	197,741	60,521	421	11,710	1
Porcellia steinbachii (A)	618	140,059	8	27,868	183,504	43,445[b]	678	11,060	1
Uvaria afzelii (A)	119	138,504	4	50,086	184,789	46,798	109	5,682	5
Xylopia peruviana (A)	405	139,795	3	113,421	183,304	43,509	374	5,064	5
Desmopsis bibracteata (M)	55	127,232	22	16,456	152,788	25,556	394	6,367	2
Klarobelia inundata (M)	152	132,435	5	38,708	158,478	26,043	1,769	8,194	1
Mosannona costaricensis (M)	288	129,252	24	21,901	152,357	23,105	1,441	10,509	2
Mosannona discolor (M)	489	133,247	6	39,794	159,349	26,102	796	12,215	2
Onychopetalum periquino (M)	265	133,962	13	11,929	160,018	26,056	1,040	7,225	1
Oxandra asbeckii (M)	414	133,019	8	34,726	170,985	37,966	402	10,118	1
Oxandra polyantha (M)	225	132,846	4	30,570	170,890	38,044	566	9,211	1
Pseudoxandra bahiensis (M)	990	134,073	1	134,073	160,435	26,362	912	7,635	3
Sapranthus microcarpus (M)	106	132,676	2	83,450	158,578	25,092	244	5,921	1
Stenanona costaricensis (M)	22	129,944	17	14,678	156,592	26,648	46	8,682	1

NOTE.—Cov, coverage. AL, assembly length including 1 IR only. Con, number of contigs. N50 length in bp. CHL, minimum chloroplast length. IR, inverted repeat length. O, outgroup. A, Annonoideae. M, Malmeoideae.

[a]The exact chloroplast and inverted repeat lengths of the Genbank accessions of *Liriodendron tulipifera* and *Annona cherimola* have been included for completeness.

[b]Inverted repeat length of these species only based on double coverage, boundaries not found in contigs.

2.3.2 Phylogenetic inference

Tree inference analyses of all data sets generally retrieved the Annonoideae and Malmeoideae as well-supported clades. Only in the analysis of the nuclear ribosomal data, the Annonoideae

were resolved but not supported in the maximum parsimony and only weakly with the maximum likelihood analyses. The maximum parsimony searches produced a single best tree for all datasets. The tree based on the concatenated chloroplast data was congruent with the current best estimate of phylogenetic relationships in Annonaceae (Chaowasku et al. 2014, Chatrou et al. 2012, Guo et al. 2017), with high support for almost all nodes (Figure 1a). The smaller separate gene, spacer and intron chloroplast datasets produced the same phylogeny. Sometimes the sister group relationships between *Duguetia* and *Xylopia* and *Onychopetalum* and *Pseudoxandra* were not strongly supported. The phylogenetic analyses of the nuclear ribosomal datasets generated more weakly supported relationships, especially within the Malmeoideae (Figure 1b).

2.3.3 Substitution rates

The likelihood ratio-tests from the baseml analyses were all highly significant ($P < 0.001$) indicating that the no-clock model had a better fit to the data than the clock model. The likelihood ratio tests of the gene dataset in codeml were also highly significant indicating that the branch model with different ω-rates for Annonoideae, Malmeoideae and the remaining taxa had a better fit to the data than a model in which ω has a fixed rate. The free-ratios model, allowing ω to vary across all branches, had yet a better fit.

The branch-site model test indicated that the genes *rbcL*, *petA* and *rps7* possibly are under positive selection. Using less stringent correction methods for multiple comparisons, such as the Benjamini-Hochberg procedure (Benjamini & Hochberg 1995), positive selection is inferred for the genes *atpB* and *rpl16* as well (uncorrected P-values of 0.00075 and 0.0079 resp.). The genes *rbcL*, *petA* and *atpB* are photosynthesis-related, while *rps7* and *rpl16* are part of the 40S small and 50S large ribosomal subunit, respectively (Wicke et al. 2011).

The GC-contents of the entire plastome assemblies ranged from 38.16% to 39.51% and were not significantly different between the Annonoideae and Malmeoideae. In contrast, for the subsets of introns, genes and conserved parts of the spacers, the GC-content was significantly higher in the Annonoideae. The nuclear ribosomal DNA had much higher GC-contents than the plastomes, with an overall GC-content of c. 56% but being much higher in the ITS-region and as high as 80% in the ITS2 region of *Monodora myristica*. There were no significant differences in GC-content between Annonoideae and Malmeoideae in the 28S, 5.8S and ITS2 regions, while the GC-content in the Annonoideae was significantly higher in 18S rRNA and significantly lower in ITS1 and ETS compared to the Malmeoideae (Table 2).

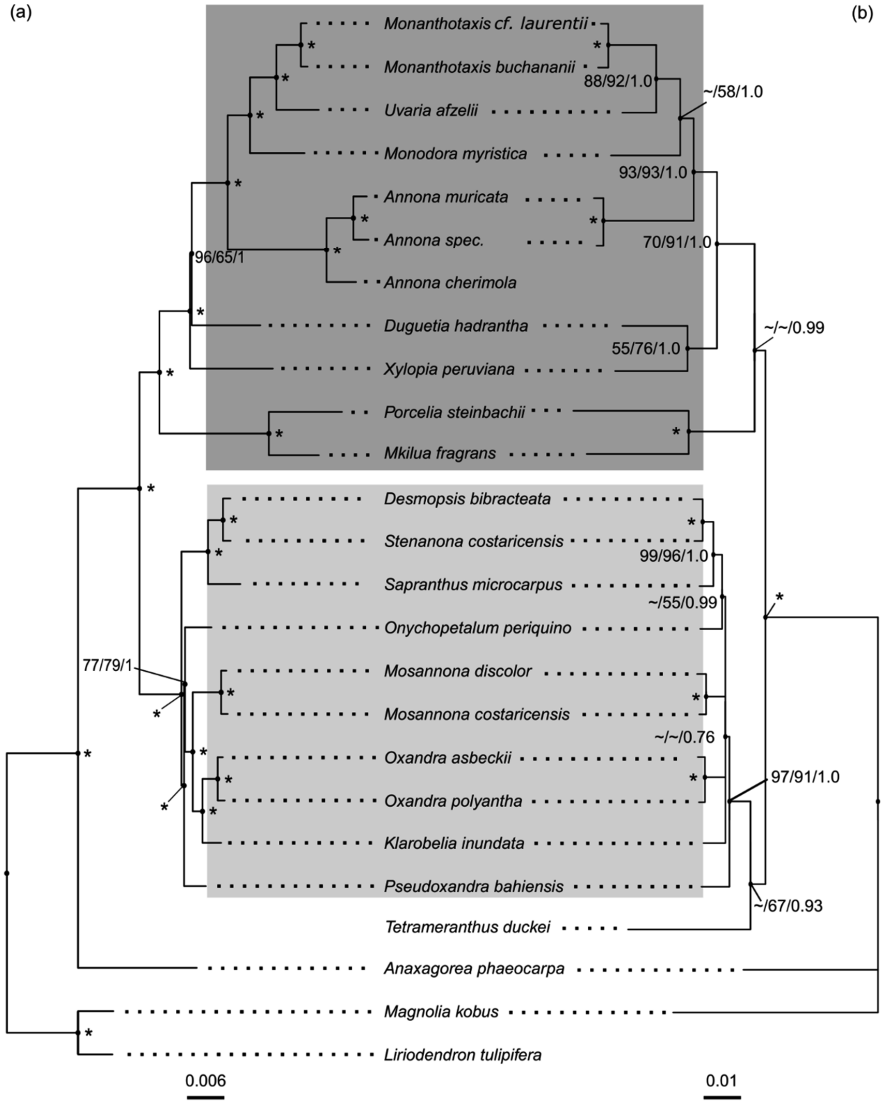

Fig. 1 Phylograms of the 50% majority rule Bayesian consensus trees of the chloroplast genome (a) and nuclear ribosomal DNA (b). Node values indicate maximum parsimony bootstrap support, maximum likelihood bootstrap support, and Bayesian posterior probabilities. Asterisks denote support values of 100/100/1.0, tildes denote bootstrap support values <50. Scale bar denotes branch lengths. The dark grey and light grey rectangles indicate the subfamilies Annonoideae and Malmeoideae, respectively.

Table 2. Summary of average GC-contents for Annonoideae and Malmeoideae.

	Average % GC-content		Difference
Genomic region	Annonoideae	Malmeoideae	P-value[a]
Chloroplasts	38.69	38.43	0.46
All spacers[b]	34.91	34.68	0.52
Conserved spacers[c]	36.59	35.86	0
Genes	40.43	40.06	0
Introns	40.54	40.01	0
Nucl Rib DNA	56.52	56.40	0.63
28S	59.38	59.37	0.96
18S	50.98	50.67	0
5.8S	59.47	59.29	0.19
ITS1	70.18	74.73	0.02
ITS2	75.75	74.70	0.36
ETS	65.47	68.23	0.01

[a]P-values of Wilcoxon rank sum test for differences between Annonoideae and Malmeoideae.

[b]All spacers including unalignable regions which were removed for the phylogenetic analyses.

[c]Conserved parts of spacers used for phylogenetic inference and analyses.

All phylogenetic analyses generated trees with significantly longer branch lengths in the Annonoideae than in the Malmeoideae (Table 3). This pattern is paralleled by significantly higher substitution rates in Annonoideae for all data partitions. Also the nonsynonymous (d_N) and synonymous (d_S)-substitutions from the ML-analyses in PAML and the substitution rates of the non-coding regions from the baseml analyses had significantly higher values in the Annonoideae compared to the Malmeoideae. Additionally, the ω-values were significantly higher for the Annonoideae compared to the Malmeoideae (Table 3). All additional analyses in which the species *Tetrameranthus duckei*, *Liriodendron tulipifera* and *Annona cherimola* were removed from the datasets gave the same highly significant results with longer branch lengths for the Annonoideae compared to the Malmeoideae, indicating that removal/addition of these taxa does not influence the results.

Table 3. P-values of Wilcoxon rank sum test for differences in branch-lengths / substitution rates between Annonoideae and Malmeoideae for each dataset.

Dataset	MP	BA	ML	baseml	d_N	d_S	ω
Chloroplast, complete	0	0.002	0.002	X	X	X	X
Chloroplast, genes	0	0.001	0.002	X	0	0.003	0.009
Chloroplast, introns	0.003	0.007	0.002	0.002	X	X	X
Chloroplast, spacers	0	0.001	0.002	0.001	X	X	X
Chloroplast, spacers + introns	0.001	0.002	0	0.001	X	X	X
Nuclear ribosomal	0.011	0	0.003	0.003	X	X	X

NOTE.— MP = Maximum parsimony analyses, BA = Bayesian analyses using MrBayes, ML = maximum likelihood analyses using RAxML, basml = baseml analyses, d_N = non-synonymous substitutions, d_S = synonymous substitutions, ω = omega-ratio (d_N/d_S).

2.4 Discussion

The branch lengths were significantly longer in the Annonoideae compared to the Malmeoideae in all analyses. For the first time we were able to demonstrate that the branch length differences between the two major clades of Annonaceae correspond to differences in substitution rates. Additionally, a novel result of our study is that chloroplast and nuclear sequences show similar patterns of branch length and rate differences between these clades. This rate heterogeneity among lineages has great implications for phylogenetic inference. Different studies have made estimations of the age of different clades in the family Annonaceae and the estimated ages varied widely depending on how the methods used cope with the rate heterogeneity in Annonaceae. Under a relaxed molecular clock model the estimated crown age of Malmeoideae was 33 Ma (Couvreur et al. 2011), while the estimated crown age of Malmeoideae was 66 Ma assuming autocorrelation of rates among lineages with penalized likelihood estimation (Pirie & Doyle 2012). The absence of fossils that can reliably be assigned to nodes within the Annonaceae phylogeny makes dating analyses even more dependent on the correct modeling of substitution rate heterogeneity. Dating studies in Annonaceae have either calibrated nodes in closely related lineages and/or the Annonaceae crown node. Failure to correctly model rate heterogeneity of a target clade in the absence of internal calibrations may lead to significant bias and even the overruling of conflicting age priors (Beaulieu et al. 2015). Disentangling the effects of rate heterogeneity among lineages is vital for developing more accurate models accommodating multimodal distributions of rates. As lineage-specific rate heterogeneity can be caused by genome-wide (Smith &

Donoghue 2008) or partial genomic lineage-specific rate heterogeneity (Sloan et al. 2012), models should correctly take into account all types of rate heterogeneity.

We showed that Annonoideae had a higher rate of evolution in both nuclear ribosomal and plastid DNA than the Malmeoideae. As these genomic regions have different inheritance and DNA repair mechanisms (Birky 2001), it is most likely that the differences between the two subfamilies are governed by processes affecting the entire genome, including mitochondria. Blazier et al. (2016) noted that the chloroplast and IR length of *Annona cherimola* from the subfamily Annonoideae was much larger than other known chloroplast genomes of related plant families. Our results show that increased chloroplast genome size as well as increased IR length are mostly confined to the subfamily Annonoideae, and that the Malmeoideae have chloroplast genome sizes and IR-lengths comparable to other Magnoliids (Cai et al. 2006). IRs in general have lower substitution rates than the single copies of the chloroplast genomes (Birky & Walsh 1992, Perry & Wolfe 2002). Since Annonoideae have a longer IR, one would expect this subfamily to have lower substitution rates than the Malmeoideae, but the contrary is true. Apparently, the effect of decreased substitution rates by the expanded IRs is overshadowed by the effects causing the increased substitution rates.

Three of the five hyperdivergent chloroplast genes, which were excluded from the codeml-analyses are positioned in the expanded IR-regions of the Annonoideae. All five genes, however, contain both well-conserved and highly divergent regions. These genes align quite well between closely related species, which makes them potentially suitable for shallow-level phylogenetic studies in Annonaceae. The reasons why these genes are so variable in the Annonaceae is unclear and could involve multiple factors as the genes have different functions and locations in the chloroplast genome. A few Annonoideae species contain a frameshift in the accD gene making that gene twice as short as in Malmeoideae and Magnoliaceae and four times shorter than the accD gene in *Mkilua fragrans* with the length ranging from 828 to 3,441 bp. It is to be tested whether this gene has retained its function in all species or if it has been transferred to the nucleus, as has been found in some other plant groups such as Campanulaceae (Rousseau-Gueutin et al. 2013).

A peculiar result is that the genes, introns and the conserved parts of the spacers of the chloroplast have a higher GC-content in the Annonoideae than the Malmeoideae, while there is no significant difference in GC-content in the entire chloroplast genome and for the spacers including highly divergent regions. An opposite pattern can be found in the GC-content of the nuclear ribosomal DNA with higher GC-content in ITS1 and ETS for the Malmeoideae than the Annonoideae (Table 2). GC content was found to be correlated with substitution rates in plants (DeRose-Wilson & Gaut 2007, Zheng et al. 2007), however these and most other studies investigating GC-content only looked at site and context specific substitutions and mutations and have found for example that G:C to A:T transitions occur more frequently than other mutations (Morton et al. 2006, Ossowski et al. 2010), and that the GC-content of surrounding

sites has an effect on the mutation rate (Morton 2003, Morton & Clegg 1995). To our knowledge there are no studies which have looked at the effect of lineage-specific rate heterogeneity on GC-content, while this would be quite simple with the current available genomic data and could enhance our knowledge of patterns correlated with molecular evolution.

Of the functional traits reported to be correlated with molecular rate of evolution, most do not seem very applicable to Annonaceae. Generation time has been suggested to influence plant substitution rates. Reproductive cells are produced in the apical meristems in plants, therefore mutations accumulate incrementally during the lifetime of an individual, which could explain the absence of a correlation with generation time in some studies. In Annonaceae, all plants are woody shrubs, trees or lianas, the lianescent habit only occurring within the subfamily Annonoideae (Chatrou et al. 2012). There is hardly any data available on generation time of either the lianas or the non-climbing species of Annonaceae, but we expect no essential different generation times between these groups. Still it would be interesting to test for any plant trait correlation with substitution rates. Besides the lianescent habit, other traits also have evolved only within the Annonoideae, such as syncarpy (Couvreur et al. 2008). Another approach would be to do a genome wide scan for positive selection to find drivers for the differences in the molecular rate of evolution within the family. In our study only the chloroplast genes were scanned for positive selection. No genes responsible for DNA-replication or reproduction related genes are included in the chloroplast. The five genes found with positive selection have different functions and work on different parts of the chloroplast. For one of those genes, i.e. *rbcL*, positive selection has been found in most land plants and it appears that the gene still is fine-tuning its performance (Kapralov & Filatov 2007). It is therefore highly unlikely that *rbcL* or any of the other 4 chloroplast genes in which positive selection takes place are the main factors causing substitution rate differences between the 2 subfamilies of Annonaceae and these genes are probably under influence of gene-specific selection pressures.

Across the tree of life, species diversification rates and molecular rates of evolution are correlated (Barraclough et al. 1996, Duchene & Bromham 2013, Eo & DeWoody 2010). This correlation seems to be corroborated by our results. The Annonoideae contain ca 1500 species, almost double the number of species compared to Malmeoideae (ca 800 spp.), and indeed have a higher rate of molecular evolution. It is unclear, however, whether there is a direct mechanistic link between these phenomena, or whether there is an additional explanatory factor. For example, environmental energy (i.e. evapotranspiration, temperature and UV radiation) was both found to be correlated with species diversity as well as with the molecular rate of evolution (Davies et al. 2004). It is noteworthy that the correlation between species diversity and rate of evolution does not occur in all phylogenies and was not found in mammals (Goldie et al. 2011) and in c. 50% of phylogenies over a range of different taxa (Webster et al. 2003). The correlation between rates of molecular evolution and

diversification rates in Annonaceae remains a hypothesis to be tested. Couvreur et al. (2011) studied the diversification rate in Annonaceae and found no difference between the Annonoideae and Malmeoideae. Given the clade-specific differences in substitution rates we found here, and the use of the uncorrelated lognormal clock model by Couvreur et al. (2011), it is likely that age estimates have been flawed, and consecutively the estimates of diversification rates. In simulation studies, Beaulieu et al. (2015) demonstrated that clade-specific rate heterogeneity causes systematic bias in the inference of node ages in angiosperms. Notably, the bias was most pronounced for nodes in the vicinity of simulated rate shifts (Beaulieu et al. 2015). In the light of these simulations, our results present a cautionary tale for the inference of the ages of deeper nodes in Annonaceae, such as crown and stem nodes of Annonoideae and Malmeoideae.

Population subdivision could lead to increased species diversification, and population size has been found to correlate with substitution rates (Moran 1996, Woolfit & Bromham 2003, Woolfit & Bromham 2005). In contrast to most other factors affecting substitution rates, an increase in substitution rate caused by effective population size should be observable in the ω-ratio (d_N/d_S). According to the nearly neutral theory synonymous substitutions are supposed to be only minimally affected by selection pressure, and as in smaller populations slightly deleterious mutations more readily get fixed, the non-synonymous substitution rate increases relatively more with decreasing population size than with synonymous substitution rates (Ohta 1992). In this study an increase in ω–ratio was found for the Annonoideae compared to the Malmeoideae. With the currently available data it is however not possible to link this to population size differences between the subfamilies, as contemporaneous population sizes do not necessarily reflect any historical fluctuations in population size, which probably have occurred multiple times with the many expansions and retractions of the tropical rainforests during the last million years. Furthermore, even the contemporaneous population sizes are not well known for most Annonaceae species with still quite some species being undescribed, including *Annona spec*. from this study (H. Rainer personal communication) or species only having been collected once or twice (Hoekstra et al. 2016). There are, however, a few indications which could imply that population size has played a role in the substitution rate differences between Annonoideae and Malmeoideae. It could be that more long-range dispersal and population subdivisions have taken place in Annonoideae than Malmeoideae, as in Annonoideae most tribes and six genera have transoceanic distributions (Couvreur et al. 2012), while in Malmeoideae only the genus *Huberantha* occurs on both sides of an ocean (Chaowasku et al. 2012). An important factor driving population isolation is dispersal limitation and a correlation between species diversification and dispersal capacity has indeed been found in tropical reef fishes (Riginos et al. 2014). Most Annonaceae are dispersed by animals and birds making long-range dispersal a rare event; further studies are needed to test if any differences between dispersal mode exist between the Annonoideae and

Malmeoideae, if there is a difference in the probability of long-range dispersal events and if this is related to their species diversity.

2.5 Conclusions

Differences in the molecular evolution of Annonoideae and Malmeoideae were apparent in all analyses. Some hypotheses explaining different rates of molecular evolution, such as transcription-coupled repair efficiency or gene-specific optimization (Zhu et al. 2014) are unsupported, as the differences between Annonoideae and Malmeoideae do not seem to be restricted to chloroplast protein-coding genes, but occur also in chloroplast spacers and the nuclear ribosomal DNA. The increased ω–ratio of the Annonoideae could indicate that purifying negative selection is less stringent in Annonoideae compared to the Malmeoideae and this could be caused by reduced population sizes. This pattern could be tested in some other groups, for example by testing if ancient island lineages have higher diversification and molecular evolutionary rates than their sister continental lineages (cf. Woolfit & Bromham 2005). Alternatively, this could be measured directly with a long-term study of colonies of a DNA-fragments exchanging bacterial species or sexually reproducing fungi in a lab in which the populations are regularly subdivided and kept small. Further studying patterns of GC-content and increased IR sizes in Annonoideae could generate new insights in molecular biological processes and how to implement them in phylogenetic analyses.

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Chapter 2 Supplementary information

Table S1 Species and voucher information with herbarium acronyms in parentheses.

Family	Subfamily	Species	Voucher	Country
Magnoliaceae	X	*Liriodendron tulipifera* L.	genbank: DQ899947.1	X
Magnoliaceae	X	*Magnolia kobus* DC.	Chatrou, L.W. 278 (U)	Cultivated in Utrecht Botanic Gardens
Annonaceae	Anaxagoroideae	*Anaxagorea phaeocarpa*	Chatrou, L.W. 717 (WAG)	Costa Rica
Annonaceae	Ambavioideae	*Tetrameranthus duckei*	Stevenson, D.W. et al.	Brazil
Annonaceae	Annonoideae	*Annona cherimola* Mill.	genbank: KU563738.1	X
Annonaceae	Annonoideae	*Annona muricata* L.	1983GR00169	Cultivated in Utrecht Botanic Gardens
Annonaceae	Annonoideae	*Annona* spec nov.	Maas, P.J.M. et al. 8759	Bolivia
Annonaceae	Annonoideae	*Duguetia hadrantha* (Diels)	Pirie, M.D. et al. 125 (U)	Peru
Annonaceae	Annonoideae	*Mkilua fragrans* Verdc.	91GR01649	Cultivated in Utrecht Botanic Gardens
Annonaceae	Annonoideae	*Monanthotaxis buchananii*	Bidgood, S. 2706 (WAG)	Tanzania
Annonaceae	Annonoideae	*Monanthotaxis cf. laurentii*	Akoegninou, A. 3296	Benin
Annonaceae	Annonoideae	*Monodora myristica*	Chatrou, L.W. 477 (U)	Cultivated in Utrecht Botanic Gardens
Annonaceae	Annonoideae	*Porcelia steinbachii* (Diels)	1999GR00210	Cultivated in Utrecht Botanic Gardens
Annonaceae	Annonoideae	*Uvaria afzelii* G.Elliot	1984GR00334	Cultivated in Utrecht Botanic Gardens
Annonaceae	Annonoideae	*Xylopia peruviana* R.E.Fr.	1984GR00271	Cultivated in Utrecht Botanic Gardens
Annonaceae	Malmeoideae	*Desmopsis bibracteata*	Chatrou, L.W. 728 (WAG)	Costa Rica
Annonaceae	Malmeoideae	*Klarobelia inundata* Chatrou	Chatrou, L.W. 205 (U)	Peru
Annonaceae	Malmeoideae	*Mosannona costaricensis*	Chatrou, L.W. 90 (U)	Costa Rica
Annonaceae	Malmeoideae	*Mosannona discolor* (R.E.Fr.)	Jansen-Jacobs, M.J. et al.	Guyana
Annonaceae	Malmeoideae	*Onychopetalum periquino*	Chatrou, L.W. 425 (U)	Bolivia
Annonaceae	Malmeoideae	*Oxandra asbeckii* (Pulle)	UG-NB-55 (U)	Guyana
Annonaceae	Malmeoideae	*Oxandra polyantha* R.E.Fr.	Chatrou, L.W. 215 (U)	Peru
Annonaceae	Malmeoideae	*Pseudoxandra bahiensis*	Lopes, J.C. et al. 141 (SPF)	Brazil
Annonaceae	Malmeoideae	*Sapranthus microcarpus*	Maas, P.J.M. et al. 8457	Honduras
Annonaceae	Malmeoideae	*Stenanona costaricensis*	Chatrou, L.W. et al. 67 (U)	Costa Rica

Table S2 Sequence platform information and statistics for each species and number of assembled chloroplast and nuclear ribosomal DNA reads.

Species	Illumina sequence platform	NCBI Biosample number	Number of reads	Read length	Number of assembled chloroplast reads	Number of assembled nuclear ribosomal DNA reads
Magnolia kobus	HiSeq 2500	SAMN07135991	26,066,52	125	357,386	42,310
Anaxagorea phaeocarpa	HiSeq 2000	SAMN07135992	20,822,14	98	302,295	15,350
Tetrameranthus duckei	NextSeq	SAMN07167652	9,230,204	150	X	2,953
Annona muricata	HiSeq 2000	SAMN07135993	22,685,32	101	797,151	44,809
Annona spec nov.	HiSeq 2500	SAMN07135994	39,139,97	125	209,763	94,141
Duguetia hadrantha	NextSeq	SAMN07167653	9,274,414	150	42,304	24,623
Mkilua fragrans	HiSeq 2000	SAMN07135995	6,915,454	101	328,225	8,548
Monanthotaxis	HiSeq 2000	SAMN07135996	11,790,27	98	213,445	55,361
Monanthotaxis cf.	HiSeq 2000	SAMN07135997	19,296,75	98	468,894	45,134
Monodora myristica	NextSeq	SAMN07167654	5,470,610	99	115,293	55,189
Porcelia steinbachii	NextSeq	SAMN07167655	7,652,544	150	613,795	54,191
Uvaria afzelii	HiSeq 2000	SAMN07135998	20,636,57	101	150,684	4,212
Xylopia peruviana	HiSeq 2000	SAMN07135999	20,767,13	101	552,710	14,834
Desmopsis bibracteata	HiSeq 2000	SAMN07136000	10,627,17	98	55,517	24,819
Klarobelia inundata	HiSeq 2500	SAMN07136001	39,509,75	125	158,154	110,033
Mosannona costaricensis	HiSeq 2500	SAMN07136002	28,908,98	125	306,269	118,660
Mosannona discolor	HiSeq 2500	SAMN07136003	31,852,94	125	520,980	77,624
Onychopetalum	HiSeq 2500	SAMN07136004	32,840,51	125	282,327	56,364
Oxandra asbeckii	HiSeq 2500	SAMN07136005	25,852,34	125	436,258	30,968
Oxandra polyantha	HiSeq 2500	SAMN07136006	29,382,42	125	237,801	37,666
Pseudoxandra bahiensis	HiSeq 2500	SAMN07136007	27,474,10	125	1,073,655	55,479
Sapranthus microcarpus	NextSeq	SAMN07167656	6,391,022	99	145,052	15,404
Stenanona costaricensis	NextSeq	SAMN07167657	4,439,558	150	17,327	2,666

Table S3 Reference genomes used in IOGA for assembly of nuclear ribosomal DNA

Species	genbank NR	region	length (bp)
Annona muricata L.	AF206850.1	18S	1665
Annona muricata L.	DQ008634.2	26S	2411
Asimina triloba (L.) Dunal	AF206856.1	18S	1725
Asimina triloba (L.) Dunal	GQ139688.1	ITS1,5.8S,ITS2	813
Asimina triloba (L.) Dunal	AY095451.1	26S	3303
Liriodendron tulipifera L.	AF206954.1	18S	1714
Liriodendron tulipifera L.	DQ499099.1	ITS1,5.8S,ITS2	598
Liriodendron chinense (Hemsl.)	AY095464.1	26S	3310

Table S4 Results of partitionfinder. Number of partitions and models of molecular evolution used for the MrBayes and RAxML analyses. In RAxML for all partitions the GTR + Gamma model of molecular evolution was used.

Dataset	RAxML	MrBayes
Chloroplast, complete	10	1 (GTR + G + I)
Chloroplast, genes	2	2 (GTR + G & GTR + G + I)
Chloroplast, introns	5	2 (HKY + G & GTR + G)
Chloroplast, spacers	5	5 (2x GTR + G & 3x GTR + G + I)
Chloroplast, spacers + introns	3	3 (3x GTR + G)
Nuclear ribosomal	2	2 (GTR + G & GTR + I)

Chapter 3

Cutting up the climbers: Evidence for extensive polyphyly in *Friesodielsia* (Annonaceae) necessitates generic realignment across the tribe Uvarieae

This chapter is based on:

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Abstract

Friesodielsia and the closely related genera *Dasymaschalon*, *Desmos*, *Exellia*, *Gilbertiella* and *Monanthotaxis* (Annonaceae subfamily Annonoideae tribe Uvarieae) are taxonomically problematic, with obscure generic delimitations and poorly known phylogenetic relationships. The present study addresses the polyphyletic status of *Friesodielsia*, using two nuclear and five chloroplast DNA regions to resolve this taxonomic confusion by circumscribing strictly monophyletic genera across the tribe. Bayesian, maximum likelihood and maximum parsimony analyses using a broad taxon sampling (101 taxa) reveal that *Friesodielsia* species form five robust and morphologically distinct clades. In order to ensure strict monophyly of genera, we restrict the generic name *Friesodielsia* to an exclusively Asian clade, and the African species that were formerly included in the genus are transferred to *Afroguatteria*, *Monanthotaxis* and *Sphaerocoryne*, necessitating ten new nomenclatural combinations. *Schefferomitra*, a monospecific genus from New Guinea, is shown to be congeneric with Asian *Friesodielsia*, and the nomenclatural implications of this are discussed. Two monospecific genera, *Exellia* and *Gilbertiella*, are furthermore synonymised with *Monanthotaxis*, necessitating two additional nomenclatural changes. New generic descriptions are provided for *Dasymaschalon* (ca. 27 species), *Desmos* (ca. 22 species), *Friesodielsia* (ca. 38 species) and *Monanthotaxis* (ca. 94 species) to reflect these revised circumscriptions.

3.1 Introduction

Although the climbing growth habit has evolved several times within the early-divergent angiosperm family Annonaceae, it only occurs with a phylogenetic bias in subfam. Annonoideae. Apart from the palaeotropical genus *Artabotrys* R.Br. (tribe Xylopieae), in which the climbing habit is achieved by persistent inflorescence hooks (Posluszny & Fisher 2000), and four species in two genera in the tribe Duguetieae (Chatrou et al. 2000), the other lianescent genera in the subfamily are restricted to the tribe Uvarieae (17 genera and ca. 400 species: Chatrou et al. 2012, Rainer & Chatrou 2006), including *Desmos* Lour., *Fissistigma* Griff., *Friesodielsia* Steenis, *Monanthotaxis* Baill., and *Uvaria* L. In rain forests of the Paleotropics, Annonaceae are amongst the most dominant plant families in the liana community (Appanah et al. 1993, Ewango et al. 2015). The tribe Uvarieae offers an excellent opportunity to investigate ecologically significant shifts in growth habit, although evolutionary research on the tribe is currently impeded by the obscure phylogenetic relationships of several constituent genera (particularly *Dasymaschalon* (Hook.f. & Thomson) Dalla Torre & Harms and *Friesodielsia*) and, in some cases, probable non-monophyly.

Phylogenetic studies (Bygrave 2000, Chatrou et al. 2012, Couvreur et al. 2011, Richardson et al. 2004, Wang et al. 2012) have consistently placed *Dasymaschalon* and *Friesodielsia* in a well-supported subclade of tribe Uvarieae (referred to here as the "*Dasymaschalon* alliance"), together with two other genera, *Desmos* and *Monanthotaxis*. This close relationship is corroborated by several diagnostic characters, including the glaucous abaxial surface of the leaves (Wang et al. 2012), inaperturate pollen with echinate-microbaculate ornamentation (Bygrave 2000, Doyle & Le Thomas 2012, Le Thomas 1980, Le Thomas 1981, Walker 1971b), and monocarps (when multi-seeded) with distinct constrictions between neighbouring seeds (Wang et al. 2012). As is generally the case in Annonaceae, however, these characters show homoplasies or reversals and therefore are not found in all species in the *Dasymaschalon* alliance. The constituent species in the *Dasymaschalon* alliance are nevertheless highly diverse morphologically, with different types of pollination chambers, stamens and monocarps (Fig. 1). *Friesodielsia* currently comprises 49 species of woody climbers (Rainer & Chatrou 2006), distributed in tropical Asia and Africa. The original generic circumscription was challenged by Sprague & Hutchinson (1916), who provisionally regarded the African and Asian species as congeneric, although they recognized that the species belong to different natural groups, and more recently by Verdcourt (1971) and Van Heusden (1992), who suggested that the Asian species may not be congeneric with those from Africa. The Asian species have elongate flowers with three inner petals that are apically connivent, forming a mitriform dome over the reproductive organs (Fig. 1E), and with subglobose monocarps containing only one or rarely two seeds (Fig. 1F); the African species, in contrast, have broader flowers with loosely coherent inner petals (Fig. 1G, I), and moniliform monocarps containing up to five seeds (Fig. 1H). Palynological data also indicate that *Friesodielsia* is heterogeneous, with Asian species

possessing pollen with anechinate exine, whereas some African species (*F. gracilipes* (Benth.) Steenis and *F. discostigma* (Diels) Steenis) have coarsely verrucate pollen (Walker 1971b). Verdcourt (1971) classified *Friesodielsia* into three subgenera: subg. *Amblymitra* Verdc., with only one species, *F. obovata* (Benth.) Verdc.; subg. *Oxymitropsis* Verdc., with three species (*F. enghiana* (Diels) Verdc. ex Le Thomas, *F. hirsuta* (Benth.) Steenis, *F. velutina* (Sprague & Hutch.) Steenis); and subg. *Friesodielsia*, comprising the remaining African and Asian species. Verdcourt (1971) also noted that the two small African subgenera (subg. *Amblymitra*, subg. *Oxymitropsis*) were strikingly different from subg. *Friesodielsia* and possibly deserved recognition as distinct genera, although he refrained from formalizing this.

The hypotheses of a distant relationship between the African and Asian species of the genus were later corroborated by molecular phylogenetic studies (Chatrou et al. 2012, Couvreur et al. 2011, Richardson et al. 2004), which consistently demonstrated that Asian species of *Friesodielsia* are closely related to *Dasymaschalon* and *Desmos*, whilst African *Friesodielsia* species were inferred to be more closely related to the African genus *Monanthotaxis*. These studies did not result in nomenclatural changes, however, because of limited taxon sampling (less than 5% of the ca. 180 species in the *Dasymaschalon* alliance). Wang et al. (2012) recently conducted a phylogenetic analysis of the *Dasymaschalon* alliance based on a more extensive taxon sampling (42 taxa, accounting for ca. 23% of species) and a concatenated dataset from five chloroplast regions (*matK*, *ndhF*, *psbA-trnH*, *rbcL*, *trnL-F*). Their results confirmed the close relationships of constituent genera within the alliance and the polyphyletic status of *Friesodielsia*, although intergeneric relationships between *Dasymaschalon*, *Desmos* and *Friesodielsia* remained unresolved due to inadequate resolution based on the chloroplast regions used, highlighting the need for further molecular phylogenetic studies based on more informative nuclear DNA markers.

Monanthotaxis currently consists of 67 species from tropical Africa and Madagascar (Hoekstra et al. 2016). In addition to the African species of *Friesodielsia*, the monospecific genera *Exellia* Boutique and *Gilbertiella* Boutique also appear to be closely related to *Monanthotaxis.* The taxonomic status of these two genera has been unclear, although they have been grouped with *Monanthotaxis* based on flower and pollen morphology (Le Thomas 1981, Van Heusden 1992, Walker 1971b). *Gilbertiella* has also been classified in the same group as *Monanthotaxis* based on fruit and seed morphology (Van Setten & Koek-Noorman 1992), while *Exellia* has very distinct fruits, comprising sessile biseriate monocarps, in contrast to the stipitate uniseriate monocarps in *Monanthotaxis* and *Gilbertiella.* In a previous phylogenetic study based on *rbcL* and *trnL-F*, *Exellia* was shown to be nested within *Monanthotaxis* (Bygrave 2000). Thus far, no studies have included DNA sequences of *Gilbertiella*.

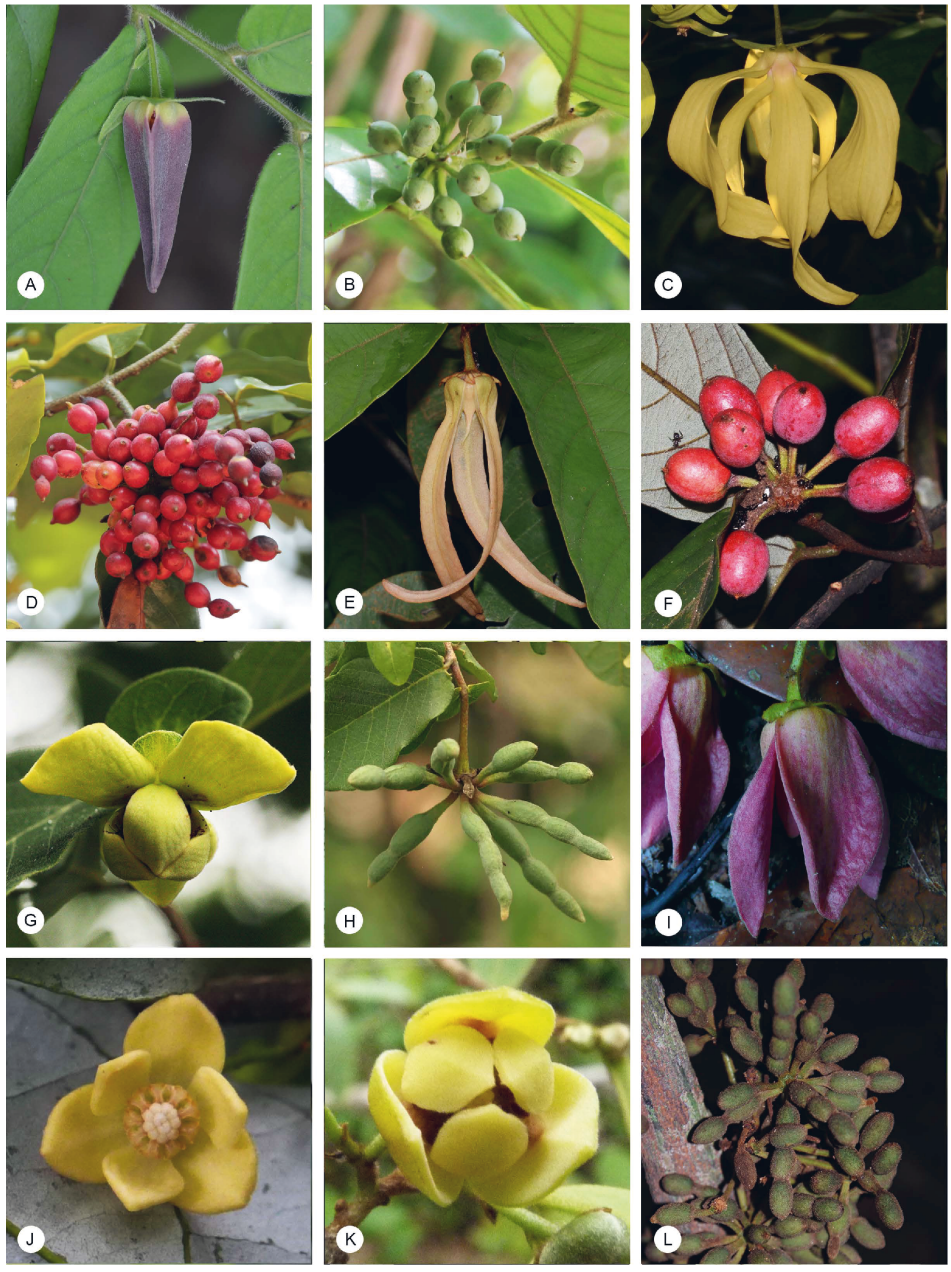

Fig. 1. Flower and fruit morphology in the *Dasymaschalon* alliance. **A,** *Dasymaschalon trichophorum* flower, with three connivent petals forming a pollination chamber; **B,** *Dasymaschalon trichophorum* fruit, composed of several multiseeded, moniliform monocarps; **C,** *Desmos chinensis* flower, with basally constricted petals forming a pollination chamber; **D,** *Desmos chinensis* fruit, with numerous multiseeded, moniliform monocarps; **E,**

Friesodielsia borneensis flower, with long outer petals and short inner petals, three inner petals apically connivent forming a pollination chamber; **F,** *Friesodielsia borneensis* fruit, composed of single-seeded monocarps; **G,** *Friesodielsia obovata* flower, with subequal inner and outer petals; **H,** *Friesodielsia obovata* fruit, with multiseeded monocarps; **I,** *Friesodielsia hirsuta* flower, which is much wider, with subequal outer and inner petals; **J,** *Monanthotaxis mannii* flower, showing a ring of obconical stamens; **K,** *Monanthotaxis buchananii* flower, with loosely coherent petals forming a pollination chamber; **L,** *Monanthotaxis diclina* fruit, with multiseeded monocarps. — Photographs: A–C, E & F, Xing Guo; D, Yuen Yung Lau; G & H, Bart T. Wursten; I & J, Carel C.H. Jongkind; K, Warren McCleland; L, Jan J. Wieringa.

In this study, molecular phylogenetic analyses are based on an expanded taxon sampling, including representatives of almost all constituent genera in the tribe Uvarieae, and based on a combined chloroplast and nuclear DNA dataset, with three main objectives: (1) to clarify intergeneric relationships within the *Dasymaschalon* alliance; (2) to investigate the phylogenetic affinities of different segregates of *Friesodielsia*, enabling validation of nomenclatural changes as necessary; and (3) to assess the phylogenetic positions of some *Friesodielsia* segregates, *Exellia* and *Gilbertiella*, allowing an assessment of the generic circumscription of *Monanthotaxis*.

3.2 Materials and methods

3.2.1 Taxon and DNA region sampling

The 42-taxon dataset generated by Wang et al. (2012) was used as the basis for an expanded taxon sampling, including additional species from the *Dasymaschalon* alliance, with a focus on *Friesodielsia* and *Monanthotaxis*, which were inadequately sampled previously (6 out of 49 *Friesodielsia* species, and 7 out of 66 *Monanthotaxis* species). A total of 101 accessions (96 species) were included in the extended dataset, with the ingroup consisting of 18 *Dasymaschalon* species, 9 *Desmos* species, 25 *Friesodielsia* species, and 27 *Monanthotaxis* species. The outgroups were selected on the basis of previous studies (Chatrou et al. 2012, Couvreur et al. 2011, Wang et al. 2012) and included 14 closely related taxa representing 11 genera from the tribe Uvarieae (*Afroguatteria* Boutique, *Cleistochlamys* Oliv., *Dielsiothamnus* R.E.Fr., *Exellia*, *Fissistigma*, *Mitrella* Miq., *Pyramidanthe* Miq., *Schefferomitra* Diels, *Sphaerocoryne* Scheff. ex Ridl., *Toussaintia* Boutique, *Uvaria*), and representative species from four more distantly related genera in the tribe Monodoreae (*Hexalobus* A.DC., *Isolona* Engl., *Sanrafaelia* Verdc., *Uvariodendron* (Engl. & Diels) R.E.Fr.).

An initial round of analyses indicated that the three *Dasymaschalon* species (*D. filipes* (Ridl.) Bân, *D. longiflorum* Finet & Gagnep., *D. tibetense* X.L.Hou) that were previously shown to be more closely related to Asian *Friesodielsia* species in the chloroplast phylogeny (Wang et al.

2012) belong to the same clade as the majority of *Dasymaschalon* species in the ribosomal DNA (rDNA) tree (Electr. Suppl.: Figs. S1 & S2, https://doi.org/10.12705/661.1). This topological discordance was strongly supported (Bayesian analysis posterior probability ≥0.95, and/or maximum parsimony or maximum likelihood analysis bootstrap / jackknife ≥75%) and hence was considered as hard incongruence, suggesting potential hybridization, incomplete lineage sorting or gene duplication (Linder & Rieseberg 2004, Slowinski & Roderic 1999, Wendel & Doyle 1998). Distinguishing different causes for gene tree incongruence requires more than two unlinked genomic datasets (Buckley et al. 2006, Joly et al. 2009); this is beyond the scope of the present study, however, and consequently *D. filipes*, *D. longiflorum* and *D. tibetense* were excluded from later analyses.

DNA sequences of five chloroplast regions (*matK*, *ndhF*, *psbA-trnH*, *rbcL*, *trnL-F*) which are commonly used in Annonaceae phylogenetics were downloaded from the nucleotide database of the National Center for Biotechnology Information (http://www.ncbi.nlm.nih.gov) or generated for the newly added samples in this study. In order to improve resolution of the phylogeny two additional nuclear ribosomal regions, the internal transcribed spacer region (ITS-5.8S-ITS2) and the external transcribed spacer (ETS), which have previously been shown to be highly variable at the species level (reviewed by: Álvarez & Wendel 2003, Feliner & Rosselló 2007, Poczai & Hyvönen 2010), were generated for all accessions, including the newly added species as well as the 42 taxa used in the chloroplast phylogeny by Wang et al. (2012). Voucher information and GenBank accession numbers for all samples included in the dataset are given in the Supplementary information.

3.2.2 DNA extraction, amplification and sequencing

DNA was extracted, amplified and sequenced using the same procedures as previously described (Guo et al. 2014, Thomas et al. 2012). For ITS and ETS, amplification reactions were performed with primers listed in Table 1 and the thermal cycling profile included template denaturation at 94°C for 2 min followed by 38 cycles of denaturation at 95°C for 1 min, primer annealing at 55°C for 1 min, and primer extension at 72°C for 1 min 30 s; followed by a final extension step at 72°C for 10 min.

3.2.3 Sequence assembly, alignment and phylogenetic analyses

Sequence fragments were edited and assembled using GeneiousPro v.7.1.9 (Biomatters; http://www.geneious.com). Sequences of individual regions were subsequently aligned automatically using the MAFFT (Katoh et al. 2002) plugin in Geneious with default settings, and then manually edited and optimised. A total of 260 ambiguously aligned positions were excluded from the analyses because of difficult homology assessment: 24 positions from 1

block of the *ndhF* region; 91 positions from 2 blocks of the *psbA-trnH* region; 35 positions from 5 blocks of the *trnL-F* region; 99 positions from 11 blocks of the ITS region; and 11 positions from 1 block of the ETS region (Table 2). An inversion of 15 positions in the *psbA- trnH* spacer of some species was identified and reverse-complemented in the alignment, following a strategy previously applied by Pirie et al. (2006) to retain substitution information in the fragments.

Table 1. Primers used for amplification and sequencing of two nuclear DNA regions.

DNA region	Primer name	Sequence (5'–3')	Source
IITS	ITS2	GCTGCGTTCTTCATCGATGC	White & al., 1990
	ITS3	GCATCGATGAAGAACGCAGC	White & al., 1990
	P17	CTACCGATTGAATGGTCCGGTGAA	Popp & Oxelman, 2001
	26S-82R	TCCCGGTTCGCTCGCCGTTACTA	Popp & Oxelman, 2001
ETS	ETS_092F	CCCATGACGGAGCGGGATGC	This study
	ETS_502R	CTGGCGGGCTCCCTGTAGGA	This study

Phylogenetic reconstruction was performed using maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI) methods. DNA sequences for the five chloroplast loci and the two rDNA gene regions were concatenated and analyzed independently of one another to resolve their respective gene trees. A simultaneous analysis (Kluge 1989, Nixon & Carpenter 1996) of all characters was then performed, which was the primary basis for phylogenetic inference.

For the MP analyses, all characters were treated as independent and of equal weight, with gaps treated as missing data. A heuristic search was performed in PAUP* v.4.0b10 (Swofford 2002) with 2000 random addition sequence replicates with TBR branch-swapping, saving 10 trees per replicate. The most parsimonious trees were summarised using a strict consensus tree. Clade support was evaluated using the jackknife (JK) method (Farris et al. 1996) with the removal probability set to approximately e^{-1} (36.7879%), and "jac" resampling emulated. One thousand JK replicates were performed with 100 random addition tree bisection-reconnection searches (each with a maximum of 10 trees held) per replicate.

Maximum likelihood analyses were performed in RAxML v.8.2.6 (Stamatakis 2006) provided by the CIPRES Science Gateway (Miller et al. 2010). The dataset was divided into seven

partitions based on DNA region identity and run under the general time-reversible model with rate heterogeneity modeled by a gamma distribution (GTR + Γ). Fifty inferences were run from distinct random stepwise addition sequence MP starting trees. Branch support was subsequently estimated with 1000 non-parametric bootstraps under the partition data model.

Bayesian analysis was undertaken using MrBayes v.3.2.6 (Ronquist et al. 2012) with both partitioned (partitions based on DNA region identity) and non-partitioned (regions concatenated without partitioning) strategies. For the partitioned dataset, the parameter values for each locus were allowed to evolve independently using the unlinked setting. The appropriate DNA substitution model for each locus and the concatenated matrix (Table 2) was determined in MrModeltest v.2.3 (Nylander 2004) using the Akaike information criterion.

For analyses of both the partitioned and the non-partitioned datasets, four independent Metropolis-coupled Markov chain Monte Carlo analyses were run. Each search used three incrementally heated and one cold Markov chain, and was run for 10 million generations and sampled every 1000th generation. The temperature parameter was set to 0.08. The mean branch length prior was reset from the default mean (0.1) to 0.01 (brlenspr=unconstrained: exponential (100.0)) to reduce the likelihood of stochastic entrapment in local tree length optima (Brown et al. 2010, Marshall 2009). Convergence was assessed using the standard deviation of split frequencies, with values <0.01 interpreted as indicating good convergence. The first 25% of samples (2500 trees) were discarded as burn-in, and the post-burn-in samples summarized as a 50% majority-rule consensus tree. Overall performance of analyses was assessed in Tracer v.1.5 (Rambaut & Drummond 2009) to determine whether the parameter samples were drawn from a stationary, unimodal distribution, and whether adequate effective sample sizes (ESS) for each parameter (ESS > 200) had been reached. Stationarity of posterior probabilities of splits within runs, and convergence of posterior probabilities of splits between different runs were visually checked using the Cumulative and Compare functions in AWTY (Nylander et al. 2007). Inference of non-partitioned and partitioned nucleotide datasets was assessed with Bayes factor comparison. The standard criterion of 2 ln Bayes factor >10 was used as a benchmark, indicating very strong evidence against an alternative strategy (Kass & Raftery 1995, Nylander et al. 2004).

Bootstrap/jackknife values of 50%–74% were considered as weak support by the data, 75%–84% as moderate support, and 85%–100% as strong support. In BI, the estimation of branch support accompanies the tree estimation and is reflected by posterior clade probability (Larget & Simon 1999); branches with values ≥0.95 are considered well supported, and <0.95 not supported (Yang & Rannala 1997).

Table 2. Descriptive statistics and best-fitting substitution models for each of the five chloroplast and two nuclear DNA regions and the concatenated datasets.

							Parsimony-informative		
DNA region	Alignment length	Excluded sites	Entire dataset	Ingroup	Entire dataset	Ingroup	Entire dataset	Ingroup	AIC model selection
Chloroplast DNA data									
matK	729	0	7.3	6.5	150 (20.6)	91 (12.5)	71 (9.7)	43 (5.9)	GTR+Γ
ndhF	2044	24	30.7	30.8	597 (29.6)	342 (16.9)	301 (14.9)	169 (8.4)	GTR+I+Γ
rbcL	1327	0	22.6	22.5	131 (9.9)	77 (5.8)	63(4.7)	35 (2.6)	GTR+I+Γ
psbA-trnH	477	91	9.9	9.2	144 (37.3)	104 (26.9)	84 (21.8)	58 (15)	GTR+Γ
trnL-F	922	35	11.2	12.4	155 (17.5)	95 (10.7)	72 (8.1)	47 (5.3)	GTR+Γ
Combined data	5499	150	21.9	22.1	1177 (22)	709 (13.3)	591 (11)	352 (6.6)	GTR+I+Γ
Nuclear DNA data									
ITS	959	99	51.4	44.4	187 (21.7)	160 (18.6)	97 (11.3)	70 (8.1)	GTR+I+Γ
ETS	430	11	35.7	22.5	–	150 (35.8)	–	98 (23.4)	HKY+I+Γ
Combined data	1389	110	46.2	37.3	337 (26.3)	310 (24.2)	195 (15.2)	168 (13.1)	HKY+I+Γ
Combined chloroplast and nuclear data									
	6888	260	26.4	24.9	1514 (22.8)	1019 (15.4)	786 (11.9)	520 (7.8)	GTR+I+Γ
			% missing data		Variable characters (%)		characters (%)		

3.3 Results

The concatenated alignment of five chloroplast regions and two nuclear ribosomal regions consisted of 6628 aligned positions. Characteristics and the best-fitting nucleotide substitution model of each data matrix are presented in Table 2. The chloroplast and rDNA analyses with all available accessions are presented in Figs. S1 & S2 to exhibit the mutually well-supported topological incongruence within the clade comprising three *Dasymaschalon* species (*D. filipes*, *D. longiflorum*, *D. tibetense*). Apart from the exclusion of the observed topological discordance, the simultaneous analysis (Fig. 2) was shown to be the best resolved amongst all three data matrices. For this reason, it was considered to be the best estimate of the phylogeny and selected as the basis for further discussion of relationships and systematic inferences.

For the BI analysis, partitioning considerably improved mean $-\ln L$ value (mean $-\ln L_{\text{non-partitioned}}$ = 27,529, mean $-\ln L_{\text{partitioned}}$ = 26,755). Bayes factor comparison indicated that the partitioned analyses based on region identity provided distinctly better explanations of the data than the analyses of the non-partitioned model: 2lnB (partitioned over non-partitioned) = 1540, significantly above the threshold value of 10. The 50% majority-rule consensus tree derived from the analyses using the partitioned strategy was therefore selected to present the results of the Bayesian analyses.

The MP, ML, and Bayesian analyses yielded similar topologies, differing mainly in the relative posterior probability (PP), MP jackknife (JK) and ML bootstrap (BS) values for particular groups (Fig. 2). The *Dasymaschalon* alliance (except *Friesodielsia discostigma* and *F. gracilipes*, which are distantly related to the majority of this genus) is unambiguously supported as monophyletic, with two sister clades (I and II) retrieved, showing a clear geographic pattern corresponding with African and Asian distributions, respectively.

Within the African Clade I (PP = 1; JK = 96; BS = 96), *Friesodielsia obovata* is shown to be sister to a clade comprising two weakly to strongly supported subclades, IA (PP = 1; JK = 93; BS = 75, consisting of 27 species of *Monanthotaxis* and *Exellia scamnopetala* (Exell) Boutique), and IB (PP = 1; JK = 57; BS = 76, comprising 8 species of African *Friesodielsia*).

Clade II (PP = 1; JK = 94; BS = 90) consists of the Asian species sampled, with the 10 accessions of *Desmos* forming an early-divergent branch, Clade IIA (PP = 1; JK = 95; BS = 95). The sister lineage to Clade IIA is strongly supported (PP = 1; JK = 93; BS = 93), and comprises two sister clades: Clade IIB (PP = 1; JK = 99; BS = 97), consisting of the Asian *Friesodielsia* taxa sampled and *Schefferomitra subaequalis* Diels; and Clade IIC (PP = 1; JK = 100; BS = 100), comprising the *Dasymaschalon* species sampled.

The results suggest that *Dasymaschalon* and *Desmos* are both monophyletic. *Friesodielsia* is highly polyphyletic, however, with the sampled species scattered across five different

lineages, viz.: (1) the Asian Clade IIB, which includes the type, *F. cuneiformis* (Blume) Steenis; (2) *F. obovata* (the early- divergent branch within Clade I); (3) Clade IB, which is the sister to the *Monanthotaxis* clade; (4) *F. gracilipes*, which is sister to a clade comprising four accessions of *Sphaerocoryne*; and (5) *F. discostigma*, which is sister to *Afroguatteria bequaertii* (De Wild.) Boutique. The Asian *Friesodielsia* group and the African genus *Monanthotaxis* are furthermore paraphyletic, with *Schefferomitra subaequalis* and *Exellia scamnopetala* deeply nested within Clades IIB and IA, respectively.

3.4 Discussion

3.4.1 Phylogenetic relationships within the Dasymaschalon alliance

The present study corroborates and expands the results of previous phylogenetic analyses, which have suggested a close relationship between the genera within the *Dasymaschalon* alliance and the polyphyletic status of *Friesodielsia* (Chatrou et al. 2012, Couvreur et al. 2011, Wang et al. 2012). The *Dasymaschalon* alliance is shown to be collectively monophyletic and can easily be distinguished morphologically from other lineages in the tribe Uvarieae by its inaperturate pollen with a thin exine, the glaucous abaxial surface of the leaves with parallel tertiary venation (Wang et al. 2012, and references therein; pers. obs.), and often by basal leaf glands (Turner 2012). The sister relationship retrieved between the African Clade I (comprising *Exellia*, *Monanthotaxis* and some *Friesodielsia* species) and the Asian Clade II (including *Desmos*, *Dasymaschalon*, *Schefferomitra* and some *Friesodielsia* species) is consistent with floral, pollen and fruit morphology: species belonging to Clade I have open or loosely coherent floral chambers (Fig. 1G, I–K), petals that are wide and short and pollen with a microbaculate exine; whereas species in Clade II have flowers with partially enclosed floral chambers, petals that are narrow and elongate (Fig. 1A, C, E) and echinate-scabrate pollen (Saunders 2010, Verdcourt 1971, Walker 1971b, Wang et al. 2009, Wang et al. 2012, pers. obs.).

Relationships within the African clade (Clade I) are well resolved (Fig. 2). After the early-divergent species *Friesodielsia obovata*, the 27 species of *Monanthotaxis* form a well-supported lineage (Clade IA, PP = 1; J K = 93; BS = 75), as do the 7 other *Friesodielsia* species (Clade IB), although the MP analysis provides only weak support (PP = 1; JK = 57; BS = 76). *Exellia scamnopetala* is deeply nested within Clade IA, rendering *Monanthotaxis* paraphyletic. A subclade (Clade IAi) comprising all sampled Madagascan species (*M. ambrensis* (Cavaco & Keraudren) Verdc., *M. boivinii* (Baill.) Verdc., *M. komorensis* P.H.Hoekstra, *M. heterantha* (Baill.) Verdc., *M. micrantha* (Baker) Verdc., *M. sororia* (Diels) Verdc.) was retrieved, with one species (*M. filipes* P.H.Hoekstra) from East Africa as sister to the remaining species. The latter species and some Madagascar representatives of this subclade possess filiform pedicels, in contrast with all other members of *Monanthotaxis*, which have thicker pedicels. All continental African species with leaf-opposed or extra-axillary inflorescences formed another

strongly supported subclade (Clade IAii) comprising seven species, whilst both (supra-)axillary and extra-axillary inflorescences are present in the Madagascar clade and all other species in Clade IA have (supra-) axillary inflorescences. The presence of staminodes seems to be restricted to the Madagascan clade and to more than half of the species of a moderately supported subclade (Clade IAiii) comprising nine *Monanthotaxis* species (including its type) and *Exellia scamnopetala*. The sections *Popowiopsis* Verdc. and *Enneastemon* (Exell) Verdc., defined by Verdcourt (1971) based on petal aestivation, are revealed to be highly polyphyletic, with the species of the former (sampled species including *M*. *ambrensis*, *M*. *boivinii*, *M*. *buchananii* (Engl.) Verdc., *M*. *ferruginea* (Oliv.) Verdc., *M*. *heterantha*, *M*. *micrantha*, *M*. *parvifolia* (Oliv.) Verdc., *M*. *pellegrinii* Verdc., *M*. *sororia*, and *M*. *trichocarpa* (Engl. & Diels) Verdc.) retrieved in four different clades and the latter (sampled species including *M*. *angustifolia* (Exell) Verdc., *M*. *foliosa* (Engl. & Diels) Verdc., *M*. *fornicata* (Baill.) Verdc., and *M*. *schweinfurthii* (Engl. & Diels) Verdc.) in three clades. Furthermore, the species *M. klainei* (Engl.) Verdc., with multiple accessions that represent different varieties, is not monophyletic, with *M. angustifolia* and *M. atopostema* P.H.Hoekstra nested within the clade (Fig. 2). These phylogenetic relationships suggest that the delimitations of *M. klainei* and the previously defined sections are problematic: on-going research involving detailed morphological examination and increased phylogenetic sampling of specimens will lead to a new subgeneric classification and will show whether the varieties described in some species should be elevated to species rank.

The intergeneric relationships within the Asian Clade II have historically proven difficult to resolve despite the fact that the three constituent genera are morphologically very distinct, with different pollination chambers and monocarp shapes (Fig. 1). *Dasymaschalon*, *Desmos* and *Friesodielsia* s.str. repeatedly formed a polytomy in previous analyses (Bygrave 2000, Chatrou et al. 2012, Couvreur et al. 2011, Wang et al. 2012). The resolution of the deeper nodes is significantly improved in the present study (Fig. 2) following the incorporation of two nuclear regions. *Dasymaschalon* is strongly supported as sister to *Friesodielsia* s.str., and these two genera are collectively sister to *Desmos*. The inferred relationships within this clade are consistent with floral morphology and pollination chamber types: *Friesodielsia* flowers have an enclosed floral chamber formed by the apical connivence of the three inner petals (Fig. 1E); *Dasymaschalon* flowers have a superficially similar floral chamber (Fig. 1A), although the petals that are apically connivent are inferred to be homologous with the outer petals of other Annonaceae; and *Desmos* f lowers (Fig. 1C) possess a partially enclosed floral chamber formed by basally constricted petals, with the apical parts spreading outwards.

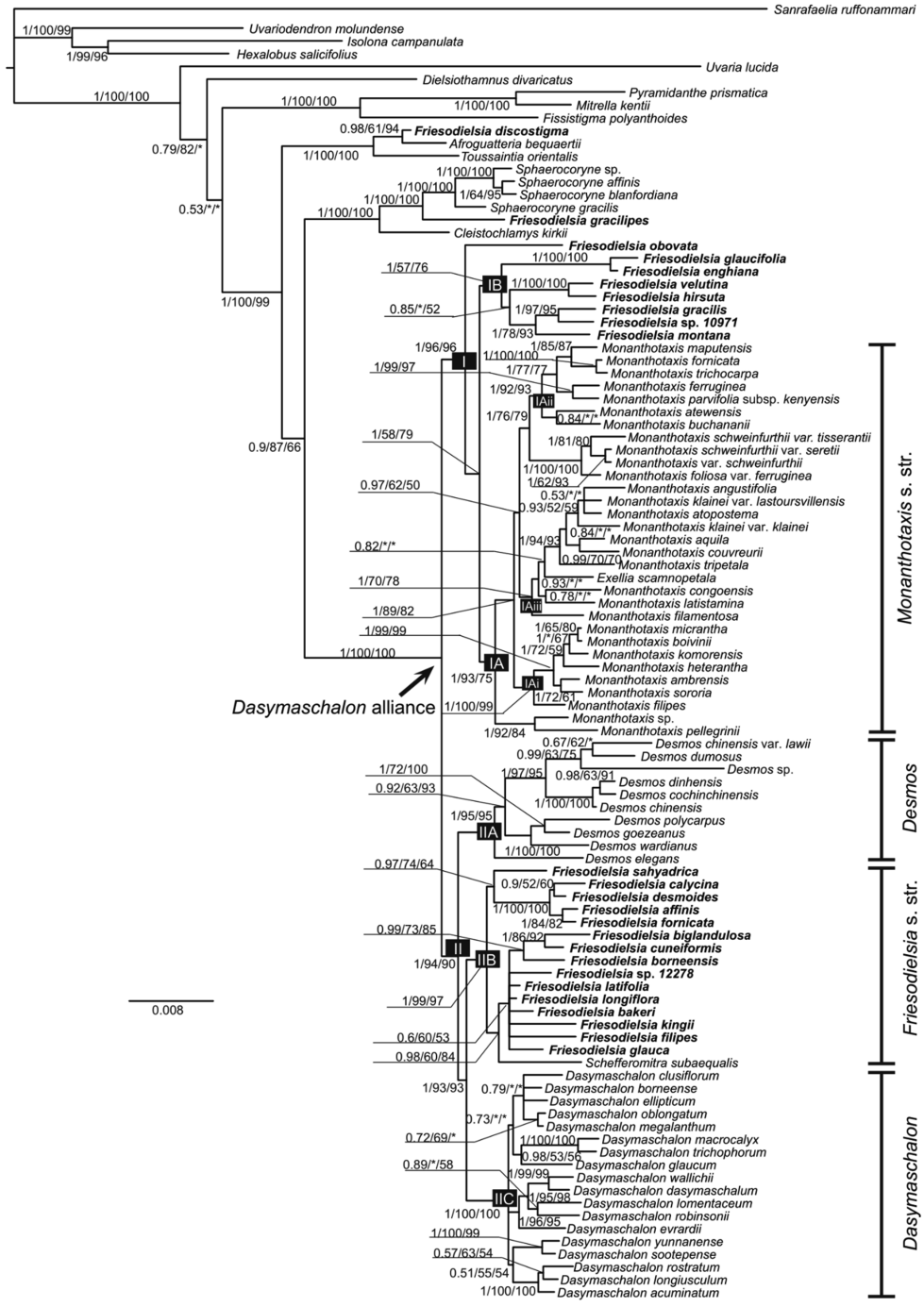

Fig. 2. Bayesian 50% majority-rule consensus tree of a simultaneous analysis of seven markers (*matK*, *ndhF*, *rbcL*, *psbA-trnH*, *trnL-F*, ITS, ETS). *Friesodielsia* accessions shown in bold. Bayesian

posterior probabilities (PP) values ≥0.5, MP jackknife (JK) values ≥ 50 and ML bootstrap (BS) values ≥50 are indicated at each node: PP / JK / BS. Asterisks represent clade support values <50%.

Whereas the subclades differentiated within *Dasymaschalon* (Clade IIC) received only weak support, several strongly supported subclades are retrieved in *Desmos* (Clade IIA) and the Asian *Friesodielsia* lineage (Clade IIB). Relationships within Clade IIA are well resolved and show a clear geographic pattern: the Sri Lankan species *Desmos elegans* Saff. is well supported as sister to the other *Desmos* species sampled, which form two subclades consisting of species from Australia (*D. goezeanus* (F.Muell.) Jessup, *D. polycarpus* Jessup, *D. wardianus* (F.M.Bailey) Jessup) and continental Asia (*D. chinensis* Lour., *D. chinensis* var. *lawii* (Hook.f. & Thomson) Bân, *D. cochinchinensis* Lour., *D. dinhensis* (Pierre ex Finet & Gagnep.) Merr., *D. dumosus* Saff.). Within Clade IIB, two main subclades with moderate to strong support can be distinguished. One subclade (comprising *F. affinis* (Hook.f. & Thomson) D.Das, *F. calycina* (King) Steenis, *F. desmoides* (Craib) Steenis, *F. fornicata* (Roxb.) D.Das, *F. sahyadrica* N.V.Page & Survesw.) is characterised by flowers with three outer petals that are freely spreading (Fig. 3A) and have a flat petal base, whereas the other subclade (including the remaining Asian *Friesodielsia* representatives sampled) has flowers with outer petals that are connivent before anthesis (Fig. 3B, C) and possess a distinctly concave petal base.

3.4.2 Polyphyly and classification of Friesodielsia

The polyphyletic status of *Friesodielsia*, in which the African species are not congeneric with the Asian species, was previously indicated by palynological data (Walker 1971b) and molecular phylogenetic analyses (Chatrou et al. 2012, Couvreur et al. 2011, Wang et al. 2012). Our increased sampling of both taxa and DNA markers reveals more extensive polyphyly: the African species of *Friesodielsia* are not only phylogenetically distinct from the Asian species, but are themselves not monophyletic, with the sampled species scattered across several different clades.

All Asian representatives of *Friesodielsia* sampled form a strongly supported clade, including the type, *F. cuneiformis*. This Asian group can be distinguished from the African species by their elongate flowers (Fig. 1E) with partially closed floral chambers (Wang et al. 2012), and unequal outer and inner petals (Verdcourt 1971). We therefore recommend that a narrower circumscription of *Friesodielsia* should be adopted, restricting the generic name to Asian species only; the African species should accordingly be transferred to other genera.



Fig. 3. Flower morphology of selected species of *Friesodielsia*. **A,** Flower bud of *Friesodielsia desmoides*, showing free-spreading outer petals; **B,** Flower bud of *Friesodielsia borneensis*, showing firmly connivent outer petals; **C,** Mature flower of *Friesodielsia borneensis*, showing three outer petals separating at base. – Photographs: Xing Guo

Among the 10 species (inclusive of a currently undescribed species) of African *Friesodielsia* sampled (out of a total of 11 species), eight form a basal grade within Clade I and are phylogenetically associated with the African genus *Monanthotaxis*, whereas two species (*F. gracilipes*, *F. discostigma*) are retrieved outside the accepted circumscription of the *Dasymaschalon* alliance (Fig. 2). Within Clade I, *F. obovata* is sister to all other African species, and seven species within Clade IB are retrieved as sister to Clade IA, which includes all the *Monanthotaxis* species sampled. These phylogenetic results suggest that *F. obovata* and the seven *Friesodielsia* species in Clade IB should be transferred to *Monanthotaxis*, or alternatively treated as new genera; the diagnostic morphological characters of each clade will be discussed in detail below (see "Delimitation of *Monanthotaxis*") to assess these two alternative classifications.

Friesodielsia gracilipes is sister to the palaeotropical genus *Sphaerocoryne*, corroborating the results of previous phylogenetic analyses based on *rbcL* and *trnL-F* sequences (Bygrave 2000), which indicated that *F. gracilipes* was located in the *Cleistochlamys-Sphaerocoryne-Toussaintia* clade (Clade 13 in Bygrave 2000: fig. 6.3b). The inferred close relationship between these two groups is consistent with their morphological similarities, as they both have reticulate tertiary leaf venation and axillary flowers. In contrast, the African species of *Friesodielsia* in Clade IB and *Monanthotaxis* have parallel tertiary leaf venation and extra-axillary flowers. Based on our assessment of the morphological affinities and phylogenetic relationships of these two groups, we believe that *F. gracilipes* is best considered congeneric with *Sphaerocoryne*, necessitating a new nomenclatural combination.

Friesodielsia discostigma, which differs from the *Friesodielsia* species in Clade IB in having reticulate tertiary leaf venation and axillary flowers, is shown to be closely related to the African genus *Afroguatteria* rather than the other four segregates of *Friesodielsia*. Great care was taken with older leaf material of *F. discostigma* (over 100 years) to avoid technical errors, including repeated DNA extraction, PCR and sequencing. Sequence similarity of *matK*, *psbA-trnH* and *trnL-F* (assessed by blast searching data in GenBank) support its relationship in the concatenated analysis (Fig. 2), indicating that our finding is not an artefact resulting from missing data. This inferred relationship between *F. discostigma* and *Afroguatteria* is consistent with their similarity in morphological characters, including subequal inner and outer petals, and numerous stipitate monocarps with one or two seeds. Van Heusden (1992: 73) recognized their similarity in secondary and tertiary leaf venation, stating that the "leaves of *F. discostigma* closely resemble those of *Afroguatteria*." Species of the *Dasymaschalon* alliance share eucamptodromous leaf venation (sensu Hickey 1979) (Fig. 4A), with parallel secondary veins lacking prominent marginal arches, and parallel tertiary veins connecting adjacent secondaries (Klucking 1986). In contrast, *Friesodielsia discostigma* and *Afroguatteria* have "festooned brochidodromous" leaf venation (Fig. 4B) with reticulate tertiary veins (sensu Hickey & Wolfe 1975), in which the secondary veins anastomose and link to form prominent

loops, with secondary arches outside the prominent loops that gradually diminish towards the margin (Guo et al. 2014, Klucking 1986, Xue et al. 2012). Based on their close phylogenetic relationships and similar morphological characters, we propose that *F. discostigma* should be transferred to the genus *Afroguatteria*.



Fig. 4. Leaf venation patterns of selected species of *Friesodielsia*. **A,** *Friesodielsia cuneiformis* (abaxial view), showing eucamptodromous venation with parallel and upturned secondary veins, and parallel tertiary veins (type, *C.L. Blume s.n.*, P barcode P00732380); **B,** *Friesodielsia discostigma* (adaxial view), showing brochidodromous venation with curved anastomosing secondary veins and reticulate tertiary veins (isotype, *G.A. Zenker 2980*, P barcode P00363341).

3.4.3 Congeneric status of Friesodielsia s.str. and Schefferomitra

The phylogenetic analyses presented here (Fig. 2) suggest that the Asian *Friesodielsia* lineage is not monophyletic due to the inclusion of *Schefferomitra subaequalis* (sole representative of this monospecific genus) in Clade IIB (PP = 1; JK = 99; BS = 97). *Schefferomitra* is currently

placed in tribe Uvarieae based on morphology (Chatrou et al. 2012), although its phylogenetic position was previously unknown due to the unavailability of DNA sequences.

Detailed examination of the morphological characters of *S. subaequalis* failed to reveal any character that supports the continued recognition of *Schefferomitra* as a genus distinct from *Friesodielsia* s.str.: the only consistent difference is the shape of the staminal connective, which is tongue-shaped in *Schefferomitra* (Couvreur et al. 2012, Keßler 1993), whereas the staminal connectives of Asian *Friesodielsia* species have a truncate discoid apex.

The phylogenetic position of *S. subaequalis* within the Asian *Friesodielsia* clade and their considerable morphological similarity therefore provide convincing evidence that *Friesodielsia* s.str. and *Schefferomitra* are congeneric. Since the name *Schefferomitra* (first published by Diels 1912) antedates that of *Friesodielsia* (first published by Van Steenis 1948), strict application of the principle of priority would therefore require adoption of the former, necessitating the transfer of about 38 species names to *Schefferomitra* (excluding the African *Friesodielsia* species, which, as described elsewhere in this study, need to be transferred for taxonomic reasons). This change would create unnecessary confusion because *Friesodielsia* is firmly rooted in the Annonaceae literature owing to its species richness in tropical Asia. In an effort to promote nomenclatural stability we therefore propose conservation of the name *Friesodielsia* against *Schefferomitra* (Guo et al. 2017). The formal transfer of the name *S. subaequalis* to *Friesodielsia* is accordingly postponed pending a ruling by the Nomenclature Committee for Vascular Plants.

3.4.4 Delimitation of Monanthotaxis

The MP, ML, and BI phylogenetic analyses consistently retrieved Clades I, IA and IB as well-supported lineages. This is consistent with two alternative interpretations of generic circumscription: either a broad delimitation of *Monanthotaxis* s.l. with the inclusion of *F. obovata* and species within Clade IB; or retaining the current delimitation of *Monanthotaxis* (equivalent to clade IA) and the segregation of *F. obovata* and the species within Clade IB as two new genera.

Friesodielsia obovata is sister to all other species of Clade I and can be readily distinguished from the remaining taxa in the alliance by the combination of peduncles that bear a conspicuous leafy bract (Verdcourt 1971) and stellate hairs (Couvreur et al. 2012). Verdcourt (1971) noted the remarkable differences between *F. obovata* and the other species of *Friesodielsia* (including African and Asian species), and placed it in a new monospecific subgenus, *Friesodielsia* subg. *Amblymitra* Verdc. Clade IB is retrieved as sister to Clade IA, which comprises *Exellia* and *Monanthotaxis* species. There are no obvious synapomorphies for the seven species in Clade IB, although diagnostic plesiomorphic character states in

stamens can distinguish this lineage from Clade IA: the species in Clade IB have numerous (up to 125) stamens in three to six whorls, compared to only a few (3–15[–40]) stamens in one or two, rarely three, whorls in Clade IA (Van Heusden 1992, Verdcourt 1971, pers. obs.). The narrower delimitation of *Monanthotaxis*, in which case *F. obovata* and the species in Clade IB would be treated as two distinct genera, would clearly be undesirable due to the lack of morphological synapomorphies. We therefore adopt a broader delimitation of *Monanthotaxis*, which possesses three characters that are likely to be synapomorphic, viz.: the climbing growth habit, loosely coherent floral chambers and moniliform monocarps. This broad *Monanthotaxis* shows very wide variation in several characters (e.g. inflorescence characters, see Hoekstra et al. 2014), but a more narrow approach would not have reduced most of this variation for core *Monanthotaxis*.

Phylogenetic results in all MP, ML, and BI analyses suggest that *Exellia scamnopetala* is deeply nested within Clade IA, rendering *Monanthotaxis* paraphyletic. The monospecific genus *Exellia* is characterized by globose and sessile monocarps (Boutique 1951b) and differs from *Monanthotaxis* that possess moniliform monocarps with an obvious stipe (Couvreur et al. 2012, Keßler 1993). *Exellia* and *Monanthotaxis* are nevertheless very similar in several characters, including: small flowers (petals generally 2–13 mm long, with the exception of *M. bokoli*, which has petals up to 27 mm) and few stamens (3–15[–40]) that are mostly obconical with a broad connective and a narrow filament. These character states are very different in *Dasymaschalon*, *Desmos* and *Friesodielsia* (including African and Asian species): these genera have large flowers (petals 15–145 mm long) and numerous (up to 200) oblong stamens (Van Heusden 1992). On the basis of these floral morphological similarities, Van Heusden (1992) placed *Exellia* in the "*Monanthotaxis* group". Furthermore, both genera have microbaculate pollen exines (Walker 1971a, Walker 1971b). Given the close affinity of *Exellia* and *Monanthotaxis*, supported by both molecular and morphological data, we consider *Exellia* congeneric with *Monanthotaxis*, thereby rendering the genus monophyletic.

Another monospecific genus, *Gilbertiella*, was placed in the "*Monanthotaxis* group" by Van Heusden (1992). The genus was described by Boutique (1951b) based on linear stamens, the outer petals that cover the slightly smaller inner petals only at the top and that have a curved hook of the petals towards the centre of the flower. All of these characters occur in at least some species of *Monanthotaxis.* Furthermore, it is highly similar to van Heusden's "*Monanthotaxis* group", in having small flowers (petals ca. 2–4 mm long), few (12) stamens, and multi-seeded monocarps (ca. 6 seeds) and the pollen are similar in having microbaculate exine (Walker 1971a, Walker 1971b). We were unable to successfully sequence DNA from herbarium samples of the only described species in the genus, *Gilbertiella congolana* Boutique, due to the poor quality of leaf materials. Fortunately, a recently described new species, *Monanthotaxis latistamina* P.H.Hoekstra (Hoekstra et al. 2016), closely resembles *G. congolana*, and this species is shown here to be nested within the *Monanthotaxis* clade (Fig.

2). We therefore propose that the generic name *Gilbertiella* should be reduced to synonymy with *Monanthotaxis*, necessitating a new nomenclatural combination.

3.5 Generic descriptions

Dasymaschalon (Hook.f. & Thomson) Dalla Torre & Harms, Gen. Siphon.: 174. 1901, nom. cons. ≡ *Unona* sect. *Dasymaschalon* Hook.f. & Thomson, Fl. Ind., 1: 134. 1855 ≡ *Desmos* sect. *Dasymaschalon* (Hook.f. & Thomson) Saff. in Bull. Torr. Bot. Club 39: 507. 1912 – Type: *Dasymaschalon dasymaschalum* (Blume) I.M.Turner.

Small trees (rarely climbers), indument of simple hairs. Leaves elliptic to ovate-oblong, 8–18 pairs of secondary veins, abaxial surface glaucous. Inflorescences axillary, 1-flowered. Flowers bisexual. Sepals 3, valvate, ovate-triangular. Petals 3 (rarely 2), ovate-triangular, in 1 whorl alternate with sepals, valvate, apically connivent to form a mitriform dome (floral chamber) over reproductive organs and often with very small basal apertures between petals; inner petal whorl absent. Stamens numerous; connectives apically truncate or apiculate; pollen inaperturate, in monads. Carpels numerous, free; ovaries densely hairy; ovules 1–7 per carpel, uniseriate. Fruit apocarpous; monocarps stipitate, globose or ellipsoid (1-seeded) or moniliform (multi-seeded); seeds 1–7 per monocarp, globose to ellipsoid, ruminations lamelliform.

Circa 27 species in tropical and subtropical Asia.

Desmos Lour., Fl. Cochinch.: 329, 352. 1790 – Type (designated by Safford in Bull. Torrey Bot. Club 39: 505. 1912): *Desmos cochinchinensis* Lour.

Woody climbers, indument of simple hairs. Leaves ovate-oblong, 7–16 pairs of secondary veins, abaxial surface glaucous. Inflorescences axillary, supra-axillary, or leaf-opposed, 1- or 2-flowered. Flowers bisexual. Sepals 3, valvate, ovate-triangular. Petals 6, in 2 whorls; each whorl valvate, subequal or outer whorl slightly longer than inner whorl; inner whorl basally constricted around reproductive organs to form enclosed floral chamber. Stamens numerous; connectives apically truncate or rounded; pollen inaperturate, in monads. Carpels numerous, free; ovary densely hairy; ovules 1–8 per carpel, uniseriate. Fruit apocarpous; monocarps stipitate, moniliform (rarely globose); seeds 1–8 per monocarp, subglobose to ellipsoid, ruminations lamelliform.

Circa 22 species in tropical and subtropical Asia and Australia.

Friesodielsia Steenis in Bull. Jard. Bot. Buitenzorg, sér. 3, 17: 458. 1948 ≡ *Polyalthia* sect. *Oxymitra* Blume in Blume & Fischer, Fl. Javae, Anonaceae: 71, pl. 34–37. 1830 ≡ *Oxymitra* (Blume) Hook.f. & Thomson, Fl. Ind.: 145. 1855, nom. illeg., non Bisch. ex Lindenb. in Nova

Acta Phys.- Med. Acad. Caes. Leop.-Carol. Nat. Cur. 14, Suppl. 1: 124. 1829 – Type: *Friesodielsia cuneiformis* (Blume) Steenis (≡ *Polyalthia cuneiformis* Blume).

= *Schefferomitra* Diels in Bot. Jahrb. Syst. 49: 152. 1912 [proposed as rejected against *Friesodielsia*: Guo et al. 2017].

Woody climbers, indument of simple hairs. Leaves oblong-lanceolate, 8–13 pairs of secondary veins, abaxial surface glaucous. Inflorescences axillary, supra-axillary or extra-axillary, 1-lowered. Flowers bisexual. Sepals 3, valvate, ovate-triangular. Petals 6, in 2 whorls; each whorl valvate, outer whorl much longer than inner whorl; inner whorl apically connivent, forming enclosed floral chamber. Stamens numerous; connectives apically truncate or rounded; pollen inaperturate, in monads. Carpels numerous, free; ovary densely hairy; ovules 1 (rarely 2) per carpel. Fruit apocarpous; monocarps stipitate, globose or ellipsoid (rarely cylindrical), seeds 1 (rarely 2) per monocarp, subglobose, ruminations lamelliform.

Circa 38 species in tropical and subtropical Asia.

Monanthotaxis Baill. in Bull. Mens. Soc. Linn. Paris 2: 878. 1890 – Type: *Monanthotaxis congoensis* Baill.

= *Clathrospermum* Planch. ex Benth. in Bentham & Hooker, Gen. Pl. 1: 29. 1862, nom. rej. against *Enneastemon* Exell – Type: *Clathrospermum vogelii* (Hook.f.) Benth. (≡ *Uvaria vogelii* Hook.f.).

= *Enneastemon* Exell in J. Bot. 70 (Suppl. 1): 209. 1932, nom. cons. – Type: *Enneastemon angolensis* Exell.

= *Atopostema* Boutique in Bull. Jard. Bot. État Bruxelles 21: 121. 1951 – Type: *Atopostema klainei* (Engl.) Boutique.

= *Exellia* Boutique in Bull. Jard. Bot. État Bruxelles 21: 117. 1951 – Type: *Exellia scamnopetala* (Exell) Boutique (≡ *Popowia scamnopetala* Exell), **syn. nov.**

= *Gilbertiella* Boutique in Bull. Jard. Bot. État Bruxelles 21: 124. 1951 – Type: *Gilbertiella congolana* Boutique, **syn. nov.**

Shrubs or woody climbers, indument of simple hairs (stellate in a few species). Leaves lanceolate, elliptic, ovate, oblong-lanceolate or obovate, 6v–23 pairs of secondary veins, abaxial surface glaucous. Inflorescences axillary, supra-axillary, extra-axillary, leaf-opposed or cauline, 1 to many-flowered. Flowers unisexual or bisexual. Sepals 3, valvate, broadly ovate to lanceolate. Petals 6 (rarely 3, 4, or 5), in 2 whorls (rarely 1), each whorl valvate, subequal or in some species outer whorl significantly longer than inner whorl; inner whorl freely spreading or loosely coherent. Stamens 3 to numerous; connectives apically truncate or apiculate; pollen inaperturate, in monads. Carpels 3 to numerous, free; ovary densely hairy or glabrous; ovules

1–7 per carpel, uniseriate (rarely biseriate). Fruit apocarpous; monocarps stipitate (rarely sessile), globose, ellipsoid or subcylindrical, seeds 1–7 per monocarp, subglobose or ellipsoid to subcylindrical, ruminations lamelliform.

Circa 94 species in tropical and subtropical Africa and Madagascar.

3.6 Nomenclatural changes

The present study reveals that the traditional circumscription of *Friesodielsia* is highly polyphyletic, with currently accepted species in this genus belonging to four different genera, viz. *Afroguatteria*, *Friesodielsia* s.str., *Monanthotaxis* and *Sphaerocoryne*. The two monospecific genera *Exellia* and *Gilbertiella* are furthermore shown to be congeneric with *Monanthotaxis*. A total of 12 nomenclatural changes are accordingly validated here, with types and synonymy provided.

Afroguatteria discostigma (Diels) X.Guo & R.M.K.Saunders, **comb. nov.** ≡ *Cleistopholis discostigma* Diels in Bot. Jahrb. Syst. 39: 474. 1907 ≡ *Oxymitra discostigma* (Diels) Ghesq. ex Pellegr. in Bull. Soc. Bot. France 1949: 66. 1950 (“1949”) ≡ *Richella discostigma* (Diels) R.E.Fr. in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 17a(2): 139. 1959 ≡ *Friesodielsia discostigma* (Diels) Steenis in Blumea 12: 359. 1964 – Holotype: Cameroon, Bipinde, 1904, *G.A. Zenker 2980* (B barcode B 10 0153055!; isotypes: BM barcode BM001125042!, BR barcode 000008800398!, G barcode G00308361!, GOET barcode GOET005676 [photo!], HBG barcode HBG-502538 [photo!], K barcode K000198949!, L barcode L.1754813!, M barcode M-0107910 [photo!], MA [photo!], P barcode P00363341!, S No. S03-2239!, WAG barcode WAG0053550 [photo!]).

Monanthotaxis congolana (Boutique) P.H.Hoekstra, **comb. nov.** ≡ *Gilbertiella congolana* Boutique in Bull. Jard. Bot. État Bruxelles 21: 124. 1951 – Holotype: Democratic Republic of the Congo, Orientale, Yangambi, rive gauche, Litulombo, 8 Dec 1939, *R.G.A. Germain 17* (BR [on 2 sheets] barcodes 000008799586! & 000008799913!; isotypes: B barcode B 10 0153067!, K barcode K000198957!, NY [photo!], P!).

Monanthotaxis dielsiana (Engl.) P.H.Hoekstra, **comb. nov.** ≡ *Unona dielsiana* Engl. in Bot. Jahrb. Syst. 39: 476. 1907 ≡ *Oxymitra dielsiana* (Engl.) Sprague & Hutch in Bull. Misc. Inform. Kew 1916: 156. 1916 ≡ *Richella dielsiana* (Engl.) R.E.Fr. in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 17a(2): 139. 1959 ≡ *Friesodielsia dielsiana* (Engl.) Steenis in Blumea 12: 359. 1964 – Holotype: Cameroon, South Province, Bipinde, Dec 1901, *G.A. Zenker 2473* (B [on 4 sheets] barcodes B 10 0154098!, B 10 0154096!, B 10 0154097! & B 10 0154099!; isotypes: BM barcode BM001125043!, BR barcode 000008801388!, COI barcode COI00071518 [photo!], E [photo!], G barcode G00308364!, GOET [on 2 sheets] barcodes GOET005688 & GOET005689 [photos!], HBG [photo!], K barcode K000198948!, L barcode L 0182291!, M

barcode M-0240178, [photo!], P [on 3 sheets] barcodes P00363342!, P00363343! & P01988326!, S [photo!], WAG barcode WAG0057970!, WU [photo!]).

Monanthotaxis enghiana (Diels) P.H.Hoekstra, **comb. nov.** ≡ *Popowia enghiana* Diels in Mildbraed, Wiss. Erg. Deut. Zentr.-Afr. Exped., Bot.: 213. 1911 ≡ *Friesodielsia enghiana* (Diels) Verdc. ex Le Thomas, Fl. Gabon 16: 240. 1969 – Holotype: Democratic Republic of the Congo, Nord- Kivu, Fort Beni a Semliki, 1907–1908, *G.W.J. Mildbraed 2213* (B barcode B 10 0153056!).

= *Unona obanensis* Baker f. in Rendle & al., Cat. Pl. Oban: 4. 1913 ≡ *Oxymitra obanensis* (Baker f.) Sprague & Hutch. in Bull. Misc. Inform. Kew 1916: 154. 1916 ≡ *Richella obanensis* (Baker f.) R.E.Fr. in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 17a(2): 139. 1959 ≡ *Friesodielsia obanensis* (Baker f.) Steenis in Blumea 12: 359. 1964 – Holotype: Nigeria, Cross River State, Oban, 1911, *P.A. Talbot 1246* (BM barcode BM000547069!).

= *Oxymitra grandiflora* Boutique in Bull. Jard. Bot. État Bruxelles 21: 116. 1951 ≡ *Richella grandiflora* (Boutique) R.E.Fr. in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 17a(2): 139. 1959 ≡ *Friesodielsia grandiflora* (Boutique) Steenis in Blumea 12: 359. 1964 – Holotype: Democratic Republic of the Congo, Orientale, Yalibutu, 45 km NW of Yangambi, 22 Jan 1948, *R.G.A. Germain 883* (BR!; isotypes: K [on 2 sheets] barcodes K000913652! & K000913653!, MO!).

= *Popowia mangenotii* Sillans in Bull. Mus. Natl. Hist. Nat., sér. 2, 24: 578. 1953 – Holotype: Central African Republic, Lobaye, Station de Boukoko, Boukoko, 14 Dec 1948, *C. Tisserant (Équipe) 1285* (P barcode P00363339!; isotypes: BR!, K barcode K000913654!, P barcode P00363338!).

= *Popowia mangenotii* f. *concolor* Sillans in Bull. Mus. Natl. Hist. Nat., sér. 2, 24: 580. 1953 – Holotype: Central African Republic, Lobaye, Station de Boukoko, Boukoko, 5 Apr 1951, *C. Tisserant (Équipe) 2062* (P barcode P00363336!; isotypes: BM barcode BM000547068!, BR!, P [on 2 sheets] barcodes P00363335! & P01985781!).

Monanthotaxis glaucifolia (Hutch. & Dalziel) P.H.Hoekstra, **comb. nov.** ≡ *Oxymitra glaucifolia* Hutch. & Dalziel in Bull. Misc. Inform. Kew 1927: 153. 1927 ≡ *Richella glaucifolia* (Hutch. & Dalziel) R.E.Fr. in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 17a(2): 139. 1959 ≡ *Friesodielsia glaucifolia* (Hutch. & Dalziel) Steenis in Blumea 12: 359. 1964 – Holotype: Nigeria, Cross River State, Oban, 1911, *P.A. Talbot 403* (BM barcode BM000843988!).

Monanthotaxis gracilis (Hook.f.) P.H.Hoekstra, **comb. nov.** ≡ *Uvaria gracilis* Hook.f., Niger Fl.: 210. 1849 ≡ *Oxymitra gracilis* (Hook.f.) Sprague & Hutch. in Bull. Misc. Inform. Kew 1916: 154. 1916 ≡ *Richella gracilis* (Hook.f.) R.E.Fr. in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 17a(2): 139. 1959 ≡ *Friesodielsia gracilis* (Hook.f.) Steenis in Blumea 12: 359. 1964 – Holotype: Sierra Leone, *G. Don s.n.* (BM barcode BM000547066!).

= *Oxymitra platypetala* Benth. in Trans. Linn. Soc. London 23: 472. 1862 ≡ *Cleistopholis platypetala* (Benth.) Engl. & Diels, Monogr. Afrik. Pflanzen-Fam. 6: 34. 1901 – Holotype: Sierra Leone, Southern Province, Bagroo river, Apr 1861, *G. Mann 857* (K barcode K00198952!).

= *Unona millenii* Engl. & Diels, Monogr. Afrik. Pflanzen- Fam. 6: 40. 1901 – Holotype: Nigeria, Lagos, Mar 1896, *H. Millen 149* (K n.v.).

= *Oxymitra rosea* Sprague & Hutch. in Bull. Misc. Inform. Kew 1916: 154. 1916 ≡ *Richella rosea* (Sprague & Hutch.) R.E.Fr. in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 17a(2): 139. 1959 ≡ *Friesodielsia rosea* (Sprague & Hutch.) Steenis in Blumea 12: 361. 1964, **syn. nov.** – Holotype: Nigeria, Cross River State, Oban, 1911, *P.A. Talbot 199* (BM barcode BM000547067!).

Note. – Sprague & Hutchinson (1916) described *Friesodielsia rosea* as distinct from *F. gracilis* based on leaf and petal form. These characters are highly variable, however, and all intermediate sizes and shapes are found in *Monanthotaxis gracilis*. We therefore synonymize the former name with the latter.

Monanthotaxis hirsuta (Benth.) P.H.Hoekstra, **comb. nov.** ≡ *Unona hirsuta* Benth. in Trans. Linn. Soc. London 23: 469. 1862 ≡ *Oxymitra hirsuta* (Benth.) Sprague & Hutch. in Bull. Misc. Inf. Kew 1916: 155. 1916 ≡ *Richella hirsuta* (Benth.) R.E.Fr. in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 17a(2): 139. 1959 ≡ *Friesodielsia hirsuta* (Benth.) Steenis in Blumea 12: 360. 1964 – Holotype: Equatorial Guinea, Bioco, Fernando Poo, 1860, *G. Mann 559* (P barcode P00363313!; isotypes: K barcode K000198950!, P barcode P00363314!).

= *Uvaria caillei* A.Chev. ex Hutch. & Dalziel, Fl. W. Trop. Afr. 1: 50. 1927 – Holotype: Guinea, Mamou, Timbou, Kouria, 28 Nov 1905, *A.J.B. Chevalier 14817* (P barcode P00363329!; G barcode G00308375!, L barcode L.1765233!, P [on 3 sheets] barcodes P00363319!, P00363320! & P01954813!).

Monanthotaxis montana (Engl. & Diels) P.H.Hoekstra, **comb. nov.** ≡ *Unona montana* Engl. & Diels in Notizbl. Königl. Bot. Gart. Berlin 2: 296. 1899 ≡ *Oxymitra montana* (Engl. & Diels) Sprague & Hutch. in Bull. Misc. Inform. Kew 1916: 155. 1916 ≡ *Richella montana* (Engl. & Diels) R.E.Fr. in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 17a(2): 139. 1959 ≡ *Friesodielsia montana* (Engl. & Diels) Steenis in Blumea 12: 360. 1964 – Holotype: Cameroon, Central Province, Yaúnde-station, 11 Jan 1894, *G.A. Zenker 431* (B barcode B 10 0153061!).

= *Unona glauca* Engl. & Diels in Notizbl. Königl. Bot. Gart. Berlin 2: 296. 1899, pro parte ≡ *Oxymitra soyauxii* Sprague & Hutch. in Bull. Misc. Inform. Kew 1916: 155. 1916 ≡ *Richella soyauxii* (Sprague & Hutch.) R.E.Fr. in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 17a(2): 139. 1959 ≡ *Friesodielsia soyauxii* (Sprague & Hutch.) Steenis in Blumea 12: 361. 1964 –

Lectotype (designated here): Gabon, Estuaire, Sibange farm, 6 Feb 1881, *H. Soyaux 203* (B barcode B 10 0153059!; isolectotype: K barcode K000198946!).

= *Oxymitra mortehanii* De Wild., Pl. Bequaert. 1: 472. 1922 – Holotype: Democratic Republic of the Congo, Equateur, Dundusana, Sep 1913, *M.G. Mortehan 512* (BR [on 3 sheets] barcodes 000008800459!, 000008800060! & 000008800787!).

Note. – *Unona glauca* was described based on two types, *H. Soyaux 203* and *Dupuis s.n.* Boutique (1951a) assigned the latter specimen to *Monanthotaxis oligandra* Exell., and we therefore designate *Soyaux 203* as the lectotype here to avoid confusion.

Monanthotaxis obovata (Benth.) P.H.Hoekstra, **comb. nov.** ≡ *Unona obovata* Benth. in Trans. Linn. Soc. London 23: 469. 1862 = *Popowia obovata* (Benth.) Engl. & Diels, Monogr. Afrik. Pflanzen-Fam. 6: 44. 1901 ≡ *Friesodielsia obovata* (Benth.) Verdc. in Kew Bull. 25: 18. 1971 – Holotype: Mozambique, Zambezia, foot of Mt. Morambala, 31 Dec 1858, *J. Kirk s.n.* (K [2 sheets] barcodes K000199033! & K000199034!; isotype: B barcode B 10 0153064!).

= *Popowia stormsii* De Wild. in Ann. Mus. Congo Belge, Bot., sér. 5, 1: 242. 1906 – Holotype: Tanzania, Rukwa, Karema, *E.P.J. Storms s.n.* (BR barcode 000008799258!).

Monanthotaxis scamnopetala (Exell) P.H.Hoekstra, **comb. nov.** ≡ *Popowia scamnopetala* Exell in J. Bot. 70(Suppl. 1): 207–208. 1932 ≡ *Exellia scamnopetala* (Exell) Boutique in Bull. Jard. Bot. État Bruxelles 21: 118. 1951 – Holotype: Buco-Zau, Cabinda, Angola, 1873, *J. Gossweiler 6884* (BM barcode BM000547053!; isotypes: COI [photo!], K barcode K000198958!, LISC [on 2 sheets] barcodes LISC 000082 & LISC 000084 [photos!], LISU!).

Monanthotaxis velutina (Sprague & Hutch.) P.H.Hoekstra, **comb. nov.** ≡ *Oxymitra velutina* Sprague & Hutch. In Bull. Misc. Inform. Kew 1916: 156. 1916 ≡ *Richella velutina* (Sprague & Hutch.) R.E.Fr. in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 17a(2): 139. 1959 ≡ *Friesodielsia velutina* (Sprague & Hutch.) Steenis in Blumea 12: 361. 1964 – **Lectotype (designated here):** Sierra Leone, Northern Province, Tonkolili, Makump, 18 Jul 1914, *N.W. Thomas 968* (K barcode K000041195!).

Note. – Sprague & Hutchinson (1916) described this species based on three specimens, *N.W. Thomas 968*, *4701* and *5005*. We did not see the specimen *Thomas 4701*, and *Thomas 968* is better preserved than *5005*.

Sphaerocoryne gracilipes (Benth.) X.Guo & R.M.K.Saunders, **comb. nov.** ≡ *Oxymitra gracilipes* Benth. in Trans. Linn. Soc. London 23: 471–472. 1862 ≡ *Cleistopholis gracilipes* (Benth.) Engl. & Diels in Engler, Monogr. Afrik. Pflanzen- Fam. 6: 34. 1901 ≡ *Richella gracilipes* (Benth.) R.E.Fr. in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 17a(2): 139. 1959 ≡ *Friesodielsia gracilipes* (Benth.) Steenis in Blumea 12: 359. 1964 – Holotype: Equatorial Guinea, Fernando Po, 1860, *G. Mann 251* (K barcode K000198951!).

= *Unona albida* Engl. in Notizbl. Königl. Bot. Gart. Berlin 2: 297. 1899 ≡ *Cleistopholis albida* (Engl.) Engl. & Diels in Engler, Monogr. Afrik. Pflanzen-Fam. 6: 34, t. 12 fig. Aa–h. 1901 ≡ *Oxymitra albida* (Engl.) Sprague & Hutch. in Bull. Misc. Inform. Kew 1916: 153–154. 1916 ≡ *Richella albida* (Engl.) R.E.Fr. in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 17a(2): 139. 1959 ≡ *Friesodielsia albida* (Engl.) Steenis in Blumea 12: 358. 1964 – **Lectotype (designated here):** Cameroon, Bipinde, 1898, *G.A. Zenker 1715* (B barcode B 10 0153057!; isolectotypes: B barcode B 10 0153058!, BM [on 2 sheets] barcodes BM000547065! & BM000843987!, BR barcode 000008800121!, E barcode E00181435 [photo!], G barcode G00308362!, HBG barcode HBG-502539 [photo!], K barcode K000198947!, L barcode L 0187107!, M barcode M-0107909!, NY barcode 0026308 [photo!], P [on 2 sheets] barcodes P00363331! & P00363333!, S!, U barcode U 0269929 [wood sample] n.v., US n.v., WAG barcode WAG0061084!, WU No. 025877 [photo!]).

= *Cleistopholis albida* var. *longipedicellata* Baker f . in Rendle & al., Cat. Pl. Oban: 3–4. 1913 ≡ *Oxymitra longipedicellata* (Baker f.) Sprague & Hutch. in Bull. Misc. Inform. Kew 1916: 154. 1916 ≡ *Richella longipedicellata* (Baker f.) R.E.Fr. in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 17a(2): 139. 1959 ≡ *Friesodielsia longipedicellata* (Baker f.) Steenis in Blumea 12: 360. 1964 – **Lectotype (designated here):** Nigeria, Oban, 1912, *P.A. Talbot 1677* (BM!; isolectotype: BM!).

Key to *Friesodielsia* and closely related genera

1 Receptacle columnar; pollen released as tetrads ..... ***Toussaintia***

1 Receptacle convex or flat; pollen released as monads **2**

2 Sepals connate and enclosing petals in bud..... ***Cleistochlamys***

2 Sepals free, not enclosing petals in bud **3**

3 Leaf venation brochidodromous, with secondary veins anastomosing and linking to form prominent loops **4**

3 Leaf venation eucamptodromous, with parallel secondary veins lacking prominent marginal arches **5**

4 Inflorescences axillary; inner petals coherent above reproductive organs .***Sphaerocoryne***

4 Inflorescences leaf-opposed; inner petals not coherent above reproductive organs .....***Afroguatteria***

5 Petals loosely coherent or free spreading; tropical Africa and Madagascar .....***Monanthotaxis***

5 Petals (partially) enclosing the reproductive organs; tropical Australasia..... **6**

6 Petals three per flower, in one whorl..... ***Dasymaschalon***

6 Petals six per flower, in two whorls..... **7**

7 Monocarps globose or ellipsoid; seeds 1 (rarely 2) per monocarp.....***Friesodielsia***

7 Monocarps moniliform; seeds >1 per monocarp..... ***Desmos***

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Chapter 3 Supplementary information

Species names and GenBank accession numbers of DNA sequences used in this study. Voucher data is given for accessions, for which DNA sequences were newly obtained, using the following format: Taxon name, *collector(s)* and *collector number*, herbarium code,country, largest political subdivision, GenBank accession numbers (*matK*, *ndhF*, *psbA-trnH*, *trnL-F*, *rbcL*, ITS, ETS). –: missing data; *: newly generated sequences.

Afroguatteria bequaertii (De Wild.) Boutique, *J. Lejoly 4865* (BR), Congo, KX786588*, –, –, KX786629*, KX786627*,–, –; ***Cleistochlamys kirkii*** (Benth.) Oliv., *Couvreur & Mbago 58* (WAG), Tanzania, Pwani, –, KM924880, KM924981, KM924948, –, –, –; ***Dasymaschalon acuminatum*** Jing Wang & R.M.K.Saunders, *Chalermglin 490520* (HKU), Thailand, cultivated in the private collection of P. Chalermglin (Bangkok), JQ768546, JQ768587, JQ768625, JQ768706, JQ768666, KX786542*, KX786585*; ***Dasymaschalon borneense*** Nurmawati, *Ambriansyah & Arifin 1687* (L), Indonesia, Kalimantan Timur, JQ768547, –, JQ768626, JQ768707, JQ768667, –, –; ***Dasymaschalon clusiflorum*** (Merr.) Merr., *Ramos & Edaño 45293* (NY), Philippines, Luzon, JQ768548, –, JQ768627, JQ768708, JQ768668, –, –; ***Dasymaschalon dasymaschalum*** (Blume) I.M.Turner, *Saunders 04/26* (HKU), Thailand, cultivated in the private collection of P. Chalermglin (Bangkok), JQ768549, JQ768588, JQ768628, JQ768709, JQ768669, KX786537*, KX786578*; ***Dasymaschalon ellipticum*** Nurmawati, *Kalat & al. 15734* (L), Brunei, JQ768550, JQ768589, JQ768629, JQ768710, JQ768670, KX786540*, KX786581*; ***Dasymaschalon evrardii*** Ast, *Poilane 9615* (P), Vietnam, Annam, JQ768551, JQ768590, JQ768630, JQ768711, JQ768671, KX786536*, KX786577*; ***Dasymaschalon glaucum*** Merr. & Chun, *Chalermglin 510521* (HKU), Thailand, Ratchaburi, JQ768553, JQ768592, JQ768632, JQ768713, JQ768673, KX786533*, KX786574*; ***Dasymaschalon lomentaceum*** Finet & Gagnep., *Saunders 04/5* (HKU), Thailand, cultivated in the private collection of P. Chalermglin (Bangkok), JQ768554, JQ768593, JQ768633, JQ768714, JQ768674, KX786538*, KX786579*; ***Dasymaschalon longiusculum*** (Bân) Jing Wang & R.M.K.Saunders, *Van der Werff & Nguyen 14292* (L), Vietnam, Tonkin, JQ768556, –, JQ768635, JQ768716, JQ768676, KX786543*, KX786586*; ***Dasymaschalon macrocalyx*** Finet & Gagnep., *Saunders 04/6* (HKU), Thailand, cultivated in the private collection of P. Chalermglin (Bangkok), JQ768557, JQ768595, JQ768636, JQ768717, JQ768677, –, KX786573*; ***Dasymaschalon megalanthum*** (Merr.) Jing Wang & R.M.K.Saunders, *Ramos & Edaño 46641* (UC), Philippines, Luzon, JQ768596, JQ768596, JQ768637, JQ768718, JQ768678, –, KX786583*; ***Dasymaschalon oblongatum*** Merr., *Merrill 9703* (NY), Philippines, Luzon, JQ768559, JQ768597, JQ768638, JQ768719, JQ768679, KX786541*, KX786582*; ***Dasymaschalon robinsonii*** Ast, *Poilane 6132* (P), Vietnam, Annam, JQ768561, –, JQ768640, JQ768721, JQ768681, KX786539*, KX786580*; ***Dasymaschalon rostratum*** Merr. & Chun, *Wang 0626* (HKU), China, Guangdong, JQ768562, JQ768599, JQ768641, JQ768722, JQ768682, –, KX786584*; ***Dasymaschalon sootepense*** Craib, *Kerr 1364*

(L), Thailand, Chiang Mai, JQ768563, JQ768600, JQ768642, JQ768723, JQ768683, KX786544*, KX786587*; ***Dasymaschalon trichophorum*** Merr., *Wang 63* (HKU), China, Guangdong, JQ768565, JQ768602, JQ768644, JQ768725, JQ768685, KX786535*, KX786576*; ***Dasymaschalon wallichii*** (Hook.f. & Thomson) Jing Wang & R.M.K.Saunders, *David 257* (P), Malaysia, Johore, JQ768566, –, JQ768645, JQ768726, JQ768686, –, KX786572*; ***Dasymaschalon yunnanense*** (Hu) Bân, *Keßler 3271* (L), Thailand, Chiang Rai, JQ768560, JQ768598, JQ768639, JQ768720, JQ768680, KX786534*, KX786575*; ***Desmos chinensis*** Lour., *Pang N2* (HKU), China, Hong Kong, JQ768567, JQ768603, JQ768646, JQ768727, JQ768687, KX786520*, KX786556*; ***Desmos chinensis*** var. ***lawii*** (Hook.f. & Thomson) Bân, *N.V. Page s.n.* (CAL), India, Western Ghats, KC933937, KC933943, KC933941, KC933939, KC933935, –, –; ***Desmos cochinchinensis*** Lour., *Wang 0612* (HKU), China, Yunnan, JQ768568, JQ768604, JQ768647, JQ768728, JQ768688, KX786519*, KX786555*; ***Desmos dinhensis*** (Finet & Gagnep.) Merr., *Meinke & Chalermglin MEI013* (L), Vietnam, JQ768569, JQ768605, JQ768648, JQ768729, –, –, –; ***Desmos dumosus*** (Roxb.) Saff., *Wang 068* (HKU), China, Yunnan, JQ768570, JQ768606, JQ768649, JQ768730, JQ768689, KX786517*, KX786553*; ***Desmos elegans*** (Thwaites) Saff., *Kostermans 24761* (L), Sri Lanka, Galle, JQ768571, –, JQ768650, JQ768731, JQ768690, –, –; ***Desmos goezeanus*** (F.Muell.) Jessup, *Ford & Cinelli 04780* (BRI), Australia, Queensland, JQ768572, JQ768607, JQ768651, JQ768732, JQ768691, KX786518*, KX786554*; ***Desmos polycarpus*** Jessup, *Sankowsky 3167* (HKU), Australia, cultivated in the private collection of G. Sankowsky, KX786589*, KX786607*, KX786613*, KX786630*, –, –, –; ***Desmos* sp.,** *Sasidharan 3132* (L), India, JQ768573, –, JQ768652, JQ768733, JQ768692, –, –; ***Desmos wardianus*** (Bailey) Jessup, *Sankowsky 2664* (BRI), Australia, Queensland, JQ768574, JQ768608, JQ768653, JQ768734, JQ768693, KX786521*, KX786557*; ***Dielsiothamnus divaricatus*** (Diels) R.E.Fr., *D. Johnson 1903* (OWU), Tanzania, EU169692, –, EU169736, EU169781, EU169759, –, –; ***Exellia scamnopetala*** (Exell) Boutique, *Sosef & al. 2220* (WAG), Gabon, Ogooué- Ivindo, KX761286*, KX787006*, KX786945*, KX786975*, KX761317*, KX761261*, KX761234*; ***Fissistigma polyanthoides*** (A.DC.) Merr., *Keßler 3232* (WAG), Thailand, cultivated in Khao Hin Son Botanical Garden, JQ768575, JQ768609, JQ768654, JQ768735, JQ768694, KX786505*, –; ***Friesodielsia affinis*** (Hook.f. & Thomson) D.Das, *Guo & Pang 20130629-1* (HKU), Thailand, Chanthaburi, KX786590*, –, KX786614*, KX786631*, –, KX786524*, KX786561*; ***Friesodielsia bakeri*** (Merr.) Steenis, *Ng 2015-184* (SING), Singapore, Cultivated in the "Gardens by the Bay" (originally from Philippines), KX786591*, –, KX786615*, KX786632*,–, –, –; ***Friesodielsia biglandulosa*** (Blume) Steenis, *Slik 3809* (L), Indonesia, KX786592*, JQ768610, JQ768655, JQ768736, –, KX786526*, KX786563*; ***Friesodielsia borneensis*** (Miq.) Steenis, *Keßler 2018* (A), Indonesia, ITCI Kenangan, KX786593*, KX786608*, KX786616*, KX786633*, –, KX786529*, KX786566*; ***Friesodielsia calycina*** (King) Steenis, *Latiff 4029* (L), Malaysia, Temenggor Forest Reserve, KX786594*, –, KX786617*, KX786634*, –, KX786522*, KX786559*; ***Friesodielsia cuneiformis*** (Blume) Steenis, *Ardi 54* (HKU), Indonesia, cultivated at Kebun Raya, Bogor, JQ768576, JQ768611, –, JQ768737, JQ768695, KX786528*, KX786565*; ***Friesodielsia desmoides*** (Craib) Steenis, *Keßler 3189* (WAG), Thailand, cultivated

in Khao Hin Son Botanical Garden, JQ768577, JQ768612, JQ768656, JQ768738, JQ768696, KX786523*, KX786560*; ***Friesodielsia discostigma*** (Diels) Steenis, *G. Zenker 3023* (P), Cameroon, Bipinde, KX786595*, –, KX786623*, KX786635*, –, –, –; ***Friesodielsia enghiana*** (Diels) Verdc. ex Le Thomas, *Harris & al. 8708* (E), Gabon, Ogooué-Maritime, JQ768578, JQ768613, JQ768657, JQ768739, JQ768697, KX786510*, KX786546*; ***Friesodielsia filipes*** (Hook.f. & Thomson) Steenis, *Sinclair 40762* (L), Malaysia, Besut, KX786596*, –, –, KX786636*, –, KX786531*, KX786569*; ***Friesodielsia fornicata*** (Roxb.) D.Das, *Tagane & al. 4331* (HKU), Cambodia, Kampot, KX786597*, –, KX786618*, KX786637*, –, KX786525*, KX786562*; ***Friesodielsia glauca*** (Hook.f. &Thomson) Steenis, *Guo & Chen GX074* (SING), Singapore, KX786598*, –, KX786619*, KX786638*, –, KX786532*, KX786570*; ***Friesodielsia glaucifolia*** (Hutch. & Dalziel) Steenis, *Ghogue & al. 500* (WAG), Cameroon, Kupe-Muanenguba, KX761298*, KX787018*, KX786957*, KX786987*, KX761329*, KX761273*, KX761245*; ***Friesodielsia gracilipes*** (Benth.) Steenis, *Tchouto Mbatchou & al. 0202853* (WAG), Cameroon, South Province, KX786599*, KX786609*, KX786620*, KX786639*, –, KX786507*, –; ***Friesodielsia gracilis*** (Hook.f.) Steenis, *Linder 794* (A), Liberia, Bong, KX786600*, KX786610*, KX786621*, KX786640*, –, KX786511*, KX786547*; ***Friesodielsia hirsuta*** (Benth.) Steenis, *Jongkind & Sambolah 12704* (WAG), Liberia, Grand Cape Mount, KX761293*, KX787013*, KX786952*, KX786982*, KX761324*, KX761268*, KX761240*; ***Friesodielsia kingii*** (J.Sinclair) Steenis, *Gardette & al. 2086* (L), Malaysia, Serting, KX786601*, –, –, KX786641*, –, –, KX786568*; ***Friesodielsia latifolia*** (Hook.f. & Thomson) Steenis, *Guo & Chen GX073* (SING), Singapore, KX786602*, –, KX786622*, KX786642*, –, KX786530*, –; ***Friesodielsia longiflora*** (Merr.) Steenis, *Barbon & al. 5701* (L), Philippines, KX786603*, –, –, –, –, –, KX786567*; ***Friesodielsia montana*** (Engl. & Diels) Steenis, *De Wilde & Van der Maesen 10959* (WAG), Gabon, Ogooué-Maritime, KX786604*, KX786611*, KX786624*, KX786643*, –, KX786512*, KX786548*; ***Friesodielsia obovata*** (Benth.) Verdc., *Chase 40526* (K), U.K., cultivated at the Royal Botanic Gardens, Kew, JQ768579, JQ768614, JQ768658, JQ768740, JQ768698, KX786509*, KX786545*; ***Friesodielsia sahyadrica*** N.V.Page & S.Surveswaran, *Page 110949* (CAL), India, Western Ghats, KC933936, KC933942, KC933940, KC933938, KC933934, –, KX786558*; ***Friesodielsia* sp.,** *De Wilde & Van der Maesen 10971* (WAG), Gabon, Ogooué-Maritime, KX761305*, KX787025*, KX786964*, KX786994*, KX761336*, KX761279*, KX761251*; ***Friesodielsia* sp.,** *Thomas 12278* (A), New Guinea, KX786605*, KX786612*, KX786625*, KX786644*, –, KX786527*, KX786564*; ***Friesodielsia velutina*** (Sprague & Hutch.) Steenis, *Jongkind & al. 11824* (WAG), Liberia, Lofa, KX761292*, KX787012*, KX786951*, KX786981*, KX761323*, KX761267*, KX761239*; ***Hexalobus salicifolius*** Engl., *Sosef & al. 2376* (WAG), Gabon, Ogooué-Maritime, EU169694, EU169714, EU169738, EU169783, EU169761, –, –; ***Isolona campanulata*** Engl. & Diels, *UUBG 86GR00240*, cultivated in University of Utrecht Botanical Garden (origin in tropical Africa), AY238963, EU169715, DQ125127, AY231287 and AY238947, AY238954, –, –; ***Mitrella kentii*** (Blume) Miq., *Gardette 2239* (L), Malaysia, Pasoh Forest Reserve, FJ743751, JQ768616, FJ743789, AY841711, AY841633, KX786506*, –; ***Monanthotaxis ambrensis*** (Cavaco & Keraudren) Verdc., *Hong-Wa & al. 221* (WAG),

Madagascar, Antsiranana, KX761295*, KX787015*, KX786954*, KX786984*, KX761326*, KX761270*, KX761242*; ***Monanthotaxis angustifolia*** (Exell) Verdc., *Sinsin 3380* (WAG), Benin, Zou, KX761303*, KX787023*, KX786962*, KX786992*, KX761334*, KX761277*, –; ***Monanthotaxis aquila*** P.H.Hoekstra, *Geerling & Bokdam 2327* (WAG), Ivory Coast, Sassandra, KX761309*, KX787029*, KX786968*, KX786998*, KX761340*, –, KX761254*; ***Monanthotaxis atewensis*** P.H.Hoekstra, *Hall & Lock GC43672* (WAG), Ghana, Eastern Region, KX761307*, KX787027*, KX786966*, KX786996*, KX761338*, –, KX761253*; ***Monanthotaxis atopostema*** P.H.Hoekstra, *Louis 3434* (BR), DR Congo, Orientale, KX761310*, KX787030*, KX786969*, KX786999*, KX761341*, –, KX761255*; ***Monanthotaxis boivinii*** (Baill.) Verdc., *Wohlhauser & Andriamalaza 60232* (WAG), Madagascar, Antsiranana, KX761299*, KX787019*, KX786958*, KX786988*, KX761330*, KX761274*, KX761246*; ***Monanthotaxis buchananii*** (Engl.) Verdc., *Robertson 7544* (WAG), Kenya, coast, JQ768581, JQ768617, JQ768660, JQ768742, JQ768700, KX786514*, KX786550*; ***Monanthotaxis congoensis*** Baill., *Wieringa & al. 7686* (WAG), Gabon, Estuaire, KX761287*, KX787007*, KX786946*, KX786976*, KX761318*, KX761262*, KX761235*; ***Monanthotaxis couvreurii*** P.H.Hoekstra, *Couvreur 762* (WAG), Cameroon, Central Province, KX761311*, KX787031*, KX786970*, KX787000*, KX761342*, KX761281*, KX761256*; ***Monanthotaxis ferruginea*** (Oliv.) Verdc., *Bidgood & al. 2870* (WAG), Tanzania, Kigoma, KX761306*, KX787026*, KX786965*, KX786995*, KX761337*, KX761280*, KX761252*; ***Monanthotaxis filamentosa*** (Diels) Verdc., *Couvreur & al. 417* (WAG), Cameroon, Central Province, KX761291*, KX787011*, KX786950*, KX786980*, KX761322*, KX761266*, KX761238*; ***Monanthotaxis filipes*** P.H.Hoekstra, *Bidgood & al. 1402* (WAG), Tanzania, Southern, KX761315*, KX787035*, KX786973*, KX787004*, KX761346*, KX761284*, KX761259*; ***Monanthotaxis foliosa*** var. ***ferruginea*** (Robyns & Ghesq.) Verdc., *Couvreur & al. 601* (WAG), Gabon, Estuaire, KX761290*, KX787010*, KX786949*, KX786979*, KX761321*, KX761265*, KX761237*; ***Monanthotaxis fornicata*** (Baill.) Verdc., *Couvreur & Mbago 89* (WAG),Tanzania, Morogoro, JQ768583, JQ768619, JQ768662, JQ768744, JQ768702, KX786515*, KX786551*; ***Monanthotaxis heterantha*** (Baill.) Verdc., *Callmander & Phillipson 684* (MO), Madagascar, Mahajanga, KX761297*, KX787017*, KX786956*, KX786986*, KX761328*, KX761272*, KX761244*; ***Monanthotaxis klainei*** (Engl.) Verdc. var. ***klainei*****,** *Fruth 03/1231/c* (M), D.R. Congo, Bandundu, KX761304*, KX787024*, KX786963*, KX786993*, KX761335*, KX761278*, KX761250*; ***Monanthotaxis klainei*** var. ***Lastoursvillensis*** (Pellegr.) Verdc., *Couvreur & al. 599* (WAG), Gabon, Estuaire, KX761289*, KX787009*, KX786948*, KX786978*, KX761320*, KX761264*, –; ***Monanthotaxis komorensis*** P.H.Hoekstra, *Barthelat & al.* 671 (MO), Mayotte, Grande Terre, KX761296*, KX787016*, KX786955*, KX786985*, KX761327*, KX761271*, KX761243*; ***Monanthotaxis latistamina*** P.H.Hoekstra, *Couvreur & al. 565* (WAG), Gabon, Ogooué-Ivindo, KX761288*, KX787008*, KX786947*, KX786977*, KX761319*, KX761263*, KX761236*; ***Monanthotaxis maputensis*** P.H.Hoekstra, *Koning 7766* (WAG), Mozambique, Maputo, KX761308*, KX787028*, KX786967*, KX786997*, KX761339*, –, –; ***Monanthotaxis micrantha*** (Baker) Verdc., *Madiomanana & al. 184* (WAG), Madagascar, Antsiranana, KX761300*, KX787020*, KX786959*, KX786989*, KX761331*, KX761275*,

KX761247*; ***Monanthotaxis parvifolia*** subsp. ***kenyensis*** Verdc., *Luke & Luke 7299* (EA), Kenya, Eastern, KX761312*, KX787032*, KX786971*, KX787001*, KX761343*, –, KX761257*; ***Monanthotaxis pellegrinii*** Verdc., *Breteler & al. 14014* (WAG), Gabon, Ngounié, KX761302*, KX787022*, KX786961*, KX786991*, KX761333*, –, KX761249*; ***Monanthotaxis schweinfurthii*** (Engl. & Diels) Verdc. var. ***schweinfurthii*****,** *Madidi 453* (MO), D.R. Congo, Orientale, KX761313*, KX787033*, –, KX787002*, KX761344*, KX761282*, KX761258*; ***Monanthotaxis schweinfurthii*** var. ***seretii*** (De Wild.) Verdc., *Fay 6534* (WAG), Central African Republic, Bamingui-Bangoran, KX761294*, KX787014*, KX786953*, KX786983*, KX761325*, KX761269*, KX761241*; ***Monanthotaxis schweinfurthii*** var. ***tisserantii*** (Le Thomas) Verdc., *Sosef & al. 2238* (WAG), Gabon, Ogooué-Ivindo, JQ768585, JQ768621, JQ768664, JQ768746, JQ768704, KX786513*, KX786549*; ***Monanthotaxis sororia*** (Diels) Verdc., *Schatz & Lowry 1439* (WAG), Madagascar, Mahajanga, KX761301*, KX787021*, KX786960*, KX786990*, KX761332*, KX761276*, KX761248*; ***Monanthotaxis*** **sp.,** *Couvreur & al. 869* (WAG), Gabon, Woleu-Ntem, KX761314*, KX787034*, KX786972*, KX787003*, KX761345*, KX761283*, –; ***Monanthotaxis trichocarpa*** (Engl. & Diels) Verdc., *Couvreur & al. 14* (WAG), Tanzania, Tanga, JQ768586, JQ768622, JQ768665, JQ768747, JQ768705, KX786516*, KX786552*; ***Monanthotaxis tripetala*** P.H.Hoekstra, *Leeuwenberg 5828* (WAG), Cameroon, East Province, KX761316*, KX787036*, KX786974*, KX787005*, KX761347*, KX761285*, KX761260*; ***Pyramidanthe prismatica*** (Hook.f. & Thomson) J.Sinclair, *Keßler 2773* (L), Indonesia, JN175163, –, JN175178, JN175208, JN175193, –, –; ***Sanrafaelia ruffonammari*** Verdc., *Kayombo & Ntemi Sallu 3027* (MO), Tanzania, Tanga, EU169703, EU169724, EU169746, EU169790, EU169768, –, –; ***Schefferomitra subaequalis*** (Scheff.) Diels, *R.D. Hoogland 10431* (WAG), Papua New Guinea, KX786606*, –, KX786626*, KX786645*, KX786628*, –, KX786571*; ***Sphaerocoryne affinis*** (Teijsm. & Binn.) Ridl., *Ardi 96* (KRB), cultivated in Kebun Raya, Bogor, KM924852, KM924886, KM924990, KM924953, –, –, –; ***Sphaerocoryne blanfordiana*** C.E.C.Fisch., *Chaowasku 36* (L), Myanmar, KM924853, KM924887, KM924991, KM924954, –, –, –; ***Sphaerocoryne gracilis*** (Oliv. ex Engl. & Diels) Verdc., *Robertson 7554* (WAG), Kenya, coast, EU169688, JQ768623, EU169732, EU169777, EU169755, KX786508*, –; ***Sphaerocoryne*** **sp.,** *Saunders 07/4* (HKU), Thailand, cultivated in the private collection of P. Chalermglin (Bangkok), AY518878, JQ768624, FJ743788, AY319185, AY319071, –, –; ***Toussaintia orientalis*** Verdc., *Johnson 1957* (OWU), Tanzania, Bagamoyo, EU169689, EU169710, EU169733, EU169778, EU169756, –, –; ***Uvaria afzelii*** G.Elliot, *UUBG 84GR00334*, cultivated in University of Utrecht Botanical Garden (origin in West Africa), AY238966, EF179310, AY841440, EF179319, AY238957, –, –; ***Uvariodendron molundense*** (Diels) R.E.Fr., *Sosef & al. 2219* (WAG), Gabon, Ogooué-Ivindo, EU169707, EU169727, EU169750, EU169794, EU169772, –, –.

Chapter 4

Revision of the African species of *Monanthotaxis* (Annonaceae)

This chapter is based on:

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(leaf anatomy by E.J. van Marle)

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Abstract

This taxonomic revision of the continental African species of *Monanthotaxis* (Annonaceae) includes 79 species and one variety. Twelve new species (*M. aestuaria*, *M. confusa*, *M. glabra*, *M. hexamera*, *M. mcphersonii*, *M. quasilanceolata*, *M. sterilis*, *M. submontana*, *M. suffruticosa*, *M. ursus*, *M. vulcanica* and *M. wieringae*) are described and 5 new combinations (*M. biglandulosa*, *M. kenyensis*, *M. ochroleuca*, *M. pynaertii* and *M. seretii*) are made. The genus *Monanthotaxis* consists of lianas or lianescent shrubs. It occurs throughout forests in tropical Africa and the highest species diversity is found in the Western Central African rainforests. A key for flowering material is provided, just like a synoptic key including 45 characters. Topics included in the revision are the history of the taxonomy of *Monanthotaxis*, morphology, leaf anatomy, floral biology, distribution and habitat, phylogeny and finally ethnobotany and phytochemistry. Each species is fully described including synonymy, notes on distribution, habitat & ecology, vernacular names, uses and a preliminary IUCN conservation status. Distribution maps are provided for all species, illustrations for 48 species and photographs of 22 species. An index of exsiccatae and an index of the scientific names are included at the end.

4.1 Introducion

The family Annonaceae consists of around 2450 species and occurs worldwide in the tropics (Rainer & Chatrou 2006). Africa currently has 41 genera and c. 400 species of Annonaceae (Couvreur et al. 2012, 2015; Ghogue et al. 2017; Guo et al. 2017) with 39 genera occurring in mainland Africa. Several small and medium-sized genera have been revised in the last 20 years (e.g., Chatrou 1998; Maas et al. 2003; Versteegh & Sosef 2007; Couvreur 2009, 2014; Botermans et al. 2011; Fero et al. 2014; Ghogue et al. 2017; Johnson & Murray 2018). However, the last revision on a continental-wide scale of the three most species-rich genera of Africa, i.e. *Artabotrys* R.Br., *Monanthotaxis* Baill. and *Uvaria* L., was more than 100 years ago (Engler & Diels 1901). *Monanthotaxis* is the second-largest genus in Africa, currently comprising 94 species. The revision of Engler & Diels (1901) of over a century ago described 30 of these species, which were scattered over four different genera at the time. *Monanthotaxis* belongs to the tribe *Uvarieae*, a group of mostly lianescent Annonaceae (Chatrou et al. 2012). The generic delimitation of *Uvarieae* has long been unstable and since 1900 some species have been classified into six different genera. With the increasing availability of DNA sequence-based phylogenies, it has become clear that several Annonaceae genera as historically demarcated were not monophyletic (e.g., *Annona* L., Chatrou et al. 2009; *Brieya* De Wild. and *Piptostigma* Oliv., Ghogue et al. 2017; *Guatteria* Ruiz & Pav., Erkens et al. 2007; *Polyalthia* Blume, Mols et al. 2004; *Uvaria* L., Zhou et al. 2009) and that most morphological characters used to delimit genera are homoplasious. Similarly, the delimitation of *Monanthotaxis* has been adjusted based on phylogenetic analyses including one third of the African species of *Monanthotaxis* (Guo et al. 2017). Two monotypic genera, *Exellia* Boutique and *Gilbertiella* Boutique, and most African species of *Friesodielsia* Steenis were synonymised with *Monanthotaxis* rendering the latter a well-supported monophyletic genus. In most parts of Africa *Monanthotaxis* can easily be recognized by its lianescent habit and glaucous lower side of the leaves. These characters also occur in the genera *Afroguatteria* Boutique and *Sphaerocoryne* (Boerl.) Scheff. ex Ridl., but these can be distinguished by brochidodromous leaf venation, in contrast to eucamptodromous venation in *Monanthotaxis.* *Monanthotaxis* occurs across Africa and Madagascar in tropical forests, but also in riverine forests of drier regions. In this article the 79 species of *Monanthotaxis*, excluding the species from Madagascar and the Comoro Islands, are being revised.

4.2 History of *Monanthotaxis*

The oldest specimens known that are now attributed to *Monanthotaxis* were collected by Adam Afzelius, one of Linnaeus' apostles, in Sierra Leone in 1795. It took more than 200 years before these specimens were identified as *M. barteri* (Baill.) Verdc. Compared to other large genera of Annonaceae, it has taken a long time for the species in *Monanthotaxis* to be

recognized as a coherent group of similar species representing a genus. In 1890 Baillon described the genus *Monanthotaxis* with the sole species *M. congoensis* Baill., with a single whorl of petals and stamens as distinguishing characters (Baillon 1890). At that point, almost 30 species now classified in *Monanthotaxis*, had already been described in other genera (*Clathrospermum* Planch. ex Benth., *Guatteria* Ruiz & Pav., *Oxymitra* (Blume) Hook.f. & Thomson, *Popowia* Endl., *Unona* L. fil. and *Uvaria* L.), yet Baillon did not transfer any of these into the genus he described. As a matter of fact, Baillon described several species currently placed in this genus as members of *Bocagea* St. Hil., *Clathrospermum*, *Popowia*, and *Unona*. Still in 1969 the genus was portrayed as "a small African genus comprising four species" (Le Thomas 1969).

After Baillon several additional species were described culminating in the revision of African Annonaceae by Engler & Diels (1901). In that revision more than 45 names relevant for this revision were included in the genera *Monanthotaxis*, *Oxymitra*, *Popowia* and*Unona*, 30 of which are currently accepted species in *Monanthotaxis*.

In 1932 Exell described the new genus *Enneastemon* Exell (Exell 1932), which he stated was related to the genera *Monanthotaxis* and *Popowia.* It differed from *Popowia* and *Monanthotaxis* in the arrangement of the petals. For his treatment of the Annonaceae in the Flora of Tropical West Africa, Keay (1953) synonymized *Clathrospermum* with *Enneastemon* based on the fact that both genera had the same petal aestivation. Keay & Boutique (1953) proposed to conserve *Enneastemon* over *Clathrospermum* based on four reasons, including that the name of *Clathrospermum* had not been used in 50 years, while *Enneastemon* already had been adopted in several floras, because *Clathrospermum* was incorrectly diagnosed by a single flower, which no longer exists and to avoid at least 9 specific transfers (Keay & Boutique 1953). This proposal got rejected (Rickett 1958), upon which Wild (1959) proposed a second time to conserve *Enneastemon* against *Clathrospermum* stressing out the fact that 4 modern floras had used the name *Enneastemon* and that Keay had consulted many colleagues working on the African flora. This proposal got accepted (Rickett 1961).

Polyalthia section *Oxymitra* Blume was raised to genus level in 1855 by Hooker & Thomson. However, the name *Oxymitra* (Blume) Hook.f. & Thomson had been preceded by the moss genus *Oxymitra* Bisch. ex Lindenb. A proposal to conserve the Annonaceae genus name *Oxymitra* over the moss genus name *Oxymitra* got rejected (Pichi-Sermolli 1954). Fries (1959) considered *Oxymitra* a synonym of *Richella* A.Gray (Gray 1852), and transferred the recognized species. Subsequently, van Steenis (1964) examined the types of *Richella* and *Oxymitra* and decided that *Richella* was distinct from *Oxymitra* based on several characters among which clearly distinct seeds. Therefore, as the name *Oxymitra* was not available, he reassigned those species to *Friesodielsia*.

In 1951 Boutique published three new genera; *Atopostema* Boutique, *Exellia* Boutique and *Gilbertiella* Boutique (Boutique 1951b).

During the fifties and sixties several important treatments of Annonaceae were published in regional floras (Boutique 1951a; Cavaco & Keraudren 1958; Robson 1960; Le Thomas 1969). They all placed the current species of *Monanthotaxis* in several distinct genera with the majority in *Popowia.* Verdcourt (1971b) critically revised those genera and concluded that the Asian species of *Popowia* were distinct from the African species and that the African species were most closely related to *Monanthotaxis*. He therefore united the majority of African species names of *Popowia* with *Monanthotaxis* together with all species of *Enneastemon*. As the name *Enneastemon* has priority over *Clathrospermum* and *Monanthotaxis* is an older name than *Enneastemon*, all species were recombined into *Monanthotaxis*, in which 55 species were then recognized (Verdcourt 1971b). Based on the shape of the stamens Verdcourt (1971b) divided the genus in three subgenera: *Monanthotaxis, Neopopowia* Verdc. and *Neopopowiopsis* Verdc.. Subsequently he subdivided the subgenus *Monanthotaxis* into five sections, mostly based on petal aestivation. Verdcourt did not include *Friesodielsia* into *Monanthotaxis* as the African species of *Friesodielsia* have many stamens with thick connective appendages forming a tight polygonal pavement when viewed from above, while his circumscription of *Monanthotaxis* included only species with less than 40 stamens of which the thecae are visible when viewed from above (Verdcourt 1971b). This classification remained as such for 40 years, till a phylogenetic study (Guo et al. 2017) using one third of the current species diversity found that most African species of *Friesodielsia* were paraphyletic with *Monanthotaxis* and not related to the Asian species of *Friesodielsia.* In addition, this study showed that the genera *Exellia* and *Gilbertiella* clustered within the genus *Monanthotaxis*. This resulted in the transfer of eight African species names of *Friesodielsia* to *Monanthotaxis* as well as the inclusion of the genera *Exellia* and *Gilbertiella* (Guo et al. 2017).

4.3 Phylogeny

A phylogeny based on 5 plastid DNA markers (*matK*, *ndhF*, *rbcL*, *psbA-trnH* and *trnL-F*) and 2 nuclear DNA markers (ETS and ITS regions of nuclear ribosomal DNA) was constructed for 80 specimens representing 75 species of *Monanthotaxis* (Hoekstra et al. 2018). The materials and methods can be found in Hoekstra et al. (2018). In Fig. 1 most outgroup species were trimmed with the exception of the most closely related species of *Monanthotaxis* (for support values see Hoekstra et al. 2018, supplementary fig. S1).

Monanthotaxis is a well-supported monophyletic genus. In Africa it is the only genus of Annonaceae with the combination of a lianescent habit with glaucous leaf undersides and eucamptodromous venation. In Asia this combination of characteristics also occurs in the

genera *Dasymaschalon* (Hook.f. & Thomson) Dalla Torre & Harms*., Desmos* Lour. and *Friesodielsia*, but in those genera the petals, at least partially, enclose the reproductive organs on the upper side, while the petals in *Monanthotaxis* do not enclose the reproductive organs

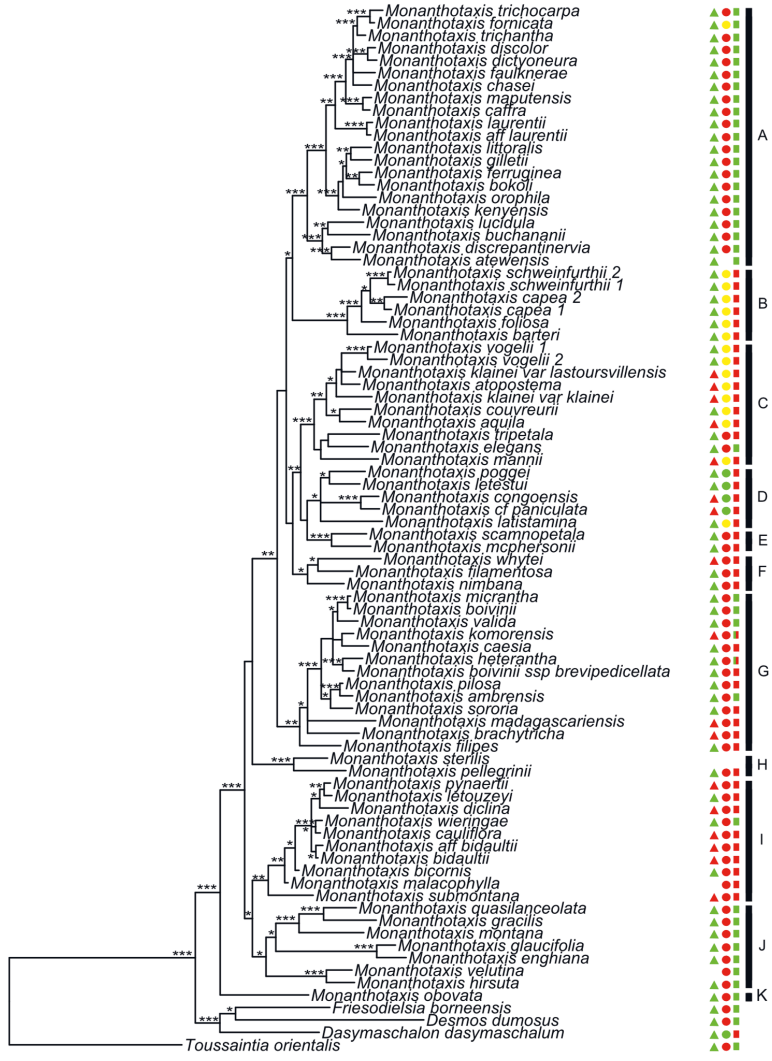


Fig. 1 Bayesian 50% majority rule consensus tree of the genus *Monanthotaxis.* Asterisks at nodes indicate node support, i.e. *** Strong node support, ** moderate node support, * weak node support, see Hoekstra et al. (2018). The letters A to K with adjacent black bars indicate the clades. The triangles, circles and squares represent morphological characters of the species which are of some use to distinguish the clades. Green triangles = staminodes absent, red triangles = staminodes present. Green circles = petals in one whorl, red circles = petals in

two whorls, yellow circles = petals in bud basally in one whorl, at the top outer petals overlapping the inner ones. Green squares = inflorescences extra-axillary or if cauliflorous also extra-axillary inflorescences present, red squares = inflorescences axillary, supra-axillary or cauliflorous, red and green squares = both extra-axillary and axillary inflorescences present.

on the upper side. *Monanthotaxis* can be divided into 11 clades, most of which are well recognizable based on a few morphological characters of the inflorescences and flowers.

The species of the well-supported clade A are recognizable by the extra-axillary inflorescences, bisexual flowers and 6–32 stamens. Based on these characters and other similarities, the unsampled and in this article described species, *M. vulcanica* P.H.Hoekstra and *M. suffruticosa* P.H.Hoekstra, are expected to belong to this clade. A subclade within clade A consists of the Ghanese endemic *M. atewensis* P.H.Hoekstra, the Tanzanian endemic *M. discrepantinervia* Verdc., the central-African *M. lucidula* (Oliv.) Verdc. and the east-African *M. buchananii* (Engl.) Verdc. Within this clade the two subsets of most closely related species, the first two and the last two, show similar disjunct distributions, indicating long-range dispersal or an African wide distribution of their ancestors and subsequent vicariance or a combination of both (Couvreur et al. 2008). These four species share the synapomorphies of pale brown coloured stems and long sepals (more than half the length of the petals). Based on these characters, the Sierra Leonean endemic *M. stenosepala* (Engl. & Diels) Verdc., which was not included in the phylogeny probably also belongs to this subclade.

Both the well-supported clades B and C are recognizable by the axillary inflorescences and the petals basally arranged in one whorl, but with the outer petals overlapping the inner petals distally, whereby the flower buds of clade B are rounded, while those of clade C have an acute tip.

The weakly supported clade D consists of species with both the petals and stamens each in one whorl and contains the type species of *Monanthotaxis* (*M. congoensis* Baill.), however the species *M. latistamina* P.H.Hoekstra has the outer petals overlapping the inner petals just at the tip in the flower bud. The non-included *M. congolana* (Boutique) P.H.Hoekstra is expected to be sister to *M. latistamina* based on that character and as both share papillate petals and stamens and 6 ovules per carpel (Hoekstra et al. 2016). Also, *M. oligandra* Exell is expected to belong to this clade as its inflorescence and flower characters are similar to *M. letestui* Pellegr.

Clade E consists of species formerly included in the genus *Exellia*. These species differ from all other clades by the synapomorphies of having 3 sessile carpels with each more than 10 ovules (versus stipitate carpels and max 8 ovules).

The weakly to moderately supported clade F is highly diverse in morphological features and no single synapomorphy was identified. All species have axillary inflorescences with bisexual

flowers, the flower buds can be rounded or ovoid, the petal size ranges from 3–22 mm, the number of stamens from 9–40 and number of carpels from 2 –30. Staminodes and some cauliflorous flowers only occur in *M. whytei* (Stapf) Verdc. The question remains if this clade will receive higher support, or if the composition of the species will change with additional markers.

In the moderately supported Clade G the South-East Tanzanian *M. filipes* P.H.Hoekstra is sister to the remainder of the clade, entirely consisting of Malagasy endemic species. *Monanthotaxis filipes* has filiform pedicels, a character that also occurs in some of the Madagascar species (Hoekstra et al. 2016). There are no synapomorphies for this clade, however, characters such as lanceolate leaves or an outer whorl of 15 staminodes occur in multiple species and only occur rarely outside clade G.

The well-supported clade H consists of only 2 species, *M. pellegrinii* Verdc., which occurs in Gabon and Cameroon, and *M. sterilis* P.H.Hoekstra, of which flowers nor fruits are known, which occurs in Cameroon, Gabon, Equatorial Guinea and in the Democratic Republic of the Congo. Sofar no synapomorphies were identified for this clade, but once flowers and fruits of *M. sterilis* are discovered, these may quite likely be present.

Species with unisexual flowers are confined to clade I. This clade contains 2 aberrant species, *M. malacophylla* (Diels) Verdc. and *M. bicornis* (Boutique) Verdc. The flowers of the Malagasy species *M. malacophylla* are unknown. It has a dense pubescence of the leaves and stem in common with most of the cauliflorous species from this clade. *Monanthotaxis bicornis* has bisexual flowers and only sparse pubescence on the leaves and stem, but has stamens with the thecae on top. This feature further only occurs in the unsampled *M. zenkeri* P.H.Hoekstra, which has many vegetative characters in common with the cauliflorous species of clade I, including a dense ferrugineous pubescence (Hoekstra et al. 2016). The unsampled *M. mortehanii* (De Wild.) Verdc. and *M. glomerulata* (Le Thomas) Verdc. most probably also belong to clade I because of the unisexual flowers with cauliflorous pistillate flowers. It is interesting to note that the presence of staminodes in clade I only occurs in staminate flowers and not in the pistillate flowers, except for *M. submontana* P.H.Hoekstra, splitting off at the base of the clade, which has some staminodes in the pistillate flowers.

Finally, clades J and K contain species, which were formerly included in *Friesodielsia* and differ from the other clades of *Monanthotaxis* in having more than 40 stamens per flower. Another typical character is the extra-axillary inflorescences. *Monanthotaxis obovata* (Benth.) P.H.Hoekstra of clade K, which is sister to the rest of *Monanthotaxis*, differs from the species in clade J in having a large leaf-like bract. The non-sampled species *M. dielsiana* (Engl.) P.H.Hoekstra and *M. glabra* P.H.Hoekstra most likely belong to clade J, because of the high number of stamens and because of the great similarity between *M. dielsiana* and *M. enghiana*

(Diels) P.H.Hoekstra and the similarity between *M. glabra* and *M. gracilis* (Hook.f.) P.H.Hoekstra.

Verdcourt (1971b) divided *Monanthotaxis* in three subgenera and one subgenus in five sections. This classification is now obsolete as the circumscription of *Monanthotaxis* has changed (Guo et al. 2017). Furthermore, several sections of Verdcourt's classification are polyphyletic, for example representatives of the section *Popowiopsis* now occur in clades A, C, F, G and H. However, we refrain from creating a subgeneric classification as some clades are weakly supported and other clades are morphologically ill-defined.

4.4 Materials and methods

More than 2500 herbarium collections were examined for this revision. Measurements were performed on herbarium specimens, although a few characters were measured on material preserved in spirit. Leaf and flower colour were only described when information was available from herbarium labels or field notes. The colours of dried material were not described as the intensity of the glaucous lower leaf surface and colour of the upper leaf surface greatly varies depending on the drying method. The different colours of dried leaves have been erroneously assigned to different varieties in the past (e.g., Sillans 1953). The collections of the following herbaria have been studied: A, AMD, B, BM, BNRH, BR, BRLU, C, E, EA, FHO, G, GC, K, L, LBV, LISC, LISU, M, MA, MO, NU, NY, P, SRGH, U,US, WAG and YA and types of the following herbaria have been verified using online databases such as https://plants.jstor.org/: COI, CORD, GH, GOET, HBG, LD, MEL, PRE, S, UPS and WU (for herbarium abbreviations see Thiers continuously updated, http://sweetgum.nybg.org/science/ih/). For the species descriptions the same terminology is used as in Hoekstra et al. (2016) with the addition that for the terminology of shapes Ball et al. (1962) is followed with the exception of the term lanceolate. With lanceolate we mean narrowly ovate, shapes which are around 3 times longer than wide or longer and have the widest point below the middle.

Preliminary conservation status assessments were performed for each species following the IUCN Red List Category Criteria (IUCN Standards and Petitions Subcommittee 2016). The Extent of Occurrence (EOO) and Area of Occupancy (AOO) were calculated using GeoCAT (Bachman et al. 2011). The AOO was calculated with a grid cell size of 2 x 2 km. The maps were created with ArcMap v.10.3 (ESRI, https://desktop.arcgis.com/en/arcmap).

4.5 Morphology

4.5.1 Habit

Young plants of almost all species of *Monanthotaxis* are self-supporting; they start as a small shrub-like tree and shift to a climbing habit during later phases of their life-history. This climbing growth habit occurs within the Annonaceae only in the tribe *Uvariae* to which *Monanthotaxis* belongs and a few species in the tribe *Duguetiae* and in the genus *Artabotrys* (Guo et al. 2017). Several species incidentally flower and have fruit as a shrub and in some species, e.g., *M. mannii* (Baill.) Verdc. and *M. obovata*, the majority of fertile specimens have been collected from shrubs. One species has a suffrutescent-like habit, i.e. *M. suffruticosa*, and this habit only very rarely occurs within the Annonaceae, e.g., in some species of *Annona* (Robson 1960). Several collection labels indicate the habit to be a small tree. The question remains if those species remain a tree during their entire life. Depending on the species the plant can reach a length of more than 100 m. Stem diameter has only been recorded for a few collections and rarely for mature lianas. The sparse observations indicate it may reach 10 cm in diam. Stems are normally cylindric but can be angulate in *M. letouzeyi* (Le Thomas) Verdc., *M. oligandra*, *M. trichocarpa* (Engl. & Diels) Verdc. and *M. whytei* and grooved in several species such as *M. atopostema* P.H.Hoekstra, *M. couvreurii* P.H.Hoekstra, *M. diclina* (Sprague) Verdc., *M. gracilis*, *M. klainei* (Engl.) Verdc. and *M. pyaertii* (De Wild.) P.H.Hoekstra. The colour of the stems is dark brown or black in most species, however it is reddish brown in nine species and is pale grey to pale brown in eight species. Several species have lenticels on the stems and branches, but the intensity is highly variable; almost all specimens of *M. caffra* (Sond.) Verdc., *M. fornicata* (Baill.) Verdc. and *M. trichocarpa* have many lenticels on the branches, however, some specimens of these species hardly contain lenticels. Most species from dense forest hardly have lenticels, but you can often still find a few lenticels on the branches, and sometimes a specimen contains one branch, which has many lenticels.

4.5.2 Indument

Young stems, leaves and flowers in most species of *Monanthotaxis* are hairy, but quite some species become glabrous and some species, such as *M. atopostema* appear to have almost entirely glabrous leaves and only very young leaves and branches are pubescent. Only *M. glabra* is from the start entirely glabrous on the stem, leaves and petals. The presence and aspect of indument are useful taxonomic characters to distinguish species within the genus. Most species have appressed hairs, but some have erect hairs, while the hairs of other species are intermediate between appressed and erect. These intermediate types are referred to in the descriptions as “ascending”. Some species have very short papillae, while hair length reaches 2 mm in others. The colour of the indument varies from white to dark brown with

most species having yellow-brown or reddish brown hairs. The hairs are simple with the exception of *M. obovata* in which sometimes the hairs grow in tufts and those tufts can therefore appear stellate as mentioned in some studies (Couvreur et al. 2012). The upper side of the leaves is glabrous in most species, but there may be whitish hairs in very young leaves that are different from the rest of the indument. The lower leaf surface of almost all species is hairy. In some species there are only a few hairs visible near the primary vein on the lower leaf surface.

4.5.3 Leaves

The leaves are petiolate, entire, alternate and distichous as for most Annonaceae. The petiole can vary from 1–13 mm in length and from 0.5–2.9 mm in diam and is mostly grooved on the upper side, but sometimes terete. The leaf blades of most species are obovate or oblong-elliptic, in some species they are narrowly obovate and in several Malagasy species the leaves are narrowly ovate. *Monanthotaxis sterilis* is the only species with linear to narrowly elliptic leaves (length/width ratio >5). Leaves are chartaceous to coriaceous and almost all species have a glaucous lower leaf surface, which can vary from almost white-greyish in *M. enghiana*, to grass-green with only a slight bluish hue in several specimens of *M. buchananii* and *M. foliosa* (Engl. & Diels) Verdc. The combination of a lianescent habit with glaucous leaves occurs in Africa only in the genera *Afroguatteria*, *Monanthotaxis* and *Sphaerocoryne*.

In some species the leaves are weakly to strongly punctate, this becomes more obvious when dried and then the leaf can be entirely covered by bumpy dots. These punctations occur also in some other genera of Annonaceae and they could be caused by osteosclereids or crystals (van Marle 2003).

Leaf blade length can vary from 1.4–35 cm with the majority of species having leaf lengths between 6–15 cm. Leaf blade size can also vary considerably within species. Canopy leaves are often smaller than understory leaves and leaves on young branches are sometimes larger than leaves on older branches. In most species the leaf base varies from cuneate to rounded, or rounded to subcordate. However, in some species the shape of the leaf base is constant, like always subcordate or cuneate to attenuate. The majority of species has thickened margins or gland-like structures near the leaf base, a feature almost exclusively present in *Monanthotaxis*, and not found in other Annonaceae. These are often darker coloured than the rest of the leaf margin, and can vary from only slightly thickened to clearly enlarged globose structures of c. 2 mm diam like in *M. biglandulosa* (Boutique) P.H.Hoekstra. In some species, e.g., *M. tripetala* P.H.Hoekstra, the margins at the base of the leaves can be recurved. In the majority of species the leaf apex is acute to acuminate, occassionally obtuse, rounded or emarginate.

The primary vein is impressed on the upper side of the lamina as in most Annonaceae. On the lower side it often has a yellowish or reddish colour in sicco, contrasting with the glaucous lamina on the lower side. The venation is eucamptodromous, i.e. the secondary veins normally do not join near the leaf margin. The number of secondary veins per side of the leaf varies from 5–23. The angle between midrib and secondary veins is generally between 60 and 75°, but can range from c. 30° in *M. vogelii* to almost 90° in *M. sterilis*. The veins normally curve gradually towards the margin, however in some species the basal half or first two-thirds of the veins are straight, before starting to curve. In a few species and/or collections the secondary veins are hardly visible, e.g., *M. littoralis* (Bagsh. & Baker f.) Verdc. Tertiary venation is in most species distinctly percurrent on the lower side of the lamina. Some species, however, have a venation that is intermediate between reticulate and percurrent and there are also some species, such as *M. littoralis*, with hardly visible tertiary venation. In several species (e.g., *M. foliosa* and *M. dictyoneura* (Diels) Verdc.) the quaternary venation is almost as well-developed as the tertiary venation and these veins are raised on the upper side of the lamina. Therefore, in these species the venation appears percurrent on the lower side and reticulate on the upper side of the lamina, this is described in the descriptions as raised reticulate on the upper side.

4.5.4 Inflorescences

The majority or probably all species of *Monanthotaxis* are monoecious. Most collections of specimens with unisexual flowers that only contain staminate or pistillate flowers, however, for some species there are collections whereby both staminate and pistillate inflorescences were collected from the same liana (e.g., *M. diclina*, *M. letouzeyi* and *M. wieringae* P.H.Hoekstra). For some other species with unisexual flowers all collections contain only staminate or pistillate flowers, it could be that these species are dioecious. The majority of species of *Monanthotaxis* have an inflorescence typical for Annonaceae. Inflorescences appear extra-axillary or leaf-opposed, but inflorescence development starts with a terminal flower, which gets overtopped by an axillary bud (Weberling & Hoppe 1996). In contrast, just over one-third of the species have axillary inflorescences. In other Annonaceae genera these axillary inflorescences have been described as terminal on a short axillary shoot (Chatrou 1998). It is, however, quite unique within the Annonaceae that in *Monanthotaxis* both axillary and terminal inflorescences can occur within the same plant. It is unclear if the axillary inflorescences in *Monanthotaxis* actually are terminal on short axillary shoots and further detailed studies are needed to clarify this. In some species the axillary inflorescences remain on the branches for a long time and flower multiple times on the same spot. These appear ramiflorous after the leaves have fallen off. Other species are entirely cauliflorous, while in some species such as *M. cauliflora* (Chipp) Verdc., *M. confusa* P.H.Hoekstra, *M. diclina* and *M. pynaertii* (De Wild.) P.H.Hoekstra, pistillate inflorescences are cauliflorous and staminate

inflorescences axillary on leafy branches. There are also quite some species with axillary inflorescences, which have a part of their inflorescences 1 or a few mm above the leaf axils, while other species such as *M. letestui* have all their inflorescences a few mm above the leaf axils. This is called supra-axillary in the descriptions and is ontogenetically probably related to axillary inflorescences. These inflorescences should not be confused with extra-axillary in which the inflorescences are not consistently placed a few mm above the axils, but often leaf-opposed. The supra-axillary inflorescences are probably caused by metatopic displacement of axillary inflorescences (Weberling & Hoppe 1996), but ontogenetic studies are needed to verify this. Most species in general have solitary flowers, but the majority of these sometimes have second or third flowers in the same inflorescence at the same time. Other species always have multiple flowers per inflorescence or even many flowers per inflorescence, such as the species with unisexual flowers. The inflorescences with multiple flowers look like fascicles, especially when the sympodial rachis is very short. Because of this resemblance they are called fascicle-like rhipidia in the species descriptions. In some species the rhipidia can superficially resemble a panicle in *M. paniculata* P.H.Hoekstra, a raceme in *M. congoensis* or a glomerule in a few species, e.g., *M. glomerulata.* These inflorescences are referred to as panicle-like rhipidia, raceme-like rhipidia and glomerule-like rhipidia in the descriptions, respectively. The sympodial rachis can vary from almost absent to up to 12 cm, while most species have a rachis length of 1–15 mm. The pedicels normally are up to 20 mm long, but can vary from 1–112 mm. They can be very slender, from 0.2 mm in diam in *M. filipes*, to robust and up to 2.5 mm in diam in *M. hirsuta* (Benth.) P.H.Hoekstra. Species with slender pedicels often have pendulous flowers, as in *M. filipes* and *M. montana* (Engl. & Diels) P.H.Hoekstra.

The inflorescences generally have at least two bracts, the single or multiple bracts on the sympodial rachis just below the articulation are referred to as lower bracts, while the single bract on the pedicel is referred to as upper bract. Often the lower bracts soon drop off, however in some species they are persistent. They are always small and the biggest reach 4 mm in length. The upper bracts are much more variable in size and shape across species. In most species the bract is placed halfway up the pedicel or in the lower half of the pedicel, but in a few species, e.g., *M. faulknerae* Verdc., it is placed in the upper half of the pedicel. In a few species, such as in *M. obovata and M. orophila* (Boutique) Verdc., the upper bract is large and almost leaf-like; the size can range from 0.3 mm in *M. trichanta* (Diels) Verdc. to 30 mm in *M. quasilanceolata* P.H.Hoekstra, while in some species the upper bract is absent. The shape of the upper bract is mostly ovate, but lanceolate in a few species and circular in *M. obovata*.

4.5.5 Flowers

Flower buds are depressed globose to ovoid, sometimes ellipsoid, and rarely deltoid. The flowers are bisexual in the majority of species, but are unisexual in nine species. In the species

with unisexual flowers the staminate flowers are smaller than the pistillate flowers and generally have smaller inflorescences with shorter and more slender pedicels.

The sepals are normally appressed to the flowers, however, in a few species such as *M. montana* they are reflexed at anthesis. In four species the sepals are larger than the petals and cover the petals in bud, but in the majority of species the sepals are much smaller than the petals. The sepals are valvate and are basally connate in about half of the species, however in some species they can be almost entirely connate and then they form a cup-like disc around the flower. In most species the sepals are ovate, but in a few species the sepals are lanceolate (*M. quasilanceolata*). The length of the sepals varies from 0.2–16 mm and the apex is acute or in some species obtuse.

Flowers of *Monanthotaxis* have 6 petals; rarely flowers with 7 petals occur. Only in *M. poggei* Engl. & Diels the flowers have 4 or 5 petals. Variation in the number of petals is rare within genera in the Annonaceae, but occurs for example also in *Uvariopsis* Engl. (Kenfack et al. 2003). The petals can be arranged in one whorl as in *M. poggei* and *M. oligandra*, or in two whorls of three petals each as in the majority of species. Also the flowers of some species have an intermediate form in which the petals are basally placed in one whorl, but in flower buds the outer petals overlap the inner petals at the top, leaving a part of the inner petals visible (e.g., fig 2d, 6c). This intermediate form can vary from where only a small part of the inner petals is visible in flower buds as in *M. mannii*, to the situation where a large part of the inner petals is visible as the outer petals only overlap the inner petals near the top, such as in *M. fornicata* and *M. latistamina*. The inner petals can be highly reduced in *M. tripetala* and *M. bidaultii* P.H.Hoekstra. The petals are hairy on the outside in almost all species and hairy on the inside with the exception of a glabrous patch near the base of the petal in the majority of species. Sometimes there is a difference in the indument between the inner and outer petals. In *M. bokoli* (De Wild. & T. Durand) Verdc. for example the inner petals are entirely glabrous, while the outer petals are densely hairy on the outside and near the apex and margins on the inside. All petals have the same shape when placed in one whorl, but the outer petals are always larger than the inner petals when placed in two whorls or when the outer petals only overlap the inner ones at the top. In some species, such as *M. quasilanceolata*, the outer petals are more than twice as long as the inner petals, while in other species the outer and inner petals are subequal. The outer petals are ovate in most species, but lanceolate in a few species such as *M. quasilanceolata*. The size ranges from 1.5 mm in *M. oligandra* to up to 50 mm in *M. hirsuta*. The inner petals are mostly elliptic, but ovate in quite some species and in other species rhombic, cordate or spathulate; the inner petals are lanceolate in *M. quasilanceolata* and linear-lanceolate in *M. velutina* (Sprague & Hutch.) P.H.Hoekstra. The size ranges from < 0.1–25 mm in *M. hirsuta*, but in most species the size ranges from 1–5 mm. The receptacle is flat or slightly convex in the majority of species and it is torus-like in a few species such as *M.*

montana. In some species, such as *M. paniculata*, the receptacle can be a slightly elevated hexagonal disc.

4.5.6 Stamens

The shape and number of stamens varies greatly within *Monanthotaxis* and is of crucial importance for species identification. This is in contrast to most other Annonaceae genera in which there is hardly any variability in the number of stamens. The number of stamens ranges from 3 in one whorl in *M. bidaultii* to up to 120 in five or six whorls in *M. gracilis*. The majority of species has 9–15 stamens in one whorl or around 24 stamens in three whorls. The length of the stamens ranges from 0.4–2.3 mm, but the majority of species have stamens between 0.8–1.2 mm long. In most species the shape of the stamens is obconical to obovoid (e.g., Fig. 13e–g, 20j–m, 22f–h, 27g). The stamens are clavate in species related to *M. schweinfurthii* (Engl. & Diels) Verdc. (e.g., Fig. 28e–f), oblong in other species (e.g., Figs. 9d–e, 25l) and some species have linear stamens (e.g., Fig. 16h–j). The colour of the stamens is only known in a few species, it is creamy white to yellowish in *M. bidaultii*, *M. caffra*, *M. couvreurii*, *M. foliosa* and *M. mannii*, they have a slightly greenish tinge in *M. latistamina*. *Monanthotaxis poggei* has reddish brown stamens and *M. buchananii*, *M. mcphersonii* P.H.Hoekstra, *M. vogelii* (Hook.f.) Verdc. and *M. whytei* have brownish stamens. The prolonged stamen connective is hairy only in a few species, usually restrained to the inside of the connective. Some species, like *M. zenkeri*, have hairs on all parts of the stamen, including the edges of the thecae (Fig. 35f–h). The filament varies from short to almost absent in *M. hirsuta* to being more than 80% of the total stamen length in *M. hexamera* P.H.Hoekstra (e.g., Fig. 16h–j). The thecae are latrorse to extrorse in the majority of species, rarely introrse. Some species, such as *M. vulcanica*, have the thecae introrse in the inner whorl and extrorse in the outer whorl. In *M. klainei* the thecae are rotated 90º and they open transversally. The majority of species have the two thecae separated by connective tissue, but in *M. bicornis* and *M. pellegrinii* the thecae almost converge at the apex of the stamens (Fig. 7l). In *M. filamentosa* (Diels) Verdc., *M. hexamera* and *M. zenkeri* the thecae cover entirely the apex of the stamens (e.g., Figs. 16h–j, 35f–h). In the species previously belonging to *Friesodielsia* the connective entirely covers the thecae (e.g., Fig. 10k–l), while in the majority of species the thecae are still visible from above. When present, the connective is truncate from above in almost all species, however it is conical in *M. quasilanceolata* (Fig. 26f–g). From the upper view the connective is circular to quadrate in some species and rectangular to ovate in the majority of species as the connective is broadened inward or outward or both. In 15 species staminodes are present as an external whorl to the stamens. In the species with unisexual flowers, the staminodes only occur in the staminate flowers, with the exception of *M. submontana,* which has staminodes in the pistillate flowers. In *M. bidaultii* three staminodes are present, while most species with

staminodes have six to nine staminodes and in some specimens of *M. mannii* 15 staminodes per flower occur. Staminodes are mainly arranged in one whorl, but an ontogenetic study of *M. whytei* (Ronse Decraene & Smets 1990, as *Popowia whitei*) showed that actually two whorls of staminodes are initiated, however the development of the outer whorl already gets interrupted in young flower buds and is not visible in mature flowers. They can vary in length from smaller than 0.1 mm to almost as long as the stamens, but in most species they are between 0.2–0.4 mm long. Thecae-like appendages are not visible in most staminodes, but the staminodes in some species such as *M. congoensis* and *M. submontana* have small thecae-like structures.

4.5.7 Carpels

The number of carpels can vary from 1 in some flowers of *M. nimbana* (Schnell) Verdc. to up to 150 in *M. pynaertii*. Most species have between 6–20 carpels per flower. In most species the carpels are densely hairy, but a group of 11 species has glabrous carpels with sometimes a few hairs near the bases. Some specimens of *M. orophila* have only a hairy outside of the carpels, and a glabrous inside. Carpels were only measured if the stamens were still present in the flowers, the size ranges from 0.8–4 mm. In most species the stigma is present on a 0.1–1.2 mm long style, while some other species have globose sessile stigmas. The style easily breaks off and in some species, of which only limited flower material is present, it is not entirely sure if the stigmas are sessile or not. There are only 3 species with hairy stigmas, i.e. *M. gracilis*, *M. quasilanceolata* and *M. ursus* P.H.Hoekstra, all other species have glabrous stigmas. During the pistillate phase the styles and stigmas are covered in a slimy exudate, probably excreted by the stigmas. The ovules are uniseriate in most species, but *M. mcphersonii* and *M. scamnopetala* (Exell) P.H.Hoekstra have biseriate ovules. The number of ovules varies from 1–9 in the uniseriate species and 12–16 in the biseriate species. The number of ovules is somewhat variable within species and even within flowers of the same plant. In species which normally have 1 ovule per carpel, rarely two ovules can occur, and in species which have normally three to four ovules per carpel, also sometimes one or two ovules per carpel occur.

4.5.8 Fruit

The fruits of *Monanthotaxis* are apocarpous as in most Annonaceae genera and consist of 1 to 26 monocarps (i.e. fruit developing from single carpel). Most species have red fruits when ripe, but some have yellow or orange fruits when ripe. The monocarps are generally moniliform (i.e. constricted between the seeds, resembling a string of beads), however they

are ellipsoid or subcylindric in some species and globose in *M. mcphersonii* and *M. scamnopetala*. The length of the monocarps varies from 7.5–175 mm and they are 4–12 mm in diam and to 26 mm diam in the biseriate species *M. scamnopetala*. The fruiting pedicels are normally thicker than the flowering pedicels and sometimes longer and have a similar but less dense indument. In *M. letestui* the fruiting pedicels reach a length of 120 mm. Monocarps are generally stipitate with stipes ranging from 1–30 mm. Only *M. mcphersonii* and *M. scamnopetala* have sessile monocarps. The stipes are grooved in about half of the species and terete in the other half. The surface of the monocarps is slightly verrucose in the majority of species, smooth in some species and tuberculate-rugose in *M. capea* (E.G.Camus & A.Camus) Verdc. The majority of species has glabrous or glabrescent monocarps. In the species with glabrescent monocarps normally some hairs can still be found on the apex and on the stipe. There are c. 30 species in which the monocarps are densely hairy. In a few species, like *M. filamentosa* and *M. trichocarpa*, these hairs are erect, while the majority of those species has appressed or appressed ascending hairs. The apex of the monocarps is normally apiculate and in some species obtuse. The species with obtuse apices can have apiculate apices when not all ovules have developed into seeds. Most species have 1 or 2 seeds per monocarp, while other species have 1–6 seeds per monocarp. A few species have more than 6 seeds per monocarps such as *M. filamentosa* and *M. scamnopetala*. The seeds are ellipsoid in the majority of species, but globose in a few species and subcylindric in 12 species. The apex is obtuse or apiculate and the colour is generally tawny brown, or reddish brown in a few species. The seeds are generally 5–18 mm long, but can reach up to 27 mm in *M. hirsuta*. The raphe is in most species slightly visible from beginning to end, but in some species completely invisible and in others only visible in the centre of the seed. The ruminations in the seeds are lamellate.

4.6 Leaf anatomy

(E.J. van Marle, Naturalis, Leiden, the Netherlands)

4.6.1 Material and methods

The collections studied are given in Table 1. Samples were taken from mature leaves at 1/3 of the leaf length, seen from the base. These leaf parts were rehydrated by shortly boiling in water and were used for the preparation of transverse sections of the central part of the lamina including the primary vein, as well as cuticular macerations. All sections were bleached and stained with Astra-blue and Safranin. Cuticular macerations were put in equal volumes of acetic acid 100% and 30% hydrogen acid at 60 C° for several days and stained with Sudan IV.

Examination was done with a Leitz Dialux microscope. Slides used in this study are deposited at Naturalis, Leiden. Results are summarized in the description and in Table 2.

Table 1. Vouchers for leaf anatomical study.

Species	Collections	Slide	Barcodes of herbarium sheets
Monanthotaxis barteri	*F.J. Breteler* & *H.C.D. de Wit 5466*	B - 1710	L.1089173; L.1089174; L.1089175; L.1089176
Monanthotaxis boivinii	*J.N. Labat 2665*		WAG0175122
Monanthotaxis capea	*N. Hallé 3555*	B - 1730	L.1089043; L.1089044; L.1089045; L.1089046
Monanthotaxis congolana	*J.L.P. Louis 11414*	B - 1732	L.1089076; L.1089077; L.1089078
Monanthotaxis diclina	*Y. Azizet Issembé 278*		WAG0158117
Monanthotaxis elegans	*G. Zenker 199*	B - 1709	L.1089177; L.1089178; L.1089179; L.1089180
Monanthotaxis hirsuta	*F.J. Breteler* & *H.C.D. de Wit 5302*	B - 1483	L.1089070; L.1089071
Monanthotaxis klainei var. *klainei*	*J.L.P. Louis 6440*	B - 1722	L.1088945; L.1088946; L.1088947; L.1088948
Monanthotaxis obovata	*G.L. Maggs 144*		WAG0108114
Monanthotaxis scamnopetala	*L. Toussaint 205*	B - 1731	L.1089050; L.1089051; L.1089053

Table 2. Leaf anatomical Characters of *Monanthotaxis*.

Species	Primary vein		Lamina			Palisade parenchyma			Spongy parenchyma				Crystals
	1	2	3	4	5	6	7	8	9	10	11	12	13
M. barteri	+	+/+	1,2/1	-/+	+	2	1	+	c/l	e,r	-	-	+/+
M. boivinii	+	-/+	1/1	-/+	+	1	1	+	l	e,r	-	-	+/+
M. capea	+	+/+	1/1	+/+	+	1	1	+	l	e,r	-	-	+/+
M. congolana	+	+/+	1/1	+/+	+	1	1	+	l	r	-	-	+/?
M. diclina	+	+/+	1/1	+/+	-	1	1	+	l	r	-	-	+/?
M. elegans	+	+/+	1/1	+/?	-	1	1	+	l	r	-	-	+/+
M. hirsuta	-	+/-	1/1	?/?	+	2	1	+	l	r	-	-	+/+
M. klainei	-	+/+	1/1	+/+	-	2	1	+	l	e	-	-	+/+
M. obovata	+	+/+	1/1	+/+	-	1	1	-	l	-	-	-	+/+
M. scamnopetala	-	+/+	1/1	+/+	+	1	1	+	l	r	-	-	+/+

+ = present; - = absent; for the characters 2, 3, 4, 13: the data are given both for the adaxial and the abaxial side, left and right of the slash, respectively. 1. Oil cells; 2. Indument adaxially/abaxially; 3. Cuticula thickness (adaxially/abaxially): 1 = < 4 µm; 2 = 4-8 µm; 3 = > 8 µm; 4 = cuticula absent; 4. Indument adaxially/abaxially; 5. Papillae; 6. 1 = isobilateral; 2 = dorsiventral; 7. Number of layers of palisade parenchyma adaxially: 1 = 1 or 2 layers; 2 = 3 or 4 layers; 8. Oil cells; 9. Structure: c = compact; l = loose; 10. Shape of oil cells: e = elongate, el = elliptical, r = rounded; 11. Osteosclereids; 12. Silica bodies; 13. Crystals in adaxial/abaxial epidermis.

4.6.2 Description of the leaf anatomy

1 – In surface view

Indument mostly present on the abaxial side, regularly also but less dense at the adaxial side, consisting of appressed or upright, uniserate simple, one- to more-cellular trichomes, 100–800 µm long, apical cell pointed; often the trichomes are easily shed, especially on the adaxial side. *Cuticle* 1–2(–5) µm above, 0–2(–3) µm abaxially, with smooth outer surface. *Unspecialized epidermal cells* polygonal (more or less 4-sided to jigsaw like); adaxial cells 10–40 by 7–25 µm, abaxial cells 15–40 by 10–25 µm; the anticlinal walls on both sides straight to undulate. *Stomata* restricted to the abaxial side and regularly distributed, paracytic with 2–4 subsidiary cells, rounded to elongated, not sunken, 15–25 by 10–15(–25) µm, 100–400/mm^2. *Crystals* often present in epidermal cells as crystal sand, druses, or rhombic crystals of varying shape and size

2 – In transverse section

Lamina dorsiventral or isobilateral. *Epidermis* adaxially 1-layered, smooth, (2–)5–20(–30) µm thick, abaxially 1-layered, (2–)4–15(–18) µm, smooth to papillate. *Stomata* on the same level as the unspecialized epidermal cells. *Mesophyll* composed of 1- (or 2-)layered palisade parenchyma and (1–)2–6(–10) layers of loosely packed sponge parenchyma; oil cells occur in the palisade parenchyma, in the sponge parenchyma or in both tissues; sclereids and silica-bodies absent. *Primary vein* consisting of one vascular bundle surrounded by a continuous sclerenchyma layer; vascular bundle arc-shaped with interrupted phloem at the adaxial side of the xylem tissue; adaxial side of the primary vein sunken to flattened, at the abaxial side often collenchyma present, as well as a layer of flattened parenchyma cells, oil cells and druses. *Terminal veins* collateral with narrow sclerenchymatic caps or sheaths; sheaths sometimes connected with both adaxial and abaxial epidermis by collenchymatic or sclerenchymatic extensions. *Crystals* often found in the epidermal cells as druses, or rhombic crystals of varying shape and size (10–25 µm diam); in the sponge- and palisade parenchyma mostly absent.

4.6.3 Discussion

The results presented here are in accordance with, and in addition to those given earlier by van Setten & Koek-Noorman (1986). *Monanthotaxis* falls within the leaf anatomical variation as known for the Neotropical genera of the Annonaceae (van Setten & Koek-Noorman, 1986), as well as the Palaeotropical genera (van Marle, unpublished results).

Leaf anatomically, *Monanthotaxis* is recognizable by a combination of characters: the topography of the primary vein, the presence of large crystals in the epidermis, especially on the adaxial side, and the total absence of sclereids and silica. Within the Annonaceae these large crystals are furthermore only found in *Cyathostemma* Griff., *Friesodielsia* and *Schefferomitra* Diels.

There are no individual features by which *Monanthotaxis* can be distinguished from the closely related Asian genus *Friesodielsia* with certainty on the base of leaf anatomy. Papillae are not found within *Friesodielsia*, but they also lack in many species of *Monanthotaxis*.

The punctation of the leaves present in several species of *Monanthotaxis* are caused by the large cristals in the epidermis on the adaxial side of the leaves.

4.7 Floral biology, pollination and dispersion

No studies on the floral biology and pollination of *Monanthotaxis* have been published. In related genera of *Monanthotaxis*, such as *Desmos* and *Friesodielsia*, flowers are protogynous, entering the pistillate phase first followed by a non-receptive interim phase and finally the staminate phase (Saunders 2012). This also seems to be the case for the majority of species in *Monanthotaxis*, as many flowers on herbarium specimens were seen either in the pistillate or staminate phase, never in both. Furthermore, the stamens were always closed in flowers during the pistillate phase. The pollinators of *Monanthotaxis* are unknown. In other genera within the *Uvarieae*, most pollinators reported are small beetles, but in the genus *Uvaria* also some reports of pollination by bees and cockroaches exist (Saunders 2012). *Monanthotaxis* exhibits a high variety in number of stamens, shape of stamens and size of flowers and stamens, which could suggest that different pollination strategies exist within the genus, such as different insect or even wind or self-pollination (Hoekstra et al. 2018).

The fruits of most species of *Monanthotaxis* are red when ripe and have a thick fleshy pericarp, which tastes and smells sweet and acid. This suggest that endozoochory is the main dispersal mechanism. There are multiple reports of *Monanthotaxis* fruits being eaten by primates, such as man, gorillas, chimpansees and several species of monkeys, galagos and lemurs. Humans eat the fruit of at least three species of *Monanthotaxis*, and there are a few reports of fruits being eaten by birds and rodents (see Table 3).

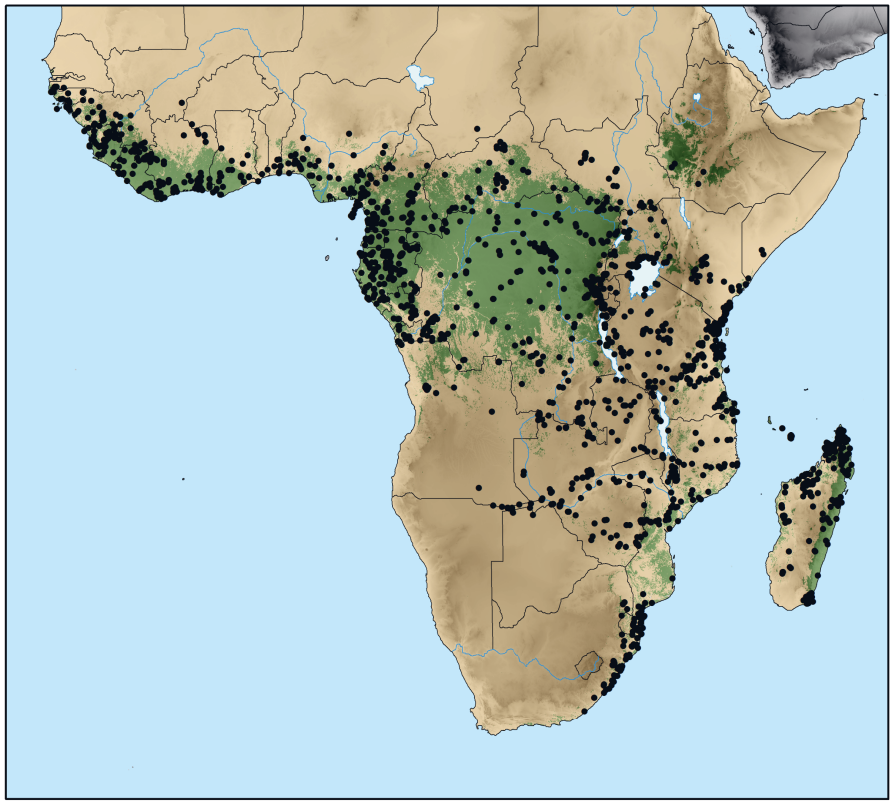
Table 3. List of animal species recorded to eat fruits of *Monanthotaxis*.

Species of *Monanthotaxis*	Eaten by	Reference
M. barteri	Chimpanzee (*Pan troglodytes*)	Arroyo-Rodríguez et al. 2015
M. boivinii	Northern sportive Lemur (*Lepilemur septentrionalis*)	Dinsmore et al. 2016
M. caffra	Human (*Homo sapiens*)	Van Wyk 2011
M. congoensis	Gorilla (*Gorilla gorilla*)	Rogers et al. 1990
	Mandrill (*Mandrillus sphinx*)	Rogers et al. 1996
M. ferruginea	Chimpanzee (*Pan troglodytes*)	McLennan 2013
M. fornicata	Northern greater galago (*Otolemur garnettii*)	Harcourt & Nash 1986
	Zanzibar bushbaby (*Galago zanzibaricus*)	Harcourt & Nash 1986
M. cf. *malacophylla*	Collared brown lemur (*Eulemur collaris*)	Bollen 2007
	Fat-tailed dwarf lemur (*Cheirogaleus medius*)	Bollen 2007
	Malagasy blue pigeon (*Alectroenas madagascariensis*)	Bollen 2007
	Black rat (*Rattus rattus*)	
	Webb's tuft-tailed rat (*Eliurus webbi*)	Bollen 2007
		Bollen 2007
M. obovata	Human (*Homo sapiens*)	Facciola 1998
M. poggei	Chimpanzee (*Pan troglodytes*)	Foerster et al. 2016
	Human (*Homo sapiens*)	Ruffo et al. 2002
M. schweinfurthii	Monkeys	Gautier-Hion et al.1985
	Moustached Guenon (*Cercopithecus cephus*)	Sourd & Gautier-Hion 1986
M. valida	Brown lemur (*Eulemur fulvus*)	Valenta et al. 2015

4.8 Distribution and habitat

Monanthotaxis occurs across tropical Africa and Madagascar and can be found in all major tropical rainforests. In the drier parts of tropical Africa, such as the Sahel zone, species are mostly confined to gallery forest along rivers (Map 1). The highest diversity of 54 species occurs in the central African rainforests with 29 species in both the Democratic Republic of the Congo and in Cameroon, while 27 species have been found in Gabon. The second highest diversity is in the upper Guinean forest of western Africa with 15 species occurring in Ivory Coast and several additional species in Liberia, Sierra Leone and Guinea. It has to be mentioned that several sterile specimens have been collected from Liberia, which cannot be assigned to any of the known species of *Monanthotaxis*. Therefore, the actual number of species in that part of Africa will almost certainly be higher. Madagascar also has a high diversity with currently 11 described species , but at least 10 additional species will have to be described, which, however, is beyond the scope of this revision. The fourth centre of diversity of *Monanthotaxis* is the eastern Arc Mountains of Tanzania with 14 species. The highest number of endemics besides Madagascar occurs in Gabon with seven species and third is

Cameroon with six endemic species. Other countries with endemic species are Tanzania with four species, the Democratic Republic of the Congo with three species, Ivory Coast with two endemic species and in both Ghana and Sierra Leone one endemic species occurs. There are only a few species with wide distributions and only *M. enghiana* and *M. laurentii* (De Wild.) Verdc. occur from Guinea in West Africa up to the east of the Democratic Republic of the Congo in Central Africa. In east Africa *M. buchananii* and *M. obovata* have wide distributions.



Map 1 Distribution of the genus *Monanthotaxis* based on all georeferenced herbarium collections seen for this study, including species from Madagascar and surrounding islands not revised here.

Most species occur in tropical rain forests and quite some species also occur in gallery forests. Nine species occur in coastal forests or thickets and a few species in east Africa occur in drier mixed woodlands. *Monanthotaxis buchananii* and *M. obovata* can occur in savannahs and open woodland in east Africa. Most species occur in the lowlands below 1000 m, but a few

species occur in submontane forests with as highest *M. orophila* occurring in Afromontane forest up to 2700 m above sea level in Rwanda.

4.9 Ethnobotany and phytochemistry

Most species of *Monanthotaxis* have sweet tasting fruits and of three species it is known that they are locally eaten, i.e. *M. caffra, M. obovata* and *M. poggei* (Facciola 1998; Ruffo et al. 2002; Van Wyk 2011). The wood of most species in East Africa is also used to construct withies, storage pots and is used for firewood (Ruffo et al. 2002). *Monanthotaxis fornicata* is locally planted in Kenya for medicinal purposes (Wekesa et al. 2015), the outer root bark is scraped off, burnt and the smoke is inhaled against mental diseases (Hedberg et al. 1982) and powdered leaves are used against snake bites (Hedberg et al. 1982; Kimaro & Lulandala 2013). Also the roots of *M. obovata* and *M. poggei* are used against snake-bites (Ruffo et al. 2002). The boiled roots of these two species and of an unidentified species of *Monanthotaxis* from Ghana are used to treat stomach aches (Ruffo et al. 2002; Asase et al. 2005). There are three species of *Monanthotaxis,* which are used locally to treat malaria, i.e. *M. heterantha* (Baill.) Verdc. in Madagascar, *M. kenyensis* (Verdc.) P.H.Hoekstra in Kenya and an unidentified species of *Monanthotaxis* from Ghana (Rasoanaivo et al. 1992; Asase et al. 2005; Mungai 2015). Recent investigations indeed have found antiplasmodial effects of extracts from leaves and twigs of *Monanthotaxis kenyensis* (Mungai 2015) and leaves and bark of *M. obovata* (Joseph et al. 2007). Currently, phytochemical constituents have been identified for 14 species of *Monanthotaxis* (Table 4). Several of these constituents can have potential benefits for humanity. Some flavonoids of *M. littoralis* have antifungal effects on mycotoxigenic fungi of maize (Clara et al. 2014) and initial studies show that the oil extracts of *M. littoralis* are potentially safe for mice (Nakavuma et al. 2016). Oil extracts of *M. parvifolia* (Oliv.) Verdc. from Benin (but see note under the species description of *M. parvifolia*) show acaricidial activity against cattle ticks. Furthermore, several species of *Monanthotaxis* contain crotepoxides, which have cancer-cell inhibiting activities as has been shown for *M. congoensis* (Starks et al. 2012) and *M. fornicata* (Choi et al. 2015).

Table 4. Phytochemical studies performed on *Monanthotaxis* species.

Species of *Monanthotaxis*	References
Monanthotaxis buchananii	Liang et al. 1988
Monanthotaxis caffra	Mulholland et al. 2000
Monanthotaxis capea	Mevy et al. 2004
Monanthotaxis cauliflora	Panichpol & Waterman 1978
	Waterman & Pootakahm 1979a
	Waterman & Pootakahm 1979b
Monanthotaxis congoensis	Starks et al. 2012
Monanthotaxis diclina	Fournier et al. 1997
Monanthotaxis discolor	Parmena et al. 2012
Monanthotaxis enghiana	Fleischer et al. 1997
Monanthotaxis fornicata	Choi et al. 2015
Monanthotaxis kenyensis	Mungai 2015
Monanthotaxis littoralis	Clara et al. 2014
Monanthotaxis obovata	Joseph et al. 2007
Monanthotaxis cf. *parvifolia*	Dedome et al. 2017
Monanthotaxis velutina	Achenbach & Hemrich 1991

4.10 Taxonomic treatment

4.10.1 ***Monanthotaxis*** Baill.

Monanthotaxis Baill. (1890) 878. —Type: *Monanthotaxis congoensis* Baill.

Clathrospermum Planch. ex Benth. in Benth. & Hook.f. (1862) 29, nom. rej. (versus *Enneastemon* Exell (1932), nom. cons.) — Type: *Clathrospermum vogelii* (Hook.f.) Planch. ex Benth. (= *Monanthotaxis vogelii* (Hook.f.) Verdc.).

Enneastemon Exell (1932) 209, nom. cons. (versus *Clathrospermum* Planch. ex Benth.) — *Monanthotaxis* Baill. subgen. *Monanthotaxis* sect. *Enneastemon* (Exell) Verdc. (1971b) 20. — Type: *Enneastemon angolensis* Exell (= *Monanthotaxis seretii* (De Wild.) P.H.Hoekstra).

Exellia Boutique (1951b) 117. — Type: *Exellia scamnopetala* (Exell) Boutique (= *Monanthotaxis scamnopetala* (Exell) P.H.Hoekstra).

Atopostema Boutique (1951b) 121. — *Monanthotaxis* Baill. subgen. *Monanthotaxis* sect. *Atopostema* (Boutique) Verdc. (1971b) 30. — Type: *Atopostema klainei* (Engl.) Boutique (= *Monanthotaxis klainei* (Engl.) Verdc.).

Gilbertiella Boutique (1951b) 124. — Type: *Gilbertiella congolana* Boutique (= *Monanthotaxis congolana* (Boutique) P.H.Hoekstra).

Friesodielsia Steenis subgen. *Amblymitra* Verdc. (1971b) 18. — Type: *Friesodielsia obovata* (Benth.) Verdc. (= *Monanthotaxis obovata* (Benth.) P.H.Hoekstra).

Friesodielsia Steenis subgen. *Oxymitropsis* Verdc. (1971b) 18. — Type: *Friesodielsia enghiana* (Diels) Verdc. (= *Monanthotaxis enghiana* (Diels) P.H.Hoekstra).

Monanthotaxis Baill. subgen. *Monanthotaxis* sect. *Popowiopsis* Verdc. (1971b) 23. — Type: *Monanthotaxis trichocarpa* (Engl. & Diels) Verdc.

Monanthotaxis Baill. subgen. *Monanthotaxis* sect. *Diclinanthus* Verdc. (1971b) 30. — Type: *Monanthotaxis cauliflora* (Chipp) Verdc.

Monanthotaxis Baill. subgen. *Neopopowia* Verdc. (1971b) 31. — Type: *Monanthotaxis filamentosa* (Diels) Verdc.

Monanthotaxis Baill. subgen. *Neopopowiopsis* Verdc. (1971b) 31. —Type: *Monanthotaxis bicornis* (Boutique) Verdc.

Lianas, scandent shrubs or shrubs, rarely small trees or a suffrutex, 0.2–100 m long or more, to 10 cm diam; bark pale grey, pale brown, reddish brown, dark brown or black; young twigs terete, angular or grooved, densely to sparsely covered with appressed to erect, simple or rarely tufted hairs, soon becoming glabrous in the majority of species. *Leaves* distichous, simple, entire, petiolate, estipulate; petiole mostly grooved above, sometimes terete; lamina obovate to oblong-elliptic, sometimes oblanceolate or lanceolate and in *M. sterilis* linear to narrowly elliptic, chartaceous to coriaceous, sometimes weakly or strongly punctate, upper side glabrous or sometimes sparsely to densely covered with erect or appressed hairs, lower side glaucous and glabrous or more frequently sparsely to densely covered with erect or appressed hairs, base attenuate, cuneate, rounded or subcordate, often with thickened margins near the base or rarely margins recurved, apex obtuse, rounded, acute or acuminate, rarely emarginate; venation eucamptodromous, primary vein impressed above, secondary veins distinct or sometimes indistinct, 5–23 on either side of primary vein, angle of secondary veins with primary vein (30–)60–75 (–90)°, straight, curving or first straight and then curving, tertiary venation flat to raised above, percurrent, reticulate, sometimes hardly visible. *Inflorescences* cauliflorous, ramiflorous, axillary, extra-axillary or terminal, 1- to many-flowered; pedicels bibracteate, slender or thick, almost glabrous to densely covered with appressed or erect hairs; lower bracts ovate or elliptic or lanceolate, soon falling off, sometimes persistent; upper bract ovate, or sometimes lanceolate or circular, small, but sometimes leaf-like and up to 30 mm long, placed halfway or in lower part of pedicel, sometimes in upper part of pedicel or absent. Flower *buds* globose, depressed globose, ovoid,

sometimes ellipsoid, deltoid or rarely lanceoloid. *Flowers* actinomorphic, bisexual or unisexual, perianth consisting of one whorl of sepals and one or two whorls of petals; sepals 3 or rarely 2, valvate, free or connate, ovate or lanceolate, appressed or sometimes reflexed, much smaller than petals or sometimes as large or larger than petals; petals 6, in one or two whorls, or rarely 3, 4 or 5 in only a single whorl, mostly hairy on the outside and near the apex and margins on the inside, rarely entirely glabrous, if in two whorls then outer petals slightly or much larger than inner petals, inner petals sometimes absent; outer petals ovate or sometimes lanceolate; inner petals elliptic, ovate, rhombic, cordate or sometimes lanceolate or linear-lanceolate; receptacle flat, slightly convex, an elevated hexagonal disc or rarely torus-like; stamens 3–120, arranged in 1–6 whorls, appearing spiral-like if more than 30 stamens, obconical, obovoid, clavate, linear, linear-oblong or oblong; filament very short to long, thecae extrorse, latrorse or sometimes introrse, connective apex truncate, or rarely conical or absent, glabrous or sometimes hairy; staminodes absent or sometimes present, to 15, in one or rarely two external whorls, glabrous or hairy; carpels 1–150, free, hairy or sometimes glabrous, ovary 1-locular with 1–16 ovules, uniseriate or rarely biseriate, basal or lateral; stigma spheroid or elongate, glabrous or rarely hairy. *Fruit* apocarpous, consisting of 1 to numerous, indehiscent, stipitate or rarely sessile monocarps, yellow, orange or red, moniliform, sometimes globose, ellipsoid or subcylindric, glabrous or covered with appressed, ascending or erect hairs, smooth or sometimes verrucose; stipes terete or grooved, sometimes absent; seed 1, basal, or 1–16, lateral, uniseriate or rarely biseriate, globose, ellipsoid or subcylindric, smooth, yellowish brown or ochre brown, apex rounded or apiculate; raphe impressed or flat; endosperm ruminations lamellate.

Distribution — About 100 species endemic to Africa (including Madagascar). Seventy-nine species in (sub-)tropical Africa, from Senegal in the west, to Somalia in the east and from south Mali in the north to the Eastern Cape province in South Africa in the south. The 11 species described to date and more than 10 undescribed species from Madagascar and the Comores are not treated in this revision.

Habitat & Ecology — Lowland rain forests, gallery forests, swamps, sometimes submontane forest, open woodlands, coastal shrub or savannahs. At low elevations up to 2700 m.

4.10.2 Key to the species

1. Leaf blades linear to narrowly elliptic, at least 5 times longer than wide, widest in middle or lower half of the leaf, secondary veins almost perpendicular to the primary vein (>75°) .....
.....67. *M. sterilis*
1. Leaf blades oblong, elliptic, obovate or oblanceolate, if blades 5 times longer than wide,

than widest in upper half of the leaf and secondary veins having acute angle with the primary vein (<60°) 2

2. Flowers unisexual 3
2. Flowers bisexual 12

3. Young branches covered with erect hairs 0.4–1.2 mm long..... 4
3. Young branches covered with appressed to ascending hairs 0.05–0.2(–0.3) mm long 6

4. Staminate flowers with 31–40 fertile stamens in 4 whorls; young branches with erect, reddish brown hairs, c. 0.4 mm long.....44. *M. letouzeyi*
4. Staminate flowers with 6 stamens in 1 whorl and an external whorl of 12(–16), small (0.2–0.5 mm long) staminodes; young branches covered with yellowish brown hairs or if reddish brown then hairs > 0.5 mm long 5

5. Young branches covered with yellowish brown hairs 0.4–0.6 mm long; connective sparsely hairy; carpels 80–100 ..... 19 *M. diclina*
5. Young branches covered with reddish brown hairs 0.6–1.2 mm long; connective glabrous; carpels 95–150 .....61 *M. pynaertii*

6. Most pistillate flowers with some staminodes or rarely a stamen (check at least 2 flowers) .....68. *M. submontana*
6. Pistillate flowers always lacking stamens and staminodes..... 7

7. Petiole 2.4–2.9 mm diam; leaf base rounded to subcordate; pistillate inflorescences densely covered with erect hairs 0.4–0.6 mm long ..... 51. *M. mortehanii*
7. Petiole 0.9–2.1 mm diam; leaf base rounded to cuneate; pistillate inflorescences covered with appressed hairs, or erect hairs < 0.3 mm long..... 8

8. Staminate flowers with 3–6 stamens; pistillate flowers with < 80 carpels 9
8. Staminate flowers with > 10 stamens (unknown for *M. glomerulata*); pistillate flowers with > 80 carpels 10

9. Staminate flowers with 3 stamens and 3 staminodes; pistillate flowers with 1, 2 or rarely 4 ovules per carpel; stipes 3.5–5 mm long .....7. *M. bidaultii*
9. Staminate flowers with 6 stamens and 12 staminodes; pistillate flowers with 5 or 6 ovules per carpel; stipes (6–)9–12 mm long .....13. *M. cauliflora*

10. Stamens 36, in 3 or 4 whorls; leaf base cuneate; petiole 0.9–1.3 mm diam..... .....78. *M. wieringae*
10. Stamens 19–22, in two whorls (but staminate flowers unknown in *M. glomerulata*); leaf base rounded; petiole 1.5–1.9 mm diam..... 11

11. Carpels > 100; petiole 7–10 mm long; pistillate inflorescences with sympodial rachis 5–15 mm long; flowering pedicels 21–25 mm long ..... 15. *M. confusa*
11. Carpels 80–95; petiole 5–7 mm long; pistillate inflorescences with sympodial rachis to 5 mm long; flowering pedicels to 10 mm long..... 35. *M. glomerulata*

12. Inflorescences cauliflorous, axillary or supra-axillary and then consistently 1–8 mm above the leaf axils..... 13
12. Inflorescences leaf-opposed or extra-axillary, but not consistently a few mm above the leaf axils 46

13. Carpels 65–85; 1 or 2 stamens and additionally 0–12 staminodes per flower in 1 whorl. .....68. *M. submontana*
13. Carpels 1–36; at least 6 well-developed stamens per flower, staminodes present or absent 14

14. Flower bud just before anthesis with only 3 petals visible, inner petals completely covered by outer petals, inner petals normally clearly different in shape and smaller than outer petals 15
14. Flower bud just before anthesis with at least a part of one of the inner petals visible and thus 4–6 petals visible (only a slight difference present in shape and size between inner and outer petals), or 4–6 petals in one whorl..... 26

15. Thecae converging on top of the stamen, connective not visible from above, or if visible, then width of connective much smaller than width of filament 16
15. Thecae not converging on top of the stamen, connective clearly visible from above and as wide or wider than filament..... 20

16. Filaments > 1 mm long, much longer than half of the total length of the stamens..... 17
16. Filaments < 1 mm long, about half of the total length of the stamens 18

17. Young branches covered with erect hairs 0.7–1.4 mm long; stamens 17–46; carpels 8–14 .....28. *M. filamentosa*
17. Young branches covered with appressed to ascending hairs 0.1–0.2 mm long; stamens 6; carpels 6 .....37. *M. hexamera*

18. Stamens 35, in 3 or 4 whorls, with some hairs near the edges of the thecae; young branches covered with erect hairs..... 79. *M. zenkeri*
18. Stamens 15–24, in 1 or 2 whorls, glabrous; young branches covered with appressed to ascending hairs..... 19

19. Young branches covered with appressed, yellow-brown hairs ..... 6. *M. bicornis*
19. Young branches covered with ascending, reddish brown hairs ..... 59. *M. pellegrinii*

20. Carpels 3; ovules 12–16, in 2 rows; monocarps sessile 21
20. Carpels 2–34; ovules 1–4, in 1 row; monocarps stipitate 22

21. Young branches covered with erect hairs c. 2 mm long; inflorescences supra-axillary; flowering pedicels 31–48 mm long ..... 49. *M. mcphersonii*
21. Young branches covered with appressed, hairs c. 0.2 mm long; inflorescences axillary; flowering pedicels 4.5–15 mm long. ..... 63. *M. scamnopetala*

22. Flowers with staminodes; carpels 12–34 23
22. Flowers without staminodes; carpels 2–9 24

23. Carpels 12–14(–18); inflorescences axillary; leaf blades oblong-elliptic to slightly obovate, base rounded to slightly cuneate ..... 47. *M. mannii*
23. Carpels 26–34; majority of inflorescences mainly cauliflorous or ramiflorous, some axillary; leaf blades obovate, base narrowly subcordate ..... 77. *M. whytei*

24. Carpels 2–5, each with 1 ovule; stamens 16–18, in two whorls — West Africa.....
.....52. *M. nimbana*
24. Carpels 9, each with 2–4 ovules; stamens 9 or 15, in one or two whorls, respectively — Central and East Africa 25

25. All 3 inner petals present; stamens 15; inflorescences supra-axillary, 2–6 mm above leaf axils; each carpel with 2 ovules — Tanzania .....29. *M. filipes*
25. Inner petals reduced, 1 or none present; stamens 9; inflorescences axillary; each carpel with 3 or 4 ovules — Cameroon and Gabon ..... 72. *M. tripetala*

26. Flower buds with all 4–6 petals in 1 whorl, all petals visible in bud. 27
26. Flower buds with petals in 2 whorls, outer 3 petals overlapping inner 3 petals towards the top, outer petals and the basal part of inner 3 petals visible in bud. 31

27. Lower side of leaves with silky-like indument, densely covered with appressed hairs >1 mm long 28
27. Lower side of leaves sparsely covered with appressed hairs <0.6 mm long, or densely covered with erect hairs..... 30

28. Inflorescence consisting of a solitary flower or an up to 4-flowered fascicle-like rhipidium; petals 4, sometimes 5 or 6 ..... 60. *M. poggei*
28. Inflorescence consisting of a 4–10-flowered raceme-like rhipidium, or a many-flowered panicle-like rhipidium; petals always 6 29

29. Inflorescence consisting of a 4–10-flowered raceme-like rhipidium; flower buds deltoid-ovoid ..... 16. *M. congoensis*

29. Inflorescence consisting of a many-flowered panicle-like rhipidium; flower buds depressed globose ..... 57. *M. paniculata*

30. Lower side of leaves densely covered with erect hairs; stamens 12–14; carpels 8–16 .... 43. *M. letestui*
30. Lower side of leaves sparsely covered with appressed to ascending hairs; stamens 6; carpels 7 ..... 55. *M. oligandra*

31. Staminodes 6–15, 0.2–-0.5 mm long, in one or two whorls outside the stamens 32
31. Staminodes absent 36

32. Staminodes 9, alternating with 9 stamens; carpels 16–26 ..... 33 (40. *M. klainei*)
32. Staminodes 6, alternating with 9 stamens (the ones in front of the inner petals absent); carpels 8–15 34

33. Flowering pedicels 8–20 mm long; seeds globose to ellipsoid .... 40a. *M. klainei* var. *klainei*
33. Flowering pedicels to 3 mm long; seeds ellipsoid..... 40b.*M. klainei* var. *lastoursvillensis*

34. Ovule 1; leaf blades obovate to narrowly obovate; carpels 8–12 ..... 75. *M. vogelii*
34. Ovules 2 or 3; leaf blades oblong-elliptic; carpels 12–15 35

35. Carpels 12 or 13; outer petals 3.4–4.5 mm long; stamens 0.7–0.8 mm long; filaments 0.3–0.4 mm long — Ivory Coast ..... 2. *M. aquila*
35. Carpels 15–20; outer petals 2.9–3.4 mm long; stamens c. 0.6 mm long; filaments c. 0.2 mm long — Republic of the Congo and Democratic Republic of the Congo ..... 4. *M. atopostema*

36. Petals and stamens entirely papillate 37
36. Petals with a very short indument, sometimes partly papillate; stamens glabrous 38

37. Stamens 12, obconical to clavate, circular as seen from above; petiole 0.7–0.8 mm diam ..... 17. *M. congolana*
37. Stamens 6, oblong, wider than thick; petiole 1.3–1.7 mm diam ..... 41. *M. latistamina*

38. Stamens 13–15, basally connate; flower buds ovoid; inflorescences cauliflorous, ramiflorous or axillary ..... 18. *M. couvreurii*
38. Stamens 9, free; flower buds rounded or slightly ovoid; inflorescences axillary or slightly supra-axillary 39

39. Ovules 2 or 3; monocarps smooth; tertiary venation of leaves strongly raised above; inflorescences normally 3–16-flowered; sympodial rachis 3–17 mm long ..... 30. *M. foliosa*
39. Ovules 4–6; monocarps slightly verrucose to strongly tuberculate-rugose; inflorescences 1–6-flowered; if tertiary venation of leaves raised, sympodial rachis absent..... 40

40. Hairs on young branches reddish brown 41
40. Hairs on young branches yellow-brown..... 43

41. Monocarps strongly tuberculate-rugulose (Fig. 6f–g); young branches covered with ascending to erect hairs 0.2–0.3 mm long; leaf base cuneate to rounded ..... 12. *M. capea*
41. Monocarps slightly to strongly verrucose (Figs. 6a, 28b); young branches covered with appressed to ascending hairs 0.1–0.2 mm long, if with ascending hairs, then leaf base subcordate or sometimes rounded..... 42

42. Carpels 7–13; leaf base cuneate to rounded; flowering pedicels 7.5–20 mm long, the majority > 13 mm long; seeds ellipsoid, 5–7 mm wide..... 54. *M. ochroleuca*
42. Carpels 6; leaf base subcordate or sometimes rounded; flowering pedicels 5–17 mm long, the majority < 13 mm long; seeds globose to ellipsoid, 8–11 mm wide ..... 65. *M. seretii*

43. Carpels 10–14 ..... 8. *M. biglandulosa*
43. Carpels 6 44

44. Inflorescences 2–6-flowered; sympodial rachis 3–10 mm long..... 1. *M. aestuaria*
44. Inflorescences 1- (or 2-)flowered; sympodial rachis absent or < 1 mm long 45

45. Upper bract during anthesis usually in upper half of the pedicel; leaf base attenuate to cuneate; pericarp < 1 mm thick — West Africa ..... 5. *M. barteri*
45. Upper bract during anthesis usually in lower half of the pedicel; leaf base cuneate to rounded; pericarp > 1 mm thick — Central Africa ..... 64. *M. schweinfurthii*

46. Sepals 9–12 mm long; stamens in a single whorl 47
46. Sepals < 6 mm long, or if longer than 8 mm, then stamens in 3–5 whorls 48

47. Monocarps 1–5-seeded; old branches pale brown; young branches covered with erect hairs 0.3–0.5 mm long — Ghana..... 3. *M. atewensis*
47. Monocarps 1-seeded; old branches reddish brown to blackish brown; young branches covered with erect hairs 0.1–0.2 mm long — Tanzania ..... 23. *M. discrepantinervia*

48. Carpels glabrous or with few hairs at the base; monocarps glabrous or with at the most few scattered hairs on the stipe..... 49
48. Carpels hairy; monocarps hairy, if becoming glabrous, then still hairs visible at the apex of the monocarp and several hairs on the stipe 59

49. Stamens 6–15, in 1 or 2 whorls 50
49. Stamens 22–32, in 3 or 4 whorls 55

50. Upper bract leaf-like, 3.4–20 mm long 51
50. Upper bract small or absent, to 1.2 mm long 52

51. Young branches, lower side of leaves, and pedicels covered with erect hairs; carpels 21–28 ..... 32. *M. gilletii*
51. Young branches, lower side of leaves, and pedicels covered with appressed hairs or glabrous; carpels 10–18 ..... 45. *M. littoralis*

52. Stamens 6; carpels 7; flower buds before anthesis with outer 3 petals overlapping the inner 3 petals at the apex, base of the inner 3 petals visible ..... 31. *M. fornicate*
52. Stamens 9–15; carpels 10–17; flower bud just before anthesis with only 3 petals visible, inner petals completely covered by outer petals 53

53. Flowering pedicels 15–18 mm long; leaf base subcordate; petiole 4.5–7 mm long — Kenya, Uganda and Ethiopia ..... 39. *M. kenyensis*
53. Flowering pedicels 6–14 mm long; leaf base cuneate to rounded; petiole 2–5 mm long — Mozambique, Swaziland and South Africa 54

54. Filaments less than half of the total stamen length, 0.2–0.3 mm long; fruiting pedicels 1–1.5 mm diam, stipe 3.5–5 mm long ..... 11. *M. caffra*
54. Filaments more than half of the total stamen length, 0.4–0.8 mm long; fruiting pedicels 0.4–0.9 mm diam; stipe 2.5–4 mm long ..... 48. *M. maputensis*

55. Young branches densely covered with erect hairs 0.4–1.3 mm long 56
55. Young branches with appressed to ascending hairs 0.2–0.4 mm long, if c. 0.4 mm long, then hairs appressed 57

56. Outer petals 15–19 mm long; carpels 27–38; seeds cylindric, 14–21 mm long; stipes 7–10(–25) mm long ..... 9. *M. bokoli*
56. Outer petals 5.8–6.7 mm long; carpels 12–24; seeds ellipsoid, 7–8 mm long; stipes 3–4(–6.5) mm long ..... 27. *M. ferruginea*

57. Carpels 17–18, 2–2.3 mm long ..... 14. *M. chasei*
57. Carpels 9–12, 1.1–1.8 mm long 58

58. Stipes 10–23 mm long; seeds subcylindric, 14–19 mm long; ripe fruit yellow to orange; young branches covered with yellowish hairs ..... 42. *M. laurentii*
58. Stipes 1.5–4 mm long; seeds ellipsoid, 6.5–10.5 mm long; ripe fruit orange to red; young branches covered with reddish brown hairs ..... 58. *M. parvifolia*

59. Stamens 36–130 (number of stamen unknown for *M. velutina*, but that species has the outer petals > 14 mm long and the inner petals lanceolate) 60
59. Stamens 9–34; outer petals < 13 mm long, inner petals never lanceolate 70

60. Inner petals linear-lanceolate; sepals reflexed ..... 74. *M. velutina*
60. Inner petals ovate, cordate or lanceolate, if lanceolate then sepals not reflexed 61

61. Young branches covered with erect hairs 0.9–2 mm long 62
61. Young branches covered with appressed or ascending hairs 0.1–0.5 mm long, if hairs erect than 0.1–0.2 mm long 64

62. Old branches drying pale brown; outer petals lanceolate; stamen connective conically prolonged; carpels 13, with 8 ovules per carpel ..... 62. *M. quasilanceolata*
62. Old branches drying dark brown to black; outer petals ovate to elliptic; stamen connective truncate above thecae; carpels 22–60, with 2–4 ovules per carpel 63

63. Thecae small, covering less than half of the stamen length; outer petals 12–22 mm long; carpels 40–60 ..... 25. *M. enghiana*
63. Thecae large, covering more than half of the stamen length; outer petals 21–50 mm long; carpels 22–24 ..... 38. *M. hirsuta*

64. Stigma hairy 65
64. Stigma glabrous 66

65. Lower side of leaves glabrous except for few appressed hairs 0.1–0.2 mm long on the primary vein; pedicels 15–50 mm long; leaves 1.4–5.7 cm wide ..... 36. *M. gracilis*
65. Lower side of leaves densely covered with ascending to erect hairs 0.3–0.4 mm long; pedicels 5–7 mm long; leaves 5.3–9 cm wide ..... 73. *M. ursus*

66. Upper bract leaf-like, 8–16 mm long; old branches greyish brown ..... 53. *M. obovata*
66. Upper bract small or absent, 0–4.5 mm long; old branches reddish brown, greyish to black 67

67. Petals glabrous ..... 33. *M. glabra*
67. Petals hairy 68

68. Pedicels 0.4–0.5 mm diam; carpels 11–14; stamens 36–48 ..... 50. *M. montana*
68. Pedicels 1.4–2.1 mm diam; carpels 41–50; stamens > 60 69

69. Young branches orange-brown, densely covered with appressed, orange-brown hairs; stamens c. 65 ..... 21. *M. dielsiana*
69. Young branches brown, densely covered with appressed, pale brown hairs; stamens > 100 ..... 34. *M. glaucifolia*

70. Stamens 23–34 71
70. Stamens 9–15 74

71. Upper bract leaf-like, 5–21 mm long; leaves not or hardly punctate in sicco; fruit covered with few, appressed hairs at the stipe ..... 56. *M. orophila*
71. Upper bract small or absent, 0–2.4 mm long; leaves slightly to strongly punctate in sicco; fruit covered with erect hairs 72

72. Subshrub to 40 cm tall; carpels 14–16; upper bract in upper half of the pedicel ..... 69. *M. suffruticosa*
72. Shrub or liana, >40 cm tall; carpels 8–14; upper bract halfway or in lower half of the pedicel 73

73. Leaf blades mostly oblong-elliptic, 1.4–5.5 by 0.7–2.6 cm; petiole 1.5–3 mm long; carpels 8–10 ..... 26. *M. faulknerae*
73. Leaf blades obovate, elliptic or oblanceolate, 4.5–13 by 2.6–5.9 cm; petiole 2.7–4.7 mm long; carpels 9–14 ..... 71. *M. trichocarpa*

74. Sepals covering petals in bud; petals as long as sepals or to 1.5 times as long as the sepals 75
74. Sepals not covering petals in bud; petals much longer than sepals, at least 2 times longer than the sepals 76

75. Stigma 0.3–0.5 mm long; filaments c. 0.3 mm long; leaf blades obovate to narrowly obovate, base rounded to subcordate or rarely cuneate — Central Africa ..... 46. *M. lucidula*
75. Stigma 0.7–1.2 mm long; filaments c. 0.1 mm long; leaf blades obovate to oblong-elliptic or narrowly so, base cuneate to rounded — Sierra Leone ..... 66. *M. stenosepala*

76. Flower buds ovoid; stamens 9, with an external whorl of 6 staminodes ..... 24. *M. elegans*
76. Flower buds globose; stamens 9–15, staminodes absent 77

77. Upper bract leaf-like, 7–15 mm long; carpels with 5 ovules ..... 76. *M. vulcanica*
77. Upper bract very short to 1 mm long or absent; carpels with 1 or 2 ovules 78

78. Old branches pale grey to pale brown; young branches sparsely covered with appressed, reddish brown hairs ..... 10. *M. buchananii*
78. Old branches blackish brown to blackish; young branches densely covered with ascending to erect hairs, if sparsely covered with appressed hairs, then hairs yellowish 79

79. Young branches densely covered with ascending to erect, yellowish hairs; flower buds before anthesis with outer 3 petals overlapping inner 3 petals at apex, only the base of the inner 3 petals visible ..... 70. *M. trichantha*
79. Young branches densely covered with ascending to erect, reddish brown hairs or sparsely

covered with appressed, yellowish hairs; flower buds just before anthesis with only 3 petals visible, inner petals completely covered by outer petals 80

80. Young branches and lower side of leaves sparsely covered with appressed hairs 0.1–0.2 mm long; leaf blades obovate to narrowly oblong-oblanceolate (leaf blades 2.3–3.2 times as long as wide), apex acute to acuminate.....20. *M. dictyoneura*
80. Young branches and lower side of leaves densely covered with ascending to erect hairs 0.2–0.6 mm long; leaf blades oblong-elliptic to oblong-obovate (leaf blades 1.7–2.6 times as long as wide), apex acute ..... 22. *M. discolor*

4.10.3 Synoptical key

In *Monanthotaxis* there is quite some variability in the vegetative characters within species and even within the same plant. This makes it very hard to construct a working dichotomous key based on vegetative characters. Also for 13 species no fruiting specimens are known. However, still quite some fruiting and sterile specimens can be named after looking at a variety of characters. Therefore, following other taxonomic revisions of large Annonaceae genera (e.g., Maas & Westra 1992; Maas et al. 2003, 2015) a synoptic key is presented, which can aid in identifying a specimen. The names of the species are abbreviated in four letter codes. The names of species present in one lead are in normal font, when occurring in more than 1 lead then written in italics and species rarely occurring in a lead are between parentheses.

aest = *M. aestuaria*
aqui = *M. aquila*
atew = *M. atewensis*
atop = *M. atopostema*
bart = *M. barteri*
bico = *M. bicornis*
bida = *M. bidaultii*
bigl = *M. biglandulosa*
book = *M. bokoli*
buch = *M. buchananii*
caff = *M. caffra*
cape = *M. capea*
caul = *M. cauliflora*
chas = *M. chasei*
cone = *M. congoensis*
conf = *M. confusa*
conl = *M. congolana*
couv = *M. couvreurii*
dicl = *M. diclina*
dict = *M. dictyoneura*
diel = *M. dielsiana*
diso = *M. discolor*
disr = *M. discrepantinervia*
eleg = *M. elegans*
engh = *M. enghiana*
faul = *M. faulknerae*
ferr = *M. ferruginea*
fila = *M. filamentosa*
fili = *M. filipes*
foli = *M. foliosa*
forn = *M. fornicata*
gill = *M. gilletii*
glab = *M. glabra*
glau = *M. glaucifolia*
glom = *M. glomerulata*
grac = *M. gracilis*
hexa = *M. hexamera*
hirs = *M. hirsuta*
keny = *M. kenyensis*
klkl = *M. klainei var. klainei*
klla = *M. klainei var. lastoursvillensis*
lati = *M. latistamina*
laur = *M. laurentii*
lete = *M. letestui*
leto = *M. letouzeyi*
litt = *M. littoralis*
luci = *M. lucidula*
mann = *M. Mannii*
mapu = *M. maputensis*
mcph = *M. mcphersonii*
mont = *M. montana*
mort = *M. mortehanii*
nimb = *M. nimbana*
obov = *M. obovata*
ochr = *M. ochroleuca*
olig = *M. oligandra*

orop = *M. orophila*
pani = *M. paniculata*
parv = *M. parvifolia*
pell = *M. pellegrinii*
pogg = *M. poggei*
pyna = *M. pynaertii*
quas = *M. quasilanceolata*
scam = *M. scamnopetala*
schw = *M. schweinfurthii*
sere = *M. seretii*
sten = *M. stenosepala*
ster = *M. sterilis*
subm = *M. submontana*
suff = *M. suffruticosa*
tria = *M. trichantha*
trio = *M. trichocarpa*
trip = *M. tripetala*
ursu = *M. ursus*
velu = *M. velutina*
voge = *M. vogelii*
vulc = *M. vulcanica*
whyt = *M. whytei*
wier = *M. wieringae*
zenk = *M. zenkeri*

1. Habit

Subshrub (versus shrub, scandent shrub or liana) — suff.

2. Old branches

Grooved or angulate (versus terete or unknown) — *atop*, *caul*, *couv*, *dicl*, *leto*, *mort*, *olig*, *pyn*, *trico*, *whyt.*

3. Old branches colour

Pale brown, pale grey, tawny brown — *aest*, atew, *bigl*, buch, (*cape*), *couv, diel*, grac, luci, obov, quas, sten.

Orange-brown or reddish brown — *aest*, conl, *disr*, (*forn*), (*gill*), glab, laur, *parv*, *sere*, suff, *ursu*, *velu*, *vulc*.

Dark brown, dark grey to black — aqui, atop, bart, bico, bida, *bigl*, boko, caff, *cape*, caul, chas, conf, cone, *couv,* dicl, dict, *diel*, diso, *disr*, eleg, engh, faul, ferr, fila, fili, foli, *forn*, *gill*, glau, glom, hexa, hirs, keny, klkl, klla, lati, lete, leto, litt, mann, mapu, mcph, mont, mort, nimb, ochr, olig, orop, pani, *parv*, pell, pogg, pyna, scam, schw, *sere*, ster, subm, tria, trio, trip, *ursu*, *velu*, voge, *vulc*, whyt, wier, zenk.

4. Indument on young twigs

covered with erect hairs > 0.5 mm long — boko, *dicl*, engh, ferr, fila, gill, hirs, mcph, pyna, quas, *suff*, (*tria*), *trio*, *velu*.

covered with ascending to erect hairs < 0.5 mm long — atew, bida, bigl, (*boko*), *caff*, cape, couv, *dicl*, diso, disr, *eleg*, faul, *fili*, *foli*, *glau*, (*grac*), *hexa*, keny, *laur*, *lete*, leto, *mapu*, *mont*, obov, *ochr*, *olig*, *parv*, pell, (*pogg*), *sere*, *ster*, (*subm*), *suff*, tria, *trio*, ursu, *velu*, *whyt*, zenk.

covered with appressed hairs or very short hairs (< 0.1 mm long) or glabrous — aest, aqui, atop, bart, bico, buch, *caff*, caul, chas, conf, cone, conl, dict, diel, *eleg*, *fili*, *foli*, forn, glab,

glau, glom, grac, *hexa*, klkl, klla, lati, *laur*, *lete*, litt, luci, mann, *mapu*, *mont*, mort, nimb, *ochr*, *olig*, orop, pani, *parv*, pogg, scam, schw, *sere*, sten, *ster*, subm, trip, *velu*, voge, vulc, *whyt*, wier.

5. Colour of indument on young twigs

whitish, yellowish, yellow-brown — aest, bart, bico, bigl, *caff*, chas, cone, conl, dicl, *dict*, *diel*, faul, fili, *foli*, forn, glab, glau, *grac*, hexa, *klla*, lati, laur, *litt*, mapu, obov, olig, orop, schw, sten, subm, suff, tria, *trio*, *velu*, vulc, wier.

reddish brown to dark brown or blackish — aqui, atew, atop, bida, boko, buch, *caff*, cape, caul, conf, couv, *dict*, *diel*, diso, disr, eleg, engh, ferr, fila, *foli*, gill, glom, *grac*, hirs, keny, klkl, *klla*, lete, leto, *litt*, luci, mann, mcph, mont, mort, nimb, ochr, pani, parv, pell, pogg, pyna, quas, scam, sere, ster, *trio*, trip, ursu, *velu*, voge, whyt, zenk.

6. Petiole > 5 mm long (versus **≤ 5 mm) —** *aest*, *aqui*, *bart*, bida, *boko*, *cape*, caul, *chas*, conf, *cone*, conl, diel, *diso*, *disr*, *ferr*, *fila*, foli, *forn*, (*gill*), *glau*, glom, *hirs*, *keny*, *klkl*, *klla*, lati, *laur*, leto, *litt*, *luci*, *mcph*, *mont*, mort, *nimb*, *obov*, *ochr*, orop, *pani*, *pell*, pyna, *scam*, *schw*, sere, subm, *tria*, *trip*, ursu, *vulc*, (*whyt*), wier, *zenk*.

7. Leaf surface punctate in sicco (versus **not distinctly punctate)** — *bida*, *boko*, caff, *chas*, *cone*, *conl*, faul, *ferru*, lati, *lete*, mapu, olig, *pani*, *parv*, suff, trio.

8. Leaf index (length/width) > 4:1 (versus **< 4:1)** — *bart*, *buch*, *cone*, *diel*, *eleg*, *engh*, *pani*, (*pyna*), ster, *subm*, (*voge*).

9. Leaf shape

oblanceolate — *aest, bida, cape, caul, cone dict, diel, disr, eleg, engh, ferr, fila, glau*, glom, grac, *laur, leto, luci, mont, nimb*, *ochr*, *pyna*, *quas*, *schw*, (*sere*), *sten*, *trio*, velu, *voge*, *vulc*.

ovate to lanceolate — *conf, dict, diso, gill, litt, mapu, orop, pani, pogg*.

linear to narrowly elliptic — ster.

oblong-elliptic to obovate — all other species

10. Leaf base

cordate, subcordate — *atew,* boko, *buch, chas, cone, dicl, dict,* diel, *diso, disr, eleg, engh, faul,* ferr, *fila, fili, foli, forn, gill, glab,* glau, *grac,hexa, hirs,* keny, klkl, *klla, lati, laur, lete, leto, luci, mcph,* mont, *mort, nimb, obov, olig, orop, parv, pell, pogg, pyna,* quas, *sere, suff, tria, trio,* ursu, velu, *whyt.*

cuneate, attenuate — aest, *aqui*, bart, bico, *bida*, *bigl, buch, caff, cape, caul, cone,* conl, *couv, foli, glab, glom, grac, lati, laur, litt, luci, mann, mapu, mcph, ochr,* pani, *pell, scam, schw, sten,* ster, subm, *voge, vulc,* wier.
rounded — all other species

11. Leaf apex truncate, obtuse or rounded (versus **acute or acuminate) —** *boko, buch, dicl, faul, ferr, foli, forn, gill, glab,* keny, *lete, leto*, *mapu,* obov, *orop, parv, schw,* suff, *tria, trio, zenk.*

12. Hairs on lower side of leaves ascending to erect (versus **appressed or glabrous) —** atew, bida, boko, dicl, *diel,* diso, disr, engh, faul, ferr, fila, fili, gill, hirs, lete, leto, mcph, *obov*, *olig*, *pell*, pyna, quas, suff, *tria*, trio, ursu, velu, *vulc,* zenk.

13. Secondary venation indistinct (versus **distinct) —** *aest*, bico, litt.

14. Number of secondary veins on one side of primary vein

< 8 — *aest, aqui, atop*, *bart*, *bigl, boko, cape, conl, couv, diel, disr, faul, ferr, fili, foli, forn, gill, glab, grac, klla, lati, laur, lete, litt, mann, mapu, mont, orop, parv, pell, quas, sere, suff, tria, trio, trip, voge.*
> 14 — *bida, buch, caul, conf, cone,* dicl, *dict, disr, engh, ferr, fila, glom, hirs, leto, luci, mort, pani, pogg, pyna,* ster, *subm,* (*trio*), velu.
8–14 — all other species.

15. Tertiary venation reticulate and raised on the upper side (versus **percurrent or indistinct and flat on the upper side)** — *bico, buch,* caff*, cone, conl,* dict, diso, *faul,* foli, *forn, gill,* keny, lati, mapu, *obov,* orop, *pani, pell, suff, tria, trio, vulc*.

16. Inflorescence position (in most species also terminal occurs)

Extra-axillary — atew, boko, buch, caff, chas, dict, diel, diso, disr, eleg, engh, faul, ferr, forn, gill, glab, glau, grac, hirs, keny, laur, litt, luci, mapu, mont, obov, orop, parv, quas, sten, suff, tria, trio, ursu, velu, vulc, *wier.*
Supra-axillary (most inflorescences a few mm above axils) — *aest, aqui, atop, bico,* fili, *foli,* lete, mcph, olig, *sere.*
Axillary — *aest, aqui,* bart, *bico, bida*, bigl, cape, *caul, conf,* cone, conl, *couv, dicl,* fila, *foli,* hexa, *klla,* lati, mann, nimb, ochr, pani, pell, pogg, *pyna*, scam, schw, *sere,* trip, voge, *whyt*, zenk.
Cauliflorous — *aqui, atop, bida, caul, conf, couv, dicl,* glom, klkl, *klla,* leto, mort, *pyna*, subm, *whyt, wier.*
Unknown — ster.

17. Inflorescence more than 5-flowered (versus **1–4-flowered)** — *aest,* caul, conf, *cone, couv, dicl, eleg, fila, foli, glom, klkl, lati, leto, luci,* mort, *olig, pani, pell, pyna, sere,* subm*, wier*.

18. Sympodial rachis > 10 mm long (versus **< 10 mm or absent)** – *bigl, caul, conf,* cong, *couv, dicl, engh, fila, foli, gill, lati,* lete, *leto, litt,* (*mann*), mort, olig, pani, *pogg, pyna,* subm, *wier*.

19. Pedicels > 20 mm long (versus **< 20 mm long)** — atew, *bart*, *bico*, *bigl, boko, buch, conf, dicl, diels, diso, engh, faul, ferr,* fili, *gill,* glab, *glau,* grac, *hexa, litt, luci,* mcph, *mont, mort, nimb,* obov, *ochr, orop, pani, pell, pyna,* quas, *subm, trio, vulc, wier*.

20. Upper bract > 5 mm long (versus **< 5 mm long or absent)** — *ferr, fila,* gill, *hirs, litt,* obov, orop, *pani,* quas, vulc.

21. Flowers unisexual (versus **bisexual) —** bida, caul, conf, dicl, glom, mort, pyna, *subm*, wier.

22. Flower buds acute (versus **rounded or obtuse)** — *aest,* aqui, atop, *bida, boko, buch,* conf, cone, couv, *dicl, disr,* eleg, fila, grac, *hexa,* hirs, klkl, klla, lete, leto, *mann*, mapu, mcph, mont, mort, pogg, *pyna,* quas, sten, *subm,* ursu, voge, *vulc, wier*.

23. Aestivation of petals in bud

in one whorl — cone, lete, olig, pani, pogg.
at the base in one whorl, but overlapping at top — aest, aqui, atop, bart, bigl, cape, conl, couv, foli, forn, klkl, klla, lati, ochr, schw, sere, voge.
in two whorls — bico, bida, boko, buch, caff, caul, chas, conf, dicl, dict, diel, diso, disr, eleg, engh, faul, ferr, fila, fili, gill, glab, glau, glom, grac, hexa, hirs, keny, laur, leto, litt, luci, mann, mapu, mcph, mont, mort, nimb, obov, orop, parv, pell, pyna, quas, scam, sten, subm, suff, tria, trio, trip, ursu, vulc, whyt, wier, zenk.
unknown — atew, ster, velu.

24. Sepals covering petals in bud (versus **sepals not covering petals in bud, petals distinctly larger than sepals in bud)** — atew?, disr, luci, sten.

25. Sepals > 5 mm long (versus **sepals <5 mm)** — atew, disr, *fila*, grac, hirs, obov, quas, *sten, velu*.

26. Largest petals >10 mm long (versus **largest petals < 10 mm)** — boko, diel, engh, *fila*, glau, grac, hirs, *mont*, *obov,* quas, suff, velu.

27. Inner petals glabrous (versus **inner petals at least near top with hairs)** — *boko, conl, diel, engh,* glab, *glau, grac,* klkl, klla, *lati*, *leto*, mont.

28. Number of stamen whorls

One whorl — aest, aqui, atew, atop, bart, bico, bida, bigl, buch, caff, cape, caul, cone, conl, couv, dicl, dict, diso, disr, eleg, *fili,* foli, forn, *gill,* hexa, keny, klkl, klla, lati, lete, litt, luci, mann, *mapu*, ochr, olig, pani, *pell*, pogg, pyn, schw, sere, sten, subm, tria, trip, voge, whyt.
Two whorls — conf, faul, *fila*, *fili, gill, mapu,* mcph, nimb, *orop*, *pell*, scam, suff, trio, vulc.
Three or more whorls – boko, chas, diel, engh, ferr, *fila,* glab, glau, grac, hirs, laur, leto, mont, obov, *orop*, parv, quas, ursu, wier, zenk.
Unknown — glom, mort, ster, velu.

29. Number of stamens per flower

(1**–**)3 — bida, *subm*.
6 — caul, cone, dicl, forn, hexa, lati, olig, pani, pyn, *subm*.
(7**–**)9**–**15(**–**18) — aest, aqui, atop, bart, bico, bigl, buch, caff, cape, conl, couv, dict, diso, disr, eleg, (*fila*), fili, foli, gill, keny, klkl, klla, lete, litt, luci, mann, mapu, mcph, nimb, ochr, *pell,* pogg, (*pyn*), scam, schw, sere, sten, (*subm*), tria, voge, vulc, whyt.
19**–**48 — boko, chas, conf, faul, ferr, fila, laur, leto, mont, orop, parv, *pell,* suff, trio, wier, zenk.
> 49 — diel, engh, glab, glau, grac, hirs, obov, quas, ursu.
Unknown — atew, glom, mort, ster, velu.

30. Connective of stamens hairy (versus **glabrous)** — bart, bida, bigl, cape, caul, conf, dicl, foli, hexa, leto, *nimb*, ochr, schw, sere, subm, wier, zenk.

31. Filament as long as or longer than half the stamen length (versus **filament shorter than half the stamen length)** — *aqui*, bart, bigl, cape, *cone*, disr, fila, *foli*, hexa, *keny*, *lete*, *mapu*, *nimb*, *orop*, parv, pell, schw, sere, subm, *tria, trip, zenk*.

32. Anther dehiscence introrse (versus **latrorse or extrorse)** — cone, fila, *gill*, hexa, *klkl, klla, mann,* nimb, *pani, pogg, vulc*.

33. Stamen connective

conical prolonged – quas
reduced, thecae on top of stamen — bico, fila, hexa, pell, zenk.

34. Number of staminodes per flower

3 — bida, *subm*.
6 — aqui, atop, cone, eleg, pani, *subm,* voge.
9 — klkl, klla, *mann, subm,* whyt.
12 — caul, dicl, *mann, pyn, subm*.
13**–**16 — *mann*, *pyn*.
absent — all other species.

35. Number of carpels per flower

(2 or) 3 — mcph, *nimb,* scam.
4**–**6 — aest, bart, *bico, cape,* conl, foli, hexa, *lati, nimb*, schw, sere.
7**–**9 — *bico, buch, cape, couv, dict,* diso, *disr, faul, fila,* fili, (*foli*), forn, *lati, laur, lete, luci, ochr,* olig, *sten*, *trio,* trip, *voge.*
10**–**15 — aqui, *atop*, bigl, *buch*, caff, *cone, couv, dict,* (*diso*), *disr, eleg, faul, ferr, fila, glab, keny, laur, lete, litt, luci,* mann, mapu, mont, *ochr, orop, pani,* parv, *pell,* pogg, quas, *sten, suff,* tria, *trio, voge,* vulc.
16**–**26 — *atop,* chas, *cone, eleg, ferr,* gill, *glab,* grac, hirs, *keny*, klkl, klla, *lete, litt, luci,* (*mann*), *obov, orop, pani, pell, suff,* (*whyt*), zenk.
27**–**38 — boko, *obov*, whyt.
> 39 — bida, caul, conf, dicl, diel, engh, glau, glom, leto, mort, pyn, subm, ursu, wier.
unknown — atew, ster, velu.

36. Carpels glabrous or with only a few hairs near base (versus **carpels almost completely covered with hairs)** — boko, caff, chas, ferr, forn, gill, keny, laur, litt, mapu, parv.

37. Number of ovules per carpel

1 or 2 — *aqui*, *atop*, *bico, bida,* buch, caff, cone, dict, diel, diso, disr, eleg, engh, *faul, ferr,* fili, *foli,* forn, glau, *grac,* hexa, *hirs,* keny, klkl, klla, *lete, litt, luci,* mann, mapu, *mont,* nimb, olig, pani, *parv, pell,* pogg, *sten,* tria, *trio,* voge.
3**–**6 — all other species.
> 6 — fila, *glab*, *glom,* leto, mcph, quas, scam.

38. Ovules biseriate (versus **uniseriate)** — mcph, scam.

39. Stigma hairy (versus **glabrous)** — grac, quas, ursu**.**

40. Monocarp indument

erect hairs — atew, *cape, dicl, diel, diso,* faul, fila, hirs, pyn, quas, suff, trio, *ursu, velu*,
glabrous or only a few hairs at stipe — boko, caff, *chas,* conl, ferr, forn, gill, keny, laur, litt, mapu, *orop,* parv, tria, *vulc,*
monocarps unknown — aqui, bico, couv, fili, glom, hexa, lati, mcph, mort, pell, ster, wier, zenk.
appressed hairs, if glabrescent some hairs present near apex and stipe – all other species.

41.Stipe length

0**–**1 mm — mcph, scam.
1**–**3 mm — *bart,* cone, *diel*, disr, eleg, *engh, forn, klkl, klla, litt, luci,* mann, *mapu, nimb, parv, pogg, sten, suff, tria, trio, ursu, voge*.

3–8 mm — all other species.
> 8 mm long — *bigl, boko,* caul, conl, dicl, fila, *gill, hirs,* laur, *lete, leto,* obov, orop, pyn, quas, *subm, trip, vulc, whyt*.

42. Monocarp surface verrucose or tuberculate-rugulose (versus **smooth or slightly verrucose)** — aest, bart, cape, *chas*, diel, scam, *sere,* trip, *vulc,* whyt.

43. Seed shape

globose — *cone, faul, klkl,* leto, *mann, mapu, schw, sere, trio, whyt.*
subcylindric to cylindric — *bigl*, boko, conl, *diel*, fila, *hirs,* laur, *obov, olig,* quas, velu*, vulc*.
elliptic — all other species.

44. Distribution

Upper Guinea (Senegal to Benin) — aqui, atew, *bart, cape, engh, foli,* glab, *grac, hirs, laur,* mann, nimb, sten, ursu, velu, *voge, whyt.*
Nigeria — *bart, engh, foli, glau, grac, hirs, laur, voge, vulc, whyt.*
West-Central Africa (Cameroon, Gabon, Equatorial Guinea) — aest, *bico,* bida, *boko, cape,* caul, cone, couv, *dicl,* diel, eleg, *engh, ferr, fila, foli, glau,* glom, *grac,* hexa, *hirs, klkl, klla, lati, laur,* lete, *leto, luci,* mcph, *mont,* pani, *pell, pyn,* quas, *scam, ster,* subm, trip, *vulc, whyt,* wier, zenk.
Central Africa (Angola, CAR, Democratic Republic of the Congo, Republic of the Congo, South Sudan) — atop, *bico,* bigl, *boko, buch, cape,* conf, conl, *dicl, engh, ferr, fila, foli, gill, klkl, klla, lati, laur, leto, litt, luci, mont,* mort, *obov, ochr,* olig, *orop, parv, pell, pogg, pyn, scam,* schw, sere*, ster.*
East Africa (Ethiopia, Kenya, Tanzania, Somalia, Uganda, Burundi, Rwanda) — *buch,* dict, diso, disr, *engh,* faul, *ferr,* fili, forn, *gill,* keny, *litt, obov, ochr, orop, parv, pogg, suff, tria, trio.*
Southern Africa (Malawi, Namibia, Zambia, Zimbabwe, Mozambique, Swaziland, South Africa) — *buch,* caff, chas, mapu, *obov, ochr, parv, suff, tria, trio.*

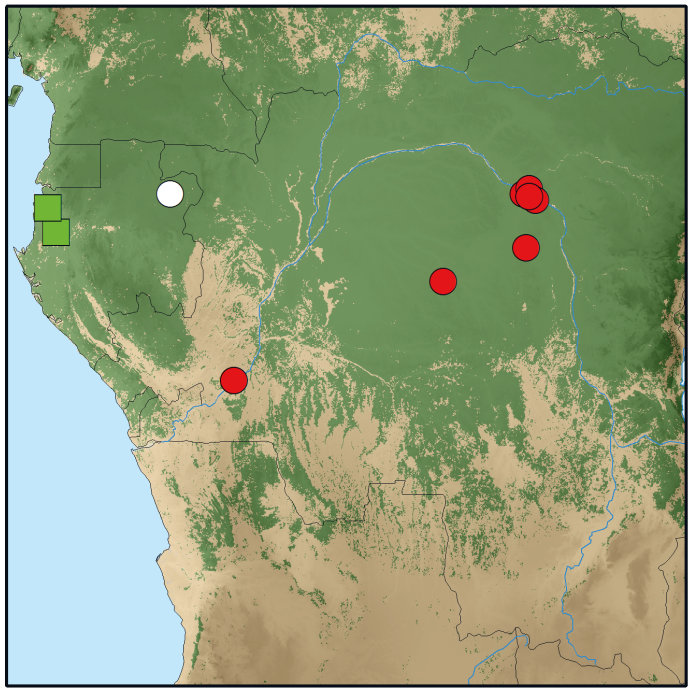
45. Elevation above 1000 m (versus **0–1000 m)** — *buch, chas, conf,* dict, diso, *disr, engh, ferr, fila, foli,* gill, *glau*, *hirs, keny, lati*, *laur, lete*, *litt, luci, mont*, *nimb, obov, ochr,* orop, *parv, pell, pogg, schw, sere, subm, trio, vulc*.

4.10.4 Species descriptions

1. *Monanthotaxis aestuaria* P.H.Hoekstra, *sp. nov.* — Fig. 2; Map 2

Monanthotaxis aestuaria belongs to the *M. schweinfurthii* complex. It is distinguishable from the other species in this complex by the elliptic to oblanceolate leaves with attenuate to cuneate base, hardly visible tertiary venation, and yellow-brown branches densely covered

with appressed, yellowish brown hairs. — Type: *J. Floret 1456* (holo: P (P01967244); iso: LBV not seen, WAG0076149), Gabon, Estuaire, 5 km au NW de Mebba, 25 Sep. 1983. Paratype: *G.D. McPherson 15091* (LBV, MO, P, WAG), Gabon, Estuaire, along Remboué River, British Gas site, 10 m, 9 Jan. 1991.



Map 2 Distribution of *Monanthotaxis aestuaria* (green squares) and *M. atopostema* (red circles, white circle uncertain det of *M. atopostema*).

Liana; young branches densely covered with appressed, yellowish brown hairs c. 0.1 mm long, becoming glabrous; old branches yellowish brown to orange-brown. *Leaves*: petiole 3–9 mm long, 0.7–1.5 mm diam, grooved, indument as on branches; lamina elliptic to obovate or oblanceolate, 6–13 by 2.5–4.5 cm, 2–3 times longer than wide, chartaceous, not punctate, above glabrous except appressed, yellow hairs c. 0.1 mm long on primary vein, below densely covered with appressed, yellow hairs c. 0.1 mm long, base attenuate to cuneate, with a thickened black margin or with very thick, globose, black glands, apex acute to acuminate, acumen to 10 mm long; secondary veins 6–10 per side, sometimes hardly visible, slightly curving upwards, tertiary venation percurrent, hardly visible. *Inflorescences* axillary or c. 2 mm above axil, composed of 2–6-flowered fascicle-like rhipidia; sympodial rachis 3–10 mm long, densely covered with appressed, yellowish hairs c. 0.1 mm long; pedicels 6–10 mm long, 0.6–0.8 mm diam, fruiting pedicels to 30 mm long and 0.7 mm diam, indument as on rachis; lower

bracts broadly ovate to ovate, 0.6–1 by 0.6–0.8 mm, indument as on om rachis; upper bract halfway up the pedicel, broadly ovate, 0.4–0.7 by 0.5–0.8 mm, indument as on rachis; flower buds globose to slightly ovoid. *Flowers* bisexual; sepals connate at the base, ovate to depressed ovate, 0.6–0.9 by 1.1–1.2 mm, apex obtuse, densely covered with hairs, persistent in fruit; receptacle c. 1.3 mm diam, flat; petals colour in vivo unknown, 6, in two whorls, base of inner petals visible in bud, outer petals ovate, c. 3.4 by 2.1–2.2 mm, outside densely covered with appressed, yellowish brown hairs c. 0.2 mm long, inside with yellow hairs at the apex and margins, inner petals narrowly elliptic, c. 3.2 by 1.1 mm, indument as on outer petals; stamens 9, in one whorl, free, obconical, 0.9–1 mm long, filaments c. 0.4 mm long, thecae extrorse, connective truncate, slightly prolonged inward, hiding thecae, glabrous, staminodes absent; carpels 6, subcylindric, c. 2.1 by 0.4–0.5 mm, densely hairy, ovules 6, lateral, stigma elongate, c. 0.7 mm long, glabrous. *Monocarps* 1–6, colour in vivo unknown, moniliform, 1–3-seeded, each part ellipsoid, 15–61 by c. 4 mm, verrucose, densely covered with appressed, pale green-brown hairs, apex apiculate, apiculum 1–3 mm long, stipes 3–6 mm long. *Seeds* unknown.

Distribution — Gabon (Estuaire).

Habitat & Ecology — In old secondary forest, clay soil. Altitude: c. 10 m. Flowering: September; young fruits: January.

Preliminary IUCN conservation status —Endangered (EN): B2ab(iii). AOO: 8 km^2. Only known from 2 collections from the Estuaire province in Gabon, both outside protected areas and under heavy threat of expanding villages or oil exploitation.

Ethymology — Named after the province and habitat where the two known specimens have been collected (Estuaire, Gabon).

Notes — 1. *Monanthotaxis aestuaria* belongs to the *M. schweinfurthii* complex (Fig. 1, clade B) based on the flower and stamen morphology, but is one of the more easily recognisable species from this complex based on vegetative characters as denoted in the diagnosis.

2. *G.D. McPherson 15091* has huge glands near the leaf base (see Fig. 2b), which are absent in the type specimen. Also in related species, such as *M. biglandulosa* the size of the basal leaf glands can vary largely between specimens.

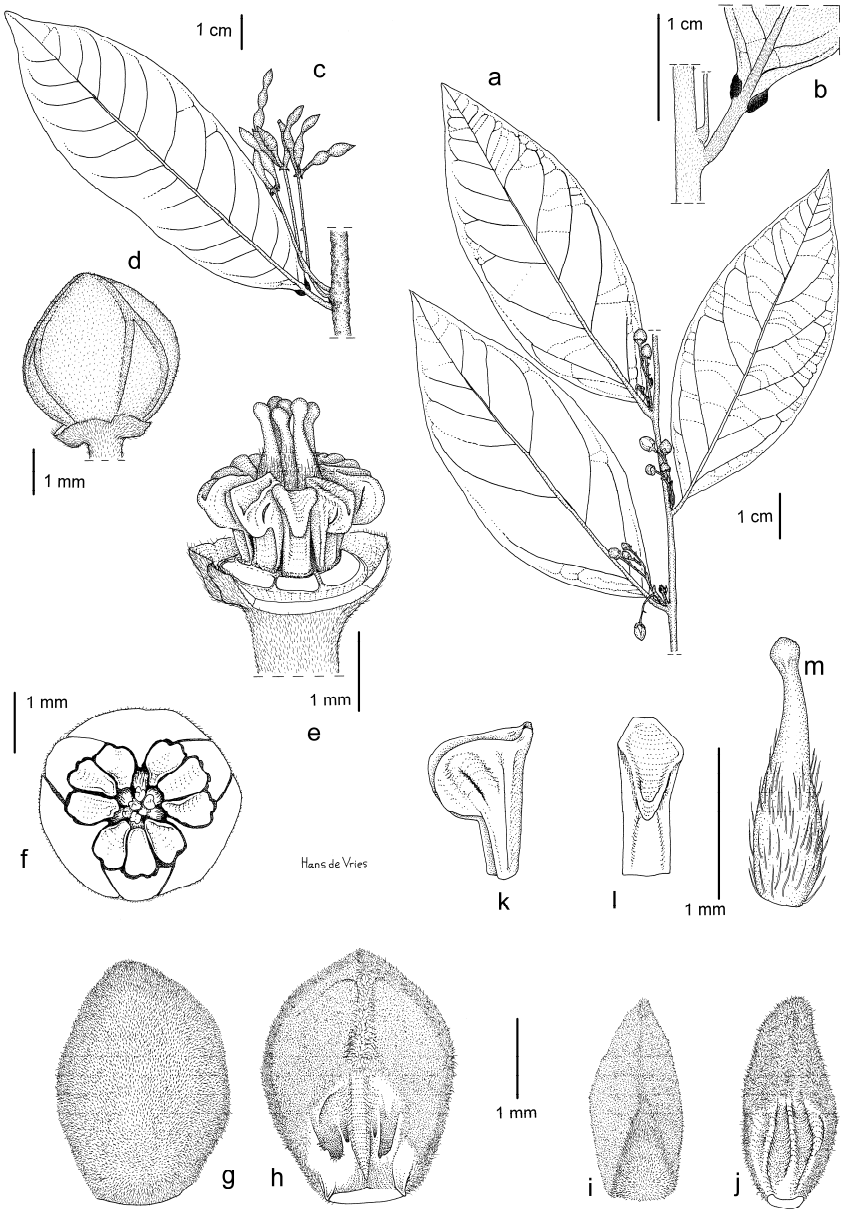


Fig. 2 *Monanthotaxis aestuaria* P.H.Hoekstra. a. Habit of flowering branch; b. leaf base abaxially; c. young fruiting inflorescence; d. flower bud; e. flower with petals removed; f. cross section flower bud; g. outer petal, outside view; h. outer petal, inside view; i. inner petal, outside view; j. inner petal, inside view; k. stamen, side view; l. stamen, front view; m. carpel (a, d–m: *J.J. Floret* & *A.M. Louis 1456*; b, c: *G.D. McPherson 15091*). Drawing by H. de Vries.

2. *Monanthotaxis aquila* P.H.Hoekstra **—** Fig. 3; Map 3

Monanthotaxis aquila P.H.Hoekstra in P.H.Hoekstra et al. (2016) 74. — Type: *C. Geerling 2327* (holo: WAG (consisting of 2 sheets: WAG0005568, WAG0005569); iso: BR0000015315335), Ivory Coast, Sassandra, Dakpadou-Sago, 27 March 1968.

Liana; young branches covered with short reddish brown hairs c. 0.1 mm long, becoming glabrous; old branches dark brown. *Leaves*: petiole 4–6 mm long, 0.7–1.1 mm diam, terete, indument as on branches; lamina oblong-elliptic to slightly obovate, 3.5–11.5 by 1.9–4.8 cm, 1.8–2.7 times longer than wide, chartaceous, not punctate, glossy dark green above, dark silvery green below, above glabrous or primary vein covered with few, short hairs, below becoming glabrous, primary vein of young leaves covered with appressed, yellowish hairs 0.1–0.2 mm long, base cuneate to rounded, glands hardly visible, apex acute to acuminate, acumen to c. 10 mm long, secondary veins 6–8 per side, from base curving upwards, tertiary venation percurrent. *Inflorescences* ramiflorous, axillary or supra-axillary, composed of solitary flowers or 2- or 3- flowered rhipidia; sympodial rachis 0.5–2 mm long, densely covered

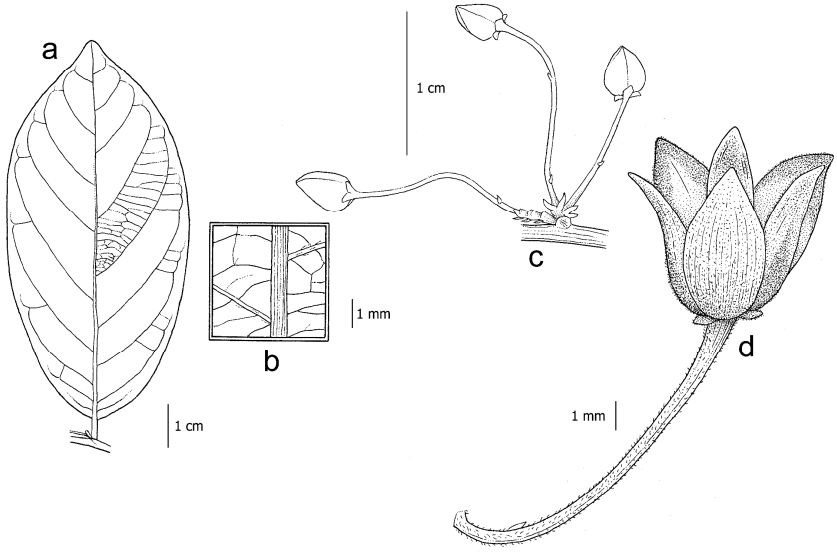
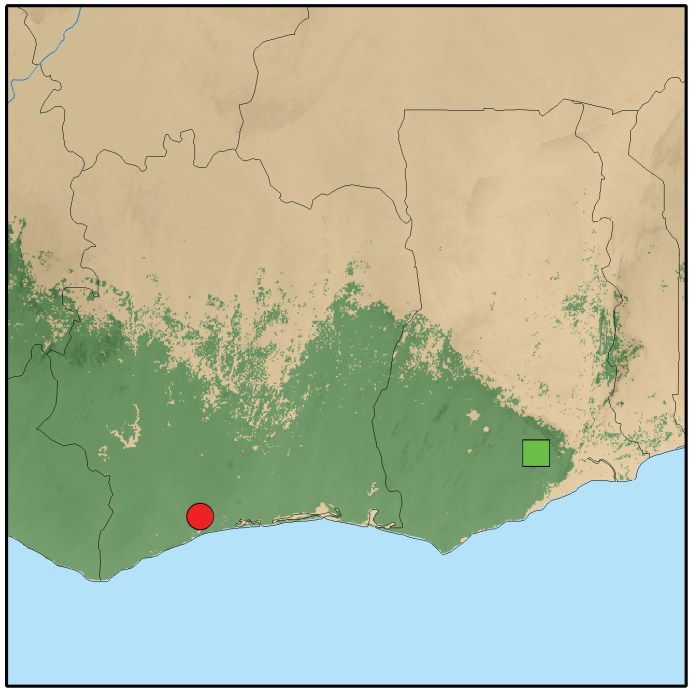


Fig. 3 *Monanthotaxis aquila* P.H.Hoekstra. a. Leaf; b. leaf detail; c. inflorescence; d. flower (all from *Geerling & Bokdam 2327*). Drawing by M. Spitteler, reproduced from Hawthorne & Jongkind (2006).

with appressed, short hairs; flowering pedicels 10–18 mm long, 0.3–0.4 mm diam, sparsely covered with appressed hairs; lower bracts ovate, 0.6–0.9 by 0.3–-0.5 mm, indument as on rachis; upper bract in lower half of pedicel, broadly ovate to narrowly ovate, 0.4–0.7 by 0.3–0.4 mm, indumentum as on pedicel; flower buds ovoid to deltoid. *Flowers* bisexual; sepals connate at the base, depressed ovate, c. 0.6 by 1.2–1.3 mm, apex obtuse, covered with appressed, yellowish hairs; receptacle 1.6–2 mm diam, flat; petals yellow, 6, in two whorls, base of inner petals visible in bud, outer petals ovate, 3.4–4.5 by 2.1–2.8 mm, outside sparsely covered with appressed, yellowish hairs, inside with appressed, very short hairs at the apex, inner petals elliptic to slightly rhombic, 2.3–3.5 by 1.3–1.5 mm, outside covered with very short yellowish hairs at the apex and in the centre, inside only with hairs at the apex; stamens 9, in one whorl, free, clavate, 0.7–0.8 mm long, filaments 0.3–0.4 mm long, thecae latrorse, connective truncate, quadrate seen from above, slightly papillate, staminodes 6, alternating with the stamens, but absent where in front of inner petals, c. 0.3 mm long, glabrous; carpels 12 or 13, ellipsoid, 0.9–1 by 0.4–0.5 mm, densely hairy, ovules 2 or 3, lateral, stigma subsessile, globose, c. 0.1 mm diam, glabrous. *Monocarps* and *seeds* not seen.

Distribution — Ivory Coast (Sassandra).



Map 3 Distribution of *Monanthotaxis aquila* (red circle) and *M. atewensis* (green square).

Habitat & Ecology — In secondary forest, on sandy soil. Flowering: end of March.

Preliminary IUCN conservation status — Critically Endangered (CR): B2ab(iii). AOO: 4 km^2. Only known from the type collection and the forests of that area are under serious threat (Chatelain et al. 1996).

Notes — 1. *Monanthotaxis aquila* belongs to a group of species with bisexual flowers, ovoid flower buds, axillary, cauliflorous or ramiflorous inflorescences and where staminodes are present these alternate with the stamens. It differs from the majority of the species of this group in having oblong-elliptic leaves, a character shared with *M. couvreurii* and *M. atopostema*. *Monanthotaxis couvreurii* differs from those species by having 13–16 basally connate stamens and the absence of staminodes. Although *M. aquila* is phylogenetically less related to *M. atopostema* than *M. couvreurii* (Fig. 1 clade C) it looks morphologically more similar to *M. atopostema.* The petals are more broadly ovate in *M. atopostema* with the petals only being slightly longer than wide, while in *M. aquila* the petals are much longer than wide; *M. atopostema* has 15–20 carpels per flower, and the staminodes are only slightly smaller than the stamens, while *M. aquila* has 12 or 13 carpels per flower and the stamens are twice as large as the staminodes. The difference in number of ovules as noted by Hoekstra et al. (2016) is incorrect, it was based on the number of seeds per monocarp of a misidentified specimen in BR. Furthermore, one of the few flowers existing of *M. atopostema* has now been examined and it has 2 or 3 ovules per carpel, just as *M. aquila.*

2. Within West Africa this species can be confused with *M. mannii*, which has globose flower buds and 9–15 staminodes, instead of 6. Vegetatively, it can generally be distinguished by a slightly shorter petiole (4–6 mm in *M. aquila* versus 2–3.5 mm in *M. mannii*).

3. *Monanthotaxis atewensis* P.H.Hoekstra — Fig. 4; Map 3.

Monanthotaxi atewensis P.H.Hoekstra in P.H.Hoekstra et al. (2016) 76. — Type: *J.B. Hall GC43672* (holo: consisting of 2 sheets: WAG0019665, WAG0019666; iso: GC, K000040198, MO), Ghana, Eastern Region, Atewa Range Forest Reserve, 2 June 1973.

Scandent shrub or liana, to 9 m long; young branches sparsely covered with erect, reddish brown hairs 0.3–0.5 mm long, becoming glabrous; old branches pale brown. *Leaves*: petiole 3–5 mm long, 1–1.2 mm diam, grooved, indument as on branches; lamina oblong-elliptic to obovate or slightly oblanceolate, 5.7–15.9 by 2.4–5.4 cm, 2–3.1 times longer than wide, chartaceous, not punctate, above greyish, glabrous except for a few short hairs near the base of the primary vein, below sparsely to densely covered with erect, reddish brown hairs 0.4–0.6 mm long, base rounded, truncate or subcordate, glands hardly visible, apex acute to acuminate, acumen to 15 mm long, secondary veins 8–14 per side, straight and halfway

curving upwards, tertiary venation percurrent. *Inflorescences* leaf-opposed, composed of solitary flowers to 3-flowered rhipidia; sympodial rachis 2–4 mm long; pedicels c. 21 mm long, c. 0.7 mm diam, fruiting pedicels 20–37 mm long, 0.6–1.1 mm diam, coverered with ascending to erect, yellowish, short hairs; lower bracts strongly reduced or absent; upper bract around the middle of the pedicel, broadly ovate, c. 1.7 by 1.4 mm, densely covered with appressed, short hairs. *Flowers* bisexual; sepals free, lanceolate, 10–12 by 2.6–2.7 mm, apex acute, densely covered with appressed, short hairs, persistent in fruit or falling off; receptacle c. 3 mm diam, flat; petals unknown; stamens unknown, scars in a single whorl; carpel number unknown, ellipsoid, c. 1.2 by 0.5 mm, densely hairy, ovules unknown, stigma elongate, c. 0.5 mm long, grooved, glabrous. *Monocarps* 1–9, green when young, ellipsoid to narrowly ellipsoid, 13–35 by 5–6 mm, slightly to strongly constricted between the seeds, slightly

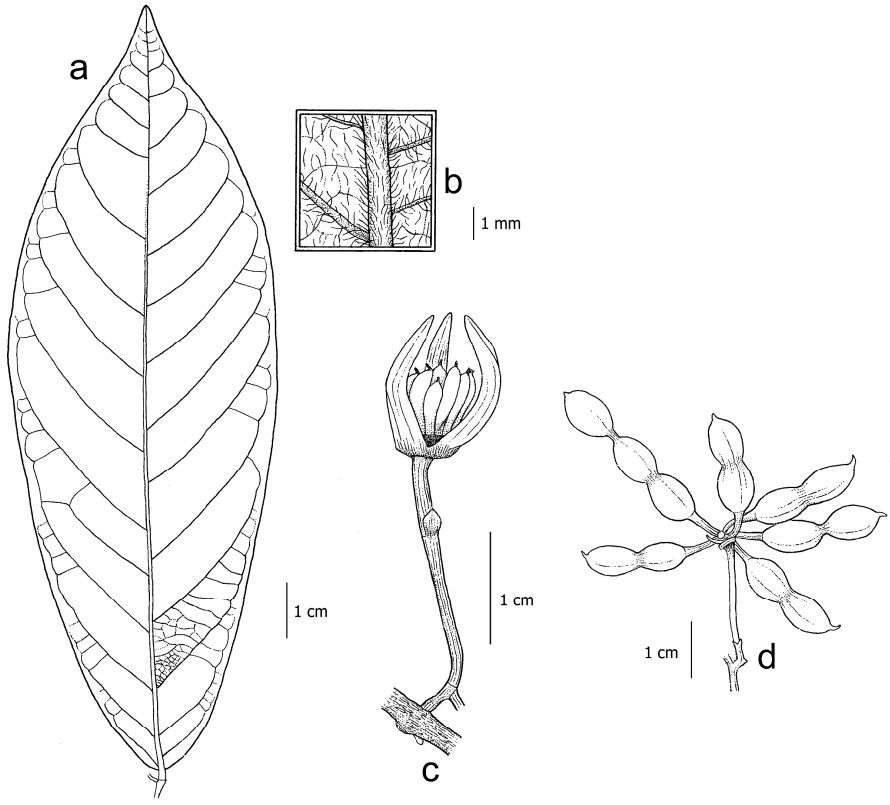


Fig. 4 *Monanthotaxis atewensis* P.H.Hoekstra. a. Leaf; b. leaf detail; c. old flower; d. fruit (a, b, d: *Hall & Lock GC43672*; c: *Hall & Enti GC36426*). Drawing by M. Spitteler, reproduced from Hawthorne & Jongkind (2006).

verrucose, sparsely covered with erect, short hairs, apex apiculate, apiculum to 2 mm long, stipes 4–6 mm long, slightly grooved. *Seeds* 1–5, ellipsoid, c. 9 by 6 mm, tawny brown, base and apex rounded, raphe visible from base to apex.

Distribution — Ghana (Eastern Region).

Habitat & Ecology — In forest, in thicket. Altitude: c. 750 m. Fruiting: May, June.

Preliminary IUCN conservation status — Critically Endangered (CR): B2ab(iii). AOO 4 km^2. This species is only known from the Atewa Range Forest Reserve and has not been collected in more than 40 years. Furthermore, the reserve is under threat of bauxite mining and logging (Kusimi 2015; Ntiamoa-Baidu et al. 2000), even more so since in 2020 the actual exploration has started, and already a few procent of the upland forest was destroyed for exploration tracks (pers. observation Wieringa).

Notes — 1. *Monanthotaxis atewensis* is easily distinguishable from all other *Monanthotaxis* species by the large, lanceolate sepals. This species is closely related to *M. stenosepala* from Sierra Leone and *M. discrepantinervia* from Tanzania based on sepals, which are as large as the petals. It differs from both species by the erect hairs on the leaves and branches. It differs from *M. stenosepala* in the larger sepals and the larger number of seeds per monocarp, while the sepals of *M. discrepantinervia* are ovate (versus lanceolate).

2. In Liberia there are two fruiting specimens (*J-G Adam 26189* and *FSC Stoop 331*) which resemble *M. atewensis*, but the monocarps are more densely verrucose, the sympodial rachis is shorter and the pedicels are larger than the specimens from Ghana. Furthermore, no sepals are present to verify the identification and for now we refrain from assigning them to this species.

4. *Monanthotaxis atopostema* P.H.Hoekstra — Map 2

Monanthotaxis atopostema P.H.Hoekstra in P.H.Hoekstra et al. (2016) 73. — *Atopostema angustifolia* Boutique (1951b) 121. — *Popowia klainei* Engl. var. *angustifolia* (Boutique) Le Thomas (1963) 291. — *Monanthotaxis klainei* (Engl.) Verdc. var. *angustifolia* (Boutique) Verdc. (1971b) 30, non *Monanthotaxis angustifolia* (Exell) Verdc. — Lectotype (designated here): *J.L.P. Louis 15324* (lecto BR (BR0000008820334); isolecto: BR0000008820358), Democratic Republic of the Congo, Orientale, à 20 km au Nord-Est de Yambao, 23 June 1939.

Shrub or liana, to 6 m long; young branches dark brown to blackish, sparsely covered with appressed, reddish brown hairs c. 0.1 mm long, soon becoming glabrous. *Leaves*: petiole 3–5

mm long, 0.9–1.1 mm diam, grooved, indument as on branches; lamina oblong-elliptic to narrowly so, 8.4–14 by 2.9–5.2 cm, 2–2.9 times longer than wide, chartaceous, not punctate, discolorous, shiny green above, dull glaucous green below, above densely covered with appressed, yellowish hairs when young, soon becoming glabrous, below sparsely covered with appressed, reddish brown hairs 0.1–0.2 mm long, soon becoming glabrous, base rounded, glands hardly visible, apex acuminate, acumen 10–35 mm long, primary vein often distinctly contrasting with darker petiole, secondary veins 5–8 per side, curving upwards, tertiary venation percurrent. *Inflorescences* cauliflorous or axillary, composed of solitary flowers or few-flowered fascicle-like rhipidia; sympodial rachis 0.8–5 mm long, densely covered with appressed, yellowish white hairs; pedicels 0–17 mm long, 0.3–0.4 mm diam, fruiting pedicels 0.6–1.8 mm diam, sparsely covered with appressed hairs, lower bracts ovate, c. 0.4 by 0.3 mm, indument as on rachis; upper bract in lower half of the pedicel, triangular to ovate, c. 0.7 by 0.4–0.8 mm, covered with appressed, yellowish hairs; flower buds ovoid. *Flowers* bisexual; sepals free, broadly to depressed ovate, 0.7–1 by 1–1.3 mm, apex acute, densely covered with appressed hairs, not persistent in fruit; receptacle 1.8–2.2 mm diam, flat; petals yellowish white, 6, in two whorls, base of inner petals visible in bud, outer petals broadly ovate, 2.9–3.4 by 2.6–3.2 mm, outside sparsely covered with yellow hairs, inside densely covered with yellowish hairs < 0.1 mm long, inner petals elliptic, 2.5–2.9 by 1.3–1.9 mm, outside densely covered with very short hairs along the middle line, inside densely covered with hairs in the upper half, but the base glabrous; stamens 9, in one whorl, free, linear-oblong, c. 0.6 mm long, filaments c. 0.2 mm long, thecae latrorse, connective truncate, slightly prolonged inward and outward, not hiding thecae, glabrous, staminodes 6, alternating with the stamens, but not in front of the inner petals, c. 0.5 mm long, glabrous; carpels 15–20, ellipsoid, c. 1 by 0.4 mm, densely hairy, ovules 2 or 3, lateral, stigma subsessile, globose, 0.1–0.2 mm long, glabrous. *Monocarps* 1–6, red when ripe, narrowly ellipsoid, 18–30 by c. 7 mm, covered with appressed, reddish brown, short hairs, becoming glabrous, but longer persistent at stipe and apex, apex apiculate or rounded, stipes 3–6 mm long, grooved. *Seeds* 1 or 2, ellipsoid, 10–11 by 6–7 mm, ochre-brown to reddish brown, apex apiculate or rounded, raphe not visible.

Distribution — Republic of the Congo (Pool), Democratic Republic of the Congo (Equateur, Orientale).

Habitat & Ecology — In tropical rainforests, swamp forests and riparian forests. Altitude: c. 470 m. Flowering: May, June, October; fruiting: February, March, May, August, October.

Vernacular names — Democratic Republic of the Congo: Lumwembe (Turumbu name) (*JLP Louis 15324*), Inaolo a Lumwemwe (Turumbu name) (*RGA Germain 271*).

Preliminary IUCN conservation status — Vulnerable (VU): B2ab(iii). EOO: 88,402 km^2, AOO: 28 km^2.This species is known from 9 collections and max 7 locations of which the majority are outside protected areas.

Notes — *Monanthotaxis atopostema* is the only species of *Monanthotaxis* in Congo with oblong-elliptic leaves and cauliflorous inflorescences. It is very similar to *M. couvreurii* from Cameroon and *M. aquila* from Ivory Coast. It differs from *M. couvreurii* by the presence of 6

staminodes (versus staminodes absent), free stamens (versus connate) and in having more carpels (15–20 versus 9–12). For the differences with *M. aquila* see under that species.

5. *Monanthotaxis barteri* (Baill.) Verdc. — Fig. 5a–d; Map 4

Monanthotaxis barteri (Baill.) Verdc. (1971b) 21. — *Popowia barteri* Baill. (1868) 324. — *Enneastemon barteri* (Baill.) Keay (1953) 72. — Type: *C. Barter s.n.* (holo: P00362783; iso: K000198913, K000198914), Sierra Leone, Western Area, Sugarloaf mountain, 8 May 1857.

Popowia heudelotii Baill. (1868) 321. — *Clathrospermum heudelotii* (Baill.) Scott Elliot (1894) 71. — Lectotype (designated here): *J. Heudelot 878* (lecto: P (P00362765); iso: P00362764), Guinea, Boké, Senegambia, Karkandy, 1837.

Popowia nigritana Baker f. (1913) 4. — *Enneastemon nigritanus* (Baker f.) Exell (1934) 281. — Type: *P.A. Talbot 1550* (holo: BM000547357; iso: K000198912), Nigeria, Cross River State, Oban, 1912.

Shrub, scandent shrub or liana, to 12 m long; young branches densely covered with appressed, yellowish brown hairs 0.2–0.3 mm long, becoming glabrous; old branches dark brown to blackish brown. *Leaves*: petiole 2.5–6 mm long, 0.6–1.3 mm diam, terete, indument as on branches; lamina oblong-elliptic, elliptic, obovate to oblanceolate, 4.8–12.1(–14.2) by 2.4–5.1 cm, 2–4.3 times longer than wide, subcoriaceous to chartaceous, not punctate, glossy above, glaucous below, above glabrous, but primary vein sparsely covered with appressed, white-yellow hairs 0.1–0.3 mm long, becoming glabrous, below sparsely covered with appressed, yellow hairs 0.1–0.3 mm long, base attenuate to cuneate, sometimes rounded, with thickened black margins, apex acute to acuminate, acumen to 10 mm long, secondary veins 6–10 per side, curving upwards, tertiary venation percurrent, not or hardly visible above. *Inflorescences* axillary, composed of solitary flowers to a 2- (or 3-)flowered fascicle-like rhipidia; sympodial rachis absent; pedicels (8–)10–25 mm long, 0.2–0.4 mm diam, fruiting pedicels 17–32 mm long, 0.6–1.5 mm diam, densely covered with appressed, yellowish brown hairs; lower bracts absent; upper bract in the upper half of the pedicel, halfway or sometimes in lower half of pedicel, ovate to lanceolate, 0.9–1.3 by 0.4–0.7 mm, indument as on pedicel; flower buds globose. *Flowers* bisexual; sepals connate at the base, depressed ovate, 0.8–1.5 by 1.4–1.8 mm, apex obtuse to slightly acute, densely covered with appressed hairs, persistent in fruit; receptacle 1.5–1.8 mm diam, flat; petals colour in vivo unknown, 6, in two whorls, base of inner petals visible in bud, outer petals ovate, 3.2–3.6(–5) by 2.2–2.6(–3.4) mm, outside and apical part and margins of inside densely covered with appressed, yellow-brown hairs, inner petals elliptic to rhombic, 2.7–3.1(–4.5) by 1.5–2.3 mm, densely hairy outside and near the apex on the inside; stamens 9, in one whorl, free, clavate, 1.2–1.4 mm long, filaments 0.8–0.9 mm long, thecae extrorse, connective truncate, prolonged inward and slightly outward, glabrous, but hairy on the inside, staminodes absent; carpels 6, ellipsoid, c. 1.4 by 0.6 mm,

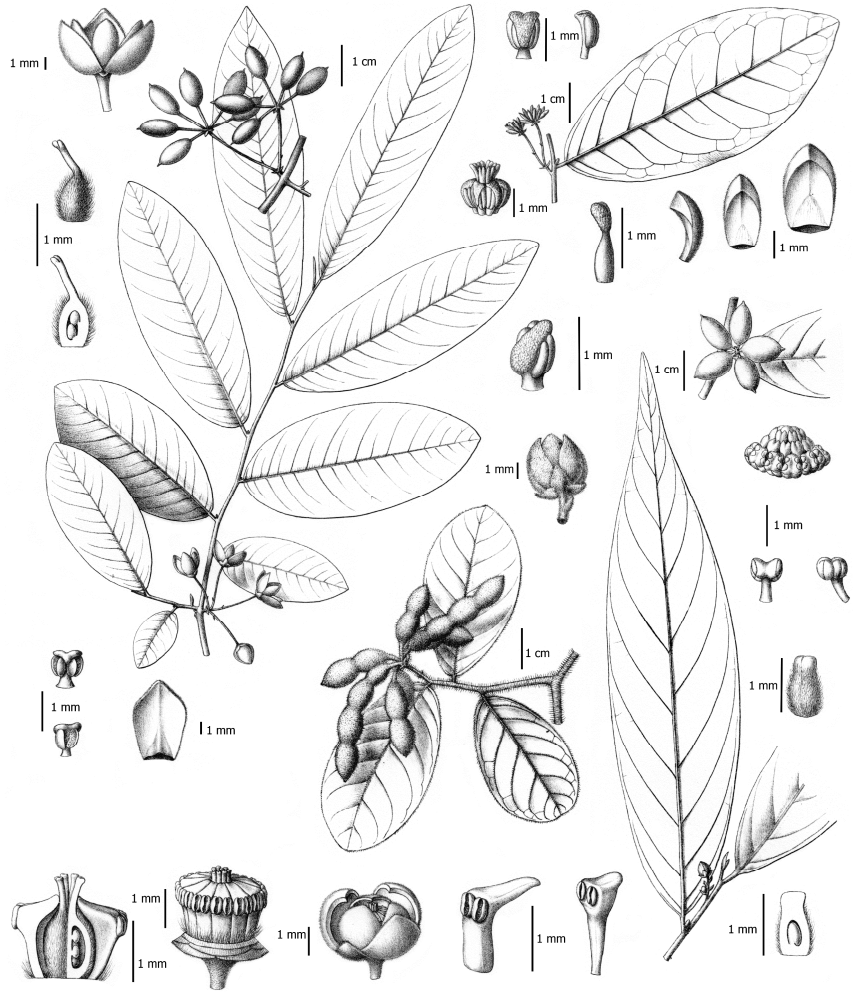
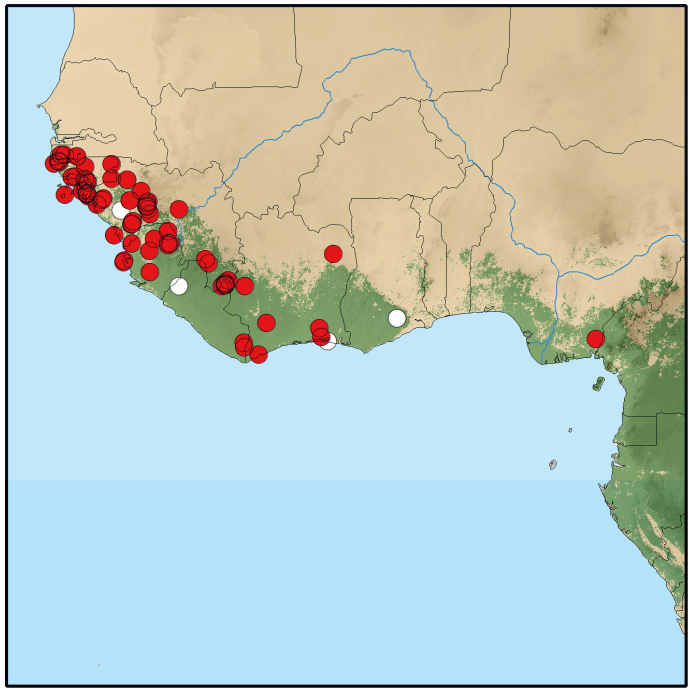


Fig. 5 a–d. *Monanthotaxis barteri* (Baill.) Verdc.: a. Flower; b. flower with petals removed; c. stamens; d. longitudinal section of flower. — e–i. *M. buchananii* (Engl.) Verdc.: e. Flowering branch and fruiting inflorescence; f. flower; g. petal, inside view; h. stamens; i. carpel and longitudinal section of carpel. — j–p. *M. elegans* (Engl. & Diels) Verdc.: j. Flowering branch; k. flower bud; l. stamens and carpels; m. stamens, front and side view; n. carpel; o. carpel longitudinal section; p. fruiting inflorescence. — q–v. *M. fornicata* (Baill.) Verdc.: q. Flowering branch; r. outer petal, inside view; s. inner petal, inside view; t. stamens and carpels; u. stamens, front and side view; v. carpel. — w. *M. trichocarpa* (Engl. & Diels) Verdc.: w. Fruiting branch. — x. *M. vogelii* (Hook.f.) Verdc.: x. Stamen. – Modified from Engler & Diels (1901) table 18 and 19.

densely hairy, ovules 4 (or 5), lateral, stigma elongate, c. 0.4 mm long, glabrous. *Monocarps* 1–6, colour unknown in vivo, moniliform with each part ellipsoid to narrowly ellipsoid, 13–55 by 7–8 mm, verrucose, densely covered with appressed, yellowish brown hairs, becoming glabrous, apiculate, apiculum 0.5–1.5 mm long, stipes 2–5 mm long. *Seeds* 1–5, ellipsoid, 11–19 by 6–7 mm, ochre-brown, apex rounded or slightly apiculate, raphe visible.

Distribution — Senegal, Guinea-Bissau, Guinea, Sierra Leone, Liberia, Ivory Coast, Ghana, Nigeria.



Map 4 Distribution of *Monanthotaxis barteri* (red circles, white circles are uncertain dets or aberrant specimens).

Habitat & Ecology — In primary rainforests, gallery forests, forest edges, swamp forests and wooded savannahs. Altitude: 0–1000 m. Flowering: March to August, fruiting: all year round.

Vernacular names — Guinea: Setinan Lanhtè (Balantè name) (*CA Couch 478*).

Preliminary IUCN conservation status —Least concern (LC). EOO: 1,017,067km^2, AOO: 260 km^2. This species is known from many localities and nature reserves and therefore is currently not under threat of extinction.

Notes — 1. *Monanthotaxis barteri* is the only species of *Monanthotaxis* in West Africa that is densely covered with appressed yellow-brown hairs on the young branches and cuneate to attenuate leaf bases.

2. Some specimens of *M. barteri* can be similar to *M. schweinfurthii* from Central Africa, but differ by having the upper bract generally in the upper half of the pedicel, by having smaller leaves with more cuneate to even attenuate leaf base with only 6–10 secondary veins per side, while *M. schweinfurthii* has larger leaves with cuneate to rounded leaf base with 9–13 secondary veins per side and the upper bract generally in the lower half of the pedicel. Furthermore, the pericarp thickness is less then 1 mm in ripe fruits of *M. barteri* and more than 1 mm in ripe fruits of *M. schweinfurthii*.

3. The single specimen from Nigeria (*PA Talbot 1550*), has longer leaves, shorter pedicels and larger flowers than specimens of *M. barteri* from West-Africa. Two specimens from an elevation of 2000 m in the Atewa Range (*DK Abbiw 275* and *JM Lock GC43945*) differ in having shorter leaves, shorter pedicels and a more reddish brown indument.

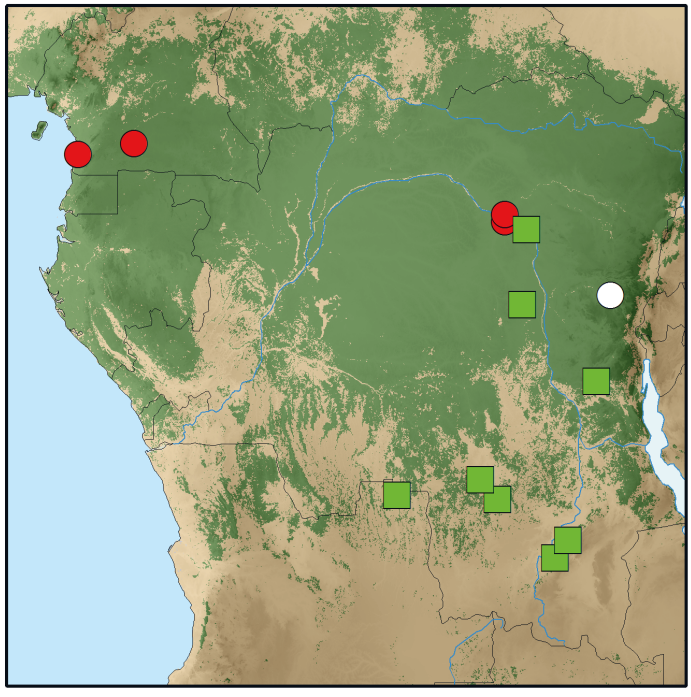
6. *Monanthotaxis bicornis* (Boutique) Verdc. — Map 5

Monanthotaxis bicornis (Boutique) Verdc. (1971b) 31. — *Popowia bicornis* Boutique (1951b) 115. — Lectotype (designated here): *J.L.P. Louis 8957* (lecto: BR (BR0000008805386); isolecto: BR0000008805379, BR6102005255172, K000913657, P00362792), Democratic Republic of the Congo, Orientale, Yamboa, 25 km au N.W. de Yangambi, 21 April 1938.

Liana, to 30 m long; young branches yellow-brown, densely covered with appressed, yellow-brown hairs 0.2–0.4 mm long, becoming glabrous; old branches blackish brown. *Leaves*: petiole 3–5 mm long, 0.6–1 mm diam, terete, indument as on branches; lamina narrowly oblong-elliptic, 6–12 by 1.9–3.5 cm, 2.6–3.7 times longer than wide, chartaceous, not punctate, medium green above, glaucous below, above sparsely covered with appressed, whitish hairs 0.5–0.8 mm long, primary vein above densely covered with long-persistent, yellowish hairs 0.2–0.4 mm long, below densely to sparsely covered with appressed, yellowish hairs 0.1–0.2 mm long, base cuneate, with thickened black margin, apex acuminate, acumen 5–15 mm long, secondary veins 11–14 per side, hardly visible, tertiary venation percurrent, slightly raised above and reticulate, hardly visible below. *Inflorescences* axillary or c. 1 mm above axils or terminal, composed of solitary flowers to 3-flowered fascicle-like rhipidia; sympodial rachis absent or up to 7 mm long, densely covered with appressed, yellowish hairs; flowering pedicels 15–60 mm long, 0.3–0.6 mm diam, densely to sparsely covered with appressed, yellowish hairs 0.1–0.2 mm long; lower bracts absent or broadly to narrowly ovate, 0.5–1.3 by c. 0.4 mm, indument as on sympodial rachis; upper bract in lower half of the pedicel, ovate, 0.4–0.7 by 0.3–0.5 mm, indument as on pedicel; flower buds globose. *Flowers* bisexual; sepals free, depressed ovate, 1–1.3 by 2.3–2.6 mm, apex acute, densely covered with

appressed hairs; receptacle 2.3–3.3 mm diam, flat; petals yellow to white, 6, in two whorls, outer petals broadly ovate, 4–6.7 by 4.6–6 mm, outside densely covered with appressed, yellow-brown hairs 0.1–0.2 mm long, inside and base densely covered with ascending, very short hairs, sometimes glabrous, inner petals broadly rhombic, 2.5–2.8 by 2.2–3 mm, indument as on outer petals; stamens 15–17, in one whorl, free, oblong, 0.8–0.9 mm long, filaments 0.3–0.4 mm long, broader than connective, thecae latrorse, almost convergent apically, only leaving a very small part of the connective visible, connective slightly prolonged inward, glabrous, staminodes absent; carpels 6–9, ellipsoid, 1.3–1.4 by c. 0.6 mm, densely hairy, ovules 2 or 3, lateral, stigma deeply bifurcate, 0.2–0.5 mm long, glabrous. *Monocarps* and *seeds* not seen.

Distribution —Cameroon (South Region), Democratic Republic of the Congo (Orientale).



Map 5 Distribution of *Monanthotaxis bicornis* (red circles, white circle uncertain det) and *M. biglandulosa* (green squares).

Habitat & Ecology — In swamp and secondary forests. Altitude: 470–600 m. Flowering: March, April.

Preliminary IUCN conservation status —Endangered (EN): B2ab(iii). EOO: 68,251^{km2}, AOO: 16 km^2. This species is known from only four localities outside reserves and has not been collected in the the last 45 years.

Notes — 1. *Monanthotaxis bicornis* is closely related to *M. pellegrinii* based on the thecae almost converging apically; *M. bicornis* differs in having appressed, yellow-brown hairs (versus ascending reddish brown hairs).

2. *Monanthotaxis bicornis* can be distinguished from the other species with apically convergent thecae by the cuneate leaf bases and 15–17 stamens in one whorl.

7. *Monanthotaxis bidaultii* P.H.Hoekstra, *sp. nov.* — Plate 1; Map 6

Monanthotaxis bidaultii has unisexual flowers and is closely related to *M. cauliflora* (Chipp) Verdc., but it is differentiated from all species of *Monanthotaxis* by the staminate flowers with 3 stamens and 3 staminodes. It is differentiated from *M. mortehanii* (De Wild.) Verdc. and *M. glomerulata* (Le Thomas) Verdc. for which no staminate flowers are known by the pistillate flowers with < 60 carpels and 2–4 ovules per carpel, while the latter two species have > 80 carpels and 6 or 7 ovules per carpel. — Type: *T.L.P. Couvreur et al. 918* (holo: WAG (consisting of 2 sheets: WAG.1576038, WAG.1576039); iso: LBV not seen, YA not seen), Gabon, Moyen-Ogooué, 30 km ESE of Lambaréné, 3–4 km on road after Mabounié 'camp de vie, 103 m, 22 Nov. 2015. Paratypes: *E. Bidault et al. 551* (LBV, MO), Gabon, Moyen-Ogooué, Mabounié, forest west of camp, 100 m, 13 May 2012. *E. Bidault & Akouangou 1528* (BR, BRLU, LBV, MO, P), Gabon, Moyen-Ogooué, zone de Mabounié, à 45 km au sud-ouest de Lambaréné, rive nord de la rivière Ngounié, 80 m, 16 May 2014. *E. Bidault & Akouangou 1632* (BR, BRLU, LBV, MO), Gabon, Moyen-Ogooué, zone de Mabounié, à 45 km au sud-ouest de Lambaréné, rive nord de la rivière Ngounié, 80 m, 19 June 2014. *E. Bidault et al. 1641* (BRLU, LBV, MO), Gabon, Moyen-Ogooué, zone de Mabounié, à 45 km au sud-ouest de Lambaréné, rive nord de la rivière Ngounié, 77 m, 20 June 2014. *E. Bidault et al. 1647* (BR, BRLU, LBV, MO, P, WAG), Gabon, Moyen-Ogooué, zone de Mabounié, à 45 km au sud-ouest de Lambaréné, rive nord de la rivière Ngounié, 94 m, 21 June 2014. *E. Bidault et al. 1876* (BRLU, LBV, MO), Gabon, Moyen-Ogooué, Mabounié, à 35 km au sud-est de Lambaréné, en bordure du site de la Base Vie 2, 22 m, 31 Oct. 2014. *F.J. Breteler 9756* (LBV, WAG), Gabon, Ogooué-Maritime, Rabi, Divangui road, 3 Apr. 1990. *T.L.P. Couvreur et al. 914* (LBV, WAG, YA), Gabon, Moyen-Ogooué, 30 km E SE of Lambaréné, on main road to Mabounié mine exploitant "camp“de vie”, c 9 km the Ngounié, 62 m, 21 Nov. 2015.

Small shrub or liana, to 20 m long, to 1 cm diam; young branches densely covered with appressed to slightly ascending or erect, reddish brown hairs 0.1–0.3 mm long, becoming glabrous; old branches dark brown to blackish. *Leaves*: petiole 5–8 mm long, 1.2–1.6 mm diam, grooved, indument as on branches; lamina narrowly oblong-elliptic to oblanceolate, 9–19 by 3–6.1 cm, 2.4–3.3 times longer than wide, chartaceous, slightly punctate, discolorous,



Plate 1 *Monanthotaxis bidaultii* P.H.Hoekstra: a–c. leafy branches; d, e. staminate inflorescences; f, g. staminate flower; h. fruit (a: cultivated specimen, same plant as *Bidault 1528*; b, c, f: *Bidault 1528*; d, g: *Bidault 551*; e: *Bidault 1632*; h: *Bidault 1647*). Photos: a: P.H. Hoekstra; b–h: E. Bidault.

dark glossy green above, glaucous below, above with appressed to ascending, yellowish hairs 0.1–0.3 mm long, becoming glabrous except for the primary vein, below densely covered with ascending to erect, yellowish hairs 0.1–0.3 mm long, base cuneate to rounded, with thickened black margin at the base, apex acute to slightly acuminate, acumen to 10 mm long, secondary veins 10–15 per side, straight to slightly curving upwards towards the margin, tertiary venation percurrent. *Flowers* unisexual. *Staminate inflorescences* cauliflorous, ramiflorous or axillary, composed of 2–5-flowered fascicles or rhipidia; sympodial rachis 1–3 mm long, densely covered with erect hairs 0.1–0.2 mm long; pedicels 1–2 mm long, c. 0.4 mm diam, fruiting pedicels 10–15 mm long, 1.2–1.9 mm diam, densely covered with appressed hairs; bracts ovate, c. 0.8 by 0.5 mm, indument as on rachis; flower buds depressed globose; sepals free, ovate, c. 0.8 by 0.6 mm, densely covered with appressed, short hairs; receptacle 0.8–1.2 mm diam, flat; petals beige, 3, in one whorl, broadly ovate, 1.9–2.2 by 1.8–2.1 mm, outside covered with appressed, short hairs, inside covered with appressed, very short hairs to papillate; stamens 3, in one whorl, free, alternating with the petals, oblong, 0.6–0.7 mm long, filaments very short, less than 0.1 mm long, thecae latrorse, connective truncate, hairy on the inside, staminodes 3, alternating with the stamens, 0.2–0.3 mm long, sparsely hairy, hairs < 0.1 mm long. *Young pistillate inflorescences* cauliflorous, few-flowered glomerules to 2 cm long; sympodial rachis densely covered with erect, reddish brown hairs 0.1–0.2 mm long; flowering pedicels c. 11 mm long, 0.5–0.7 mm diam; bracts ovate, c. 0.7 by 0.5 mm, indument as on rachis; flower buds globose to ovoid; sepals ovate to broadly ovate, 1.1–1.4 by 0.8–1.4 mm, densely covered with hairs, not persistent in fruit; receptacle unknown; petal colour in vivo unknown, at least 3 in at least 1 whorl, outer petals depressed ovate, at least 2–2.2 by 2.7–2.8 mm, outside densely covered with dark brown hairs, inside densely covered with yellowish hairs c. 0.05 mm long, inner petals absent or not yet developed; carpels c. 52, ellipsoid, c. 1 by 0.4 mm, densely hairy, ovules 2(–4), lateral, stigma subglobose, c. 0.4 mm long, glabrous. *Monocarps* 4–23, brown, ellipsoid or moniliform, each part ellipsoid to narrowly ellipsoid, 12–28 by 6.5–7.5 mm, slightly verrucose, densely covered with hairs, apex apiculate, apiculum 1–1.5 mm long, stipes 3.5–5 mm long. *Seeds* 1–2(–4), ellipsoid, 12–13 by c. 6.5 mm, ochre-brown, apex rounded, raphe slightly visible.

Distribution — Gabon (Moyen-Ogooué, Ogooué-Maritime).

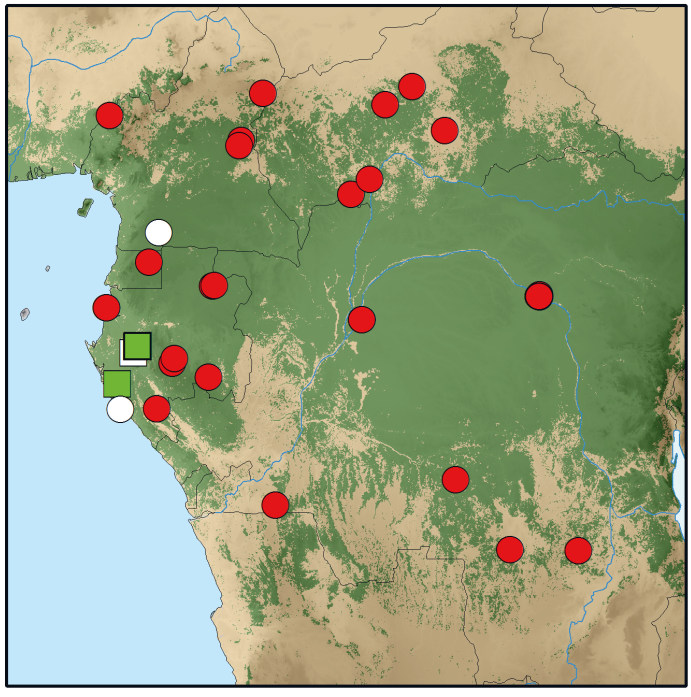
Habitat & Ecology — In terra firme forest, swamp forest and secondary forest. Altitude: 22–180 m. Flowering : April to June; fruiting: June, October, November.

Preliminary IUCN conservation status —Endangered (EN): B2ab(iii). EOO: 336 km^2, AOO: 8 km^2. This species is only known from 2 localities, both outside protected reserves.

Ethymology — *Monanthotaxis bidaultii* is named after Ehoarn Bidault, the discoverer of the population in Mabounié and collector of the majority of specimens of this species.

Notes — 1. *Monanthotaxis bidaultii* can be distinguished from other species as indicated in the diagnosis.

2. *F.J. Breteler 9756* from Ogooué-Maritime has a slightly different facies caused by more dense and slightly more ascending/erect hairs than the specimens from Moyen-Ogooué. This specimen is identified here as *M. bidaultii* because of the similarity in leaf shape, inflorescence and DNA-sequences (Fig. 1, clade I). The description of the pistillate inflorescence is based on that specimen.



Map 6 Distribution of *Monanthotaxis bidaultii* (green squares, white square is uncertain det) and *M. bokoli* (red circles, white circles are uncertain dets).

8. *Monanthotaxis biglandulosa* (Boutique) P.H.Hoekstra, *comb. nov.* — Fig. 6i; Map 5

Monanthotaxis biglandulosa (Boutique) P.H.Hoekstra, comb. nov. — *Enneastemon biglandulosus* Boutique (1951b) 125. — Lectotype (designated here): *J.A.A. Gillardin 183* (lecto: BR (BR0000008820440); iso: BR0000008820266, BR0000008820273), Democratic Republic of the Congo, Kasai-Oriental, Kanda Kanda, Concession Laridon, Versaut vallée, 940 m, 4 Dec 1936.

Shrub or liana, to 3 m long; young branches densely covered with ascending, yellowish brown hairs 0.2–0.4 mm long, becoming glabrous; old branches grey-black. *Leaves*: petiole 2.5–4.5 mm long, 1.5–1.7 mm diam, terete, indument as on branches; lamina elliptic to narrowly

elliptic-obovate, 8.2–15.7 by 2.8–7.1 cm, 2.2–3.5 times longer than wide, chartaceous, not punctate, above sparsely covered with appressed, whitish hairs 0.2–0.3 mm long, primary vein more covered with ascending, yellowish hairs, below sparsely covered with appressed, yellow hairs c. 0.2 mm long, primary vein densely covered with appressed to ascending hairs, base slightly cuneate to rounded, with or without thick, globose, black glands, apex acute to acuminate, acumen to 15 mm long, secondary veins 7–13 per side, slightly curving upwards towards the margin, tertiary venation percurrent, hardly visible above. *Inflorescences* axillary, composed of solitary flowers to 3-flowered fascicle-like rhipidia; sympodial rachis 0–12 mm long, densely covered with ascending, yellowish hairs; pedicels 7–25 mm long, 0.4–0.6 mm diam, fruiting pedicels 22–35 mm long, 0.7—1.2 mm diam, densely covered with ascending, yellow hairs; lower bracts absent or a dense tuft of yellow-brown hairs; upper bract in the lower half of the pedicel or to almost halfway, ovate, 0.7–1.2 by 0.4–0.7 mm, densely covered with hairs as pedicels; flower buds globose. *Flowers* bisexual; sepals connate at the base, depressed ovate to shallowly triangular, 0.7–1 by 1.5–1.7 mm, apex acute, densely covered with appressed hairs, persistent in fruit; receptacle 1.5–2 mm diam, flat; petals colour in vivo unknown, 6, in two whorls, base of inner petals visible in bud, outer petals ovate, 3.5–4.2 by 2.3–3.7 mm, outside densely covered with appressed, yellowish brown hairs c. 0.2 mm long, but hairs shorter and ascending near the apex of the inside and glabrous at the base, inner petals rhombic, 2.9–3.1 by 2–2.1 mm, outside and apical part on inside covered with yellowish brown, short hairs; stamens 9, in one whorl, free, clavate, 1.3–1.6 mm long, filaments 0.8–1 mm long, thecae extrorse, connective truncate, prolonged outward and inward, hiding thecae, glabrous, but sparsely hairy on the underside of the inward extension, staminodes absent; carpels 10–14, subcylindric, 1.3–1.6 by c. 0.5 mm, densely hairy, ovules 5 or 6, lateral, stigma elongate, 0.4–0.5 mm long, glabrous. *Monocarps* 1–7, colour yellowish brown, moniliform,18–39 by 6–8 mm, slightly verrucose, covered with appressed, yellowish brown hairs, apex apiculate, apiculum 1–4 mm long, stipes 7–11 mm long. *Seeds* 1–5, subcylindric to ellipsoid, 13–18 by 5–8 mm, ochre-brown, apex rounded, raphe visible or not.

Distribution —Democratic Republic of the Congo (Kasai-Oriental, Katanga, Maniema, Orientale), Angola (Lunda Norte).

Habitat & Ecology — In primary rainforest, secondary rainforest and gallery forest. Altitude: 470–995 m. Flowering: February, May, December; fruiting: April, May.

Vernacular names — Democratic Republic of the Congo: Lukukuma (*R. Desenfans 5176*).

Preliminary IUCN conservation status —Endangered (VU): B2ab(iii). EOO: 438,453 km^2, AOO: 28 km^2. This species is known from 7 scattered locations of which 4 fall outside reserves.

Notes — 1. Verdcourt (1971b) refrained from changing *Enneastemon biglandulosus* to *Monanthotaxis biglandulosa*, because he was not sure if this species should be synonymised with *M. schweinfurthii* as the size of the leaf glands varies. However, *M. biglandulosa* differs from the latter in having 10–14 carpels per flower, while *M. schweinfurthii* consistently has 6 carpels. Furthermore, the sympodial rachis in *M. biglandulosa* is generally 4–12 mm long and

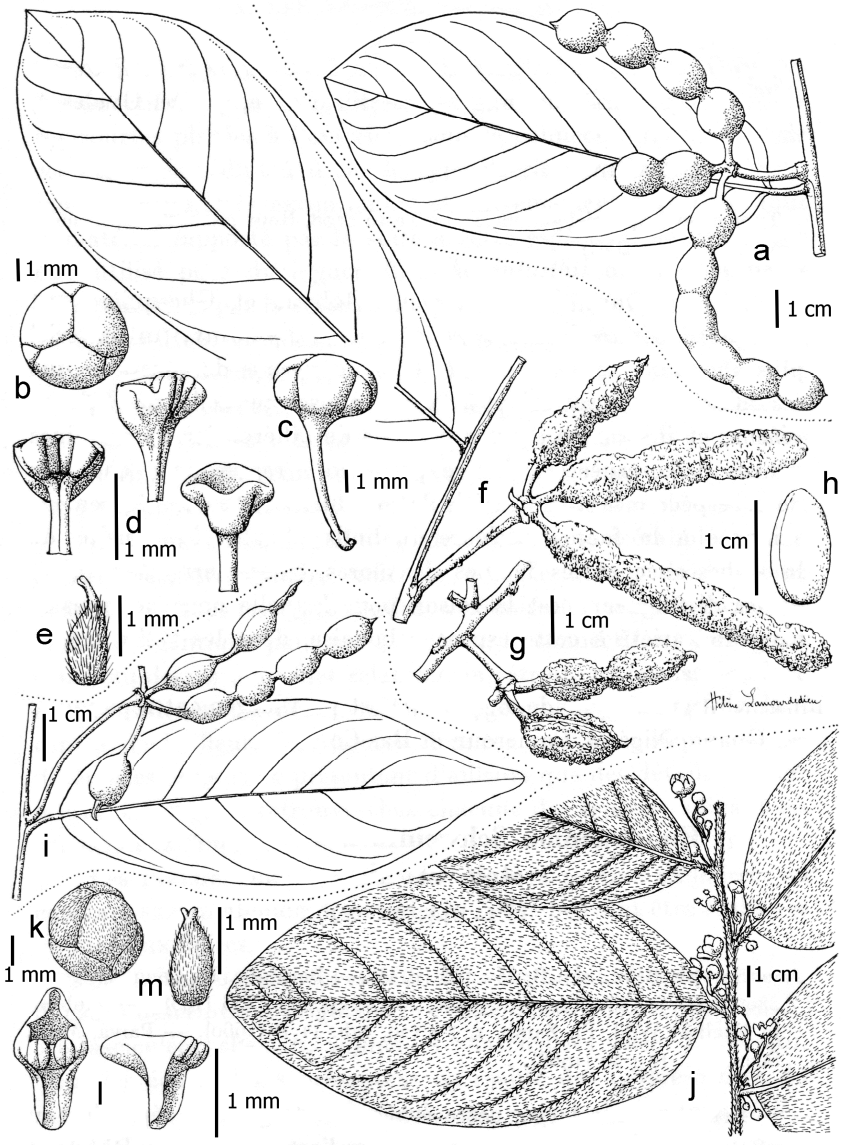


Fig. 6 a. *Monanthotaxis seretii* (De Wild.) P.H.Hoekstra: a. Fruiting branch. — b–h. *M. capea* (E.G.Camus & A.Camus) Verdc.: b. Flower bud, seen from above; c. flower bud, side view; d. stamen, outer, inner and side view; e. carpel; f. fruiting branch; g. fruiting branch; h. seed. — i. *M. biglandulosa* (Boutique) P.H.Hoekstra: i. Fruiting branch. — j–m. *M. foliosa* (Engl. & Diels) Verdc.: j. Flowering branch; k. flower bud, seen from above; l. stamen, outer and side view; m. carpel (a: *J.L.P. Louis 11405*; b–h: *Hallé 3561*; i: *Bamps 600*; j–m: *Le Testu 2108*). Modified from Le Thomas (1969) plate 44.

the seeds are normally subcylindric, while the sympodial rachis is generally absent or up to 1 mm long in *M. schweinfurthii* and the seeds are ellipsoid to subglobose.
2. *P. Bamps 500* differs from the other specimens in having appressed instead of ascending hairs on the young branches.

9. *Monanthotaxis bokoli* (De Wild. & T.Durand) Verdc. — Fig. 7a–g; Map 6

Monanthotaxis bokoli (De Wild. & T.Durand) Verdc. (1971b) 24. — *Xylopia bokoli* De Wild. & T.Durand (1900) 2. — *Popowia bokoli* (De Wild. & T. Durand) Boutique (1951a) 349. — Lectotype (designated here): *A.P. Dewèvre 785* (lecto: BR (BR0000024941433), not seen; isolecto: BR0000008804020, BR0000008804358), Democratic Republic of the Congo.
Popowia iboundjiensis Pellegr. (1949) 212. — Lectotype (designated here): *G.M.P.C. Le Testu 5729* (lecto: P (P00362791); isolecto: BM000553827, LISC000388, P00362789, P00362790), Gabon, Ngounié, Ndingui, Mullerville, 11 nov 1925; other syntype: *G.M.P.C. Le Testu 8626* (BM000553826, P01954740, P01954741), Gabon, Ogooué-Lolo, region de Lastoursville, Mont Iboundji, 27 Dec. 1930.

Scandent shrub or liana, to 6 m long; young branches densely covered with erect, reddish brown hairs 0.4–1.3 mm long, becoming glabrous; old branches blackish, sometimes with reddish tint. *Leaves*: petiole 2.5–6.3 mm long, 0.9–1.3 mm diam, terete, indument as on branches; lamina oblong-elliptic, 4.4–12.6 by 2.3–6.9 cm, 1.6–2.6 times longer than wide, subcoriaceous to chartaceous, slightly punctate, glaucous above, above covered with appressed, white hairs 0.5–1 mm long, soon becoming glabrous, primary vein above covered with ascending to erect, yellow hairs c. 0.2 mm long, below sparsely covered with ascending to erect, reddish brown hairs 0.5–0.8 mm long, slightly more densely so on primary vein, base subcordate, glands hardly visible, apex rounded or acute, secondary veins 7–11 per side, straight then halfway curving upwards, tertiary venation percurrent, hardly visible above. *Inflorescences* extra-axillary, leaf-opposed or terminal, composed of solitary flowers; sympodial rachis absent; pedicels 11–24 mm long, 0.5–0.9 mm diam, fruiting pedicels 0.9–1.1 mm diam, sparsely to densely covered with erect, reddish brown hairs 0.5–0.6 mm long; lower bracts absent; upper bract in the lower half of the pedicel, ovate, 1.4–2.2 by 0.7–0.9 mm, indument as on pedicel; flower buds globose, but ovoid before anthesis. *Flowers* bisexual; sepals connate at the base, depressed ovate, 2.8–4.1 by 4.5–6.8 mm, apex rounded, covered with ascending, yellow-brown hairs, persistent in fruit; receptacle 3.7–5.8 mm diam, flat; petals colour in vivo unknown, 6, in two whorls, outer petals ovate, 15–19 by 8.4–10.8 mm, outside and apical part and margins of inside densely covered with yellowish hairs, inner petals lanceolate, c. 13 by 4.5–5.2 mm, outside glabrous, except for few hairs near the apex; stamens 24–32, in three or four whorls, free, obovoid, 1–1.1 mm long, filaments 0.3–0.4 mm long, thecae latrorse to extrorse, connective truncate, prolonged inward, hiding thecae, slightly papillate, staminodes absent; carpels 27–38, subcylindric, c. 2.7 by 0.4 mm, glabrous or with

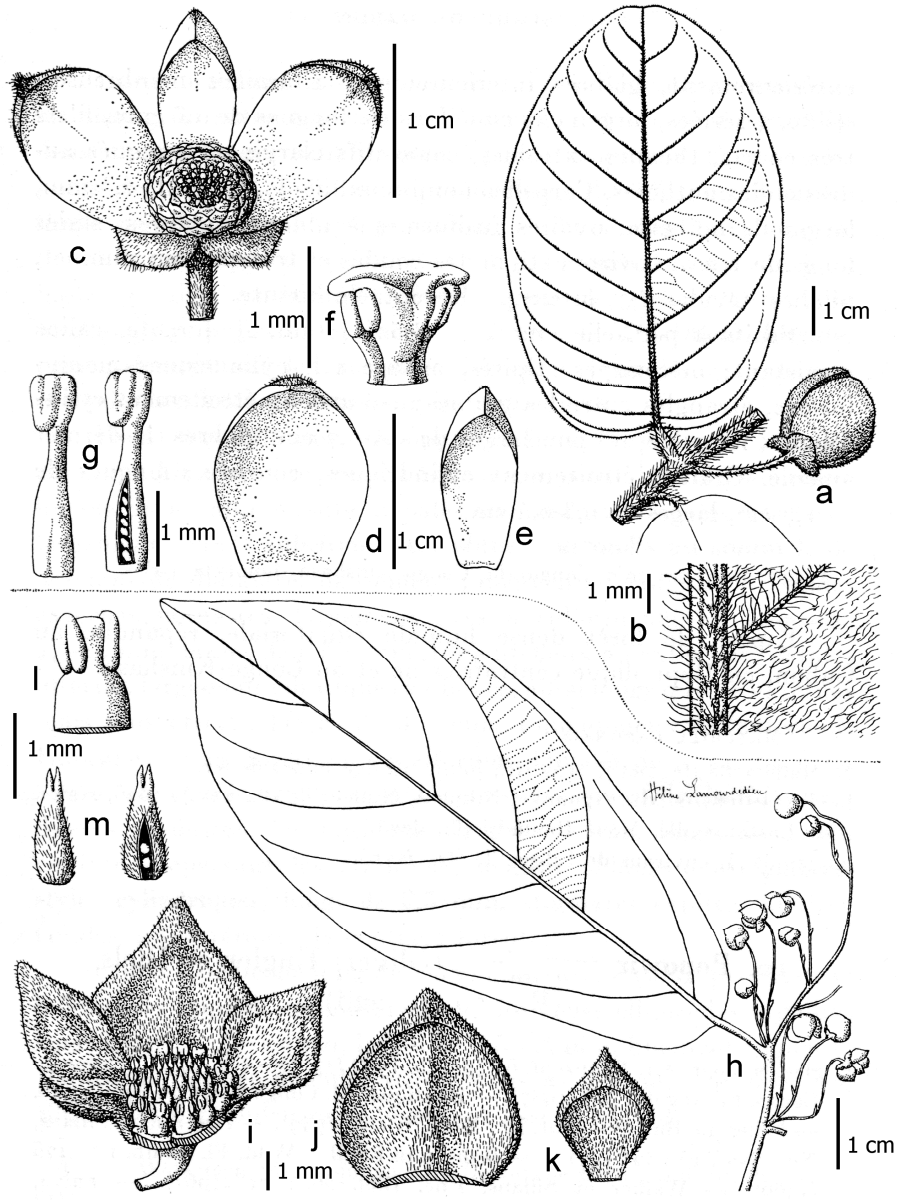


Fig. 7 a–g. *Monanthotaxis bokoli* (De Wild. & T.Durand) Verdc.: a. Flowering branch; b. detail leaf abaxially; c. flower with three petals removed; d. outer petal, inside view; e. inner petal, inside view; f. stamen; g. carpel and longitudinal section of carpel. — h–m. *M. pellegrinii* Verdc.: h. Flowering branch; i. flower with three petals removed; j. outer petal, inside view; k. inner petal, inside view; l. stamen; m. carpel and longitudinal section of carpel (a–g: *Le Testu 5729*; h–m: *Le Testu 9028*). Modified from Le Thomas (1969) plate 41.

a few hairs at the base, ovules 4 or 5, lateral, stigma subcylindric, c. 0.9 mm long, glabrous. *Monocarps* 1–25, yellow, maturing orange, subcylindric, 26–65 by 5–8 mm, slightly verrucose, glabrous or with a few hairs on the stipe, apex rounded or apiculate, apiculum to 4 mm long, stipes 7–10(–25) mm long. *Seeds* 1–4, cylindric, 14–21 by 4–6 mm, ochre-brown, apex flattened, rounded or apiculate, raphe not visible.

Distribution — Cameroon, Central African Republic, Democratic Republic of the Congo, Equatorial Guinea, Gabon.

Habitat & Ecology — In swamp forests, gallery forests, primary and secondary rain forests. Altitude: 350–800 m. Flowering: March to December; fruiting: all year round.

Vernacular names — Democratic Republic of the Congo: Bocodji (*A.P. Dewèvre 785*).

Preliminary IUCN conservation status — Least concern (LC). EOO: 2,157,212 km^2, AOO: 108 km^2. This species is known from many localities including a few national parks. Therefore, *M. bokoli* is currently not under threat of extinction.

Notes — 1. *Monanthotaxis bokoli* resembles *M. ferruginea* and both species share a dense indument of erect, reddish brown hairs on the branches and leaves and glabrous carpels. *Monanthotaxis bokoli* can, however, easily be distinguished by the much larger flowers, almost glabrous inner petals and subcylindric seeds and monocarps with long stipes. However, the leaves of *M. ferruginea* are highly variable between different populations and those on specimens from eastern Africa may look highly similar to *M. bokoli*.

2. A specimen from southwest Gabon (*F.J. Breteler 14616*) differs from the other specimens of *M. bokoli* in having shorter hairs and slightly more obovate leaves.

3. The lectotype designated here was not seen. However this sheet has been appointed by Johnson & Murray (2018) as the holotype, they should have stated that it is a lectotype as previous authors did not indicate which of the 3 sheets is the holotype.

10. *Monanthotaxis buchananii* (Engl.) Verdc. — Fig. 5e–i; Plate 2a; Map 7

Monanthotaxis buchananii (Engl.) Verdc. (1971b) 24. — *Unona buchananii* Engl. (1895) 179. — *Popowia buchananii* (Engl.) Engl. & Diels (1901) 47. — Lectotype (designated by Johnson & Murray 2018): *J. Buchanan 1152* (lecto: B100153048; isolecto: BM000553828, K000198971), Malawi, 1891; other syntypes: *F.L. Stuhlmann 6238* (B not seen), Tazania, Pwani, Usaramo, Kisserewe, Jan. 1894; *F.L. Stuhlmann 6703* (B not seen), Tanzania, Pwani, Usaramo, Kisserewe, Feb. 1894.

Popowia djurensis Engl. & Diels (1901) 49. — Lectotype (designated here): *G.A. Schweinfurth 1931* (lecto: B (B100154092); isolecto: E00624347, K000198981, K000198982, MEL2382325, P00362788, S, WU0025874), South Sudan, Western Equatoria, “im lande der Djur, grosse Seriba Ghatta”, 12 June 1869; other syntypes: *G.A. Schweinfurth 2046* (B, K000198983, P00362787, WU0025873), South Sudan, Western Equatoria, im lande der

Djur, Seriba Ghattas, 10 July 1869; *F.L. Stuhlmann 1470* (B not seen, BR), Uganda, South Buganda, Sese Isl., Jan. 1891.

Small tree, shrub, scandent shrub or liana, 0.7–7 m long; young branches pale brown (rarely? green in vivo), sparsely covered with appressed, reddish brown hairs c. 0.4 mm long, becoming glabrous; old branches pale grey or pale brown, sometimes purplish brown in living specimens. *Leaves*: petiole 2–4 mm long, 0.5–1 mm diam, grooved, covered with appressed, reddish brown or white hairs; lamina narrowly oblong-elliptic, 4.5–10.7(–13.2) by 1.1–3.8(–4.9) cm, (2.2–)3–5.3 times longer than wide, chartaceous, not punctate, young leaves above sparsely covered with long, white hairs, soon becoming glabrous except for the primary vein, below covered with appressed, pale brown hairs c. 0.2 mm long, base cuneate to rounded or slightly subcordate, with small black glands, apex acute to rounded, primary vein yellowish or reddish, often distinctly contrasting with darker petiole, secondary veins 9–16 per side, straight upwards, tertiary venation slightly reticulate, slightly raised above and below or not visible above. *Inflorescences* leaf-opposed, composed of solitary flowers or up to 4-flowered rhipidia; sympodial rachis 0–3 mm long in flower, to 5 mm long in fruit; pedicels 8–32 mm long, 0.3–0.6 mm diam, fruiting pedicels 0.5–0.8 mm diam, covered with with reddish brown hairs; lower bracts depressed ovate, c. 1 by 2 mm, covered with reddish brown hairs; upper bract ovate, 0.5–1 by 0.2–0.5 mm, indumentum as pedicel; flower buds depressed globose to deltoid-ovoid. *Flowers* bisexual; sepals free, depressed triangular-ovate, 0.8–1.5 by 1.5–2 mm, covered with reddish brown, short hairs, persistent in fruit; receptacle 2–3 mm diam, flat, covered with short, brown hairs between the carpels and stamens; petals yellowish green to bright yellow, 6, in two whorls, outer petals ovate to broadly ovate, 4.6–7 by 3–5.5 mm, outside covered with white to yellowish, short hairs, base and apex of inside covered with hairs < 0.1 mm long, inner petals narrowly ovate, 3–6 by 1–2.4 mm, indumentum as on outer petals; stamens 11–15, in one whorl, adnate to base of petals or free, obconical to clavate, 0.8–1 mm long, filaments 0.2–0.3 mm long, thecae latrorse to extrorse, connective truncate, circular or quadrate seen from above, slightly prolonged inward, glabrous, staminodes absent; carpels 9–14, subcylindric to ellipsoid, 1–1.2 by c. 0.5 mm, densely hairy, ovules 1 or 2, basal or lateral, stigma elongate, 0.2–0.4 mm long, grooved to almost bifurcate, glabrous. *Monocarps* up to 13, dull orange to red when ripe, fusiform, narrowly ellipsoid to subglobose, 13–23 by 5–6 mm, rugulose to smooth, base and apex sparsely covered with appressed, short hairs, apex apiculate, apiculum 1–1.5 mm long, stipes 4.5–7 mm long, slightly to strongly grooved. *Seeds* 1 or 2, ellipsoid, 7.5–10.5 by 5.5–7 mm, ochre-brown, both ends rounded to sometimes slightly apiculate, raphe slightly visible as a longitudinal furrow from base to apex.

Distribution — Central African Republic, South Sudan, Kenya, Uganda, Tanzania, Zambia, Malawi, Mozambique, Zimbabwe.

Habitat & Ecology — In mixed woodland, evergreen forest, semi-deciduous forest, dry forest, secondary forest, riverine woodland, dry coastal woodland, submontane forest,

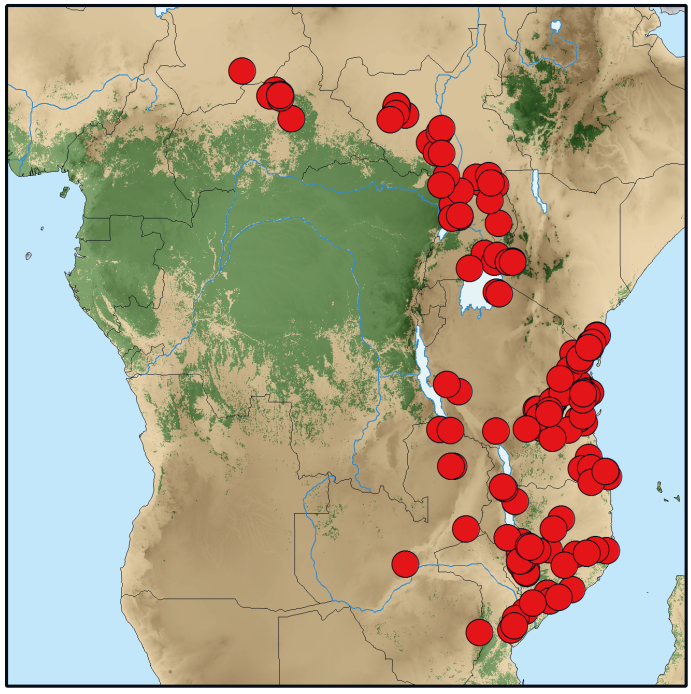


Plate 2 a. *Monanthotaxis buchananii* (Engl.) Verdc.: flowering branch. — b. *Monanthotaxis caffra* (Sond.) Verdc.: flowering branch. — c–e. *Monanthotaxis couvreurii* P.H.Hoekstra: c. Leaves; d. inflorescence; e. flower. — f. *Monanthotaxis diclina* (Sprague) Verdc.: pistillate inflorescence with flower buds and young fruits (a: *J. Burrows 9828*; b: *Wieringa 8018*; c–e: *Couvreur 762*; f: *Couvreur 537*). Photos: a: M.C. Lötter; b: J.J. Wieringa; c–f: T.L.P. Couvreur.

savannah, wooded grassland; stony hillslopes, on sandy soils, sandy loam, rocky river banks, flat laterite, near termite hills. Altitude: 0–1430 m. Flowering and fruiting all year round.

Vernacular names — Kenya: Mbulushi (Kikambe name) (*W.D. Hawthorne 258*). Malawi: Nkhokwe (*I.H. Patel 881, 909* & *J.L. Balaka 71)*, Njokondo (Tonga name) (*J. Pawek 6108*). South Sudan: Chulu (Dinkwa name) (*F.W. Andrews 628*), Milili (Kakwa name) (*J.G. Myers 13841*), Mo'ba (Mödö name) (*J. Persson 55*). Tanzania: Kizanaki (Kinaswa name) (*R.E.S. Tanner 4350*),

Milegeselegese (Kihehe name) (*F. Haerdi 219*), Mkeja (*Frontier-Tanzania Coastal Forest Research Programme 1943*), Mpegeho (*H.J. Ndangalasi 0624*), Msafu-simba (Kidoe name) (*Y.S. Abeid 445*), Mugoweko (Kisagara name) (*F. Haerdi 219*).



Map 7 Distribution of *Monanthotaxis buchananii*.

Preliminary IUCN conservation status — Least concern (LC). EOO: 4,256,330 km^2, AOO: 592 km^2. This species is known from many localities and national parks.

Notes — 1. Ripe fruits smell as overripe bananas when opened.

2. *Monanthotaxis buchananii* can easily be distinguished from all other species of *Monanthotaxis* by having pale brown branches and narrowly oblong-elliptic leaves. It is sometimes confused with *Cleistochlamys kirkii* (Benth.) Oliv., which has sessile flowers on leafless branches. Sterile specimens can be distinguished in the different tertiary venation, which is more reticulate and slightly more raised above in *Cleistochlamys.*

3. There are 3 syntypes mentioned in the protologue, *J. Buchanan 1152, F.L. Stuhlmann 6238 & 6703*. The collections from Stuhlmann should be present in Berlin, but have not been seen by us. *J. Buchanan 1152* is present in three different herbaria and therefore the most complete sheet from Berlin, which, therefore, has been designated as lectotype. *G.A. Schweinfurth 1931* is designated as lectotype for *Popowia djurensis* as it contains better material and is present in more herbaria than the parasyntype *G.A. Schweinfurth 2046*.

4. *N.A. Mwangulango 408* and *H.J. Ndangalasi 624* from Tanzania have very large leaves and the fruits of *Mwangulango 408* are more cylindric (c. 10 by 5 mm). However, no other characters have been found which could distinguish these from the other collections

5. *R.B. Drummond 3882* from coastal Kenya has a purplish brown bark, which dries grey and the leaf base is cuneate to almost attenuate.

11. *Monanthotaxis caffra* (Sond.) Verdc. — Fig. 8; Plate 2b; Map 8

Monanthotaxis caffra (Sond.) Verdc. (1971b) 24. — *Guatteria caffra* Sond. in Harv. & Sond. (1860) 9. —*Popowia caffra* (Sond.) Benth. in Benh. & Hook.f. (1862) 470. — Lectotype (designated here): *J.F. Drège 4082* (lecto: B (B100153015); isolecto: FHO not seen, HBG-502507, K000198959, P01954699, P01986740), South Africa, Kwazulu-Natal, prope Port Natal; other syntype: *W. Gueinzius s.n.* (G00308299), South Africa, Kwazulu-Natal, Natal, 1847.

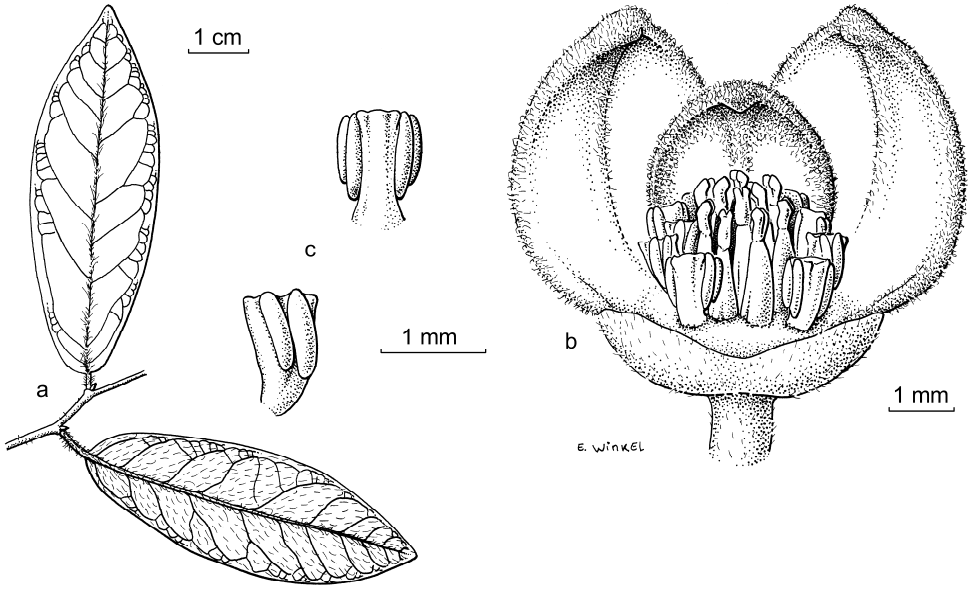


Fig. 8 *Monanthotaxis caffra* (Sond.) Verdc. a. Leafy branch; b. flower with three petals removed; c. stamen, outer and side view (a–c: *Huntley 71*). Drawing by E. Winkel.

Small tree, shrub, scandent shrub or liana, to 10 m long, c. 1 cm diam; young branches green in vivo, reddish brown in sicco, sparsely covered with appressed or erect, reddish brown to pale brown hairs c. 0.4 mm long, becoming glabrous; old branches dark brown. *Leaves*: petiole 3–5 mm long, c. 1 mm diam, grooved, indument as on branches; lamina narrowly elliptic to narrowly obovate, 5.5–10.8 by 2.1–3.5 cm, 2.6–3.4 times longer than wide, chartaceous to coriaceous, punctate, glaucous below, above becoming glabrous, but covered with long-

persistent hairs at the base of the primary vein, below covered with appressed, yellowish brown to pale brown hairs c. 0.2 mm long, base cuneate to rounded, with slightly thickened margins, apex acute to slightly acuminate, acumen to 10 mm long, primary vein yellowish or reddish, often contrasting with darker petiole, secondary veins 9 or 10 per side, curving upwards, tertiary venation reticulate, raised above and slightly so below or not visible below. *Inflorescences* leaf-opposed, composed of solitary flowers or 2–4-flowered cymes; sympodial rachis 0–2 mm long, indument as branches; pedicels 6–12 mm long, 0.5–1 mm diam, fruiting pedicels 10–17 mm long, 1–1.5 mm diam, indument as branches; lower bracts broadly ovate to lanceolate, 1–3.5 by c. 1 mm, indument as branches; upper bract broadly triangular to ovate, 1.5–1.6 by 0.7–1.2 mm, indument as pedicel; flower buds depressed globose to globose. *Flowers* bisexual; sepals basally slightly connate, depressed ovate, 0.6–0.8 by 2.5–4 mm, apex obtuse, densely covered with reddish brown, short hairs, persistent in fruit; receptacle 4–5 mm diam, flat, covered with short, brown hairs between the carpels and stamens; petals pale yellowish to yellow, inside drying reddish brown to purple, 6(–8), in two whorls, outer petals broadly ovate, 3, 6–7 by 6–7 mm, outside covered with yellowish, short hairs, inside with hairs at the apex, inner petals 3(–5), ovate, 3–4 by 2–3 mm, outside covered with short hairs, inside covered with hairs at the apex and base; stamens 15 or 16, in three groups of 5(–6), opposite to the inner petals, free, obconical, 0.9–1.1 mm long, filaments 0.2–0.3 mm long, thecae latrorse, 0.7–0.8 mm long, connective truncate, glabrous, staminodes absent; carpels 11–15, ellipsoid, 0.9–1.1 by c. 0.5 mm, glabrous, except for some hairs at the base, ovules 1(or 2), basal, stigma elongate, 0.4–0.5 mm long, grooved, glabrous. *Monocarps* up to 8, orange to bright red when ripe, narrowly ellipsoid, 12–20 by 5–6 mm, sparsely covered with appressed hairs at the stipe, 2-seeded ones slightly constricted between the seeds, rugulose to smooth, apex apiculate, apiculum c. 1 mm long, stipes 3.5–5 mm long, slightly to strongly grooved. *Seeds* 1–2, ellipsoid, c. 7.5 by 6.2 mm, ochre-brown, both ends rounded to sometimes slightly apiculate, raphe not visible.

Distribution — South Africa (Eastern Cape, Kwazulu-Natal, Mpumalanga), Swaziland (Lubombo). Habitat & Ecology — On rock outcrops, coastal forest, mountain forest, gallery forest, swamp forest and secondary forest; on sandstone, black turf soil and sandy mixed soil. Altitude: 0–914 m. Flowering: September to April; fruiting all year round.

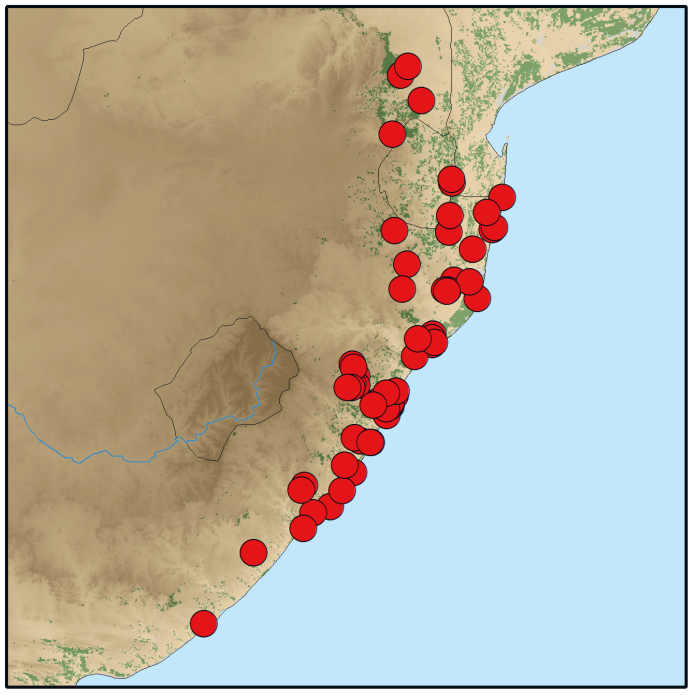
Vernacular names — South Africa (Foden & Potter 2005): Dwababessie (Afrikaans); Dwaba-berry (English); Idwabe, Isidwaba, Iviriga (Xhosa); Ithunganhlanzi, Mkonjane, Umavumba, Umazwenda Omhlophe, Umazwende, Umgogawezinhlanya, Umgogi Wezihlanya (Zulu).

Preliminary IUCN conservation status — Least concern (LC). EOO: 142,438 km^2, AOO: 260 km^2. This species is known from many localities including some nature reserves and some recent collections.

Uses — The fruits are edible (van Eck et al. 1997, Van Wyk 2011).

Notes — *Monanthotaxis caffra* is the only species of *Monanthotaxis* occurring in its distribution range. The distribution almost overlaps with the closely related *M. maputensis* in Kwazulu-Natal. The only reliable character to distinguish *M. caffra* from *M. maputensis* are

the stamens, which have short filaments in *M. caffra* (Fig. 8c) and long filaments in *M. maputensis* (Fig. 21g, h). Furthermore, the majority of specimens of *M. caffra* can be distinguished from *M. maputensis* in having larger and hairier leaves, thicker pedicels and larger stipes.



Map 8 Distribution of *Monanthotaxis caffra*.

12. *Monanthotaxis capea* (E.G.Camus & A.Camus) Verdc. — Fig. 6b–h; Map 9

Monanthotaxis capea (E.G.Camus & A.Camus) Verdc. (1971b) 21. — *Popowia capea* E.G.Camus & A.Camus (1913) 5. — *Enneastemon capeus* (E.G.Camus & A.Camus) Ghesq. (1939) 141. — Lectotype (designated here): *G.-L. Angoulvant s.n.* (lecto: P (P00362786); isolecto: BM001125039, E00624344, K000041008, P00362784, P00362785), Ivory Coast, de l'est du pays d'Attié, 1910.

Enneastemon seretii (De Wild.) Robyns & Ghesq. var. *tisserantii* Le Thomas (1963) 292, syn. nov. — *Enneastemon schweinfurthii* (Engl. & Diels) Robyns & Ghesq. var. *tisserantii* (Le Thomas) Le Thomas (1969) 254. — *Monanthotaxis schweinfurthii* (Engl. & Diels) Verdc. var. *tisserantii* (Le Thomas) Verdc. (1971b) 21. — Type: *C. Tisserant (Équipe) 1710* (holo: P01982418), Central African Republic, Lobaye, Boukoko, 10 April 1950.

Shrub or liana, several meters long; young branches densely covered with ascending to erect, reddish brown hairs 0.2–0.3 mm long, becoming glabrous; old branches dark brown to grey-brown. *Leaves*: petiole 4.5–8 mm long, 1.4–2.6 mm diam, slightly grooved, indument as on branches; lamina oblong-elliptic, obovate to oblanceolate, (7.4–)11.7–19.7 by 3.4–7.7 cm, 1.7–3.1 times longer than wide, subcoriaceous, not punctate, medium green above, glaucous below, above sparsely covered with appressed, whitish hairs 0.3–0.5 mm long, soon becoming glabrous, primary vein more densely covered with erect, reddish brown, below sparsely covered with appressed, yellow-brown 0.1–0.2 mm long hairs, primary vein more densely covered with ascending hairs 0.2–0.3 mm long, base cuneate to rounded, with thickened black margins or thick, globose, black glands, apex acute to acuminate, acumen to 15 mm long, secondary veins 7–12 per side, slightly curving upwards, tertiary venation percurrent, hardly visible above. *Inflorescences* axillary, composed of solitary flowers to 4-flowered fascicle-like rhipidia; sympodial rachis absent or as a cushion up to 1 mm long, densely covered with reddish brown hairs; pedicels 6–9 mm long, 0.3–0.7 mm diam, fruiting pedicels 11–16 mm long, 1.1–1.9 mm diam, densely covered with ascending to erect, reddish brown hairs; lower bracts absent; upper bract in the lower half of the pedicel, broadly ovate or represented by a tuft of hairs, c. 0.6 by 0.7–0.8 mm, indument as on pedicel; flower buds globose. *Flowers* bisexual; sepals connate at the base to almost entirely fused, depressed ovate, c. 0.7 by 1.2 mm, apex obtuse, densely covered with hairs, persistent in fruit; receptacle 1.5–2 mm diam, flat; petals colour in vivo unknown, 6, in two whorls, base of inner petals visible in bud, outer petals ovate, 3.5–5 by 2–3.8 mm, outside and upper half of the inside densely covered with appressed to ascending, yellowish brown hairs, inner petals rhombic to slightly obovate, 2.5–3.5 by 1.5–2.4 mm, outside and apical part of the inside densely covered with yellowish brown hairs; stamens (8 or) 9 (or 10), in one whorl, free, clavate, 1.4–1.5 mm long, filaments 0.8–0.9 mm long, thecae extrorse, connective truncate, slightly prolonged inward and outward, glabrous, but hairy on the inside, staminodes absent; carpels 6–9, subcylindric, c. 1.8 by 0.5 mm, densely hairy, ovules 4–6, lateral, stigma elongate, 0.2–0.6 mm long, glabrous. *Monocarps* 1–6, colour in vivo unknown, moniliform with each part narrowly ellipsoid to elipsoid, 20–79 by 8–10 mm, strongly tuberculate-rugulose, densely covered with ascending, white to brown hairs, apex apiculate, apiculum 2–4 mm long, stipes 3–6 mm long. *Seeds* 1–6, ellipsoid, c. 12 by 7–8 mm, ochre-brown, apex rounded, raphe visible.

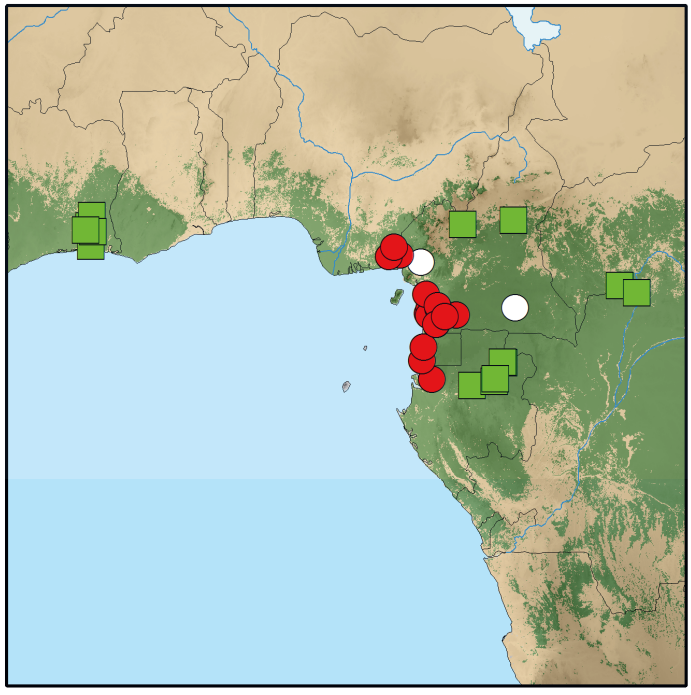
Distribution — Ivory Coast, Cameroon, Gabon, Central African Republic, Democratic Republic of the Congo.

Habitat & Ecology — In gallery forests, swamp forests, evergreen forest and old secondary forest. Altitude: 350–530 m. Flowering: April to August, November; fruiting: May, July to November.

Vernacular names — Central African Republic: Nolo tsanga (Lissongo name) (*R. Sillans s.n.*).

Preliminary IUCN conservation status —Vulnerable (VU): B2ab(iii). EOO: 1.004.525 km^2, AOO: 56 km^2. This species has a wide distribution range, however, it has only been collected

a few times recently and occurs in 9 localities of which only one is in a nature reserve. For these reasons the category “vulnerable” is assigned to this species. There is, however, quite some variation in morphological characters within Central Africa, especially the 2 specimens from central Cameroon are different. Therefore, each population separately has a much higher extinction risk and requires protection.



Map 9 Distribution of *Monanthotaxis capea* (green squares) and *M. cauliflora* (red circles, white circles are uncertain dets).

Notes — 1. *Monanthotaxis capea* is the only species of *Monanthotaxis* with strongly tuberculate-rugulose monocarps. Flowering material is difficult to distinguish from other species of the *M. schweinfurthii* complex (Fig. 1, clade B). It can be distinguished by the combination of ascending to erect reddish brown 0.2–0.3 mm long hairs on the young branches, the cuneate to rounded leaf bases and 4–6 ovules per carpel. There is quite some variation in the vegetative characters over the distribution. The specimens from Ivory Coast have more oblong-elliptic leaves, while in Central Africa the specimens have more obovate leaves and these were previously assigned to *M. schweinfurthii* var. *tisserantii*. However, no other distinguishable characters have been found between those populations and no different base-pairs were found in the few DNA-markers that could be sequenced for a specimen from

Ivory Coast compared to one from Gabon (Fig. 1, clade B), therefore these names are here synonymised.
2. Two specimens from the Adamawa region in central Cameroon (*R.G. Letouzey 7570* and *8738*) have narrowly obovate leaves and smaller monocarps than specimens from other regions, more material, especially flowering, is needed to verify if this should be a different taxon.
3. Some flowering specimens from the Central African Republic are hardly distinguishable from *M. seretii*, because fruits are lacking and more material especially from the north of the Democratic Republic of the Congo and the Republic of the Congo is needed to assess the exact status of *M. capea* and *M. seretii*.

13. *Monanthotaxis cauliflora* (Chipp) Verdc. — Map 9

Monanthotaxis cauliflora (Chipp) Verdc. (1971b) 30. — *Popowia cauliflora* Chipp (1923) 182. —— Lectotype (designated by Le Thomas 1969: 218): *W.C. Thomson s.n.* (lecto: K000198911; isolecto: P not seen), Nigeria, Cross River State, Old Calabar, 1863.
Clathrospermum mannii auct. non Oliv.: Oliv. (1868) 25, pro parte, quoad specim. ♀. — *Popowia mannii* aunct. non (Oliv.) Engl. & Diels: Engl. & Diels (1901) 49, pro parte, quoad specim. ♀. — *Popowia diclina* auct. non Sprague: Sprague (1908) 53, pro parte, quoad specim. ♀.

Liana, to 25 m long, to 3.5 cm diam; young branches dark brown to blackish, covered with erect, reddish brown hairs 0.05–0.1 mm long, becoming glabrous; old branches dark brown. *Leaves*: petiole 5–9 mm long, 1.2–2.1 mm diam, grooved, indument as on branches; lamina oblong-elliptic to oblanceolate, 12.5–15.2 by 4.8–5.8 cm, (2–)2.2–3.1(–3.9) times longer than wide, chartaceous, not punctate, glaucous below, above glabrous except primary vein densely covered with yellowish hairs c. 0.1 mm long, below sparsely covered with white hairs to 0.4 mm long, becoming glabrous, veins more densely covered with appressed to slightly erect hairs, base rounded to cuneate, with thickened black margin, apex acute to acuminate, acumen to 10 mm long, secondary veins 11–16 per side, straight, tertiary venation percurrent. *Flowers* unisexual. ♂ *Inflorescences* axillary, composed of solitary flowers to up to 6-flowered fascicles; sympodial rachis 2–15 mm long, densely covered with hairs c. 0.1 mm long; pedicels 5–6 mm long, 0.3–0.4 mm diam, densely covered with reddish brown hairs c. 0.05 mm long; bracts ovate, 0.5–0.7 by 0.3–0.4 mm, indument as on rachis; flower buds depressed globose; sepals slightly connate basally, broadly triangular, 0.5–0.8 by 0.5–0.7 mm, densely covered with very short hairs; receptacle 0.6–1.1 mm diam, convex; petals colour in vivo unknown, 6, in two whorls, outer petals depressed ovate, 1.2–2.3 by 1.9–2.7 mm, outside densely covered with brownish hairs, inside covered with yellowish, very short papillae, inner petals elliptic, 0.5–0.7 by 0.3–0.5 mm, outside and inside covered with yellowish to whitish, very short hairs; stamens 6, in one whorl, in groups of 2, oblong, 0.7–1.1 mm long, filaments 0.1–0.3 mm long,

thecae latrorse, connective truncate, sparsely hairy, staminodes 12 (or 13), c. 0.2 mm long, sparsely hairy. ♀ *Inflorescences* cauliflorous, condensed, many-flowered panicles to c. 12 cm diam; sympodial rachis 1.5–10 cm long, densely covered with reddish brown hairs c. 0.1 mm long; pedicels 6–20 mm long, 0.6–0.8 mm diam, fruiting pedicels 30–40 mm long, 1.1–1.8 mm diam, densely covered with reddish brown, very short hairs; bracts ovate to broadly ovate, 1–1.6 by 0.7–0.9 mm, indument as on rachis; flower buds depressed globose; sepals free to basally slightly connate, ovate to lanceolate, 0.7–1.3(–1.8) by 0.4–0.6(–1.4) mm, densely covered with appressed, very short hairs; receptacle 1.2–1.3 mm diam, convex; petals dull green on the outside, yellowish on the inside, 6, in two whorls, outer petals depressed ovate, 2.8–3.3(–4.2) by 3.7–4(–5) mm, outside densely covered with appressed, yellowish brownish hairs 0.1–0.2 mm long, inside covered with yellowish, very short papillae, inner petals elliptic, 1.3–1.4 by 0.5–0.6 mm, outside and inside covered with yellowish, very short hairs; carpels 48–60(–76), ellipsoid, 1.2–1.4 by 0.4–0.5 mm, densely hairy, ovules 5 or 6, lateral, stigma elongate, 0.2–0.4 mm long, grooved, glabrous. *Monocarps* up to 8, narrowly ellipsoid to ellipsoid, 15–57 by 6–9 mm, constricted between the seeds, smooth to slightly verrucose, rather densely covered with yellowish hairs 0.1–0.2 mm long, becoming glabrous, apex apiculate, apiculum 0.5–1 mm long, stipes (6–)9–12 mm long, slightly grooved. *Seeds* 1–4, ellipsoid, 12–15 by 5–8 mm, yellowish brown to reddish brown, both ends rounded, raphe not visible.

Distribution — Cameroon, Equatorial Guinea, Gabon.

Habitat & Ecology — In primary rainforest, old secondary forest and gallery forest. Altitude: 50–720 m. Flowering: January, August; fruiting: February, June.

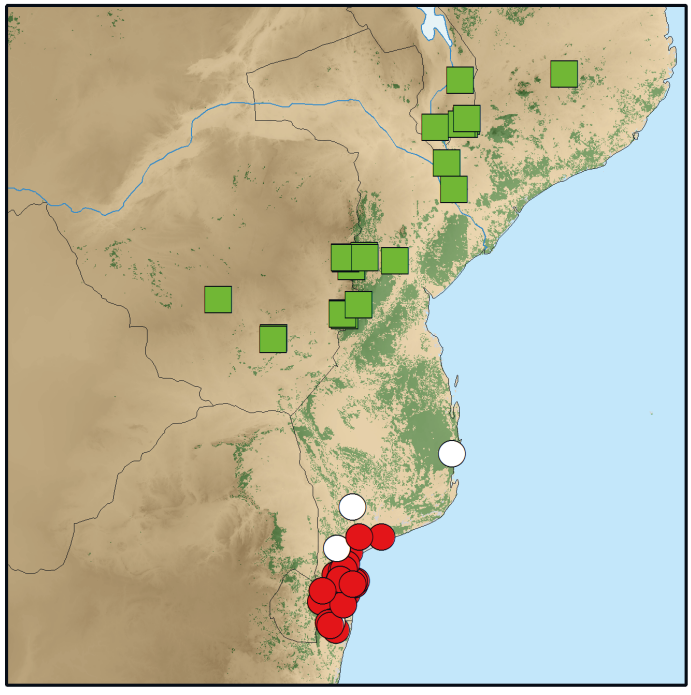
Preliminary IUCN conservation status —Vulnerable (VU). EOO: 67,001 km^2, AOO: 64 km^2. This species is known from 17 collections from 9 locations of which 2 in national parks and one in a nature reserve. However, the majority of collections are very old and the last collections from Nigeria and Gabon are more than 50 years old.

Notes —*Monanthotaxis cauliflora* resembles *M. diclina* and *M. pynaertii*. Typical specimens are easily distinguishable by their very short indument on the young branches and lower side of the leaves and the smaller pistillate flowers with 48–60 carpels. In the south of Cameroon and very north of Gabon *M. cauliflora* and *M. diclina* occur sympatrically and some intermediate forms can be found. *J.J. Bos 6037*, for example, has large pistillate flowers with up to 76 carpels and is therefore intermediate between *M. diclina* and *M. cauliflora*, however, the indument is more like *M. cauliflora* than *M. diclina*. All other specimens of *M. cauliflora* can be distinguished by the staminate flowers, which have 6 stamens and 9 very small staminodes.

14. *Monanthotaxis chasei* (N.Robson) Verdc. —Map 10

Monanthotaxis chasei (N.Robson) Verdc. (1971b) 25. — *Popowia chasei* N.Robson (1958) 155. — Type: *N.C. Chase 5375* (holo: K000198970; iso: BM000553829, LISC000389, S, SRGH not seen), Zimbabwe, Manicaland, Mutare, Umtali, S.T. Commonage, 610 m, 26 Dec. 1951.

Scandent shrub or liana, to 10 m long; young branches reddish brown, densely covered with appressed, yellow-brown hairs 0.2–0.4 mm long, becoming glabrous, old branches dark brown. *Leaves*: petiole 4–7 mm long, 1–1.5 mm diam, terete, indument as on branches; lamina elliptic to obovate, 5.7–14.6 by 2.7–7.6 cm, 1.5–2.5 times longer than wide, chartaceous, sometimes slightly punctate, dark green above, glaucous below, above covered with appressed, white hairs 0.2–0.3 mm long, becoming glabrous, primary vein covered with slightly longer-persistent, yellow hairs, below sparsely to rather densely covered with appressed, yellowish hairs 0.2–0.3 mm long, more densely so



Map 10 Distribution of *Monanthotaxis chasei* (green squares) and *M. maputensis* (red circles, white circles are uncertain dets).

on the primary vein, base rounded to subcordate, with slightly thickened black margin, apex acute to acuminate, acumen to 15 mm long, secondary veins 9–13 per side, slightly curving or straight and curving at end near margin, tertiary venation percurrent, hardly visible above. *Inflorescences* extra-axillary or leaf-opposed, composed of solitary flowers to 3-flowered fascicle-like rhipidia; sympodial rachis absent or up to 3 mm long, covered with appressed to ascending, yellowish hairs c. 0.2 mm long; pedicels 4–17 mm long, 0.6–0.8 mm diam, fruiting pedicels 8–35 mm long, 1–1.4 mm diam, indument as on rachis; lower bracts ovate, 1.3–1.8 by 0.6–0.9 mm, indument as on rachis; upper bract in the lower half of the pedicel or halfway, broadly ovate, 0.5–1.2(–4) by 0.9–1.4(–3.9) mm, indument as on sympodial rachis; flower buds globose. *Flowers* bisexual; sepals free or connate at the base, depressed ovate, 1.5–2.5 by 3.4–4.4 mm, apex rounded to mucronate, densely covered with appressed, yellow hairs, persistent in fruit; receptacle 3–3.5 mm diam, flat; petals colour in vivo unknown, 6, in two whorls, outer petals ovate, 7–8.5 by 5.2–8.4 mm, outside and margins of the inside covered with yellow-brown hairs, inner petals elliptic, 6.6–7 by 3.8–5.2 mm, outside and apical part of the inside covered with yellowish hairs; stamens 24, in three whorls, free, obovoid, c. 1.3 mm long, filaments c. 0.4 mm long, thecae latrorse, connective truncate, prolonged slightly inward and outward or not prolonged, not hiding thecae, glabrous, staminodes absent; carpels 17 or 18, subcylindric, 2–2.3 by 0.4–0.5 mm, glabrous or sparsely covered with few hairs, ovules 4, lateral, stigma elongate, 0.8–1.1 mm long, glabrous. *Monocarps* 4–8, reddish orange, ellipsoid to narrowly ellipsoid, 11–38 by 6–9 mm, verrucose, sparsely covered with few hairs or glabrous, apex rounded to apiculate, apiculum c. 1 mm long, stipes 3–6 mm long. *Seeds* 1–4, ellipsoid, 6–8.5 by 4.8–5.2 mm, ochre-brown, apex rounded or flattened, raphe hardly visible.

Distribution — Malawi, Mozambique, Zimbabwe.

Habitat & Ecology — In mixed evergreen forest, gallery forest, dense woodland; on sandy loam soil. Altitude: 396–1500 m. Flowering: October to January; fruiting: January to May.

Vernacular names — Mozambique: Mutadza (*E.C. Andrada 1026*).

Preliminary IUCN conservation status — Near threatened (NT). EOO: 192,050 km^2, AOO: 96 km^2. This species is known from 13 locations including 3 nature reserves, however, the area of occupancy is quite small and several of the locations are under threat of forest degradation or mining activities.

Notes — *Monanthotaxis chasei* is the only species of *Monanthotaxis* in Zimbabwe, Malawi and the north of Mozambique with almost glabrous carpels. The yellowish brown, appressed hairs on the young branches and the veins on the lower side of the leaves set it apart from other species of *Monanthotaxis* with extra-axillary flowers and 24 stamens in three whorls.

15. *Monanthotaxis confusa* P.H.Hoekstra, *sp. nov.* — Fig. 9a–d; Map 11

Monanthotaxis confusa has unisexual flowers and can be distinguished from other species by the staminate flowers with 19–22 stamens in two whorls and a lack of staminodes. The

staminate flowers of *M. mortehanii* and *M. glomerulata* are unknown, but it can be distinguished from *M. mortehanii* by the very short appressed hairs c. 0.1 mm long on the pedicels, while *M. mortehanii* has erect, 0.4–0.6 mm long hairs on the pedicels of the pistillate inflorescence; it differs from *M. glomerulata* in the number of carpels (>100 versus 80–95), the petiole size (7–10 mm versus 5–7 mm long, the length of the sympodial rachis of the pistillate inflorescences (5–15 mm versus < 5 mm) and the length of flowering pedicels (21–25 mm versus <10 mm). — Type: *G.C.C. Gilbert GCC14442* (holotype: WAG (WAG.1587477); iso: BR0000013186098), Democratic Republic of the Congo, Bandundu, Bankaie, Lac Leo II, 14 July 1953. Paratypes: *J.H.P.A. Ghesquière 6665* (K, P), Democratic Republic of the Congo, Nord-Kivu, nord de Rutshuru, forêt de Makwera, 1300 m, 29 May 1938; *J.-P.A. Lebrun 6134* (BR, K, P), Democratic Republic of the Congo, Kasai-Oriental, Katakokombe, Nov. 1932; *J.L.P. Louis 5882* (B, BR, K, P), Democratic Republic of the Congo, Orientale, Isangi, Yangambi, 470 m, 29 Aug. 1937. *J.L.P. Louis 7000* (BR, C, MO, US), Democratic Republic of the Congo, Orientale, Yangambi, 470 m, 13 July 1937; *J.L.P. Louis 9282* (BR, FHO, K, P), Democratic Republic of the Congo, Orientale, route d'Isangi, 470 m, 9 May 1938; *J.L.P. Louis 9966* (B, BR), Democratic Republic of the Congo, Orientale, Yangambi, 470 m; *J.L.P. Louis 12169* (BR, C, MO, US), Democratic Republic of the Congo, Orientale, Isangi, Yangambi, 470 m, 25 Oct. 1938.

Growth form unknown; young branches dark brown, covered with brown hairs c. 0.1 mm long, becoming glabrous; old branches dark brown to blackish. *Leaves*: petiole 7–10 mm long, 1.5–1.9 mm diam, grooved, indument as on branches; lamina ovate to obovate or narrowly so, 13.3–20.7 by 5.5–8.5 cm, 1.8–2.9 times longer than wide, chartaceous, not punctate, above glabrous, but primary vein covered with erect, whitish hairs c. 0.3 mm long, below covered with appressed hairs 0.1–0.2 mm long, base rounded, with thickened black margin, apex acute, secondary veins 13–16 per side, straight at end curving slightly upwards, tertiary venation percurrent. *Flowers* unisexual. ♂ *Inflorescences* axillary or ramiflorous, composed of 1–7-flowered, fascicle-like rhipidia; sympodial rachis 2–8 mm long, densely covered with appressed, dark brown hairs; pedicels 3–8 mm long, 0.8–0.9 mm diam, densely covered with appressed to ascending, reddish brown hairs; lower bracts broadly to depressed ovate, 0.5–1 by 0.7–0.9 mm, indument slightly more dense as on rachis; upper bract broadly ovate, 0.7–0.9 by 0.8–1 mm, indument as on lower bract, flower buds broadly ovoid; sepals free, broadly ovate, 1–1.7 by 1.2–1.5 mm, densely covered with appressed hairs; receptacle 1–2 mm diam, convex; petals colour in vivo unknown, 6, in two whorls, free, outer petals depressed ovate, 2.5–3.6 by 3.3–4.7 mm, outside densely covered with dark brown hairs 0.1–0.2 mm long, inside densely covered with yellow-brown hairs < 0.1 mm long, inner petals elliptic, 1.6–1.9 by 0.8–0.9 mm, outside and inside densely covered with yellow-brown, very short hairs; stamens 19–22, in two whorls, free, oblong, 0.7–0.8 mm long, filaments c. 0.1 mm long, thecae extrorse, connective truncate, connective and filaments hairy, staminodes absent. ♀ *Inflorescences* cauliflorous, many-flowered; sympodial rachis 5–15 mm long, covered with brownish hairs c. 0.1 mm long; bracts ovate, 1.1–1.7 by c. 1 mm, densely covered with

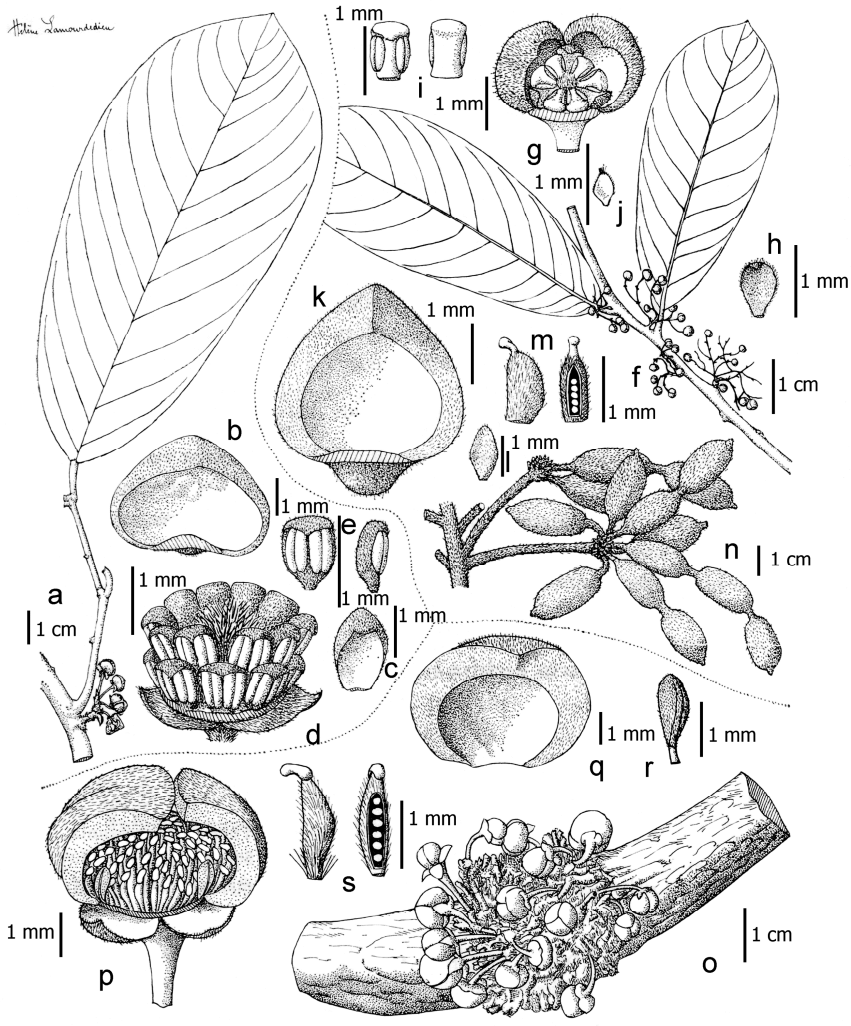
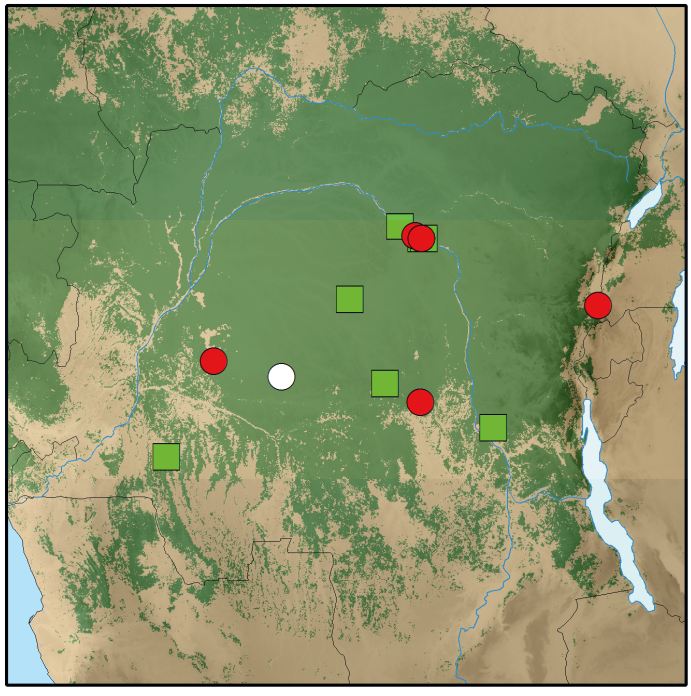


Fig. 9 a–e. *Monanthotaxus confusa* P.H.Hoekstra: a. Staminate flowering branch; b. staminate flower, outer petal, inside view; c. staminate flower, inner petal, inside view; d. staminate flower with petals removed; e. stamen, outer and side view. — f–n. *M. diclina* (Sprague) Verdc.: f. Staminate flowering branch; g. staminate flower with one outer petal removed; h. staminate flower inner petal, inside view; i. stamen, outside and inside view; j. staminate flower staminode; k. pistillate flower, outer petal, inside view; l. pistillate flower, inner petal, inside view; m. carpel and longitudinal section of carpel; n. fruits. — o–s. *M. glomerulata* (Le Thomas) Verdc.: o. Pistillate inflorescence; p. pistillate flower with one outer petal removed; q. pistillate flower, outer petal, inside view; r. pistillate flower, inner petal, inside view; s. carpel and longitudinal section carpel (a–e: *Lebrun 6134*; f–j: *Klaine 2881*; k–m: *Klaine 1382*; n: *Klaine 404*; o–s: *Le Testu 8700*). Modified from Le Thomas (1969) plate 38.

brownish hairs; flower buds ovoid; flowering pedicels 21–25 mm long, 0.8–0.9 mm diam, indument as on rachis; sepals free, broadly ovate to spathulate, 2–3 by 1.5–3 mm, densely covered with brownish hairs; receptacle to 2.5 mm high, c. 1.5 mm diam, convex; petals colour in vivo unknown, 6, in two whorls, free, outer petals broadly ovate, 6–6.5 by 6.5–7.5 mm, outside covered with dark hairs c. 0.1 mm long, inside papillate; inner petals obovate, c. 3 by 2 mm, both sides densely covered with yellowish papillae; carpels c. 128, ellipsoid to rhombic, 1.1–1.3 by 0.5–0.6 mm, densely hairy, ovules 6, lateral, stigma globose and to 0.2 mm long in the middle of the flower, elongate and to 0.4 mm long in the outer whorls, glabrous. *Monocarps* up to at least 5, colour in vivo unknown, ellipsoid to narrowly ellipsoid, at least 10 mm long, 6–7 mm wide, slightly verrucose, sparsely covered wtih appressed, short hairs, apex rounded to slightly apiculate, apiculum to 0.5 mm long, stipes c. 5 mm long. *Seeds* at least 3, ellipsoid, 8–9 by c. 6 mm, reddish brown, with ends flattened, with a c. 4 mm long funiculus, raphe visible.

Distribution — Democratic Republic of the Congo (Bandundu, Kasai-Oriental, Nord-Kivu, Orientale).



Map 11 Distribution of *Monanthotaxis confusa* (red circles, white circle is uncertain det) and *M. congolana* (green squares).

Habitat & Ecology — In terra firme forest and inundated forest. Altitude: 300–1300 m. Flowering: July to September; fruiting: October.

Preliminary IUCN conservation status —Endangered (EN): B2ab(iii). EOO: 295,065 km^2, AOO: 20 km^2. This species is only known from 9 collections in 4 localities and was last collected in 1953. Field work is needed to verify if this species still exists.

Ethymology — Named *confusa* because this species has been confused with *Monanthotaxis cauliflora*. The fact that Le Thomas (1969) described and depicted a staminate flower of *M. confusa* as *M. cauliflora* added to this confusion.

Notes — The specimens of *Monanthotaxis confusa* were previously identified as *M. cauliflora*. The staminate flowers are very different from that species, they have 19–22 stamens and no staminodes (versus 6 stamen and 12–13 staminodes), whereas the pistillate flowers have twice the number of carpels compared to *M. cauliflora*. The description of the staminate flowers of *M. cauliflora* in Le Thomas (1969) was based on the staminate flowers of *J.-P.A. Lebrun 6134*, which is now included in *M. confusa.*

16. *Monanthotaxis congoensis* Baill. — Fig. 10a–g; Map 12

Monanthotaxis congoensis Baill. (1890) 878. — Lectotype (designated by Le Thomas 1969: 258) : *F.R. Thollon 813* (lecto consisting of 3 sheets: P00362762, P00362763, P00362766; isolecto: K000198992, MA630761, MA698356, WAG0003586, WAG0003587), Gabon, Congo, Ogooué, July 1887.

Small understory tree, shrub or liana, 1.5–5 m long; young branches densely covered with appressed, pale brown hairs 0.7–1.2 mm long, becoming glabrous; old branches dark brown to blackish. *Leaves*: petiole 3–8 mm long, c. 1 mm diam, grooved, densely covered with hairs; lamina narrowly obovate to narrowly oblong-elliptic, 7.5–25 by 1.9–6 cm, (2.3–)3.1–4.4 times longer than wide, chartaceous, sometimes slightly punctate, glaucous below, young leaves above sparsely covered with appressed white hairs 2–3 mm long, becoming glabrous, below densely covered with appressed, white hairs 1–2.5 mm long below, less densely so in older leaves, base rounded to slightly cordate, sometimes broadly cuneate, sometimes with small, thickened black margin, apex acute to acuminate, acumen to 15 mm long, secondary veins 9–16 per side, oblique, curving upwards, tertiary venation percurrent to somewhat reticulate, slightly raised above, below only visible in older leaves. *Inflorescences* axillary or terminal, 6–13 cm long, 4–10-flowered raceme-like rhipidia; sympodial rachis sparsely to densely covered with white, short hairs, internodes up to 25 mm long, 1 (or 2) flowers in the axil of each lower bract; flowering and fruiting pedicels up to 12 mm long and 0.5 mm diam, indument as on rachis; lower bracts lanceolate, 2–3 by c. 0.5 mm, indument as on rachis, upper bract absent; flower buds deltoid-ovoid. *Flowers* bisexual; sepals free or slightly connate, broadly ovate to triangular, 0.5–2.5 by 0.5–1.5 mm, densely covered with white hairs, apex acute; receptacle

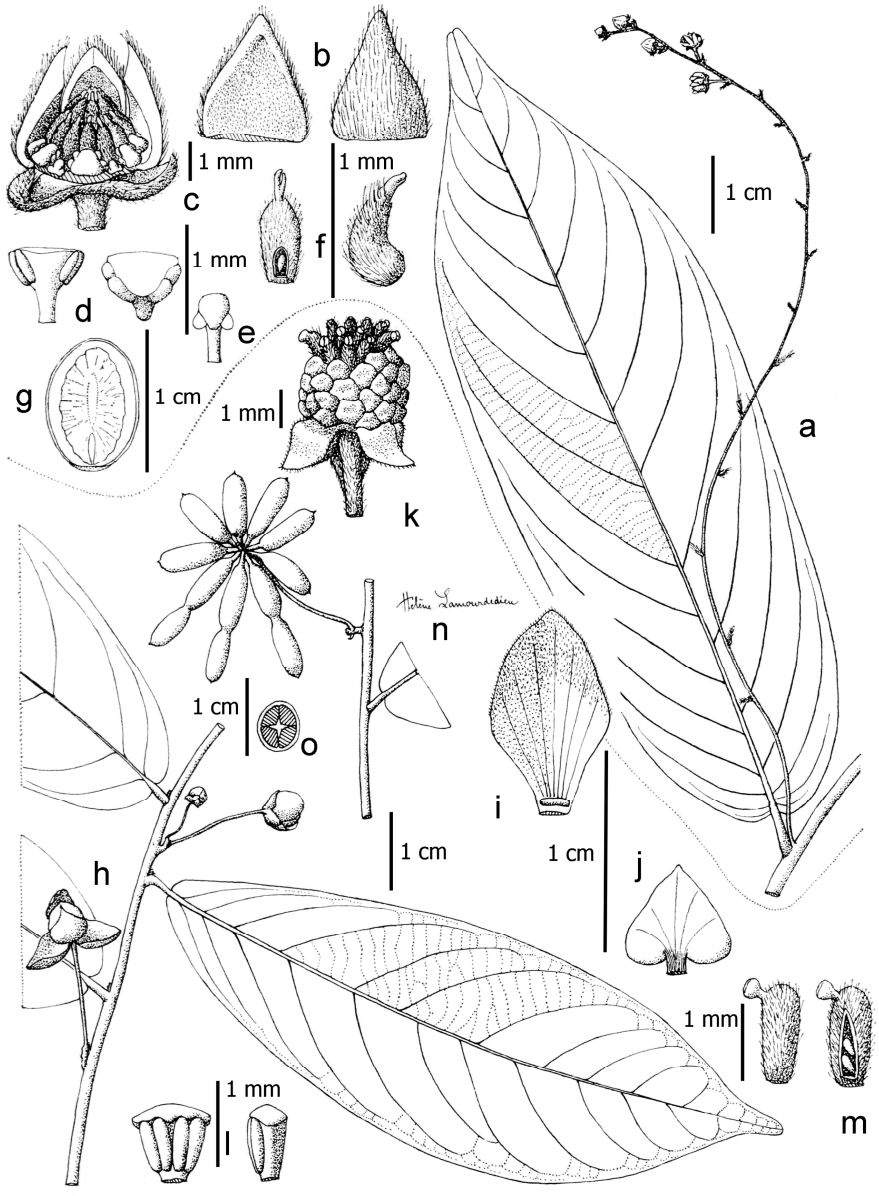
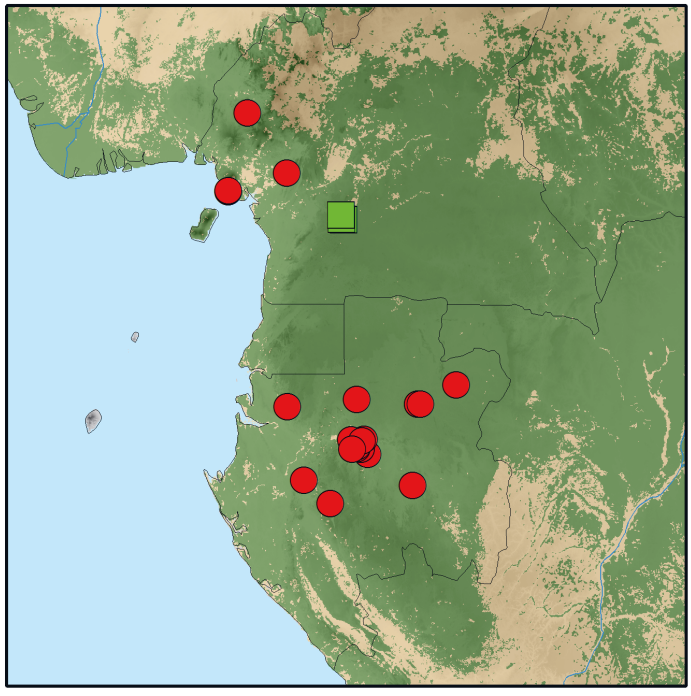


Fig. 10 a–g. *Monanthotaxis congoensis* Baill.: a. Flowering branch; b. petal inner and outside view; c. flower with three petals removed; d. stamen front view and seen from above; e. staminodes; f. carpel and longitudinal section of carpel; g. longitudinal section of seed. — h–o. *M. montana* (Engl. & Diels) P.H.Hoekstra: h. Flowering branch; i. outer petal; j. inner petal; k. flower with petals removed; l. stamen, front and side view; m. carpel and longitudinal section of carpel; n. fruiting branch; o. transverse section of seed (a–g: *Thollon 813*; h–m: *Le Testu 4364*; n–o: *Tisserant 1362*). Modified from Le Thomas (1969) plates 42 and 45.

c. 2 mm diam, convex; petals greenish to yellow, inside paler, 6, in one whorl, ovate to lanceolate, 3–4 by 1–2 mm, outside densely covered with hairs, inside covered with hairs < 0.1 mm long; stamens 6, in one whorl, opposite the petals, free, obconical, c. 0.7 mm long, filaments c. 0.4 mm long, thecae introrse, connective truncate, apex c. 0.8 mm wide, not hiding the thecae, glabrous, staminodes 6, alternating with the stamens, c. 0.6 mm long, filaments c. 0.3 mm long, thecae introrse, staminodes with 2 dorsal theca-like appendages c. 0.4 mm wide, carpels 15–21, ellipsoid, c. 0.7 by 0.3 mm, densely covered with reddish brown hairs, ovule 1, basal, stigma bifurcate, c. 0.2 mm long, glabrous. *Monocarps* up to 4, dull orange to red, ellipsoid to subglobose, 12–15 by 9–10 mm, densely covered with pale brown hairs c. 0.5 mm long, apex rounded; stipes 2–3 mm long. *Seeds* 1, ellipsoid to globose, 8–9 by 7–8 mm, ochre-brown, both ends rounded, raphe a longitudinal furrow.

Distribution — Cameroon (Littoral, South-West Region), Gabon (Estuaire, Moyen-Ogooué, Ngounié, Ogooué-Ivindo, Ogooué-Lolo).



Map 12 Distribution of *Monanthotaxis congoensis* (red circles) and *M. couvreurii* (green squares).

Habitat & Ecology — In primary periodically inundated forest, gallery forest, forest edges, primary rainforest and old secondary forest on rocky soil. Altitude: 90–626 m. Flowering: March to May, November, December; fruiting all year round.

Preliminary IUCN conservation status — Least concern (LC). EOO: 168,369 km^2, AOO: 88 km^2. This species is known from many locations, including a few national parks.

Notes — 1. *Monanthotaxis congoensis* can easily be distinguished from all species of *Monanthotaxis* by its raceme-like inflorescences.

2. The sterile specimen *K. Schmitt 66* from the Cross River National Park in Nigeria has also a dense indument of appressed hairs on the lower side of the leaves, but has shorter and wider leaves than typical specimens of *M. congoensis*. Fertile material is needed to verify if *M. congoensis* also occurs in Nigeria.

3. Le Thomas (1969) cited *F.R. Thollon 813* (P) as holotype. Likely, P was the only herbarium holding this gathering at the time of description and the P set hence could be considered as holotype, since all traced sheets in other herbariums arrived after 1890. But, when doubted, Le Thomas's remark should be regarded as a lectotypification, where the sheets in P become the lectotype. The set of sheets in P mentions the set consists of 4 sheets, but only 3 were traced by us.

17. *Monanthotaxis congolana* (Boutique) P.H.Hoekstra — Map 11

Monanthotaxis congolana (Boutique) P.H.Hoekstra in Guo et al. (2017) 14. — *Gilbertiella congolana* Boutique (1951b) 124. — Lectotype (designated here): *R.G.A. Germain 17* (lectotype: BR (BR000008799586); isolecto: B100153067, BR000008799913, K000198957, NY00025920, P00046763), Democratic Republic of the Congo, Orientale, Yangambi, rive gauche, Litulombo, 470 m, 8 Dec. 1939.

Liana; young branches yellowish orange to greenish, sparsely covered with appressed, yellowish hairs 0.1–0.2 mm long, soon becoming glabrous; old branches reddish brown. *Leaves*: petiole 5–8 mm long, 0.7–0.8 mm diam, grooved, indument as on branches; lamina oblong-elliptic to ovate or narrowly so, 6.5–12.5 by 2.6–5.2 cm, 2.4–2.8 times longer than wide, chartaceous to subcoriaceous, punctate, but not well visible in older leaves, young leaves below sparsely covered with appressed hairs c. 0.1 mm long, soon becoming glabrous, base cuneate to broadly cuneate, with thickened margin, apex acute to acuminate, acumen to 15 mm long, secondary veins 6–8 per side, oblique, curving upwards, tertiary venation reticulate, raised above. *Inflorescences* axillary or terminal, solitary, flowers in fascicles or in to 2 cm long lax panicle-like, up to 4-flowered rhipidia; sympodial rachis absent or 1–5 mm long, sparsely covered with appressed, yellowish hairs; flowering and fruiting pedicels 6–14 mm long, 0.4–0.7 mm diam, covered with appressed, short hairs; lower bracts absent or ovate, 0.5–0.7 by c. 0.4 mm, densely covered with appressed, yellow hairs; upper bract ovate, 0.3–0.8 by 0.2–0.3 mm, indument as on lower bract, placed halfway up the pedicel; flower buds globose to slightly ellipsoid. *Flowers* bisexual; sepals free, shallowly triangular, 0.2–0.5 by 0.5–0.7 mm, apex acute, covered with appressed, yellowish, short hairs; receptacle 1.3–1.8 mm diam, flat; petals yellow-green, 6, in one whorl, outer petals overtopping inner petals in bud,

elliptic to ovate, with inward hook at top, 1.8–2.7 by 1.1–2.1 mm, outside papillate to sparsely covered with appressed, short hairs, inside papillate, often denser so at apex and base; stamens 12, in one whorl, free, alternating with and opposite the petals, obconical to slightly clavate, wider than thick, length 0.8–1.1 mm, width 0.3–0.4 mm, radial width 0.3–0.4 mm, densely papillate, filaments c. 0.05 mm long, thecae 2, latrorse or extrorse, connective truncate, circular seen from above, densely papillate, staminodes absent; carpels 7 or 8, ellipsoid, 0.8–1.2 by 0.4–0.6 mm, densely covered with reddish brown hairs, ovules 6, lateral, stigma subsessile, globose, < 0.1 mm long, grooved, glabrous. *Monocarps* up to 4, orange-red, cylindric, 90–110 by 6–8 mm, slightly constricted between the seeds, glabrous, apex apiculate, apiculum c. 1 mm long, stipes 9–12 mm long. *Seeds* 1–3, cylindric, 24–26 by c. 5 mm, ochre-brown, apex apiculate, apiculum c. 1 mm long, raphe not visible.

Distribution — Democratic Republic of the Congo (Bandundu, Equateur, Maniema, Orientale).

Habitat & Ecology — In periodically inundated primary forest and terra firme forest. Altitude: c. 470 m. Flowering: February, May, June, September, December; fruiting: February, December.

Vernacular names — Democratic Republic of the Congo: Nginko e Likebe (Turumbu name) (*R.G.A. Germain 17*).

Preliminary IUCN conservation status —Endangered (EN): B2ab(iii). EOO: 332,197 km^2, AOO: 28 km^2. This species is known from 5 localities, including one nature reserve. However, it has not been collected since 1959 and its present existence is doubtful.

Notes — *Monanthotaxis congolana* and *M. latistamina* are the only two species of *Monanthotaxis* with densely papillate petals and stamens. Flowers of *M. congolana* have 12 linear stamens (versus 6 oblong stamens in *M. latistamina*), which are circular in cross-section (versus ellipsoid in cross-section).

18. *Monanthotaxis couvreurii* P.H.Hoekstra — Plate 2c–e; Map 12

Monanthotaxis couvreurii P.H.Hoekstra in Hoekstra et al. (2016) 79. — Type: *T.L.P. Couvreur 762* (holo consisting of 3 sheets: WAG.1576998, WAG.1576999, WAG.1577000; iso: MPU1374962), Cameroon, Central Province, Ottotomo Forest Reserve, 45 km SW of Yaoundé, c.5 km on main path into reserve, 3°35.21'N; 11°17.63'E, 700 m, 24 Apr. 2015.

Liana; young branches densely covered with ascending, reddish brown hairs 0.1–0.2 mm long, old branches greyish brown. *Leaves*: petiole 3–5 mm long, 0.8–0.9 mm diam, slightly grooved, indument as on branches; lamina oblong-elliptic to obovate or narrowly so, 4.5–12 by 1.8– 4.3 cm, 2.1–2.9 times longer than wide, chartaceous, not punctate, discolorous, glossy green above, pale greyish green below, above sparsely covered with appressed, whitish hairs c. 0.1 mm long, soon becoming glabrous, below sparsely covered with appressed, whitish yellowish hairs 0.1–0.2 mm long, base cuneate to rounded, glands hardly visible, apex acute to

acuminate, acumen to 10 mm long, secondary veins 7–11 per side, from base curving upwards, tertiary venation percurrent, sometimes hardly visible. *Inflorescences* cauliflorous, ramiflorous or axillary, composed of 2-flowered rhipidia in the axils of the leaves to many-flowered clusters on the trunk; sympodial rachis 1–15 mm long; flowering pedicels 4–20 mm long, 0.2–0.6 mm diam, sparsely covered with ascending to erect hairs c. 0.1 mm long; lower bracts strongly reduced or absent; upper bract absent; flower buds ovoid. *Flowers* bisexual; sepals slightly connate basally, broadly triangular, 0.8–0.9 by 0.9–1 mm, apex acute, densely covered with yellowish hairs; receptacle 1.2–2 mm diam, flat; petals pale yellow to white, 6, in two whorls, base of inner petals visible in bud, outer petals elliptic-ovate, 3.5–5 by 2–3.5 mm, outside densely covered with yellowish, short hairs, inside with a few hairs near the margins, inner petals narrowly elliptic to narrowly ovate, 3–4.5 by 1.2–1.5 mm, outside covered with yellowish hairs at the apex and centre, inside glabrous or with few hairs at the margins; stamens 13–15, in one whorl, connate at the base, linear-obconical, 0.8–0.9 mm long, filaments c. 0.4 mm long, thecae latrorse to extrorse, connective truncate, circular from above, papillate, staminodes absent; carpels 9–12, subcylindric to narrowly ellipsoid, 1.2–1.3 by 0.3–0.4 mm, densely hairy, ovules 4, lateral, stigma subsessile, globose, c. 0.2 mm diam, glabrous. *Monocarps* and *seeds* not seen, but see the label of *C. Farron 7359*.

Distribution — Cameroon (Central Province).

Habitat & Ecology — In old secondary forest, on slope. Altitude: c. 700 m. Flowering: April, May.

Preliminary IUCN conservation status — Critically Endangered (CR): B2ab(iii). AOO: 8 km^2. Only known from the Ottotomo Forest Reserve in Cameroon. The surrounding forests of this reserve are increasingly degrading and the increase of human population intensifies the pressure on the forest (Sassen & Jum 2007).

Notes — *Monanthotaxis couvreurii* is the only species in the genus with basally connate stamens. *Monanthotaxis couvreurii* resembles *M. aquila* from Ivory Coast and *M. atopostema* from the Republic of the Congo and Democratic Republic of the Congo, but differs in having slightly more secondary veins with smaller spaces in between, and in the absence of staminodes.

19. *Monanthotaxis diclina* (Sprague) Verdc. — Fig. 9f–n; Plate 2f; Map 13

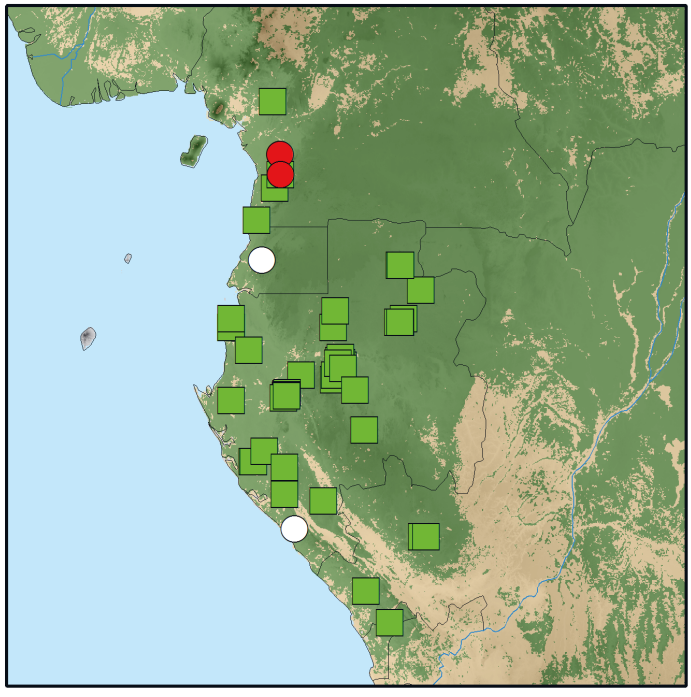
Monanthotaxis diclina (Sprague) Verdc. (1971b) 31, non *M. mannii* (Baill.) Verdc (1971b). — *Clathrospermum mannii* Oliv. (1868) 25, pro parte, quoad *Mann 960*. — *Popowia mannii* (Oliv.) Engl. & Diels (1901) 49, pro parte, quoad *Mann 960*, nom. illeg., non *Popowia mannii* Baill. (1868) 320. — *Popowia diclina* Sprague (1908) 53, pro parte, quoad *Mann 960*; Chipp (1923) 182. — Lectotype (selected by Le Thomas, 1969: 216): *G. Mann 960* (lecto: K000198989), Gabon, Estuaire, Gaboon River, July 1861.

Popowia caulantha Exell (1932) 208. — Type: *J. Gossweiler 6721* (holo: BM000553848; iso: COI 00004904, LISC000104, LISC000264, LISC000265, LISC000266, LISU), Angola, Cabinda, BucoZau-Maiombe, na colina próximo do posto administrative, 29 Sep. 1916.

Liana, to 25 m long; young branches densely covered with erect to curly, yellow-brown hairs 0.4–0.6 mm long, becoming glabrous; old branches dark brown. *Leaves*: petiole 3–5 mm long, 1.5–2 mm diam, grooved, indument as on branches; lamina oblong-elliptic, obovate to oblanceolate, 8.5–18.2 by 3.5–6.9 cm, 2.4–2.9(–3.5) times longer than wide, chartaceous to subcoriaceous, not punctate, discolorous, glossy dark green above, glaucous below, above sparsely covered with few, white to yellow hairs 0.3–0.5 mm long, primary vein densely covered with erect, yellow hairs, below densely covered with erect yellow hairs c. 0.5 mm long, base rounded to subcordate, with thickened black margin, apex acute to almost rounded, secondary veins 15–19 per side, 10–12 per side on young leaves, straight to curving upwards, tertiary venation percurrent. *Flowers* unisexual. ♂ *Inflorescences* axillary or ramiflorous, composed of solitary flowers to few-flowered fascicles, sometimes up to 25-flowered rhipidia; sympodial rachis 1–3 mm long, densely covered with erect, yellow-brown hairs 0.3–0.4 mm long; pedicels 2–5 mm long, c. 0.4 mm diam, densely covered with erect, yellow-brown hairs; bracts ovate, c. 0.5 by 0.4 mm, indument as on rachis; flower buds depressed globose; sepals slightly connate at the base, broadly ovate, c. 0.5 by 0.5 mm, densely covered with appressed, brown hairs, persistent in fruit; receptacle 1–1.2 mm diam, convex; petals yellowish brown, 6, in two whorls, outer petals depressed ovate, c. 1.6 by 2 mm, outside densely covered with yellowish brown, short hairs, inside covered with yellowish hairs c. 0.05 mm long, inner petals elliptic, 0.5–0.8 by 0.3–0.4 mm, outside and the apex of the inside, covered with yellowish hairs c. 0.05 mm long, base of inside glabrous; stamens 6, in one whorl, in pairs, free, oblong, 0.8–0.9 mm long, filaments 0.3–0.4 mm long, thecae latrorse, connective truncate, sparsely hairy, staminodes 12, in one whorl 0.2–0.3 mm long, sparsely hairy. ♀ *Inflorescences* cauliflorous, glomerules or condensed, many-flowered panicle-like rhipidia; sympodial rachis 1.5–6 cm long, to 9 cm long in fruit, densely covered with erect, yellowish brown hairs c. 0.5 mm long; pedicels 15–25 mm long, 0.9–1 mm diam, fruiting pedicels to 45 mm long, 1.1–1.6 mm diam, densely covered with erect, yellowish brown hairs; bracts ovate, 1.3–1.7 mm long, indument as on sympodial rachis; flower buds globose to slightly ovoid; sepals free or slightly connate, broadly ovate, 1.2–1.7 by 1.3–1.4 mm, densely covered with appressed, brown hairs, persistent in fruit; receptacle 1.6–2 mm diam, convex to globose; petals pale brown on the outside, creamy on the inside, 6, in two whorls, outer petals broadly ovate, 3–5 by 3.5–5.4 mm, outside densely covered with appressed brown hairs 0.2–0.3 mm long, inside covered with yellowish hairs c. 0.05 mm long, inner petals elliptic, 1.3–1.7 by 0.6–0.7 elliptic, outside and inside covered with yellowish hairs c. 0.05 mm long; carpels 80–100, narrowly ellipsoid, 1.3–1.4 by 0.3–0.4 mm, densely hairy, ovules 4 or 5, lateral, stigma elongate, c. 0.2 mm long, grooved, glabrous. *Monocarps* up to 14, medium green when ripe, narrowly ellipsoid to moniliform,, 23–55 by 7–8 mm, slightly verrucose, rather densely

covered with erect to curly, brownish hairs 0.3–0.4 mm long, apex apiculate, apiculum 0.5–1 mm long, stipes (6–)8–11(–14) mm long, slightly grooved. *Seeds* 1–5, ellipsoid, 12–15 by 6–8.5 mm, reddish brown, both ends rounded, raphe slightly visible as a longitudinal furrow from base to apex.

Distribution —Cameroon, Gabon, Republic of the Congo, Angola.



Map 13 Distribution of *Monanthotaxis diclina* (green squares) and *M. dielsiana* (red circles, white circles are uncertain dets).

Habitat & Ecology — In primary forest, old secondary forest, submontane forest, swamp forest and gallery forest. Altitude: 30–650 m. Flowering and fruiting all year round.

Preliminary IUCN conservation status —Least concern (LC). EOO: 277,679 km^2, AOO: 172 km^2. This species is known from many locations and recent collections. It is one of the commonest species of *Monanthotaxis* encountered in the forests of Gabon.

Notes — 1. *Monanthotaxis diclina* can be distinguished from all other *Monanthotaxis* species with unisexual flowers by the dense indument of yellowish brown hairs to 0.5 mm long on the young branches and lower side of the leaves. Other species have reddish brown hairs or shorter hairs.

2. The sterile specimens *W.D. Hawthorne 2262* and *C.C.H. Jongkind 8515* from Liberia look very similar to *M. diclina*. These would be the first records of the species in West Africa, and

flowering or fruiting material is needed to assess whether they represent *M. diclina*. The specimen cited in Keay (1954) as *M. diclina* from Liberia probably is more similar to *M. velutina* than to *M. diclina*.

3. Exell (1932) explicitely mentions that his paper is based on material that was sent to BM, hence we consider the BM sheet of *J. Gossweiler 6721* as the holotype of *Popowia caulantha*.

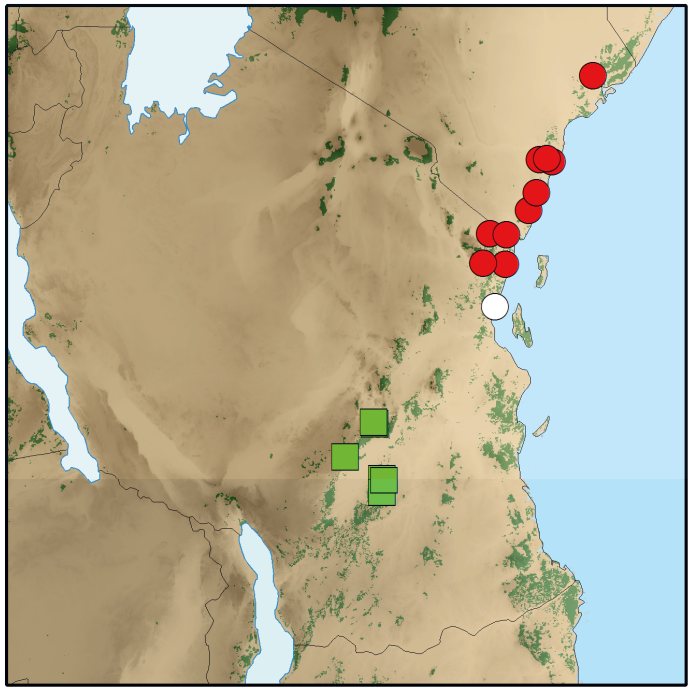
20. *Monanthotaxis dictyoneura* (Diels) Verdc. — Map 14

Monanthotaxis dictyoneura (Diels) Verdc. (1971b) 25. — *Popowia dictyoneura* Diels in Mildbr. (1933) 811. — Lectotype (designated by Verdcourt 1971a: 98): *H.-J.E. Schlieben 1686* (lecto: B100153027; isolecto: BM000553830, BR0000008803993, BR0000008804327, BR0000008804655, G00308306, HBG-502536, LISC000380, M0107933, MA384770, MA384770-2, P00362611, S), Tanzania, Morogoro, Ulanga district, Mahenge, Muhulu Mts, SSW von station Mahenge, c.1200 m, 30 Jan. 1932.

Small tree or scandent shrub, to 8 m tall; young branches blackish, sparsely covered with appressed hairs 0.1–0.2 mm long, becoming glabrous; old branches blackish. *Leaves*: petiole 3–4 mm long, 0.8–1.2 mm diam, grooved, sparsely covered with appressed, yellow hairs c. 0.1 mm long; lamina narrowly obovate, narrowly oblong-elliptic to narrowly ovate, 5.4–12.8(–14.7) by 2.4–4.3(–6.5) cm, 2.3–3.2 times longer than wide, subcoriaceous, not punctate, discolorous, shiny dark green above, glaucous below, above glabrous or primary vein covered with appressed, very short hairs, below glabrous or sparsely covered with appressed, yellowish hairs c. 0.1 mm long, base rounded to subcordate, glands hardly visible, apex acute to acuminate, acumen to 25 mm long, secondary veins 11–15 per side, from base straight, halfway curving upwards, tertiary venation reticulate to slightly percurrent, distinctly raised and reticulate above. *Inflorescences* extra-axillary, leaf-opposed or terminal, composed of solitary flowers to 4-flowered rhipidia; sympodial rachis 1.3–2.5 mm long, sparsely covered with appressed, yellowish, short hairs; pedicels 7–12 mm long, 0.4–0.6 mm diam, fruiting pedicels c. 16 mm long, c. 1.2 mm diam, indument as on sympodial rachis; lower bracts absent or ovate to orbicular, 0.5–0.8 by c. 0.5 mm, indument as on rachis; upper bract in the lower half of the pedicel or halfway or absent, broadly ovate, c. 0.5 by 0.5 mm, densely covered with appressed, yellowish hairs; flower buds globose. *Flowers* bisexual; sepals slightly connate at the base, depressed ovate to shallowly triangular, 0.6–1.4 by 2–2.2 mm, apex obtuse to acute, sparsely covered with appressed hairs c. 0.1 mm long, persistent in fruit; receptacle 1.7–3 mm diam, flat; petals colour in vivo unknown, 6, in two whorls, outer petals broadly ovate, 4.5–5.1 by 4.8–5.5 mm, outside and apical part and margins of the inside sparsely covered with appressed hairs c. 0.1 mm long, inner petals elliptic, 4–4.6 by 2.7–2.8 mm, elliptic, outside and inside covered with very short hairs; stamens 9–14, in one whorl or in three groups of 4–5 opposite the inner petals, free, linear-oblong, 1.4–1.6 mm long, filaments 0.6–0.7 mm long, thecae latrorse to extrorse, connective truncate, prolonged inward and outward, slightly

papillate, staminodes absent; carpels 9–14, subcylindric, 1.9–2 by 0.4–0.5 mm, densely hairy, ovules 2, lateral, stigma elongate, 0.7–0.8 mm long, glabrous. *Monocarps* 2, colour in vivo unknown, narrowly ellipsoid, 15–21 by 6–7 mm, slightly constricted between the seeds, slightly verrucose, sparsely covered with appressed hairs c. 0.1 mm long, apex rounded to mucronate, stipes 3.5–5 mm long. *Seeds* 1–2, ellipsoid, c. 8 by 6 mm, ochre-brown.

Distribution — Tanzania (Iringa, Morogoro).



Map 14 Distribution of *Monanthotaxis dictyoneura* (green squares) and *M. faulknerae* (red circles, white circle is uncertain det).

Habitat & Ecology — In montane forest. Altitude: 1200–1760 m. Flowering: December, January; fruiting: October.

Preliminary IUCN conservation status —Endangered (EN): B2ab(iii). EOO: 5,246 km^2, AOO: 24 km^2. This species is known from 3 localities of which one is at the edge of the Udzungwa Mountains National Park. The locations are threatened by forest clearance for agriculture.

Notes — 1. *Monanthotaxis dictyoneura* can be distinguished from other species in East Africa by the almost glabrous narrowly obovate to narrowly oblong-elliptic leaves with clearly raised reticulate venation on the upper side. The leaves of some specimens of *M. orophila* can

appear similar, but that species has large, leafy bracts, in contrast to the very small or absent bracts in *M. dictyoneura.*

2. Only a single fruit with two monocarps has been seen.

3. Despite some similarity, *C. Frimodt-Moller TZ517* and *W.R.Q. Luke 6669* have not been assigned to this species, due to the incompleteness of the material and the larger-sized leaves.

21. *Monanthotaxis dielsiana* (Engl.) P.H.Hoekstra — Map 13

Monanthotaxis dielsiana (Engl.) P.H.Hoekstra in Guo et al. (2017) 14. — *Unona dielsiana* Engl. in Diels (1907) 476. — *Oxymitra dielsiana* (Engl.) Sprague & Hutch. (1916) 156. — *Richella dielsiana* (Engl.) R.E.Fr. in Engl. & Harms (1959) 139. — *Friesodielsia dielsiana* (Engl.) Steenis (1964) 359. — Lectotype (designated here): *G.A. Zenker 2473* (lectotype: B (B100154098); isolecto: B100154096, B100154097, B100154099, BM001125043, BR000008801388, COI00071518, E, G00308364; GOET005688, GOET005689, HBG502481, K000198948, KFTA 0001554, KFTA 0001555, L 0182291, M-0240178, P00363342, P00363343, P01988326, S07-13404, WAG0057970, WU 0025876), Cameroon, South Province, Bipinde, Dec. 1901.

Liana; young branches densely covered with appressed, orange-brown hairs c. 0.5 mm long, becoming glabrous; old branches greyish. *Leaves*: petiole 6–11 mm long, 1.6–2 mm diam, terete, indument as on branches; lamina narrowly oblong-elliptic to oblanceolate, 10.3–21.3 by 3.3–3.8 cm, 3.1–4.8 times longer than wide, membranous to subcoriaceous, not punctate, glaucous below, glabrous above, but primary vein densely covered with appressed yellowish white hairs 0.1–0.3 mm long, below subglabrous, but primary vein sparsely covered with appressed to erect, whitish hairs, base slightly subcordate, with a thickened, black margin, apex acuminate, acumen 5–25 mm long, secondary veins 7–14 per side, first straight but curving upwards at end, tertiary venation percurrent, not raised above. *Inflorescences* leaf-opposed, composed of solitary flowers or 2- or 3-flowered fascicles; sympodial rachis c. 8 mm long, rather densely covered with erect, orange-brown hairs 0.2–0.4 mm long; pedicels 15–27 mm long, 1.4–2.1 mm diam, fruiting pedicels to 2.9 mm diam, indument more dense than on sympodial rachis; lower bracts ovate to lanceolate, c. 3.5 by 1–2 mm, indument as on sympodial rachis; upper bract placed halfway or in upper half of pedicel, broadly ovate, c. 4.5 by 4.2 mm, indument as on pedicel; flower buds globose. *Flowers* bisexual; sepals free, broadly triangular, c. 4 by 4 mm, apex acute, densely covered with appressed yellow-brown hairs; receptacle c. 4.5 mm diam, convex; petals colour in vivo unknown, 6, in two whorls, outer petals ovate, 10–15 by 8–9 mm, outside densely covered with yellow-brown, short hairs, inside glabrous at the base, inner petals broadly ovate, c. 8 by 7.7 mm, outside densely covered with hairs, but less densely so near the margins, inside glabrous; stamens c. 65, in three whorls, free, linear, c.1.2 mm long, filaments c. 0.1 mm long, thecae latrorse, connective truncate, circular seen from above, hiding thecae, c. 0.2 mm thick above the thecae, glabrous, staminodes absent; carpels c. 41, ellipsoid, c. 1.7 by 0.7 mm, densely hairy, ovules 1 or 2, basal,

stigma subsessile, globose, c. 0.1 mm diam, glabrous. *Monocarps* 1–6, brown when young, narrowly ellipsoid to cylindric, c. 45 by 10–12 mm, tuberculate-rugulose, densely covered with erect, yellow-brown hairs c. 0.7 mm long, apex rounded, stipes c. 3 mm long. *Seeds* 1–2, cylindric-ellipsoid, c. 15 by 9 mm.

Distribution — Cameroon (Central Region, South Region).

Habitat & Ecology — In primary rainforest. Altitude: c. 200 m. Flowering: December; fruiting: March.

Preliminary IUCN conservation status —Critically endangered (CR): B2ab(iii). AOO: 8 km^2. This species is only known from 2 collections from southern Cameroon of more than 50 years ago, from unprotected areas.

Notes — The flowers and leaves of *M. dielsiana* are very similar to *M. enghiana* and *M. glaucifolia*, but *M. dielsiana* differs in the dense indument of appressed, yellow to orange-brown hairs on the young branches, while *M. enghiana* has longer and erect dark brown hairs and *M. glaucifolia* has a dense indument of appressed, pale brown hairs. Additionally, *M. dielsiana* has a much lower number of stamens compared to the other 2 species and the seeds are cylindric-ellipsoid instead of ellipsoid.

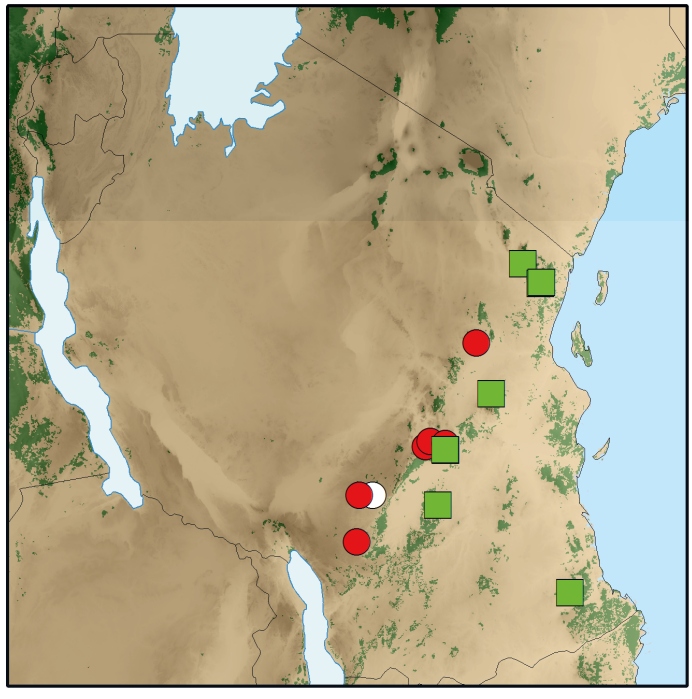
22. *Monanthotaxis discolor* (Diels) Verdc. — Map 15

Monanthotaxis discolor (Diels) Verdc. (1971b) 25. — *Popowia discolor* Diels in Mildbr. (1932) 398. — Lectotype (designated here): *H.-J.E. Schlieben 36* (lectotype: B (B100153024); isolecto: B100153025, B100153026, BM000553831, BR0000008804983, BR0000008805317, G00308307, M0107932, MA384769, P00362608, S), Tanzania, Iringa, Stromgebiet des oberen Ruhudje, Landschaft Lupembe, nördlich des Flusses, Jan. 1931.

Shrub, scandent shrub or liana, to 4 m long; young branches densely covered with ascending to erect, reddish brown hairs 0.2–0.3 mm long, becoming glabrous; old branches grey-black to blackish. *Leaves*: petiole 3–8 mm long, 0.9–1.6 mm diam, grooved, densely covered with ascending to erect, reddish brown hairs; lamina oblong-ovate, oblong-elliptic to oblong-obovate, 4.8–12.8 by 2.5–5.4 cm, 1.7–2.6 times longer than wide, chartaceous, not punctate, glaucous below, above sparsely covered with ascending, whitish hairs 0.2–0.4 mm long, primary vein more densely covered with yellowish hairs, below sparsely covered with ascending to erect, white hairs 0.4–0.6 mm long, primary vein covered with yellowish hairs, base truncate to subcordate, glands hardly visible, apex acute, secondary veins 8–12 per side, from base straight, halfway curving upwards, tertiary venation percurrent below, distinctly reticulate and raised above. *Inflorescences* extra-axillary, leaf-opposed or terminal, composed of solitary flowers to 4-flowered rhipidia; sympodial rachis 1.5–2.5 mm long, densely covered with ascending to erect hairs; pedicels 8–24 mm long, 0.4–0.5 mm diam, fruiting pedicels 23–34 mm long, 0.8–1.6 mm diam, densely covered with ascending to erect hairs 0.2–0.3 mm

long; lower bracts ovate, 0.5–0.8 by 0.4–0.5 mm, indument as on sympodial rachis; upper bract in the lower half of the pedicel or absent, broadly ovate, c. 0.5 by 0.5 mm, indument as on pedicels; flower buds globose. *Flowers* bisexual; sepals free, depressed ovate, 1.2–1.5 by 1.5–1.7 mm, apex obtuse, densely covered with hairs, persistent in fruit; receptacle 1.5–2 mm diam, flat; petals colour in vivo unknown, 6, in two whorls, outer petals ovate to broadly ovate, 3.6–3.7 by 2.1–3.5 mm, outside and apical part and margins of the inside densely covered with ascending, yellowish hairs, inner petals elliptic, c. 2.9 by 1.4 mm, outside and apical part of the inside covered with short hairs; stamens 8–12, in one whorl, free, linear-oblong, c. 1.4 mm long, filaments c. 0.5 mm long, thecae latrorse, connective truncate, prolonged outward, not hiding thecae, glabrous, staminodes absent; carpels 8–9(–14), subcylindric to narrowly ellipsoid, c. 1.5 by 0.4 mm, densely hairy, ovules 2, lateral, stigma subglobose, c. 0.2 mm long, glabrous. *Monocarps* up to 14, colour in vivo unknown, narrowly ellipsoid, 15–24 by 5–6 mm, constricted between the seeds, slightly verrucose, sparsely covered with ascending, short hairs, apex apiculate, apiculum 1–1.5 mm long, stipes 4–8 mm long. *Seeds* 1–2, ellipsoid, 7–8.5 by 5–6 mm, ochre-brown, apex rounded, raphe visible.

Distribution — Tanzania (Iringa, Mbeya).



Map 15 Distribution of *Monanthotaxis discolor* (red circles, white circle is uncertain det) and *M. discrepantinervia* (green squares).

Habitat & Ecology — In montane forest. Altitude: 1440–2050 m. Flowering: January, October; fruiting: March, May, September.

Preliminary IUCN conservation status —Endangered (EN): B2ab(iii). EOO: 20,471 km^2, AOO: 24 km^2. This species is known from 4 localities of which 2 fall inside nature reserves. The other localities are under high threat of clearance of natural vegetation for tobacco and tea plantations.

Notes — 1. *Monanthotaxis discolor* can be recognised in East Africa by the raised and reticulate venation on the upper side of the leaves and the dense indument of ascending to erect, reddish brown hairs on the young branches and lower side of the leaves. Some specimens of *M. ochroleuca* can show this combination of vegetative characters, but that species has very different flowers, which are axillary and not extra-axillary as in *M. discolor*.

2. *G.S. Bidgood 542* is exceptional, it is slightly more densely hairy than the type specimen and with up to 14 monocarps, while in the flowering specimens only 8 or 9 carpels were counted.

23. *Monanthotaxis discrepantinervia* Verdc. — Plate 3a; Map 15

Monanthotaxis discrepantinervia Verdc. (1986) 295. — Type: *L.B. Mwasumbi 12077* (holo: DSM not seen; iso: K000198980), Tanzania, Morogoro, morningside, on road to Bondwa, N. Uluguru Mountains, 1500 m, 30 Nov. 1980.

Scandent shrub or liana, to 6 m long; young branches covered with erect, reddish brown hairs 0.1–0.2 mm long, becoming glabrous; old branches reddish brown to blackish brown. *Leaves*: petiole 3–6 mm long, 1–1.1 mm wide, grooved, indument as on branches; lamina oblong-elliptic, obovate to oblanceolate, 3.5–15.3 by 2.1–6.1 cm, 1.3–3.6 times longer than wide, chartaceous, not punctate, discolorous, green above, pale green and glaucous below, above sparsely covered with ascending, white hairs 0.2–0.3 mm long, primary vein densely covered with erect, yellowish hairs, below sparsely covered with ascending, yellow hairs 0.2–0.4 mm long, primary vein and veins more densely so, base rounded, truncate to slightly subcordate, glands hardly visible, apex acute to acuminate, acumen to 10 mm long, secondary veins 7–16 per side, curving upwards or from base straight, halfway curving upwards, tertiary venation percurrent, hardly visible above. *Inflorescences* extra-axillary, leaf-opposed or terminal, composed of solitary flowers or 2-flowered rhipidia; sympodial rachis c. 1 mm long, densely covered with yellow hairs; flowering and fruiting pedicels 9–13 mm long, 0.7–1 mm diam, densely covered with ascending hairs c. 0.2 mm long; lower bract depressed ovate to ovate, 0.5–4 by 1–3 mm; upper bract halfway up the pedicel, broadly to narrowly ovate, 2–4 by 0.8–3.5 mm, densely covered with yellow hairs; flower buds globose to slightly ovoid. *Flowers* bisexual; sepals free, broadly ovate, 9–11 by c. 8.5 mm, apex obtuse, sparsely covered with yellowish, short hairs, persistent in fruit; receptacle 2–3 mm diam, flat; petals colour in vivo unknown, 6, in two whorls, outer petals ovate to broadly ovate, 3–7 by 3.2–5 mm, outside and apical part of the inside densely covered with yellowish hairs c. 0.1 mm long, inner petals



Plate 3 a. *Monanthotaxis discrepantinervia* Verdc.: Flowering branch. — b. *Monanthotaxis enghiana* (Diels) P.H.Hoekstra: Leaves. — c. *Monanthotaxis filamentosa* (Diels) Verdc.: Flower. — d. *Monanthotaxis foliosa* (Engl. & Diels) Verdc.: Flowering branch. — e. *Monanthotaxis glabra* P.H.Hoekstra: Leaves and fruit. — f. *Monanthotaxis hirsuta* (Benth.) P.H.Hoekstra: Flowers (a: *Couvreur 94*; b: not collected; c: *Letouzey 14591*; d: *Couvreur 601*; e: *Jongkind 7965*; f: *Jongkind 8836*). Photos: a, d: T.L.P. Couvreur; b, e, f: C.C.H. Jongkind; c: P.H. Hoekstra.

elliptic, 2.7–5 by 1.3–2 mm, outside covered with short hairs, glabrous along the margins, inside glabrous except for some hairs near the apex; stamens 15 or 16, in one whorl, free, linear-oblong, c. 0.9 mm long, filaments c. 0.5 mm long, thecae latrorse to extrorse, connective truncate, prolonged outward, not hiding thecae, glabrous, staminodes absent; carpels 8–10, narrowly ellipsoid, 1.2–1.4 by c. 0.3 mm, densely hairy, ovules 1 or 2, lateral, stigma subglobose to ellipsoid, 0.2–0.5 mm long, glabrous. *Monocarps* 1–3, colour in vivo unknown, ellipsoid, 12–16 by 5–7 mm, smooth, sparsely covered with yellowish, short hairs, apex

apiculate, apiculum c. 1 mm long, stipes 1–1.5 mm long. *Seed* 1, ellipsoid, 9.5–12 by 6–6.5 mm, ochre-brown, apex flattened or rounded, raphe not visible.

Distribution — Tanzania (Iringa, Lindi, Morogoro, Tanga).

Habitat & Ecology — In submontane and montane forest. Altitude: 760–1425 m. Flowering: April, May, September, November; fruiting: November.

Vernacular names — Tanzania: Msitu (Kitongwe name) (*Y.S. Abeid 1302*).

Preliminary IUCN conservation status —Endangered (EN): B2ab(iii). EOO: 89,549 km^2, AOO: 32 km^2. This species is known from 8 collections from 5 locations. Three are in protected areas; however, in two of these locations the collections are more than 100 years old and the other two locations are under threat of habitat destruction.

Notes — 1. *Monanthotaxis discrepantinervia* is the only species in Eastern Africa of which the sepals are as large as or larger than the petals. It differs from other species with large sepals from West and Central Africa in having broadly ovate sepals and only one seed per monocarp.

2. Floral measurements were taken from a terminal, quite small flower; the largest measurements were copied from the protologue.

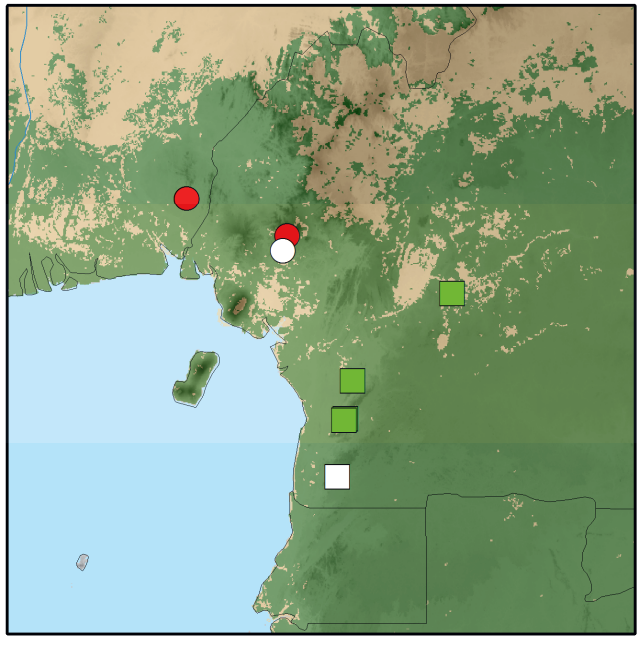
24. *Monanthotaxis elegans* (Engl. & Diels) Verdc. — Fig. 5j–p; Map 16

Monanthotaxis elegans (Engl. & Diels) Verdc. (1971b) 25. — *Unona elegans* Engl. in Engl. & Diels (1899) 296, nom. illeg., non Thwaites in Thwaites & Hooker (1864) 398. — *Popowia elegans* Engl. & Diels (1901) 45 — Type: *G.A. Zenker 1321* (holo: B100153023; iso: BM000553832, BM000553833, E00181437, G00308366, HBG-502506, K000198990, K000198991, M-0198713, P00362605, P00362606), Cameroon, South Province, Bipinde, 23 Mar. 1897.

Shrub, to 4 m tall; young branches reddish brown to blackish brown, densely covered with appressed to ascending, reddish brown hairs 0.1–0.2 mm long, becoming glabrous; old branches blackish brown to dark greyish brown. *Leaves*: petiole 2.5–5 mm long, 0.9–1.3 mm diam, slightly grooved, indument as on branches; lamina narrowly oblong-elliptic, slightly oblanceolate or rarely obovate, (4.6–)9–15.4 by 2.3–4.6 cm, (2–)2.9–5.5 times longer than wide, chartaceous, not punctate, medium green above, glaucous below, above covered with appressed, yellowish hairs 0.1–0.2 mm long, below sparsely covered with appressed, white to yellow hairs 0.1–0.2 mm long, base rounded to narrowly subcordate, with slightly thickened dark brown margin, apex acute to acuminate, acumen to 30 mm long, secondary veins 11–14 per side, straight, but curving halfway, tertiary venation percurrent, slightly visible above. *Inflorescences* extra-axillary or terminal, composed of 1–8-flowered, glomerule-like rhipidia; sympodial rachis 1.5–4 mm long, indument as on branches; pedicels 1.2–2 mm long, 0.6–0.7 mm diam, fruiting pedicels 3.5–5 mm long, 1–1.2 mm diam, densely covered with appressed,

yellowish hairs 0.1–0.2 mm long; lower bracts ovate, 0.6–0.9 by c. 0.4 mm, indument as on rachis; upper bract in lower half or halfway up the pedicel, ovate, 0.5–0.8 by c. 0.3 mm, indument as on pedicel; flower buds ovoid. *Flowers* bisexual; sepals free, broadly triangular-ovate, 1.1–1.4 by 1.2–1.5 mm, apex acute, densely covered with appressed hairs, persistent in fruit; receptacle c. 2 mm diam, flat; petals creamy yellow, 6, in two whorls outer petals broadly ovate, 2.6–4.3 by 2.6–3.5 mm, outside densely covered with yellow-brown hairs, inside glabrous except for few hairs near the apex and margins, inner petals rhombic, c. 3.5 by 1.9 mm, centre and base of the outside covered with yellow hairs, inside glabrous, except for few hairs at the apex; stamens 9, in one whorl, free, linear-oblong, c. 0.9 mm long, filaments c. 0.4 mm long, thecae latrorse, connective truncate, prolonged inward and outward, not hiding thecae, glabrous, staminodes 6, alternating with the stamens, but not in front of the inner petals, 0.1–0.2 mm long, glabrous; carpels 12–20, narrowly ellipsoid, c. 1.1 by 0.3 mm, densely hairy, ovules 1 (or 2), basal, stigma globose, c. 0.2 mm diam, glabrous. *Monocarps* 2–8, colour unknown in vivo, ellipsoid to narrowly ellipsoid, 9–16 by 5–5.5 mm, slightly verrucose, sparsely covered with appressed, yellow-brown hairs, becoming glabrous, apex apiculate, apiculum 0.2–0.3 mm long, stipes 1.5–2 mm long. *Seeds* 1 or 2, ellipsoid, 6.7–9.4 by 4.6–5.5 mm, ochre-brown, apex rounded, raphe visible.

Distribution —Cameroon (Central Region, South Region).



Map 16 Distribution of *Monanthotaxis elegans* (green squares, white square is uncertain det) and *M. glaucifolia* (red circles, white circle is uncertain det).

Habitat & Ecology — In primary and gallery forest; once on an open rocky spot on sandy soil. Altitude: 200–400 m. Flowering: March, June, July; fruiting: March.

Preliminary IUCN conservation status —Endangered (EN): B2ab(iii). EOO: 2,259 km^2, AOO: 16 km^2. This species is known from 10 collections from 3 locations, all outside protected areas and the last collection dated from more than 50 years ago.

Notes — 1. *Monanthotaxis elegans* can easily be recognized by the mostly oblong-lanceolate leaves and extra-axillary or terminal glomerule-like inflorescences with yellow-brown indument.

2. *E. Annet 348* is aberrant in having obovate instead of the typical oblong-lanceolate leaves, but the inflorescence and flowers are identical to *M. elegans*.

25. *Monanthotaxis enghiana* (Diels) P.H.Hoekstra — Fig. 11; Plate 3b; Map 17

Monanthotaxis enghiana (Diels) P.H.Hoekstra in Guo et al. (2017) 14. — *Popowia enghiana* Diels in Mildbr. (1911) 213. — *Friesdielsia enghiana* (Diels) Verdc. in Le Thomas (1969) 240. — Type: *G.W.J. Mildbraed 2213* (holo: B100153056), Democratic Republic of the Congo, Nord-Kivu, Fort Beni a Semliki, 1907-1908.

Unona obanensis Baker f. (1913) 4. — *Oxymitra obanensis* (Baker f.) Sprague & Hutch. (1916) 154. — *Richella obanensis* (Baker f.) R.E.Fr. in Engl. & Harms (1959) 139. — *Friesodielsia obanensis* (Baker f.) Steenis (1964) 359. — Type: *P.A. Talbot 1246* (holo: BM000547069), Nigeria, Cross River State, Oban, 1911.

Oxymitra grandiflora Boutique (1951b) 116. — *Richella grandiflora* (Boutique) R.E.Fr. in Engl. & Harms (1959) 139. — *Friesodielsia grandiflora* (Boutique) Steenis (1964) 359. — Lectotype (designated here): *R.G.A. Germain 883* (lectotype: BR; iso: K000913652, K000913653, MO), Democratic Republic of the Congo, Orientale, Yalibutu, 45 km NW of Yangambi, 22 Jan. 1948.

Popowia mangenotii Sillans (1953) 578. — Lectotype (designated here): *C. Tisserant (Équipe) 1285* (lectotype: P (P00363339); iso: BR, K000913654, P00363338), Central African Republic, Lobaye, Station de Boukoko, Boukokok, 14 Dec. 1948.

Popowia mangenotii Sillans f. *concolor* Sillans (1953) 580. — Lectotype (designated here): *C. Tisserant (Équipe) 2062* (lectotype: P (P00363336); iso: BM000547068, BR, P003633385, P01985781), Central African Republic, Lobaye, Station de Boukoko, Boukokok, 5 Apr. 1951.

Shrub, scandent shrub or liana, to 15 m long, to 6 cm diam; young branches densely covered with erect, dark brown hairs 0.9–1.4 mm long, becoming glabrous; old branches dull silvery-grey, drying black. *Leaves*: petiole 3–4 mm long, 1.3–2.2 mm diam, terete, indument as on branches; lamina narrowly oblong-oblanceolate, 10.8–35 by 3.3–7.5 cm, (2.2–)3–4.4(–5.9) times longer than wide, membranous to subcoriaceous, not punctate, discolorous, slightly bright to pale green above, glaucous below, above sparsely covered with appressed, whitish hairs c. 0.7 mm long, soon becoming glabrous, primary vein densely covered with erect hairs,

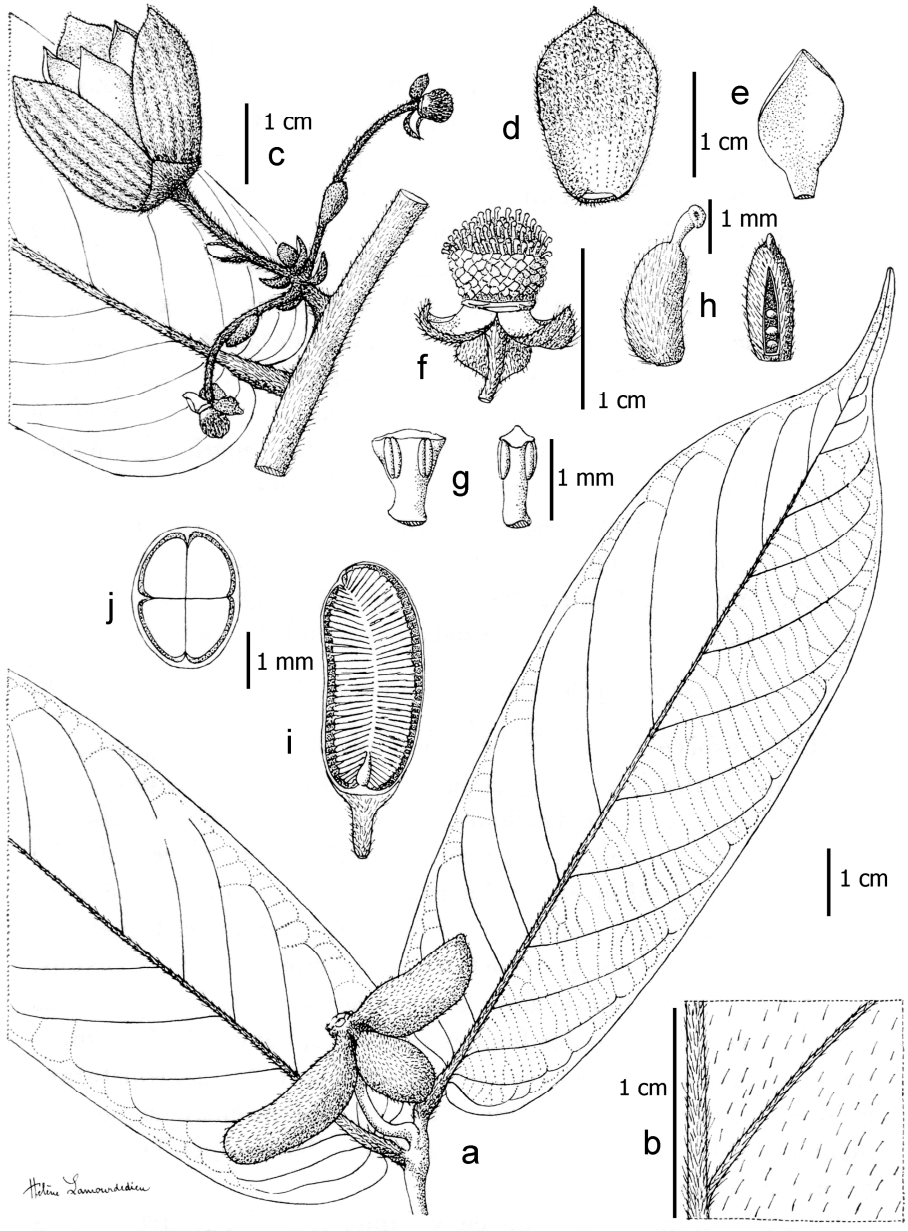


Fig. 11 *Monanthotaxis enghiana* (Diels) P.H.Hoekstra: a. Fruiting branch; b. detail leaf abaxially; c. inflorescence; d. outer petal; e. inner petal; f. flower with petals removed; g. stamen, front and side view; h. carpel and longitudinal section of carpel; i. longitudinal section of carpel; j. transverse section of carpel (a: *Sillans 1701*; b–h: *Tisserant 1941*; i, j: *Sillans 1701*). Modified from Le Thomas (1969) plate 43.

below rather densely covered with erect, brown hairs 0.5–0.8 mm long, more densely so on the primary vein, base rounded to subcordate, glands hardly visible, apex acute to acuminate, acumen to 50 mm long, secondary veins 11–20 per side, curving upwards near margin, tertiary venation distinctly percurrent, not raised above. *Inflorescences* extra-axillary or sometimes supra-axillary, composed of corymb-like (1–)2–5-flowered rhipidia; sympodial rachis 3–12 mm long, densely covered with hairs, flowering and fruiting pedicels 18–22 mm long, 0.6–1.8 mm diam, densely covered with ascending to erect hairs; lower bracts broadly ovate 1.5–2 by 1.5–2.5 mm, indument as on pedicels; upper bract halfway or at one-third of the pedicel, broadly ovate, 2.7–4.5 by 3.5–4 mm, semi-amplexicaul, outside glabrous, inside densely covered with hairs; flower buds globose. *Flowers* bisexual; sepals connate at the base, depressed ovate, 2.5–5 by 4.7–8 mm, apex rounded, densely covered with appressed, dull brown hairs, persistent in fruit; receptacle convex; petals dull black, purplish brown in sicco, 6, in two whorls, outer petals ovate to elliptic, 12–22 by 7–14 mm, outside densely covered with yellow-brown hairs, inside covered with reddish, short hairs at the apex, glabrous at the base, inner petals ovate-rhombic, 9–14 by 8–10 mm, outside and inside glabrous, sometimes with few, solitary hairs at the base; stamens 90–110, in three or four whorls, free, obconical, 1.2–1.3 mm long, filaments c. 0.4 mm long, thecae latrorse, connective truncate, rectangular from above, prolonged inward and outward, hiding thecae, glabrous, staminodes absent; carpels 40–60, subcylindric, c. 2.9 by 0.5 mm, densely hairy, ovules 2(–4), lateral, stigma elongate, c. 1 mm long, glabrous. *Monocarps* 5–15, glaucous green, ellipsoid, 14–34 by 8–9 mm, densely covered with brown hairs, apex rounded to apiculate, stipes 2–5 mm long. *Seeds* 1–2(–3), ellipsoid, 11–12 by 7–11 mm, tawny to reddish brown, ends rounded, raphe slightly visible on both sides.

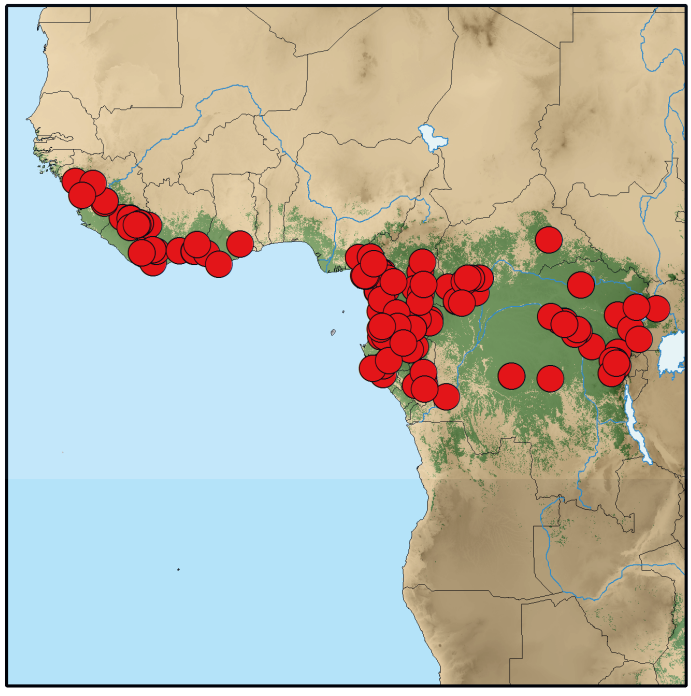
Distribution — Guinea, Sierra Leone, Liberia, Ivory Coast, Ghana, Nigeria, Cameroon, Equatorial Guinea, Gabon, Republic of the Congo, Central African Republic, Democratic Republic of the Congo, Uganda.

Habitat & Ecology — In evergreen primary forest, moist semi-deciduous forest, submontane forest, secondary forest, gallery forest, swamp forest, on rocky soil. Altitude: 0–1,375 m. Flower: October to July; fruiting: October to July.

Vernacular names — Cameroon: Mavembegne (Pygmée name) (*R.G. Letouzey 5071*). Central African Republic: Mo-Fembe Fembe (Lissongo name) (*C. Tisserant Équipe 2062*), Fembe (Lissongo name) (*C. Tisserant Équipe 1701*), Molo-Mindowali (Lissongo name) (*C. Tisserant Équipe 1257*), Vembenye (Bambindjere name) (*D.J. Harris 1721*). Democratic Republic of the Congo: Lukumbula (Kirega and Kitembe name) (*A.R. Christiaensen 1802*, *G.M.D.J. Troupin 12466*). Amàphaphasà (Kikumu name) (*J. Bokdam 3574*). Amapapasia (*C.E.N. Ewango 258*), Esaa (Babua name) (*P. Gérard* 517), Etumu (Mukire name) (*J. Claessens 629*). Impimbo ya pembe (Nkundo name) (*B.I. Fruth 1894*), Impimbo ya dzamba (Nkundo name) (*B.I. Fruth 123*). Gabon: Maboom-Mamiala (Bongom name) (*J.J. Wieringa 3605*).

Preliminary IUCN conservation status —Least concern (LC). EOO: 4,370,609 km^2, AOO: 468 km^2. This species occurs in many countries, locations and reserves. In the wet tropical forests of Central and West Africa this probably is the most common species of *Monanthotaxis*.

Notes — *Monanthotaxis enghiana* is generally easily recognizable by the narrowly oblong-oblanceolate leaves with a dense indument of erect, dark brown, long hairs on the young branches and lower side of the leaves. Some sterile specimens can have more narrowly oblong-elliptic leaves, and are not distinguishable with certainty from *M. hirsuta.* However, the petals and stamens of *M. enghiana* are very different from those of *M. hirsuta*. The outer petals of *M. enghiana* are shorter (12–22 mm versus 21–50 mm in *M. hirsuta*) and the inner petals of *M. enghiana* are ovate-rhombic (versus lanceolate). The thecae of *M. enghiana* are very short, they cover less than half the stamen length, while in *M. hirsuta* the thecae cover much more than half the stamen length. *Monanthotaxis enghiana* is closely related to *M. dielsiana* and *M. glaucifolia*, but differs clearly in the indument type. See the notes under those species.



Map 17 Distributin of *Monanthotaxis enghiana* (red circles).

26. *Monanthotaxis faulknerae* Verdc. — Map 14

Monanthotaxis faulknerae Verdc. (1971b) 25. — Type: *H.G. Faulkner 1624* (holo: K000198979; iso: B100153028, BR0000008802002), Tanzania, Tanga, Tanga-Mombasa road, 16 km from Tanga, 60 m, 28 May 1955.

Scandent shrub or liana, to 3 m long; young branches reddish brown, covered with erect, yellowish hairs 0.2–0.5 mm long, becoming glabrous; old branches dark brown, grey-black to blackish. *Leaves*: petiole 1.5–3 mm long, 0.4–0.7 mm diam, terete, indument as on branches; lamina oblong-elliptic or sometimes obovate to narrowly so, 1.4–5.5(–6.7) by 0.7–2.6 cm, 1.5–2.8 times longer than wide, subcoriaceous, punctate, discolorous, olive-green above, dull greenish white below, young leaves above sparsely covered with ascending, white hairs 0.4–0.6 mm long, becoming glabrous, primary vein more densely hairy, below sparsely covered with ascending to erect, white hairs 0.3–0.6 mm long, base rounded or sometimes slightly subcordate, glands hardly visible, apex rounded to acute, secondary veins 7–10 per side, from base curving upwards, tertiary venation percurrent, slightly raised and reticulate above. *Inflorescences* terminal or extra-axillary, mostly leaf-opposed, composed of solitary flowers; sympodial rachis absent; pedicels 4–22 mm long, 0.4–0.6 mm diam, fruiting pedicels 0.7–1.1 mm diam, sparsely covered with erect hairs 0.3–0.5 mm long; lower bracts absent; upper bract in the lower half of the pedicel or absent, ovate, 1.2–2.4 by 0.7–1.7 mm, indument as on pedicel; flower buds globose. *Flowers* bisexual; sepals free, depressed ovate to orbicular, 1.8–3.7 by 2.8–4.2 mm, apex rounded, densely covered with ascending, white, short hairs, punctate, persistent in fruit, slightly accrescent; receptacle 2.2–2.7 mm diam, flat; petals colour in vivo unknown, 6, in two whorls, outer petals broadly ovate to ovate, 4.2–8.8 by 4.8–7.5 mm, outside and apex and margins on the inside covered with ascending, white-yellow, short hairs, inner petals elliptic, 3.8–5.2 by 2.3–4.6 mm, outside and apex of the inside covered with short hairs; stamens 23–27, in two whorls, free, linear-obovoid, c. 1.2 mm long, filaments c. 0.4 mm long, thecae latrorse to extrorse, connective truncate, prolonged outward and inward, not hiding thecae, glabrous, staminodes absent; carpels 8–10, subcylindric, c. 1.7 by 0.5 mm, densely hairy, ovules 2 or 3, lateral, stigma elongate, c. 0.8 mm long, glabrous. *Monocarps* up to 9, orange, narrowly ellipsoid, 14–23 by 4.8–5.5 mm, constricted between the seeds, slightly verrucose, densely covered with erect, yellowish white hairs, apiculate, apiculum 1–2 mm long, stipes 3.2–5.5 mm long. *Seeds* 1–3, subglobose to ellipsoid, 6.2–9.8 by 3.8–4.7 mm, ochre-brown, apex flattened, rounded or apiculate, raphe hardly visible as a longitudinal furrow from base to apex.

Distribution — Kenya (Coast), Tanzania (Tanga).

Habitat & Ecology — In lowland forest, *Brachystegia* woodland, coastal thicket on tan sand. Altitude: 20–370 m. Flowering: May, June;f ruiting: February, July, December.

Preliminary IUCN conservation status —Vulnerable (VU): B2ab(iii). EOO: 12,700 km^2, AOO: 40 km^2. This species is known from 10 collections from 7 locations along the coast of Kenya and north-east of Tanzania of which only three are in protected areas.

Notes — *Monanthotaxis faulknerae* is morphologically closely resembling *M. suffruticosa* and *M. trichocarpa*. All three species have punctate leaves in sicco and have extra-axillary inflorescences, c. 25 stamens and erect hairs on the monocarps. *Monanthotaxis faulknerae* can be distinguished from *M. suffruticosa* in the lower number of carpels (8–10 versus 14–16) and a different growth form (shrub or liana versus a subshrub). *Monanthotaxis faulknerae* is difficuilt to distinguish from *M. trichocarpa,* but generally has oblong-elliptic leaves, which are much smaller than those of *M. trichocarpa*, which has generally obovate leaves that are normally double the size of those of *M. faulknerae.* Further *M. faulknerae* has 8–10 carpels per flower, while *M. trichocarpa* normally has around 12 carpels per flower. There is some overlap in the characters and generally a combination of characters has to be used when a specimen has leaves in the length of 4.5–6 cm. More material of *M. faulknerae* and field and DNA-studies are needed to assess if it merely is an extreme form of *M. trichocarpa* or a good species.

27. *Monanthotaxis ferruginea* (Oliv.) Verdc. — Fig. 12k–q; Map 18

Monanthotaxis ferruginea (Oliv.) Verdc. (1971b) 26. — *Unona ferruginea* Oliv. (1868) 35. — *Popowia ferruginea* (Oliv.) Engl. & Diels (1901) 46. — Lectotype (designated by Paiva 1966: 41): *F.M.J. Welwitsch 761* (lecto: LISU206061; isolecto: B100153029, BM000553834, BM000553835, BR0000008805324, COI00004905, G00308369, K000198968, LISU206062, P00362602), Angola, Cuanza Norte, distr. Golungo Alto, 305 m, July 1855.

Unona eminii Engl. (1895) 179. — Syntypes: *F.L. Stuhlmann 1556* (B not seen), Tanzania, Kagera, Bukoba; *F.L. Stuhlmann 4022* (B not seen), Tanzania, Kagera, Bukoba.

Popowia djumaensis De Wild. (1909) 76. — Type: *J. Gillet 2803* (holo divided over 2 sheets: BR0000008803160, BR0000008803962), Democratic Republic of the Congo, Bandundu, vallée de la Djuma, July 1907.

Shrub, scandent shrub or liana, to 6 m long; young branches densely covered with erect, reddish brown hairs 0.5–0.9 mm long, becoming glabrous; old branches blackish brown. *Leaves*: petiole 3.5–7.5 mm long, (0.7–)1.2–1.5 mm diam, terete, indument as on branches; lamina oblong-elliptic, obovate or oblanceolate, 3.6–17.2 by 1.8–6.8 cm, (1.7–)1.8–3.3 times longer than wide, hardly to slightly punctate, chartaceous, not punctate, glossy dark green above, dull greyish green below, above densely covered with ascending to erect, white-yellowish hairs 0.3–0.6 mm long, becoming glabrous, primary vein with longer persistent, ascending to erect, yellow hairs, below sparsely covered with erect, reddish brown hairs 0.5–0.9 mm long, more densely so on veins, base subcordate with thickened black margin, apex acute to slightly obtuse, secondary veins 7–15 per side, from base straight, halfway curving

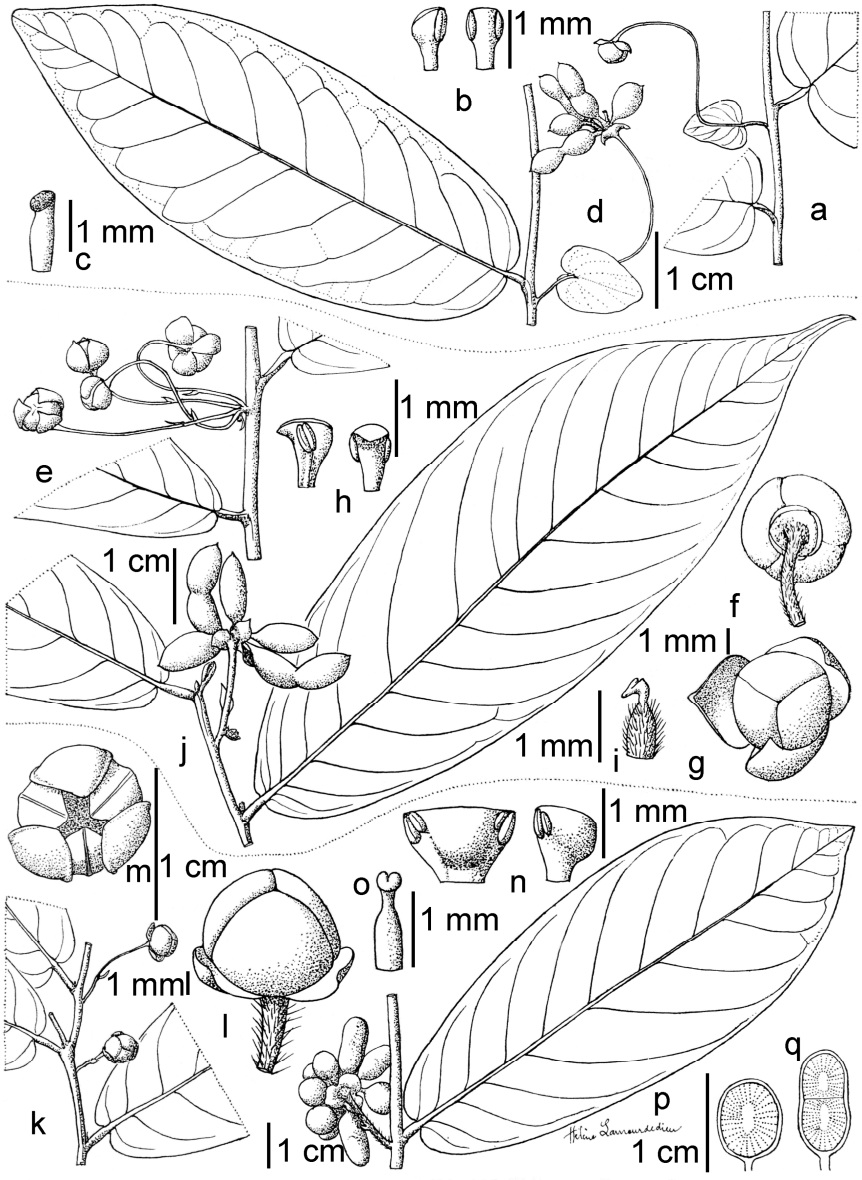


Fig. 12 a–d. *Monanthotaxis littoralis* (Bagsh. & Baker f.) Verdc.: a. Flowering branch; b. stamen, front and side view; c. carpel; d. fruiting branch. — e–j. *M. lucidula* (Oliv.) Verdc.: e. Flowering branch; f. flower bud with sepals removed, seen from below; g. flower bud seen from above; h. stamen, side and front view; i. carpel; j. fruiting branch. — k–q. *M. ferruginea* (Oliv.) Verdc.: k. Flowering branch; l. flower bud; m. flower seen from above; n. stamen, front and side view; o. carpel; p. fruiting branch; q. longitudinal sections of carpels (a–c: *Koechlin 671*; d: *Thollon 938*; e–i: *Bouquet 792*; j: *Hallé 3539*; k–q: living material of *Hallé 3081 & 3103*). Modified from Le Thomas (1969) plate 40.

upwards, tertiary venation percurrent, hardly visible. *Inflorescences* extra-axillary, leaf-opposed or terminal, composed of solitary flowers; sympodial rachis absent; flowering and fruiting pedicels (5–)10–36 mm long, 0.4–0.8 mm diam, covered with ascending to erect, reddish brown hairs 0.4–0.8 mm long; lower bract absent; upper bract in the lower half of the pedicel or halfway, ovate to narrowly ovate, 2–5.5 by 0.5–4.5 mm, indument as on pedicel; flower buds globose. *Flowers* bisexual; sepals free, depressed ovate to almost orbicular, 1.5–2.7 by 2.7–3.3 mm, apex rounded, sparsely covered with ascending, yellow-brown hairs, persistent in fruit; receptacle 4.5–5 mm diam, flat; petals colour in vivo unknown, 6, in two whorls, outer petals ovate, 5.8–6.7 by 4.5–6 mm, outside and near the margins of the inside densely covered with yellowish hairs; inner petals elliptic to ovate, 3–5.4 by 2.7–2.9 mm, outside and apical part of the inside densely covered with yellow hairs; stamens 22–25, in three whorls, free, obovoid, 1.1–1.5 mm long, filaments 0.3–0.5 mm long, thecae latrorse to extrorse, connective truncate, prolonged inward, not hiding thecae, glabrous, staminodes absent; carpels 12–24,
narrowly ellipsoid, 1–1.8 by c. 0.5 mm, glabrous except for few hairs at the base, ovules 2–4, lateral, stigma subsessile to elongate, 0.1–0.7 mm long, glabrous. *Monocarps* 2–17, orange to red, moniliform, each part ellipsoid to narrowly ellipsoid, 12–35 by 6–9 mm, slightly verrucose, glabrous or with few hairs on the stipe, apex rounded or apiculate, apiculum to 4 mm long, stipes 3–4(–6.5) mm long. *Seeds* 1–3(–5), ellipsoid, 7–8 by 5–6 mm, ochre-brown, apex rounded, raphe hardly visible.

Distribution — Cameroon, Gabon, Republic of the Congo, Democratic Republic of the Congo, South Sudan, Ethiopia, Uganda, Rwanda, Burundi, Tanzania, Angola.

Habitat & Ecology — In gallery forest, lowland rainforest, *Brachystegia* woodland, forest edges, old secondary forest, montane forest and rock plateaus. Altitude: 20–1800 m. Flowering and fruiting: all year round.

Vernacular names — Democratic Republic of the Congo: Mugoya (Kindande name) (*R. Pierlot 3082*), Mubugu (Kihavu name) (*D. van der Ben 765*). Tanzania: Lujongololo (*S. Uehara 534*).

Preliminary IUCN conservation status —Least concern (LC). EOO: 3,769,635 km^2, AOO: 228 km^2. This species is known from many locations and several reserves.

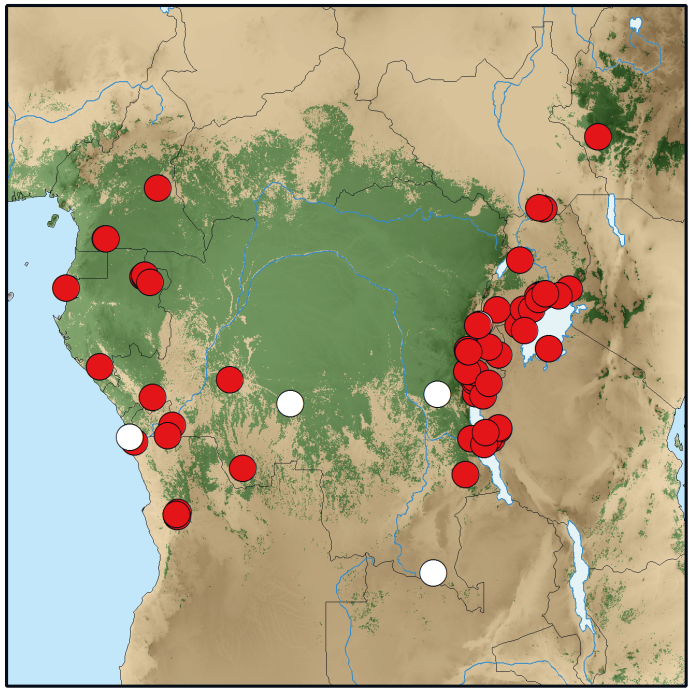
Notes — 1. *Monanthotaxis ferruginea* is resembling *M. bokoli*, both species having erect, reddish brown hairs on the young branches and lower side of the leaves, and flowers with 24 stamens and glabrous carpels. For the differences see the key and the note under *M. bokoli*.

2. *Monanthotaxis ferruginea* is a highly variable species with some of the variation geographicaly clustered. Specimens from the highlands in the eastern part of the distribution area have in general larger upper bracts and *A.B. Katende 1301* from Uganda has leafy bracts of c. 5.5 by 4.5 mm. Furthermore, the majority of specimens have acute leaf tips, but some specimens in the east of Africa have obtuse leaf tips and are vegetatively difficult to distinguish

from *M. bokoli*. More material in combination with DNA-analyses are needed to test if all the poplations of *M. ferruginea* belong to the same entity.

3. *A. Dumont 241* from the Kasai Oriental province in the Democratic Republic of the Congo looks vegetatively like *M. ferruginea*, but has filiform supra-axillary pedicels and only 15 stamens per flower. This is probably a new species, but more material from that area is needed.

4. *J.F. Brunel 7715*, with a single old flower, is from Togo, which is far outside the range of the species. Better material is needed to assess if this specimen really belongs to *M. ferruginea*.



Map 18 Distribution of *Monanthotaxis ferruginea* (red circles, white circles are uncertain dets).

28. *Monanthotaxis filamentosa* (Diels) Verdc. — Plate 3c; Map 19

Monanthotaxis filamentosa (Diels) Verdc. (1971b) 31. — *Popowia filamentosa* Diels (1907) 478. —Type: *G.A. Zenker 2985* (holo: B not seen; iso: BR0000008804297, E00624352, GOET005686, HBG-502505, K000198988, L 0038042, M0107931, P00362600, S, WAG0071434, WU0025872), Cameroon, South Region, Bipinde, Apr. 1904.

Popowia malchairii De Wild. (1911) 309. — Type: *L. Malchair 295* (holo, divided over 2 sheets: BR0000008804624, BR0000008804952), Democratic Republic of the Congo, Equateur, Budjala, environs a Likimi, 25 Apr. 1910.

Popowia setosa Diels (1915) 442, syn. nov. — Lectotype (designated here): *G.W.J. Mildbraed 5989* (lectotype: B (B100154095); iso HBG502503), Cameroon, South Region, 58 km E of Kribi, Fenda, 1911.

Liana, to 10 m long; young branches densely covered with erect, reddish brown hairs 0.7–1.4 mm long, becoming glabrous; old branches black to blackish brown. *Leaves*: petiole 2.5–6 mm long, 1–2.5 mm diam, slightly grooved, indument as on branches; lamina oblong-elliptic, obovate or oblanceolate, 12.5–28.6 by 4.1–12.5 cm, 1.8–3.1 times longer than wide, subcoriaceous, not punctate, dark green above, glaucous below, above sparsely covered with ascending to erect, whitish hairs 0.5–1 mm long, on primary vein indument more dense and composed of yellow hairs, below sparsely covered with erect, yellowish hairs 0.5–1.4 mm long, more densely so on primary vein, base rounded to subcordate, with slightly thickened black margin, apex acute to acuminate, acumen 5–10 mm long, secondary veins 12–19 per side, curving or straight and halfway curving upwards, tertiary venation percurrent. *Inflorescences* axillary or terminal, composed of solitary flowers or 2–10-flowered, raceme-like rhipidia; sympodial rachis absent or to 10 cm long, densely covered with erect, reddish brown hairs; pedicels 1–18 mm long, 0.6–1 mm diam, fruiting pedicels 9–31 mm long, 0.6–2.1 mm diam, covered with erect, reddish brown hairs 0.5–1 mm long; lower bract absent or narrowly ovate, c. 2.1 by 0.5 mm, indument as on pedicel; upper bract absent or very large, sepal-like, just below the flower, ovate, 1.1–8 by 0.5–4.1 mm, indument as on pedicel; flower buds ovoid. *Flowers* bisexual; sepals free, covering flower in bud, ovate, 4.5–10 by 3.2–5.5 mm, apex acute, densely covered with appressed to ascending hairs, not persistent in fruit; receptacle c. 2 mm diam, flat; petals colour in vivo unknown, 6, in two whorls, outer petals ovate to narrowly ovate, 8–22 by 4.7–8.5 mm, outside and inside (except for the glabrous base) densely covered with appressed, yellow hairs, inner petals ovate to elliptic, 6.5–14 by 3–5 mm, indument as on outer petals; stamens 17–46, in two to four whorls, free or connate at the base, linear, 1.8–2.3 mm long, filaments 1.3–1.9 mm long, thecae introrse, convergent apically, hiding connective, glabrous, staminodes absent; carpels 8–14, subcylindric, 2.3–2.5 by 0.5–0.6 mm, dense hairy, ovules 7–9, lateral, stigma elongate, c. 0.7 mm long, glabrous. *Monocarps* 1–7, yellow to red, subcylindric, 110–175 by 6.5–8 mm, slightly verrucose, densely to sparsely covered with erect, reddish brown hairs, apex apiculate, apiculum 1–3 mm long, stipes 8–15 mm long. *Seeds* 1–7, subcylindric, 17–25 by 4–5 mm, ochre-brown.

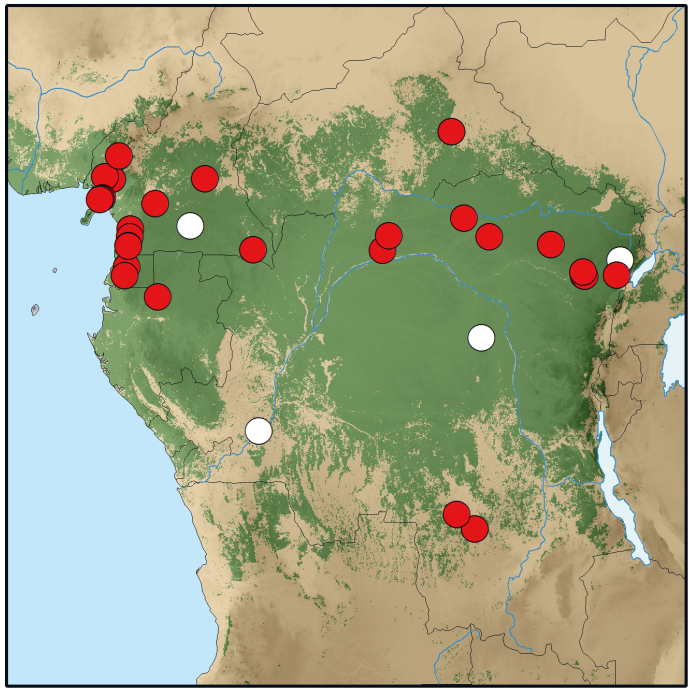
Distribution — Cameroon, Central African Republic, Democratic Republic of the Congo, Equatorial Guinea, Gabon.

Habitat & Ecology — In primary forest, secondary forest, submontane forest and gallery forest, on rocky soil. Altitude: 120–1700 m. Flowering: October to July; fruiting: February, March, June, September, November.

Vernacular names — Democratic Republic of the Congo: Lisis (Kibila name) (*Nasanga 45*), Amapapasia (Bila name) (*F. Amsini 283*), Nginko e Likebe e Tokembe (*L. Toussaint 858*).

Preliminary IUCN conservation status —Least concern (LC). EOO: 2,090,176 km^2, AOO: 108 km^2. This species has a large extent of occupancy and occurs in quite some locations and protected areas. Furthermore, it has in recent years been collected relatively often, including in several new locations.

Notes — *Monanthotaxis filamentosa* is easily recognizable by the dense indument of erect, reddish brown hairs on the young branches and the leaves, and by the large, ovoid flower buds. Specimens from the western part of the distribution area generally have oblong-elliptic or sometimes obovate leaves, while some specimens from the eastern part of the distribution area have more obovate to oblanceolate leaves. The monocarps appeared more densely hairy in the eastern part of the distribution. More flowering and fruiting material, especially from the Democratic Republic of the Congo, is needed to verify if those populations belong to the same species.



Map 19 Distribution of *Monanthotaxis filamentosa* (red circles, white circles are uncertain dets).

29. *Monanthotaxis filipes* P.H.Hoekstra **—** Fig. 13; Map 20

Monanthotaxis filipes P.H.Hoekstra in P.H.Hoekstra et al. (2016) 82. — Type: *G.S. Bidgood 1402* (holo : K 2 sheets; iso: BR0000013186036, C, EA, MO4027188, P01967237, UPS, WAG0071696), Tanzania, Lindi district, Rondo plateau, Rondo forest Reserve, 10°07'S; 39°13'E, 700 m, 7 Feb. 1991.

Shrub, c. 1 m tall; young branches yellow-brown, densely covered with appressed to ascending, yellowish hairs 0.3–0.7 mm long, becoming glabrous; old branches dark brown to greyish brown. *Leaves*: petiole 3–5 mm long, 0.7–1 mm diam, slightly grooved, indument as on branches; lamina oblong-elliptic to narrowly obovate, 3.7–10.7 by 1.5–4.4 cm, 1.6–3.3 times longer than wide, chartaceous, not punctate, discolorous, pale bluish green below, above sparsely covered with whitish appressed hairs when young, soon becoming glabrous, below densely covered with ascending, yellowish white hairs 0.3–0.5 mm long, base rounded, truncate or slightly subcordate, with thickened margin at the base, apex acute, secondary veins 7–10 per side, first straight, halfway curving upwards, tertiary venation percurrent. *Inflorescences* supra-axillary, 2–6 mm above leaf axil, 1–2-flowered rhipidia; sympodial rachis 0–1 mm long; flowering pedicels 18–55 mm long, c. 0.2 mm diam, sparsely covered with ascending to erect hairs; lower bracts strongly reduced or absent; upper bract halfway up the pedicel, ovate, c. 0.3 by 0.1 mm or just a dense tuft of hairs or absent, indument as on pedicels; flower buds globose. *Flowers* bisexual, pendulous; sepals connate at the base, depressed ovate to almost cup-shaped, c. 0.5 by 1.1–1.2 mm, apex obtuse to rounded, densely covered with appressed, yellow hairs; receptacle 1.5–2 mm diam, flat; petals creamy white, 6, in two whorls, outer petals broadly ovate, 2.5–2.7 by 2.8–3.6 mm, outside and apex of the inside densely covered with yellowish, short hairs, base of inside glabrous; inner petals ovate to rhombic, 1.9–2 by 1.2–1.4 mm, indument as on in outer petals; stamens (13?–)15, in one to two whorls, free, obovoid, 1.1–1.3 mm long, filaments 0.3–0.4 mm long, thecae extrorse, connective truncate, not hiding thecae, glabrous, staminodes absent; carpels 9, subcylindric, c. 1.2 by 0.2–0.3 mm, densely hairy, but glabrous near the apex, ovules 2, lateral, stigma elongate, c. 0.4 mm long, grooved, glabrous. *Monocarps* and *seeds* not seen.

Distribution — Tanzania (Lindi).

Habitat & Ecology — In steep escarpment densely covered with thickets; stony-gravelly soil. Altitude: c. 700 m. Flowering: February.

Preliminary IUCN conservation status — Critically endangered (CR): B2a(ii,iii). AOO: 8 km^2. This species is only known from the Rondo Forest Reserve. Although it is a reserve, a major part of the forest in the reserve has been cleared in recent years as can be seen in satellite images provided by Google Earth (assessed April 2017).

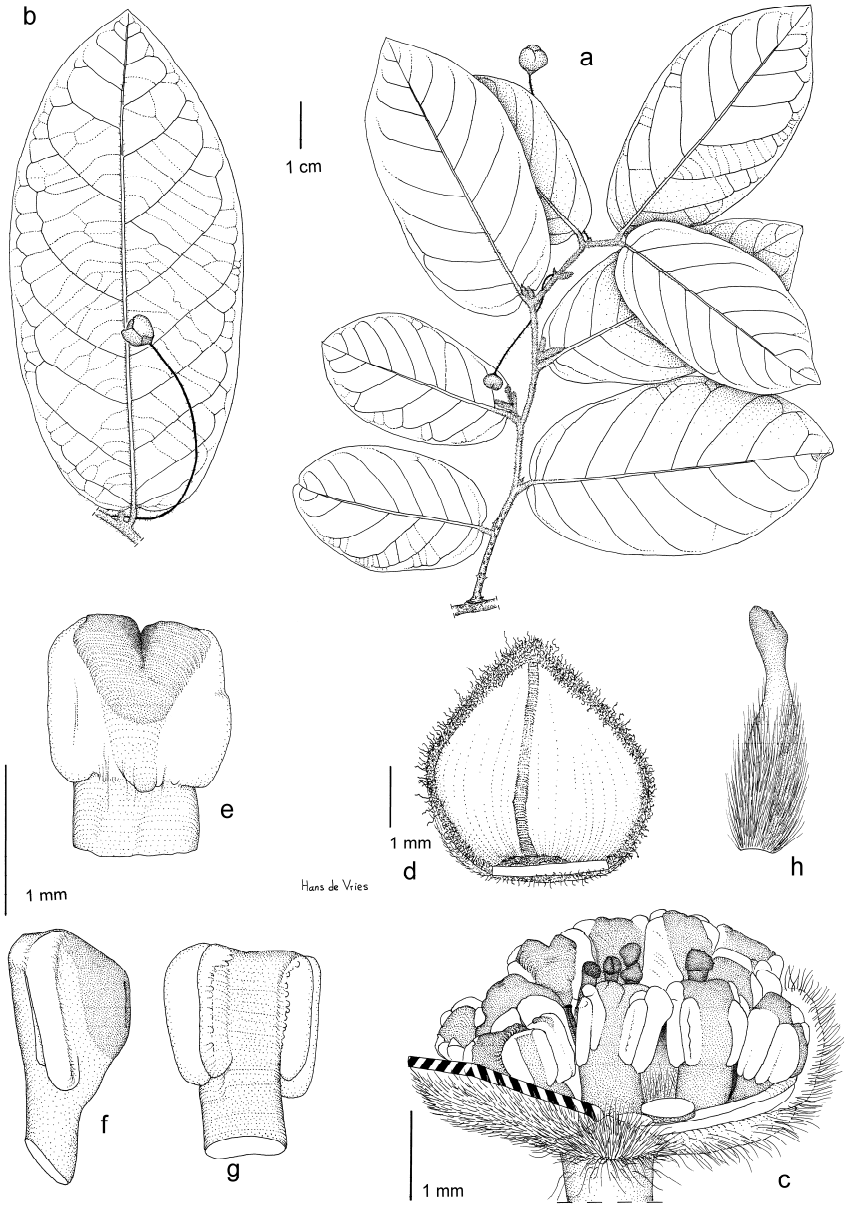
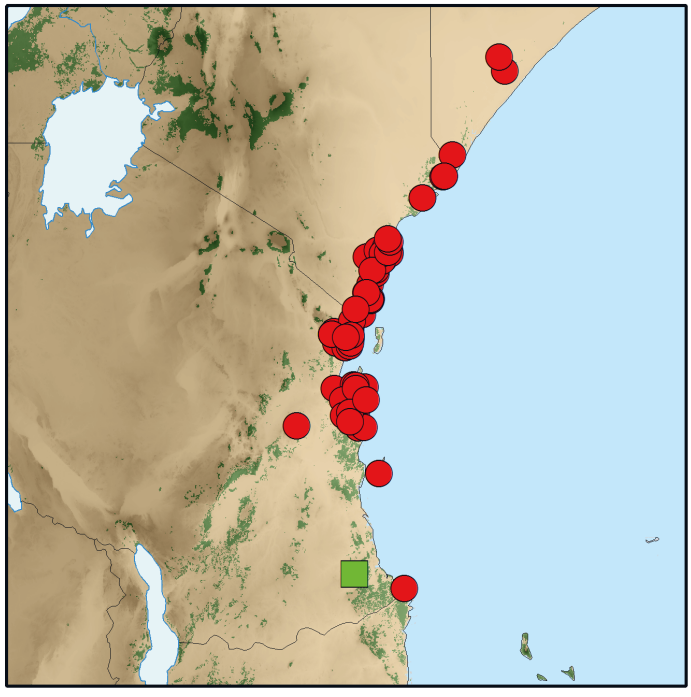


Fig. 13 *Monanthotaxis filipes* P.H.Hoekstra. a. Habit showing flowering branch; b. leaf with flower; c. flower with petals removed; d. outer petal, inside view; e. stamen, inside view; f. stamen, side view; g. stamen, outside view; h. carpel (a–h: *Bidgood 1402*). Drawing by Hans de Vries.

Notes — *Monanthotaxis filipes* is easily recognisable by the long and filiform pedicels and a dense indument of appressed to ascending, yellow hairs on the young branches and lower side of the leaves. In East Africa *M. trichantha* has a similar yellow indument, but that species has extra-axillary inflorescences, shorter pedicels and the flowers are very different. Filiform pedicels also occur in some *Monanthotaxis* species on Madagascar (e.g., *M. heterantha*). The phylogenetic analyses place *M. filipes* as sister to the Malagasy species.



Map 20 Distribution of *Monanthotaxis filipes* (green square) and *M. fornicata* (red circles).

30. *Monanthotaxis foliosa* (Engl. & Diels) Verdc. — Fig. 6j–m; Plate 3d; Map 21

Monanthotaxis foliosa (Engl. & Diels) Verdc. (1971b) 21. — *Popowia foliosa* Engl. & Diels (1901) 52. — *Enneastemon foliosus* (Engl. & Diels) Robyns & Ghesq. (1933) 165. — Lectotype (designated here): *G.A. Zenker 2050* (lectotype B (B100153030); isolecto: B100153031, BM001125038, BR0000008820280, E00624353, G00014883, G00014884, HBG-502537, K000198987, L.1754335, M-0205486, MO, P00362595, P00362598, S, WU0025871), Cameroon, South Province, Bipinde, 1899.

Enneastemon ferrugineus Robyns & Ghesq. (1934) 90. — *Monanthotaxis foliosa* (Engl. & Diels) Verdc. var. *ferruginea* (Robyns & Ghesq.) Verdc. (1971b) 21, syn. nov. —*Enneastemon foliosus* (Engl. & Diels) Robyns & Ghesq. var. *ferrugineus* (Robyns & Ghesq.) Le Thomas

(1969) 246. — Type: *G.M.P.C. Le Testu 2108* (holo consisting of 3 sheets: P00362594, P00362596, P00362597; iso: BM000547358, BR0000008820235, BR0000008820242, E00624354, LISC000377, US), Gabon, Nyanga, Tchibanga area, Roungala, 9 Sep. 1915.

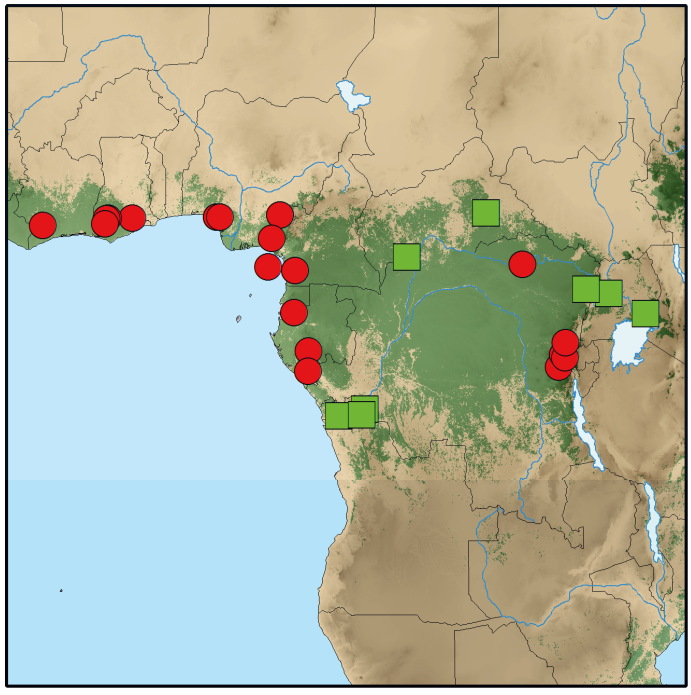
Shrub, scandent shrub or liana, to 3.5 m long; young branches reddish brown to yellowish brown, densely covered with erect, reddish brown hairs c. 0.2 mm long, or ascending, yellow-brown to reddish brown hairs 0.05–0.1 mm long, becoming glabrous; old branches dark brown to blackish brown. *Leaves*: petiole 5–7 mm long, 1.2–1.8 mm diam, slightly grooved, indument as on branches; lamina oblong-elliptic to elliptic, 8.8–20.8 by 5.2–8.9 cm, 1.5–2.6 times longer than wide, subcoriaceous, not punctate, mid green and glossy above, glaucous below, above sparsely covered with appressed, whitish hairs 0.2–0.3 mm long, becoming glabrous, primary vein more densely covered with ascending, reddish brown hairs c. 0.2 mm long, below sparsely to densely covered with appressed, yellow-brown hairs 0.1–0.2 mm long, base rounded to subcordate or sometimes slightly cuneate, with thickened black margins, apex obtuse to acute, secondary veins 7–10 per side, straight, but halfway slightly curving, tertiary venation percurrent, distinctly raised above. *Inflorescences* axillary or sometimes supra-axillary, c. 1 mm above axil, sometimes composed of solitary flowers, but normally 3–16-flowered rhipidia; sympodial rachis normally present, 3–17 mm long, densely covered with erect, reddish brown hairs 0.1–0.2 mm long; pedicels 5.5–11 mm long, 0.4–0.5 mm diam, fruiting pedicels 7–15 mm long, 0.7–0.8 mm diam, indument as on rachis; lower bract ovate, 0.5–0.7 by 0.6–0.8 mm, indument as on rachis; upper bract in the lower half of the pedicel or halfway, ovate, 0.4–0.5 by 0.5–0.6 mm, indument as on sympodial rachis; flower buds globose. *Flowers* bisexual; sepals connate at the base, depressed ovate, 0.5–0.7 by 1.1–1.4 mm, apex obtuse to acute, densely covered with appressed, yellow-brown hairs, persistent in fruit; receptacle 1.5–1.7 mm diam, flat; petals colour in vivo unknown, 6, in two whorls, base of inner petals visible in bud, outer petals, ovate, 2.5–6.5 by 2–4.2 mm, outside densely covered with appressed, yellow-brown hairs, apical part of inside covered with short white-yellow hairs; inner petals rhombic, 2.4–6.1 by 1.4–3.4 mm, outside and apical part of the inside densely covered with hairs; stamens 8 or 9, in one whorl, free, clavate, 0.8–1.3 mm long, filaments 0.4–0.8 mm long, thecae extrorse, connective truncate, prolonged inward and outward, not hiding thecae, glabrous, but hairy on the introrse side, staminodes absent; carpels 6 (or 7), subcylindric to narrowly ellipsoid, 1.3–1.6 by 0.4–0.5 mm, densely hairy, ovules 2 or 3, lateral, stigma elongate, 0.3–0.5 mm long, glabrous. *Monocarps* 1–3, colour in vivo unknown, moniliform to subcylindric, 16–24 by 9–11 mm, smooth, densely covered with appressed, yellow hairs, becoming glabrous, apex apiculate, apiculum 0.7–1.2 mm long, stipes c. 4 mm long. *Seeds* 1–3, ellipsoid, c. 11 by 8 mm, ochre-brown, apex rounded, raphe visible.

Distribution — Ivory Coast, Ghana, Nigeria, Cameroon, Equatorial Guinea, Gabon, Democratic Republic of the Congo.

Habitat & Ecology — In primary rain forest, secondary forest and gallery forest. Altitude: 50–1700 m. Flowering: August to May; fruiting: January, March, April, November.

Vernacular names — Democratic Republic of the Congo: Amapupu (*T.B. Hart 1143*). Hunanga (Kindega name) (*R. Gutzwiller1812*).

Preliminary IUCN conservation status —Endangered (EN): B2ab(iii). EOO: 2,908,934 km^2, AOO: 80 km^2. Although this species has a wide extent of occurrence and is known from 13 locations, the locations are severely fragmented and the species has only been collected twice in the last 20 years and it has not been collected in Ghana and Democratic Republic of the Congo for more than 50 years.



Map 21 Distribution of *Monanthotaxis foliosa* (red circles) and *M. gilletii* (green squares).

Notes — 1. *Monanthotaxis foliosa* belongs to the *M. schweinfurthii* complex, which has axillary inflorescences, globose flower buds in which the 3 outer petals overlap the 3 inner petals at the top and with 9 stamens per flower (Fig. 1, clade B). It differs from the other species of this complex in the strongly raised and reticulate venation on the upper side of the leaves, and by having 2 or 3 ovules per carpel (versus 4–6 ovules) and smooth monocarps, not tuberculate-rugulose.

2. The indument of *M. foliosa* is highly variable: specimens from central and south Gabon have the densest indument and the longest hairs; these specimens previously belonged to *M.*

foliosa var. *ferruginea*. However, in Cameroon all different indument types occur with the densest indument found in *D.W. Thomas 4721* and the most glabrous specimen, *G.A. Zenker 2050*. More specimens from Gabon are needed to assess if there is a real gradient in indument type.

3. In the introduction of the protologue of *Enneastemon ferrugineus* it is stated that they received new material at the herbarium in Paris, thus the holotype is from P and as the 3 sheets are linked no lectotype has to be designated.

31. *Monanthotaxis fornicata* (Baill.) Verdc. — Fig. 5q–v; Map 20

Monanthotaxis fornicata (Baill.) Verdc. (1971b) 21. — *Popowia fornicata* Baill. (1868) 318. — *Enneastemon fornicatus* (Baill.) Exell (1939) 320. — Lectotype (designated here): *L.H. Boivin s.n.* (lectotype: P (P01954770); isolecto: P01954769), Tanzania, Zanzibar, Mombaza, 1848.

Clathrospermum biovulatum S. Moore in Baker & S.Moore (1877) 65. — Lectotype (designated by Verdcourt 1971a: 97): *J.M. Hildebrandt 1294* (lecto: BM000547359; iso: B, CORD00002675, K, L 0188035, 00008567), Tanzania, Zanzibar, Bagamofs, May 1874.

Shrub or scandent shrub, 1.5–5 m tall; young branches reddish brown, greenish brown or olive green-brown, sparsely covered with appressed to ascending, yellowish hairs 0.1–0.3 mm long, becoming glabrous; old branches dark brown to purple brown. *Leaves*: petiole 2–6 mm long, 0.9–1.5 mm diam, grooved, indument slightly more dense than on branches; lamina oblong-elliptic, 4.2–10.7 by 2.3–6.5 cm, 1.5–2.2 times longer than wide, chartaceous, not punctate, glaucous or pale green below, above glabrous, below sparsely covered with appressed, yellowish hairs c. 0.2 mm long, primary vein with more persistent hairs, base rounded to subcordate, with thickened margin, apex obtuse to acute, primary vein often strongly contrasting in colour with the petiole, secondary veins 6–9 per side, straight to curving upwards, tertiary venation below percurrent, above with slightly raised reticulation (visible with hand lens). *Inflorescences* leaf-opposed, composed of solitary flowers to 5-flowered fascicles; sympodial rachis 0–1 mm long densely covered with appressed hairs; pedicels 4–12 mm long, 0.4–0.5 mm diam, fruiting pedicels 10–20 mm long, 0.5–0.9 mm diam, sparsely covered with appressed, yellowish, short hairs to glabous; lower bracts ovate, c. 0.8 by 0.8 mm, densely covered with hairs, or absent; upper bract halfway up the pedicel, ovate, 0.8–1.2 by 0.4–0.6 mm, densely covered with appressed, yellow hairs; flower buds ellipsoid. *Flowers* bisexual; sepals connate at the base, triangular to broadly triangular, 0.5–0.8 by 0.5–1.2 mm, apex acute, covered with with appressed, yellow hairs, persistent in fruit; receptacle c. 1.5 mm diam, flat; petals creamy yellow to fleshy yellow with white at the base of inside, 6, in one whorl, outer petals overtopping inner petals in bud, outer petals elliptic, 3.5–4.2(–6.7) by 1.5–1.6(–2.2) mm, outside and apex of the inside covered with appressed yellowish, short hairs, base of inside glabrous, inner petals elliptic, 2.8–3.8(–5.7) by 1.1–1.3(–2) mm, indument as outer petals; stamens 6, in one whorl, free, obconical, 0.7–1.1 mm long, filaments 0.2–0.3 mm

long, thecae extrorse to latrorse, connective truncate, triangular prolongation pointing outward, not hiding thecae, glabrous and slightly verrucose, staminodes absent; carpels 7 (or 8), subcylindric, 1.3–1.4 by 0.2–0.3 mm, glabrous, ovules 2 (or 3), lateral, stigma elongate, c. 0.5 mm long, glabrous, verrucose, slightly 2-lobed. *Monocarps* 1–7, yellow-orange or red, narrowly ellipsoid, 12.5–24 by 4–5.5 mm, glabrous, apex rounded to apiculate, apiculum 0.1–1 mm long, stipes 1.5–5 mm long. *Seeds* 1–2(–3), ellipsoid, 9–10 by 4.5–5 mm, tawny brown, ends apiculate, raphe not visible.

Distribution — Somalia, Kenya, Tanzania.

Habitat & Ecology — In dry lowland forest, wooded grassland, coastal forest, closed *Afzelia* forest, gallery forest, secondary forest; on white sandy soil, red sandy soil, sandstone and on coral rock. Altitude: 0–400 m. Flowering all year round; fruiting: January, March, May to November.

Vernacular names — Kenya: Nguku (Swa name) (*H.M .Gardner 1426*), Mudzala (Friana name) (*R.M. Graham 1979*), Mgweni (Digo name) (*S.A. Robertson 4252*), Mrori (Giriama name) (*W.P. Langridge 42)*, Mbalushi (*P.W. Mulwa 100*), Mwala ga Kuku *(R. Mapperley 31*). Somalia: Osmandow *(M. Maunders* 67), Cismaan-Dooy (*C.F. Hemming 114*). Tanzania: Mkalia (Nyamio name) (*P.R.O. Bally 12105*), Msofu-simba (Kidoe name) (*Y.S. Abeid* 225).

Preliminary IUCN conservation status —Least concern (LC). EOO: 270,531 km^2, AOO: 252 km^2. This species is known from many locations and protected areas near the coasts of Tanzania, Kenya and south Somalia. It is quite common in some locations.

Uses — It has been reported to be used against snake bites around the Ngumburunu Forest Reserve in Tanzania (Kimaro & Lulandala 2013) and *M. fornicata* is domesticated by Mijikenda farmers in Kenya for their medicinal value (Wekesa et al. 2015).

Notes — 1. *Monanthotaxis fornicata* can be recognized by the oblong-elliptic leaves and by having only a few hairs on the leaves and young branches. It is also the only species of *Monanthotaxis* which has extra-axillary inflorescences in combination with ellipsoid flower buds and the 3 outer petals overlapping the 3 inner petals at the top.

2. *Frontier Tanzania Coastal Forest 2205* has hairy fruits, but for the rest fits *M. fornicata*.

32. *Monanthotaxis gilletii* (De Wild.) Verdc. — Map 21

Monanthotaxis gilletii (De Wild.) Verdc. (1971b) 26. — *Popowia gilletii* De Wild. (1905a) 241. — Type: *J. Gillet 3592* (holo: BR0000008805294), Democratic Republic of the Congo, Bas-Congo, Madimba, environ de Kisantu, 1903.

Scandent shrub or liana, to 4 m long; young branches covered with erect, brown hairs 0.5–1 mm long; old branches blackish to dark reddish brown. *Leaves*: petiole 3–5.5 mm long, 0.8–1.2 mm diam, slightly grooved, indument slightly denser than on branches; lamina oblong-elliptic to elliptic-ovate or narrowly so, 6.2–13.5 by 2.7–4.9 cm, 1.7–2.9 times longer than wide, membranous to subcoriaceous, not punctate, glaucous below, above sparsely covered

with erect hairs on primary vein, soon becoming glabrous, below sparsely covered with erect, brown hairs 0.5–1 mm long, more densely so on the primary vein, base rounded to subcordate, with thickened black margin, apex obtuse to sometimes slightly acute, secondary veins 6–13 per side, curving upwards, tertiary venation intermediate between percurrent and reticulate, slightly raised above. *Inflorescences* terminal or extra-axillary, composed of solitary flowers or sometimes 2-flowered rhipidia; sympodial rachis 5–11 mm long, covered with erect, yellowish brown hairs; pedicels 10–25 mm long, c. 0.5 mm diam, fruiting pedicels 25–35 mm long, 0.5–1.2 mm diam, covered with erect hairs c. 0.5 mm long; lower bract absent; upper bract large and leafy, broadly ovate, 7–17 by 6–16 mm, base semi-amplexicaul, sparsely covered with erect hairs; flower buds globose. *Flowers* bisexual; sepals connate, at the base almost forming a cup-like disc, depressed ovate, c. 1 by 3 mm, apex obtuse, densely covered with appressed to ascending hairs; receptacle 1.5–2.5 mm diam, flat, covered with hairs between carpels; petals yellowish to olive-reddish, 6, in two whorls, outer petals ovate, 5–8.1 by 3.6–4.3 mm, outside covered with ascending, yellow-brown hairs, inside densely covered with yellow, short hairs, glabrous at the base, inner petals rhombic, narrowed at the base, not covering stamens entirely in bud, 4.5–6 by 3.2–3.4 mm, outside densely covered with yellow, short hairs, inside glabrous at the base; stamens 15, in one or two whorls, free, linear-obconical, 1.6–1.9 mm long, filaments 0.3–0.6 mm long, thecae latrorse to introrse, connective truncate, subquadrate, pentagonal to squarish seen from above, prolonged outwards, staminodes absent; carpels 21–28, narrowly subcylindric-ellipsoid, c. 2.1 by 0.2–0.3 mm, glabrous, ovules 6, lateral, stigma elongate, c. 0.9 mm long, glabrous. *Monocarps* up to 12, yellow to red when ripe, narrowly ellipsoid to moniliform, 16–55 by 6–9 mm, glabrous or with few hairs at the base, apex apiculate, apiculum to 3 mm long, stipes 5–10 mm long. *Seeds* 1–4, ellipsoid, 7–9 by 5.5–6 mm, tawny, ends rounded, raphe not visible.

Distribution — Central African Republic, Democratic Republic of the Congo, Uganda.

Habitat & Ecology — In rainforest. Altitude: 1130–1243 m. Flower: February, March, June, December; fruiting: January, May, October.

Preliminary IUCN conservation status —Endangered (EN): B2ab(iii). EOO: 1,460,344 km^2, AOO: 32 km^2. This species is known from 12 collections from 7 locations. The distribution is highly fragmented and it has only been collected once in the last 50 years.

Notes — 1. *Monanthotaxis gilletii* is easily recognizable by the leafy upper bract and the erect, reddish brown hairs of young stems, pedicels and lower leafside.

2. Specimens from Bas-Congo (including the type) have much smaller seeds than specimens of the Central African Republic, Uganda and the east of the Democratic Republic of the Congo.

33. *Monanthotaxis glabra* P.H.Hoekstra, sp. nov. — Fig. 14; Plate 3e; Map 22

Monanthotaxis glabra is the only species of *Monanthotaxis* with both the outer and inner petals entirely glabrous. Additionally, it can be distinguished by the almost entirely glabrous young branches, the many stamens in three or four whorls and 11–20 carpels with 6 to 7

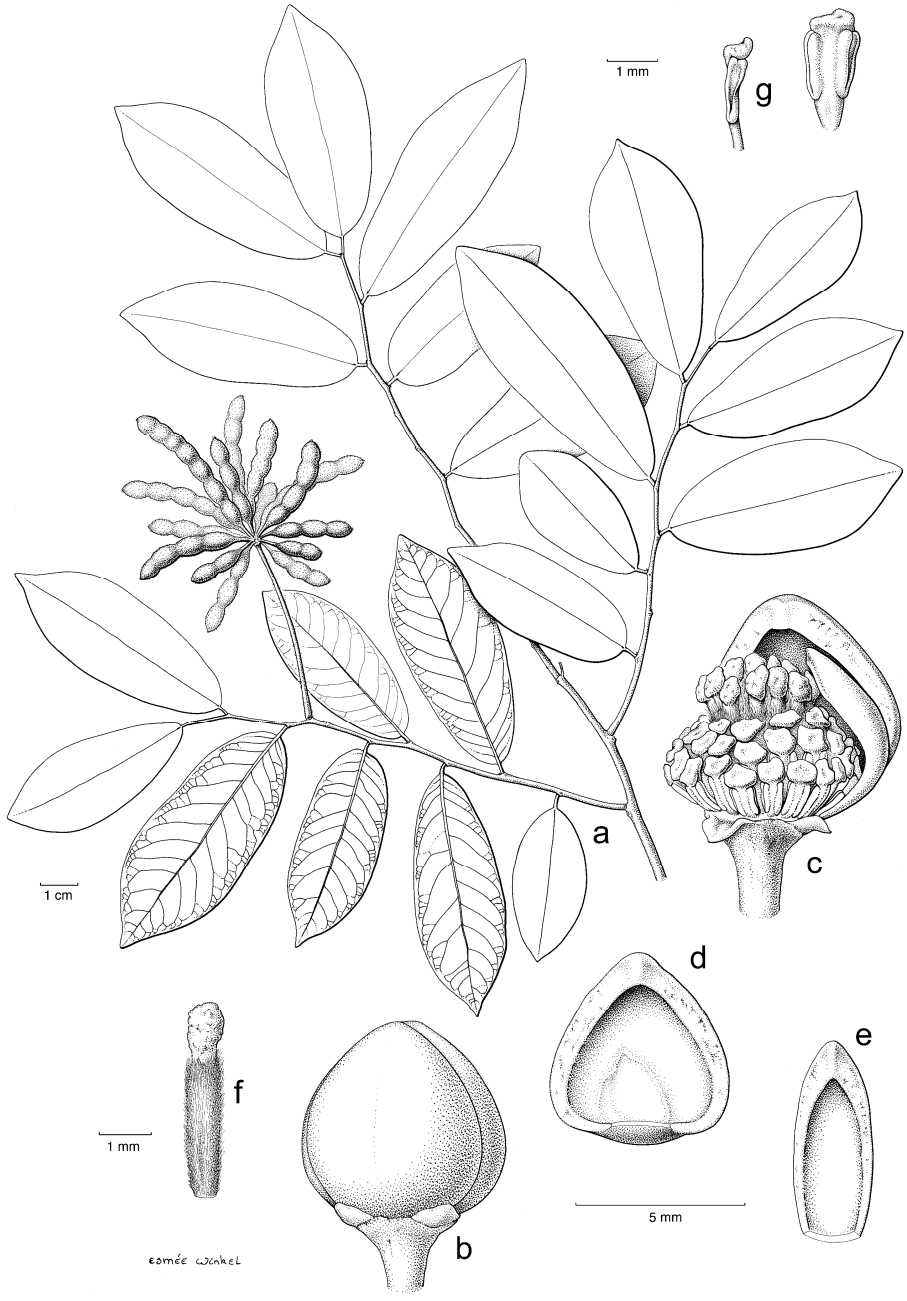


Fig. 14 *Monanthotaxis glabra* P.H.Hoekstra: a. Fruiting branch; b. flower bud; c. flower bud with two outer and two inner petals removed; d. outer petal, inside view; e. inner petal, inside view; f. carpel; g. stamen, side and front view (a: *Versteegh 536*; b–g: *Demange 2830*). Drawing by E. Winkel.

ovules per carpel. — Type: *R. Demange 2830* (holotype: P (P01982488); iso: P01982489), Mali, Sikasso, Kléla, galerie du Lotio, 14 July 1965. Paratypes: *L. Aké Assi et al. 4049* (FR), Burkina Faso, Comoé, Banfora, Ouangolodou, à 10 km de Ouangolodougou, en allant vers Folonzo, 371 m, 20 Oct. 2007; *L. Aké Assi 4933* (G), Ivory Coast, Bouna, Ouango-Fitini, au bord de la Comoe, 13 July 1958; *J. Bokdam 2865* (BR, K, WAG), Ivory Coast, Bouna, 47 km S of Bavé, 20 June 1968; *J.-P. Essou & Agbani 1516* (BENIN not seen, MO, WAG), Benin, Mono, Lokossa, Aguidahoué, 19 Feb. 1999; *J.B. Hall & Swaine GC 46214* (GC not seen, K), Ghana, Brong-Ahafo Region, Bui by Black Volta, 24 July 1976; *C.C.H. Jongkind et al. 7965* (BR, G, K, MA, MO, P, WAG), Guinea, Nzérékoré, Nimba Mountains, Gba valley, 625 m, 14 July 2007; *A. Le Thomas & Deroin 11* (P), Ivory Coast, Grands-Ponts, N'Douci, station de la Lamto, 6 July 1985; *C. Versteegh & den Outer 536* (WAG), Ivory Coast, Korhogo, 50 km SE of Korhogo, at river Bandama-Blanc, 17 July 1969.

Shrub or liana, to 4 m long and 4 cm diam; young branches reddish brown, glabrous or sparsely covered with few whitish hairs c. 0.2 mm long; old branches reddish brown. *Leaves*: petiole 2.5–5 mm long, 0.7–1 mm diam, grooved, glabrous or sparsely covered with appressed hairs; lamina oblong-elliptic to obovate or narrowly so, 2.9–10.5 by 1.4–3.9 cm, 1.7–3.3 times longer than wide, chartaceous, not punctate, glabrous above, below sparsely covered with appressed, reddish brown hairs c. 0.2 mm long, becoming glabrous, base rounded or slightly subcordate or cuneate, glands hardly visible, apex rounded to acute, secondary veins 7–10 per side, curving upwards, tertiary venation hardly visible, slightly reticulate to percurrent. *Inflorescences* extra-axillary or terminal, composed of solitary flowers; sympodial rachis absent; pedicels 28–52 mm long, 0.3–0.5 mm diam, fruiting pedicels 0.6-1.1 mm diam, glabrous or sparsely covered with short hairs; lower bract absent; upper bract halfway up the pedicel or absent, lanceolate, c. 0.5 by 0.2 mm or just a tuft of yellowish hairs; flower buds globose. *Flowers* bisexual; sepals free, shallowly triangular, c. 0.7 by 1.6 mm, apex acute, glabrous; receptacle c. 2.3 mm diam, slightly convex; petals colour in vivo unknown, 6, in two whorls, outer petals broadly ovate, c. 8.6 by 8.5 mm, glabrous, inner petals elliptic, 6.5–7.5 by 3.3–3.5 mm, glabrous; stamens 50–80, in three or four whorls, free, obovoid-obconical, 2–2.2 mm long, filaments 0.4–0.7 mm long, thecae latrorse in young buds to extrorse, connective hiding thecae, papillate, staminodes absent; carpels 11–20, subcylindric, 3.4–3.5 by 0.6–0.7 mm, densely hairy, ovules 6 or 7, lateral, stigma elongate, 0.7–0.8 mm long, glabrous. *Monocarps* 6–20, red-brown, narrowly ellipsoid, 13–46 by 4–5 mm, densely to sparsely covered with appressed, yellowish brown hairs, apex rounded or apiculate, apiculum 0–2 mm long, stipes 4–5 mm long, slightly grooved. *Seeds* 1–7, ellipsoid, 6–7 by c. 4 mm, tawny brown, ends flattened, raphe not visible.

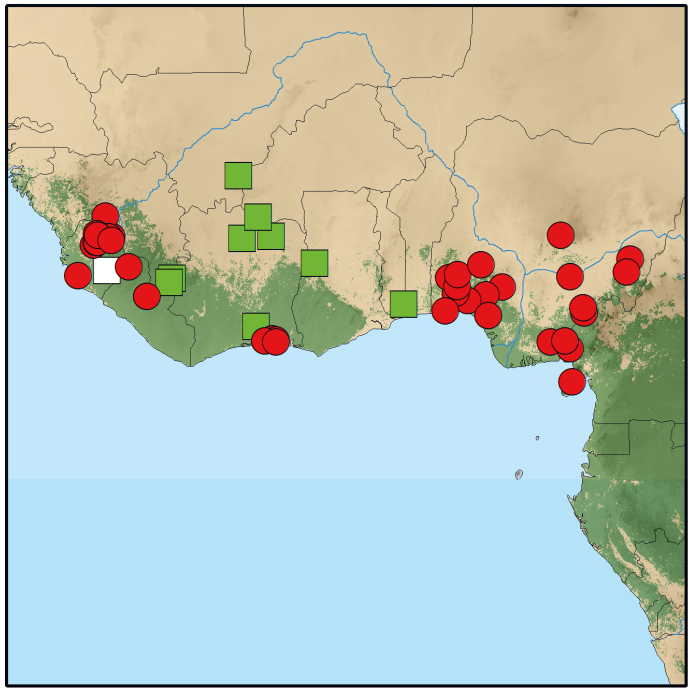
Distribution — Guinea, Liberia, Ivory Coast, Mali, Burkina Faso, Ghana, Benin.

Habitat & Ecology — In gallery forest and dense humid semi-deciduous forest. Altitude: 371–625 m. Flowering: June, July; fruiting: May to July.

Preliminary IUCN conservation status —Vulnerable (VU): B2ab(iii). EOO: 353,482 km^2, AOO: 36 km^2. *Monanthotaxis glabra* is known from 9 collections and 8 locations of which 4 in protected areas. The other areas are under severe threat of deforestation and habitat degradation.

Ethymology — This species is named *M. glabra* as it is the only species of *Monanthotaxis* with glabrous petals and sepals.

Notes — *Monanthotaxis glabra* differs from all species of *Monanthotaxis* by the glabrous petals and sepals. The specimens had originally been identified as *M. parvifolia*, however, that species has a subcordate leaf base, young branches densely covered with short hairs and very different flowers with stamens only in two whorls, hairy sepals and petals and glabrous carpels and fruits.



Map 22 Distribution of *Monanthotaxis glabra* (green squares, white square is uncertain det) and *M. gracilis* (red circles).

34. *Monanthotaxis glaucifolia* (Hutch. & Dalziel) P.H.Hoekstra — Map 16

Monanthotaxis glaucifolia (Hutch. & Dalziel) P.H.Hoekstra in Guo et al. (2017) 14. — *Oxymitra glaucifolia* Hutch. & Dalziel (1927b) 153. — *Richella glaucifolia* (Hutch. & Dalziel) R.E.Fr.

(1959) 139. — *Friesodielsia glaucifolia* (Hutch. & Dalziel) Steenis (1964) 359. — Type: *P.A. Talbot 403* (holo: BM000843988), Nigeria, Cross River State, Oban, 1911.

Liana; young branches brown, densely covered with appressed to ascending, pale brown hairs 0.2–0.5 mm long, becoming glabrous; old branches dark brownish black. *Leaves*: petiole 4–7 mm long, 1.7–2.8 mm diam, terete, indument as on branches; lamina narrowly oblong-elliptic to oblanceolate, 11–25.8 by 3.7–8.6 cm, 2.6–3.8 times longer than wide, membranous to subcoriaceous, not punctate, glaucous to whitish below with blackish green venation, above glabrous, below glabrous or sometimes sparsely covered with pale-brown hairs c. 0.4 mm long, primary vein covered with pale brown hairs 0.1–0.3 mm long, base subcordate to narrowly subcordate, glands hardly visible, apex acuminate, acumen 5–25 mm long, primary vein reddish brown below in sicco, secondary veins 10–13 per side, first straight but slightly curving upwards at end near margin, tertiary venation percurrent, flat above. *Inflorescences* extra-axillary, leaf-opposed or sometimes terminal, composed of solitary flowers; sympodial rachis c. 1 mm long, densely covered with erect, yellow-brown hairs 0.2–0.3 mm long; pedicels 5–21 mm long, c. 1.4 mm diam, fruiting pedicels to 2.1 mm diam, indument as on sympodial rachis; lower bracts ovate, c. 2.5 by 1.6 mm; upper bract placed at the base of pedicel, broadly ovate, c. 3 by 2.4 mm, indument as on rachis; flower buds globose. *Flowers* bisexual; sepals free, depressed ovate, c. 4.5 by 7 mm, apex obtuse, densely covered with appressed, yellow-brown hairs; receptacle c. 5 mm diam, torus to 3 mm high, convex; petals colour in vivo unknown, 6, in two whorls, outer petals ovate, 30–35 by 23–25 mm, outside densely covered with appressed, yellow-brown hairs, inside glabrous except for some very short scattered hairs, inner petals rhombic, c. 21 by 26 mm, leaving open space at the base, outside sparsely covered with hairs 0.1–0.2 mm long, inside glabrous; stamens >100, in five or six whorls, free, obconical, c. 1.3 mm long, filaments c. 0.5 mm long, thecae latrorse, connective truncate, rectangular seen from above, not hiding thecae, glabrous, staminodes absent; carpels 45–50, subcylindric to narrowly ellipsoid, 1.7–2 by c. 0.7 mm, densely covered with yellow hairs, ovules 2, lateral, stigma subsessile, globose, 0.1–0.2 mm diam, glabrous. *Monocarps* at least 8, colour in vivo unknown, ellipsoid, 1-seeded monocarps c. 15 by 9–10 mm, 2-seeded ones to 26 by 9–10 mm, smooth, densely covered with yellow-brown hairs 0.1–0.2 mm long, apex rounded to apiculate, stipes 3–4 mm long, slightly grooved. *Seeds* 1 or 2, ellipsoid, c. 10 by 8 mm, reddish brown to tawny-brown, raphe visible.

Distribution — Nigeria (Cross River State), Cameroon (South-West Region).

Habitat & Ecology — In submontane forest. Altitude: c. 950 m. Flowering: December.

Preliminary IUCN conservation status —Endangered (EN): B2ab(iii). AOO: 8 km^2. *Monanthotaxis glaucifolia* is known from 2 locations, of which the one near the Oban-Group Forest Reserve has not been collected in more than 100 years.

Notes — *Monanthotaxis glaucifolia* closely resembles *M. dielsiana* and *M. enghiana* based on the flowers and leaf shape. It differs from *M. dielsiana* in having more than 100 stamens and by having pale brown hairs on the young branches, while *M. dielsiana* has orange-brown

hairs and c. 65 stamens. *Monanthotaxis enghiana* differs from *M. glaucifolia* in having longer and erect hairs on the branches and leaves, *M. enghiana* generally has 2–5 flowers per inflorescence and *M. glaucifolia* only one. Some specimens of *M. enghiana*, however, have less and more ascending instead of erect hairs, especially specimens at higher altitudes. More collections from the provinces bordering Cameroon and Nigeria are needed to verify if *M. glaucifolia* is merely a high-altitude variant of *M. enghiana* or if it is indeed a valid species. For now we refrain from synonymizing *M. glaucifolia* with *M. enghiana*.

35. *Monanthotaxis glomerulata* (Le Thomas) Verdc. — Fig. 9 o–s; Map 23

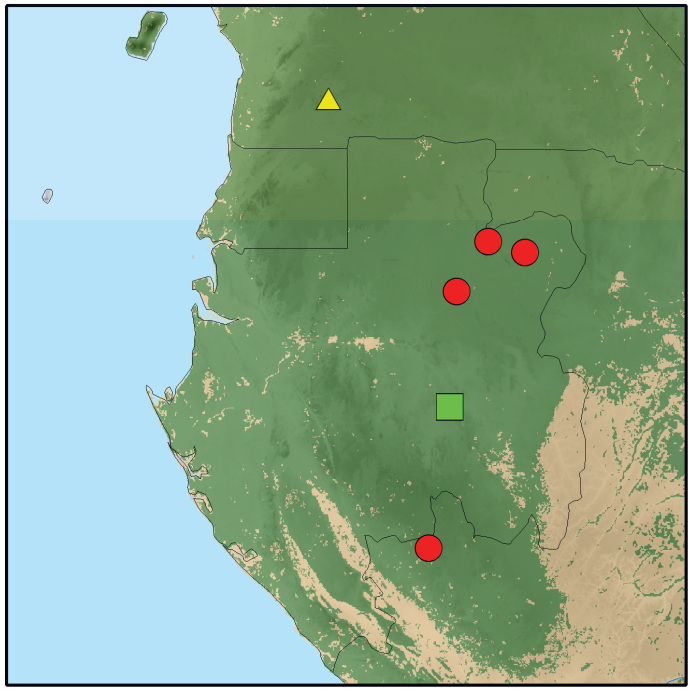
Monanthotaxis glomerulata (Le Thomas) Verdc. (1971b) 31. — *Popowia glomerulata* Le Thomas (1963) 288. — Type: *G.M.P.C. Le Testu 8700* (holo consisting of 2 sheets: P00362634, P00362635; iso: BM000553849, BR0000008823755, BR0000008823762, BR0000008823854), Gabon, Ogooué-Lolo, region de Lastoursville, Lastoursville, 13 Mar. 1931.

Liana; young branches blackish brown, densely covered with appressed, reddish brown hairs 0.1–0.2 mm long, becoming glabrous; old branches blackish brown. *Leaves*: petiole 5–6.5 mm long, 1.1–1.9 mm diam, terete, indument as on branches; lamina obovate to oblanceolate, 9.6–24.1 by 4.3–8.1 cm, 2.2–3 times longer than wide, chartaceous, not punctate, glabrous above, primary vein sparsely covered with ascending yellow-brown hairs 0.2–0.3 mm long, below sparsely covered with appressed, yellowish hairs 0.1–0.2 mm long, base cuneate to rounded, with thickened black margin, apex acute to slightly acuminate, acumen to 5 mm long, secondary veins 12–17 per side, slightly curving, tertiary venation percurrent. ♂ *Inflorescences* unknown. ♀ *Inflorescences* cauliflorous, consisting of glomerule-like rhipidia; sympodial rachis to 5 mm long, densely covered with appressed, reddish brown hairs; flowering pedicels 5–10 mm long, 1.1–1.5 mm diam, densely covered with appressed, reddish brown hairs; lower bracts ovate, c. 1.4 by 0.7 mm, indument as on sympodial rachis; upper bract in lower half of the pedicel, depressed ovate, 1–1.2 by 1.3–1.7 mm; ♀ flowers; sepals free to slightly connate, broadly to depressed ovate, 1.7–2 by 1.8–2.5 mm, apex acute, densely covered with hairs; receptacle c. 1.5 mm diam, convex; petals colour in vivo unknown, 6, in two whorls, outer petals depressed ovate, 4–6 by 5.5–7.5 mm, outside and inside densely covered with yellow-brown hairs; inner petals elliptic, 1.5–2 by 0.5–1 mm, indument as on outer petals; staminodes absent; carpels 80–95, subcylindric, 1.7–1.9 by 0.4–0.5 mm, densely hairy, ovules 6 or 7, lateral, stigma elongate, 0.3–0.4 mm long, glabrous. *Monocarps* and *seeds* not seen.

Distribution — Gabon (Ogooué-Lolo).
Habitat & Ecology — Flowering: March.

Preliminary IUCN conservation status —Critically endangered (CR): B2ab(iii). AOO: 4 km^2. This species is only known from the type collection, which was collected more than 80 years ago and is outside a protected area. This species is possibly already extinct.

Notes — *Monanthotaxis glomerulata* can be distinguished from other cauliflorous *Monanthotaxis* species by the glomerule-like inflorescences. *Monanthotaxis bidaultii* has few-flowered glomerule-like inflorescences, but differs in having c. 50 carpels, with 2–4 ovules and *M. bidaultii* has a denser indument of ascending to erect hairs on the lower leafside.



Map 23 Distribution of *Monanthotaxis glomerulata* (green square), *M. hexamera* (yellow triangle) and *M. latistamina* (red circles).

36. *Monanthotaxis gracilis* (Hook.f.) P.H.Hoekstra — Fig. 15a–g; Map 22

Monanthotaxis gracilis (Hook.f.) P.H.Hoekstra in Guo et al. (2017) 14. — *Uvaria gracilis* Hook.f. in Hook.f. & Benth. (1849) 210. — *Oxymitra gracilis* (Hook.f.) Sprague & Hutch. (1916) 154. — *Richella gracilis* (Hook.f.) R.E.Fr. (1959) 139. — *Friesodielsia gracilis* (Hook.f.) Steenis (1964) 359. —Type: *G. Don s.n.* (holo: BM000547066), Sierra Leone.

Oxymitra platypetala Benth. in Benh. & Hook.f. (1862) 472. — *Cleistopholis platypetala* (Benth.) Engl. & Diels (1901) 34. — Type: *G. Mann 857* (holo: K00198952), Sierra Leone, Southern Province, Bagroo river, Apr. 1861.

Unona millenii Engl. & Diels (1901) 40. — Type: *H. Millen 149* (holo: K not seen), Nigeria, Lagos, Mar. 1896.

Oxymitra rosea Sprague & Hutch. (1916) 154. — *Richella rosea* (Sprague & Hutch.) R.E.Fr. (1959) 139. — *Friesodielsia rosea* (Sprague & Hutch.) Steenis (1964) 361. — Type: *P.A. Talbot 199* (holo: BM000547067), Nigeria, Cross River State, Oban, 1911.

Scandent shrub or liana, 4–20 m long, 2–10 cm diam; young branches pale brown to brown, covered with appressed to ascending hairs c. 0.1 mm long, becoming glabrous; old branches pale grey. *Leaves*: petiole 2–4 mm long, 0.4–0.9 mm diam, grooved, indument as on branches; lamina oblanceolate, 4–16.5 by 1.4–5.7 cm, 2.4–3.3 times longer than wide, subcoriaceous, not punctate, glaucous below, above glabrous, but primary vein covered with few, yellowish, short hairs, below glabrous except for a few yellowish hairs 0.1–0.2 mm long on the primary vein, base narrowly subcordate, appearing cuneate, with thickened black margin, apex acute to acuminate, acumen to 20 mm long, secondary veins 7–9(–10) per side, curving upwards, tertiary venation slightly percurrent. *Inflorescences* extra-axillary or leaf-opposed, composed of lax (1–)2–3-flowered rhipidia; sympodial rachis 2–5 mm long, covered with appressed, yellowish, short hairs; pedicels 15–50 mm long, 0.3–0.4 mm diam, fruiting pedicels 0.3–0.8 mm diam, indument as on sympodial rachis; lower bracts lanceolate, 1–2 by 0.4–0.6 mm, densely to sparsely covered with appressed, yellowish, short hairs; upper bract in lower half of the pedicel, ovate to lanceolate, 1.5–2.5 by 0.8–1 mm, sparsely covered with appressed, yellow hairs; flower buds ovoid to deltoid. *Flowers* bisexual; sepals free, ovate, 3 (or 4), 6–6.2 by 3.8–4.5 mm, apex obtuse, sparsely covered with appressed hairs, persistent in fruit or not; receptacle c. 3 mm diam, convex; petals greenish, yellowish, olive or tinged with pink, 6, in two whorls, outer petals ovate to lanceolate, 12–30 by 7–12 mm, outside covered with appressed, yellowish hairs, becoming glabrous, apex of inside covered with glandular-like hairs, base glabrous; inner petals ovate to rhombic, 5–9 by 3–5 mm, outside covered with appressed, short hairs, inside glabrous or sparsely covered with hairs; stamens 80–125, in three to five whorls, free, linear-oblong, 0.7–1.2 mm long, filaments c. 0.1 mm long, thecae latrorse, connective truncate, circular seen from above, hiding thecae, glabrous, staminodes absent; carpels 17–24, subcylindric, 1.2–1.9 by 0.2–0.4 mm, densely hairy, ovules 2–5, lateral, stigma elongate, 0.4–0.6 mm long, hairy. *Monocarps* 10–20, red when ripe, moniliform, each part globose to ellipsoid with 1–5 seeds, 13–35 by 4–5 mm, sparsely covered with appressed hairs, densely so when young, apex apiculate, apiculum 1–2 mm long, stipes 4–8 mm long, slightly grooved. *Seeds* 1–5, ellipsoid, c. 6 by 4 mm, tawny brown, ends rounded, raphe not visible or slightly visible from base to apex on both sides.

Distribution — Guinea, Sierra Leone, Liberia, Ivory Coast, Ghana, Nigeria, Cameroon, Equatorial Guinea.



Fig. 15 a–g. *Monanthotaxis gracilis* (Hook.f.) P.H.Hoekstra: a. Flowering branch; b. sepal; c. outer petal; d. inner petal; e. stamen, side and front view; f. carpel and longitudinal section of carpel; g. fruit. — h–o. *M. obovata* (Benth.) P.H.Hoekstra: h. Flowering branch; i. sepal; j. outer petal; k. inner petal, inner and side view; l. androecium and gynoecium; m. stamen, front and side view; n. carpel and longitudinal section of carpel; o. fruits. — p–u. *M. stenosepala* (Engl. & Diels) Verdc.: p. Flowering branch; q. flower, side view; r. inner petal, inner and side view; s. stamen from behind and side view; t. gynoecium; u. longitudinal section of carpel. Modified from Engler & Diels (1901) table 15, 17 and 18.

Habitat & Ecology — In primary forest, secondary forest, swamp forest and gallery forest, on river banks and summit ridges. Altitude: 10–870 m. Flowering: January, March, April, August to November; fruiting: October to April, June, July.

Vernacular names — Sierra Leone: Mabwe (*N.W. Thomas 1461*).

Preliminary IUCN conservation status —Least concern (LC). EOO: 1,240,501 km^2, AOO: 148 km^2. This species is known from many locations and quite some reserves.

Notes — 1. *Monanthotaxis gracilis* and *M. quasilanceolata* can easily be distinguished from all other *Monanthotaxis* species by the long and slender pedicels with ovoid to deltoid flower buds and ovate to lanceolate outer petals. *Monanthotaxis gracilis* differs from *M. quasilanceolata* by having pale grey branches, very short hairs on the branches and pedicels, small lanceolate bracts, a globose instead of conical connective, more and shorter carpels, and much smaller monocarps and seeds.

2. The number of stamens differs between Upper Guinea with 110–125 stamens and Lower Guinea with 80–90 stamens. However, stamens of only 2 flowers from the west of Upper Guinea have been counted and more material in flower of especially Ghana and Ivory Coast is needed to verify if there is a gradient in the stamen number.

37. *Monanthotaxis hexamera* P.H.Hoekstra, *sp. nov.* — Fig. 16; Map 23

Monanthotaxis hexamera has the thecae on top of the stamens and a very long filament, a character shared with *M. filamentosa*. It differs from that species in having short, appressed to ascending white-yellowish hairs on the young branches, while *M. filamentosa* has long, erect, reddish brown hairs. Furthermore, *M. hexamera* has 6 stamens and 6 carpels with each 1 ovule, while *M. filamentosa* has 17–46 stamens and 9–14 carpels with each 7–9 ovules. — Type: *R.G. Letouzey 10288* (holotype: P (P01960096); iso:YA0002998), Cameroon, South Region, près Zingui, 20 km WSW d'Ebolowa, Kribi, 5 Apr. 1970.

Liana, to 3 m long; young branches reddish brown, densely covered with appressed to ascending, white-yellowish hairs 0.1–0.2 mm long, becoming glabrous; old branches blackish brown. *Leaves*: petiole 3–5 mm long, 0.8–1.1 mm diam, slightly grooved, indument as on branches; lamina narrowly oblong-elliptic, 9.5–11.5 by 3.3–4.1 cm, 2.6–3 times longer than wide, chartaceous, not punctate, glaucous below, above glabrous except primary vein densely covered with asending to erect, white-yellowish hairs 0.1–0.2 mm long and becoming glabrous, below sparsely covered with appressed, whitish hairs 0.1–0.2 mm long, base rounded to narrowly subcordate, with slightly thickened black margin, apex acute, secondary veins 11–13 per side, slightly curving, tertiary venation percurrent, hardly visible above. *Inflorescences* axillary, slightly supra-axillary or terminal, composed of solitary flowers to 4-flowered fascicle-like rhipidia; sympodial rachis 0.5–4 mm long, densely covered with ascending, white-yellowish hairs; flowering pedicels 15–24 mm long, c. 0.4 mm diam, sparsely

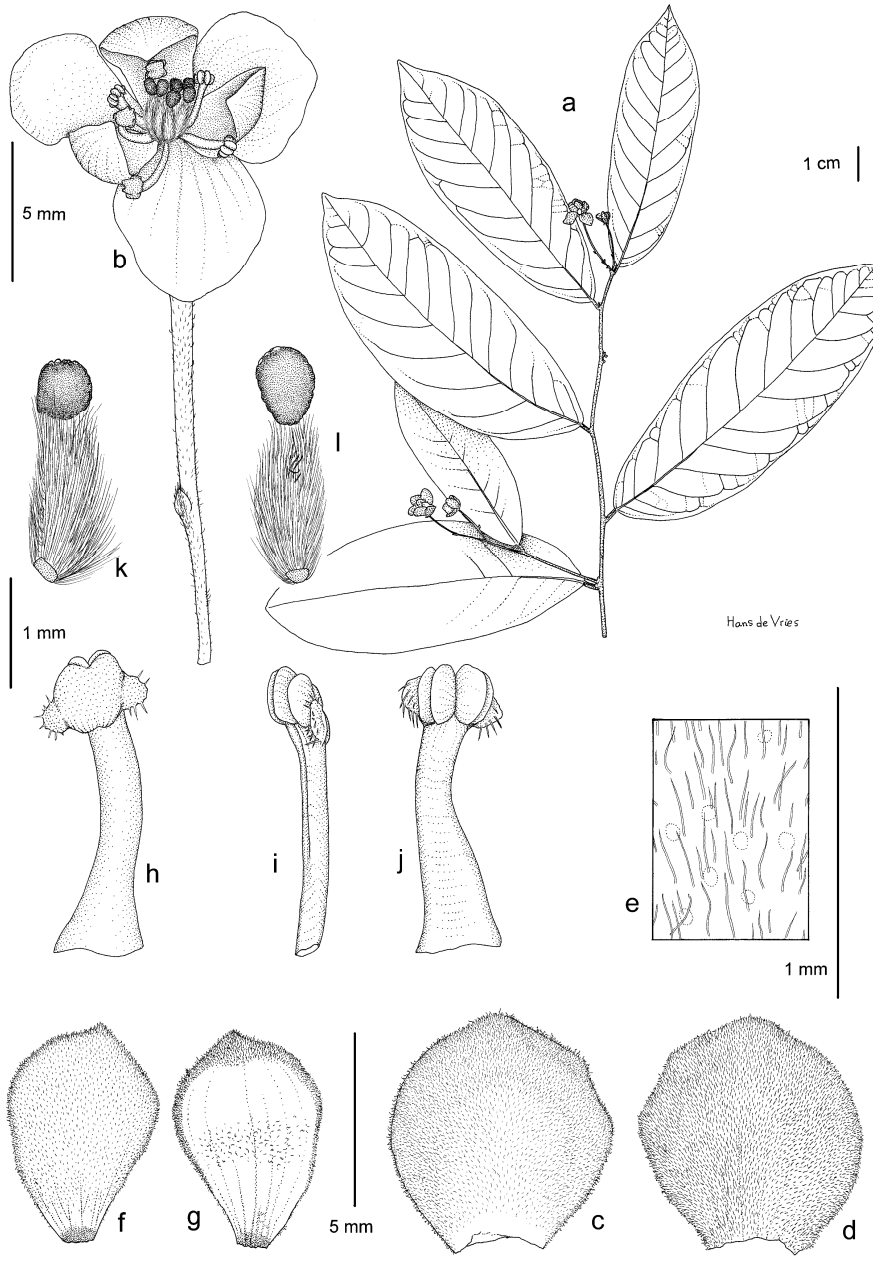


Fig. 16 *Monanthotaxis hexamera* P.H.Hoekstra: a. Flowering branch; b. flower; c. outer petal, inside view; d. outer petal, outside view; e. detail of outer petal, outside; f. inner petal, outside view; g. inner petal, inside view; h. stamen, back view; i. stamen, side view; j. stamen, front view; k. carpel, side view; l. carpel, front view (*Letouzey 10288*). Drawing by H. de Vries.

covered with appressed, white-yellowish hairs 0.1–0.2 mm long; lower bract ovate, 0.6–0.9 by 0.3–0.4 mm, indument as on pedicel; upper bract in the lower half of the pedicel, ovate, 0.5–0.9 by 0.4–0.6 mm, indument as on pedicel; flower buds globose to slightly ovoid. *Flowers* bisexual; sepals connate at the base, ovate to depressed ovate, 0.8–1 by 1–1.4 mm, apex acute, sparsely covered with yellowish white hairs; receptacle 1.5–1.8 mm diam, flat; petals white-orange, 6, in two whorls, outer petals ovate, 4.5–8 by 3.7–5.8 mm, outside sparsely covered with yellowish white hairs, inside densely so, but glabrous at the base, inner petals elliptic, c. 5.1 by 2.7–2.9 mm, outside densely covered with yellowish white hairs, base of the inside glabrous; stamens 6, in one whorl, free, linear, c. 2.2 mm long, filaments c. 1.7 mm long, thecae introrse, on top of the filament, connective irregular circular, present on the extrorse side, filament and connective sparsely hairy, staminodes absent; carpels 6, narrowly ellipsoid, 1.6–1.9 by 0.6–0.7 mm, densely covered with whitish hairs, ovule 1, basal, stigma globose, 0.2–0.4 mm diam, glabrous. *Monocarps* and *seeds* not seen.

Distribution — Cameroon (South Region).

Habitat & Ecology — In bushy scrub. Flowering: April.

Preliminary IUCN conservation status —Critically endangered (CR): B2ab(iii). AOO: 4 km^2. This species is only known from the type collection, which was collected more than 45 years ago outside a protected area.

Ethymology — named *hexamera* as this species has six petals, six stamens and six carpels.

38. *Monanthotaxis hirsuta* (Benth.) P.H.Hoekstra — Fig. 17; Plate 3f; Map 24

Monanthotaxis hirsuta (Benth.) P.H.Hoekstra in Guo et al. (2017) 14. — *Unona hirsuta* Benth. in Benth. & Hook.f. (1862) 469. — *Oxymitra hirsuta* (Benth.) Sprague & Hutch. (1916) 155. — *Richella hirsuta* (Benth.) R.E.Fr. (1959) 139. — *Friesodielsia hirsuta* (Benth.) Steenis (1964) 360. — Type: *G. Mann 559* (holo: K000198950; iso: P00363313, P00363314), Equatorial Guinea, Bioco, Fernando Poo, 1860.

Uvaria caillei A.Chev. ex Hutch. & Dalziel (1927a) 50. — Lectotype (designated here): *A.J.B. Chevalier 14817* (lectotype: P (P00363329); isolecto: G00308375, L.1765233, P00363319, P00363320, P01954813), Guinea, Mamou, Timbou, Kouria, 28 Nov. 1905.

Small tree, shrub or liana, to at least 3 m tall; young branches dark brown to black, covered with erect, reddish brown hairs 1.2–1.7 mm long, becoming glabrous; old branches dark brown to black. *Leaves*: petiole 4.5–6 mm long, 1.8–2.5 mm diam, terete, indument as on branches; lamina oblong-elliptic, obovate to oblanceolate, 8.3–28.5 by 4.9–7.5 cm, 1.7–3.8 times longer than wide, membranous to subcoriaceous, not punctate, glaucous below, above sparsely covered with erect hairs on primary vein, soon becoming glabrous, below covered

with erect, brown hairs 0.5–1.5 mm long, more densely so on the primary vein, base obtuse to subcordate, sometimes acute, glands hardly visible, apex acute to short acuminate, acumen to 5(–20) mm long, secondary veins 9–23 per side, curving upwards near margin end, tertiary venation distinctly percurrent, flat above. *Inflorescences* leaf-opposed or sometimes terminal, composed of 1- or sometimes 2-flowered fascicles; sympodial rachis to 2 mm long, covered with yellowish hairs; pedicels 7–12 mm long, 1.3–2.5 mm diam, fruiting pedicels 13–31 mm long, 1.6–2.1 mm diam, densely covered with erect hairs 0.2–0.4 mm long; lower bracts ovate, c. 5.2 by 2.8 mm; upper bract in upper part of the pedicel, ovate to triangular, c. 5 by 4.5–4.9 mm, outside and inside densely covered with ascending to erect hairs; flower buds ovoid. *Flowers* bisexual; sepals free, ovate to triangular, 6–9 by 5–7 mm, apex obtuse to acute, densely covered with yellowish brown hairs, not persistent in fruit; receptacle 8–12 mm diam, flat; petals yellow to reddish, 6, in two whorls, outer petals narrowly ovate to narrowly elliptic, 21–50 by 9–17 mm, outside densely covered with yellow-brown hairs, inside similar but becoming glabrous near base, inner petals lanceolate-elliptic, 16–25 by 6–8 mm outside densely covered with appressed to ascending, yellow-brown, short hairs, inside covered with erect hairs c. 0.1 mm long; stamens 100–120, in four or five whorls, free, cylindric to obconical, 1.2–1.6 mm long, filaments c. 0.3 mm long, thecae latrorse, connective truncate, quadrately thickened above thecae, hiding thecae seen from above, glabrous, staminodes absent; carpels 22–24, narrowly ellipsoid, c. 1.8 by 0.7 mm, densely hairy, ovules 2 or 3, lateral, stigma elongate, c. 1.2 mm long, glabrous. *Monocarps* 2–9, orange when ripe, ellipsoid to subcylindric, 1-seeded monocarps 23–30 by 9–13 mm, 3-seeded monocarps to 52 mm long,

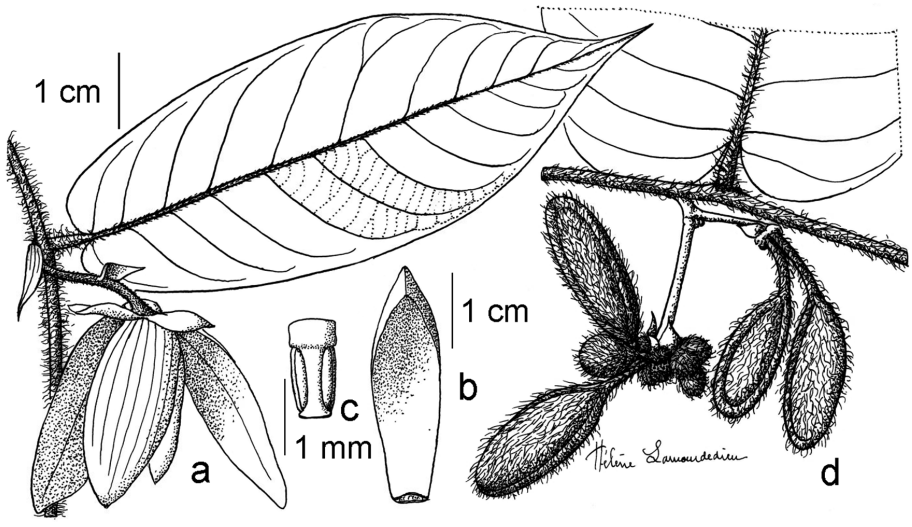
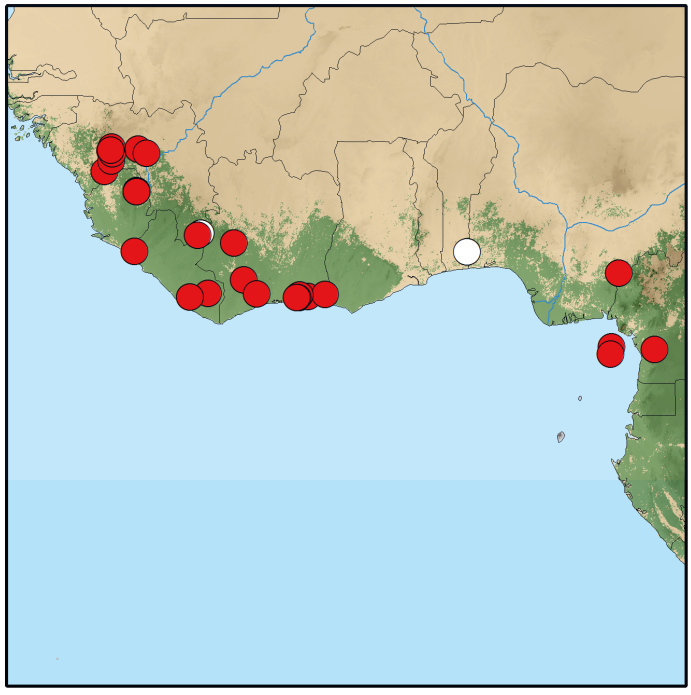


Fig. 17 *Monanthotaxis hirsuta* (Benth.) P.H.Hoekstra: a. Flowering branch; b. outer petal, inside view; c. stamen, front view; d. fruiting branch (a–c: *Chevalier 14817*; d: *FHI 19738*). Drawing by H. Lamourdedieu, © Muséum national d'Histoire naturelle, Paris.

densely covered with erect hairs 1–1.5 mm long, apex rounded to apiculate, stipes 7–11 mm long. *Seeds* 1–3, ellipsoid to narrowly ellipsoid, 17–27 by 9–10 mm, tawny to reddish brown, ends rounded, raphe slightly visible on both sides.

Distribution — Guinea, Sierra Leone, Liberia, Ivory Coast, Nigeria, Cameroon, Equatorial Guinea.

Habitat & Ecology — In swamp forest, gallery forest, primary forest and secondary forest. Elevation: 40–1300 m. Flowering: November to January, March, June; fruiting: January to March, May to July, October.



Map 24 Distribution of *Monanthotaxis hirsuta* (red circles, white circles are uncertain dets).

Preliminary IUCN conservation status —Least concern (LC). EOO: 1,066,157 km^2, AOO: 112 km^2. This species is known from many locations and several reserves. It can be quite common locally in West-Africa. However, it must be noted that it has only been collected four times east of the Dahomey gap of which only one collection is recent and the other three were more than 50 years ago.

Notes — 1. *Monanthotaxis hirsuta* is in flower easily distinguishable from related species such as *M. enghiana* and *M. velutina* by the long thecae covering more than half of the length of the stamens and the more than 25 mm long reddish outer petals. Because of the variability

in vegetative characters *M. hirsuta* is sometimes difficult to distinguish from *M. enghiana*. *Monanthotaxis enghiana* normally has oblanceolate leaves with a narrow subcordate base and an acuminate apex, while *M. hirsuta* normally has more obovate to oblong-elliptic leaves with a broader subcordate base and an obtuse to acute apex. Furthermore, the erect hairs on young branches are normally longer in *M. hirsuta*, but exceptions occur. Also *M. filamentosa* can resemble *M. hirsuta* vegetatively, but normally has broader obovate leaves with a rounded leaf base. Some sterile specimens cannot be identified with certainty.

2. In the protologue of *Unona hirsuta* it is indicated that Bentham (in Bentham & Hooker 1862) revised material received at Kew herbarium. The holotype is thus the specimen from Kew and not Paris as stated in Guo et al. (2017).

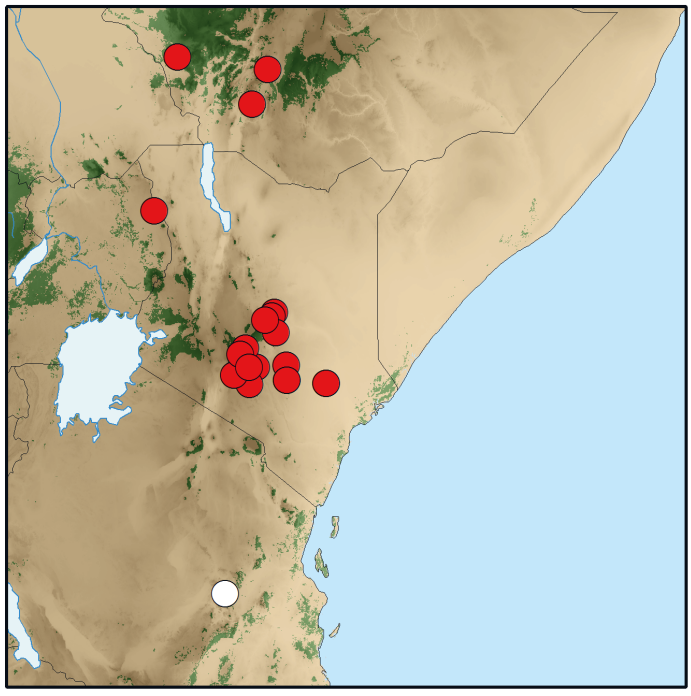
39. *Monanthotaxis kenyensis* (Verdc.) P.H.Hoekstra, *comb. nov.*, *stat. nov.* — Map 25

Monanthotaxis parvifolia (Oliv.) Verdc. subsp. *kenyensis* Verdc. (1971b) 27. — Type: *B. Verdcourt 2620* (holo: K000198975; iso: BR0000008801685, EA, PRE0396142-0), Kenya, Central, 14 falls, near where Donyo Subuk Road crosses river Athi, 14 Jan. 1960.

Shrub, scandent shrub or liana, to 5 m tall; young branches sparsely to densely covered with erect, reddish brown hairs 0.2–0.3 mm long, becoming glabrous; old branches grey-black to blackish. *Leaves*: petiole 4.5–7 mm long, 1–1.5 mm diam, grooved, indument as on branches; lamina oblong-elliptic to narrowly so, 4.5–10.8 by 1.9–4.8 cm, 2–2.9 times longer than wide, chartaceous, not punctate, glaucous below, primary vein yellowish or reddish, often contrasting with darker petiole, above glabrous, below sparsely covered with appressed, yellowish to pale brown hairs 0.2–0.3 mm long, becoming glabrous, base subcordate, with slightly thickened margins, apex obtuse, secondary veins 9–12 per side, curving upwards, tertiary venation reticulate, raised above, not visible below. *Inflorescences* leaf-opposed or extra-axillary, composed of solitary flowers; sympodial rachis 0–1.5 mm long, densely covered with erect hairs; pedicels 15–18 mm long, c. 0.3 mm diam, fruiting pedicels c. 0.7 mm diam, sparsely covered with ascending to erect, short hairs; lower bracts absent, upper bract in lower half to halfway up the pedicel, ovate to lanceolate, 0.7–1.1 by 0.3–0.4 mm, indument as on pedicel; flower buds globose. *Flowers* bisexual; sepals connate at the base, depressed ovate, 1.2–1.3 by 1.8–2 mm, apex obtuse, densely covered with appressed, yellowish hairs, persistent in fruit; receptacle c. 2.2 mm diam, flat, covered with brown, short hairs between carpels and stamens; petals yellow, 6, in two whorls, outer petals broadly ovate, 6.1–7 by 5.6–6.7 mm, outside covered with yellowish hairs, inside with hairs at the apex and margins, inner petals elliptic to rhombic, 5.2–5.5 by 2.9–3.8, outside covered with hairs, inside with hairs at the apex; stamens 9–15, in one whorl, free, obconical, 1.1–1.2 mm long, filaments 0.5–0.7 mm long, thecae extrorse, connective truncate, glabrous, staminodes absent; carpels 12–17, subcylindric, 1.3–1.4 by 0.3–0.4 mm, glabrous, ovules 1 or 2 (or 3), basal or lateral, stigma elongate, c. 0.5 mm long, glabrous. *Monocarps* 1–6, orange to red when ripe, narrowly

ellipsoid, 13–26 by 5–5.5 mm, glabrous, apex apiculate, apiculum c. 1 mm long, stipes 3–4 mm long, terete to slightly grooved. *Seeds* 1 or 2, ellipsoid, 7–8 by 4.5–5 mm, ochre-brown, ends slightly apiculate, raphe not visible or slightly visible.

Distribution — Ethiopia, Uganda, Kenya.



Map 25 Distribution of *Monanthotaxis kenyensis* (red circles, white circle is uncertain det).

Habitat & Ecology — In dry rocky forest, submontane forest, gallery forest, woodland and rocky outcrops on rocky hillsides, river banks. Altitude: 770–1945 m. Flowering: January to June; fruiting: February, April to July, September, November, December.

Preliminary IUCN conservation status —Least concern (LC). EOO: 337,422 km^2, AOO: 76 km^2. There are more than 10 populations of which the majority from forest reserves and the species is locally common.

Notes — *Monanthotaxis kenyensis* was treated by Verdcourt (1971b) as a subspecies of *M. parvifolia*. *Monanthotaxis parvifolia* is very variable in leaf shape and indument density, and the leaves of some specimens resemble those of *M. kenyensis.* The two species are set apart by the number of stamens per flower: 9–15 stamens in a single whorl in *M. kenyensis*, and 24 stamens in three whorls in *M. parvifolia*. *Monanthotaxis kenyensis* shares the single whorl of stamens with *M. maputensis* and *M. caffra*, but differs from the latter two species in its longer pedicels and petiole, and subcordate leaf base.

40. *Monanthotaxis klainei* (Engl.) Verdc. — Fig. 18a–i; Map 26

Monanthotaxis klainei (Engl.) Verdc. (1971b) 30. — *Popowia klainei* Engl. in Engler & Diels (1901) 52 (‘*klainii*’). — *Atopostema klainei* (Engl.) Boutique (1951b) 122 (‘*klainii*’). — Lectotype (designated by Le Thomas 1969: 220): *T.-J. Klaine 1539* (lecto: P00362628; isolecto: P00362629), Gabon, Estuaire, environs de Libreville, 25 Mar. 1899.

Liana to 7 m tall, 1–4 cm diam; young branches dark brown to blackish covered with reddish brown hairs 0.1 mm long, soon becoming glabrous; old branches dark brown to blackish. *Leaves*: petiole 3–7(–11) mm long, 0.9–2.9 mm diam, grooved, indument as on branches; lamina obovate, 9.8–26.8 by 4.6–10.8 cm, 1.6–2.7 times longer than wide, chartaceous to subcoriaceous, not punctate, glaucous below, primary vein red-brown in sicco, only slightly contrasting with petiole, above glabrous, below sparsely covered with appressed, reddish brown hairs c. 0.1 mm long, base subcordate, glands hardly visible, apex acute to shortly acuminate, acumen to 15 mm long, secondary veins 7–12 per side, straight to curving upwards, tertiary venation percurrent. *Inflorescences* cauliflorous, composed of solitary flowers or many-flowered fascicles; sympodial rachis 0–4 mm long; pedicels 0–20 mm long, 0.5–0.6 mm diam, fruiting pedicels 1–24 mm long, 0.8–1.9 mm diam, densely covered with appressed, very short hairs to glabrous; lower bracts absent or broadly triangular, c. 0.5 by 0.5 mm, indument as on pedicels; upper bract in the lower half of the pedicel or near the base, ovate to narrowly triangular, small, 0.5–1.4 by 0.5 mm, indument as on pedicels; flower buds ovoid. *Flowers* bisexual; sepals connate at the base, depressed ovate, 0.5–0.8 by 1.0–1.4 mm, sparsely covered with appressed, very short hairs, persistent in fruit; receptacle 1.5–2.2 mm diam, flat; petals creamy pink to red pink, 6, in two whorls, base of inner petals visible in bud, outer petals ovate, 3.3–4.5 by 2.5–3.4 mm, outside covered with appressed, yellowish to reddish brown, very short hairs, inside glabrous except for a few hairs at the apex, inner petals elliptic, 3.2–3.7 by 1.2–2.1, outside covered with short hairs on the midline, inside glabrous; stamens 9, in one whorl, connate at the base, oblong to slightly ellipsoid, 0.8–1 mm long, filaments 0.2–0.3 mm long, thecae placed on top of each other at the lateral inside of the stamen, transversally dehiscent, connective truncate, glabrous, staminodes 9, in one whorl alternating with the stamens, 0.3–0.4 mm long, ellipsoid to spathulate, glabrous; carpels 16–26, subcylindric to narrowly ellipsoid, 1.1–1.5 by 0.3–0.5 mm, densely hairy, ovules 1 or 2, basal or lateral, stigma subsessile, square or globose, c. 0.2 mm diam, glabrous. *Monocarps* up to 10, colour in yellow to red when ripe, ellipsoid to narrowly ellipsoid, 14–27 by 7–10 mm, slightly verrucose, sparsely covered appressed, yellowish, short hairs, becoming glabrous but longer persistent at stipe and top, apex rounded to apiculate, apiculum to 1 mm long, stipes 1–4 mm long, grooved to round. *Seeds* 1 or 2, globose to ellipsoid, 8–12 by 6–9 mm, ochre-brown to reddish brown, both ends rounded, raphe visible as a longitudinal furrow from base to apex.

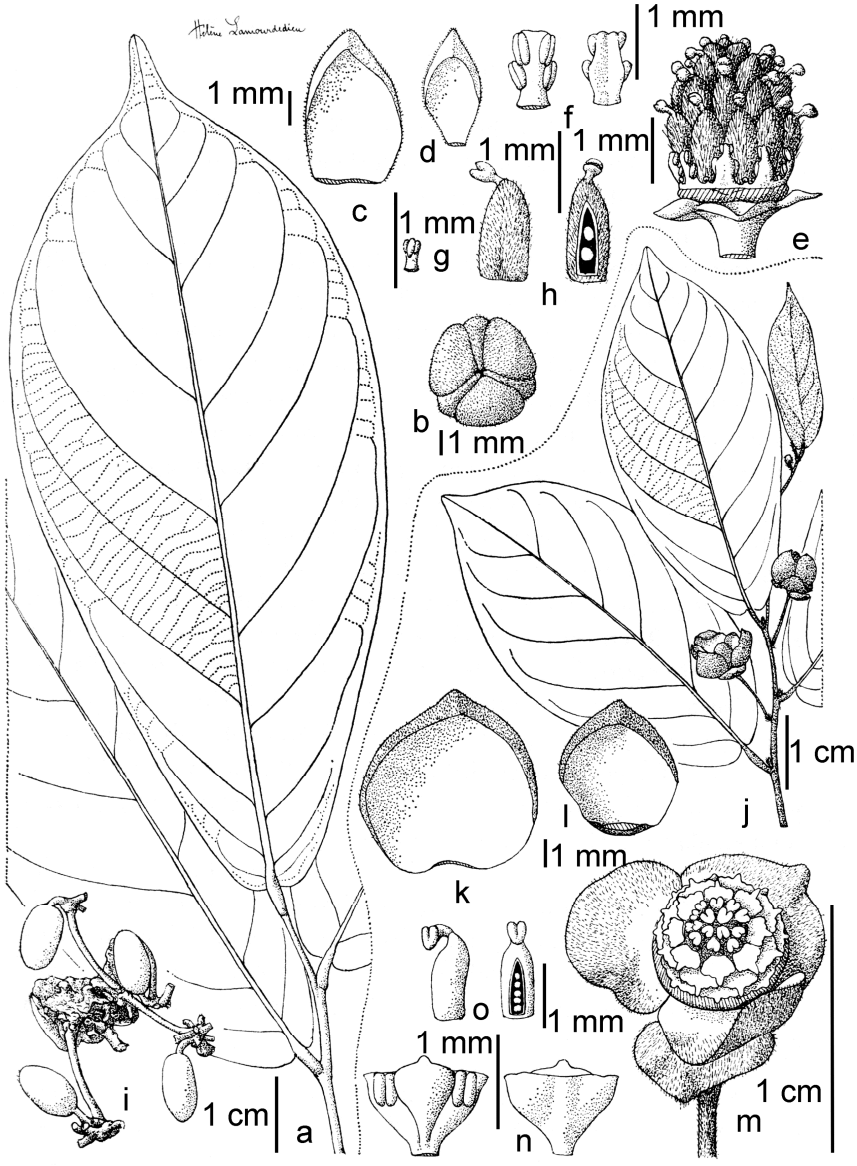


Fig. 18 a–i. *Monanthotaxis klainei* (Engl.) Verdc.: a. Leaves; b. flower bud seen from above; c. outer petal, inside view; d. inner petal, inside view; e. flower with petals removed; f. stamen, inside view and outside view; g. staminode; h. carpel and longitudinal section of carpel; i. fruits. — j–o. *M. laurentii* (De Wild.) Verdc.: j. Flowering branch; k. outer petal, inside view; l. inner petal, inside view; m. flower with petals removed; n. stamen, outside and inside view; o. carpel and longitudinal section of carpel (a–h: *Klaine 2662*; i: *Klaine 1539*; j–o: *Le Testu 4512*). Modified from Le Thomas (1969) plate 39.

Notes — 1. *Monanthotaxis klainei* can be distinguished from other species of *Monanthotaxis* by having 9 stamens, with transversally dehiscent thecae. It has more carpels (16–26) than closely related species, such as *M. vogelii* (8–12) and *M. aquila* (12–13) and it has more staminodes (9 versus 6).

2. *Monanthotaxis klainei* was named after T.-J. Klaine, therefore, the epithet *klainii* has been corrected to *klainei* according to ICBN article 60.7 (Turland et al. 2018).

a. var. ***klainei*** — Map 26

Leaves: lamina 1.6–2.3 times longer than wide, primary vein red-brown in sicco, only slightly contrasting with petiole, secondary veins 8–12 per side. *Inflorescences* cauliflorous, composed of solitary flowers or many-flowered fascicles; pedicels 8–20 mm long, fruiting pedicels 15–24 mm long. *Flowers*; carpels 16–20. *Seeds* 1 or 2, globose in Congolese specimens, ellipsoid in Gabonese specimens, 8–12 by 8–9 mm.

Distribution — Democratic Republic of the Congo (Bandundu, Bas-Congo, Equateur, Kinshasa, Orientale), Gabon (Estuaire, Ogooué-Ivindo, Ogooué-Lolo, Ogooué-Maritime).

Habitat & Ecology — In primary forest, gallery forest and swamp forest. Altitude: 470–495 m. Flowering: May, July, October, December; fruiting: January, March to August, October.

Vernacular names — Democratic Republic of the Congo: Bodzingo kodzi (Nkundo name) (*B.I. Fruth 1231*), Tsaka tsamba (*L. Pauwels 3564*).

Preliminary IUCN conservation status —Least concern (LC). EOO: 1,088,343 km^2, AOO: 132 km^2. This variety has a wide distribution from many locations. There is however only one recent collection from Democratic Republic of the Congo. Pending the taxonomic status of the Congolese specimens the conservation status could therefore change to 'endangered'.

Notes —

The variety *klainei* was distinguished from the variety *lastoursvillensis* by Le Thomas (1969) based on longer pedicels and a larger number of flowers per inflorescences in var. *klainei*. With the availability of more material, the number of flowers per inflorescence cannot be maintained as distinctive character. Seed shape, globose in Congolese specimens of var. *klainei* and ellipsoid in var. *lastoursvillensis*, further adds to the distinction. The paucity of fertile material from (the north of) Gabon has restricted the study of distinquishing characters across the distributional range.

b. var. ***lastoursvillensis*** (Pellegr.) Verdc. — Map 26

Monanthotaxis klainei (Engl.) Verdc. var. *lastoursvillensis* (Pellegr.) Verdc. (1971b) 30. — *Popowia lastoursvillensis* Pellegr. (1949) 213. — *Popowia klainei* Engl. var. *lastoursvillensis* (Pellegr.) Le Thomas (1963) 290. — Lectotype (designated by Le Thomas 1969: 221): *G.M.P.C. Le Testu 8595* (lecto consisting of 2 sheets: P00362624, P00362625; iso:

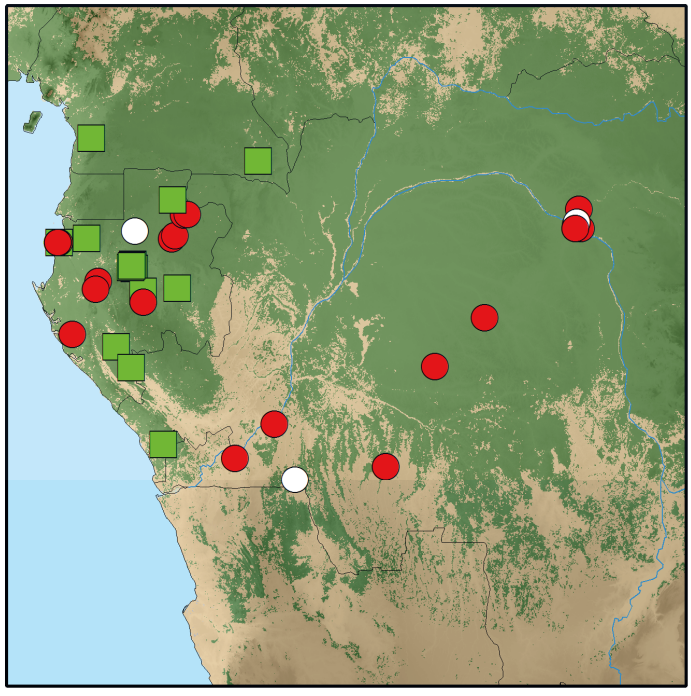
BM000553844, BR0000008823748, BR0000008823847), Gabon, Ogooué-Lolo, region de Lastoursville, Poungwé, 19 Dec. 1930.

Leaves: lamina 1.9–2.7 times longer than wide, primary vein yellowish or reddish, often clearly contrasting with petiole, secondary veins 7–10 per side. *Inflorescences* cauliflorous, ramiflorous or axillary, composed of solitary flowers or a few-flowered fascicles; pedicels 0–3 mm long, fruiting pedicels 1–10 mm long. *Flowers*; carpels 20–26. *Seeds* 1, ellipsoid, 10–12 by 6–7 mm.

Distribution —Cameroon, Gabon, Angola.

Habitat & Ecology — In rain forest, gallery forest, river banks and forest near savannas. Altitude: 35–200 m. Flowering: January, March, May, December; fruiting: January to May, October.

Preliminary IUCN conservation status —Near threatened (NT). EOO: 306,766 km^2, AOO: 60 km^2. This variety is currently known from 11 locations and is probably quite common in Lope National Park, however the most recent collections from Cameroon and Angola are from more than 100 years ago, and the variety might have disappeared from various localities.



Map 26 Distribution of *Monanthotaxis klainei* var. *klainei* (red circles, white circles are uncertain dets), *M. klainei* var. *lastoursvillensis* (green squares).

41. *Monanthotaxis latistamina* P.H.Hoekstra **—** Fig. 19; Plate 4a–c; Map 23

Monanthotaxis latistamina P.H.Hoekstra in P.H.Hoekstra et al. (2016) 88. — Type: *T.L.P. Couvreur 565* (holo consisting of 3 sheets: WAG.1577028, WAG.1577029, WAG.1577030; iso: LBV not seen, YA not seen), Gabon, Ogooué-Ivindo, Ivindo National Park, along main trail departing from behind the herbarium at the Research station of Ipassa, 0°30.23'N, 12°47.59'E, 519 m, 11 Nov. 2013.

Scandent shrub or liana, to 4 m long; young branches sparsely covered with appressed, yellowish hairs 0.1–0.2 mm long, soon becoming glabrous; old branches dark brown to blackish. *Leaves*: petiole 5–12 mm long, 1.3–1.7 mm diam, grooved, indument as on branches; lamina oblong-elliptic to obovate or narrowly so, 6–13 by 3.5–7.2 cm, 1.6–2.7 times longer than wide, chartaceous to subcoriaceous, punctate, although hardly visible in older leaves, green above, pale greyish green below, young leaves above and below sparsely covered with appressed hairs 0.1–0.2 mm long, soon becoming glabrous, base cuneate, rounded to subcordate with thickened black margin, apex acute to acuminate, acumen to 13 mm long, secondary veins 7–8(–10) per side, oblique, from base curving upwards, tertiary venation reticulate, raised above. *Inflorescences* axillary or terminal, solitary, in fascicle-like rhipidia or in to 4 cm long lax panicle-like, up to 6-flowered rhipidia; sympodial rachis from almost absent to at least 1 cm long, covered with appressed hairs to becoming glabrous; flowering pedicels 8–17 mm long, 0.3–0.4 mm diam, indument as on sympodial rachis; lower bracts strongly reduced or absent; upper bract placed halfway up the pedicel, ovate, 0.6–0.7 by 0.4–0.6 mm, indument as on rachis; flower buds globose to slightly ellipsoid. *Flowers* bisexual; sepals connate at the base, depressed ovate, 0.8–1 by 1.2–1.5 mm, apex obtuse to slightly acute, covered with appressed, yellowish, short hairs; receptacle 1.2–1.5 mm diam, flat; petals green when young, 6, in one whorl, outer petals overtopping inner petals in bud, elliptic to slightly ovate, with inwardly reflexed appendage at apex, 1.6–2.5 by 0.7–1.2 mm, outside papillate to covered with appressed, short hairs, inside papillate, most densely so at the apex; stamens 6, in one whorl, free, alternating with the petals, oblong, wider than thick 1–1.2 by 0.6–0.7 mm, radial width 0.2–0.3 mm, densely papillate, filaments c. 0.1 mm long, thecae extrorse, connective truncate to conical, densely papillate, staminodes absent; carpels 6–9, narrowly ellipsoid, 1–1.4 by 0.4–0.6 mm, densely covered with reddish brown hairs, ovules 6, lateral, stigma globose to slightly elongate, 0.1–0.2 mm long, grooved to almost bifurcate, glabrous. *Monocarps* and *seeds* not seen, but reported as yellowish.

Distribution — Gabon (Ogooué-Ivindo), Republic of the Congo (Niari).

Habitat & Ecology — In evergreen forest and forest on shallow soil at summit of hill. Altitude: 520–1020 m. Flowering: May, October, November.

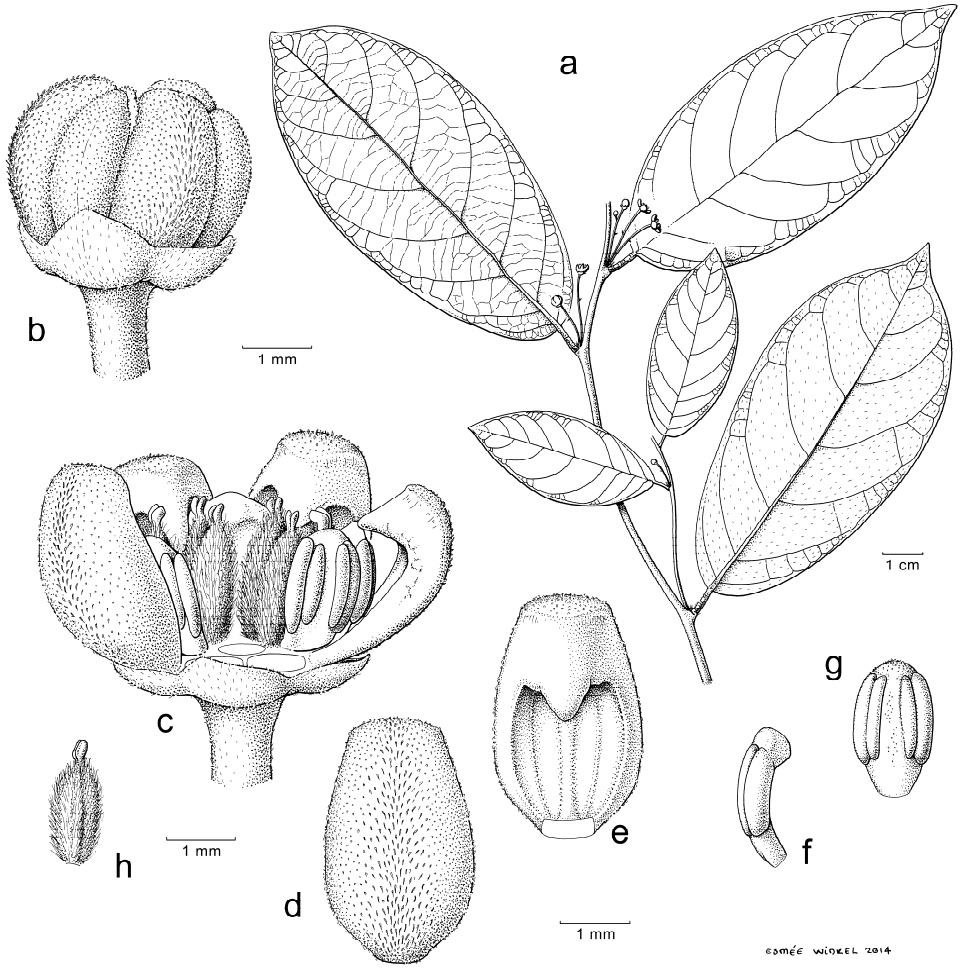


Fig. 19 *Monanthotaxis latistamina* P.H.Hoekstra: a. Flowering branch; b. flower bud; c. flower with 2 petals removed; d. outer petal, outside view; e. outer petal, inside view; f. stamen, side view; g. stamen inside view; h. carpel (*Couvreur 565*). Drawing by E. Winkel.

Preliminary IUCN conservation status — Endangered (ED): B2ab(iii). EOO: 17,682 km^2, AOO: 16 km^2. Of the four collections of this species only one is from a protected area, while the other locations are under threat of logging and habitat destruction.

Notes — *Monanthotaxis latistamina* closely resembles *M. congolana*, the only other species of *Monanthotaxis* with papillate petals and stamens. For the differences with *M. congolana* see note under that species.



Plate 4 a–c. *Monanthotaxis latistamina* P.H.Hoekstra: a. Leaves; b. inflorescence; c. flowers. — d. *Monanthotaxis letouzeyi* (Le Thomas) Verdc.: Leaves. — e, f. *Monanthotaxis mannii* (Baill.) Verdc.: e. Leaves; f. leaves and flower (a–c: *Couvreur 565*; d: *Couvreur 752*; e, f: *Jongkind 11848*). Photos: a–d: T.L.P. Couvreur; e, f: C.C.H. Jongkind.

42. *Monanthotaxis laurentii* (De Wild.) Verdc. — Fig. 18j–o; Map 27

Monanthotaxis laurentii (De Wild.) Verdc. (1971b) 26. — *Popowia laurentii* De Wild. (1905b) 19. — Type: *É. Laurent 92* (holo: BR0000008805010), Democratic Republic of the Congo, Equateur, Bikoro, Lukolela, 13 Dec. 1903.

Unona congensis Engl. & Diels (1899) 296. — *Popowia congensis* (Engl. & Diels) Engl. & Diels (1901) 44. — Type: *É. Laurent s.n.* (holo: BR0000008804686), Democratic Republic of the Congo, Equateur, Bomongo, Bangala, 20 Feb. 1896.

Scandent shrub or liana, to 20 m long; young branches reddish brown, sparsely covered with appressed to ascending, yellowish hairs 0.2–0.3 mm long, becoming glabrous; old branches reddish brown. *Leaves*: petiole 3–6.5 mm long, 0.7–1.3 mm diam, slightly grooved, indument slightly more dense than on branches; lamina oblong-elliptic to obovate or narrowly so, 4.7–18.3 by 2.4–7.2 cm, 1.7–2.6 times longer than wide, chartaceous, not punctate, dull green above, glaucous below, above sparsely covered with appressed, white hairs 0.3–0.5 mm long, becoming glabrous, primary vein with longer persistent white-yellowish hairs 0.3–0.5 mm long, below sparsely covered with appressed, yellowish hairs 0.1–0.3 mm long, slightly more dense on veins, becoming glabrous, base rounded or slightly subcordate, glands hardly visible, apex acute to acuminate, acumen to 20 mm long, secondary veins 7–14 per side, slightly curving upwards, tertiary venation percurrent. *Inflorescences* extra-axillary, leaf-opposed or terminal, composed of solitary flowers or 2-flowered rhipidia; sympodial rachis absent or up to 5 mm long, densely covered with appressed, yellowish hairs; pedicels 5–9(–11) mm long, 0.5–0.8 mm diam, fruiting pedicels 15–23 mm long, 1.1–1.8 mm diam, sparsely covered with appressed to ascending, yellowish hairs c. 0.2 mm long; lower bract absent or lanceolate, c. 1.2 by 0.4 mm, indument as on rachis; upper bract in the upper half of the pedicel or halfway, ovate, 1.2–1.6 by 0.9–1.6 mm, densely covered with yellow hairs; flower buds globose. *Flowers* bisexual; sepals free or slightly connate at the base, depressed ovate, 1.1–1.7 by 2.5–3.4 mm, apex rounded, densely covered with appressed, yellow-brown hairs, persistent in fruit; receptacle 1.5–2.5 mm diam, slightly convex; petals colour in vivo unknown, 6, in two whorls, outer petals broadly ovate, 6–8 by 5.2–8.1 mm, outside and near the margins of the inside sparsely to densely covered with white-yellowish hairs, inner petals ovate to rhombic, 4.5–5.3 by 3.5–3.9 mm, outside densely covered with white-yellow hairs, inside glabrous except for the apical part; stamens 23 or 24, in three whorls, free, obovoid, 1–1.2 mm long, filaments 0.3–0.4 mm long, thecae latrorse to extrorse, connective truncate, prolonged outward, not hiding thecae, glabrous, staminodes absent; carpels 9–12, subcylindric, 1.5–1.8 by 0.4–0.5 mm, glabrous or sometimes with few hairs at the base, ovules 5 or 6, lateral, stigma elongate, obconical, 0.6–0.8 mm long, glabrous. *Monocarps* 3–11, yellow to orange, moniliform to subcylindric, each part subcylindric, 25–85 by 5–6 mm, slightly verrucose, glabrous or covered with few, yellowish hairs on the stipe, apex apiculate, apiculum 1–2 mm long, stipes 10–23 mm long. *Seeds* 1–6, subcylindric, 14–19 by 5–6 mm, ochre-brown, apex flattened to rounded, raphe not visible.

Distribution — Guinea, Sierra Leone, Liberia, Ivory Coast, Ghana, Nigeria, Cameroon, Central African Republic, Democratic Republic of the Congo, Equatorial Guinea, Gabon, Angola.

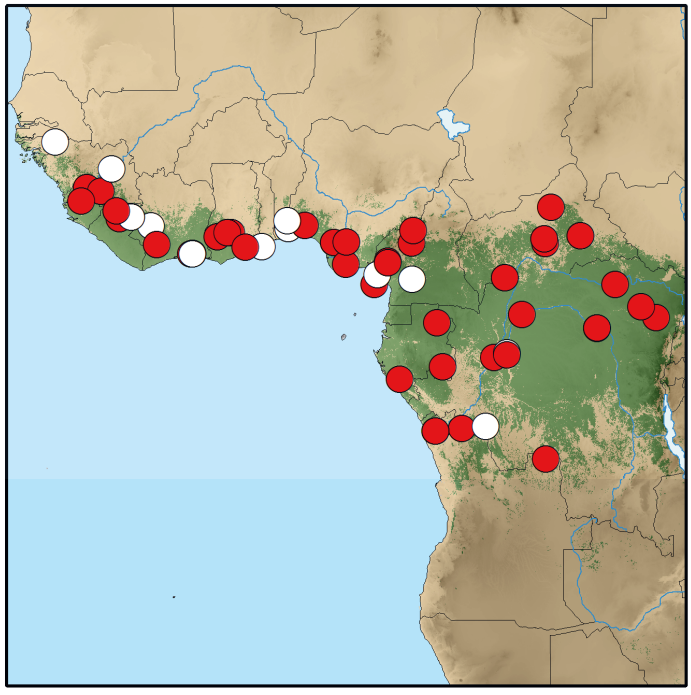
Habitat & Ecology — In primary forest, secondary forest, savanna with forest pockets and gallery forest. Altitude: 70–1524 m. Flowering: September to May; fruiting: all year round.

Vernacular names —Sierra Leone: Jenbigbili (*N.W. Thomas 1642*).

Preliminary IUCN conservation status —Least concern (LC). EOO: 4,617,777 km^2, AOO: 184 km^2. This species has a very wide distribution with several collections made in protected reserves and therefore this species is currently not under threat of extinction.

Notes — *Monanthotaxis laurentii* can easily be recognized in fruit by the long, subcylindric seeds, extra-axillary inflorescences, and the sparse indument of yellow hairs on the young branches. In flower it can be recognized by having 23 or 24 stamens in three whorls, glabrous carpels and the indument of the young branches.

In West Africa there are fruiting specimens in Benin, Togo and north-east Ivory Coast with fruits as *M. parvifolia*, i.e. with red fruits and ellipsoid seeds. However, the DNA and the leaves match *M. laurentii* (Fig. 1, clade A). Flowering material from this area is needed to verify if these specimens really belong to *M. laurentii.*



Map 27 Distribution of *Monanthotaxis laurentii* (red circles, white circles are uncertain dets).

43. *Monanthotaxis letestui* Pellegr. — Fig. 20; Map 28

Monanthotaxis letestui Pellegr. (1950) 75. — Lectotype (designated by Le Thomas 1969: 259): *G.M.P.C. Le Testu 7845* (lecto consisting of 2 sheets: P00362620, P00362622; iso: BM000547354, BM000547355, BR0000008801678, BR0000008802347, P00734029, P00734030), Gabon, Ogooué-Lolo, région de Lastoursville, 8 Jan. 1930.

Popowia hallei Le Thomas (1965) 443, syn. nov. — *Monanthotaxis letestui* Pellegr. var. *hallei* (Le Thomas) Le Thomas (1969) 259. —Type: *N. Hallé 3508* (holo: P00362619), Gabon, Ogooué-Ivindo, Bélinga, 14 Dec. 1964.

Scandent shrub or liana, 1.5–5 m long; young branches densely covered with appressed to ascending, reddish brown hairs c. 0.2 mm long; old branches dark brown to blackish. *Leaves*: petiole 2–5 mm long, 0.7–1 mm diam, grooved, indument as on branches; lamina elliptic to slightly obovate, 4–12.4 by 1.8–5.2 cm, 1.9–3 times longer than wide, chartaceous, sometimes punctate, discolorous, glossy green and glabrous above, dull and glaucous green below, primary vein dark brown below, above densely covered with yellowish to brownish hairs, below densely covered with erect, pale yellowish hairs 0.2–0.4 mm long, base subcordate to slightly truncate with thickened margin, apex emarginate, rounded to acute, primary vein above impressed, secondary veins 6–11 per side, straight, curving upwards, tertiary venation percurrent, not visible above. *Inflorescences* mostly supra-axillary, originating 1–4(–7) mm above axil, lax, pending, 1–4-flowered rhipidia to 12.5 cm long; sympodial rachis 2.4–6(–12) cm long, sparsely covered with appressed hairs; pedicels 1.5–3.9 cm long, 0.3–0.4 mm diam, fruiting pedicels 3.5–5.5(–11.6) cm long, sparsely covered with hairs; lower bracts absent; upper bract halfway or in upper half of pedicel, lanceolate 1–2 by 0.3–0.5 mm, densely covered with reddish brown hairs; flower buds ovoid. *Flowers* bisexual; sepals slightly connate, depressed ovate, 0.8–1.3 by 1.7–1.8 mm, apex rounded to slightly acute, densely covered with appressed hairs; receptacle c. 1.5 mm diam, flat; petals cream, yellow-green or yellow-violet, 6, in one whorl, narrowly ovate to lanceolate, 3–6 by 1–3 mm outside covered with appressed, reddish brown, short hairs, inside papillate; stamens 12–14, in one whorl, free, obconical, 1–1.3 mm long, filaments 0.4–0.7 mm long, thecae extrorse, connective truncate, with short triangular prolongation pointing outward, papillate, staminodes absent; carpels 8–16, narrowly ellipsoid, 1.1–1.4 by 0.4-0.6 mm, densely covered with reddish brown hairs, ovules 2–4, lateral, stigma ellipsoid to cup-shaped, 0.2–0.3 mm long, grooved, glabrous. *Monocarps* at least up to 6, yellow to red, ellipsoid to subcylindric, 14–47 by 6–7 mm, slightly to strongly constricted between the seeds, slightly rugulose with appressed reddish brown hairs, apex apiculate, apiculum c. 1 mm long, stipes 4–10 mm long, terete. *Seeds* 1–4, ellipsoid, 8.5–9.5 by 4.5–5.5 mm, tawny-brown, seed ends rounded, raphe visible on both sides.

Distribution — Gabon (Haut-Ogooué, Ogooué-Ivindo, Ogooué-Lolo, Woleu-Ntem).

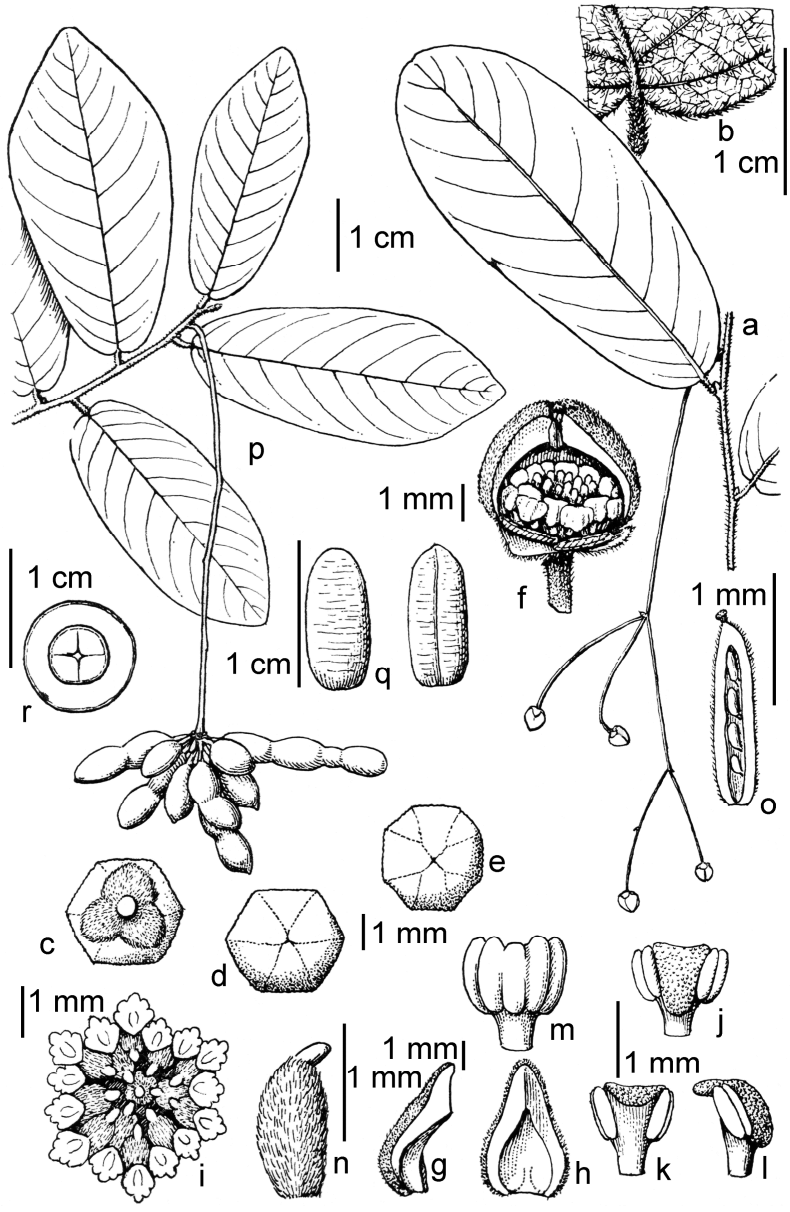
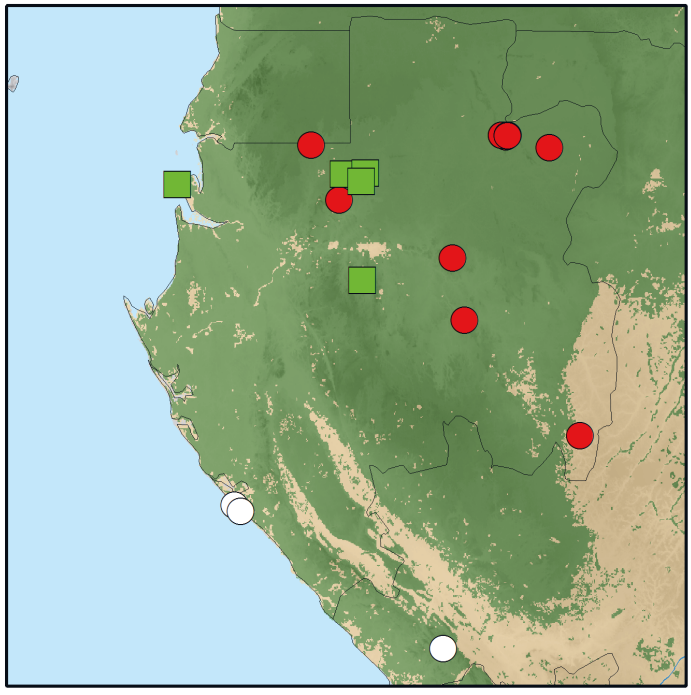


Fig. 20 *Monanthotaxis letestui* Pellegr.: a. Flowering branch; b. leaf base abaxially; c. flower bud seen from below; d, e. flower bud seen from above; f. flower with one sepal and one petal removed; g. petal, side view; h. petal, inside view; i. arrangement of stamens and carpels seen from above; j. stamen, seen from above; k. stamen, inside view; l. stamen, side view; m. stamen, outside view; n. carpel; o. longitudinal section of carpel; p. fruiting branch; q. seed; r. transverse section of fruit (a, b, f–h, j–l, o: *Hallé 3508*; c–e, i, m, n, p–r: living specimen Hallé). Modified from Le Thomas (1969) plate 46.

Habitat & Ecology — In forests with shallow rocky soil. Altitude: 460–1025 m. Flowering: January, February, May, July, September, October, December; fruiting: March, May to July, September, November, December.



Map 28 Distribution of *Monanthotaxis letestui* (red circles, white circles are uncertain dets or aberrant specimens) and *M. mcphersonii* (green squares).

Preliminary IUCN conservation status —Vulnerable (VU): B2ab(iii). EOO: 58,689 km^2, AOO: 36 km^2. This species is known from seven populations of which two fall inside National Parks, but the other five are in unprotected areas and under threat of habitat degradation and deforestation.

Notes — 1. *Monanthotaxis letestui* is easily recognised by the supra-axillary, lax and pending rhipidia. This character is only shared with the allopatric *M. oligandra*. It can be distinguished from that species by the number of stamen (12–14 versus 6) and the more densely hairy lower leafside.

2. Le Thomas (1969) distinguished 2 different subspecies based on filament length, presence or absence of a style, and impressions or not from the stamens in the petals. However, we found all intermediate forms, including those from the same locality. Therefore, subspecific taxa within *M. letestui* should not be recognized.

3. *J.J.F.E. De Wilde 11213* and *11391* from the coastal forest on sand near Gamba in Gabon are possibly a different (sub)species. The leaves and stems are less densely hairy and the sympodial rachis above the bract is < 5 mm long, while in most collections of *M. letestui* it is > 10 mm long. However, the flowers are indistinguishable from *M. letestui* and therefore these specimens are tentatively identified as *M. letestui*.

4. *G.H.J. Cusset 1311* from the Republic of the Congo has very elongated seeds, measuring c. 26 by 6 mm. The supra-axillary inflorescence and leaves suggest it probably belongs to *M. letestui*.

5. The epithet of *M. le-testui* has been corrected to *letestui* according to ICBN article 60.11 (Turland et al. 2018).

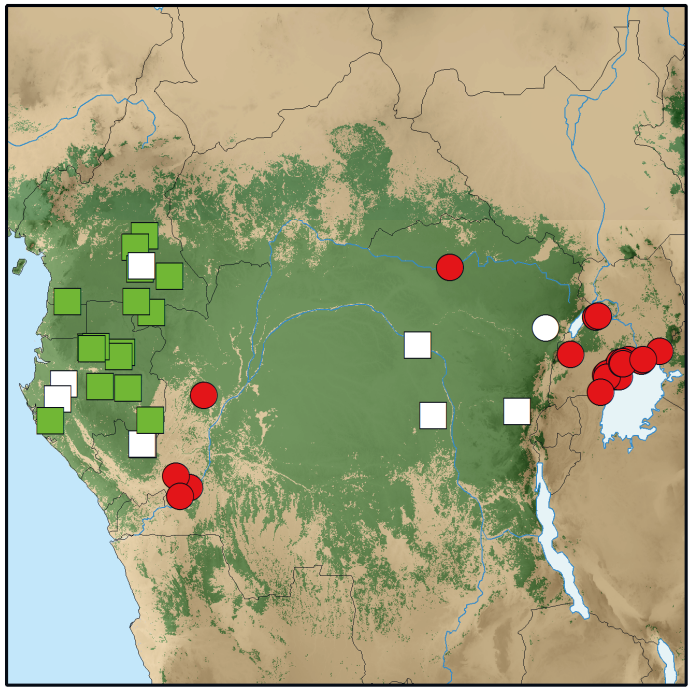
44. *Monanthotaxis letouzeyi* (Le Thomas) Verdc. — Plate 4d; Map 29

Monanthotaxis letouzeyi (Le Thomas) Verdc. (1971b) 31. — *Popowia letouzeyi* Le Thomas (1968) 241. — Type: *R.G. Letouzey 3066* (holo: P00362617; iso: YA0002635), Cameroon, East Province, Nkoum, 19 Feb. 1960.

Liana, to 30 m long; young branches green, densely covered with erect, reddish brown hairs c. 0.4 mm long, becoming glabrous; old branches dark brown to blackish. *Leaves*: petiole (6–)7–10(–15) mm long, 2–3.4 mm diam, grooved, indument as on branches; lamina oblong-elliptic, obovate to oblanceolate, 6–23 by 6–12.2 cm, 1.6–2.9 times longer than wide, chartaceous, not punctate, discolorous, dark green above, glaucous below, above sparsely covered with hairs, becoming glabrous, primary vein densely covered with erect, reddish brown hairs, below densely covered with erect, yellow to reddish brown hairs c. 0.4 mm long, base rounded to subcordate, with thickened black margin, apex emarginate, rounded or rounded with small apicule to 10 mm long, secondary veins 14–19 per side, straight to slightly curving upwards, tertiary venation percurrent. ♂ *Inflorescences* cauliflorous, composed of 3–many-flowered fascicles or glomerules; sympodial rachis 5–25 mm long densely covered with erect, reddish brown hairs 0.2–0.4 mm long; pedicels 6–10 mm long, 0.8–1.2 mm diam, indument as on rachis; lower bracts absent; upper bracts c. halfway the pedicel, ovate, 0.6–1 by 0.8–1 mm, indument as on sympodial rachis; flower buds broadly ovoid; sepals slightly connate, elliptic to ovate, 1.1–1.2 by 0.7–0.8 mm, densely covered with reddish brown hairs; receptacle 1.2–1.4 mm diam, convex; petals colour in vivo unknown, 6, in two whorls, slightly connate at the base, outer petals depressed ovate, c. 3.5 by 4.7 mm, outside densely covered with erect, yellowish to reddish brown hairs, inside covered with few whitish to yellowish papillae c. 0.05 mm long, inner petals elliptic to ovate, 1.5–2.2 by 1–1.1 mm, outside and inside covered with yellowish papillae, apex covered with few hairs c. 0.05 mm long; stamens 31–40, in four whorls, free, oblong, 1.3–1.4 mm long, filaments 0.3–0.5 mm long, thecae extrorse, connective truncate, connective and filaments hairy, staminodes absent. ♀ *Inflorescences* cauliflorous, condensed many-flowered panicle-like rhipidia; sympodial rachis 2.5–4 cm long,

densely covered with erect, reddish brown hairs 0.2–0.4 mm long; pedicels 8–15 mm long, 1.3–1.6 mm diam, fruiting pedicels 10–30 mm long, c. 2.1 mm diam, indument as on rachis; lower bracts ovate to broadly ovate, 0.7–2 by 1–1.5 mm, indument as on rachis; upper bracts in lower half of pedicel, size and indument as upper bracts; flower buds broadly ovoid; sepals slightly connate at base, ovate to depressed ovate, 1.5–1.7 by 1–2 mm, densely covered with reddish brown hairs; receptacle 2.5–3 mm diam, convex; petals colour in vivo unknown, 6, in two whorls, free; outer petals broadly ovate, 5–5.7 by 4.8–6.1 mm, outside densely covered with appressed, brownish hairs, inside densely covered with yellowish papillae and with few, yellowish hairs c. 0.05 mm long, inner petals spathulate, 1.8–2 by 1.2–1.4 mm, outside and inside densely covered with yellowish papillae; carpels c. 120, ellipsoid to rhombic, 1–1.2 by 0.5–0.7 mm, densely hairy, ovules 7 or 8, lateral, stigma ellipsoid to globse, 0.2–0.4 mm long, glabrous. *Monocarps* > 3, blackish green, moniliform, each part globose, 20–80 by 9–10 mm, smooth, rather densely covered with brownish hairs 0.2–0.4 mm long, apex rounded to slightly apiculate, apiculum to 0.5 mm long, stipes 7–10 mm long, slightly grooved to terete. *Seeds* 1–6, globose, c. 9 by 9 mm, reddish brown, both ends rounded, raphe not visible.

Distribution — Cameroon, Gabon, Republic of the Congo.



Map 29 Distribution of *Monanthotaxis letouzeyi* (green squares, white squares are uncertain dets) and *M. littoralis* (red circles, white circle is uncertain det).

Habitat & Ecology — In evergreen forest, gallery forest, secondary forest and swamp forest on sandy clay. Altitude: 40–850 m. Flowering: February, April, September, November; fruiting: March.

Preliminary IUCN conservation status —Least concern (LC). EOO: 264,066 km^2, AOO: 64 km^2. This species is known from 13 locations, five of which are protected areas. Several collections were made recently, and we do not consider this species under threat of extinction.

Notes — *Monanthotaxis letouzeyi* can be recognized by the cauliflorous inflorescences and the dense indument of erect, reddish brown hairs c. 0.4 mm long on the young branches. *Monanthotaxis letouzeyi* can be confused with *M. diclina*, but that species has yellow-brown hairs and very different staminate flowers, which are axillary and have only 6 stamens and 12 staminodes, while *M. letouzeyi* has the staminate inflorescences cauliflorous and each flower has 31–40 stamens and no staminodes.

45. *Monanthotaxis littoralis* (Bagsh. & Baker f.) Verdc. — Fig. 12a–d; Map 29

Monanthotaxis littoralis (Bagsh. & Baker f.) Verdc. (1971b) 27. — *Popowia littoralis* Bagsh. & Baker f. (July 1908) 221. — Lectotype (designated here): *M.T. Dawe 191* (lectotype: K (K000198976); isolecto: B100154091), Uganda, Central, Busiro, 1905.

Popowia dawei Diels (Aug. 1908) 328. — Lectotype (designated here): *M.T. Dawe 191* (lecotype: B (B100154091); iso: K000198976), Uganda, Central, Busiro, 1905.

Popowia bequaertii De Wild. (1922) 467. — Syntypes: *J. Bequaert 6252* (BR not seen), Democratic Republic of the Congo, Kivu, Rutshuru; *J. Bequaert 2746* (BR not seen), Democratic Republic of the Congo, Irumu; *J. Bequaert 7393* (BR not seen), Democratic Republic of the Congo, Kinshasa.

Shrub, scandent shrub or liana, to 8 m long; young branches sparsely covered with appressed hairs 0.2–0.3 mm long to glabrous; old branches blackish to dark brown. *Leaves*: petiole 2–6.5 mm long, 0.6–1 mm diam, slightly grooved, indument as branches; lamina elliptic to elliptic-ovate, 3.6–11.3 by 1.5–4.5 cm, 2.1–3.5 times longer than wide, membranous, not punctate, glaucous or pale green below, above sparsely covered with erect hairs on primary vein, soon becoming glabrous, below sparsely covered with appressed short hairs 0.1–0.4 mm long on the primary vein, becoming glabrous, base rounded to slightly cuneate, with thickened black margin, apex acute, secondary veins inconspicuous 6–12 per side, curving upwards, tertiary venation slightly reticulate, often hardly visible. *Inflorescences* extra-axillary or leaf-opposed, composed of solitary flowers; sympodial rachis 1–11 mm long, glabrous or sparsely covered with apressed hairs; pedicels 13–33 mm long, 0.2–0.5 mm diam, fruiting pedicels 25–45 mm long, glabrous or sparsely covered with appressed, yellowish, short hairs; lower bract absent; upper bract near the base of the pedicel; large and leafy, circular, ovate to narrowly ovate, 3.4–20 by 4.2–14 mm, base semi-amplexicaul, outside sparsely covered with appressed hairs;

flower buds globose. *Flowers* bisexual; sepals connate at the base and almost forming a ring, depressed ovate, c. 1.3 by 2.2 mm, apex obtuse, densely covered with appressed, yellowish hairs; receptacle 1.5–2.5 mm diam, flat; petals dull waxy yellow, pale yellow to yellow-green, 6, in two whorls, outer petals broadly elliptic-ovate, 4.3–5.4 by 4–4.8 mm, outside densely covered with yellow-brown, short hairs, inside glabrous at the base, inner petals elliptic to rhombic, 3.1–3.2 by 2.1–2.4, outside densely covered with appressed, yellow hairs, inside glabrous at the base; stamens 15, in one whorl, free, linear-obconical, c. 1.1 mm long, filaments c. 0.5 mm long, thecae latrorse, connective truncate, square to circular seen from above, glabrous, staminodes absent; carpels 10–18, narrowly subcylindric-ellipsoid, c. 1.6 by 0.4 mm, glabrous or with few hairs at the base, ovules 2 or 3, lateral, stigma elongate, c. 0.6 mm long, glabrous, bifurcate at the apex. *Monocarps* up to 10, pendant, orange when ripe, narrowly ellipsoid to moniliform, 8–18 by 4–6 mm, apex apiculate, apiculum to 1 mm long, stipes 2–4 mm long. *Seeds* 1 or 2, ellipsoid, 6–7 by 4–5 mm, tawny, ends rounded, raphe not visible.

Distribution — Democratic Republic of the Congo, Uganda, Republic of the Congo.

Habitat & Ecology — In primary forest, secondary forest, woodland thickets, moist semi-deciduous forest and forest edges. Altitude: 754–1260 m. Flowering: March to May, July to December; fruiting: March to May, July to November.

Vernacular names — Democratic Republic of the Congo: Babua (Embaye na Kamba name) (*P. Gérard 2478*). Uganda: Lakolya (Lasese name) (*J.W. Purseglove 1700*).

Preliminary IUCN conservation status —Near-threatened (NT). EOO: 913,461 km^2, AOO: 104 km^2. This species is known from quite some locations, however, only a very few collections have been made in protected areas, and the majority of collections are old and in areas that are currently highly degraded. Furthermore, all collections from the western part of the distribution are more than 50 years old.

Notes — 1. *Monanthotaxis littoralis* belongs together with *M. gilletii*, *M. orophila* and *M. vulcanica* to a group of species easily recognisable by the leafy bract. *Monanthotaxis littoralis* can be distinguished from *M. gilletii* by the short, appressed hairs on the stems and pedicels and by having less carpels (10–18 versus 25–28). It can be distinguished from *M. orophila* by having inconspicuous veins on the leaves and by having fewer stamens (15 versus 24–33). *Monanthotaxis littoralis* can be distinguished from *M. vulcanica* by the glabrous carpels, shorter stipes (2–4 mm versus 6–10 mm long) and shorter, more ellipsoid seeds (6–7 mm versus 8–15 mm).

2. The carpels of *M. littoralis* are glabrous or sometimes covered with a few hairs at the base, however, *Bashonga ATBP 790* in Uganda has hairy carpels.

3. *Popowia bequaertii* was synonymised with *M. littoralis* by Boutique (1951a), however we could not find any of the specimens mentioned by Boutique.

4. The 2 specimens of collection *M.T. Dawe 191* arrived around the same time in the herbaria of Kew and Berlin. Bagshawe and Baker (1908) working in Kew published it as

Popowia littoralis one month before Diels (1908), who worked in Berlin and published the specimen as *Popowia dawei*.

46. *Monanthotaxis lucidula* (Oliv.) Verdc. — Fig. 12e–j; Map 30

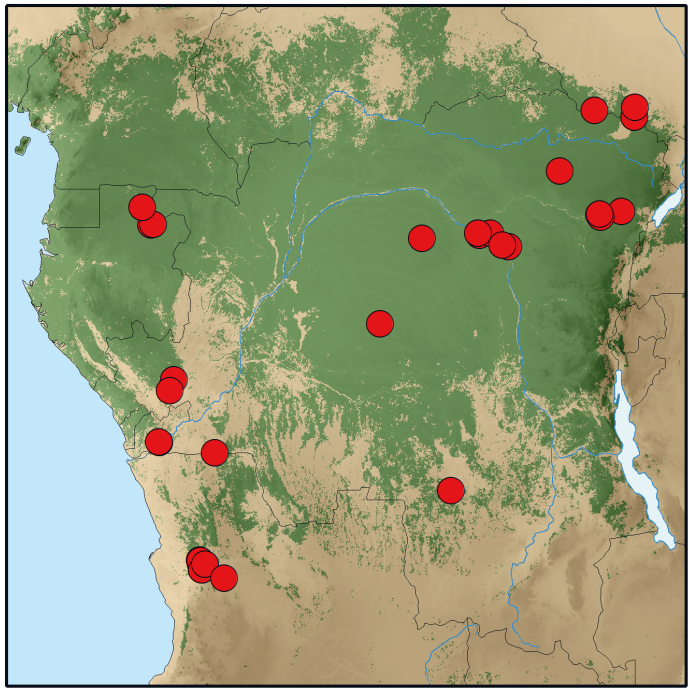
Monanthotaxis lucidula (Oliv.) Verdc. (1971b) 27. — *Unona lucidula* Oliv. (1868) 35. — *Popowia lucidula* (Oliv.) Engl. & Diels (1901) 45. — Lectotype (designated by Paiva 1966): *F.M.J. Welwitsch 762* (lecto: LISU not seen; isolecto: BM000553841), Angola, Malanje, distr. Pungo Adongo, barrancas da Pedra Songe ipsius Pruesidii, 731 m, Apr. 1857.

Unona lucidula Oliv. var. *scandens* Hiern (1896) 11. — Type: *F.M.J. Welwitsch 770* (holo: BM not seen; iso:B100460924, COI00004906, LISU not seen, P00362641), Angola, Cuanza Norte, distr. Golungo Alto.

Shrub or liana, to 10 m long; young branches sparsely covered with appressed, reddish brown hairs 0.2–0.3 mm long, becoming glabrous; old branches pale grey to pale brown. *Leaves*: petiole 3–6(–9) mm long, 0.8–1.4 mm diam, slightly grooved, indument as on branches; lamina obovate-oblong to oblanceolate, 7.8–16 by 2.6–6.6 cm, 1.8–3.5 times longer than wide, chartaceous, not punctate, glaucous below, strongly contrasting with reddish brown veins, above glabrous, but primary vein sparsely covered with appressed, yellow hairs 0.3–0.5 mm long, becoming glabrous, below sparsely covered with appressed, yellow hairs 0.2–0.4 mm long, becoming glabrous, hairs more contrasting on primary vein and veins, base cuneate, rounded to slightly subcordate, with thickened black margins, apex acute to acuminate, acumen to 20 mm long, secondary veins 8–16 per side, from base straight, halfway curving upwards, tertiary venation percurrent, hardly visible above. *Inflorescences* extra-axillary or leaf-opposed, composed of solitary flowers or more frequently of 2–6-flowered fascicle-like rhipidia; sympodial rachis 1–2.5 mm long, sparsely covered with appressed, yellow hairs 0.2–0.4 mm long; pedicels 5–21 mm long, 0.4–0.5 mm diam, fruiting pedicels 14–30 mm long, 1.1–1.4 mm diam, densely covered with appressed to ascending, yellow hairs; lower bract lanceolate, 2.8–4 by 0.9–1.2 mm, indument as on pedicel; upper bract in the lower half of the pedicel, ovate, 1.8–4 by 0.5–3 mm, indument as on pedicel; flower buds globose. *Flowers* bisexual; sepals free, covering petals in flower bud, ovate, 3.6–4.3 by 2.2–3.9 mm, apex acute, densely covered with appressed, yellow-brown hairs, persistent in fruit or slightly accrescent; receptacle c. 2 mm diam, flat; petals colour in vivo unknown, 6, in two whorls, outer petals broadly ovate, 3.5–7.2 by 3.4–5.7 mm, outside densely covered with yellow-brown, short hairs, inside covered with white-yellowish, very short hairs near the margins, inner petals narrowly elliptic to broadly ovate, 2.7–4.9 by 0.9–4.7 mm, outside densely covered with short hairs, inside glabrous, except for a few very short hairs near the apex and base; stamens 15, in one whorl, free, linear-oblong, 0.8–1.1 mm long, filaments c. 0.3 mm long, thecae latrorse to extrorse, connective truncate, prolonged outward, not hiding thecae, glabrous, staminodes absent; carpels 8–16, narrowly subcylindric-ellipsoid, 1.1–1.4 by c. 0.3 mm, densely hairy,

ovules 2–4, lateral, stigma elongate, 0.3–0.5 mm long, glabrous. *Monocarps* 2–15, colour in vivo unknown, moniliform, each part ellipsoid, 11–31 by 4.5–5.5 mm, slightly verrucose, sparsely covered with appressed hairs, becoming glabrous, apex apiculate, apiculum to 1 mm long, stipes 2–4.5 mm long. *Seeds* 1–4, ellipsoid, 7–9.5 by 4.2–5 mm, ochre-brown, apex flattened or rounded, raphe hardly visible.

Distribution — South Sudan, Democratic Republic of the Congo, Gabon, Republic of the Congo, Angola.



Map 30 Distribution of *Monanthotaxis lucidula*.

Habitat & Ecology — In primary mixed forest, secondary forest, swamp forest, gallery forest and *Gilbertiodendron* forest. Altitude: 300–1158 m. Flowering: January to May, September to November; fruiting: December to June, August.

Vernacular names — Democratic Republic of the Congo: Amapupu (*J.F. Kahindo 86*), Buba (Kibila name) (*T.B. Hart 1238*). Uganda: Umbusukundu (Zande name) (*F.W. Andrews 1544*).

Preliminary IUCN conservation status —Least concern (LC). EOO: 1,911,535 km^2, AOO: 136 km^2. This species has a wide distribution and occurs in many locations and there are a few recent collections. Therefore, this species is currently not under threat of extinction.

Notes — 1. *Monanthotaxis lucidula* is the only species of *Monanthotaxis* in Central Africa with the sepals covering the petals in bud. Vegetatively it can generally be recognized by the pale grey to pale brown branches and reddish brown secondary veins highly contrasting with the glaucous lower leafside. *Monanthotaxis lucidula* can be distinguished from other species with the sepals covering the petals in bud by the obovate to oblanceolate leaves and ovate sepals to 4.3 mm long.

2. There is some variation in the vegetative characters of *M. lucidula* across the distribution. In the west of the distribution area the branches are more pale brown, while in the east of Congo the branches are more grey-brown and the young branches are more densely hairy.

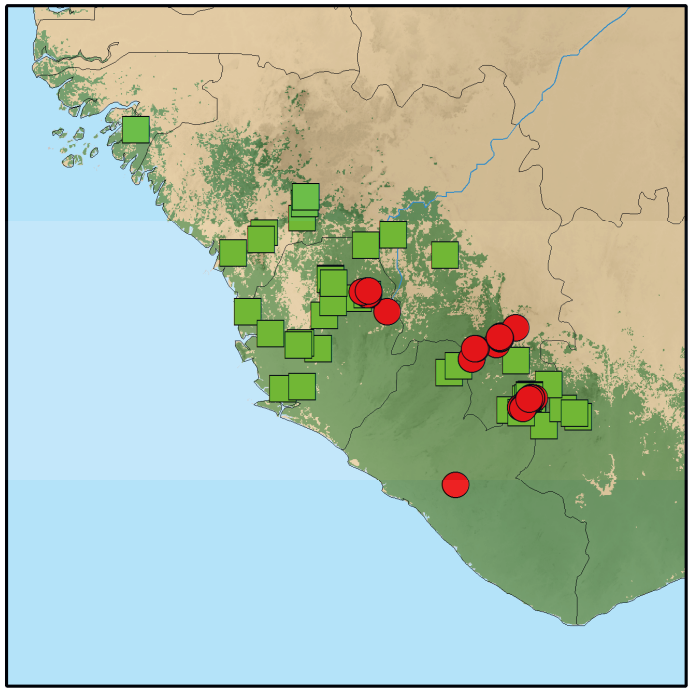
47. *Monanthotaxis mannii* (Baill.) Verdc. — Plate 4e–f; Map 31

Monanthotaxis mannii (Baill.) Verdc. (1971b) 21. — *Popowia mannii* Baill. (1868) 320. — *Clathrospermum baillonii* Scott Elliot (1894) 70, non *C. mannii* Oliv. — *Popowia baillonii* (Scott Elliot) Engl. & Diels (1901) 48, nom. superfl. — Lectotype (designated here): *G. Mann 809* (lectotype: P (P00362639); isolecto: GH, K000041018), Sierra Leone, Southern Province, Moyamba, Bagroo River, Apr. 1861.

Shrub or liana, to 3 m long; young branches densely covered with appressed, reddish brown hairs c. 0.1 mm long, becoming glabrous; old branches blackish brown to dark brown. *Leaves*: petiole 2–3.5 mm long, 0.6–1.1 mm diam, slightly grooved, indument as on branches; lamina oblong-elliptic to slightly obovate, 5.4–13 by 2–5 cm, 1.9–2.8 times longer than wide, chartaceous, not punctate, glaucous below, above glabrous, but primary vein glabrous or sparsely covered with white-yellow hairs 0.1–0.2 mm long, below sparsely covered with hardly visible appressed, white to yellow hairs 0.3–0.5 mm long, slightly more densely so on primary vein, becoming glabrous, base rounded to slightly cuneate, with slightly thickened black margin, apex acute to acuminate, acumen 5–10 mm long, secondary veins 5–9(–13) per side, curving, tertiary venation percurrent, not visible above and indistinct below. *Inflorescences* axillary, composed of solitary flowers or 2- or 3-flowered rhipidia; sympodial rachis 1.5–10(–13) mm long, densely covered with appressed to ascending, yellow hairs; pedicels 7–11 mm long, 0.2–0.3 mm diam, fruiting pedicels 5–15 mm long, 0.6–0.9 mm diam, indument as on rachis; lower bract ovate, 0.7–0.9 by 0.3–0.4 mm, indument as on rachis; upper bract in the lower half of the pedicel, ovate, c. 0.6 by 0.3–0.4 mm, indument as on rachis; flower buds globose or slightly ovoid. *Flowers* bisexual; sepals free, depressed ovate, 0.6–0.9 by 0.9–1.3 mm, apex acute, densely covered with appressed hairs, persistent in fruit or not; receptacle 1.2–1.8 mm diam, flat; petals yellow, 6, in two whorls, outer petals broadly ovate, 3.1–3.3 by 2.8–3.5 mm, outside densely covered with yellow, short hairs, base of the inside glabrous, inner petals broadly ovate to rhombic, 2.1–3.1 by 2–2.3 mm, indument as on outer petals; stamens 9 or 10, in one whorl, free, linear-oblong, 0.5–0.9 mm long, filaments 0.1–0.3 mm long, thecae introrse to latrorse, connective truncate, prolonged inward and outward, not

hiding thecae, glabrous, staminodes 9–15, in one or two whorls, inner whorl alternating with the stamens, c. 0.5 mm long, outer whorl if present c. 0.2 mm long, glabrous; carpels 12–14(–18), ellipsoid, 0.8–1 by c. 0.4 mm, densely hairy, ovules 1 (or 2), basal, stigma subsessile, globose, 0.1–0.2 mm diam, glabrous. *Monocarps* 1–10, orange, ellipsoid, 8–12 by 5–7 mm, slightly verrucose, densely covered with appressed, yellow hairs, becoming glabrous, apex rounded, stipes 1–2.5 mm long. *Seeds* 1 (or 2), ellipsoid to subglobose, 5.5–9 by 4.7–5.5 mm, ochre-brown, apex rounded, raphe visible.

Distribution — Guinea-Bissau, Guinea, Sierra Leone, Liberia, Ivory Coast.



Map 31 Distribution of *Monanthotaxis mannii* (green squares) and *M. nimbana* (red circles).

Habitat & Ecology — In gallery forest, primary forest and secondary forest on sandy clay and brown clay. Altitude: 30–957 m. Flowering: March to July; fruiting: April, June, July, September to December.

Vernacular names — Sierra Leone: Kongan (*N.W. Thomas 2993*), T'Cobwe (*N.W. Thomas 6182*), Egbor (Temne name) (*N.W. Thomas 2136*), Bowonkingime (Susu name) (*N.W. Thomas 2136*), Nomai (Limba name) (*N.W. Thomas 2136*).

Preliminary IUCN conservation status —Least concern (LC). EOO: 161,503 km^2, AOO: 168 km^2. There are many recent collections from different localities.

Notes — 1. *Monanthotaxis mannii* is together with *M. nimbana* the only species with oblong-elliptic leaves and rounded leaf base in Upper Guinea. Sterile and fruiting specimens can look very similar to *M. nimbana*, but the majority of the fruits generally have more than 3 monocarps. The flowers of *M. mannii,* however, are very different from *M. nimbana*, and the phylogeny reconstruction shows that they are not related (Fig. 1, clade C and F). The flowers of *M. mannii* consist of one whorl of stamens and one or two whorls of staminodes, while *M. nimbana* has two whorls of stamens. Also *M. mannii* has more carpels than *M. nimbana* (12–14 versus 2–5).

2. Most specimens of *M. mannii* have one whorl of staminodes and a few specimens have an additional whorl of 6 staminodes. There is one specimen from Guinea that has 15 staminodes in one whorl.

48. *Monanthotaxis maputensis* P.H.Hoekstra — Fig. 21; Map 10

Monanthotaxis maputensis P.H.Hoekstra in Hoekstra et al. (2016) 91. — Type: *J. de Koning 7766* (holo: WAG0349310; iso: LMA not seen, MO3880761), Mozambique, Maputo, Moamba, Chinhanguanine, margem esquerda do rio Incomáti, 14 Dec. 1979.

Shrub, scandent shrub or liana, to 10 m long, to 3 cm diam; young branches reddish brown, sparsely covered with appressed or erect, pale brown hairs c. 0.4 mm long, soon becoming glabrous; old branches dark brown. *Leaves*: petiole 2–4 mm long, 0.7–1 mm diam, grooved, indument as on branches; lamina elliptic, ovate to obovate or narrowly so, 2.8–6.7(–8.1) by 1.5–3.3 cm, 1.6–2.7(–3.3) times longer than wide, chartaceous to coriaceous, often punctate, discolorous, shiny dark green above, glaucous to pale green below, primary vein yellowish or reddish, above sparsely covered with appressed yellowish hairs c. 0.2 mm long, becoming glabrous, below covered with appressed yellowish to pale brown hairs c. 0.2 mm long, becoming glabrous, base cuneate to rounded, with slightly thickened margins, apex obtuse to acute, secondary veins 5–8 per side, from base curving upwards, tertiary venation reticulate, raised above and slightly raised or not visible below. *Inflorescences* leaf-opposed, composed of solitary flowers or 2- or 3-flowered rhipidia; sympodial rachis 0–3 mm long; pedicels 6–14 mm long, 0.3–0.4 mm diam, indument as on branches, fruiting pedicels 0.4–0.9 mm diam, becoming glabrous; lower bracts broadly ovate, c. 1.5 by 1.4 mm, indument as on pedicel; upper bract placed near middle of pedicel, broadly triangular to broadly ovate, c. 0.5 by 0.5 mm, indument as on pedicel; flower buds ovoid. *Flowers* bisexual; sepals slightly connate, depressed ovate, 0.5–0.7 by 1.5–2 mm, apex obtuse, covered with reddish brown, short hairs near the margins, persistent in fruit; receptacle 2–3 mm diam, flat, covered with brown, short hairs between the carpels and stamens; petals pale yellowish to yellow, inside drying reddish brown to

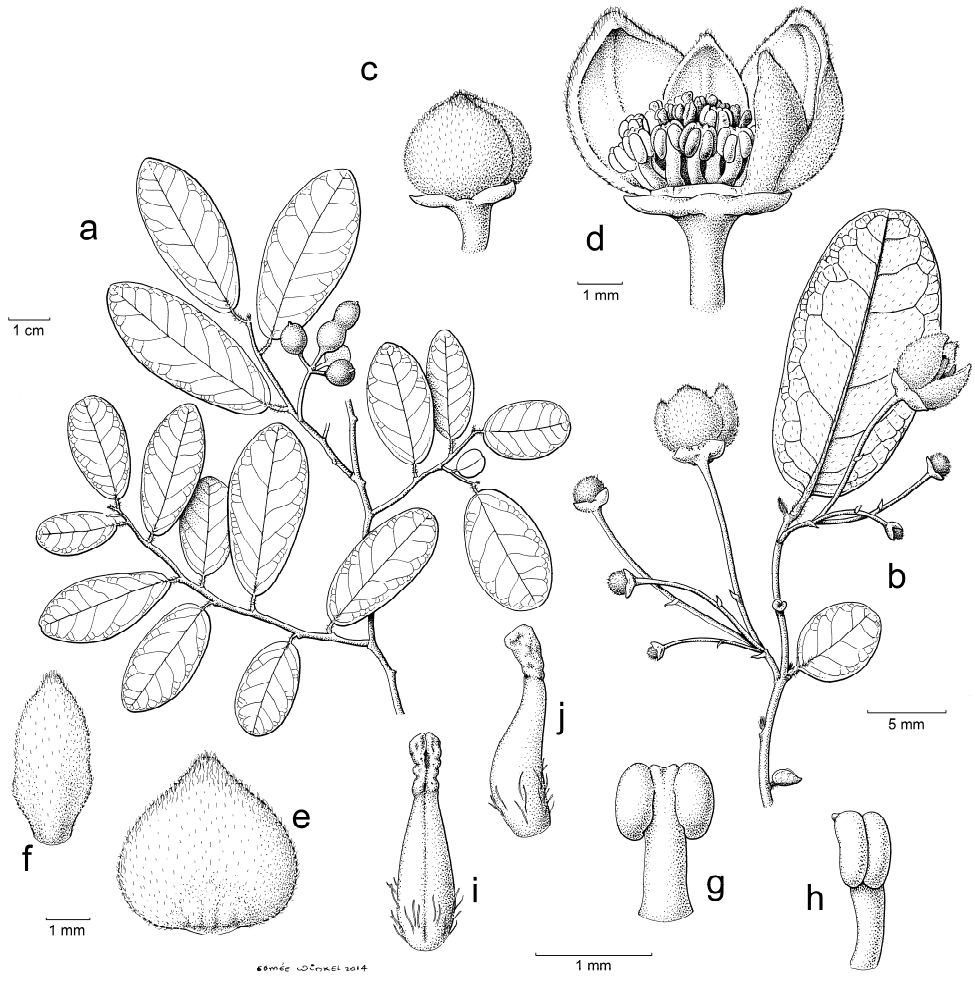


Fig. 21 *Monanthotaxus maputensis* P.H.Hoekstra: a. Fruiting branch; b. flowering branch; c. flower bud; d. flower with one outer and one inner petal removed; e. outer petal, outside view; f. inner petal, outside view; g. stamen, inside view; h. stamen, side view; i. carpel, inside view; j. carpel, side view (a: *Mendonça 4480*; b–j: *Exell 565*). Drawing by E. Winkel.

purple, 6, in two whorls, outer petals broadly ovate, 2.5–4 by 3.2–4 mm, outside covered with yellowish, short hairs, more densely so near the margins, inside densely covered with hairs at the apex, inner petals ovate to elliptic, 3–3.4 by 1.7–2.2 mm, outside and inside covered with hairs at the apex; stamens 12–15, in one or two whorls, free, obconical to clavate, 0.8–1.2 mm long, filaments 0.4–0.8 mm long, thecae latrorse, 0.3–0.5 mm long, connective truncate, glabrous, staminodes absent; carpels 10–13, narrowly subcylindric to ellipsoid, 1.2–1.6 by 0.4–0.5 mm, glabrous, except for some hairs at the base, ovules 1 (or 2), basal, stigma elongate, 0.3–0.4 mm long, grooved, glabrous. *Monocarps* 1–10, bright red when ripe, globose to

ellipsoid, 7.5–15 by c. 5 mm, 2-seeded ones to 19 mm long, rugulose to smooth, glabrous, apex apiculate, apiculum c. 0.5 mm long, stipes 2.5–4 mm long, slightly to strongly grooved, sparsely covered with appressed hairs when young. *Seeds* 1 (or 2), globose to ellipsoid, 5.5–8 by 4.5–6.6 mm, ochre-brown, both ends rounded, raphe not visible.

Distribution — Mozambique (Gaza, Maputo), South Africa (Kwazulu-Natal).

Habitat & Ecology — In different types of thickets and forests on sandy soils. Altitude: 0–150 m. Flowering: February to April, November, December; fruiting: March to September.

Preliminary IUCN conservation status —Least concern (LC). EOO: 43,433 km^2, AOO: 128 km^2. This species is known from at least 3 nature reserves and more than 10 different localities. The species can be quite common in the coastal dunes of Mozambique. Therefore, *M. maputensis* is currently not under threat of extinction.

Notes — *Monanthotaxis maputensis* is the only species of *Monanthotaxis* present in South Mozambique and just over the border in South Africa, although the distribution almost overlaps with *M. caffra*. It is closely related with that species and the only reliable characters to distinguish them are the shape of the stamens and the filament length. For further details see the note under *M. caffra*.

49. *Monanthotaxis mcphersonii* P.H.Hoekstra**, *sp. nov.*** — Fig. 22; Plate 5a, b; Map 28

Monanthotaxis mcphersonii is together with *Monanthotaxis scamnopetala* the only species in the genus with 3 sessile monocarps having seeds in 2 rows. It differs from *M. scamnopetala* in the long, erect hairs (versus short, appressed hairs) and the 3–5 cm long, supra-axillary flowering pedicels (versus 0.5–1.5 cm long axillary pedicels). — Type: *G.D. McPherson 15708* (holotype: WAG (WAG0031254); iso: B100010096, BR0000013211295, LBV, MO, NY, P01982194, US), Gabon, Ogooué-Ivindo, south of Ayem, western border of Lopé-Okanda Reserve, along lumber roads south of SEEF chantier, 200 m, 29 Dec. 1991. Paratypes: *T.L.P. Couvreur et al. 528* (WAG, YA), Gabon, Estuaire, forêts des conservateurs, near road to Cape Esterias, 35 m, 5 Nov. 2013; *T.L.P. Couvreur et al. 862* (LBV, WAG, YA), Gabon, Woleu-Ntem, c. 15 km south of Mitzic, in Foreex concession, c 4 km after leaving main road (N2), 543 m, 14 Nov. 2015; *T.L.P. Couvreur et al. 881* (LBV, WAG, YA), Gabon, Woleu-Ntem, on road from Mitzic to Lalara (N2), just after the bridge over the Lara, c 500 m in forest, 561 m, 15 Nov. 2015; *J.M. Reitsma 2977* (LBV, MO, NY, WAG), Gabon, Woleu-Ntem, c. 4 km NNE of Oveng, 887 m, 11 Feb. 1987.

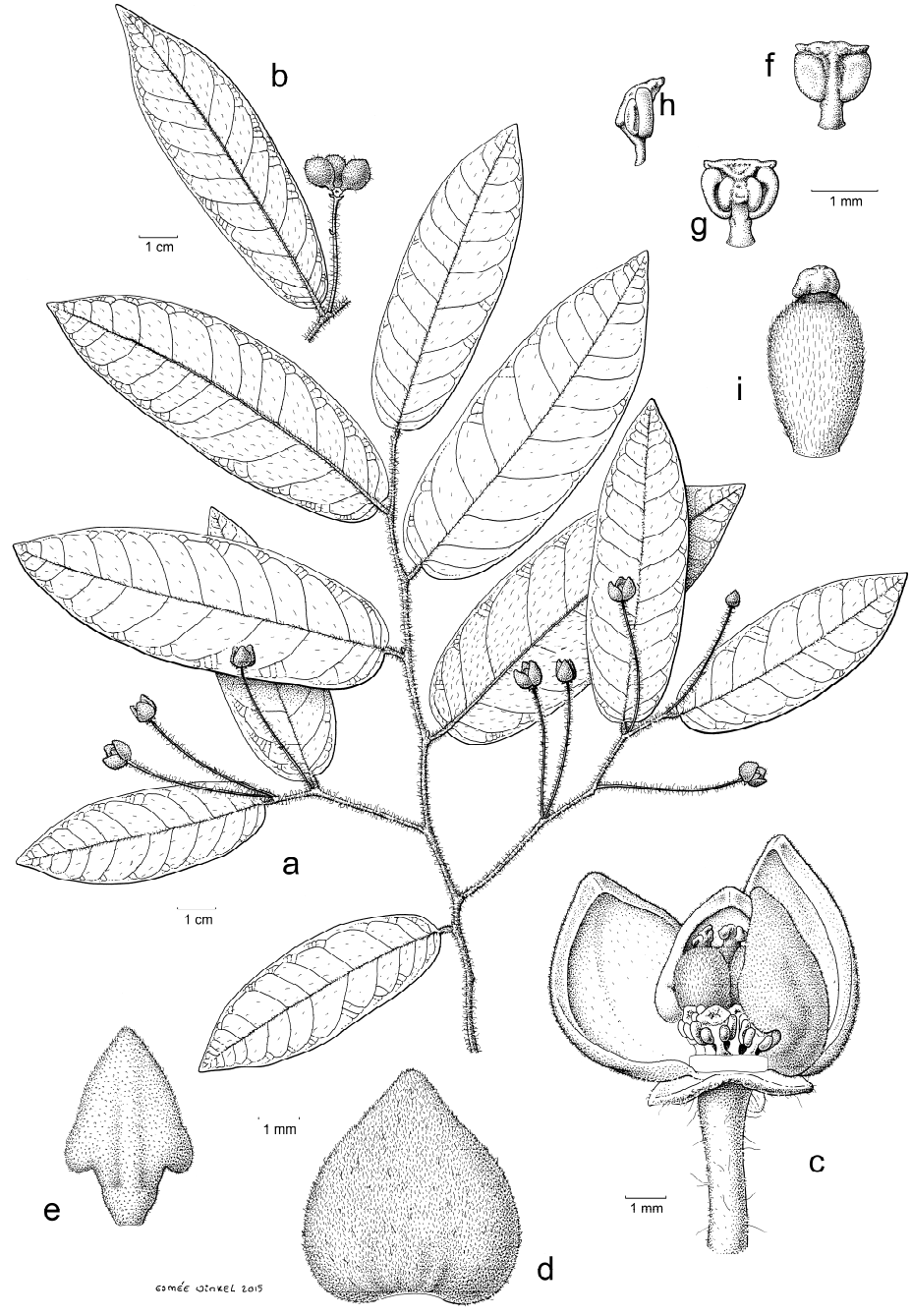


Fig. 22 *Monanthotaxis mcphersonii* P.H.Hoekstra: a. Flowering branch; b. fruiting branch; c. flower with one outer and one inner petal removed; d. outer petal, outside view; e. inner petal, outside view; f. stamen, inside view; g. stamen, outside view; h. stamen, side view; i. carpel (*G.D. McPherson 15708*). Drawing by E. Winkel.

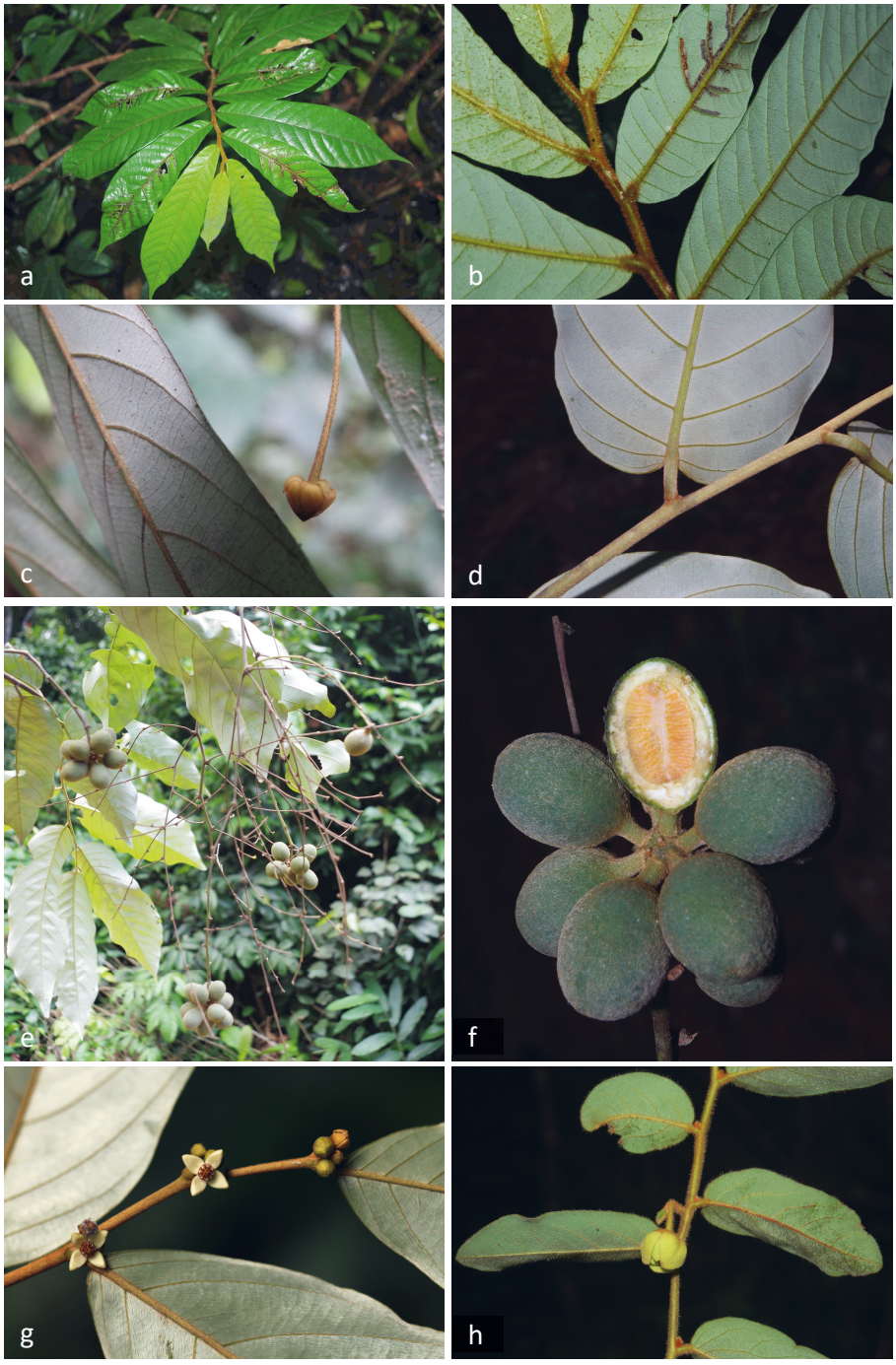


Plate 5 a, b. *Monanthotaxis mcphersonii* P.H.Hoekstra: a. Leaves above; b. leaves below. — c. *Monanthotaxis montana* (Engl. & Diels) P.H.Hoekstra: Flower bud. — d–f. *Monanthotaxis paniculata* P.H.Hoekstra: d. Leaves; e. inflorescence with fruits; f. fruit. — g. *Monanthotaxis*

poggei Engl. & Diels: Flowering branch. — h. *Monanthotaxis suffruticosa* P.H.Hoekstra: Flowering branch (a, b: *Couvreur 528*; c: *Couvreur 891*; d–f: *Couvreur 1108*; g. photographed in Democratic Republic of the Congo, no specimen collected; h: *Lötter 1741*). Photos: a, b, d–f: T.L.P.Couvreur; c: P.H.Hoekstra; g: B.Würsten; h: M.C. Lötter.

Liana, to 20 m long; young branches blackish, covered with erect, reddish brown hairs c. 2 mm long; old branches as young branches. *Leaves*: petiole 3–6 mm long, 0.8–1.2 mm diam, grooved, indument as on branches; lamina narrowly oblong-elliptic, 6.5–11.7 by 2.3–3.9 cm, 2.8–3.9 times longer than wide, chartaceous, not punctate, glaucous below, above sparsely covered with appressed hairs c. 1 mm long, more densely covered with erect hairs on primary vein, below sparsely covered with erect, yellowish hairs c. 2 mm long, base cuneate, rounded to subcordate, with slightly thickened margins, apex acute, primary vein reddish brown, secondary veins 8–14 per side, curving upwards, tertiary venation percurrent. *Inflorescences* supra-axillary, composed of solitary flowers or 2-flowered rhipidia; sympodial rachis 0–1 mm long; flowering and fruiting pedicels 31–48 mm long, 0.3–0.5 mm diam, covered with erect, reddish brown hairs; lower bracts absent; upper bract at c. one-third of the pedicel, ovate, 1–1.2 by 0.5–0.6 mm, densely covered with appressed hairs; flower buds ovoid. *Flowers* bisexual; sepals free, ovate to broadly ovate, 1.3–1.7 by 1.2–1.4 mm, apex acute, densely covered with appressed, yellowish hairs, persistent in fruit; receptacle 1.5–2 mm diam, convex; petals dull yellow at the outside, inside beige with white base, 6, in two whorls, outer petals ovate to broadly ovate, 5–7 by 5–6 mm, densely covered with appressed, yellowish hairs, except for the glabrous base of the inside, inner petals rhombic, 5–6 by 2.5–3 mm, claw c. 2 mm long, outside and apex and base of the claw on the inside densely covered with appressed hairs; stamens 15, in two whorls, free, in groups of 5 opposite the outer petals, brown, obconical, 1–1.5 mm long, filaments 0.3–0.5 mm long, thecae extrorse, connective truncate, slightly prolonged inward, hiding thecae seen from above, glabrous, staminodes absent; carpels 3, ellipsoid, c. 3 by 1.4 mm, densely covered with yellow hairs, ovules 12–14, in two rows, lateral, stigma globose, c. 0.5 mm diam, slightly grooved, glabrous. *Monocarps* 1–3, yellowish brown, immature monocarps subglobose, c. 6.5 by 7 mm, stipes to 1 mm long. *Seeds* 2, immature, dark brown.

Distribution — Gabon (Estuaire, Ogooué-Ivindo, Woleu-Ntem).

Habitat & Ecology — In primary rainforest and old secondary forest. Altitude: 35–-887 m. Flowering: December; fruiting: February.

Preliminary IUCN conservation status —Endangered (EN): B2ab(iii). EOO: 15,157 km^2, AOO: 20 km^2. This species is known from 5 collections from 3 localities of which one in the Lopé National Park. However, the location in Woleu-Ntem is under pressure of habitat degradation by logging companies and the location in Estuaire by the expanding city of Libreville

Ethymology — This species is named after Gordon McPherson, collector of the type of this species, and of several other species of *Monanthotaxis*, including the type specimen of *M. paniculata* and the single paratype of *M. aestuaria.*

Note — *Monanthotaxis mcphersonii* can easily be recognized by the narrow oblong-elliptic leaves and the long erect hairs on the stems and leaves.

50. *Monanthotaxis montana* (Engl. & Diels) P.H.Hoekstra — Fig. 10h–o; Plate 5c; Map 32

Monanthotaxis montana (Engl. & Diels) P.H.Hoekstra in Guo et al. (2017) 15. — *Unona montana* Engl. & Diels (1899) 296. — *Oxymitra montana* (Engl. & Diels) Sprague & Hutch. (1916) 155. — *Richella montana* (Engl. & Diels) R.E.Fr. (1959) 139. — *Friesodielsia montana* (Engl. & Diels) Steenis (1964) 360. — Type: *G.A. Zenker* & *A. Staudt 431a* (holo: B100153061), Cameroon, Central Province, Yaúnde-station, 11 Jan. 1894.

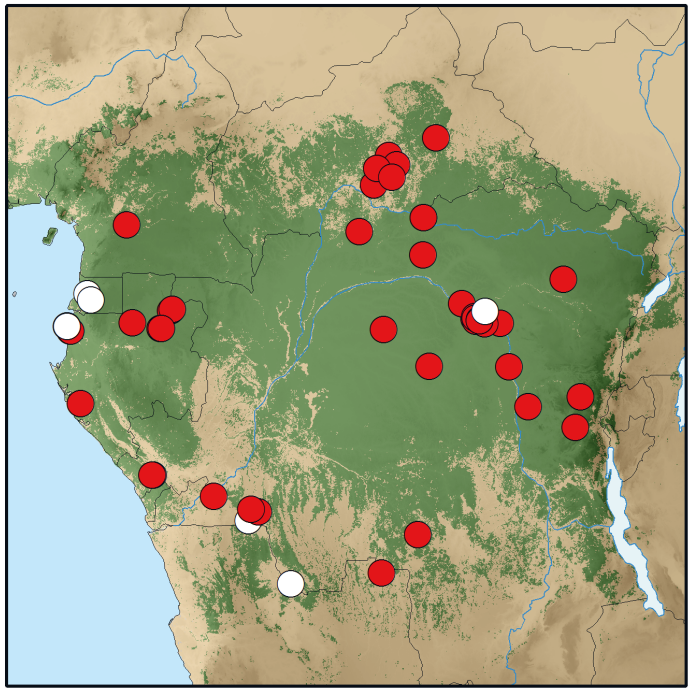
Unona glauca Engl. & Diels (1899) 296, pro parte. — *Oxymitra soyauxii* Sprague & Hutch. (1916) 155, non *O. glauca* Hook.f. & Thomson (1855: 146). — *Richella soyauxii* (Sprague & Hutch.) R.E.Fr. (1959) 139, non *R. glauca* (Hook.f. & Thomson) R.E.Fr. (1959: 139). — *Friesodielsia soyauxii* (Sprague & Hutch.) Steenis (1964) 361, non *F. glauca* (Hook.f. & Thomson) Steenis (1964: 359). — Lectotype (designated by Guo et al. 2017): *H. Soyaux 203* (lecto: B100153059; isolecto: K000198946), Gabon, Estuaire, Sibange farm, 6 Feb. 1881.

Oxymitra mortehanii De Wild. (1922) 472. — Type: *M.G. Mortehan 512* (holo consisting of 3 sheets: BR000008800459, BR000008800060, BR000008800787), Democratic Republic of the Congo, Equateur, Dundusana, Sep. 1913.

Liana, to 7 m long, to 1 cm diam; young branches blackish brown, densely covered with appressed to ascending, reddish brown hairs 0.2–0.3 mm long, becoming glabrous; old branches blackish brown to dark grey. *Leaves*: petiole 2.5–6 mm long, 0.8–1.5 mm diam, slightly grooved, indument as on branches; lamina elliptic to obovate or narrowly so, 5.5–20 by 2.8–6.7 cm, (1.3–)1.8–2.6(–3.3) times longer than wide, subcoriaceous, not punctate, glossy dark green above, drying dark grey, pale glaucous below, above glabrous, but primary vein densely covered with ascending, yellow hairs, becoming glabrous, below covered with appressed, yellow-brown hairs 0.2–0.4 mm long, more densely so on the primary vein, base subcordate, with thickened black margin, apex acute to acuminate, acumen to 15 mm long, secondary veins 7–13 per side, slightly curving, tertiary venation percurrent, not visible above. *Inflorescences* extra-axillary, composed of solitary flowers or sometimes to 4-flowered fascicle-like rhipidia; sympodial rachis 0.5–5 mm long, indument as on young branches; pedicels 13–33 mm long, 0.4–0.5 mm diam, fruiting pedicels 28–38 mm long, 0.4–0.9 mm diam, sparsely covered with ascending, reddish brown hairs c. 0.2 mm long; lower bract ovate, 1–1.1 by 0.4–0.6 mm, densely covered with appressed, yellowish hairs; upper bract absent or very close to the base of the pedicel, ovate, 0.6–0.9 by 0.4–0.5 mm, densely covered with appressed, yellowish hairs; flower buds ovoid. *Flowers* bisexual; sepals free, ovate, 1.2–2 by 0.8–1.5 mm, reflexed at anthesis, apex acute, densely covered with hairs, not persistent in fruit; receptacle 1.7–2.7 mm diam, convex to torus-like, 1.1–1.3 mm high; petals yellow to green on the outside, purple-black on the inside, 6, in two whorls, reflexed at anthesis, outer

petals ovate to spathulate, 6–15 by 5.4–6.7 mm, outside and the upper half of the inside sparsely covered with yellow hairs, inner petals cordate, 5.8–7.5 by 4.5–9 mm, glabrous; stamens 36–48, in 3–5 whorls, free, linear-oblong, 0.8–0.9 mm long, filaments c. 0.1 mm long, thecae extrorse, connective truncate, hiding thecae, glabrous, staminodes absent; carpels 11–14, narrowly ellipsoid, 1.1–1.9 by 0.5–0.6 mm, dense hairy, ovules 1–3, lateral, stigma globose, c. 0.2 mm diam, glabrous. *Monocarps* 4–11, yellow with red stripes or dull red, moniliform, each part ellipsoid, 12–33 by 4–9 mm, slightly verrucose, densely covered with appressed hairs, becoming glabrous, apex rounded to apiculate, apiculum to 1.5 mm long, stipes 3–8 mm long. *Seeds* 1–3, ellipsoid, 10.5–12 by 5–6 mm, ochre-brown, apex rounded or flattened, raphe hardly visible.

Distribution —Cameroon, Central African Republic, Democratic Republic of the Congo, Gabon, Republic of the Congo, Angola.



Map 32 Distribution of *Monanthotaxis montana* (red circles, white circles are uncertain dets).

Habitat & Ecology — In primary evergreen forest, secondary forest, swamp forest, gallery forest, terra firme forest and low spiny forest, on rocky soil and on river banks. Altitude: 5–1030 m. Flowering and fruiting all year round.

Vernacular names — Democratic Republic of the Congo: Biembré (*M.G. Mortehan 512*), Kitsaka tsamba (*L. Pauwels 3490*).

Preliminary IUCN conservation status —Least concern (LC). EOO: 2,218,732 km^2, AOO: 188 km^2. This species has a wide distribution from many locations.

Note — *Monanthotaxis montana* can be recognised by the combination of small, reflexed, ovate sepals, many stamens in multiple whorls, and a grey upper leaf side in sicco.

51. *Monanthotaxis mortehanii* (De Wild.) Verdc. — Map 33

Monanthotaxis mortehanii (De Wild.) Verdc. (1971b) 31. — *Popowia mortehanii* De Wild. (1914) 381. — Type: *M.G. Mortehan 722* (holo: BR0000008824073), Democratic Republic of the Congo, Equateur, Bumba, Dundusana, Nov. 1913.

Liana; young branches dark brown covered with erect, reddish brown hairs 0.05–0.1 mm long, soon becoming glabrous; old branches brown. *Leaves:* petiole 5–9 mm long, 2.4–2.9 mm diam, grooved, indument as on branches; lamina obovate, 15–23 by 8–10 cm, 1.9–2 times longer than wide, chartaceous, not punctate, glaucous below, above glabrous, below sparsely covered with appressed, yellowish to reddish brown hairs c. 0.1 mm long, veins with slightly more dense indument, base rounded to subcordate, with thickened black margin, apex acute to shortly acuminate, acumen to 1 mm long, secondary veins 12–15 per side, straight, tertiary venation percurrent. ♂ *Inflorescences* unknown. ♀ *Inflorescences* cauliflorous, condensed many-flowered glomerules or panicles to 6 cm long; sympodial rachis 2–3 cm long, covered with erect, reddish brown hairs 0.4–0.6 mm long; flowering pedicels 10–25 mm long, 0.8–1 mm diam, indument as on rachis; bracts broadly ovate, 1.5–1.8 by 1.5–1.8 mm, indument as on rachis; flower buds ovoid. ♀ *Flowers*: sepals free to slightly connate, broadly ovate to broadly triangular, c. 2.1 by 2.3 mm, densely covered with reddish brown hairs c. 0.1 mm long; receptacle c. 1.7 mm diam, convex; petals colour in vivo unknown, 6, in two whorls, free; outer petals broadly ovate, 6.1–6.2 by 6.1–6.3 mm, outside densely covered with reddish brown hairs c. 0.2 mm long, inside densely covered with yellowish papillae, inner petals spathulate, c. 1.8 by 0.9 mm, outside and inside densely covered with yellowish papillae; carpels c. 106, narrowly ellipsoid, 1.5–1.6 by 0.5–0.6 mm, densely hairy, ovules 6, lateral, stigma elongate, 0.4–0.5 mm long, slightly grooved at the apex, glabrous. *Monocarps* and *seeds* not seen.

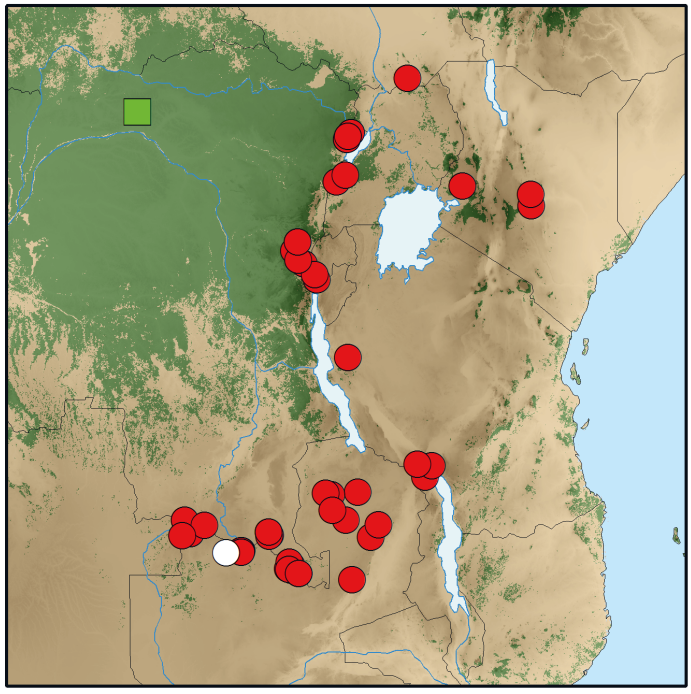
Distribution — Democratic Republic of the Congo (Equateur).

Habitat & Ecology — In forest. Flowering: November.

Preliminary IUCN conservation status —Critically endangered (CR): B2ab(iii). AOO: 4 km^2. This species is only known from one collection from more than 100 years ago.

Notes — *Monanthotaxis mortehanii* is only known from the type specimen. It can be distinguished from other cauiflorous species of *Monanthotaxis* by the appressed, short hairs on the young branches, erect, long hairs on the pedicels and by having more than 100 carpels.

Furthermore, it has wider leaves, longer and broader petioles than other species with unisexual flowers.



Map 33 Distribution of *Monanthotaxis mortehanii* (green square) and *M. ochroleuca* (red circles, white circle isuncertain det).

52. *Monanthotaxis nimbana* (Schnell) Verdc. — Map 31

Monanthotaxis nimbana (Schnell) Verdc. (1971b) 27. — *Popowia nimbana* Schnell (1953) 93. — Type: *R.A.A. Schnell 5202* (holo consisting of 2 sheets: P00362636, P00362637), Guinea, Nzérékoré, forêt montagneuse du Nimba, forêt des crêtes du Nimba S.W., Apr. 1950.

Scandent shrub or liana, to 5 m long; young branches densely covered with appressed, reddish brown hairs 0.1–0.2 mm long, becoming glabrous, old branches blackish brown. *Leaves:* petiole 2–8 mm long, 0.6–0.9 mm diam, terete, indument as on branches; lamina narrowly oblong-elliptic to narrowly obovate, 4.9–12.6 by 1.7–4.1 cm, 2.5–3.4 times longer than wide, chartaceous, not punctate, pale bluish green below, above sparsely covered with appressed, white hairs 0.4–0.5 mm long, primary vein hairs more densely covered with yellowish and longer persistent hairs, becoming glabrous, below sparsely covered with appressed, yellowish hairs 0.1–0.3 mm long, base rounded to slightly subcordate, with thickened black margin, apex

acute to acuminate, acumen to 15 mm long, secondary veins 9–13 per side, curving, tertiary venation percurrent. *Inflorescences* axillary or terminal, composed of solitary flowers; sympodial rachis absent; flowering and fruiting pedicels 9–45 mm long, 0.3–0.5 mm diam, sparsely covered with appressed, yellowish hairs; lower bract absent; upper bract in upper half of the pedicel, ovate to lanceolate, 0.7–1.8 by 0.3–0.6 mm, indument as on pedicel; flower buds globose. *Flowers* bisexual; sepals free, broadly ovate, 1–1.3 by 0.9–1.4 mm, apex acute, densely covered with appressed hairs, persistent in fruit; receptacle c. 1.5 mm diam, flat; petals colour in vivo unknown, 6, in two whorls, base of inner petals visible in bud, outer petals broadly ovate, 2.1–3.5 by 1.9–3.3 mm, outside and apical part and margins on the inside covered with yellow hairs, inner petals elliptic, 1.5–3.4 by 0.9–2.1 mm, indument as on outer petals; stamens 16–18, in two whorls, free, linear-oblong, 0.8–1.2 mm long, filaments c. 0.6 mm long, thecae introrse, connective truncate, prolonged outward, not hiding thecae, glabrous or sometimes hairy, staminodes absent; carpels 2–5, ellipsoid, 1.1–1.2 by c. 0.7 mm, densely hairy, ovule 1, basal, stigma elongate, 0.4–0.5 mm long, glabrous. *Monocarps* 1–5, orange, ellipsoid to narrowly ellipsoid, 12–18 by 5.5–6 mm, slightly verrucose, densely covered with appressed, white-yellowish hairs, becoming glabrous, apex apiculate, apiculum to 0.5 mm long, stipes 1–5 mm long. *Seed* 1, ellipsoid, 8.5–10 by 5.5–6 mm, ochre-brown, apex rounded, raphe visible.

Distribution — Guinea, Sierra Leone, Liberia, Ivory Coast.

Habitat & Ecology — In montane forest, gallery forest and sub-montane scrub, on rocky soils, steep slopes and hill-crests. Altitude: 700–1615 m. Flowering: January to August; fruiting: June to March.

Preliminary IUCN conservation status —Least concern (LC). EOO: 49,713 km^2, AOO: 112 km^2. This species is common in the Nimba mountains and some other mountain ridges in the south of Guinea. It must however be noted that this species has not been collected in Sierra Leone in the last 50 years.

Notes — 1. *Monanthotaxis nimbana* is the only species of *Monanthotaxis* with axillary inflorescences, the stamens in two whorls and with 2–5 carpels per flower. Most specimens can be readily recognised by having fruits with only 1–3 1-seeded monocarps.

2. Some specimens from Mount Loma in Sierra Leone are different from the majority of specimens in having shorter pedicels, 8–15 mm long, and narrowly obovate leaves and the only specimen with flowers has small hairs on the connectives, however, there are also specimens with longer pedicels and oblong-elliptic leaves on Mount Loma. More material is needed in combination with phylogenetic analyses of molecular characters to define if that population belongs to a different entity.

53. *Monanthotaxis obovata* (Benth.) P.H.Hoekstra — Fig. 15h–o; Map 34

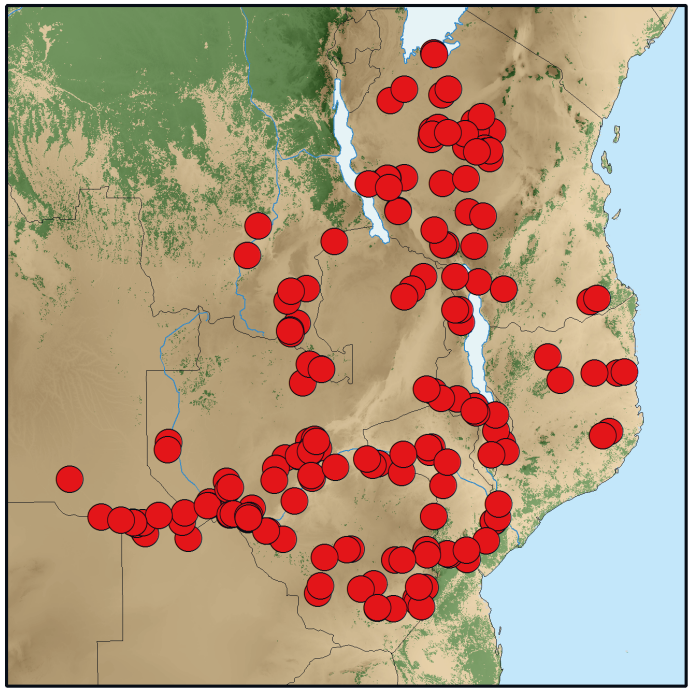
Monanthotaxis obovata (Benth.) P.H.Hoekstra in Guo et al. (2017) 15. — *Unona obovata* Benth. (1862) 469. — *Popowia obovata* (Benth.) Engl. & Diels (1901) 44. — *Friesodielsia obovata* (Benth.) Verdc. (1971b) 18. — Type: *J. Kirk s.n.* (holo consisting of 2 sheets: K000199033, K000199034; iso: B100153064), Mozambique, Zambezia, foot of Mt. Morambala, 31 Dec. 1858.

Popowia stormsii De Wild. (1905a) 242. — Type: *E.P.J. Storms s.n.* (holo: BR000008799258), Tanzania, Rukwa, Karema.

Small tree, shrub, scandent shrub or liana, 1–6(–9) m long; young branches yellowish brown, densely covered with ascending, white-yellowish hairs 0.2–0.4 mm long, becoming glabrous; old branches greyish brown. *Leaves:* petiole 3–8 mm long, c. 1 mm diam, slightly grooved, indument as on branches; lamina obovate to obovate-oblong, 4.5–14 by 3–9.5 cm, 1.2–2.5 times longer than wide, chartaceous, not punctate, discolorous, green above, paler and glaucous with yellowish veins below, above and below densely covered with simple or sometimes stellate, white or yellowish hairs 0.3–0.5 mm long, becoming glabrous, base rounded to subcordate, with small glands, apex rounded to emarginate, secondary veins 8–11 per side, curving upwards, tertiary venation slightly percurrent or loosely reticulate, slightly raised above and below. *Inflorescences* terminal or leaf-opposed, composed of solitary flowers; sympodial rachis absent; flowering and fruiting pedicels 28–50 mm long, 1–2 mm diam, indument as on petiole, but less dense; lower bract absent; upper bract near the base of the pedicel, large and leafy, circular to broadly ovate, 8–16 mm long, indument same as on leaves; flower buds depressed globose. *Flowers* bisexual; sepals free, broadly ovate to orbicular, 6–7 by 5–7 mm, apex rounded to acute, densely covered with white, short hairs, not persistent in fruit; receptacle c. 3–10 mm diam, convex; petals creamy white to yellowish green, 6, in two whorls, outer petals broadly ovate, rounded to reniform, 6–14 by 5–17 mm, outside covered with hairs, inside glabrous at the base, inner petals rhombic to broadly ovate, narrowed at the base, not covering stamens entirely in bud, 3–6 by 3–5 mm, indument as on outer petals; stamens 50–80, in three or four whorls, free, oblong to obconical, c. 1.2 mm long, filaments c. 0.2 mm long, thecae latrorse, connective truncate, square, pentagonal to rhombic seen from above, glabrous, staminodes absent; carpels 17–30, ellipsoid, c. 1.2 by 0.6 mm, densely covered with yellow hairs, ovules 4, lateral, stigma subsessile, ellipsoid, oblongoid to globose, c. 0.3 mm long, grooved, glabrous. *Monocarps* up to 11, orange-red, narrowly ellipsoid to cylindric, 27–90 by 7–8 mm, sparsely covered with appressed hairs, apex rounded or slightly apiculate, stipes 8–27 by 1–2 mm. *Seeds* 1–4, cylindric-ellipsoid, 13–18 by 6–7 mm, tawny, apiculate, raphe not visible.

Distribution — Democratic Republic of the Congo, Tanzania, Angola, Zambia, Zimbabwe, Malawi, Mozambique, Namibia, Botswana.

Habitat & Ecology — In open woodland (mostly composed of *Brachystegia*), grassland, termite mounds and rocky outcrops. Altitude: 65–1380 m. Flowering: September to March, June; fruiting: November to August.



Map 34 Distribution of *Monanthotaxis obovata*.

Vernacular names — Botswana: Muchinga (Sikololo name) (*O.B. Miller 5*). Democratic Republic of the Congo: Kapurema (Kibemba name) (*F. Malaisse 6393*). Malawi: Mchinga (*R.G.R. Townsend 3*), Mcinka (*P.G. Adlard 226*). Mozambique: Maiyako (Macua name) (*A.L. Maite 169*), Munchinga (*F.A. Mendonça 3653*), Meginga (*E.C. Andrada 1002*), N'Chinga (*J.M. de Aguiar Macêdo 4728*), Nécupo (Macua name) (*A.R. da Torre 9732*). Namibia: Kalundamambo (Kwangali name) (*S. Austaller 10*), Mkondekonde (Mbukushu name) (*H.H. Kolberg 608*). Tanzania: Msalansi (Kinyamwezi name) (*G.T. Mwiga 120*), Msalasi (Kinyiramba name) (*O.A. Kibure 1180*), Msarasi (Nyanwesi name) (*R. Ludanga 2699*), Msalusi (Nyam name) (*V.C. Gilbert 5235*). Zambia: Monchinga (*J.J.A. Jalla s.n.*), Muchinga (Tonga and Soli name) (*F. White 1907*), Muchinga-chinga (*O.B. Miller 104*), Muchinga (Lozi name) (*E. Fewdays 3*). Zimbabwe: Muchinga (Shona name) (*I. Mukuya 45*)

Preliminary IUCN conservation status —Least concern (LC). EOO: 2,642,412 km^2, AOO: 704 km^2. This is the species with the highest number of collections. It occurs in many locations including several national Parks. This species is not under threat of extinction.

Uses — Edible raw and cooked (Facciola 1998). Boiled roots are used as a medicine against snakebites, stomach-ache and infertility in women (Ruffo et al. 2002). The wood is used to make walking sticks, withies, grain stores and as firewood (Ruffo et al. 2002).

Note — *Monanthotaxis obovata* is easily recognisable by the leafy upper bract and broadly obovate leaves, which are glaucous below and have conspicuous yellow veins.

54. *Monanthotaxis ochroleuca* (Diels) P.H.Hoekstra, *comb. nov*. — Map 33

Popowia ochroleuca Diels, Bot. Jahrb. Syst. 53 (1915) 441. — *Enneastemon ochroleucus* (Diels) R.E.Fr. (1953) 41. — Lectotype (designated here): *A.F. Stolz 170* (lectotype: B (B100153045); isolecto: B100153044, BM000547360, G00308344, HBG-502504, K000198973, K000198974, L 0038041, L 0188030, M-0107926, MO, S, US, WAG0000091), Tanzania, Mbeya, Rungwe district, station Kyimbila, 1300 m, 2 Sep. 1907.

Popowia ochroleuca Diels var. *keniensis* R.E.Fr. in R.E.Fr. & T.C.E.Fr. (1925) 321. — *Enneastemon ochroleucus* (Diels) R.E.Fr. var. *keniensis* (R.E.Fr.) R.E.Fr. (1953) 41. — Lectotype (designated by Verdcourt 1971a: 94): *R.E. Fries 1998* (holo: UPS; iso: B100460760), Kenya, Eastern, Chuca, 26 Feb. 1922.

Scandent shrub or liana, to 5 m long; young branches densely covered with appressed, reddish brown hairs 0.1–0.2 mm long or ascending hairs 0.2–0.3 mm long, becoming glabrous; old branches dark brown to grey-black. *Leaves:* petiole 4–8 mm long, 1.4–1.6 mm diam, slightly grooved, indument as on branches; lamina elliptic, obovate to oblanceolate, 6.4–14.5(–18.4) by 2.8–6.4(–7.5) cm, 2–3(–3.5) times longer than wide, chartaceous to subcoriaceous, not punctate, green above, glaucous below, above sparsely covered with appressed, whitish hairs c. 0.4 mm long, becoming glabrous, primary vein more densely covered with ascending, yellowish hairs, below sparsely covered with appressed, yellow-brown to reddish brown hairs 0.1–0.2 mm long, primary vein slightly more hairy, base cuneate to rounded, with thickened black margins or thick, black glands, apex acute to acuminate, acumen to 20 mm long, secondary veins 8–12 per side, slightly curving, tertiary venation percurrent, hardly visible. *Inflorescences* axillary, composed of solitary flowers or 2-flowered fascicle-like rhipidia; sympodial rachis absent or to 1 mm long; flowering pedicels 7.5–21 mm long, 0.3–0.4 mm diam, fruiting pedicels 14–35 mm long, 0.5–1.6 mm diam, densely covered with appressed or slightly ascending, reddish brown hairs; lower bract absent; upper bract in the lower half of the pedicel, halfway or sometimes slightly above the middle of the pedicel, ovate, 0.5–1.1 by 0.7–1 mm, indument as on pedicel; flower buds globose. *Flowers* bisexual; sepals slightly connate at the base, depressed ovate to shallowly triangular, 0.6–1.1 by 1–1.7 mm, apex acute, densely covered with hairs, persistent in fruit; receptacle 1.8–2 mm diam, flat; petals colour in vivo unknown, 6, in two whorls, base of inner petals visible in bud, outer petals ovate, 3.9–5.3 by 1.9–2.9 mm, outside densely covered with appressed, reddish brown hairs, inside covered with yellowish brown, very short hairs, sometimes glabrous at the base, inner petals

rhombic to spathulate, 3.5–4.2 by 1.3–2.5 mm, outside and apical part of the inside densely covered with yellowish brown, very short hairs; stamens 7–9, in one whorl, free, obconical to clavate, 1.5–1.6 mm long, filaments 0.6–0.8 mm long, thecae extrorse, connective truncate, slightly prolonged inward or not, hiding the thecae, sparsely hairy on the inside or glabrous, staminodes absent; carpels 7–13, subcylindric, 1.7–2 by 0.5–0.7 mm, densely hairy, ovules 4–6, lateral, stigma elongate, 0.3–0.4 mm long, glabrous. *Monocarps* 1–10, colour in vivo unknown, moniliform, 12–50 by 7–9 mm, slightly verrucose, densely covered with appressed, reddish brown hairs 0.2–0.3 mm long, apiculate, apiculum 1–5 mm long, stipes 3–6 mm long. *Seeds* 1–4(–5), ellipsoid, 10–12 by 5–7 mm, ochre-brown, rounded to short apiculate apex, raphe visible.

Distribution — South Sudan, Democratic Republic of the Congo, Uganda, Burundi, Kenya, Tanzania, Zambia, Malawi.

Habitat & Ecology — In evergreen forest, upland rain forest, gallery forest and secondary forest, on top of hills, in spray of waterfall; on grey sandy loam and on steep rocky slopes. Altitude: 850–1925 m. Flowering: February, March, May to November; fruiting: January to November.

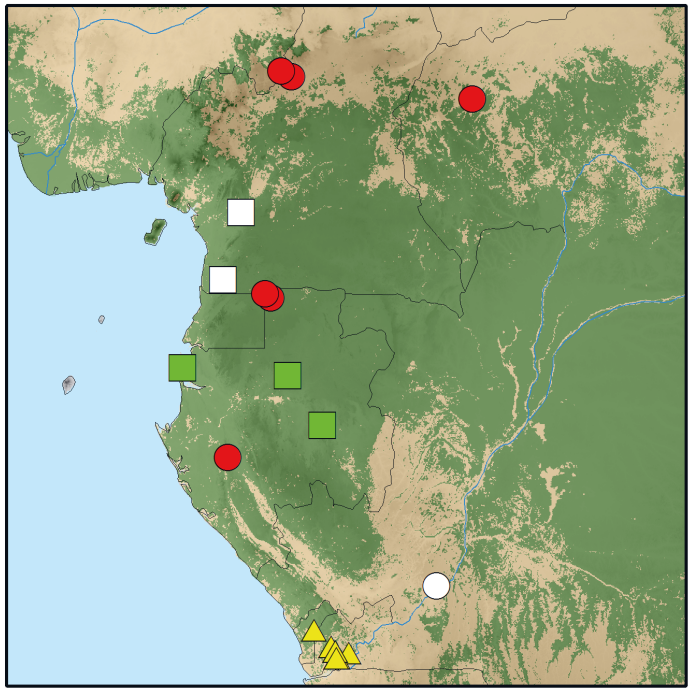
Vernacular names — Democratic Republic of the Congo: Clu (Kilendu name) (*A.S. Taton 156*). Tanzania: Mbigiri (Nyakyusa name) (*G.P. Leedal 5803*).

Preliminary IUCN conservation status —Least concern (LC). EOO: 1,531,758 km^2, AOO: 176 km^2. This species is known from many locations, including several reserves.

Notes — *Monanthotaxis ochroleuca* is the only species of *Monanthotaxis* in East Africa and Southern Africa with axillary inflorescences and reddish brown indument. *Monanthotaxis ochroleuca* belongs to the *M. schweinfurthii* complex (Fig. 1, clade B), but can be distinguished from the other species by the reddish brown indument and by having more than 6 carpels per flower. Furthermore, it can generally be recognized by the ellipsoid seeds and the leaf shape, however, some specimens from Zambia deviate from these 2 characters and can look similar to specimens from Angola of *M. seretii*. Those specimens can only be distinguished by the number of carpels. In the East of the Democratic Republic of the Congo some specimens can approach *M. schweinfurthii*, but that species has a yellow-brown indument.

55. *Monanthotaxis oligandra* Exell — Map 35

Monanthotaxis oligandra Exell (1932) 209. — Type: *J. Gossweiler 6043* (holo: BM000547353; iso: COI00004908, LISC000268), Angola, Cabinda, Pongo Monga, Mayombe, 27 Dec. 1915.



Map 35 Distribution of *Monanthotaxis oligandra* (yellow triangles), *M. paniculata* (green squares, white squares are uncertain dets) and *M. pellegrinii* (red circles, white circle is uncertain det).

Scandent shrub or liana, 1–7 m long, c. 0.5 cm diam; young branches reddish brown, covered with with appressed to ascending, yellowish hairs c. 0.2 mm long, becoming glabrous; old branches blackish. *Leaves:* petiole 2–4 mm long, 1–1.4 mm diam, grooved, indument as on branches; lamina oblong-elliptic to obovate or narrowly so, 7–15.4 by 3.4–5.9 cm, 1.7–2.9 times longer than wide, chartaceous, punctate, ash-grey below, above sparsely covered with hairs to 0.4 mm long, soon becoming glabrous, below sparsely covered with appressed to ascending, whitish hairs 0.2(–0.4) mm long, more densely so on the primary vein, base rounded to subcordate with thickened margin, apex acute to acuminate, secondary veins 8–12 per side, curving upwards, tertiary venation percurrent. *Inflorescences* supra-axillary, originating 2–8(–16) mm above axil, 1–6-flowered rhipidia; sympodial rachis 2.7–3.6 cm long, covered with erect, yellowish hairs c. 0.3 mm long; pedicels 0.7–1.5 mm long, 0.2–0.3 mm diam, fruiting pedicels to 60 mm long; indument as on rachis; lower bracts absent; upper bract placed at the nodes in the inflorescence, lanceolate, 1.1–2 by 0.2–0.4 mm, densely covered with hairs; flower buds globose. *Flowers* bisexual; sepals free at the base, broadly ovate, 0.6–1 by 0.8–0.9 mm, apex acute, outside densely covered with appressed hairs, inside glabrous

except for the hairy edges; receptacle 0.7–1.2 mm diam, flat; petals tawny at the outside, inside cream, 6, in one whorl, ovate, 1.5–2 by 1–1.5 mm, outside densely covered with hairs c. 0.1 mm long, inside at the apex covered with hairs c. 0.05 mm to papillate, base glabrous; stamens 6, in one whorl, free, obconical, 0.4–0.8 mm long, filaments 0.1–0.3 mm long, thecae extrorse, connective truncate, slightly prolonged outward, papillate, staminodes absent; carpels 7, ellipsoid, c. 0.8 by 0.4 mm, densely covered with yellowish hairs, ovules 2, lateral, stigma globose, c. 0.1 mm diam, grooved, glabrous. *Monocarps* 6, colour in vivo unknown, narrowly ellipsoid to subcylindric, 16–18 by 4–5 mm, constricted between the seeds, slightly verrucose, densely covered with appressed, reddish brown hairs, becoming glabrous, apex apiculate, apiculum 2–3 mm long, stipes c. 4 mm long, terete. *Seeds* 1 or 2, ellipsoid to cylindric, 9–12 by 4–5 mm, tawny-brown, seed ends apiculate, apiculum c. 0.5 mm long, raphe visible on both sides.

Distribution — Democratic Republic of the Congo (Bas-Congo), Angola (Cabinda).

Habitat & Ecology — In forest and secondary forest. Flowering: January, March, December; fruiting: April, June, July.

Preliminary IUCN conservation status —Endangered (EN): B2ab(iii). EOO: 1,517 km^2, AOO: 24 km^2. This species is only known a few locations from a small area near the border of Angola and the Democratic Republic of the Congo. Furthermore, it has only been collected once in the last 50 years.

Notes — *Monanthotaxis oligandra* is easily recognised by the supra-axillary rhipidium. This character is only shared with the allopatric *M. letestui*. It can be distinguished from that species by the number of stamen (6 versus 12–14) and the sparsely hairy lower leafside.

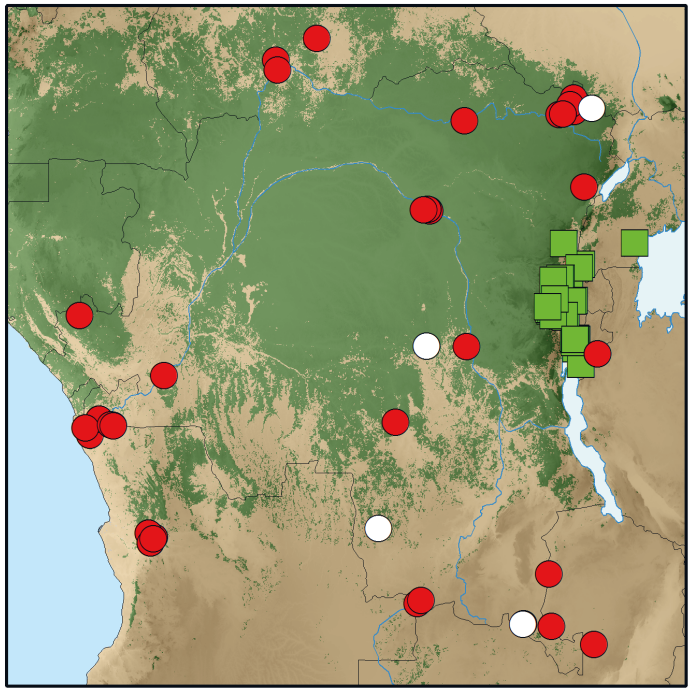
56. *Monanthotaxis orophila* (Boutique) Verdc. — Map 36

Monanthotaxis orophila (Boutique) Verdc. (1971b) 27. — *Popowia orophila* Boutique (1951b) 112. — Lectotype (designated by Verdcourt 1971a: 100): *J.-H. Humbert 7530* (lecto consisting of 2 sheets: BR0000008802019, BR0000008802675; iso: G00308337, P00362630, P00362632, P00362633), Democratic Republic of the Congo, Sud-Kivu, Kabare, montagnes à l'Ouest du Lac Kivu, Marais Kanzibi, 2200 m, 1 Feb. 1929.

Monanthotaxis germainii (Boutique) Verdc. (1971b) 26, syn. nov. — *Popowia germainii* Boutique (1951b) 113. — Lectotype (designated by Verdcourt 1971a: 101): *R.G.A. Germain 3164* (lecto: BR0000008805287; iso: BM000553836, K000198986), Democratic Republic of the Congo, Nord-Kivu, Rutshuru, Rumangabo, 27 Dec. 1944.

Shrub, scandent shrub or liana, to 15 m long and 3 cm diam; young branches covered with appressed, yellow-brown hairs 0.1–0.2 mm long, becoming glabrous; old branches blackish to dark brown. *Leaves:* petiole (3–)5–9(–12) mm long, 0.8–1.3 mm diam, grooved, indument as on branches; lamina oblong-elliptic to narrowly oblong-obovate, 3.5–15.5 by 1.2–6.2 cm, 2.3–3.3 times longer than wide, subcoriaceous, not punctate, above glabrous, below glabrous,

except for a few, appressed hairs c. 0.1 mm long on primary vein, base obtuse, rounded to subcordate, with thickened black margin, apex obtuse, acute to often shortly acuminate, acumen to 10 mm long, secondary veins 6–12 per side, curving upwards, tertiary venation reticulate, raised above.



Map 36 Distribution of *Monanthotaxis orophila* (green squares) and *M. parvifolia* (red circles, white circles are uncertain dets).

Inflorescences terminal, leaf-opposed or sometimes extra-axillary, composed of solitary flowers; sympodial rachis 3–8 mm long, sparsely covered with appressed, yellowish brown hairs; flowering pedicels 10–26 mm long, 0.4–0.5 mm diam, fruiting pedicels 0.6–1 mm diam, indument as on rachis; lower bract absent; upper bract near base of pedicel, large and leafy, broadly ovate to ovate, base semi-amplexicaul, 5–21 by 5–11 mm, glabrous except for few hairs at the margins; flower buds globose. *Flowers* bisexual; sepals connate at the base, depressed ovate to shallowly triangular, 2–2.3 by 3–3.5 mm, apex acute, sparsely covered with appressed hairs; receptacle 2.5–3 mm diam, flat; petals greenish to yellowish green, 6, in two whorls, outer petals ovate to broadly ovate, 5–9.5 by 5.5–7.5 mm, outside densely covered with yellow-brown, short hairs, inside densely covered with yellow, short hairs, glabrous at the base, inner petals rhombic to elliptic, narrowed at the base, not covering stamens entirely in bud, 5.2–7.6 by 3.3–5 mm, outside densely covered with very short hairs, inside glabrous at

the base; stamens 24–34, in two or three whorls, free, linear-obconical, 1.8–2.3 mm long, filaments 0.8–1.3 mm long, thecae latrorse, connective truncate, square, pentagonal to rhombic seen from above, glabrous, staminodes absent; carpels (7–)11–17, narrowly subcylindric-ellipsoid, c. 2 by 0.5 mm, densely hairy, ovules 4–6, lateral, stigma elongate, 0.5–0.7 mm long, 2-lobed at the apex, glabrous. *Monocarps* 2–11, red when ripe, moniliform, 19–55 by 6–9 mm, each part ellipsoid, covered with few, appressed hairs at the stipe, apex apiculate, apiculum to 3 mm long, stipes 9–17 mm long. *Seeds* 1–6, ellipsoid, 14–18 by 6–7 mm, tawny, apex apiculate, raphe not visible.

Distribution — Democratic Republic of the Congo, Uganda, Rwanda, Burundi.

Habitat & Ecology — In submontane evergreen forest, montane forest, gallery forest and secondary forest on basalt and syenite. Altitude: 1220–2700 m. Flowering and fruiting all year round.

Vernacular names — Burundi: Umukonyantoki (Kirundi name) (*J. Lewalle 4313*). Democratic Republic of the Congo: Lukumbula (Kiviga name) (*R. Gutzwiller 1984*). Rwanda: Uruhetza (*P.A.J.B. van der Veken 10949*), Urukenke (*G. Bouxin 1319*), Ingani-gani (*G. Bouxin 665*), Uruhashya (*B. Runyinya 811*).

Preliminary IUCN conservation status —Least concern (LC). EOO: 75,845 km^2, AOO: 136 km^2. This species is known from many locations, including several national parks.

Notes — 1. *Monanthotaxis orophila* belongs to a group of species with a large leafy bract. It can be distinguished from the other species by the leathery leaves, the 25–34 stamens, the hairy carpels, and by seeds longer than 12 mm.

2. *Monanthotaxis germainii* was regarded as distinct from *M. orophila* based on a number of characters by Boutique (1951b), however all characters show overlap, therefore the two names are synonymised. Only the number of stamens is slightly different between the lowland specimens (1200–1600 m above sea level) and the specimens from higher altitudes (1800–2700 m). The 2 lowland specimens have 24–25 stamens, while the highland specimens have 27–33 stamens. Also the number of carpels which according to Boutique was 15–17 for *M. germainii* and 7–10 for *M. orophila* overlap, almost all flowers which the first author opened had 11–14 carpels. We have not seen flowers with 7–10 carpels as mentioned by Boutique (1951a) and Verdcourt (1971a).

57. *Monanthotaxis paniculata* P.H.Hoekstra — Fig. 23; Plate 5d–f; Map 35

Monanthotaxis paniculata P.H.Hoekstra in P.H.Hoekstra et al. (2014) 106. — Type: *G.D. McPherson 16123* (holo consisting of 2 sheets: WAG0357246, WAG0357247; iso: LBV, MO, P01967243), Gabon, Ogooué-Ivindo, north of Koumameyong along SHM lumber roads, 0˚ 25’ N, 11˚ 55’ E, 200 m, 31 Jan. 1993.

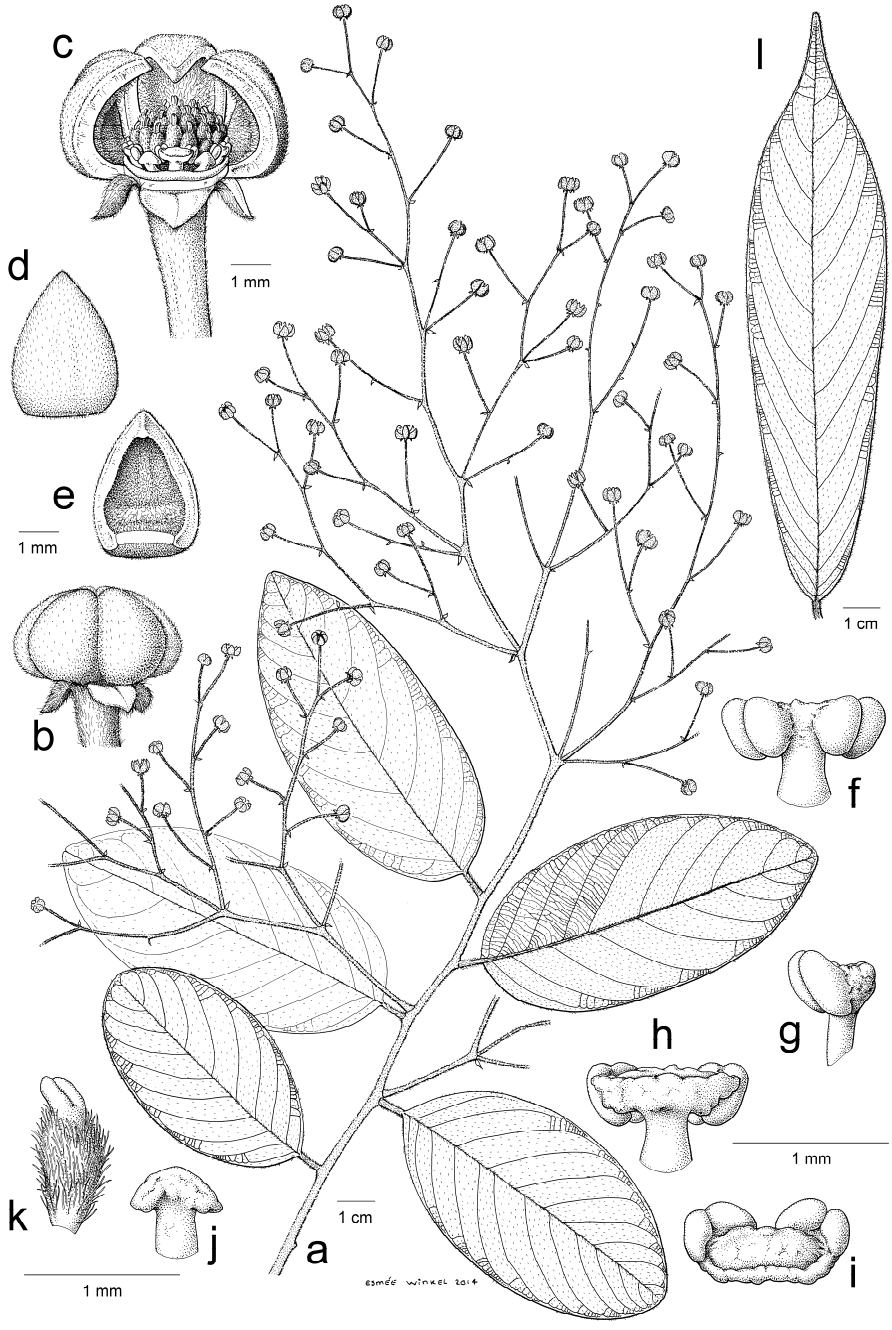


Fig. 23 *Monanthotaxis paniculata* P.H.Hoekstra: a. Flowering branch; b. flower bud; c. flower with three petals removed; d. petal, outside view; e. petal, inside view; f. stamen, inside view; g. stamen, side view; h. stamen, outside view; i. stamen, seen from above; j. staminode; k. carpel (a–k: *G.D. McPherson 16123*; l: *Reitsma 2870*). Drawing by E. Winkel.

Liana to 20 m long; young branches densely covered with appressed, reddish brown hairs c. 0.5 mm long, becoming glabrous; old branches dark brown to blackish. *Leaves:* petiole 4–8 mm long, 1–1.5 mm diam, grooved, densely covered with appressed hairs; lamina ovate to oblong-lanceolate, 8.5–23.5 by 3.3–6.6 cm, 2–4.2 times longer than wide, chartaceous, older leaves punctate below, glaucous or green below, young leaves above sparsely covered with appressed, white hairs c. 1 mm long, becoming glabrous, below densely covered with appressed yellowish hairs c. 2 mm long, less densely so in older leaves, base cuneate to broadly cuneate, with small thickened black margin, apex acute to acuminate, acumen to 25 mm long, secondary veins 10–16 per side, oblique, curving upwards, impressed above, tertiary venation percurrent to slightly reticulate, slightly raised above, below only visible in older leaves. *Inflorescences* axillary or terminal, in 5.5–27 cm long many-flowered panicle-like rhipidia; sympodial rachis often multiple times bifurcate or trifurcate, densely covered with reddish brown, short hairs, 1–3 flowers in the axil of each upper bract; flowering pedicels 5–22 mm long, 0.4–0.8 mm diam, indument as on rachis; lower bracts elliptic to lanceolate, 1–8 by 0.5–1.5 mm, same indument as on rachis, upper bract absent; flower buds depressed globose. *Flowers* bisexual; sepals free to slightly connate at base, depressed ovate, 0.6–1 by 1–1.5 mm, apex acute, outside densely covered with reddish brown hairs, inside glabrous, apex acute; receptacle 2–3.5 mm diam, flat; petals yellowish or dull yellow, 6, in one whorl, ovate, c. 3 by 1.5 mm, ovate, outside and inside covered with appressed, yellowish, short hairs; stamens 6, in one whorl, free, opposite the petals, obconical, c. 0.6 mm long, filaments c. 0.2 mm long, thecae introrse, connective truncate, prolonged, kidney-shaped seen from above, c. 1 mm wide, not hiding thecae, glabrous, staminodes 6, alternating with the stamens, c. 0.4 by 0.5 mm; carpels 14–24, ellipsoid, c. 0.9 by 0.4 mm, densely covered with reddish brown hairs, ovule 1, basal, stigma shape subglobose, c. 0.2 mm long, bifurcate, glabrous. *Fruits* seen from photographs: *Monocarps* 1–10, green, ellipsoid, covered with reddish brown hairs, apex rounded. *Seeds* 1, ellipsoid.

Distribution — Gabon (Estuaire, Ogooué-Ivindo, Ogooué-Lolo), perhaps in Cameroon.

Habitat & Ecology — In forest fringe of a marshy savannah and along lumber roads. Altitude: 0–500 m. Flowering: January; fruiting: June.

Preliminary IUCN conservation status —Endangered (EN): B2ab(iii). EOO: 15,921 km^2, AOO: 12 km^2. This species has been collected once since its publication in 2014. This third collection was from a new location, but also an area that is under threat of habitat degradation by logging and thus our estimate does not change.

Notes — 1. *Monanthotaxis paniculata* is the only species of *Monanthotaxis* with a large panicle-like rhipidium. It strongly resembles *M. congoensis,* but differs in the inflorescence-type, the depressed globose floral buds, the stamens inserted on a black hexagonal disc and the connective prolongation, that is kidney-shaped when seen from above. Vegetatively, *M. paniculata* can be distinguished by the yellowish indument of the lower leafside. However, more collections are needed to assess the variability in vegetative characters.

2. Field photos of *T.L.P. Couvreur 1108* were seen, which has fruits. No measurements are included in the description as this specimen was not yet examined by the authors.

3. Two specimens from Cameroon, *T.L.P. Couvreur 651* and *T.L.P. Couvreur 708*, probably belong to this species, but they are sterile, which precludes an identification with certainty.

58. *Monanthotaxis parvifolia* (Oliv.) Verdc. — Fig. 24; Map 36

Monanthotaxis parvifolia (Oliv.) Verdc. (1971b) 27. — *Unona parvifolia* Oliv. (1868) 36. — *Popowia parvifolia* (Oliv.) Engl. & Diels (1901) 46, nom. illeg. non Kurz (1875), nec Scheff. (1885). — *Popowia oliveriana* Exell & Mendonça (1937) 24. — Lectotype (designated by Paiva 1966): *F.M.J. Welwitsch 760* (lecto: LISU not seen; iso: BM000553842, BM001125036, BR0000008824080, C10000162, C10000163, COI00004907, G00308295, K000198966, LD1757603, LD1758499, M0107927, M0107928, P00362626, P00362627, PRE0774856-0), Angola, Cuanza Norte, District Gulongo Alto, 305 m, July 1855.

Popowia louisii Boutique (1951b) 114. — Lectotype (designated here): *J.L.P. Louis 1213* (lectotype: BR (consisting of 3 sheets: BR0000008823793, BR0000008824141, BR0000008824158); iso: B100460854, K000913658, NY00026228, P00362646), Democratic Republic of the Congo, Orientale, Isangi, île Esali, dans la fleuve, en face de Yangambi, 470 m, 7 Feb. 1936.

Popowia louisii Boutique var. *grandifolia* Boutique (1951b) 115. — Type: *C. Rossignol 9* (holo: BR0000008824127), Democratic Republic of the Congo, Maniema, Kibombo, Difuma, 8 Mar. 1934.

Shrub or liana, to 4 m long; young branches sparsely to densely covered with appressed to ascending, reddish brown hairs 0.2–0.3 mm long, becoming glabrous; old branches black, blackish brown or reddish brown. *Leaves:* petiole 2.5–4.5 mm long, 0.5–0.9 mm diam, terete, indument as on branches; lamina elliptic to obovate, 3.2–10.1 by 1.5–4.2 cm, 1.7–2.5 times longer than wide, chartaceous, slightly punctate, glaucous below, above sparsely covered with appressed, white hairs 0.3–0.5 mm long, becoming glabrous, primary vein covered with longer persistent, appressed to ascending, yellow hairs, below sparsely covered with appressed, reddish brown hairs 0.2–0.3 mm long, more densely so with hairs 0.2–0.5 mm long on veins, base rounded or subcordate with slightly thickened black margin, apex obtuse or acute, secondary veins 5–10 per side, slightly curving, tertiary venation percurrent, hardly visible. *Inflorescences* extra-axillary or leaf-opposed, consisting of solitary flowers; sympodial rachis absent; pedicels 7–11.5 mm long, 0.4–0.5 mm diam, fruiting pedicels 9.5–21(–32) mm long, 0.6–0.8 mm diam, sparsely to densely covered with ascending hairs 0.2–0.3 mm long; lower bract absent; upper bract in the lower half of the pedicel or halfway, ovate to lanceolate, 2.1–2.5 by 0.5–1.2 mm, densely covered with hairs; flower buds globose. *Flowers* bisexual; sepals free or slightly connate at the base, depressed ovate to almost orbicular, 1.5–3 by 2.3–3.9 mm, apex rounded, sparsely covered with appressed hairs, persistent in fruit; receptacle 1.7–

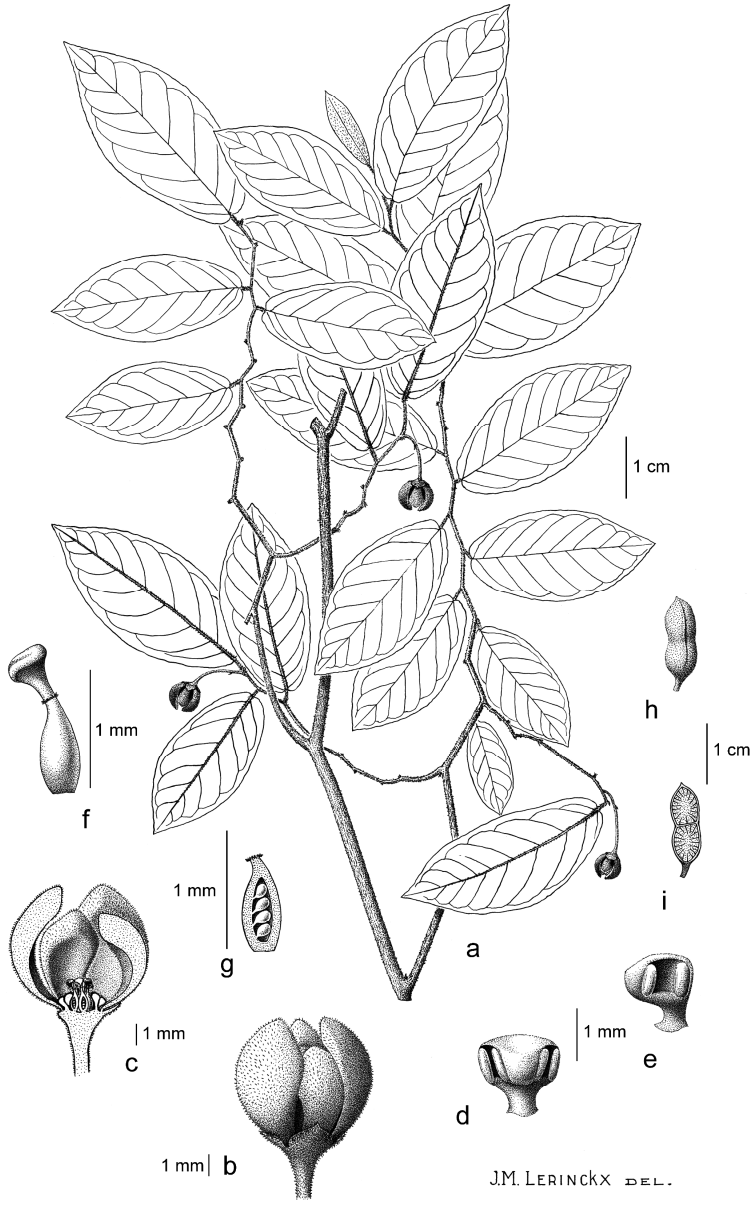


Fig. 24 *Monanthotaxis parvifolia* (Oliv.) Verdc.: a. Flowering branch; b. flower, c. longitudinal section of flower; d. stamen, front view; e. stamen, side view; f. carpel; g. longitudinal section of carpel; h. one monocarp; i. longitudinal section of monocarp (based on *Louis 12804* and *13119*). Modified from Boutique (1951a) plate 33.

3 mm diam, flat to slightly convex, hairy; petals colour in vivo unknown, 6, in two whorls, outer petals, ovate, 5.5–7 by 3.7–4 mm, outside densely covered with yellowish hairs, near the margins of the inside covered with yellowish hairs < 0.1 mm long, inner petals broadly elliptic to ovate, 2.5–4.5 by 2.1–2.5 mm, outside and apical part of the inside densely covered with yellow hairs; stamens 22–24, in three whorls, free, obovoid, 1.4–1.7 mm long, filaments 0.7–1 mm long, thecae latrorse to extrorse, connective truncate, slightly prolonged outward, not hiding thecae, glabrous, staminodes absent; carpels 12, subcylindric, 1.1–1.3 by 0.2–0.4 mm, glabrous except for few hairs at the base, ovules 2–4, lateral, stigma elongate, claviform, 0.3–0.4 mm long, glabrous. *Monocarps* 2–8, orange to red when ripe, moniliform, each part ellipsoid, 11–26 by 5–6 mm, slightly verrucose, glabrous or with a few hairs on the stipe, apex rounded or apiculate, apiculum to 1.5 mm long, stipes 1.5–4 mm long. *Seeds* 1–4, ellipsoid, 6.5–10.5 by 4–4.5 mm, ochre-brown, apex apiculate, apiculum to 1 mm long, raphe not visible.

Distribution —Central African Republic, Democratic Republic of the Congo, Republic of the Congo, Burundi, Angola, Zambia.

Habitat & Ecology — In gallery forest and savannas. Altitude: 305–1250 m. Flowering and fruiting all year round.

Preliminary IUCN conservation status —Least concern (LC). EOO: 3,108,335 km^2, AOO: 148 km^2. This species has a wide distribution and occurs in quite some localities and nature reserves.

Notes — 1. *Monanthotaxis parvifolia* can be recognized by the combination of glabrous carpels, 22–24 stamens in three whorls and a reddish brown indument on the branches and leaves.

2. It is a highly variable species and the specimens from the Congolean rainforests have much less indument on leaves and branches and slightly shorter hairs than the specimens from the rest in the distribution range. These specimens were formerly placed under *Popowia louisii*, but besides the sparser indument no other differences could be found with the typical specimens of *M. parvifolia.*

3. *Monanthotaxis parvifolia* probably does not occur in West Africa. Most specimens formerly assigned to *M. parvifolia* have very different flowers and are now described as *M. glabra*. Another group of specimens from Benin and Togo have the fruits similar to *M. parvifolia*, however the phylogenetic analysis (Fig. 1) and vegetative characters indicate that they are related to *M. laurentii*, see the note under that species. There are 2 specimens from Guinea, which look like *M. parvifolia*, but without flowers they cannot be assigned with certainty to that species.

59. *Monanthotaxis pellegrinii* Verdc. — Fig. 7h–m; Map 35

Monanthotaxis pellegrinii Verdc. (1971b) 28, non *M. letestui* Pellegr. (1950). — *Popowia letestui* Pellegr. (1949) 213. — Lectotype (designated by Le Thomas 1969: 226): *G.M.P.C. Le Testu 9028* (lecto consisting of 3 sheets: P00362618, P00362621, P00362623; iso: BM000553843, BR0000008823779, BR0000008823786, BR0000008823830), Gabon, Woleu-Ntem, region de Bitam, bords de la Kyé à Meyo, 12 Mar. 1933.

Scandent shrub or liana, to 3 m long; young branches densely covered with ascending, reddish brown hairs 0.1–0.3 mm long, becoming glabrous; old branches black to blackish brown. *Leaves:* petiole 3–9 mm long, 0.8–1.4 mm diam, grooved, indument as on branches; lamina ovate, oblong-elliptic to obovate or narrowly so, 6.2–22 by 2.8–9 cm, 2.1–3 times longer than wide, chartaceous, not punctate, above glabrous except primary vein glabrous or covered with ascending, whitish hairs, below covered with ascending to appressed, white-yellowish hairs 0.2–0.3 mm long, base cuneate, rounded to slightly subcordate, with thickened black margin, apex acute to acuminate, acumen to 15 mm long, secondary veins 6–11 per side, straight and halfway curving upwards, tertiary venation percurrent, slightly raised above. *Inflorescences* axillary or terminal, composed of solitary flowers or 2–6-flowered fascicle-like rhipidia; sympodial rachis 0.5–10 mm long, sparsely covered with ascending hairs, becoming glabrous; flowering pedicels 16–55 mm long, 0.5–0.6 mm diam, sparsely covered with ascending, reddish brown hairs; lower bract absent or ovate, c. 1 by 0.4 mm, densely covered with yellow-brown hairs; upper bract in lower half of the pedicel, broadly ovate, 0.5–0.9 by 0.5–0.7 mm, indument as on pedicel; flower buds globose. *Flowers* bisexual; sepals connate at the base, depressed ovate, 0.5–0.7 by 2–2.8 mm, apex rounded to acute, sparsely covered with white to yellowish hairs; receptacle 2.5–3 mm diam, flat; petals pale yellow, 6, in two whorls, outer petals broadly ovate, 4.7–5.5 by 4.6–5.8 mm, outside and inside densely covered with yellow-brown hairs, inner petals broadly ovate, 2.5–4 by 2.8–3 mm, indument as on outer petals; stamens 15–24, in one or two whorls, free, oblong, 0.8–1.6 mm long, filaments 0.5–0.9 mm long, broader than connective, thecae latrorse, almost convergent apically, only leaving a very small part of the connective visible, glabrous, staminodes absent; carpels 10–16(–21), subcylindric, 1.2–1.4 by c. 0.4 mm, densely hairy, ovules 2 or 3, lateral, stigma elongate, deeply bifurcate, 0.4–0.5 mm long, glabrous. *Monocarps* and *seeds* not seen.

Distribution — Cameroon, Central African Republic, Gabon.

Habitat & Ecology — Along forest road and on river bank. Altitude: 600–1300 m. Flowering: March, April, June, September.

Preliminary IUCN conservation status —Endangered (EN): B2ab(iii). EOO: 592,537 km^2, AOO: 28 km^2. This species has a wide distribution, but is only known from 5 unprotected localities and has only been collected once in the last 50 years.

Notes — 1. *Monanthotaxis pellegrinii* shares with *M. bicornis* the shape of the stamens, which have a filament wider than the connective and the thecae converging apically almost hiding the connective. *Monanthotaxis pellegrinii* differs from *M. bicornis* in the indument, which consists of ascending, reddish brown hairs on young branches, while *M. bicornis* has appressed, yellow-brown hairs on the young branches. They are not closely related as phylogenetic analysis places them in different clades (Fig. 1, clade H and I). In *M. pellegrinii* the leaf shape is highly variable, however, the type of *M. pellegrinii* has a leaf shape similar to *M. bicornis*, but it differs in the indument. Also the number of stamens is highly variable in this species. The type specimen and one other collection of north Gabon have 15–17 stamens in one whorl, while in 4 other collections the flowers have 24 stamens in two whorls. No other differences correlated to this difference in stamen number could be found. More material combined with DNA-based phylogenetic analyses are needed to verify if all specimens belong to the same entity or actually belong to 2 or more different (sub)taxa.

2. There is one fruiting specimen in the Republic of the Congo, which may belong to *M. pellegrinii*, however, the pedicels are very short, the leaf shape is different and it occurs in much drier forests than the other collections of *M. pellegrinii*. The fruit has 6 moniliform monocarps with each 2–4 ellipsoid seeds. The monocarps are 32–41 by 7–8 mm, verrucose, apex rounded to apiculate, sparsely covered with ascending, yellow-brown hairs, and the stipes 7–8 mm long.

60. *Monanthotaxis poggei* Engl. & Diels — Plate 5g; Map 37

Monanthotaxis poggei Engl. & Diels (1901) 53. — Lectotype (designated by Verdcourt 1971a: 93): *F.R.R. Schlechter 12801* (lecto consisting of 2 sheets: B100153041, B100153042; isolecto: AMD.129315, AMD.129316, BM000547352, BR0000008801708, BR0000008802033, K000198985, L 0188029, L.2362454, P01982449, P01982450, WAG0057967), Democratic Republic of the Congo, Kinshasa, Kinshasa, Nov. 1899.

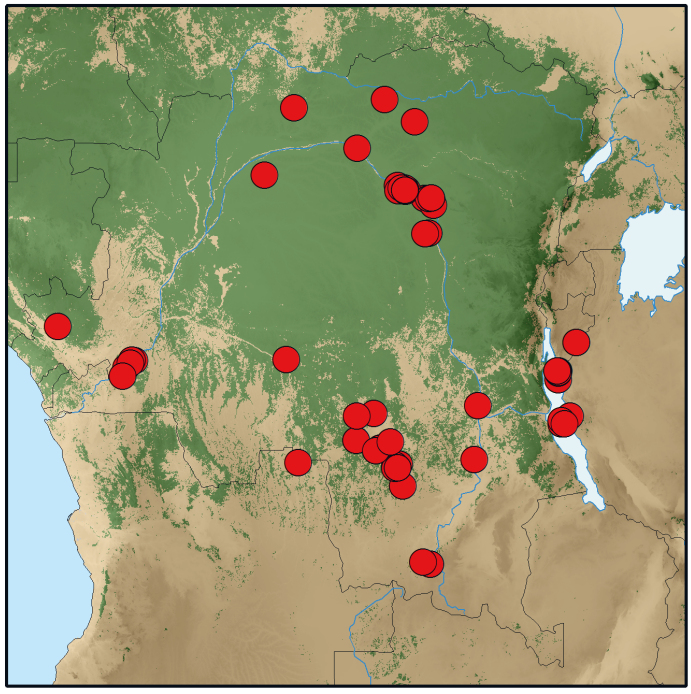
Monanthotaxis poggei Engl. & Diels var. *latifolia* Engl. & Diels (1901) 53. — Type: *P. Pogge 638* (holo: B not seen), Democratic Republic of the Congo, Manima, Kasongo, am Lufuba, Apr. 1882.

Popowia argentea De Wild. (1914) 383. — Type: *E.P. Luja s.n.* (holo consisting of 2 sheets: BR0000008802361, BR0000008802699), Democratic Republic of the Congo, Kasai-Oriental, Forêt du Sankuru, June 1911

Small tree, shrub, scandent shrub or liana, 1–3(–5) m long; young branches covered with appressed to slightly ascending, reddish brown hairs 0.5–1 mm long, becoming glabrous; old branches blackish brown. *Leaves:* petiole 3–5 mm long, c. 1 mm diam, grooved, indument as on branches; lamina oblong-elliptic to ovate or narrowly so, 6.5–18.5 by 2.8–6.7 cm, 2.2–3.6 times longer than wide, chartaceous, not punctate, young leaves above sparsely covered with appressed, whitish hairs, but soon becoming glabrous, below densely covered with appressed,

silky brownish hairs 0.8–1.5 mm long, whitish in older leaves, base rounded to subcordate, sometimes with small thickened black margin, apex broadly acute to acuminate, acumen to 17 mm long, secondary veins 8–16 per side, curving upwards, tertiary venation percurrent, slightly raised above, below only visible in older leaves. *Inflorescences* axillary, composed of solitary flowers or up to 4-flowered fascicle-like rhipidia; sympodial rachis 0–23 mm long; pedicels 3–7 mm long, c. 0.6 mm diam, fruiting pedicels (4–)8–12 mm long, 0.8–1.2 mm diam, indument as on young branches; lower bract absent; upper bract in lower half or halfway the pedicel, ovate, 1.5–2 by c. 1 mm (see note 2), indument as on young branches; flower buds ovoid-deltoid. *Flowers* bisexual; sepals free to slightly connate at base, (2 or) 3, broadly triangular-ovate, c. 1.5 by 1.5–2 mm, covered with reddish brown hairs, persistent in fruit and becoming up to 3 mm long; receptacle c. 3 mm diam, flat; petals yellowish brown, inside reddish brown in sicco, 4(–6), in one whorl, ovate-elliptic, 3–4 by 2–3 mm, outside covered with reddish brown hairs, inside glabrous; stamens 8–12, in one whorl, free, obconical, c. 0.7 mm long, filaments c. 0.3 mm long, thecae latrorse to introrse, c. 0.4 mm long, connective truncate, slightly prolonged inward, glabrous, staminodes absent; carpels 10–12, ellipsoid, c. 0.8 by 0.5 mm, densely hairy, ovules (1 or) 2 (or 3), basal or lateral, stigma subsessile, globose, c. 0.05 mm long, grooved, glabrous. *Monocarps* 1–6, green, maturing yellow-orange, ellipsoid or subcylindric, 1-seeded ones 11–16 by c. 7 mm, 2-seeded ones 19–22 by c. 7 mm and slightly constricted between the seeds, densely covered with ascending, reddish brown hairs when young, ripe fruits with less dense and more appressed hairs, apex rounded or slightly apiculate, stipes 1.5–3.5 mm long. *Seeds* 1 or 2, ellipsoid, 9–10(–14) by 5–7 mm, ochre-brown, both ends rounded, raphe a longitudinal furrow.

Distribution — Democratic Republic of the Congo, Republic of the Congo, Burundi, Tanzania Angola.



Map 37 Distribution of *Monanthotaxis poggei*.

Habitat & Ecology — In primary and secondary forest, gallery forest; on brown sandy soil or large sandstone blocks. Altitude: 470–1300 m. Flowering and fruiting all year round.

Vernacular names — Democratic Republic of the Congo: Lukukuma (*R. Desenfans 4422*), Kanimpemba (Tshiluba name) (*L. Liben 1745*), Kakumu (Tshiluba name) (*L. Liben 2384*), Kadjambuluka (*A. Thiébaud 748*). Tanzania*:* Bulyankende (Kiha name) (*Y.S. Abeid 981*), Shrubbish (*T.H. Clutton-Brock 18*), Lujongororo (Kitongwe name) (*S. Uehara 72*), Lujongololo (*S. Uehara 579*).

Preliminary IUCN conservation status —Least concern (LC). EOO: 1,712,827 km^2, AOO: 228 km^2. This species occurs in many locations including several nature reserves.

Uses — The pulp of ripe fruits is edible and freshly eaten (Ruffo et al. 2002). The roots are used as a medicine against stomach-ache and snakebites (Ruffo et al. 2002). The wood is used to make storage pots and withies and the wood is used as firewood (Ruffo et al. 2002).

Notes — 1. *Monanthotaxis poggei* is easily recognisable by the appressed, silky hairs on the lower leaf surface. Older leaves can be similar to those of *M. congoensis* or *M. paniculata*, but *M. poggei* differs by having solitary flowers or up to 4-flowered fascicle-like rhipidia, while *M. congoensis* has the flowers in raceme-like rhipidia and *M. paniculata* in panicle-like rhipidia.

2. According to the protologue and Boutique (1951a), Paiva (1966) and Verdcourt (1971a) the bracts are c. 1.5 cm long. They probably refer to the upper bract, which is 1.5 mm, not cm, long.

61. *Monanthotaxis pynaertii* (De Wild.) P.H.Hoekstra, *comb. nov.* — Fig. 25; Map 38

Popowia pynaertii De Wild. (1914) 382. — Lectotype (designated here): *L.A. Pynaert 852* (lectotype: BR, consisting of 2 sheets: BR0000008805348, BR0000008805355), Democratic Republic of the Congo, Equateur, Mbandaka, Eala, 20 Dec. 1908.

Liana, to 20 m long, 2 cm diam; young branches covered with erect, reddish brown hairs 0.6–1.2 mm long, becoming glabrous; old branches dark brown. *Leaves:* petiole 5–7 mm long, 1.1–1.5 mm diam, grooved, indument as on branches; lamina oblong-ellitpic to obovate, mostly narrowly so, 9.5–23.2 by 2.9–7 cm, 2.4–4.1 times longer than wide, chartaceous to subcoriaceous, not punctate, glaucous below, above sparsely covered with erect, yellow hairs 0.4–1 mm long, becoming glabrous, primary vein densely covered with erect and long-persisting yellow hairs, below covered with erect, yellow hairs 0.5–1 mm long, base rounded to subcordate, with thickened black margin, apex acute to acuminate, acumen to 15 mm long, secondary veins 11–17 per side, straight to curving upwards, tertiary venation percurrent. *Flowers* unisexual. ♂ *Inflorescences* axillary, flowers solitary or in up to 10-flowered fascicles; sympodial rachis 4–8 mm long, covered with erect hairs 0.3–0.6 mm long; flowering pedicels 2.5–3.5 by c. 0.3 mm, indument as on rachis; bracts ovate, 0.6–0.7 by c. 0.3 mm, indument as on pedicels; flower buds depressed globose; sepals broadly triangular to ovate, 0.7–1 by 0.6–0.7 mm, covered with appressed, short hairs; receptacle 1.1–1.3 mm diam, flat; petals colour in vivo unknown,

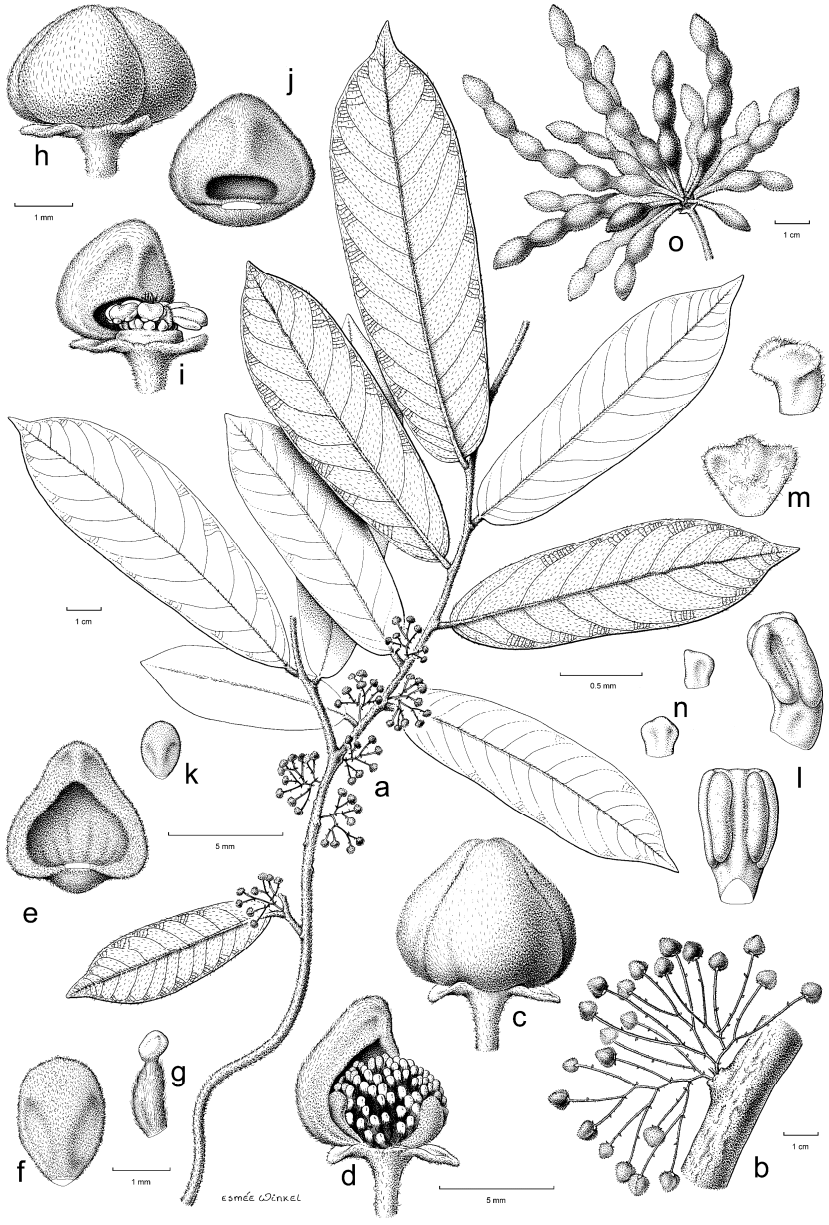


Fig. 25 *Monanthotaxis pynaertii* (De Wild.) P.H.Hoekstra: a. Branch with staminate inflorescences; b. pistillate inflorescence; c. pistillate flower bud; d. pistillate flower with two outer petals removed; e. outer petal of pistillate flower, inside view; f. inner petal of pistillate flower, inside view; g. carpel; h. staminate flower bud; i. staminate flower with two outer petals removed; j. outer petal of staminate flower, inside view; k. inner petal of staminate flower, inside view; l. stamen, front and side view; m, n. staminodes; o. fruit (a, h–n: *Evrard 5198*; b–g: *Pynaert 852*; o: *Tisserant 2035*). Drawing by E. Winkel.

6, in two whorls, outer petals broadly ovate, c. 2.7 by 3 mm, outside covered with appressed, yellowish, short hairs, inside densely covered with yellowish, very short hairs, inner petals elliptic, c. 0.8 by 0.4 mm, outside and inside densely covered with yellowish, very short hairs; stamens 6(–9), in one whorl, in pairs, oblong, free, c. 1 mm long, filaments c. 0.2 mm long, thecae latrorse, connective truncate, glabrous, staminodes 12–16, in one whorl, 0.2–0.5 mm long, sparsely hairy or glabrous. ♀ *Inflorescences* cauliflorous, condensed many-flowered panicles; sympodial rachis 3.5–5 cm long, densely covered with erect hairs 0.5–1 mm long; pedicels 20–33 mm long, 0.6–0.8 mm diam, fruiting pedicels to 2 mm diam, covered with erect, yellowish brown hairs; bracts lanceolate to ovate, 2.3–2.4 by c. 0.7 mm, indument as on rachis; flower buds ovoid; sepals depressed ovate to broadly ovate, 1–2 by 1.5–2 mm, densely covered with appressed hairs, persistent in fruit; receptacle 1.8–1.9 mm diam, convex; petals colour in vivo unknown 6, in two whorls, outer petals broadly ovate, 5–6.3 by 5–6.5 mm, outside densely covered with appressed, reddish brown hairs, inside covered with yellowish, very short hairs, inner petals ovate, 1.7–1.8 by 0.7–0.8, outside and inside covered with yellowish, very short hairs; carpels 95–150, subcylindric to ellipsoid, 1.5–1.7 by 0.4–0.5 mm, densely hairy, ovules 4–6, lateral, stigma globose to ellipsoid, 0.3–0.4 mm long, grooved, glabrous. *Monocarps* up to 20, colour in vivo unknown, ellipsoid to subcylindric, 20–60 by 7–8 mm, constricted between the seeds, slightly verrucose, rather densely covered with erect hairs 0.2–0.4 mm long, apex apiculate, apiculum 1–2 mm long, stipes 9–12 mm long, slightly grooved. *Seeds* 1–6, ellipsoid, 11–13 by 6.5–7.5 mm, reddish brown, ends slightly apiculate, raphe not visible.

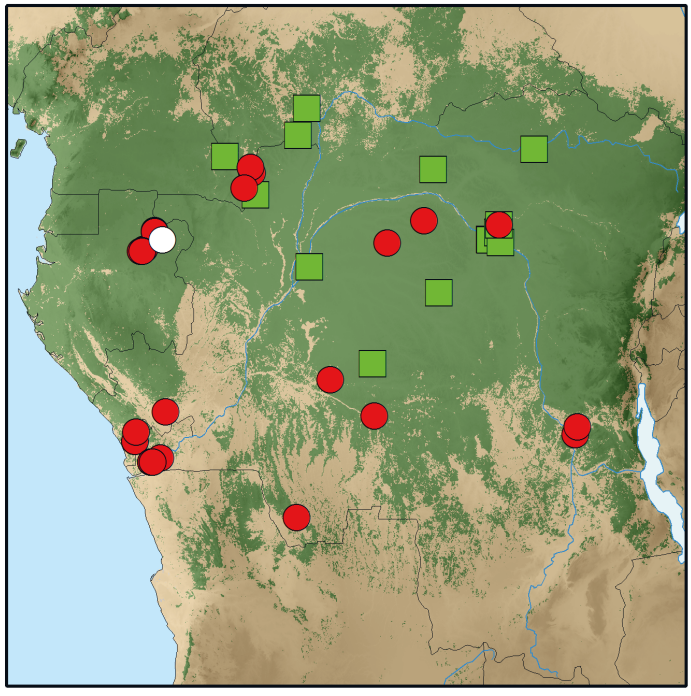
Distribution — Cameroon, Central African Republic, Democratic Republic of the Congo, Republic of the Congo.

Habitat & Ecology — In swamp forest and gallery forest. Altitude: c. 362 m. Flowering: October to February; fruiting: March, June.

Vernacular names — Central African Republic: Mindowali (Sango name) (*C. Tisserant Équipe 2035*). Democratic Republic of the Congo: Babua (Embai name) (*P. Gérard 5534*), Pome (*M.G. Mortehan 617*), Bodzingo kodzi (Nkundo name) (*B.I. Fruth 332*).

Preliminary IUCN conservation status —Vulnerable (VU): B2ab(iii). EOO: 518,446 km^2, AOO: 60 km^2. This species is only known from 9 locations and has only been collected twice in recent years.

Notes — *Monanthotaxis pynaertii* is quite easily distinguished from other caulescent species by the 0.6–1.2 mm long, erect hairs on the young branches and leaves. *Monanthotaxis pynaertii* was previously placed in the synonymy of *M. diclina*, but it differs besides the erect indument in having larger flowers, and more carpels in the pistillate flowers.



Map 38 Distribution of *Monanthotaxis pynaertii* (green squares) and *M. scamnopetala* (red circles, white circle is uncertain det).

62. *Monanthotaxis quasilanceolata* P.H.Hoekstra, *sp. nov*. — Fig. 26; Map 39

Monanthotaxis quasilanceolata can be distinguished from all species of *Monanthotaxis* by the 5–11 cm long slender pedicels in combination with a lanceoloid flower bud, lanceolate sepals and lanceolate petals. It is the only species of *Monanthotaxis* that has the connective of the stamens conically prolonged above the thecae. — Type: *J.J.F.E. de Wilde 10971* (holotype: WAG (consisting of 2 sheets: WAG0232743, WAG0232744); iso: BR0000013211448, K not seen, LBV, MO not seen), Gabon, Ogooué-Maritime, Rabi-Kounga, Rabi, Shell/Gabon, just N of Airstrip, 30 m, 26 Jan. 1993. Paratype: *M.F. de Carvalho 5371* (MA), Equatorial Guinée, Rio Muni, Litoral, Bata-Sendje, Estrada km 40, a jusante de ponte sobre o Río Benito, 10 July 1993.

Liana, 6–10 m long; young branches dark brown to blackish, densely covered with erect, reddish brown hairs c. 1.5 mm long, becoming glabrous; old branches pale brown. *Leaves:* petiole 2–5 mm long, 0.7–1 mm diam, grooved, indument as on branches; lamina obovate to oblanceolate, 7.7–14.6 by

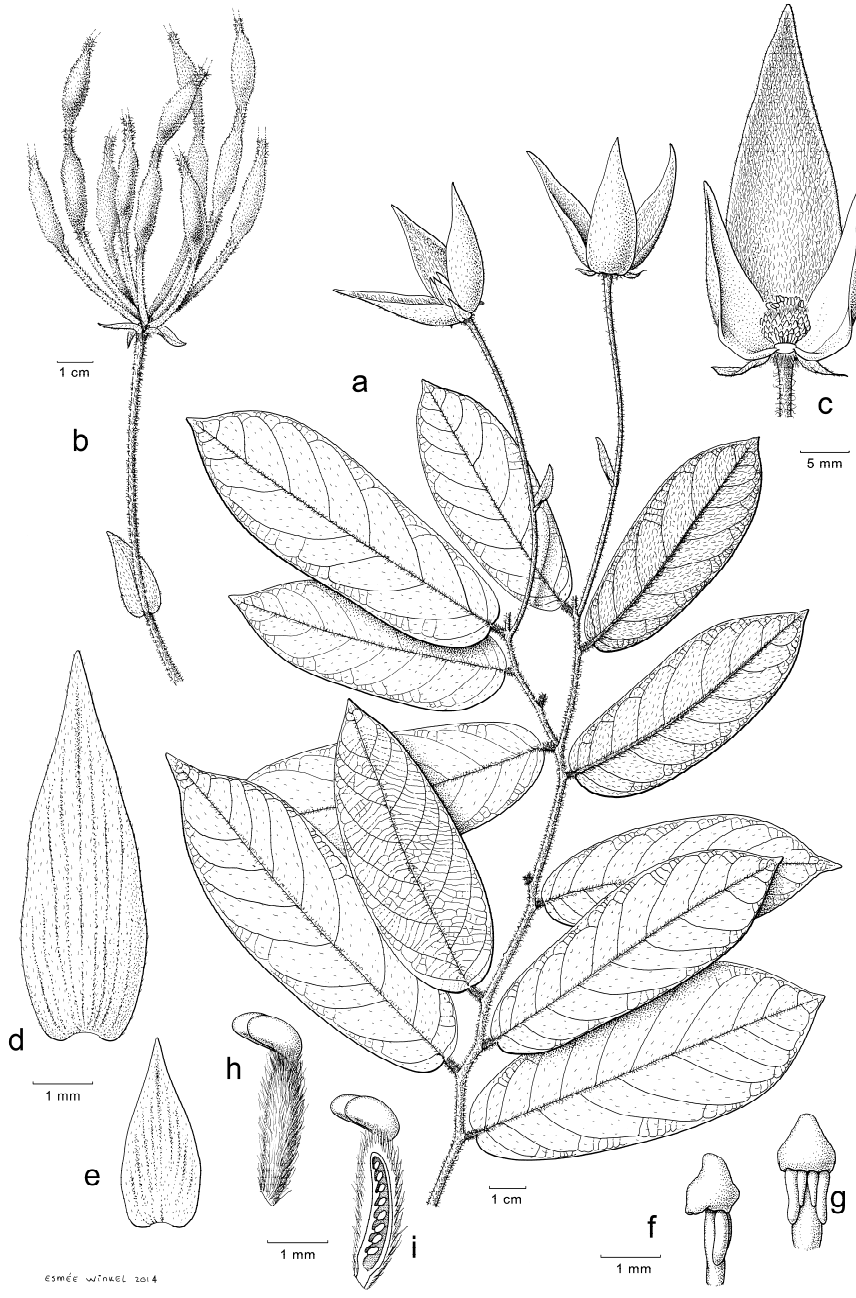


Fig. 26 *Monanthotaxis quasilanceolata* P.H.Hoekstra: a. Flowering branch; b. fruit; c. flower with two outer petals and one inner petal removed; d. outer petal; e. inner petal; f. stamen, side view; g. stamen, front view; h. carpel; i. longitudinal section of carpel (*De Wilde 10971*). Drawing by E. Winkel.

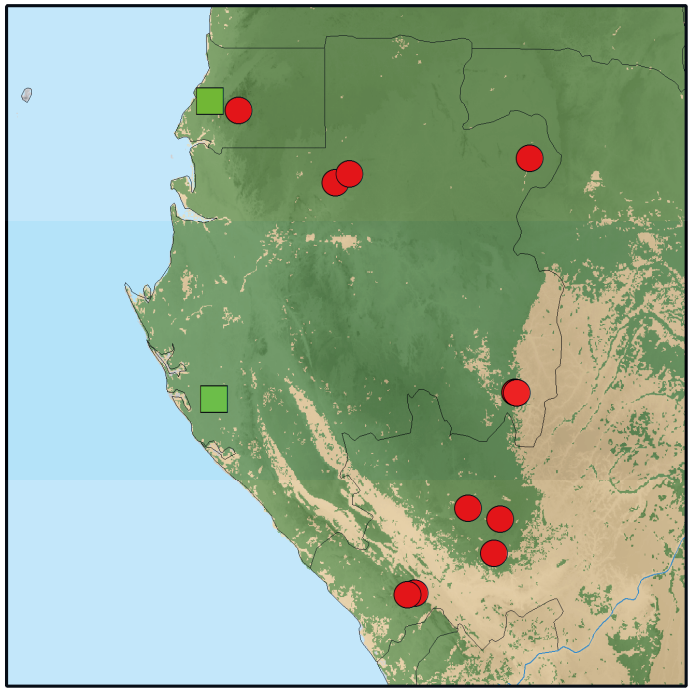
2.6–5.3 cm, 2.3–3 times longer than wide, chartaceous to subcoriaceous, not punctate, dull green above, pale glaucous below, above sparsely covered with appressed, white hairs c. 0.5 mm long, becoming glabrous, primary vein with a more dense indument and composed of erect hairs, below sparsely covered with erect, yellowish hairs 0.7–1 mm long, base subcordate, with thickened margins, apex acuminate, acumen to 25 mm long, secondary veins yellowish, 7–12 per side, curving upwards, tertiary venation percurrent. *Inflorescences* leaf-opposed, composed of solitary pendent flowers; sympodial rachis absent; flowering pedicels 50–112 mm long, 0.6–0.7 mm diam, fruiting pedicels to 2.3 mm diam, covered with erect, reddish brown hairs, becoming glabrous; lower bracts absent; upper bract halfway up the pedicel, lanceolate, 8.5–30 by 2.4–10 mm, indument as on pedicel; flower buds lanceoloid. *Flowers* bisexual; sepals ovate to lanceolate, 8–16 by 4.3–6 mm, apex acute to slightly acuminate, densely covered with appressed, yellowish hairs 0.3–0.5 mm long, persistent in fruit; receptacle 2.5–3.5 mm diam, convex; petals greenish yellow, drying reddish brown, 6, in two whorls, outer petals lanceolate, 30–35 by 11–13 mm, outside sparsely covered with appressed, white hairs, inside densely covered with appressed, white hairs giving a grey appearance, base glabrous, inner petals lanceolate, 14.5–15 by c. 6 mm, outside sparsely covered with appressed, white hairs, inside glabrous except for a few white hairs at the apex and margins; stamens > 60, in four whorls, free, oblong, 1.7–2 mm long, filaments 0.1–0.4 mm long, thecae extrorse, inner thecae smaller than the outer ones, connective conical, prolonged on top of the thecae, 0.7–0.9 mm high, hiding thecae, glabrous, staminodes absent; carpels 13, subcylindric, 3.5–4 by 0.7–0.8 mm, densely covered with yellowish hairs, ovules 8, uniseriate, lateral, stigma ellipsoid, geniculate at insertion with ovary, c. 1 mm long, hairy. *Monocarps* 10, colour in vivo unknown, fusiform to cylindric, > 60 by 4–6 mm, constricted between the seeds, constrictions to 1 cm long, slightly verrucose, apex apiculate, apiculum 5–8 mm long, covered with erect, reddish brown hairs, more densely so on constrictions and stipe, stipes 15–30 mm long, slightly to strongly grooved, rugulose. *Seeds* > 2, narrowly subcylindric, 18–19 by 3.5–5 mm, apex apiculate, apiculum to 0.5 mm long, ochre-brown, raphe visible as a longitudinal furrow from base to apex on both sides, funiculus c. 3.7 by 1.5 mm conical.

Distribution — Equatorial Guinea (Rio Muni Litoral), Gabon (Ogooué-Maritime).

Habitat & Ecology — In primary forest and in small swamp. Altitude: c. 30 m. Flowering: January, July; fruiting: July.

Preliminary IUCN conservation status —Endangered (EN): B2ab(iii).AOO: 8 km^2. This species has only been collected twice in unprotected areas.

Ethymology — The name *quasilanceolata* refers to the lanceolate shape of bracts, sepals, petals and connectives in side view, however, the leaves are oblanceolate.



Map 39 Distribution of *Monanthotaxis quasilanceolata* (green squares) and *M. sterilis* (red circles).

63. *Monanthotaxis scamnopetala* (Exell) P.H.Hoekstra — Fig. 27; Map 38

Monanthotaxis scamnopetala (Exell) P.H.Hoekstra in Guo et al. (2017) 15. — *Popowia scamnopetala* Exell (1932) 207. — *Exellia scamnopetala* (Exell) Boutique (1951b) 118. — Type: *J. Gossweiler 6884* (holo: BM000547053; iso: COI, K000198958, LISC000082, LISC000084, LISU), Angola, Cabinda, Buco-Zau-Maiombe, 18 Dec. 1916.

Liana, to 15 m long, to 20 cm diam; young branches dark brown to blackish, sparsely covered with appressed, reddish brown hairs c. 0.2 mm long, becoming glabrous; old branches blackish. *Leaves:* petiole 4–7 mm long, 1–1.8 mm diam, grooved, indument as on branches; lamina oblong-elliptic to narrowly oblong-elliptic, 5–21 by 2.2–7.6 cm, 1.8–3.4 times longer than wide, chartaceous to subcoriaceous, not punctate, glossy dark green above, glaucous below, above glabrous except for primary vein, below sparsely covered with appressed, yellowish hairs c. 0.2 mm long, becoming glabrous, base cuneate to rounded, with slightly thickened margins, apex acute to slightly acuminate, acumen to 10 mm long, primary vein reddish brown, secondary veins yellowish, 8–13 per side,

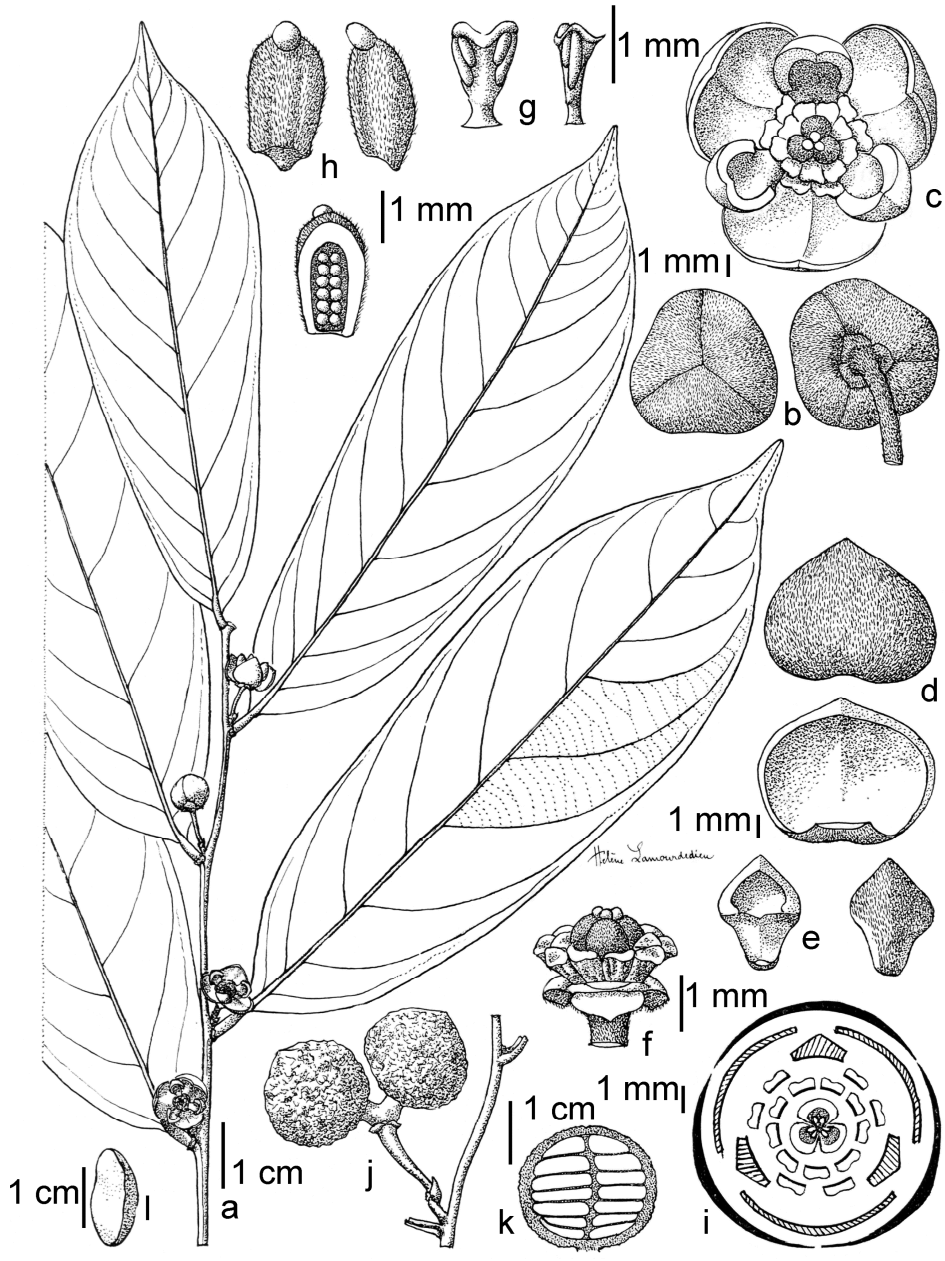


Fig. 27 *Monanthotaxis scamnopetala* (Exell) P.H.Hoekstra: a. Flowering branch; b. flower bud seen from above and below; c. flower seen from above; d. outer petal, outside and inside view; e. inner petal, inner and outside view; f. flower with petals removed; g. stamen, front and side view; h. carpel, front and side view and longitudinal section of carpel; i. floral diagram; j. fruit; k. longitudinal section of monocarp; l. seed (a–i: *N. Hallé & Le Thomas 163*; j: *Donis 2386*; k: *Flamigni 6371*; l: *Evrard 2004*). Modified from Le Thomas (1969) plate 47.

straight but at end curving upwards, tertiary venation percurrent. *Inflorescences* axillary, composed of solitary flowers; sympodial rachis 0–3 mm long; pedicels 4.5–15 mm long, 0.7–0.9 mm diam, fruiting pedicels 10–30 mm long, 2–2.5 mm diam, indument as on branches, becoming glabrous; lower bracts triangular to ovate, to 0.5 by 0.5 mm, densely covered with appressed reddish brown hairs; upper bract absent; flower buds depressed globose. *Flowers* bisexual; sepals free, depressed ovate to triangular, 0.5–1.2 by 1–1.5 mm, apex acute, densely covered with appressed, reddish brown hairs, persistent in fruit or falling off; receptacle c. 1.7 mm diam, flat; petals brownish at the outside, creamy white at the inside (the outer ones), white (the inner ones), 6, in two whorls, outer petals ovate to broadly ovate, 6–9 by 5.5–8 mm, outside covered with appressed yellowish hairs, inside only hairy at the apex, inner petals rhombic and geniculate, 5–6 by 3–3.5 mm, white, outside and apex of the inside sparsely covered with appressed hairs; stamens 14 or 15, in two whorls, in groups of (4)5, free, obconical to obovoid, 1.2–1.8 mm long, filaments 0.2–0.4 mm long, thecae latrorse to slightly extrorse, connective truncate, more or less hiding thecae, glabrous, staminodes absent; carpels 3, oblongoid to obovoid, 2.7–2.8 by 1.4–1.6 mm, densely hairy, ovules in two rows, 12–16, lateral, stigma subsessile, conical, c. 0.3 mm long, glabrous. *Monocarps* 1–3, green to golden brown in vivo, black in sicco, sessile, globose, 1.7–2.4 by 1.7–2.6 cm, verrucose. *Seeds* 10–14, half-moon shaped, outside convex, inside flat, 12–19 by 6–11 mm, ochre brown, both ends rounded.

Distribution —Central African Republic, Democratic Republic of the Congo, Gabon, Republic of the Congo, Angola.

Habitat & Ecology — In evergreen forest, gallery forest, semi-deciduous forest, old secondary forest and on rock plateau with shallow soil. Altitude: 350–900 m. Flowering: February, March, July, October, December; fruiting: February to June, August to November.

Vernacular names — Democratic Republic of the Congo: Moamba Nsinga (Pila name) (*L. Toussaint 205*), Muamba Nsinga (*L. Toussaint 398*), Ngiko e Likebe (Turumbu name) (*C.M. Evrard 2004*).

Preliminary IUCN conservation status — Least concern (LC). EOO: 1,349,342 km^2, AOO: 92 km^2. This species has been collected several times recently, including in nature reserves. Therefore, this species is likely not under threat of extinction.

Notes — 1. *Monanthotaxis scamnopetala* is together with *M. mcphersonii* the only species of *Monanthotaxis* with sessile monocarps and biseriate ovules (Fig. 1, clade E). It can easily be distinguished from *M. mcphersonii* by the appressed, short hairs on the stems and leaves.

2. According to Le Thomas (1969) *M. scamnopetala* sometimes has a geminate inflorescence.

3. According to Boutique (1951a) and Le Thomas (1969) *M. scamnopetala* has 15–20 ovules per carpel, however, in the drawings of their respective publications a row of 7 ovules (Boutique 1951a) and two rows of 6 ovules (Le Thomas 1969) are visible, which coincides with our observations of 12–16 ovules consisting of two rows of 6–8 ovules.

64. *Monanthotaxis schweinfurthii* (Engl. & Diels) Verdc. — Map 40

Monanthotaxis schweinfurthii (Engl. & Diels) Verdc. (1971b) 27. — *Popowia schweinfurthii* Engl. & Diels (1901) 51. — *Enneastemon schweinfurthii* (Engl. & Diels) Robyns & Ghesq. (1933) 165. — *Enneastemon schweinfurthii* (Engl. & Diels) Robyns & Ghesq. var. *schweinfurthii*: Le Thomas (1969) 252. — Type: *G.A. Schweinfurth 3157* (holo: B100153043; iso: K000198984), Democratic Republic of the Congo, Orientale, Dungu, Mbruole, Mar. 1870.

Shrub, scandent shrub or liana; young branches densely covered with appressed, yellowish brown hairs 0.1–0.2 mm long, becoming glabrous; old branches dark brown. *Leaves:* petiole 4–9 mm long, 1.2–1.7 mm diam, slightly grooved or terete, indument as on branches; lamina oblong-obovate to obovate or narrowly so, 6.9–18.4(–20.6) by 3.7–6.5(–7.6) cm, 1.9–2.7 times longer than wide, chartaceous, not punctate, glaucous below, above sparsely covered with appressed, whitish hairs 0.4–0.5 mm long, becoming glabrous, primary vein more densely covered with ascending to erect, yellowish brown hairs 0.2–0.3 mm long, below sparsely to densely covered with appressed, yellow-brown hairs 0.1–0.2 mm long, primary vein more densely hairy, base cuneate to rounded with thickened black margins, apex obtuse, acute to acuminate, acumen to 15 mm long, secondary veins 9–13 per side, slightly curving, tertiary venation percurrent, hardly visible. *Inflorescences* axillary, composed of a solitary flower to 2-(or 3-)flowered fascicle-like rhipidia; sympodial rachis absent or < 1 mm long; pedicels 9–20 mm long, 0.3–0.4 mm diam, fruiting pedicels 15–25 mm long, 1–1.8 mm diam, sparsely to densely covered with appressed, yellow-brown hairs; lower bract absent; upper bract in the lower half of the pedicel, ovate, 0.4–0.5 by 0.3–0.4 mm, indument as on pedicel; flower buds globose. *Flowers* bisexual; sepals connate at the base, depressed ovate, 0.7–1.2 by 1.2–1.8 mm, apex acute to obtuse, densely covered with appressed, yellow-brown hairs, persistent in fruit; receptacle 1.3–1.5 mm diam, flat; petals colour in vivo unknown, 6, in two whorls, base of inner petals visible in bud, outer petals ovate to broadly ovate, 4–4.8 by 2.8–4.6 mm, outside and inside densely covered with appressed, white-brown, short hairs, base glabrous, inner petals rhombic to elliptic, 2–4.3 by 1–3.3 mm, outside and apical part of the inside densely covered with white-brown hairs; stamens 9, in one whorl, free, clavate, 1–1.7 mm long, filaments 0.6–1.3 mm long, thecae extrorse, connective truncate, slightly prolonged inward and outward, hiding the thecae, glabrous except sparsely hairy on the inside, staminodes absent; carpels 5 or 6, subcylindric, 1.5–1.9 by 0.5–0.6 mm, densely hairy, ovules 5 or 6, lateral, stigma elongate, 0.2–0.4 mm long, glabrous. *Monocarps* 1–4, colour in vivo unknown, moniliform, each part ellipsoid, 15–34 by 8–9 mm, slightly verrucose, densely covered with appressed, whitish yellow hairs, apiculate, apiculum 3–6 mm long, stipes 3.5–4.8 mm long. *Seeds* 1–6, ellipsoid to subglobose, c. 10 by 8.5 mm, ochre-brown, ends rounded, raphe visible.

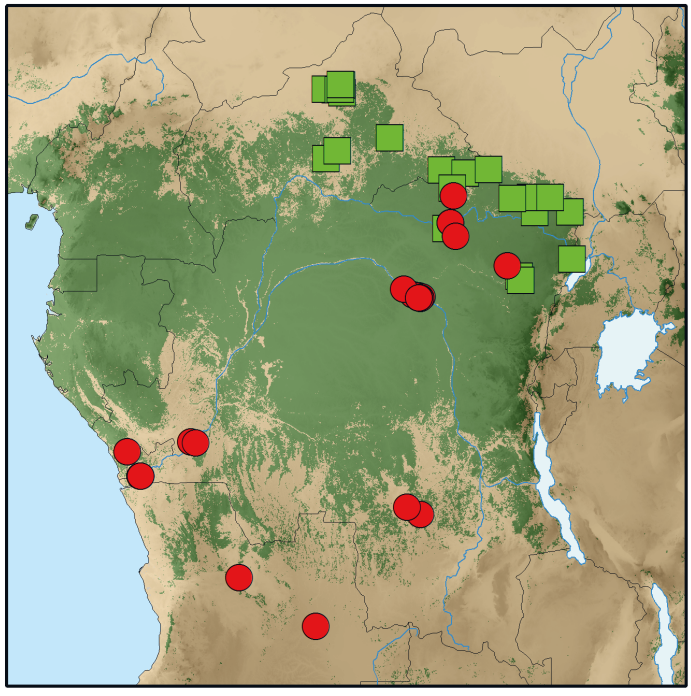
Distribution — Central African Republic, South Sudan, Democratic Republic of the Congo.

Habitat & Ecology — In gallery forest, swamp forest, and semi-deciduous forest. Altitude: 200–1290 m. Flowering: March to May, October; fruiting: December to March, May, July, October.

Vernacular names — Central African Republic: Búgù-àndima (Zande name) (*M. Buckner 120*). Democratic Republic of the Congo: Amapupu (*T.B. Hart 1545*).

Preliminary IUCN conservation status —Least concern (LC). EOO: 383,894 km^2, AOO: 92 km^2. This species has a quite wide distribution and has been collected several times recently, including in some nature reserves.

Notes — *Monanthotaxis schweinfurthii* belongs to the *M. schweinfurthii* complex (Fig. 1, clade B) and can be recognized by the combination of having 5 or 6 carpels per flower and yellow-brown indument on the stems and leaves. This combination of characters also occurs in the allopatric *M. barteri* from West-Africa, see the note under that species.



Map 40 Distribution of *Monanthotaxis schweinfurthii* (green squares) and *M. seretii* (red circles).

65. *Monanthotaxis seretii* (De Wild.) P.H.Hoekstra, *comb. nov.* — Fig. 6a, 28; Map 40

Popowia seretii De Wild. (1909) 76. — *Enneastemon seretii* (De Wild.) Robyns & Ghesq. (1933) 162. — *Enneastemon schweinfurthii* (Engl. & Diels) Robyns & Ghesq. var. *seretii* (De Wild.) Le Thomas (1969) 253. — Type: *F. Seret 870* (holo consisting of 2 sheets: BR0000008804716, BR0000008820259), Democratic Republic of the Congo, Orientale, Bambesa, Poko Zobia, 4 May 1907.

Enneastemon angolensis Exell (1932) 210. — Type: *J. Gossweiler 9488* (holo consisting of 2 sheets: BM000553823, BM000553824; iso: B100460755, COI00004901, K000198965, LISC000269, LISC000270, US00098694), Angola, Malanje, rio Lui, Quibo-Quela, 1200 m, 3 Feb. 1931.

Enneastemon affinis Robyns & Ghesq. (1933) 163. — Lectotype (designated here): *P. Quarré 2708* (lectotype: BR, consisting of 5 sheets: BR0000008820457, BR0000008820464, BR0000008820563, BR0000008820570, BR0000008820587; iso: K000198907), Democratic Republic of the Congo, Katanga, Kaniama, récolté a la Pastorale section I, Mutalala en Kil, Sep. 1931.

Liana to 25 m long; young branches densely covered with appressed to ascending, reddish brown hairs 0.1–0.2 mm long, becoming glabrous; old branches reddish brown to dark brown. *Leaves:* petiole 5.5–13 mm long, 0.8–1.7 mm diam, slightly grooved, indument as on branches; lamina oblong-elliptic to obovate, 4.2–22.4 by 2.1–11.8 cm, 1.8–2.4 times longer than wide, subcoriaceous, not punctate, glaucous below, above sparsely covered with appressed to ascending, white hairs 0.1–0.2 mm long, primary vein covered with erect, yellowish hairs, becoming glabrous, below sparsely covered with appressed, yellowish hairs 0.1–0.2 mm long, base rounded to subcordate with thickened black margin, apex acute to shortly acuminate, acumen 5–10 mm long, secondary veins 7–10(–13) per side, straight or slightly curving, tertiary venation percurrent, hardly visible. *Inflorescences* axillary or supra-axillary, solitary, but more often in up to 6-flowered fascicle-like rhipidia; sympodial rachis cushion-like, up to 4 mm long, densely covered with reddish brown hairs c. 0.1 mm long; pedicels 5–17 mm long, 0.4–0.6 mm diam, fruiting pedicels 1–2.2 mm diam, indument as on rachis; lower bracts absent; upper bract placed halfway or in lower half of the pedicel, ovate to broadly ovate, 0.4–0.5 by 0.8–1 mm, indument as on rachis; flower buds globose. *Flowers* bisexual; sepals connate at the base, depressed ovate, 0.4–1 by 1.2–2 mm, apex obtuse to slightly acute, densely covered with appressed hairs, falling off in fruit; receptacle 2–2.5 mm diam, flat; petals colour in vivo unknown, in sicco the inner petals reddish brown on the base and yellowish brown near the top of the outside, 6, in one whorl, outer petals overtopping inner petals in bud, outer petals ovate to rhombic, 4.5–7 by 3.5–4.5 mm, outside and inside densely covered with appressed to ascending, reddish brown hairs, but hairs shorter to glabrous near base of inside, inner petals elliptic to rhombic, 3.2–5.9 by 2.2–3.4 mm, outside covered with ascending to erect hairs, inside densely covered with yellowish brown, very short hairs;

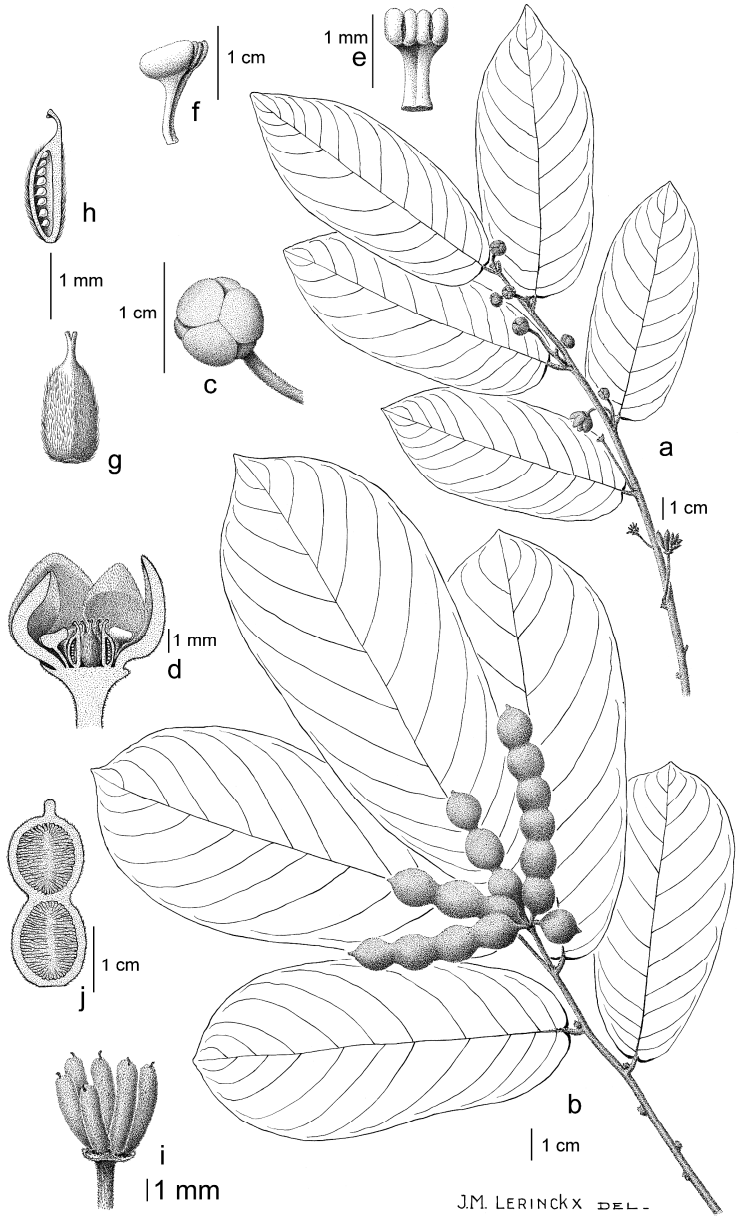


Fig. 28 *Monanthotaxis seretii* (De Wild.) P.H.Hoekstra: a. Flowering branch; b. fruiting branch; c. flower bud seen from above; d. longitudinal section of flower; e. stamen, outside view; f. stamen, side view; g. carpel; h. longitudinal section of carpel; i. young fruit; j. longitudinal section of monocarp (based on *Toussaint 127* and *396*). Modified from Boutique (1951a) plate 36.

stamens 9, in one whorl, free, clavate, 1.3–1.5 mm long, filaments 0.8–1 mm long, thecae extrorse, connective truncate, prolonged outward and inward, hiding the thecae, glabrous, but sparsely hairy on the underside of the inward appendage, staminodes absent; carpels c. 6, narrowly subcylindric to narrowly ellipsoid, 1.9–2 by 0.6–0.7 mm, grooved, densely hairy, ovules 5 or 6, lateral, stigma elongate, 0.4–0.5 mm long, glabrous. *Monocarps* 1–6, colour in vivo unknown, moniliform, 23–70 by 8–11 mm, slightly to clearly verrucose, densely covered with reddish brown, yellowish brown to whitish hairs 0.1–0.2 mm long, apex rounded to apiculate, apiciulum to 3 mm long, stipes 4–8 mm long. *Seeds* 1–5, globose to ellipsoid, 10–12 by 8–11 mm, ochre-brown, apex rounded, raphe clearly visible.

Distribution —Democratic Republic of the Congo (Bas-Congo, Kasai-Oriental, Katanga, Kinshasa, Orientale), Angola (Cabinda, Lunda Sul, Malanje).

Habitat & Ecology — In gallery forest, secondary forest and at forest at edge of savannas. Altitude: 470–1200 m. Flowering: November to May, July to September; fruiting: February to June, September and November.

Vernacular names — Democratic Republic of the Congo: Badamu (Zande name) (*P. Gérard 4514*) 1057044, Dupe Kasa keke (Babua name) (*P. Gérard 3806*) 1060891, Dupe kasa Sisi (Babua name) (*P. Gérard 4995*) 321695

Preliminary IUCN conservation status —Vulnerable (VU): B2ab(iii). EOO: 1,441,060 km^2, AOO: 80 km^2. This species is known from nine locations, of which three in nature reserves. This species has only been collected twice in the last 50 years and the majority of locations are under threat of logging and pressure of expanding populations.

Notes — 1. *Monanthotaxis seretii* belongs to the *M. schweinfurthii*-complex (Fig. 1, clade B) and can be recognized by the combination of having 6 carpels per flower and a reddish brown indument. *Monanthotaxis capea* also has these characters and can best be distinguished by the monocarps, which are strongly rugose-tuberculate in *M. capea* and weakly to strongly verrucose in *M. seretii.* Furthermore, *M. seretii* generally has a subcordate leaf base, but more collections from the north of the Democratic Republic of the Congo are needed to assess the exact boundaries in species delimitation between *M. seretii* and *M. capea.*

2. There is quite some variation in general appearance across the distribution area of *M. seretii*. The pedicel length is 5–8 mm in North and Central Democratic Republic of the Congo and 6–17 mm in Angola and Bas-Congo. Furthermore, the hairs on the monocarps are reddish brown in Angola, but yellowish brown to whitish brown in the Democratic Republic of the Congo.

66. *Monanthotaxis stenosepala* (Engl. & Diels) Verdc. — Fig. 15p–u; Map 41

Monanthotaxis stenosepala (Engl. & Diels) Verdc. (1971b) 29. — *Popowia stenosepala* Engl. & Diels (1901) 49. — Lectotype (designated here): *G.F. Scott Elliot 5564* (lectotype: K (K000198909); isolecto: B100153047, BM001125035, P00362647), Sierra Leone, Northern Province, Limba, near Madina, 11 Apr. 1892.

Small tree or thick bush, to 2.3 m tall; young branches dark brown, sparsely covered with appressed, yellowish hairs 0.1–0.2 mm long, becoming glabrous; old branches pale brown. *Leaves:* petiole 2.5–4 mm long, 0.5–0.9 mm diam, grooved, indument as on branches; lamina obovate to oblong-elliptic or narrowly so, 4.5–12.2 by 2–4 cm, 2.3–3.4 times longer than wide, chartaceous, not punctate, above glabrous, but primary vein with a few short hairs near the base, becoming glabrous, below sparsely covered with appressed, white hairs 0.2–0.3 mm long, primary vein covered with appressed, yellowish hairs, base rounded to cuneate, glands hardly visible, apex acute to acuminate, acumen to 10 mm long, secondary veins 8–13 per side, straight to curving upwards, tertiary venation slightly percurrent. *Inflorescences* leaf-opposed or extra-axillary, composed of solitary flowers to 3-flowered fascicles; sympodial rachis 0–0.5 mm long; pedicels 5–20 mm long, 0.3–0.4 mm diam, fruiting pedicels 0.4–0.6 mm diam, covered with yellowish, ascending to erect hairs; lower bract lanceolate or absent, c. 1.3 by 0.3 mm, densely covered with hairs; upper bract in lower half of the pedicel, ovate to lanceolate, 1.1–2 by 0.5–0.7 mm, densely covered with hairs; flower buds ovoid. *Flowers* bisexual; sepals free, lanceolate, 4–6 by 1.5–2.2 mm, apex acute, densely covered with appressed, short hairs, persistent in fruit or falling off; receptacle 1.5–2.5 mm diam, flat; petals colour in vivo unknown, 6, in two whorls, outer petals ovate to elliptic, c. 4.7 by 2.3 mm, outside and apical part of the inside covered with yellowish, very short hairs, base of inside glabrous, inner petals narrowly elliptic, c. 4.2 by 1.3 mm, indument as on outer petals; stamens c. 14 (see note 2), in one whorl, free, obovoid to obconical, c. 0.7 mm long, filaments c. 0.1 mm long, thecae extrorse to latrorse, connective truncate, prolongation triangular pointing outward, not hiding thecae, glabrous, staminodes absent; carpels 7–10, narrowly ellipsoid, c. 3.2 by 1.2 mm, densely hairy, ovules 2 or 3, lateral, stigma elongate, 0.7–1.2 mm long, deeply bifurcate, glabrous. *Monocarps* 1–10, yellow, ellipsoid, 8–18 by 4–5 mm, slightly constricted between the seeds, sparsely covered with appressed, short hairs, apex apiculate, apiculum to 3 mm long, stipes 2–3 mm long, terete. *Seeds* 1 or 2, ellipsoid, c. 6 by 4 mm, tawny brown.

Distribution — Sierra Leone (Northern Province).

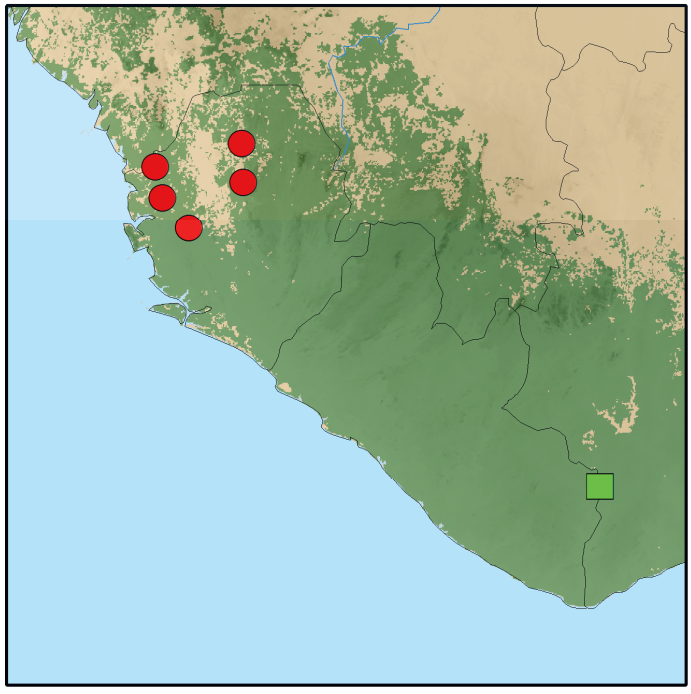
Habitat & Ecology — Flowering: April; fruiting: January, July.

Preliminary IUCN conservation status —Endangered (EN): B2ab(iii). EOO: 7,184 km^2, AOO: 20 km^2. This species is known from only 5 collections in a small area in Sierra Leone and has not been collected since 1936.

Notes — 1. *Monanthotaxis stenosepala* is the only species in Sierra Leone with sepals as long as or longer than the petals. It can be distinguished from other species with large sepals

by the lanceolate sepals and young branches sparsely covered with appressed, short hairs; it differs from *M. lucidula* by the narrower oblong-oblanceolate leaves and much shorter filaments.

2. We have only counted the stamens in one young flower bud of *N.W. Thomas 10603.* According to the protologue (Engler & Diels 1901) this species should have 6–9 stamens. Unfortunately, the stamens of all flowers of the type have fallen off, making it impossible to count the exact number of stamens, but according to the scars left in the flower of the type collection it appears that there have been more than 12 stamens per flowers.



Map 41 Distribution of *Monanthotaxis stenosepala* (red circles) and *M. ursus* (green square).

67. *Monanthotaxis sterilis* P.H.Hoekstra, *sp. nov*. — Fig. 29; Map 39

Monanthotaxis sterilis can be distinguished from all other species of *Monanthotaxis* by the linear to narrowly elliptic leaves and the secondary veins that are almost perpendicular to the primary vein. — Type: *T.L.P. Couvreur 869* (holotype: WAG (WAG.1575982); iso: LBV, YA), Gabon, Woleu-Ntem, on road from Mitzic to Lalara (N2), just after the bridge over the Lara, 150 m in forest, 382 m, 15 Nov. 2015. Paratypes: *A. Bouquet 1041* (P), Republic of the Congo, Lékoumou, village de Moutséné, Batéké, piste de Bouba, 20 Jan. 1965; *A. Bouquet 1782* (P), Republic of the Congo, Lékoumou, Monts Ndoumou, au niveau du village de Mandili, 11 Oct.

1965; *T.L.P. Couvreur et al. 628* (YA), Cameroon, Littoral, Ebo Wildlife Reserve, Djuma permanent camp, on east trail, 1000 m, 15 Feb. 2013; *T.L.P. Couvreur et al. 713* (LBV, WAG), Gabon, Haut-Ogooué, Ossélé village, 45 km on road from Franceville to Kessala, 20 Mar. 2015; *T.L.P. Couvreur et al. 731* (LBV, WAG), Gabon, Haut-Ogooué, Ossélé village, 45 km on road from Franceville to Kessala, 21 Mar. 2015; *T.L.P. Couvreur et al. 792* (IEC not seen, WAG), Republic of the Congo, Kouilou, 30 km on Dolisie-Mvouti road, just behind the telephone antenna, 703 m, 21 Sep. 2015; *G.H.J. Cusset 892* (P), Republic of the Congo, Kouilou, environs de Dimonika, au-dessus de la source Paris Sangha, 5 Mar. 1980; *C. Farron 4470* (P), Republic of the Congo, Lékoumou, 35 kms Est Sibiti, Moussoumou, chantier forestier de M. Fouet, 18 Aug. 1965; *N. Hallé & Le Thomas 371* (P), Gabon, Ogooué-Ivindo, 25 km SE de Mekambo, route canton sud, 7 Aug. 1966; *B. Senterre & Obiang Mbomio 3409* (BRLU), Equatorial Guinea, Rio Muni, Centro Sur, SE du Parc National de Monte Alén, au S du Rio Laña, près de la Cabaña Ecofac de Misergue, 850 m, 17 July 2002; *J.J. Wieringa et al. 8406* (WAG), Gabon, Woleu-Ntem, 17 km SE of Mitzic, forestry chantier St. Germain (Foreex), 500 m, 16 Nov. 2015.

Shrub or liana, to 6 m long; young branches densely covered with appressed to ascending, reddish brown hairs 0.2–0.4 mm long, becoming glabrous; old branches blackish brown. *Leaves:* petiole 2–4 mm long, 0.6–0.8 mm diam, slightly grooved, indument as on branches; lamina linear to narrowly elliptic, 9.1–15.2 by 1.4–2.1 cm, 4.9–7.6 times longer than wide, chartaceous, not punctate, glossy dark green above, dull pale greyish green below, above sparsely covered with appressed, white hairs 0.3–0.4 mm long, soon becoming glabrous, primary vein densely covered with ascending, yellowish hairs, below sparsely covered with appressed, yellowish hairs 0.2–0.3 mm long, base cuneate, with slightly thickened black margin, apex acuminate, acumen 10–20 mm long, secondary veins 15–20 per side, almost perpendicular with primary vein, straight, but curving halfway, tertiary venation slightly percurrent, hardly visible. *Flowers*, *monocarps* and *seeds* not seen.

Distribution — Cameroon, Equatorial Guinea, Gabon, Republic of the Congo.

Habitat & Ecology — In primary forest, submontane forest and secondary rain forest, on hill sides and on sand soil near stream. Altitude: 382–850 m.

Preliminary IUCN conservation status — Least concern (LC). EOO: 163,087 km^2, AOO: 44 km^2. This species has only been collected a few times as most collectors do not collect sterile material. However, recent field work has shown that this species is actually quite common in the forests of Gabon and surrounding areas (Thomas Couvreur and Paul Hoekstra personal observations).

Ethymology — This species is called *sterilis* as there are many collections, but all are sterile despite significant efforts to find fertile material.

Note — Although the leaf shape is unique within *Monanthotaxis*, the DNA-based phylogenetic analysis clearly place this species within *Monanthotaxis*. Also the lianescent

habit with glaucous leaves and eucamptodromous venation clearly place this species within *Monanthotaxis*.

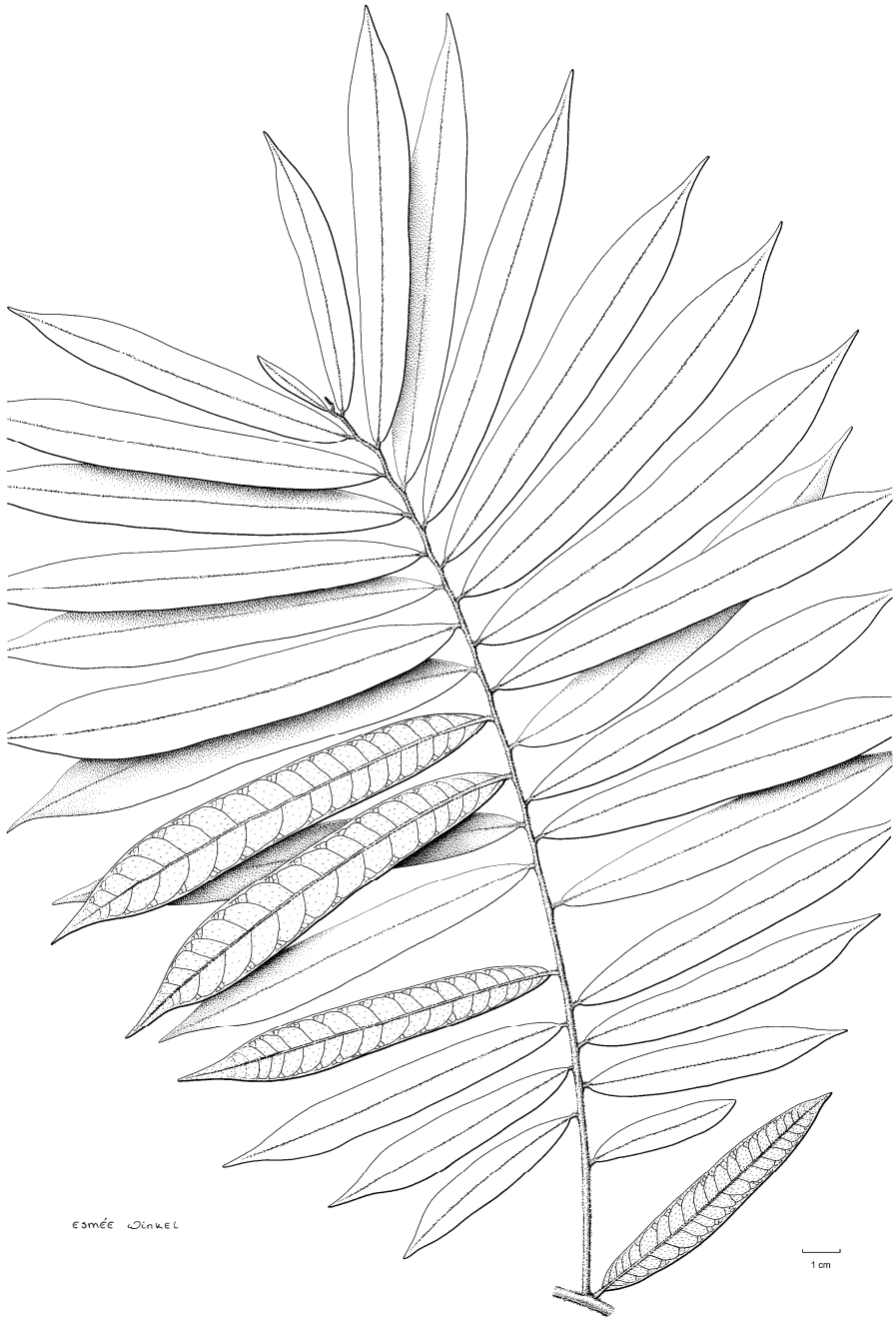


Fig. 29 *Monanthotaxis sterilis* P.H.Hoekstra: Habit (*Couvreur 869*). Drawing by E. Winkel.

68. *Monanthotaxis submontana* P.H.Hoekstra, *sp. nov.* — Fig. 30; Map 42

Monanthotaxis submontana belongs to the group of *Monanthotaxis* species with cauliflorous, unisexual flowers, but differs from all these species in the presence of stamens and/or staminodes (1– 14) in pistillate and rarely in bisexual flowers. Furthermore, it is distinguished from most cauliflorous species by the combination of having oblong-elliptic leaves with a cuneate leaf base and inflorescences with a sympodial rachis up to 7 cm long, pedicels ranging from 7–55 mm long and flowers with 65–85 carpels. — Type: *R.G. Letouzey 14476* (holotype: WAG (WAG0053953); iso: MO 2 sheets, P01982361), Cameroon, Littoral, Nlonako, 5 km SEE of Nkongsamba, 1600 m, 17 Mar. 1976. Paratypes: *M.R. Cheek et al. 9067* (K, KUPE not seen, WAG, YA), Cameroon, South-West Region, Mount Kupe, Kodmin, ridge on S side of LOH mt, 1650 m, 23 Jan. 1998; *M.R. Cheek et al. 9202* (K, KUPE not seen, WAG, YA), Cameroon, South-West Region, Mount Kupe Division, Kodmin to Nzeembeng, c. 1 km pas tjunction for Ngomin and crossing of Ndip river, 1150 m, 14 Feb. 1998; *C. Doumenge 554* (MO, P), Cameroon, South-West Region, forested slope in the Bakossi Mountains 1–8 km NNE of Menyum village, 1000 m, 22 May 1987; *M. Etuge et al. 4122* (K, WAG, YA), Cameroon, South-West Region, Nzimbeng road, 1300 m, 4 Feb. 1998; *M. Etuge et al. 4442* (K, KUPE not seen, WAG, YA), Cameroon, South-West Region, Kupe-Muanenguba division, Muahumzum, Kodmin road towards Mahusom, 1400 m, 12 Nov. 1998; *D.W. Thomas & Macleod 5274* (MO, P, YA), Cameroon, South-West Region, forested hillsides in the Bakossi Mountains, west of Bangem, 800 m, 3 Jan. 1986.

Liana, 6–10 m long, c. 5 cm diam; young branches dark brown, covered with appressed to slightly erect, yellowish hairs, 0.1–0.2 mm long, becoming glabrous; old branches dark brown spotted green in vivo. *Leaves:* petiole 6–10 mm long, 0.7–0.8 mm diam, grooved, indument as on branches; lamina narrowly oblong-elliptic to oblong-elliptic, 7.2–14.1 by 2.1–3.5 cm, 2.3–4.5 times longer than wide, chartaceous, not punctate, glaucous below, above densely covered with appressed, white to yellow hairs 0.2–0.3 mm long, primary vein more densely covered with persistent hairs, becoming glabrous, below covered with appressed,white hairs 0.2–0.3 mm long, primary vein covered with more persistent hairs, base cuneate, with thickened black margin, apex acute to acuminate, acumen to 15 mm long, secondary veins 11–18 per side, straight to curving upwards, tertiary venation percurrent. *Inflorescences* cauliflorous, composed of condensed many-flowered panicles; sympodial rachis to 7 cm long, densely covered with appressed to erect, reddish brown hairs 0.1–0.3 mm long; pedicels 7–55 mm long, 0.8–0.9 mm diam, fruiting pedicels 1.4–1.8 mm diam, densely covered with reddish brown hairs; lower bracts ovate, 1.3–2.2 by c. 0.8 mm, indument as on rachis; upper bracts in lower part of the pedicel, shape and indument as lower bracts; flower buds ovoid to globose. *Flowers* bisexual or unisexual; sepals broadly ovate, 1.5–1.8 by 1.5–1.8 mm, densely

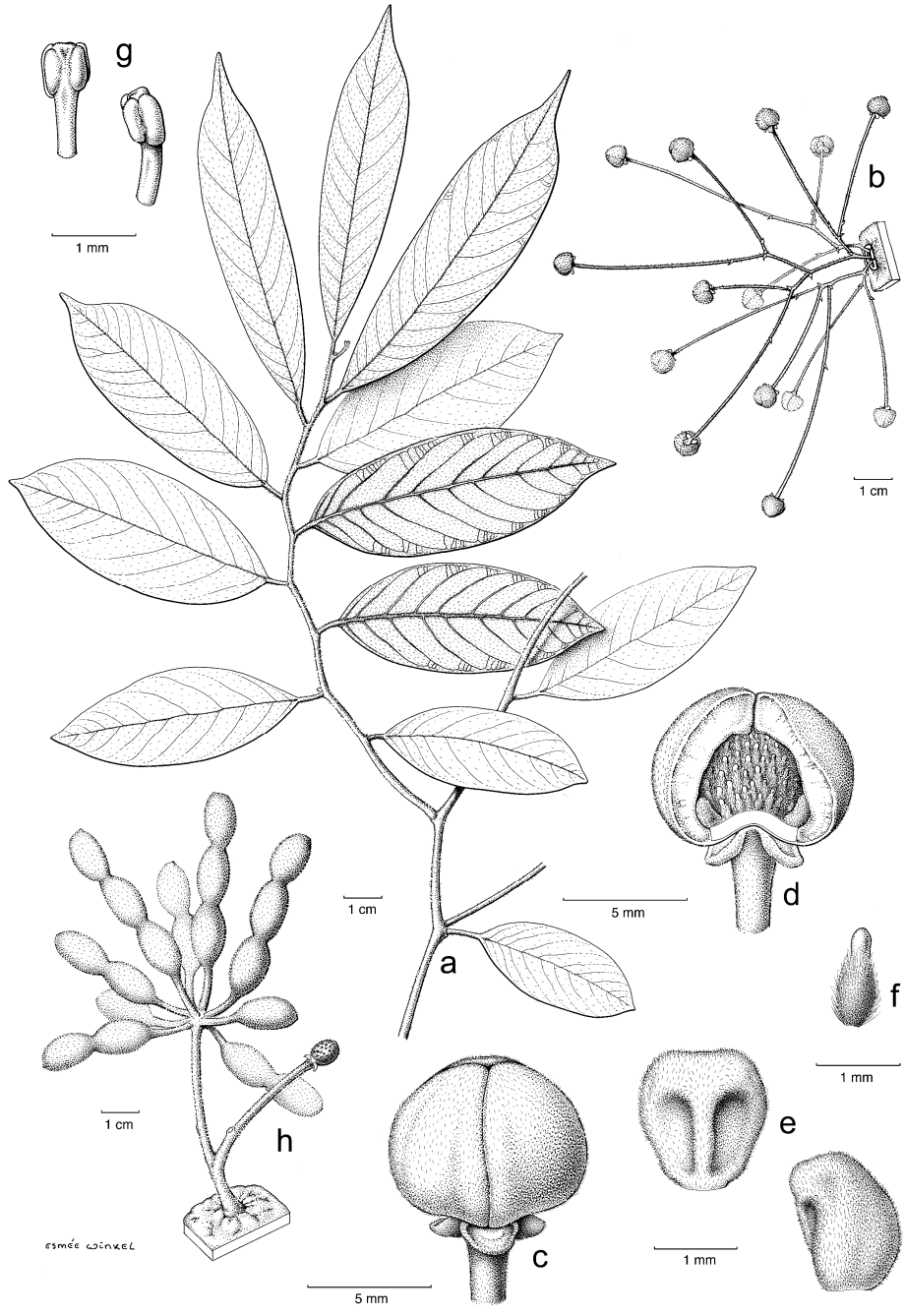
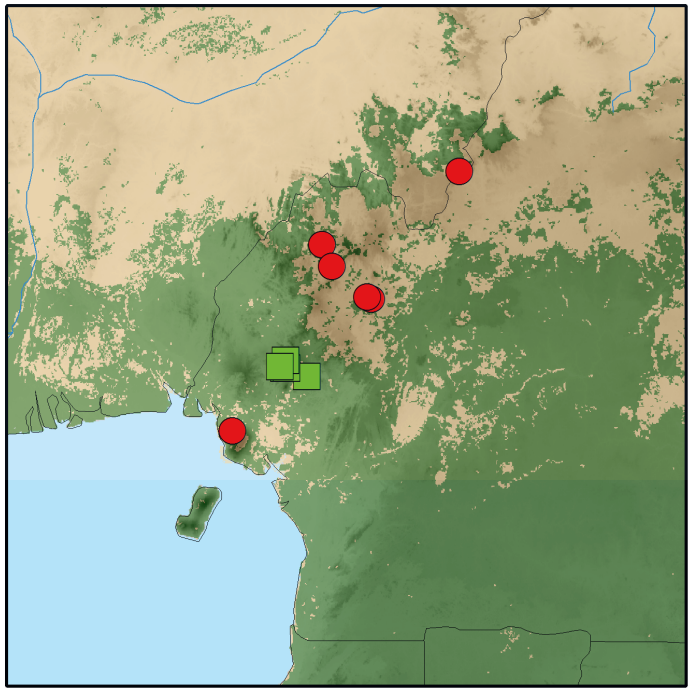


Fig. 30 *Monanthotaxis submontana* P.H.Hoekstra: a. Habit; b. inflorescence; c. flower bud; d. flower bud with one outer petal removed; e. inner petal, inner and outside view; f. carpel; g. stamen, front and side view; h. fruiting inflorescence (*Letouzey 14476*). Drawing by E. Winkel.

covered with appressed hairs, persistent in fruit; receptacle c. 2.2 mm diam, convex to globose; petals dark brown to golden green on the outside, yellowish at the inside, 6, in two whorls, outer petals broadly ovate, 3.6–5 by 3.6–5.7 mm, outside densely covered with appressed, reddish brown, short hairs, inside covered with yellowish hairs c. 0.05 mm long, inner petals sometimes strongly reduced to absent, broadly elliptic, 0.4–1.3 by 0.3–1.1 mm, outside and inside covered with yellowish hairs c. 0.05 mm long; stamens 0–2(–4), in one whorl, free, often only 1 or 2 present near the inner petals and the others reduced to staminodes, oblong to slightly clavate, c. 1 mm long, filaments c. 0.6 mm long, hairy, thecae extrorse to latrorse, on top of stamen hiding connective, staminodes 0–14 from very small to almost identical to the stamens; carpels 65–85, ellipsoid, 0.8–0.9 by 0.4–0.5 mm, densely hairy, ovules 3–5, lateral, stigma globose, c. 0.1 mm diam, glabrous. *Monocarps* up to 18, medium green, moniliform, each part ellipsoid, 23–45 by 7–9 mm, smooth to slightly verrucose, covered with appressed, reddish brown, short hairs, apex apiculate, apiculum to 2 mm long, stipes 7–14 mm long, slightly grooved. *Seeds* 1–4, ellipsoid, 13–14 by 6–8 mm, tawny brown, ends rounded to apiculate, raphe slightly visible as a longitudinal furrow from base to apex.

Distribution — Cameroon (Littoral, South-West Region).



Map 42 Distribution of *Monanthotaxis submontana* (green squares) and *M. vulcanica*(red circles).

Habitat & Ecology — In submontane forest, montane forest and swamp forest. Altitude: 800–1650 m. Flowering: January, March; fruiting: January, February, May, November.

Preliminary IUCN conservation status —Endangered (EN): B2ab(iii). EOO: 173 km^2, AOO: 20 km^2. This species is known from 7 collections from a very small area of which the largest part is under threat by habitat destruction and by degradation.

Ethymology — Named *submontana* as this species is confined to the submontane forests of Cameroon.

Notes — 1. It is unclear if the stamens in the flowers of *M. submontana* really are fertile. In most flowers there are several staminodes present, which vary from hardly developed to almost stamen-like with thecae. It is unclear if those biggest stamens contain pollen or not and material in more advanced stages of flowering are needed to assess this.

2. On the sheets of *Letouzey 14476* is written 'only pistillate flowers apparently'. Letouzey probably overlooked the small stamens and staminodes as they are only visible when the inner petals are bend backwards.

69. *Monanthotaxis suffruticosa* P.H.Hoekstra, *sp. nov*. — Plate 5h; Map 43

Monanthotaxis suffruticosa is the only species of *Monanthotaxis*, which grows as a subshrub just up to 40 cm high. It closely resembles *M. faulknerae* and *M. trichocarpa* as all 3 species have c. 24 stamens in two whorls, monocarps covered with erect hairs, and leaves punctate in sicco. Besides the growth form, *M. suffruticosa* differs from *M. trichocarpa* in the oblong-elliptic leaves, which are generally obovate in *M. trichocarpa*; from *M. faulknerae* it differs by generally broader leaves (2.1–3.8 cm versus 0.7–2.6 cm) and more carpels per flower (14–16 versus 8–10). — Type: *K.B. Vollesen MRC3362* (holotype: WAG (WAG0053977); iso: C, EA, K, UPS), Tanzania, Lindi, Selous Game Reserve, Madaba, 300 m, 7 Mar. 1976. Paratypes: *E.M.C. Groenendijk et al. 1029* (LMU not seen, MO), Mozambique, Nampula, distrito de Monapo, reserva florestal do Sr. Wolf em Monapo, 10 Feb. 1984; *M.C. Lötter & Turpin 1741* (K), Mozambique, Cabo Delgado, Pr 1040, 25 km west of Palma, 132 m, 22 Mar. 2009; *T. Rees 155* (C, EA), Tanzania, Lindi, Selous game reserve, Mkangira área, 300 m, 8 July 1971; *K.B. Vollesen MRC2714* (C, EA), Tanzania, Lindi, Selous game reserve, c. 18 km SW of Kingupira, 175 m, 10 Sep. 1975.

Subshrub, branching from the base, to 40 cm tall; young branches orange to reddish brown, glandular-punctate, densely covered with erect, yellowish hairs 0.4–0.8 mm long; old branches reddish brown, sparsely covered with hairs. *Leaves:* petiole 2–3.5 mm long, 0.6–1 mm diam, terete, indument as on branches; lamina oblong-elliptic to narrowly oblong-elliptic, 4–7.4 by 2.1–3.8 cm, 1.5–3 times longer than wide, subcoriaceous, punctate, discolorous, glossy dark green above, dull greenish white below, young leaves above sparsely covered with erect, white hairs to 1 mm long, becoming glabrous, primary vein more densely covered with

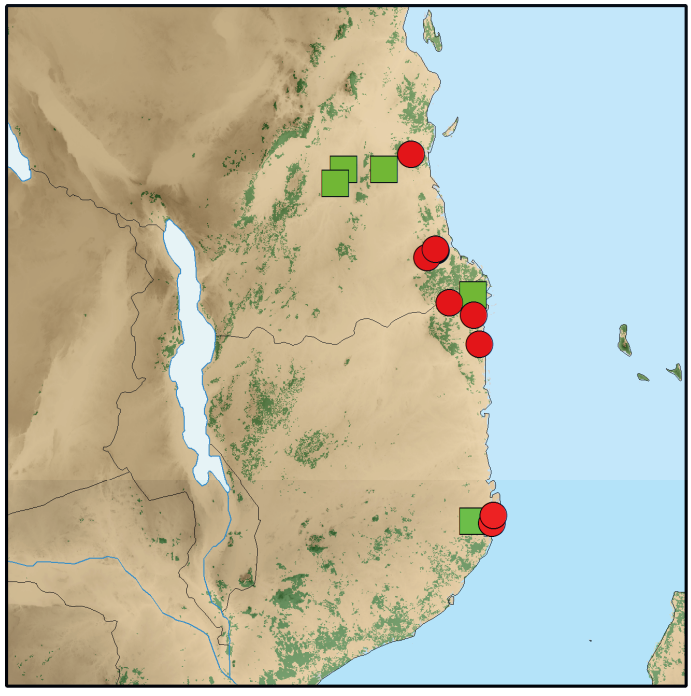
erect, white hairs, below sparsely covered with ascending to erect, white hairs 0.3–0.5 mm long, more densely so on primary vein, base rounded to slightly subcordate, glands hardly visible, apex rounded to obtuse, secondary veins 5–9 per side, from base curving upwards, tertiary venation percurrent, slightly reticulate above. *Inflorescences* extra-axillary, composed of solitary flowers; sympodial rachis absent; pedicels 11–16 mm long, 0.2–0.4 mm diam, fruiting pedicels 0.5–0.7 mm diam, sparsely covered with erect hairs 0.3–0.4 mm long; lower bract absent; upper bract in the upper half of the pedicel or sometimes absent, ovate, 1.3–1.8 by 0.7–1 mm, indument as on pedicel; flower buds globose. *Flowers* bisexual; sepals free, depressed ovate to orbicular, 2.5–3.5 by 3.2–3.4 mm, apex rounded, densely covered with erect, short hairs, persistent in fruit, slightly accrescent; receptacle c. 2.5 mm diam, slightly convex; petals colour in vivo unknown, 6, in two whorls, outer petals ovate to elliptic, 10.5–12.5 by 5.2–7.8 mm, outside sparsely covered with ascending, yellowish hairs 0.2–0.3 mm long, inside covered with very short hairs near the apex and margins, inner petals ovate, 8.2–9 by 4.1–4.6 mm, outside and apex and margins of the inside covered with yellowish, short hairs; stamens 23 or 24, in two whorls, free, linear-obovoid, 1.3–1.5 mm long, filaments 0.4–0.5 mm long, thecae latrorse to extrorse, connective truncate, prolonged outward, not hiding the thecae, glabrous, staminodes absent; carpels 14–16, subcylindric, c. 1.9 by 0.3 mm, densely hairy, ovules 3, lateral, stigma elongate, c. 0.9 mm long, glabrous. *Monocarps* up to 4, yellow, ellipsoid, 14–23 by 4.8–5.5 mm, constricted between the seeds, slightly verrucose, covered with erect, yellowish hairs, apex apiculate, stipes 2.5–4 mm long. *Seeds* 1–3, ellipsoid, c. 8.5 by 4.4 mm, ochre-brown, apex flattened, raphe slightly visible as a longitudinal furrow from base to apex.

Distribution — Tanzania (Lindi), Mozambique (Cabo Delgado, Nampula).

Habitat & Ecology — In woodland and dry coastal forest, on sandy soil. Altitude: 132–300 m. Flowering: February, March; fruiting: March, July, September.

Preliminary IUCN conservation status —Endangered (EN): B2ab(iii). EOO: 88,043 km^2, AOO: 20 km^2. This species is known from 5 collections in 4 locations of which 2 are nature reserves. However, the Selous Game Reserve was placed in 2014 on the UNESCO list of world heritage in danger and the other areas are under threat of habitat destruction and degradation.

Ethymology — This species is named *suffruticosa* as it is the only species of *Monanthotaxis* which grows as a subshrub (Latin: suffrutex).



Map 43 Distribution of *Monanthotaxis suffruticosa* (green squares) and *M. trichanta* (red circles).

70. *Monanthotaxis trichantha* (Diels) Verdc. — Plate 6a; Map 43

Monanthotaxis trichantha (Diels) Verdc. (1971b) 23. — *Popowia buchananii* (Engl.) Engl. & Diels var. *trichantha* Diels in Mildbr. (1936) 270. — *Popowia trichantha* (Diels) R.E.Fr. (1953) 39. — Lectotype (designated here): *H.-J.E. Schlieben 5890* (lectotype: B (B100471983); iso: B100471984, BM000553825, BR0000008824097, G00308304, HBG-502534, HBG-502535, MA384772, P01954700, S), Tanzania, Lindi, 40 km W of Lindi, near lake Lutamba, 240 m, 19 Jan. 1935.

Shrub or scandent shrub, 0.5–3 m tall; young branches yellow-brown, densely covered with ascending to erect, yellowish hairs 0.3–0.5 mm long, becoming glabrous; old branches brown-blackish. *Leaves:* petiole 3–6 mm long, 0.6–1.2 mm diam, terete, indument as on branches; lamina oblong-elliptic to obovate, 3.2–9 by 1.8–4.2 cm, 1.4–2.4 times longer than wide, subcoriaceous, not punctate, glaucous below, young leaves above sparsely covered with erect, white hairs, primary vein densely covered with yellowish, short hairs, becoming glabrous,

below sparsely covered with appressed to erect, yellowish hairs 0.2–0.5 mm long, primary vein sparsely to densely covered with appressed to erect hairs, base subcordate to truncate, with slightly thickened margin or not, apex obtuse to acute, secondary veins 6–10 per side, straight to slightly curving upwards, tertiary venation percurrent, slightly raised above. *Inflorescences* leaf-opposed or extra-axillary, composed of lax (1–)2(–4)-flowered fascicles; sympodial rachis 0–0.5 mm long; pedicels 2–8 mm long, 0.2–0.3 mm diam, fruiting pedicels 11–14 mm long, c. 0.5 mm diam, densely covered with erect, short, yellowish hairs; lower bract absent; upper bract halfway up the pedicel or absent, a tuft of hairs or lanceolate, to 0.3 by 0.1 mm, densely covered with yellow hairs; flower buds globose, all six petals visible at the base, at apex only 3. *Flowers* bisexual; sepals connate at the base, depressed ovate, 0.5–1 by 0.9–1.6 mm, apex obtuse, covered with appressed, yellow hairs, persistent in fruit or not; receptacle 1–1.3 mm diam, flat; petals yellow, 6, in two whorls, outer petals ovate to elliptic, 2.8–4.4 by 1.9–2.8 mm, outside covered with appressed, yellowish, short hairs, inside covered with glandular-like hairs at the apex, base glabrous, inner petals elliptic, 2.3–3.3 by 1.1–2.1 mm, indument as on outer petals; stamens 15, in one whorl, free, linear-obconical, c. 0.8 mm long, filaments c. 0.4 mm long, thecae extrorse, connective truncate, slightly prolonged outward, not hiding the thecae, glabrous, staminodes absent; carpels c. 10, subcylindric to ellipsoid, c. 1.3 by 0.4 mm, densely hairy, ovules 2, lateral, stigma elongate, c. 0.4 mm long, glabrous. *Monocarps* 2–4, bright red when ripe, ellipsoid, 10–14 by 5–6 mm, glabrous except for a few hairs at the base, apex apiculate, apiculum 0.5–1 mm long, stipes 2–4 mm long, terete. *Seed* 1, ellipsoid, c. 8 by 5 mm, tawny brown, ends rounded, raphe not visible or very slightly.



Plate 6 a. *Monanthotaxis trichantha* (Diels) Verdc.: a. Flowering branch. — b, c. *Monanthotaxis trichocarpa* (Engl. & Diels) Verdc.: b. Flowering branch; c. fruiting branch. — d–f. *Monanthotaxis whytei* (Stapf) Verdc.: d. Flower, e, f. inflorescences with flowers (a: *Lötter 1757*; b: *Lötter 1624*; c: *Lötter 1184*; d–f: photographed in Botanical gardens Utrecht, no specimen collected). Photos: a–c: M.C. Lötter; d–f: L.Y.T. Westra.

Distribution — Tanzania (Lindi, Pwana), Mozambique (Cabo Delgado, Nampula).

Habitat & Ecology — In coastal sand forest, coastal thickets and closed mixed woodland on sandy soils, stony ridges and on ferralitic soils. Altitude: 30–550 m. Flowering: January to March; fruiting: February, March.

Vernacular names — Mozambique: Sofu (Macua name) (*J. de Koning 9682*), Nankwankule (Macua name) (*E.M.C. Groenendijk 1235*).

Preliminary IUCN conservation status —Vulnerable (VU): B2ab(iii). EOO: 30,540 km^2, AOO: 40 km^2. This species is known from 10 collections from 6 locations of which the majority are under threat of habitat destruction.

Notes — *Monanthotaxis trichantha* can be recognised by the combination of a yellow-brown indument, extra-axillary flowers on a short pedicel, and the six petals in one whorl in bud, but overlapping at the top. Vegetatively it looks highly similar to the sympatric *M. filipes*, but the inflorescences are extra-axillary, the flower has a different aestivation and stamen shape and moreover, *M. filipes* has the flowers on long slender pedicels, instead of short ones.

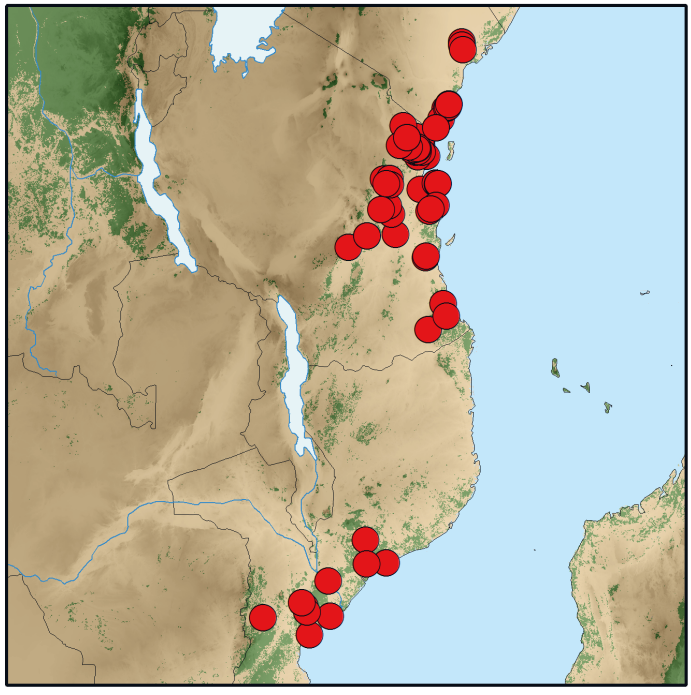
71. *Monanthotaxis trichocarpa* (Engl. & Diels) Verdc. — Fig. 5w; Plate 6b–c; Map 44

Monanthotaxis trichocarpa (Engl. & Diels) Verdc. (1971b) 29. — *Unona ferruginea* Oliv. forma *brevifolia* Engl. (1895) 179. — *Popowia trichocarpa* Engl. & Diels (1901) 47. —Type: *F.L. Stuhlmann 6972* (holo: B), Tanzania, Dar es Salaam, Uzaramo.

Shrub or liana, to 7 m long; young branches olive or reddish brown, densely covered with erect, yellow-brown to reddish brown hairs 0.3–0.6 mm long, becoming glabrous; old branches dark brown, grey-black to blackish. *Leaves:* petiole 2.7–4.7 mm long, 0.9–1.2 mm diam, slightly grooved, indument as on branches; lamina obovate to elliptic, 4.5–13(–18.2) by 2.6–5.9(–6.8) cm, 1.5–2.7(–3.2) times longer than wide, subcoriaceous, punctate, discolorous, dark green above, glaucous below, young leaves above covered with ascending, white hairs 0.3–0.5 mm long, becoming glabrous, below sparsely covered with ascending to erect, whitish yellow hairs 0.3–0.6 mm long, primary vein slightly more densely hairy, base subcordate or sometimes rounded, glands hardly visible, apex emarginate, rounded or acute, secondary veins 6–12(–17) per side, from base straight, halfway curving upwards, tertiary venation percurrent, slightly raised reticulate above. *Inflorescences* pendent, extra-axillary, composed of solitary flowers; sympodial rachis absent; pedicels 9–23 mm long, 0.4–0.5 mm diam, fruiting pedicels 0.4–0.9 mm diam, sparsely covered with erect, reddish brown hairs 0.4–0.5 mm long; lower bract absent; upper bract in the lower half of the pedicel or halfway or absent, lanceolate, 1–2 by 0.3–0.4 mm, indument as on pedicel; flower buds globose. *Flowers* bisexual; sepals free or slightly connate at the base, depressed ovate to orbicular, 1.2–2.8 by 2.6–2.8 mm, apex rounded to acute, densely covered with ascending, short hairs, persistent in fruit, slightly accrescent; receptacle 3.1–3.5 mm diam, flat; petals colour in vivo unknown, 6, in two whorls, outer petals broadly ovate, 4.5–8.8 by 4–7.6 mm, outside covered with ascending, short hairs, inside covered with very short hairs near the apex and margins, inner petals elliptic, 4.5–7.2 by 2.4–4.6 mm, outside and apex of inside covered with short hairs; stamens 24–27, in two whorls, free, linear-obovoid, 1.1–1.3 mm long, filaments c. 0.5 mm long, thecae latrorse to extrorse, connective truncate, prolonged inward, not hiding the thecae, glabrous, staminodes absent; carpels 9–14, subcylindric to ellipsoid, 1.7–2.2 by c. 0.6 mm, densely hairy, ovules 1–4(–5), lateral, stigma elongate, 0.7–0.9 mm long, glabrous.

Monocarps up to 10, orange to red, moniliform, each part ellipsoid, 13–39 by 5–7 mm, slightly verrucose, densely covered with erect, yellowish brown hairs, apiculate, apiculum 1–2 mm long, stipes 2–5 mm long. *Seeds* 1–5, subglobose to ellipsoid, 8–12 by 4.4–5.5 mm, ochre-brown, ends flattened or with an apiculate apex, raphe hardly visible as a longitudinal furrow from base to apex.

Distribution — Kenya, Tanzania, Mozambique.



Map 44 Distribution of *Monanthotaxis trichocarpa*.

Habitat & Ecology — In evergreen forest, forest edges, gallery forest, degraded vegetation, lowland moist forest, sub-montane forest and semi-deciduous forest, on limestone rocky outcrops, steep slopes, sandstone hills, along stream banks and on riverside rocks. Altitude: 20–1280 m. Flowering: November to July, September; fruiting: all year round.

Vernacular names — Kenya: Muganda wa simba (Ki-jibana name) (*L.J. Lap 256*), Usisi (Kisambaa name) (*C.J. Kayombo 1471*). Tanzania: Mpau (Kimatumbi name) (*O.A. Kibure 142*), Mkenene (Kisambaa name) (*M.A. Mwangoka 1302*), Mosfu simba (Kidoe name) (*Y.S. Abeid 1931*), Mvomero (Morogoro name) (*L.B. Mwasumbi 13893*), Mshofu (Kisambaa name) (*G.A. Peter 25761*).

Preliminary IUCN conservation status —Least concern (LC). EOO: 638,875 km^2, AOO: 284 km^2. This species is known from many locations and several nature reserves and is locally common. It is currently not in risk of extinction.

Notes — 1. *Monanthotaxis trichocarpa* closely resembles *M. faulknerae* and *M. suffruticosa*, but can generally be distinguished by the much larger and obovate leaves. For further differences see the notes under those species.

2. *Monanthotaxis. trichocarpa* is quite variable in vegetative characteristics, with especially specimens in the southern range of the distribution having more narrow obanceolate leaves with an acute apex. On the label of *W.D. Hawthorne 226* it is written that specimens on limestone have larger leaves. Especially some specimens from the Morogoro district have much larger leaves than typical specimens of *M. trichocarpa*, but no differences in flower characters could be found. More studies are needed to test whether this variable species is one entity.

3. *W.R.Q. Luke 11242*, collected at a height of 1520 m in montane forest in the Udzungwa Mountains, is probably a new species related to *M. trichocarpa*. The leaves dry grey, and have a clearly raised reticulation on the leaves, more flowering and fruiting material is needed of this highland form to assess its status.

4. Verdcourt (1971a) mentioned that this species has 18–36 stamens per flower. Most flowers however have 24 stamens and we have only seen a few flowers with up to 27 stamen.

72. *Monanthotaxis tripetala* P.H.Hoekstra — Fig. 31; Map 45

Monanthotaxis tripetala P.H.Hoekstra in P.H.Hoekstra et al. (2016) 96. — Type: *A.J.M. Leeuwenberg 5828* (holo consisting of 2 sheets: WAG0110801, WAG0110802; iso: B100190273, BR0000014126253, C not seen, EA, K, LISC not seen, MO not seen, P01967268, PRE not seen, YA not seen), Cameroon, East Province, 15 km E of Dimako, village halfway Bertoua-Doumé, 650 m, 11 June 1965.

Liana, at least 10 m long, c. 11 cm diam; young branches covered with appressed, reddish brown hairs c. 0.1 mm long, becoming glabrous; old branches dark brown, with few lenticels. *Leaves:* petiole 2–8 mm long, 0.6–1.5 mm diam, slightly grooved, indument as on branches; lamina oblong-elliptic to narrowly oblong-elliptic, 4.2–16.2 by 1.8–5.3 cm, 1.8–3 times longer than wide, subcoriaceous, not punctate, discolorous, glossy dark green above, dull greenish white below, young leaves above sparsely covered with appressed, white hairs, becoming glabrous, primary vein covered with appressed, yellowish hairs, becoming glabrous, below sparsely covered with appressed, white hairs 0.1–0.2 mm long, becoming glabrous, primary vein more densely covered with yellowish hairs, base rounded, with thick globose glands, apex acute to acuminate, acumen to 5 mm long, secondary veins 7–10 per side, from base curving upwards, tertiary venation percurrent, not visible above.

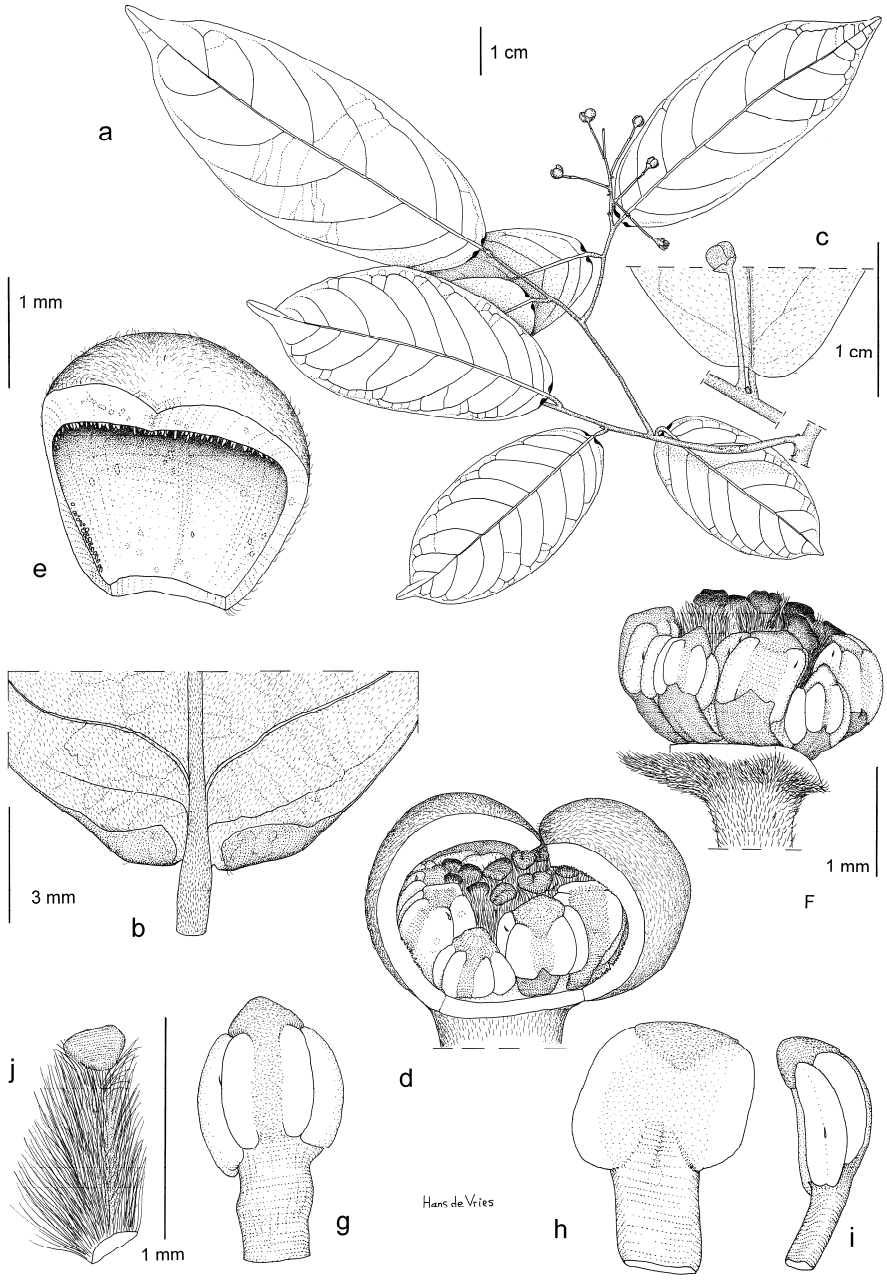


Fig. 31 *Monanthotaxis tripetala* P.H.Hoekstra: a. Flowering branch; b. leaf base abaxially; c. leaf base and inflorescence; d. flower with one petal removed; e. petal, inside view; f. flower with petals removed; g. stamen, outside view; h. stamen, inside view; i. stamen, side view; j. carpel (*Leeuwenberg 5828*). Drawing by H. de Vries.

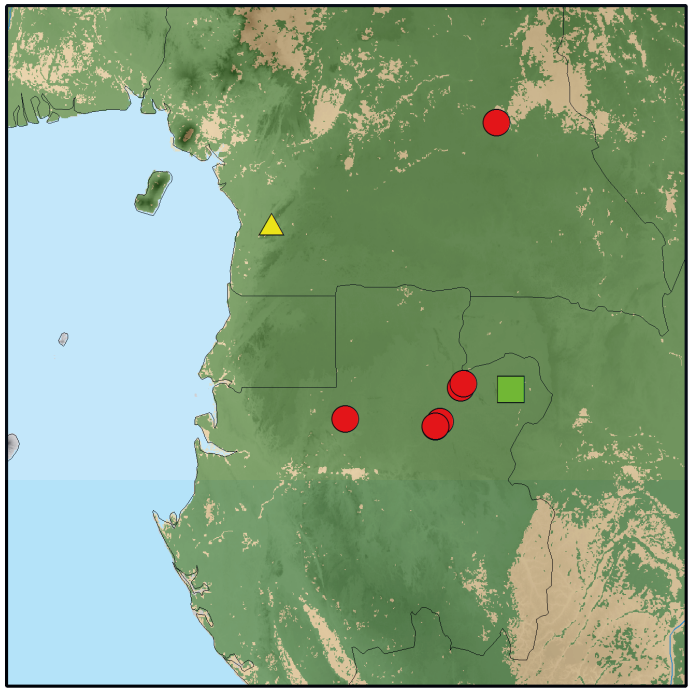
Inflorescences axillary, composed of solitary flowers or a 2-flowered rhipidia; sympodial rachis 0–6 mm long, covered with appressed, yellowish hairs; pedicels 12–20 mm long, 0.2–0.4 mm diam, fruiting pedicels 16–29 mm long, 1.5–2.2 mm diam, covered with appressed, yellowish hairs; lower bract absent; upper bract in the upper half of the pedicel or absent, ovate, c. 0.5 by 0.2 mm, densely covered with yellowish hairs; flower buds globose. *Flowers* bisexual; sepals free, depressed ovate, c. 0.5 by 0.8–1 mm, apex obtuse, densely covered with appressed, yellow hairs, not persistent in fruit; receptacle c. 1.5 mm diam, flat; petals colour in vivo unknown, 3 (or 4) in one (or two) whorls, outer petals broadly ovate, 2–2.2 by c. 2.2 mm, outside covered with appressed, yellowish hairs, apex of inside papillate, inner petals usually absent, rarely a single strongly reduced petal present, narrowly elliptic, c. 1.5 by 0.5–0.6 mm, outside and base of inside sparsely covered with yellowish papillae; stamens 9–12, in one whorl, free, linear-clavate, c. 1.2 mm long, filaments c. 0.6 mm long, thecae extrorse to latrorse, connective truncate, prolongation not hiding thecae, glabrous, staminodes absent; carpels c. 9, subcylindric to ellipsoid, 1.1–1.2 by 0.3–0.4 mm, densely hairy, ovules 3 or 4, lateral, stigma subsessile, subglobose, 0.1–0.2 mm long, glabrous. *Monocarps* 7, yellow, moniliform, each part narrowly ellipsoid, 110–130 by 7.5–8.5 mm, verrucose, sparsely covered with appressed, short hairs, apex apiculate, apiculum 5–8 mm long, stipes 7–22 mm long. *Seeds* 1–4, ellipsoid, c. 17 by 7 mm, reddish brown, apex apiculate, raphe visible.

Distribution — Cameroon (East province), Gabon (Ogooué-Ivindo).

Habitat & Ecology — In evergreen forest and old secondary forest on hill side. Altitude: 391–895 m. Flowering: June; fruiting: October.

Preliminary IUCN conservation status —Endangered (ED): B2ab(iii). EOO: 38,735 km^2, AOO: 24 km^2. This species is known from 6 collections from 4 locations of which one is a protected area. The other locations are under threat of mining companies or by an increasing human population growth.

Notes — *Monanthotaxis tripetala* can be recognized by the small axillary flowers of which the inner petals are highly reduced. This also occurs in some cauliflorous species, but those have unisexual flowers.



Map 45 Distribution of *Monanthotaxis tripetala* (red circles), *M. wieringae* (green square) and *M. zenkeri* (yellow triangle).

73. *Monanthotaxis ursus* P.H.Hoekstra, *sp. nov.* — Fig. 32; Map 41

Monanthotaxis ursus, together with *M. gracilis* and *M. quasilanceolata*, are the only species of *Monanthotaxis* with a hairy stigma. *Monanthotaxis ursus* differs from *M. quasilanceolata* in the much shorter pedicels, shorter hairs on the young branches and the truncate connective. From *M. gracilis* it differs in having a denser indument of erect, 0.3–0.4 mm long hairs on the lower side of the leaves, while *M. gracilis* has almost glabrous leaves except for a few scattered hairs on the primary vein. Furthermore, *M. ursus* has broader leaves, 5.3–9 cm wide, and short flowering pedicels, to 7 mm long, while *M. gracilis* has leaves 1.4–5.7 cm wide and the flowers pending on 15–45 mm long pedicels. — Type: *L. Aké Assi 17225* (holotype consising of 2 sheets: G), Ivory Coast, Guiglo, route de Tabou, forêt près Sièblohoula, 29 Dec. 1985.

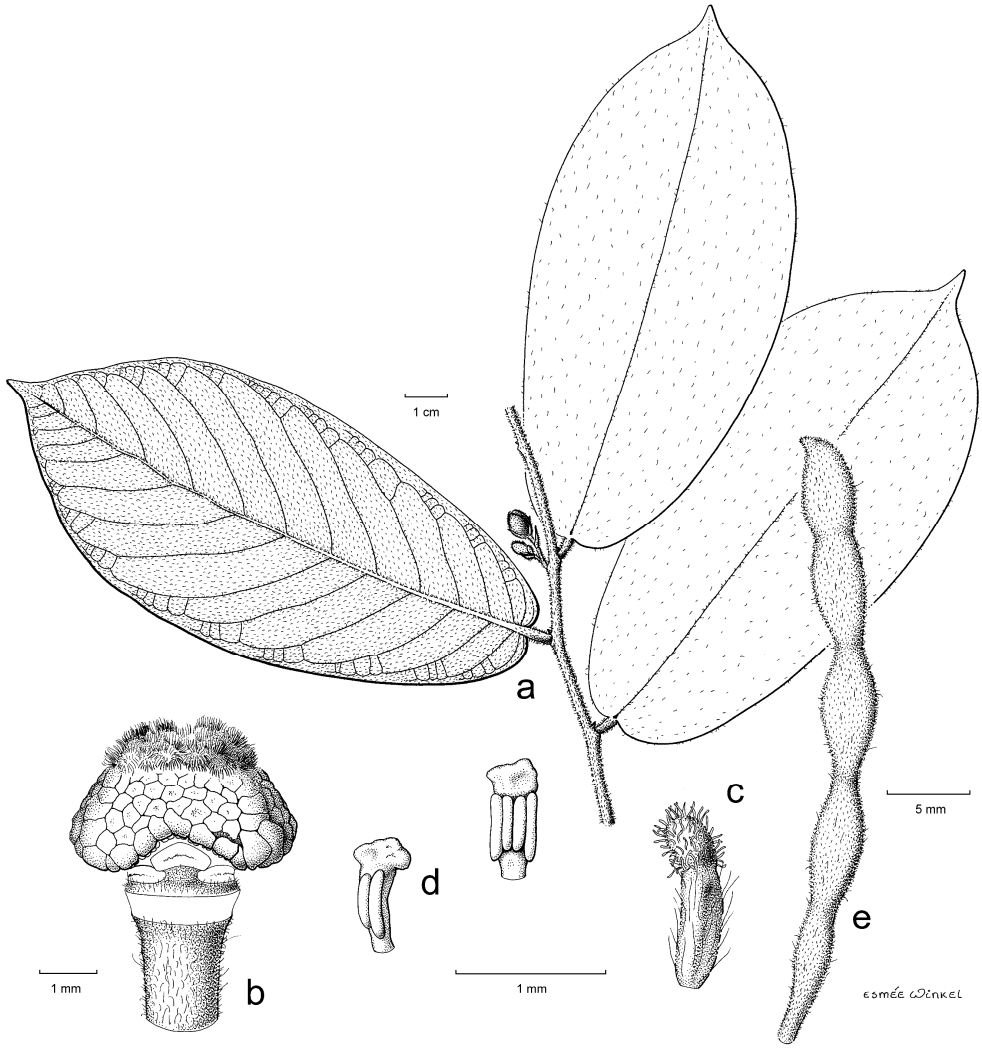


Fig. 32 *Monanthotaxis ursus* P.H.Hoekstra: a. Flowering branch; b. flower with petals and sepals removed; c. carpel; d. stamen, side and front view; e. monocarp (*Aké Assi 17225*). Drawing by E. Winkel.

Growth form unknown; young branches densely covered with erect to ascending, reddish brown hairs 0.1–0.2 mm long, becoming glabrous; old branches dark brown to reddish brown. *Leaves:* petiole 5–11 mm long, 1.7–2.2 mm diam, slightly grooved, indument as on branches; lamina obovate, 11.1–17 by 5.3–9 cm, 1.9–2.1 times longer than wide, chartaceous, not punctate, above sparsely covered with ascending to erect, white hairs 0.3–0.4 mm long, primary vein densely covered with erect, yellowish hairs, below densely covered with ascending, yellow hairs 0.3–0.4 mm long, base subcordate, with thickened black margin, apex acute to acuminate, acumen 5–10 mm long, secondary veins 12–14 per side, straight, halfway

slightly curving upwards, tertiary venation percurrent. *Inflorescences* leaf-opposed or terminal, composed of 2- or 3-flowered rhipidia; sympodial rachis 2–3 mm long, densely covered with ascending, reddish brown hairs; pedicels 5–7 mm long, 1–1.2 mm diam, fruiting pedicels c. 24 mm long, c. 1.3 mm diam, densely covered with ascending, reddish brown hairs; lower bract absent or broadly ovate, c. 0.5 by 0.5 mm, indument as on pedicel; upper bract halfway up the pedicel, ovate to lanceolate 3.5–4.5 by c. 0.8 mm, densely covered with ascending hairs; flower buds ovoid to deltoid. *Flowers* bisexual; sepals free, ovate, 3.5–4 by 1.6–2.1 mm, apex acute, densely covered with appressed, whitish hairs, persistent in fruit; receptacle c. 2 mm diam, convex; petals colour in vivo unknown, 6, in two whorls, outer petals ovate, 8.5–9 by 5–6 mm, outside and inside covered with yellowish brown hairs, inner petals elliptic, 4–4.5 by 2.4–2.7 mm, outside densely covered with yellow-brown hairs, inside glabrous; stamens c. 130, in four or five whorls, free, linear-oblong, 0.7–0.8 mm long, filaments c. 0.1 mm long, thecae extrorse to latrorse, connective truncate, globose, prolongation hiding the thecae, glabrous, staminodes absent; carpels c. 45, subcylindric, c. 1.7 by 0.2–0.3 mm, densely hairy, ovules c. 5, lateral, stigma globose to ellipsoid, c. 0.4 mm long, hairy. *Monocarps* up to 26, only young ones seen, colour in vivo unknown, 1–5-seeded, c. 40 by 4 mm, slightly constricted between the seeds, densely covered with ascending hairs, apex apiculate, stipes 2.5–4 mm long. *Seeds* 1–5, ripe seeds unknown.

Distribution — Ivory Coast (Guiglo).

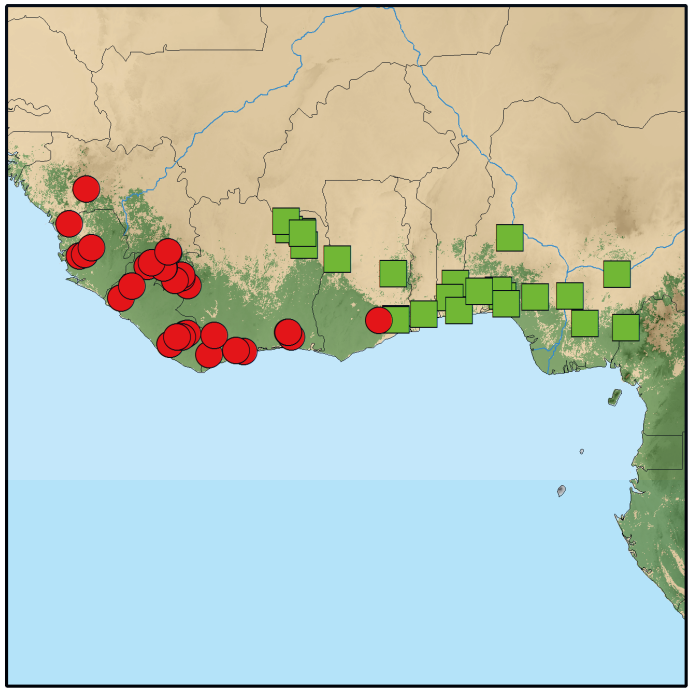
Habitat & Ecology — In forest. Flowering: December; young fruits: December.

Preliminary IUCN conservation status — Critically Endangered (CR): B2ab(iii). AOO: 4 km2. Only known from the type collection in an unprotected area. Near the type location in both Ivory Coast and Liberia are nature reserves. It should be searched for in those areas, but meanwhile as it has not been collected in more than 30 years the status of critically endangered is proposed.

Ethymology — This species is named ‘ursus’ after the genus name for bears, as this species is much more hairier than the related *M. gracilis*. Ursus is here used as a noun.

74. *Monanthotaxis velutina* (Sprague & Hutch.) P.H.Hoekstra — Map 46

Monanthotaxis velutina (Sprague & Hutch.) P.H.Hoekstra in Guo et al. (2017) 15. — *Oxymitra velutina* Sprague & Hutch. (1916) 156. — *Richella velutina* (Sprague & Hutch.) R.E.Fr. (1959) 139. — *Friesodielsia velutina* (Sprague & Hutch.) Steenis (1964) 361. — Lectotype (designated by Hoekstra in Guo et al. 2017): *N.W. Thomas 968* (lecto: K; isolecto: K), Sierra Leone, Northern Province, Tonkolili, Makump, 130 m, 18 July 1914.



Map 46 Distribution of *Monanthotaxis velutina* (red circles) and *M. vogelii* (green squares).

Shrub, scandent shrub or liana, 1–100 m long, to 6 cm diam; young branches very densely covered with appressed to erect, orange-brownish hairs 0.3–0.7 mm long, becoming glabrous; old branches medium-brown. *Leaves:* petiole 2.5–4.5 mm long, 1.5–1.9 mm diam, terete, indument as on branches; lamina obovate to oblanceolate, 8.4–25.1 by 4–9.6 cm, 2.3–3.8 times longer than wide, membranous to subcoriaceous, not punctate, discolorous, medium green above, glaucous below, above sparsely covered with appressed, whitish hairs 0.5(–1) mm long, becoming glabrous, primary vein densely covered with slightly erect, orange-brown hairs, below sparsely covered with erect, orange-brown hairs 0.5–0.8 mm long, more densely so on primary vein, base narrowly subcordate to cordate, glands hardly visible, apex acuminate, acumen 10–20 mm long, secondary veins (12–)16–22 per side, curving upwards, tertiary venation distinctly percurrent, flat above. *Inflorescences* extra-axillary or leaf-opposed, composed of solitary flowers; sympodial rachis 2–3.5 mm long, densely covered with erect, orange-brown hairs; flowering and fruiting pedicels 8–13 mm long, 1–1.6 mm diam, indument as on sympodial rachis; bracts ovate, to 1.5 mm long; flower buds unknown. *Flowers* bisexual; sepals free, reflexed, ovate, 4.5–6.5 by c. 3.5 mm, apex acute to acuminate, outside densely covered with yellow-orange hairs 0.1–0.2 mm long, inside becoming glabrous near the base, persistent in fruit; receptacle c. 5 mm diam, convex; petals colour in vivo unknown,

6, in two whorls, outer petals lanceolate, 14–16 by 5–6 mm, outside densely covered with yellow-brown hairs, inside becoming glabrous at the base, inner petals linear, 9.6–11 by c. 2 mm, outside and inside sparsely covered with yellowish, very short hairs; stamens number unknown, in at least two whorls, free, oblong, 0.7–0.9 mm long, filaments 0.2–0.3 mm long, thecae extrorse, connective truncate, prolongation hiding the thecae, glabrous, staminodes absent; carpels unknown. *Monocarps* 7–12, green-brown to dark brown, ellipsoid to cylindric, 20–24 by 9–12 mm, densely covered with hairs 0.2–0.3 mm long, apex rounded to acute, stipes 5–6 mm long. *Seeds* 1 or 2, cylindric-ellipsoid, 18–19 by 8–9 mm, tawny, ends apiculate, raphe clearly visible on both sides, very deep incising seed.

Distribution — Guinea, Sierra Leone, Liberia, Ivory Coast, Ghana.

Habitat & Ecology — In primary forest, secondary forest, gallery forest, semi-deciduous forest and open forest on shallow soil, sandy lateritic soil, sandy clay, on steep slopes, on hilltops and at river banks. Flowering: July, December; fruiting: March, May, July.

Preliminary IUCN conservation status —Least concern (LC). EOO: 387,407 km^2, AOO: 116 km^2. This species is known from many locations, including several reserves. Therefore, it is currenty not under threat of extinction.

Notes — *Monanthotaxis velutina* is easily distinguishable from the other species previously belonging to *Friesodielsia* subg. *Oxymitropsis* by the linear inner petals and reflexed sepals. Very few fertile specimens exist in the herbaria, and all 5 collections are in fruit and some with a few petals and stamens still attached. *C.C.H. Jongkind 6877* from Northwest Liberia and *Nimba Botanic Team PD283* and *C.C.H. Jongkind 11039* from South Guinea have smaller leaves with a cuneate leaf base. This could be a different (sub)species, but all 3 collections are sterile. *G.P. Cooper 199* from Liberia, which was cited in Keay (1954) as *M. diclina*, probably is related to *M. velutina* as it has extra-axillary inflorescences and large, ovate sepals, however the indument and fruits are different from *M. velutina*.

75. *Monanthotaxis vogelii* (Hook.f.) Verdc. — Fig. 5x; Map 46

Monanthotaxis vogelii (Hook.f.) Verdc. (1971b) 23. — *Uvaria vogelii* Hook.f. in Hook. (1848) 767. — *Clathrospermum vogelii* (Hook.f.) Benth. in Benth. & Hook.f. (1862) 29. — *Popowia vogelii* (Hook.f.) Baill. (1868) 324. — Type: *E. Vogel 203* (holo consisting of 2 sheets: K000198915, K000198916), Nigeria, Quorra, opposite Stirling, Sep. 1841.

Monanthotaxis angustifolia (Exell) Verdc. (1971b) 21, syn. nov. — *Enneastemon angustifolius* Exell (1937) 163. — Type: *P.W. Richards 3469* (holo consisting of 3 sheets: BM000547356, BM001125040, BM001125041; iso: MO-1889425), Nigeria, Ogun State, Ijebu, Shasha Forest reserve, 17 May 1935.

Popowia dalzielii Hutch. in Hutch. & Dalz.(1927a) 55. — Lectotype (designated here): *J.M. Dalziel 712* (lectotype: K, consisting of 2 sheets: K000198917, K000913659; isolecto:

BM001125037, MO 2 sheets, P00362644, P00362645), Nigeria, Benue State, north Nigeria, Abinsi, 13 Sep. 1972.

Shrub, scandent shrub or liana, to 3 m long; young branches sparsely covered with appressed, reddish brown hairs 0.1–0.2 mm long, becoming glabrous; old branches blackish brown to dark brown. *Leaves:* petiole 2–5 mm long, 1.1–1.5 mm diam, slightly grooved to terete, indument as on branches; lamina narrowly obovate, 9.7–17.5 by 2.5–5.6 cm, 2.4–4.1 times longer than wide, chartaceous, not punctate, dark green above, greyish green below, above glabrous, but primary vein sparsely covered with appressed, whitish hairs 0.1–0.2 mm long, below sparsely covered with appressed, yellowish hairs 0.1–0.2 mm long, base cuneate to rounded, with slightly thickened black margin, apex acute to acuminate, acumen to 15 mm long, secondary veins 7–12 per side, forming an acute angle with primary vein, straight, but curving halfway, tertiary venation percurrent, not visible above and slightly visible below. *Inflorescences* axillary, composed of solitary flowers or 2–3(–4) flowered fascicle-like rhipidia; sympodial rachis 0.5–1.5 mm long, densely covered with appressed, yellow-brown hairs 0.1–0.2 mm long; pedicels 6–14 mm long, 0.4–0.5 mm diam, fruiting pedicels 0.7–1 mm diam, sparsely covered with appressed, yellowish hairs 0.1–0.2 mm long; lower bract ovate, 1–1.5 by c. 1 mm, indument as on rachis; upper bract absent or sometimes present near the base of the pedicel, lanceolate, c. 2 by 0.7 mm, densely covered with appressed, yellowish hairs; flower buds ovoid. *Flowers* bisexual; sepals connate at the base, depressed ovate to shallowly triangular, 0.5–0.7 by 1.3–1.5 mm, apex acute to rounded, sparsely covered with appressed hairs, persistent in fruit; receptacle c. 2 mm diam, flat; petals colour in vivo unknown, 6, in two whorls, base of inner petals visible in bud, pinkish yellow, outer petals broadly ovate to ovate-elliptic, 2.4–3.3 by 2–2.1 mm, outside sparsely covered with yellow hairs, inside glabrous except for some very short hairs near the apex, inner petals elliptic, 2–2.7 by c. 1.3 mm, base and centre outside sparsely covered with yellow hairs, inside glabrous except for a few hairs at the apex; stamens 8 or 9, in one whorl, free, linear-oblong, 0.7–0.8 mm long, filaments c. 0.3 mm long, thecae extrorse to latrorse, connective truncate, slightly prolonged inward and outward, not hiding the thecae, glabrous, staminodes 6, alternating with the stamens, but not in front of the inner petals, c. 0.3 mm long, glabrous; carpels 8–12, narrowly ellipsoid, 0.9–1.3 by 0.2–0.3 mm, densely hairy, ovule 1, basal, stigma elongate, c. 0.4 mm long, glabrous or covered with few papillae. *Monocarps* 2–9, red, narrowly ellipsoid, 11–15 by 4.5–5.5 mm, slightly verrucose, densely covered with appressed, yellow-brown, very short hairs, apex apiculate, apiculum to 0.3 mm long, stipes 2–4 mm long. *Seed* 1, ellipsoid, c. 10.3 by 4–4.7 mm, ochre-brown, apex rounded, raphe visible.

Distribution — Ivory Coast, Ghana, Benin, Nigeria, Cameroon.

Habitat & Ecology — In gallery forest, swamp forest, savannah open woodland and open high forest; growing in cracks of schist rocks, on rocky islands, on loamy soil and on black clay.

Flowering: March, April, June, July, September; fruiting: April, June, September, November, December.

Vernacular names — Ghana: Jmada Adanine (*F.R. Irvine 2887*).

Preliminary IUCN conservation status —Least concern (LC). EOO: 386,040 km^2, AOO: 84 km^2. This species has a wide distribution and occurs in several reserves.

Notes — 1. *Monanthotaxis vogelii* can be recognised by the combination of narrowly obovate leaves, ovoid flower buds and flowers with 9 stamens and 6 staminodes. Furthermore, the inflorescences are often ramiflorous and each monocarp has 1 ellipsoid seed.

2. *Monanthotaxis angustifolia* is synonymised as it was only distinguished from *M. vogelii* by leaf shape, but the leaf shape is quite variable with intermediate forms present, although the narrowest obovate leaves occur in Cameroon and East Nigeria. However, no other distinguishing characters could be found and the DNA sequences are highly similar (Fig. 1, clade C).

76. *Monanthotaxis vulcanica* P.H.Hoekstra, *sp. nov.* — Fig. 33; Map 42

Monanthotaxis vulcanica belongs to a group of species with a large leafy upper bract on the pedicel. It can be distinguished from the other species of this group by the combination of 15 stamens, c. 14 hairy carpels per flower and monocarps with large stipes of 6–10 mm long. — Type: *R.G. Letouzey 15050* (holotype: P (P01982551); iso: WAG.1576469, YA0003005), Cameroon, South-West region, pentes NW du Mt. Cameroun, vers Efolofo, 30 km W. S/Préfecture Muyuka (feuille IGN 1/200.000 Buea – Douala), 750 m, 1 June 1976. Paratypes: *J.D. Chapman 3675* (FHO, K), Nigeria, Taraba state, Sardauna prov. Kurmin Dodo, Chappal Waddi escarpment, 1800 m, 8 Feb. 1975; *M. Etuge 4810* (K, YA), Cameroon, North-west region, Bali Ngemba F.R. Mantum, 1600 m, 17 Nov. 2000; *H. Jacques-Félix 3078* (P), Cameroon, West region, Mt Nkogam, Feb. 1939; *R.G. Letouzey 13046* (P, YA), Cameroon, West region, Massif du Nkogam, 25 km W of Foumban, en lisière latérale, vallon au SW du sommet principal, 1600 m, 28 Oct. 1974; *T.D. Maitland 1618* (K), Cameroon, North-west region, Bamenda, af. Bambui, 1370 m, June 1931. Liana, to 20 m long; young branches reddish brown, sparsely covered with appressed, yellowish hairs c. 0.2 mm long to almost glabrous; old branches reddish brown to blackish. *Leaves*: petiole 3–6 mm long, 0.6–1 mm diam, slightly grooved, indument as on branches; lamina oblong-elliptic to slightly oblanceolate, 5.6–11.8 by 2.3–3.9 cm, 2.3–3.6 times longer than wide, chartaceous, not punctate, glaucous below, above glabrous, primary vein covered with ascending, yellowish hairs 0.3–0.5 mm long, becoming glabrous, below sparsely covered with appressed to ascending, yellowish hairs 0.1–0.3 mm long, base rounded to slightly cuneate, with thickened black margin, apex acute to slightly acuminate, acumen to 20 mm long, secondary veins 8–12 per side, straight, halfway curving upwards, tertiary venation percurrent, slightly raised above, hardly visible below.

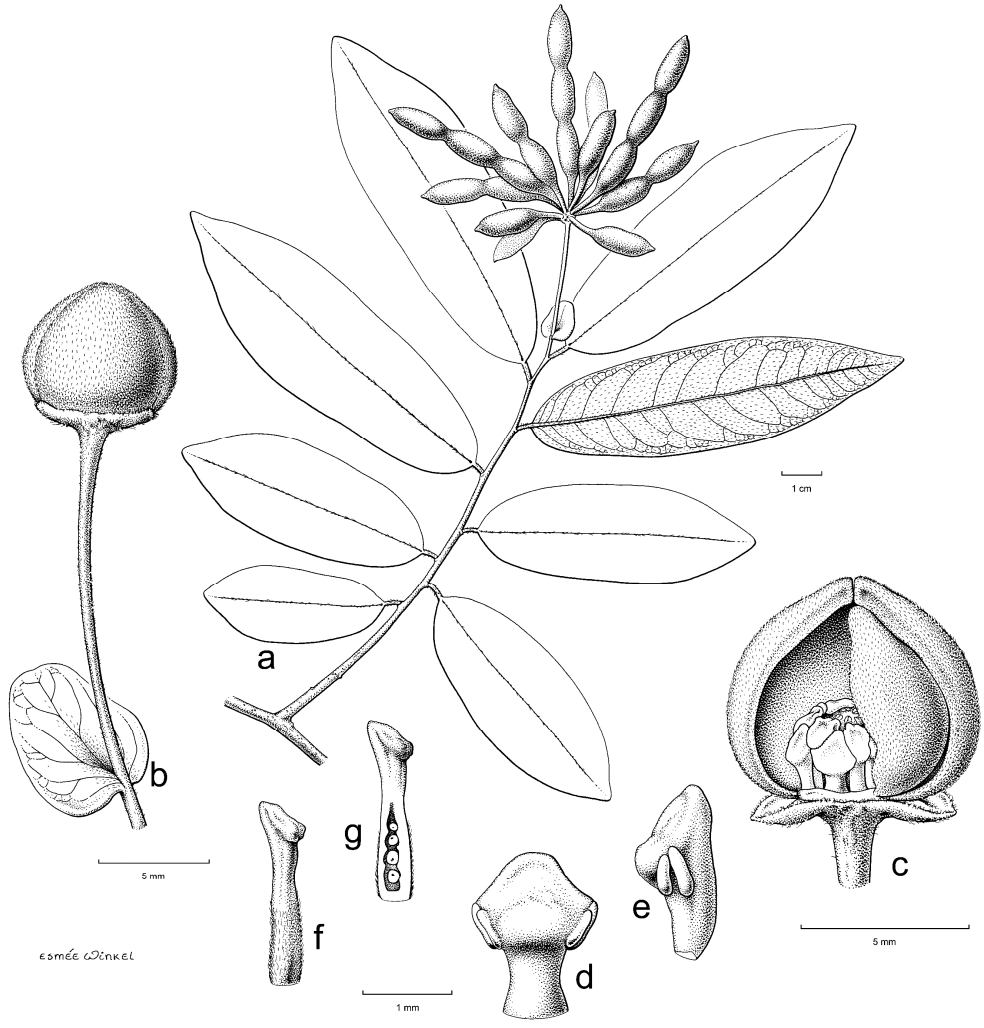


Fig. 33 *Monanthotaxis vulcanica* P.H.Hoekstra: a. Fruiting branch; b. inflorescence with flower bud; c. flower bud with one outer and one inner petal removed; d. stamen, outside view; e. stamen, side view; f. carpel; g. longitudinal section of carpel (a: *Chapman 3675*; b–g: *Letouzey 15050*). Drawing by E. Winkel.

Inflorescences extra-axillary or terminal, composed of solitary flowers; sympodial rachis absent; pedicels 19–25 mm long, 0.4–0.5 mm diam, fruiting pedicels 20–37 mm long, 0.5–1.1 mm diam, sparsely covered with appressed to ascending, yellowish hairs; lower bract absent; upper bract leaf-like, in the lower half of the pedicel, ovate, 7–15 by 5–10 mm, sparsely covered with appressed-ascending, yellowish hairs; flower buds globose to slightly ovoid. *Flowers* bisexual; sepals connate at the base, depressed ovate to shallowly triangular, 1.5–2.3 by 3–3.4 mm, apex acute, densely covered with hairs, persistent in fruit; receptacle 3.2–3.5

mm diam, flat; petals colour in vivo unknown, 6, in two whorls, outer petals ovate to broadly ovate, 6.4–8 by 6–6.3 mm, outside and inside sparsely covered with yellowish hairs, base of inside glabrous, inner petals elliptic, 5.3–5.7 by 3.9–4.1 mm, indument as on outer petals; stamens 15, in two whorls, free, linear-obovoid, c. 2 mm long, filaments 0.8–0.9 mm long, thecae introrse in inner whorl, extrorse in outer whorl, connective truncate, prolonged outward in the inner whorl, and inward in the outer whorl, not hiding the thecae, glabrous, staminodes absent; carpels c. 14, subcylindric, c. 2.1 by 0.3–0.4 mm, densely hairy, ovules 5, lateral, stigma elongate, c. 0.8 mm long, glabrous. *Monocarps* 2–13, orange, moniliform, each part ellipsoid to subcylindric, 12–50 by 4.5–6.5 mm, verrucose, covered with few hairs on the stipe, apex apiculate, apiculum to 2 mm long, stipes 6–10 mm long. *Seeds* 1–4, ellipsoid to subcylindric, 8–15 by 5–6 mm, apex rounded to apiculate, ochre-brown, raphe not visible.

Distribution — Nigeria (Taraba State), Cameroon (North-West Region, South-West Region, West Province).

Habitat & Ecology — In submontane forest and on forest edges. Altitude: 750–1800 m. Flowering: June; fruiting: February, June, October, November.

Preliminary IUCN conservation status —Endangered (EN): B2ab(iii). EOO: 18,794 km^2, AOO: 24 km^2. This species is known from 6 collections from 4 locations, of which only one in a nature reserve. The other 3 locations are under threat of habitat destruction.

Ethymology — This species is named *Monanthotaxis vulcanica* as it is confined to the volcanic belt of Cameroon and Nigeria.

77. *Monanthotaxis whytei* (Stapf) Verdc. — Plate 6d–f; Map 47

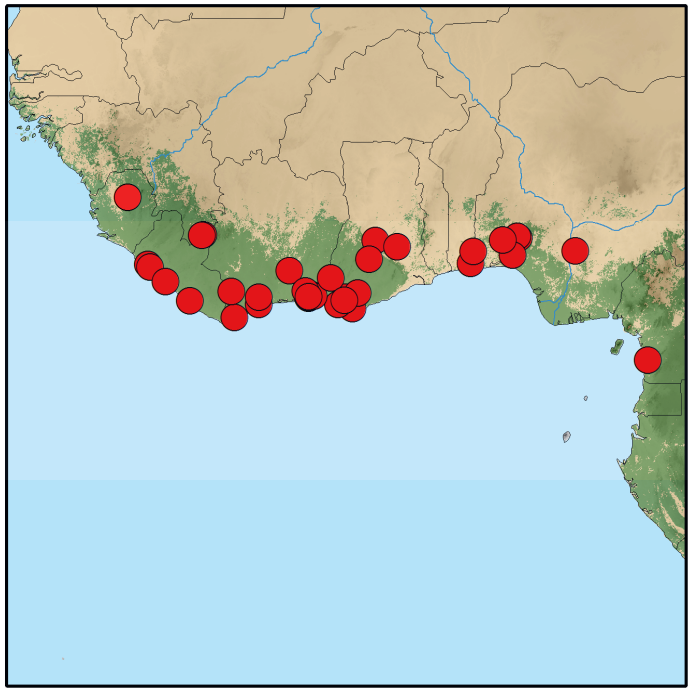
Monanthotaxis whytei (Stapf) Verdc. (1971b) 29. — *Popowia whytei* Stapf (1905) 81. — Type: *A. Whyte s.n.* (holo: K000198908), Liberia, Sino, Sinoe Basin, 1904.

[*Popowia prehensilis* A.Chev. (1920) 11, *nomen nudum*. — Based on: *A.J.B. Chevalier 16048* (P00362640), Ivory Coast, Abidjan, Bingerville, 13 Dec. 1906; *A.J.B. Chevalier 17077* (P00362642, P01982378, P01982379, P01982380), Ivory Coast, Abidjan, vallée de l'Agnieby, entre Guébo et Mbago, 2 Feb. 1907; *A.J.B. Chevalier 17701* (P01982383), Ivory Coast, Aboisso, entre Bianouan et Soubié, 27 Mar. 1907].

Shrub or liana, to 20 (–50) m long; young branches dark brown, covered with appressed to ascending, reddish brown hairs c. 0.2 mm long, becoming glabrous; old branches dark brown to blackish. *Leaves:* petiole 1–4(–7) mm long, 1.1–2.1 mm diam, grooved, indument slightly denser than that on young branches; lamina obovate to narrowly so, 8.8–19.4 by 3.5–8.5 cm, 1.7–2.8 times longer than wide, chartaceous to subcoriaceous, not punctate, discolorous, green above, glaucous below, above covered with erect, yellowish hairs, becoming glabrous, below sparsely covered with appressed, yellowish hairs c. 0.1 mm long, primary vein covered with few, yellowish hairs to 0.3 mm long, base narrowly subcordate, glands hardly visible, apex

acute to slightly acuminate, acumen to 3 mm long, secondary veins 8–14 per side, curving upwards, tertiary venation percurrent, sometimes hardly visible. *Inflorescences* cauliflorous, ramiflorous or axillary, composed of solitary flowers or few-flowered fascicles to short glomerule-like rhipidia; sympodial rachis 2–8 mm long, densely covered with slightly erect, yellowish hairs 0.1–0.2 mm long; pedicels 7–11 mm long, 0.6–0.7 mm diam, fruiting pedicels 13–20 mm long, c. 1.6 mm diam, indument as on sympodial rachis; lower bracts triangular to ovate, 0.5–1.6 by 0.5–0.7 mm, indument as on sympodial rachis; upper bract in lower half or halfway the pedicel, triangular to lanceolate, 0.7–1.5 by 0.4–0.6 mm, indument as on sympodial rachis; flower buds globose. *Flowers* bisexual; sepals free, broadly ovate, 1–1.8 by 1.1–1.8 mm, densely covered with appressed, yellowish hairs, persistent in fruit; receptacle c. 2.3 mm diam, flat; petals dirty greenish yellow to yellow, 6, in two whorls, outer petals broadly ovate, 3.4–5 by 3.4–4.5 mm, outside covered with appressed, yellowish hairs, inside glabrous except for the margins, inner petals elliptic to ovate, 3–4 by 1.5–2.2 mm, outside with yellowish, short hairs on the primary vein, inside glabrous except for a few small hairs at the apex; stamens 9, in one whorl, free, obconical, 0.9–1.1 mm long, filaments c. 0.2 mm long, thecae latrorse, connective truncate, prolonged inward and outward, square seen from above, glabrous, staminodes 9, alternating with the stamens, 0.3–0.6 mm long, ovoid-triangular, glabrous; carpels 26–34, subcylindric, 1.1–1.3 by c. 0.2 mm, densely hairy, ovules 3, lateral, stigma elongate, 0.4–0.6 mm long, grooved, glabrous. *Monocarps* up to 10, yellow to orange when ripe, often with a white exudate, ellipsoid to subglobose, 15–38 by c. 8 mm, constricted between the seeds, verrucose, densely covered with appressed/ascending yellow hairs, becoming glabrous, but longer persistent at stipe and top, apex rounded to shortly apiculate, apiculum to 1 mm long, stipes 4.5–12 mm long, grooved. *Seeds* 1–3, globose to ellipsoid, 9–10 by 6–7 mm, ochre-brown to reddish brown, both ends rounded, raphe slightly visible as a longitudinal furrow from base to apex.

Distribution — Sierra Leone, Liberia, Ivory Coast, Ghana, Benin, Nigeria, Cameroon.



Map 47 Distribution of *Monanthotaxis whytei*.

Habitat & Ecology — In primary forest, swampy forest, secondary forest, gallery forest and in savanna areas, on gravel, sandy soil, wet cliffs and on river banks. Altitude: 50–600 m. Flowering: November to February, April to July; fruiting: all year round.

Preliminary IUCN conservation status —Least concern (LC). EOO: 934,306 km^2, AOO: 160 km^2. This species has a wide distribution and occurs in several nature reserves and has been collected several times quite recently. Therefore, this species is currently not under threat of extinction.

Notes — 1. *Monanthotaxis whytei* can be recognised by the cauliflorous or ramiflorous inflorescences, globose floral buds, and flowers each with 9 stamens and 9 small staminodes. The majority of specimens have angular stems and they can easily be recognised by this character in West Africa.

2. In an ontogenetic study, Ronse Decraene& Smets (1990) found that this species actually forms two whorls of staminodes, but the outer whorl already stops very early during the development and is not visible in mature flowers.

3. There are some differences among different collections in seed shape (subglobose to ellipsoid) and in stipe length, but no consistent correlating patterns were found.

78. *Monanthotaxis wieringae* P.H.Hoekstra, *sp. nov.* — Fig. 34; Map 45

Monanthotaxis wieringae belongs to the group of species with unisexual flowers (Fig. 1, clade I). It can be distinguished from most species in having 36 stamens in three or four whorls. It differs from *M. letouzeyi* in the appressed, yellowish, short hairs on the young branches, which are erect, reddish brown, and longer in *M. letouzeyi.* It differs from *M. mortehanii* and *M. glomerulata,* of which no staminate flowers are known, in having a cuneate leaf base and long and slender petioles. — Type: *J.J. Wieringa 3833* (holotype: WAG, consisting of 3 sheets: WAG0151260, WAG0151261, WAG0151262; iso: LBV0000658, MO), Gabon, Ogooué-Ivindo, road Mékambo to Makokou, 480 m, 2 Jan. 2001.

Liana, to 30 m long; young branches dark brown, covered with appressed, yellowish hairs c. 0.1 mm long, becoming glabrous; old branches dark brown. *Leaves:* petiole 6–9 mm long, 0.9–1.3 mm diam, grooved, indument as on branches; lamina elliptic to obovate or narrowly so, 8–13.5 by 3.4–6 cm, 2–3 times longer than wide, chartaceous, not punctate, discolorous, medium-green above, grey-green below, above sparsely covered with appressed, yellowish, short hairs, becoming glabrous, primary vein with a more dense and persistent indument, below sparsely covered with appressed, yellow hairs 0.1–0.3 mm long, base cuneate, with thickened black margin, apex acute, secondary veins 10 or 11 per side, straight to curving upwards, tertiary venation percurrent. *Flowers* unisexual. ♂ *Inflorescences* leaf-opposed or ramiflorous, composed of solitary flowers to 4-flowered fascicles; sympodial rachis 6–8 mm long, covered with appressed, short hairs; flowering pedicels 6–8 mm long, c. 0.8 mm diam,

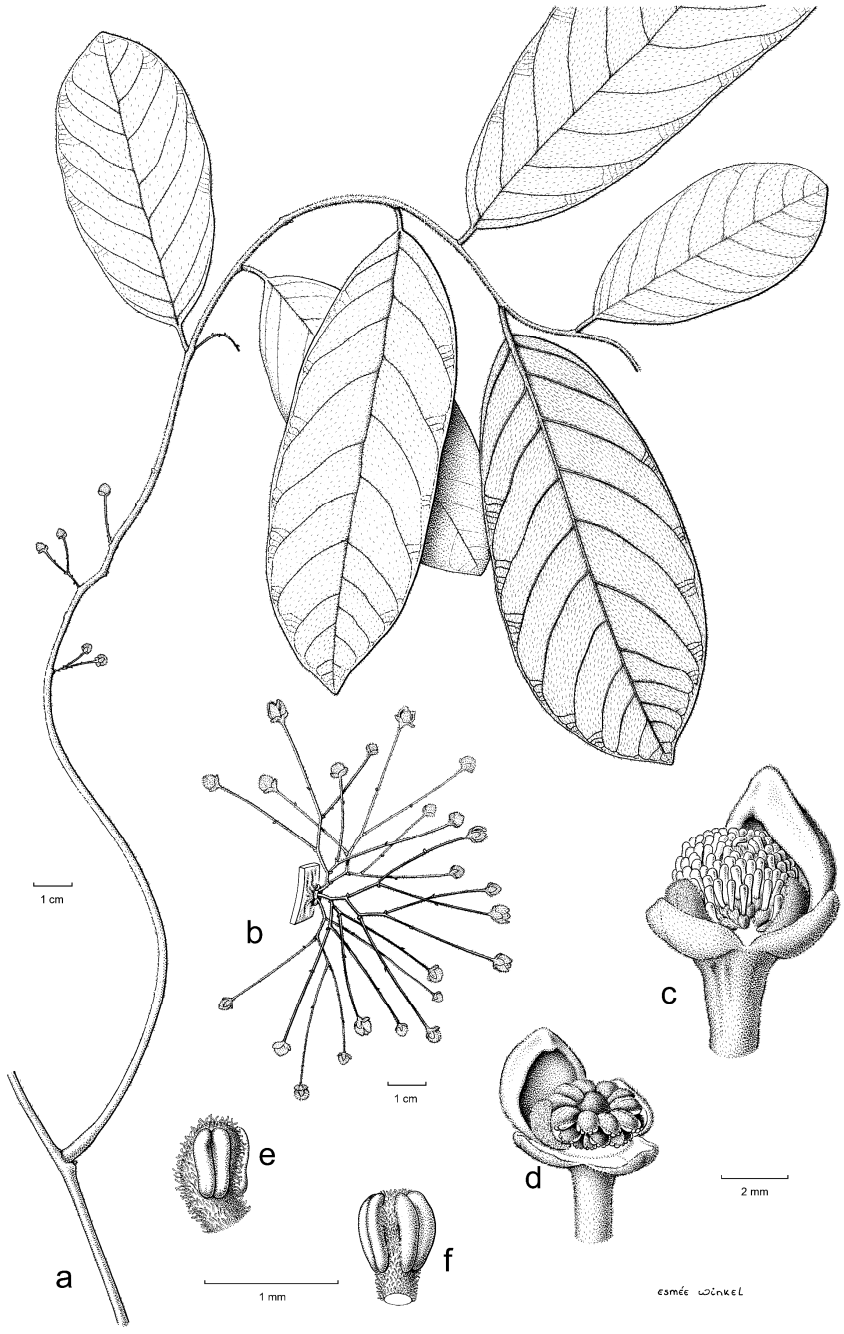


Fig. 34 *Monanthotaxis wieringae* P.H.Hoekstra: a. Branch with staminate inflorescences; b. inflorescence with pistillate flowers; c. pistillate flower with two outer petals removed; d. staminate flower with two outer petals and one inner petal removed; e. stamen, side view; f. stamen, outside view (*Wieringa 3833*). Drawing by E. Winkel.

indument as on rachis; lower bracts ovate, 0.6–0.8 by c. 0.5 mm, indument as on rachis; upper bracts halfway or in lower half of the pedicel, shape, size and indument as lower bracts; flower buds globose; sepals free to slightly connate, depressed ovate, 1.4–1.5 by 1.8–1.9 mm, densely covered with appressed hairs; receptacle c. 2.3 mm diam, convex; petals colour in vivo unknown, 6, in two whorls, outer petals depressed ovate, c. 2.5 by 3.5–3.8 mm, outside densely covered with appressed, brownish, short hairs, inside covered with yellowish, very short hairs; inner petals broadly ovate, c. 1.2 by 1.4 mm, outside and inside covered with yellowish, very short hairs; stamens 36, in three or four whorls, free, oblong to obconical, 0.7–0.9 mm long, filaments c. 0.1 mm long, thecae extrorse, connective truncate, prolongation hiding thecae, densely covered with yellowish hairs, staminodes absent. ♀ *Inflorescences* cauliflorous, a glomerule or condensed many-flowered panicle; sympodial rachis 1–3.5 cm long, densely covered with appressed hairs; flowering pedicels 10–30 mm long, 0.7–1.1 mm diam, indument as on rachis; lower bracts ovate, 1.3–1.4 by c. 1 mm, indument as on rachis; upper bracts halfway or in upper half of pedicel, shape, size and indument as lower bracts, flower buds ovoid; sepals free to slightly connate at base, broadly ovate, 2–2.4 by 2–2.3 mm, outside densely covered with appressed, brown hairs, inside only hairy at the apex; receptacle c. 2 mm diam, convex; petals green with pale brownish silvery hairs, 6, in two whorls, outer petals, broadly ovate, c. 5 by 4.5 mm, outside densely covered with appressed, pale brownish hairs, inside covered with yellowish hairs c. 0.05 mm long, inner petals elliptic, 2.2–2.4 by 1.4–1.5, outside and inside densely covered with yellowish hairs c. 0.05 mm long; carpels c. 129, narrowly ellipsoid to subcylindric, 1.4–1.5 by 0.3–0.4 mm, densely hairy, ovules 3 or 4, lateral, stigma elongate, 0.6–0.7 mm long, grooved, glabrous. *Monocarps* and *seeds* not seen.

Distribution — Gabon (Ogooué-Ivindo).

Habitat & Ecology — In secondary forest. Altitude: c. 480 m. Flowering: January.

Preliminary IUCN conservation status — Critically Endangered (CR): B2ab(iii). AOO: 4 km2. Only known from one, relatively recent collection from an unprotected area.

Ethymology — *Monanthotaxis wieringae* is named after Jan J. Wieringa, collector of the sole collection of this species. Furthermore, he has collected many species of *Monanthotaxis* with leaf material on silica gel, which greatly facilitated and improved the molecular analyses of the genus.

79. *Monanthotaxis zenkeri* P.H.Hoekstra — Fig. 35; Map 45

Monanthotaxis zenkeri P.H.Hoekstra in PH.Hoekstra et al. (2016) 98. — Type: *G.A. Zenker 3495a* (holo: G00308331; iso: BR0000013211349, E00624356, HBG, K, L.1759466, MO3726267), Cameroon, South Province, Bipinde, probably Oct. 1907.

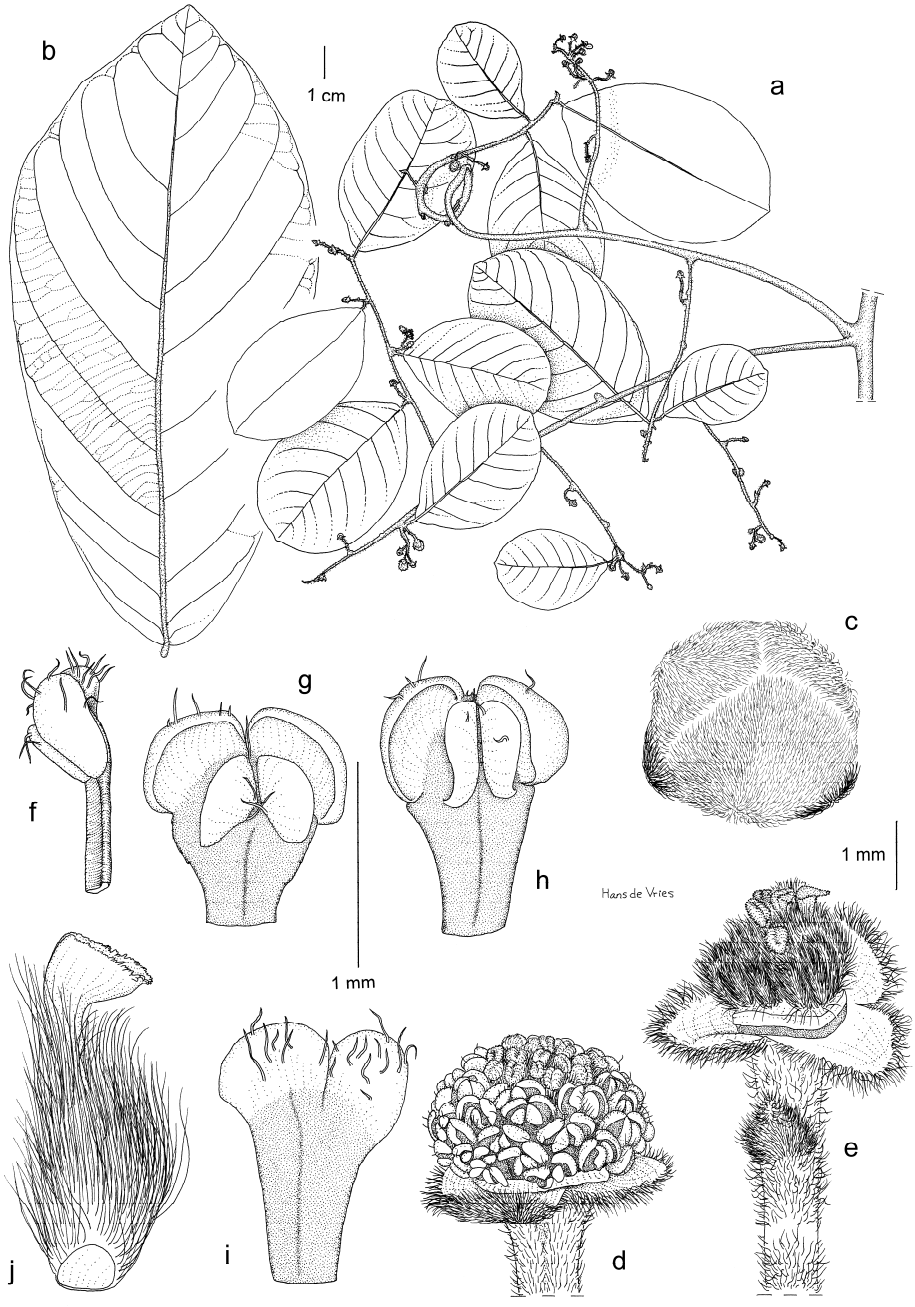


Fig. 35 *Monanthotaxis zenkeri* P.H.Hoekstra: a. Habit; b. leaf abaxially; c. flower bud; d. flower with petals removed; e. old flower; f. stamen, side view; g, h. stamen, outside view; i. stamen, inside view; j. carpel (*Zenker 3495a*). Drawing by H. de Vries.

Probably a liana; young branches brown, densely covered with erect, reddish brown hairs 0.3–0.4 mm long, becoming glabrous; old branches dark brown. *Leaves:* petiole 3–6 mm long, 0.7–2.3 mm diam, terete, indument as on branches; lamina obovate to elliptic-obovate 4.7–20.1 by 2.3–9.5 cm, 2–2.3 times longer than wide, subcoriaceous to chartaceous, not punctate, young leaves above sparsely covered with erect, yellow-brown, short hairs, becoming glabrous, below densely covered with erect, yellow-brown hairs 0.4–0.5 mm long, base rounded, with thickened margin, apex obtuse to acute, secondary veins (8–)10–12 per side, first straight, halfway curving upwards, tertiary venation percurrent. *Inflorescences* axillary, 1–3-flowered rhipidia; sympodial rachis 0–2 mm long, densely covered with ascending to erect, reddish brown, short hairs; flowering pedicels 4–6 mm long, 0.4–0.5 mm diam, densely covered with ascending to erect, short hairs; lower bract strongly reduced or absent; upper bract in the lower half of the pedicel, ovate, 0.6–0.8 by 0.5–0.8 mm, densely covered with hairs; flower buds globose. *Flowers* bisexual; sepals slightly connate at the base, depressed ovate to shallowly triangular, c. 1 by 1.5 mm, apex obtuse, densely covered with appressed, yellow hairs; receptacle c. 1.5 mm diam, flat; petals colour in vivo unknown, 6, in two whorls, outer petals broadly ovate, 2–3.1 by 2.1–2.5 mm, outside and margins of inside covered with appressed, yellowish, short hairs, base and centre of inside glabrous, inner petals rhombic, 1.8–2.4 by 1.3–1.6 mm, outside and apex of inside densely covered with yellow hairs; stamens 35, in three or four whorls, free, linear-obconical, 0.7–0.8 mm long, filaments c. 0.4 mm long, thecae extrorse, convergent apically, hiding the connective, sparsely hairy, staminodes absent; carpels c. 16, subcylindric to narrowly ellipsoid, 1.1–1.4 by c. 0.3 mm, densely hairy, ovules 4 or 5, lateral, stigma curved, elongate to subglobose, c. 0.2 mm long, glabrous, except for some hairs at the base. *Monocarps* and *seeds* not seen.

Distribution — Cameroon (South Province).

Habitat & Ecology — In forest. Flowering: October.

Preliminary IUCN conservation status — Critically Endangered (CR): B2ab(iii). AOO: 4 km^2. Only known from the type collection, more than 100 years old, from an unprotected area. It can be extinct.

Notes — *Monanthotaxis zenkeri* has unique stamens within the genus. It is the only species with the combination of hairy thecae on top and a relative short filament. Besides this, it can be distinguished from the other species of *Monanthotaxis* with thecae on top by the dense indument of erect, reddish brown, short hairs.

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Identification list

The abbreviations of species names refer to the taxa as listed for the synoptic key, i.e., they consist of the first four letters of the epithet, with the exception of the following eight names: cone = *M. congoensis*; conl = *M. congolana*; diso = *M. discolor*; disr = *M. discrepantinervia*; klkl = *M. klainei* var. *klainei*; klla = *M. klainei* var. *lastoursvillensis*; tria = *M. trichantha*; trio = *M. trichocarpa*. Unidentified *Monanthotaxis* specimens are cited as *spec*. Doubtfull identifications are indicated with a question mark.

Abbiw 271: bart? – Abeid 225: forn; 445: buch; 981: pogg; 1050: schw; 1526: spec; 1931: trio – Acocks 10960: caff – Acutt 13: caff – Adam 4343: nimb; 4579: hirs; 5265: engh; 5425: nimb; 11868: bart; 14608: hirs; 14614: bart; 16252: nimb; 20167: nimb; 20577: nimb; 20618: nimb; 21019: engh; 21170: bart; 21413: bart; 22044: hirs; 22133: hirs; 22382: nimb; 22511: hirs; 22530: nimb?; 22746: engh; 22895: nimb; 22941: hirs; 23121: grac; 23182: grac; 23274: grac; 23370: bart; 23563: bart; 23567: bart; 23621: engh; 24348: nimb; 24587: whyt; 25560: nimb; 26189: spec; 26336: hirs; 26599: engh; 26902: bart; 26903: bart; 27511: nimb; 27651: bart?; 28770: nimb; 30134: bart – Adames 674: engh – Adebusuyi 67019: voge – Adjakidjè 3341: whyt –Adlard 226: obov; 336: buch – Adomou 11: voge; 49: hirs? – Afzelius 8: bart; 27: bart – Agnew 8090: buch – Ahimbisibwe 140: buch; 396: buch – Aké Assi 4049: glab; 4933: glab; 5521: mann; 8169: cape; 8889: hirs; 12031: laur; 12154: cape; 12237: mann; 12289: mann; 12693: foli; 14775: hirs; 15155: laur?; 16533: cape; 16773: cape; 17118: pogg; 17225: ursu; 17722: cape; 19009: voge – Akoègninou 2667: spec; 3296: laur?; 5437: voge – Akpabla 906: foli; 1106: grac; 1107: grac; 1112: foli – Amsini 113: engh; 283: fila – Andoh FH5493: laur – Andrada 1002: obov; 1026: chas – Andrews 628: buch; 867: buch; 1387: luci; 1544: luci; 1756: ferr – Angus 714: obov?; 945: obov; 1342: obov; 2023: obov; 2854: obov – Annet 348: eleg – Archbold 2138: trio – Arends 479: foli – Armitage 55/103: obov; 59/278: obov; 59/306: obov; 60/10: obov; 60/87: obov – Aubréville SF 1496: cape – Austaller 10: obov – Azizet Issembé 278: dicl.

Baagøe 137: trio – Bagshawe 629: litt – Bainbridge 56/226: obov – Balaka 71: buch; 1233: obov; 2086: buch – Baldwin jr 6383: bart; 6624: bart; 10192: grac – Balkwill 1396: caff;

2999: caff; 7634: caff – Bally 11453: keny; 12105: forn; 13708: buch?; 13751: forn – Balsinhas 3187: caff – Bamps 434: mont; 600: bigl; 601: leto; 1381: hirs; 2838: orop; 4216: parv; 4221: luci; 4222: parv; 6350: forn; 8196: pogg; 8275: obov – Banda 2559: buch – Barbosa 1253: chas – Barter 1221: voge; 1335: laur – Barthelat 269: komo; 590: komo; 671: komo; 1045: komo – Bartsch 1729: obov – Bashonga ATBP 790: litt – Battiscombe 241: keny; 852: ochr – Baum 548: obov – Becquet 440: ferr – Beentje 99: velu; 1044: mann; 2310: forn; 2323: forn – Bequaert (Liberia series) 140: laur – Bequaert 6959: mont; 7691: parv – Berhaut 6047: bart; 6137: bart; 6319: bart; 6395: bart; 6471: bart; 6808: bart; 6853: bart – Betti 532: hirs?; 562: caul?; 1100: spec – Bews 1014: caff – Bezuidenhout 253: obov – Bidault 468: dicl; 551: bida; 590: klla; 789: dicl; 817: dicl; 1528: bida; 1632: bida; 1641: bida; 1647: bida; 1667: dicl; 1668: dicl; 1876: bida – Bidgood 542: diso; 1050: obov; 1402: fili; 1454: buch; 1629: tria; 1731: tria; 1736: tria; 1858: buch; 1860: obov; 2035: trio; 2279: obov; 2706: buch; 2781: ferr; 2870: ferr; 4088: ferr; 4148: ferr; 4175: pogg; 4540: ferr; 4635: ferr; 5571: ferr; 5597: obov; 5803: ochr – Biegel 1749: obov; 3699: obov – Bilivogui 11: mann; 154: mann – Bingham 8600: buch – Birch 60/474: buch – Bissiengou 435: diel? – Bjørnstad 2149: obov – Blackmore 1474: buch – Boaler 439: obov; 982: obov – Bogdan 828: keny – Bokdam 2865: glab; 3193: pogg; 3574: engh?; 3630: mont; 4368: litt? – Bolema 93: pogg; 525: boko; 637: laur; 684: pogg; 840: mont?; 854: pogg; 1161: laur; 1167: boko – Bond 10B 46: buch – Borhidi 86/315: trio; 86/573: trio; 86/713: trio? – Borle 364: obov – Bos 3854: whyt; 4069: caul; 5818: engh; 6037: caul; 6293: caul; 6653: engh; 6735: bico; 6867: caul – Bosch 308: nimb – Boudet 2632: mann – Bouquet 639: spec; 792: luci; 1041: ster; 1245: engh; 1782: ster; 1786: engh; 2388: dicl – Bourquin 9: caff – Boutique 261: mont – Bouxin 665: orop; 1319: orop – Boyekoli Ebale Congo 2010 Expedition: 255: pogg – Brand 325: caff – Braun 1679: trio – Brenan 7771: obov; 8115: ochr; 8826: foli; 8917: foli; 9125: foli; 14621: trio; 14665: trio – Breteler 1374: fila; 1874: leto; 2137: engh; 2692: bico; 5302: hirs; 5466: bart; 6697: cone; 7553: trio; 8990: cape; 9756: bida; 9865: klla; 11843: parv; 12477: boko; 14014: pell; 14616: boko?; 14995: engh – Breteler & de Wilde 549: lete – Breyne 560: fila?; 564: pogg; 809: klkl; 1417: boko; 3329: klkl; 3350: scam; 3620: pogg – Brunt 1494: keny – Buchanan 1152: buch – Buckner 120: schw – Bujo Dhego 3031: laur – Bullock 2305: obov; 3047: obov? – Burrows 4866: caff; 9828: buch; 10246: schw; 10813: tria; 11011: buch; 12794: trio; 12900: spec – Burtt Davy 20669: obov; 21059: obov – Burtt 738: obov; 1377: obov; 3453: obov; 5089: obov – Busse 1070: obov; 2263: trio – Bytebier 2788: bigl; 2957: ferr?; 3287: gill.

Cable 3526: spec – Callens 2166: mont?; 2392: laur?; 2409 B: scam; 2565: conl; 3092: ferr; 3888: luci – Campbell 239: caff; 266: caff – Carnochan 1928/76: obov; 1928/198: obov – Carvalho 4025: laur; 4108: grac; 5371: quas; 6208: caul – Catarino 252: bart – Chandler 1556: ferr; 2023: litt – Chapman 1787: obov; 1960: ochr; 2103: chas; 3675: vulc; 5092: laur; 5797: buch; 6191: buch; 6202: buch; 6611: chas; 7137: buch; 7439: buch; 7631: chas; 7649: buch; 8383: buch; 8401: chas; 8925: buch – Chase 3540: obov; 4488: chas; 5048: obov;

5375: chas; 6537: obov; 7410: chas; 7724: obov; 46032: obov – Chatelain 65: engh; 469: voge; 643: engh; 716: engh; 1003: bart; 1288: whyt – Chatrou 681: spec – Cheek 7711: caul?; 9067: subm; 9202: subm; 10154: glau?; 15447: engh – Chevalier 6021: parv; 6542: boko; 6779: buch; 7069: schw; 7344: schw; 8118: buch; 8260: buch; 10527: buch; 10631: parv; 11428: hirs; 11432: grac; 11433: grac; 14817: hirs; 15428: hirs; 15432: grac; 16048: whyt; 16408 Bis: hirs; 16490: laur; 17077: whyt; 17701: whyt; 19040: bart; 20341: hirs; 21292: mann; 21505: mann; 25826: mann; 25834: mann; 27036: dicl; 28419: olig – Chillou 352: bart; 362: mann; 507: bart; 1301: bart – Chiparawasha 385: obov – Chipunga 61: obov – Chizea FHI19780: grac – Choo 760: leto – Christiaensen 1802: engh – Claessens 495: fila; 629: engh – Clarke 3448: trio; 3541: buch – Clarkson 342: caff – Clements 579: buch; 787: buch – Clutton–Brock 18: pogg – Coates Palgrave 560: trio – Comins 480: caff – Compère 831: foli; 1028: litt; 1066: ferr; 1766: mont; 1827: parv – Conrads 5116: ferr; 5151: ferr; 13251: ferr – Conservator of Forests 237: buch – Cooper GP 199: spec – Cooper T 1226: caff – Cordonnier 77: bart; 101: bart – Cornet d'Elzius 450: parv – Correia 116: buch; 578: mapu; 1690: mapu; 2892: mapu – Couch 478: bart – Couvreur 14: trio; 49: spec; 76: trio; 89: forn; 94: disr; 406: spec; 416: spec; 417: fila; 421: spec; 439: spec; 440: spec; 443: spec; 444: spec; 458: leto; 466: engh; 509: spec; 513: spec; 524: spec; 528: mcph; 537: dicl; 565: lati; 574: lete; 579: trip; 599: klla; 601: foli; 618: engh; 626: cone; 628: ster; 629: dicl; 635: engh; 651: pani?; 653: engh; 668: spec; 669: engh; 676: caul?; 690: fila; 691: engh; 695: fila; 704: eleg?; 705: caul; 708: pani?; 713: ster; 730: leto; 731: ster; 752: leto; 754: engh; 762: couv; 772: sere?; 778: spec; 786: spec; 787: mont?; 792: ster; 852: engh; 858: dicl; 861: fila; 862: mcph; 865: leto; 869: ster; 870: trip; 871: spec; 881: mcph; 889: klai?; 890: leto; 891: mont; 901: cone?; 902: klla; 914: bida; 916: dicl; 918: bida; 929: bida?; 981: laur; 986: engh; 989: fila; 1003: engh; 1018: cone; 1024: engh; 1025: cone; 1028: engh; 1037: engh; 1049: vulc?; 1056: laur; 1060: spec; 1065: engh; 1081: spec; 1083: spec; 1101: spec; 1107: spec; 1108: pani; 1116: spec; 1117: spec; 1121: engh; 1124: engh; 1138: engh – Cribb 11089: dict; 11092: disr; 11217: buch – Croegaert 48: fila – Cunningham 877: caff; 3156: ferr? – Cusset 713: mont; 892: ster; 1311: lete?.

da Silva 782: luci; 2356: luci – da Torre 1119: obov; 2635: mapu; 3053: buch; 5201 A: buch; 9732: obov; 10641: buch; 11200: buch; 14359: trio; 14363: buch; 14422: buch; 15318: obov; 16278: buch; 16390: obov; 16481: buch; 16519: chas; 17080: trio; 17199: buch; 18269: obov – Dacremont 207: parv – Dale K 3171: ochr – Dalziel 712: voge; 761: grac; 1096: grac – Daramola 403: laur; 484: grac – Darbyshire 596: grac; 597: mann – Dauby 1064b: lete; 3063: dicl – Davies 711: obov; 1688: obov; 1743: obov – Dawe 187: ferr; 191: litt – Dawkins 409: litt; 510: ferr – De Aguiar Macêdo 4728: obov – de Koning 94: whyt; 1068: whyt; 1175: whyt; 1250: whyt; 1652: laur; 1821: whyt; 1914: laur; 2369: whyt; 2826: whyt; 2991: grac; 3403: laur; 3569: whyt; 3656: grac; 3687: laur; 3700: whyt; 4563: whyt; 4748: whyt; 4827: whyt; 5331: whyt; 5406: laur; 5760: laur; 5876: whyt; 6283: laur; 6356: whyt; 6866: bart; 6867 A: laur; 7316: mapu; 7379: mapu; 7766: mapu; 7768: mapu?; 8680:

mapu; 9063: mapu?; 9682: tria – de Kruif E23: hirs – de Rouw 286: whyt – de Saeger 120: pogg; 1198: parv; 2607: luci – de Vogel 203: voge – de Wilde JJFE 562: velu; 3436: laur; 3716: hirs; 8330: dicl; 8371 A: ferr; 8955: laur; 10896: dicl; 10959: mont; 10971: quas; 11213: lete?; 11391: lete?; 11418: cone; 11482: cone; 11773: cone; 11981: klla; 11982: cone – de Wilde WJJO 506: whyt; 1987: caul; 2709: eleg; 2787: eleg – de Winter 4251: obov; 8608: caff; 8857: caff – de Wit 7126: hirs; 7488: grac; 12996: whyt – de Witte 5404: bigl – Deighton 2498: velu; 3263: sten – Delvaux 439: scam – Demange 2830: glab – Descoings 10035: pyna; 11555: mont; 12225: schw – Desenfans 2126: pogg; 4422: pogg; 4801: obov; 5176: bigl – Desmet 14: fila – Devillé 231: ochr – Devred 1108: laur; 1163: gill; 1166: gill; 1576: luci; 2166: klkl; 2893: klkl? – Dewèvre 785: boko – Dewulf 303: mont; 987: mont – Dhetchuvi Matchu–Mandje 1526: leto; 1635: dicl – Diabate 1366: laur – Dibata 40: klai; 332: dicl – Diniz 102: mapu; 1301: bart; 2138: bart – Dinklage 2092: whyt – do Espirito Santo 592: bart; 1518: bart; 1799: bart; 1953: bart; 2037: bart; 2220: bart; 2476: mann; 3407: bart – Donis 1841: scam; 1859: olig; 2334: laur; 2340: parv; 2386: scam; 2410: laur – Doumbouya 61: mann – Doumenge 554: subm – Dowsett–Lemaire 872: chas; 907: chas; 1040: chas – Drège 4082: caff – Drummond 1955: trio; 3106: trio; 3236: forn; 3873: forn; 3882: buch; 3906: forn; 4485: buch; 7111: ochr – Dubois 224: engh – Dümmer 718: litt; 724: ferr; 724A: ferr; 724B: ferr; 4389: buch – Dumont 241: ferr? – Duvigneaud 412P: parv; 1412Au: parv.

Edwards 1577: caff – Eggeling 799: litt; 1627: buch; 2003: litt; 3296: orop – Eilu 038: engh; 168: litt; 230: orop; 282: engh – Emwiogbon FHI60005: laur – Enti GC35529: whyt; GC36381: foli; GC37439: velu – Essou 1174: laur?; 1516: glab – Etuge 1729: fila; 2377: fila; 4122: subm; 4442: subm; 4676: laur; 4810: vulc – Evrard 330: mont; 1351: cape; 1576: pogg; 2004: scam; 2014: klai; 2016: pyna; 2790: luci; 3377: pogg; 3415: mont; 4696: klkl; 4723: atop; 5111: scam; 5198: pyna; 5525: mont; 5685: conl; 5781: luci – Ewango 258: engh? – Exell 565: mapu; 1056: buch.

Faden 865: keny; 67/21: keny; 67/356: keny; 68/715: keny; 70/234: trio; 74/1236: faul; 77/449: forn; 85/35: trio – Fakih 197: trio – Fanshawe 815: obov; 1288: obov; 1474: ochr; 2818: ochr; 3304: ochr; 8842: ochr – Farmar 192: bart – Farrell 138: obov; 189: chas – Farrington MSB336: obov – Farron 4015: litt; 4023: pogg; 4470: ster; 7266: couv; 7359: couv – Faulkner 80: trio; 532: forn; 774: trio; 1040: trio; 1070: trio; 1624: faul; 1632: forn; 1652: forn; 2559: forn; 3860: buch; 4175: forn; 4891: forn – Fay 2180: mont; 4043: schw; 6330: schw; 6431: schw; 6534: schw; 6623: buch; 6697: schw; 6915: buch; 7045: schw; 7071: buch; 7156: laur; 8346: buch; 8466: engh – Festo 1303: ferr; 2635: faul – Fewdays 3: obov – Flamigni 486: ferr; 6371: scam; 10692: parv? – Florence 230: engh; 353: spec; 463: engh; 465: mont; 809: leto; 868: dicl; 875: mont; 1006: klai; 1017: mont; 1080: leto?; 1083: scam; 1165: leto?; 1241: scam; 1266: dicl; 1409: trip?; 1417: scam; 1444: scam; 1475: dicl; 1756: spec?; 1915: engh; 1965: cone; 1985: spec; 1994: leto; 2015: cone – Floret 1456: aest – Foggie 4437: foli – Fries 110: obov; 1998: ochr; 3160: caff; 3161: caff; CentrAfr 558: parv

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Raimundo ARF 719: bart – Raimundo F 294: ferr – Ralimanana 277: komo – Rammell 1086: ochr – Randrianasolo 825: cone – Raymond 314: obov – Raynal 20851: ferr – Reekmans 1332: orop; 5037: orop; 6817: ferr; 7970: orop; 8025: ferr; 8908: orop – Rees AF T 77: buch – Rees T 155: suff – Reitsma 1057: dicl; 2283: cone; 2305: dicl?; 2870: pani; 2977: mcph; 3749: dicl; 3815: dicl – Renier 232: orop – Renvoize 1831: buch – Richards MAE 18328: obov – Richards PW 3469: voge – Risopoulos 684: sere; 692: pogg – Robertson 3697: trio; 4092: forn; 4252: forn; 4704: forn; 4763: forn; 4779: buch; 4812: trio; 4840: trio; 6466: buch; 7544: buch; MDE19: buch; MDE146: buch – Roberty 10773: bart; 10776: bart; 16466: bart; 17247: mann – Robinson 255: obov – Robson 1046: buch – Robyns 403: schw; 3103: schw; 3265: parv – Rodrigues Pedro 2179: trio – Rodrigues 329: mapu – Rogers 404: keny – Ross JH 2314: caff – Ross R 232: voge – Rossignol 9: parv – Rudatis 54: voge; 807: caff; 1423: caff – Ruffo 950: obov – Runyinya 435: orop; 811: orop; 964: orop – Russell 2718: obov – Rutherford–Smith 662: obov – Rwaburindore 3072: ferr.

Sacleux 630: forn; 2038: trio – Saint Clair Thompson FH 3677: whyt – Salubeni 2706: obov; 3560: obov; 4026: obov; 4959: obov; 5132: buch; 6226: chas – Sangai EA 15691: forn – Saufferer 796: forn; 1587: forn – Scheffler 229 a: disr – Schlechter 12006: caff; 12801: pogg – Schlieben 36: diso; 1686: dict; 2239: dict; 5890: tria – Schmidt 1284: obov – Schmitt 66: spec – Schmitz 2855: ochr; 5914: boko; 6211: pogg – Schnell 1114: nimb; 2636: nimb; 3516: nimb; 3850: engh; 4399: nimb; 4414: hirs?; 4419: laur?; 4511: nimb; 4541: nimb; 4642: velu; 4651: bart; 4657: bart; 4725: hirs; 4737: bart; 4952: mann; 5115: velu; 5202: nimb; 5399: engh; 5613: bart?; 5618: engh; 6061: engh; 6631: nimb; 6833: hirs; 6846: hirs; 6869: bart; 6924: bart; 7358: hirs; 7465: bart; 7658: velu – Schoenmaker 49: klkl – Schweinfurth

1931: buch; 2046: buch; 3157: schw – Scott Elliot 4020: mann; 4382: sten; 4671: bart; 4854: hirs; 5415: mann; 5564: sten; 5656: bart; 5882: sten – Scouppe 179: velu – Semsei 2246: forn; 2404: trio; 2410: buch; 3726: buch – Senterre 764: diel?; 1328: spec; 1534: fila?; 2016: mont?; 3407: mont?; 3408: fila; 3409: ster – Seret 870: sere – Sesay 29: whyt – Seyani 1791: buch – Shantz 558: obov – Sheil 1255: litt; 1383: ferr – Sillitoe 357bis: schw; 357ter: schw; 477: buch – Sim 1016: caff; 2610: caff – Simons 1471: spec; 1476: spec; 1637: spec – Simpson 39: forn – Sinsin 3380: voge – Sita 150: pogg; 1287: dicl; 1589: atop; 1725: litt; 2074: atop; 2713: bico?; 3044: luci; 3529: parv; 3789: engh; 3966: lati; 3971: parv; 4046: dicl; 5009: cone – Smeyers 4: ochr; 63: ochr – Smith 1355: obov; 2319: obov – Sokpon B113: whyt – Sosef 2013: mont; 2056: engh; 2060: leto; 2090: engh; 2220: scam; 2238: cape; 2242: leto; 2281: engh – Southern Highlands Conservation Program 927: ferr? – Soyaux 203: mont – Spitaels 375: orop – Stolz 170: ochr; 1396: ochr – Stone 3151: cone – Stoop – vd Kasteele 331: spec – Straub 271: velu – Strey 3901: caff; 7118: caff – Strid 2690: obov; 2789: ochr – Stuhlmann 1470: buch; 6238: buch; 6703: buch; 6972: trio – Suzuki F 6: pogg – Symoens 14141: obov – Synnott 656: litt.

Talbot 41: grac; 199: grac; 323: engh; 403: glau; 1246: engh; 1255: glau; 1550: bart; 1612: caul; 3726: laur – Tanner 514: obov; 1547: obov; 3542: forn; 3683: forn; 3708: trio; 4350: buch; 4380: buch – Taton 156: ochr; 1346: ochr – Taylor 3332: gill; 3387: buch – Tchiengué 2673: nimb; 2816: fila; 3131: nimb; T 25: velu – Téré 1942: velu; 2400: laur? – Tessmann 2512: pell – Thiébaud 748: pogg – Thollon 498: laur; 813: cone; 938: litt – Thomas AS 925: ferr – Thomas DW 3624: buch; 3644: buch; 4324: caul; 4721: foli; 5274: subm; 8966: leto – Thomas NW 968: velu; 1446: sten; 1461: grac; 1642: laur; 2136: mann; 2705: laur; 2993: mann; 2998: mann; 3426: grac; 3639: mann; 4688: mann; 4701: velu; 4955: mann; 4998: mann; 5005: velu; 5250: mann; 5538: mann; 5566: mann; 6182: mann; 10603: sten – Timberlake 5669: buch – Tinguy 1028: komo – Tinley 1438: obov; 2814: buch; 2936: trio – Tisserant (Équipe) 689: engh; 763: laur; 914: cape; 1015: laur; 1120: cape; 1257: engh; 1285: engh; 1454: cape; 1594: cape; 1612: gill; 1701: engh; 1710: cape; 1755: laur; 1941: engh; 2035: pyna; 2062: engh; 2090: cape; 2132: gill; 2486: boko; 4233: engh – Tisserant 350: schw; 875: mont; 1126: parv; 1362: mont; 1468: laur; 1468 Bis: laur; 1775: laur; 2153: schw; 2532: boko; 2841: mont; 4233: engh – Topham 705: chas – Toussaint 62: sere; 127: sere; 189: olig; 205: scam; 290: laur; 362: sere; 396: sere; 398: scam; 401: scam; 685: gill; 858: fila?; 895: engh; 2123: parv – Townsend 3: obov – Trapnell 2278: buch; 2283: buch – Trochain 10434: boko – Troupin 522: parv; 792: luci; 884: parv; 1502: parv; 1737: schw; 4562: foli; 4755: ochr; 5371: foli; 12466: engh; 14481: orop – Turner 96: buch; 201: buch; 211: buch; 230: buch.

Uehara 72: pogg; 534: ferr; 579: pogg – Unwin 49: laur.

Vahrmeijer 451: caff – van den Brande 216: pogg; 565: fila – van der Ben 765: ferr; 1337: buch – van der Burg 549: laur – van der Burgt 614: grac; 1288: bart; 1872: mann; 1873: grac – van der Laan 202: whyt; 364: whyt – van der Maesen 8631: obov – van der Veken 10949: orop – van Doorn: 30: whyt – van Eijnatten 1406: grac; 2270: voge – van Lavieren 832: obov – van Meer 16: velu; 917: grac; 1054: grac; 1230: grac; 1809: foli; 1851: foli; 1868: grac – van Rensburg 1506: obov – van Setten 172: whyt; 342: whyt – van Son 28766: obov – van Wyk 4752: caff; BSA2863: chas – Vanden Berghen 5460: bart; 8788: bart – Vaughan 972: forn; 1754: trio; 1993: trio; 2005: trio; 2223: forn; 2750: buch – Venter 89: obov; 386: obov; 893: caff – Verdcourt 126: trio; 168: trio; 2620: keny; 3365: pogg; 3644: keny; 12113: keny – Verger 827: grac – Vermoesen 1483: olig; 1491: olig; 2269: boko – Verschueren 394: parv – Versteegh 536: glab – Vigne 1290: foli; FH3884: voge – Villiers 100: dicl – Volk 2088: obov – Vollesen 2704: buch; MRC2714: suff; MRC3362: suff; MRC4014: trio – Vos 249: caff; 600: caff.

Wabeke 20: bart – Wagemans 504: sere; 505: olig; 1146: laur; 1526: ferr; 1527: laur; 2193: luci; 2351: scam – Walker 3/sn: engh – Walters 1620: spec; 1637: spec – Ward 851: caff; 890: caff; 2373: caff; 2507: caff – Warnecke Amani 173: trio – Waterman 840: caul – Webster N 7: obov – Weigend 2993: obov – Wells 75: caff – Welwitsch 758: luci; 760: parv; 761: ferr; 762: luci; 770: luci; 771: ferr; 772: ferr – Whellan 2015: obov – White F 1907: obov; 3198: ochr; 3300: ochr; 3300A: ochr; 3391: parv; 3412: ochr; 3696: buch; 6098: ochr; 10432: caff; 10469: mapu – White LJT 27: spec; 231: cone; 371: dicl; 470: dicl; 558: klla; 879: klla; 1104: klla; 1224: cone; 1559: klla; ECOFAC29: klla – Wieringa 1291: dicl; 1650: dicl; 2679: leto?; 3605: engh; 3833: wier; 5452: mont?; 5898: engh; 7686: cone; 8018: caff; 8229: trip; 8235: scam; 8237: dicl; 8241: mont; 8244: engh; 8245: cone; 8287 a: cone; 8292: scam?; 8310: ferr; 8319: lete; 8320: lati; 8406: ster; 8418: leto; 8425: engh; 8542: dicl; 8572: spec; 8574: spec; 8578: spec; 8579: klla; 8632: ferr; 8633: mont? – Wigg 404: obov; 1052: trio; FH1088: obov – Wild 6629: chas– Wilks 1649: dicl; 2451: leto? – Williamson 111: cone – Wilson (Uganda) 935: keny – Wirminghaus 1005: caff; 1093: caff – Wood GHS 587: ferr; 659: buch; 1507: ferr; FD1506: litt; FD1506A: gill – Wood JM 1067: caff.

Yallah 111: glab – Yangakola 411: engh – Yongo 868: engh; 965: engh – Yonon Botanic Team 46: velu; 52: velu; 106: laur; 108: engh; 112: velu; 167: velu.

Zawa 595: engh – Zenker 132: eleg; 199: eleg; 356: caul; 357: engh; 1321: eleg; 2050: foli; 2102: dicl; 2473: diel; 2693: eleg; 2977: klla; 2985: fila; 3001: foli; 3495a: zenk; 3898: caul; 4000: eleg; 4477: eleg – Zenker & Staudt 431a: mont – Zietsman 4264: mapu – Zimmermann g6361: trio; g6362: trio – Zunguze 781: mapu.

Chapter 5

Floral evolution by simplification in *Monanthotaxis* (Annonaceae) and hypotheses for pollination system shifts

This chapter is based on:

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Abstract

Simplification by reduction has occurred many times independently in the floral evolution of angiosperms. These reductions have often been attributed to changes in reproductive biology. In the angiosperm plant family Annonaceae, most species have flowers with six petals, and many stamens and carpels. In the genus *Monanthotaxis* several deviations from this pattern have been observed, including flowers that contain three petals and three stamens only. New DNA sequences were generated for 42 specimens of *Monanthotaxis.* Five chloroplast markers and two nuclear markers for 72 out of 94 species of *Monanthotaxis* were used to reconstruct a phylogeny of the genus, which revealed several well-supported, morphologically distinct clades*.* The evolution of four quantitative and two qualitative floral characters was mapped onto this phylogeny, demonstrating a reduction in flower size and number of flower parts in *Monanthotaxis.* A large variation in stamen forms and numbers, strong correlations between petal size, stamen and carpel number, combined with a non-gradual mode of evolution and the sympatric co-occurrence of *Monanthotaxis* species from different clades suggest that the high diversity in the African rainforest of this genus is caused by switches in pollination systems.

5.1 Introduction

The evolution of life shows a trend towards increasing complexity and synorganisation. Concurrently, there is an evolutionary trend across the tree of life towards the loss of biological complexity by reduction (O'Malley et al. 2016). Examples of such simplifications in evolution are independent losses of multicellularity in a variety of fungal lineages, losses of Hox genes across different animal groups, the reduction in the complexity and size of the gametophytic generation in land plants and genome reduction in parasitic plants (Graham et al. 2017, Holland 2013, O'Malley et al. 2016, Wicke et al. 2013). Simplification also occurs widely in the evolution of flowers across the angiosperms. Despite some uncertainty in the inference of ancestral floral characters at the crown node of angiosperms, e.g. regarding the number of perianth and stamen whorls, it is evident that reductive trends are widespread in the evolution of angiosperms (Sauquet et al. 2017).

Some of these trends are evidently linked to fundamental changes in reproductive biology, such as the change from bi- to unisexual flowers with a concomitant reduction in number, or entire disappearance, of either stamens or carpels (Mitchell & Diggle 2005). Many independent reductions in flower size are correlated with changes in pollination regime. Shifts from insect pollination towards either wind pollination or self-pollination are associated with a decrease of floral complexity. The evolutionary scale of such changes ranges from local variation within a species to synapomorphies that characterize major clades (Friedman & Barrett 2008, Goodwillie & Ness 2005, Goodwillie et al. 2010). The presence of sterile stamens (staminodes) is frequently an intermediate step in the reduction of the androecium. Staminodes that do not obtain a new function, such as pollinator attractant, are often quickly lost during evolution. As a consequence, non-functional staminodes are generally only found in taxa where the reduction has occurred recently (Walker-Larsen & Harder 2000).

Before the era of molecular phylogenetics one of the hypotheses on the origin of angiosperms was the euanthial theory, arguing that the ancestral angiosperm flowers contained many spirally arranged parts and subsequent reduction has taken place (Arber & Parkin 1907). With the rise of molecular phylogenetics and the discoveries of fossil flowers from the Cretaceous (Friis et al. 2006) the current leading hypothesis is that the ancestral angiosperm flowers had more than two perianth and stamen whorls (Sauquet et al. 2017). Both increases in size and complexity, as well as simplification occurred later in evolution and can now be observed in extant angiosperms (Endress & Doyle 2009, Friis et al. 2006). A reduction in the number of whorls of tepals and stamens has occurred in most modern angiosperms. The ancestral state of many other floral characters is uncertain for angiosperms, which is likely caused by the variability of many of those states in the early diverging angiosperms, complicating the inference of ancestral states (Endress & Doyle 2009).

Among early diverging angiosperms, the Annonaceae are second in size after the Lauraceae, containing ca 2430 species (Rainer & Chatrou 2006), and are amongst the dominant plant

families in tropical forests worldwide (Cardoso et al. 2017). The flowers of most species of Annonaceae contain three perianth whorls, viz. a single whorl of three sepals and two whorls of three petals. In the majority of species the flowers have a large number of stamens in multiple whorls, with the whorled pattern often becoming irregular with increasing numbers of stamens (Endress & Armstrong 2011).

Several deviations from the general floral pattern in Annonaceae were observed in the genus *Monanthotaxis* during an ongoing taxonomic revision (Guo et al. 2017, Hoekstra et al. 2014, Hoekstra et al. 2016). This genus consists of lianas and is endemic to Africa and Madagascar. With 94 species it is one of the species-rich genera of Annonaceae and the second largest genus for Africa. In contrast to most other genera in the family, *Monanthotaxis* displays a huge variation in floral characters (Fig. 1). The flowers of most species are small relative to the range of sizes observed across Annonaceae. Species such as *M. tripetala* are amongst the smallest-flowered species in the family. Petals commonly occur in either one or two whorls. In some species, however, the petals form a single whorl at the floral base, whilst the outer petals overtop the inner petals at the apex in flower buds and give the appearance of two petal whorls in bud stage. In some species (e.g. *M. bidaultii*, *M. tripetala*), reduction of floral parts had led to a decrease in size, or even absence, of the inner whorl of petals. The number of stamens greatly varies from a few stamens in a single whorl (e.g. *M. bidaultii*, *M. heterantha*), up to 120 stamens in many whorls (e.g. *M. gracilis*). Several species possess an outer whorl of staminodes (Hoekstra et al. 2016). In most other genera of Annonaceae these characters vary hardly.

As most species have a moderate number of small flowers high up in the canopy of tropical rainforests, almost nothing is known about the ecology and pollination biology of *Monanthotaxis*. However, well-sampled phylogenies are a helpful tool to test hypotheses about evolution (Soltis et al. 1999), facilitated by observations on floral morphology made from herbarium specimens. The exact generic delimitation of *Monanthotaxis* and allied genera had long been unclear (Wang et al. 2012). Recently, the generic boundaries of the genus have been clarified with a well-supported phylogeny containing about 40% of the species of *Monanthotaxis.* This resulted in the transfer of the genera *Exellia, Gilbertiella* and most of the African species of *Friesodielsia* to the genus *Monanthotaxis*, rendering *Monanthotaxis* morphologically well delimited and monophyletic (Guo et al. 2017).

In this study, we increased the taxon sampling of *Monanthotaxis* to over 75% of the species diversity. Four quantitative and two qualitative characters, which are elements of floral reductions, were scored for these species. We traced changes in these characters over the phylogeny to produce and tested hypotheses about the evolution and diversification of the genus. More specifically, we examined the evolutionary mode of the floral characters, i.e. whether these have evolved following a gradual mode or pulsed mode of evolution, and the correlations between floral characters to test the possibility that small flowers in some

Monanthotaxis species have evolved in concert with a reduction in number of parts. This is done to create testable hypotheses about the diversification of the genus.

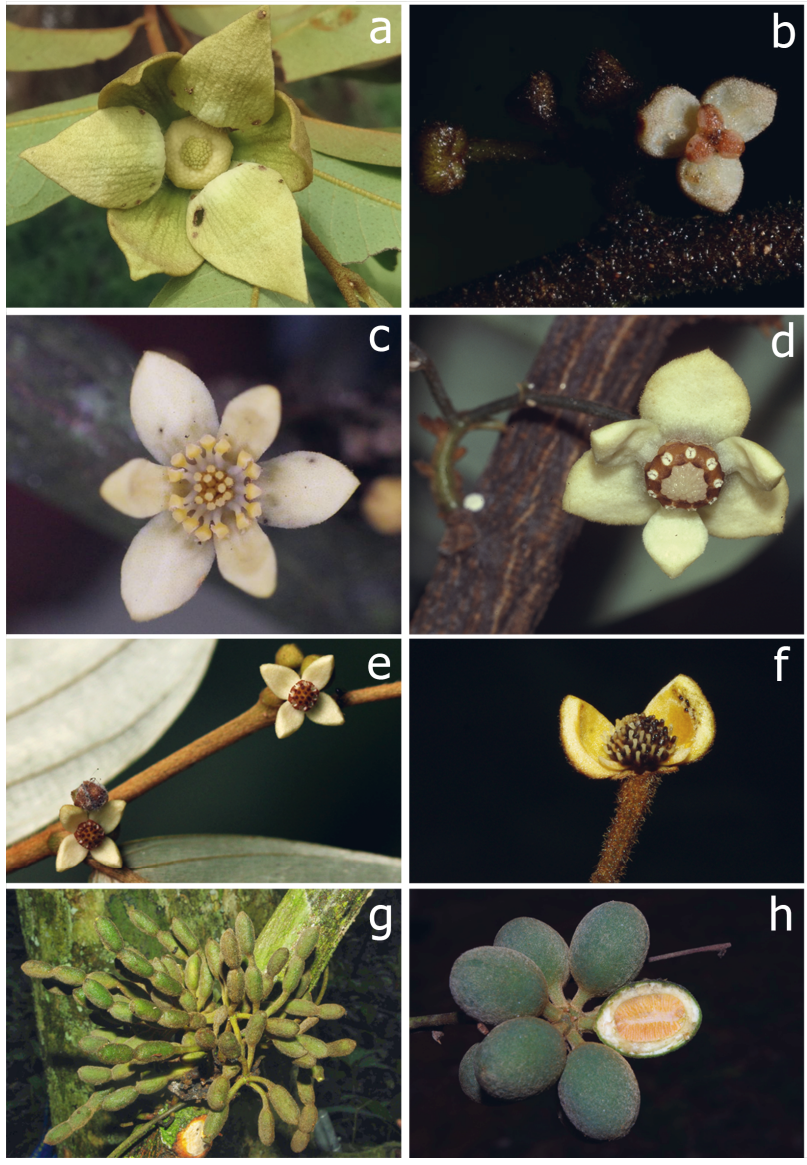

Figure 1. Flower morphology of outgroups (a) and flowers and fruits of *Monanthotaxis* (b-h). (a) *Uvaria scabrida*, flower showing many stamens and carpels; (b) *Monanthotaxis bidaultii* male flower showing three petals and three stamen; (c) *Monanthotaxis couvreurii*, flower showing basally fused stamens; (d) *Monanthotaxis whytei*, cauliflorous flower with nine hardly visible staminodes alternating with nine stamens; (e) flowers of *Monanthotaxis poggei* showing four petals and eight stamen, each in a single whorl; (f-g) *Monanthotaxis diclina,*

female flower with one petal removed showing many carpels, and fruits showing multiple seeds per monocarp; (h) *Monanthotaxis paniculata* fruits with single seed per monocarp. — Photographs: (a) Paul H. Hoekstra, (b) Ehoarn Bidault; (c, f-h) Thomas L.P. Couvreur; (d) Lubbert Y.T. Westra; (e) Bart T. Wursten.

5.2 Materials and methods

5.2.1 Taxon sampling

For each species, subspecies and variety of *Monanthotaxis* at least one representative voucher specimen was selected and six species have been included twice in this study as these belong to allopatric populations with some morphological differences. Eight outgroup species were selected based on the phylogeny of Guo et al. (2017) including all genera in the *Dasymaschalon* clade and representative genera of the tribe Uvarieae. 262 DNA sequences were newly generated for this study and 299 sequences were taken from previous studies (Chatrou et al. 2012, Guo et al. 2017). All voucher specimens were identified by the first author in the framework of a taxonomic revision of the genus *Monanthotaxis*. Sequences for a total of 72 out of the 94 species (74 of 96 taxa when including varieties) of *Monanthotaxis* were successfully produced. This includes fifteen recently described new species (Hoekstra et al. 2014, Hoekstra et al. 2016, Hoekstra et al. 2021). An initial exploration of specimens from Madagascar indicated that there are at least 12 undescribed species from that region. Of the 22 taxa not included 8 species were only very recently recognized as new species to science. The other taxa are only known from very old collections and DNA extraction and amplification failed or no permission was obtained from the herbaria to sample those old collections.

5.2.2 DNA extraction, amplification and sequencing

DNA sequences of five chloroplast markers (*matK*, *ndhF*, *psbA-trnH*, *rbcL* and *trnL-F*) and two nuclear markers (ETS and ITS1-5.8S-ITS2) were generated for 42 specimens and downloaded from genbank for 46 specimens.

DNA extraction, amplification and sequencing followed the protocol that has been previously described (Guo et al. 2014, Thomas et al. 2012) and the PCR reaction for the nuclear markers as in Guo et al. (2017) with the modification that 5 µl of 5x Betaine was added to each 25 µl PCR, because the ITS and ETS sequences have a high GC content (55-60%). The PCR products were sequenced on an ABI 3730 Sequencing platform by BaseClear (Leiden, The Netherlands). For voucher information and GenBank accession numbers see Supplementary Table S2 online.

5.2.3 Phylogenetic analyses

Trace files were checked and assembled in Sequencer 5.4 (Gene Codes Corporation, MI U.S.A.) or BioEdit 7.2.5 (Hall 1999). Sequences were aligned using the L-ins-I option in MAFFT v 7.245 (Katoh & Standley 2013) and verified manually in Mesquite v 3.11 (Maddison & Maddison 2016). Ambiguously aligned regions (in ITS and ETS) as well as microsatellites were excluded from the analyses (Chatrou et al. 2012). Some species had an inversion of 14 positions in the *psbA-trnH* spacer. Following Pirie et al. (2006), this fragment was inverted when necessary, to retain any phylogenetic information. Gaps were coded following the method of Simmons and Ochoterena (Simmons & Ochoterena 2000) using FastGap 1.2 (Borchsenius 2009).

Phylogenetic trees were inferred using maximum parsimony analyses, maximum likelihood analyses and Bayesian Inference. With the program Partitionfinder v. 1.1.1 (Lanfear et al. 2012) we inferred the best partitioning scheme as well as the best substitution models for those partitions. Individual loci, and separate codon positions for the coding genes, were defined as the data blocks. All possible partitioning schemes and substitution models were fitted on the dataset using the greedy algorithm of PhyML in Partitionfinder and the best partitioning scheme was selected based on the Bayesian Information Criterion.

Maximum parsimony analyses were performed in PAUP* version 4.0a151 (Swofford 2002) with the heuristic search option and tree bisection-reconnection (TBR) branch swapping, with 1000 random addition sequence replicates, saving 50 trees per replicate. Character states were treated as unordered and of equal weight (Fitch 1971). To assess clade support nonparametric bootstrap analyses were performed with 1000 bootstrap replicates and 100 random addition sequence replicates per bootstrap replicate, saving 50 trees per replicate.

Bayesian inference was conducted with MrBayes v3.2.6 (Ronquist & Huelsenbeck 2003) on the CIPRES gateway server (Miller et al. 2010). The best fitting model of sequence evolution as defined by Partitionfinder was applied to the DNA sequence data and the restriction site model with the setting “coding = variable” was applied to the gap-coding data. It has been shown that MCMC analyses of closely related species may get biased towards excessively long branch-length estimates (Brown et al. 2010) and therefore following Guo et al. Guo et al. (2017), the temperature parameter was set to 0.08 and the mean branch length prior was set to 0.01 (brlenspr=unconstrained: exponential(100.0)). These settings improved mixing of the chains compared to the default values of the program. Four different chains were run for 10 million generations sampling every 1000th generation. Convergence was assessed using the R-package RWTY version 1.0.1 (Warren et al. 2016) as this package includes an estimation of the effective sample size (ESS) for the tree topology parameter (Lanfear et al. 2016) as well as ESS values for other parameters and diagnostic plots.

Maximum likelihood analyses were run on the CIPRES Gateway server with RAxML version 8 (Stamatakis 2014). The GTR-gamma model of substitutions was used for the DNA sequence

data and the bingamma model for the gap-coded data. To assess clade support a rapid bootstrap analysis was performed on the best-scoring tree with 1000 nonparametric bootstrap iterations.

In many angiosperms positive selection takes place on the active sites of the *rbcL*-gene and removing those sites could improve phylogenetic resolution (Kapralov & Filatov 2007). This has been found in a family-wide study of Annonaceae (Hoekstra et al. 2017). We tested for signs of positive selection in the genes *rbcL* and *matK*, using the branch-site model of positive selection (Yang et al. 2005) in the program Codeml of the PAML4.8 package (Yang 2007). A simplified version without branch lengths of the most likely tree from the maximum likelihood analyses was used as a backbone phylogeny. We assessed the presence of positive selection for the branch subtending the *Monanthotaxis* crown node, for each gene separately. These models were compared using a likelihood ratio test against a null model in which the value ω was fixed. When the likelihood ratio test significantly demonstrated the presence of positive selection ($P < 0.05$), the Bayes empirical Bayes (BEB)(Yang et al. 2005) was used to calculate the posterior probabilities for site classes and to identify the sites under positive selection. These codons were deleted from the alignment and subsequently all phylogenetic inferences were redone with the new dataset without codons under positive selection.

Bayesian, maximum likelihood and maximum parsimony analyses were rerun separately on the nuclear and chloroplast loci to check for incongruences. Nine specimens, for which more than half of the DNA sequences were missing (3000 bp), were excluded from the dataset and all phylogenetic inferences were rerun to test if support values for any nodes improved. The support values from all different runs were summarized and compared using a customized Python script with the library Dendropy version 4.1.0 (Sukumaran & Holder 2010). Maximum parsimony and maximum likelihood bootstrap values from 85 to 100 were considered as strong node support, values from 75 to 84 as moderate support and values from 50 to 74 as weak support. Posterior probabilities higher than 0.95 were considered as supported, below 0.95 as unsupported.

5.2.4 Morphological character sampling

Six morphological characters were selected to be used as a proxy for floral reduction. Four characters are quantitative, i.e. maximum petal length, number of stamens, number of carpels and number of ovules per carpel, and two characters are qualitative, i.e. flower sexuality and presence of staminodes. For species of *Monanthotaxis* all these characters were (re-)measured from herbarium material as in published literature sometimes errors were encountered. For the outgroup species data was taken from literature (Le Thomas 1969, Turner 2012, Verdcourt 1971) and missing data (including number of stamen for all species) was measured from herbarium material.

Quantitative variables were transformed to logarithmic scale. However, variation occurs in the number of stamens and carpels within species and even within specimens, with variation increasing with the number of stamens and carpels per species. Species with generally nine stamens often may have a few flowers with eight stamens and sometimes even twelve stamens, while in a species with around 100 stamens the number can vary from 80 to 120 stamens. To take the increasing absolute value of variation with increasing number of stamens and or carpels into account, the average of the logarithm of the minimum and maximum number of stamens and carpels per species was used in the analyses.

The logarithm of the average of the maximum and minimum number of ovules per carpel was taken for species with a variable number of ovules per carpels. Species with a single ovule per carpel rarely have carpels with two ovules, and vice versa; these species were scored as having the predominantly occurring number of ovules.

The morphological characters could be observed for almost all species, with the exception of *Monanthotaxis sterilis* for which neither flowers nor fruits are known. Other species for which some of the characters could not be scored were *M. atewensis, M. malacophylla* and *M.* aff. *laurentii* for which only fruits are known, *M. aff. bidaultii* and *M. submontana* for which only female flowers are available, and *M. velutina*, the only flowering specimen has old flowers.

5.2.5 Character mapping and analyses

Morphological characters were optimized and analyzed on phylogenetic trees using BayesTraits version 2.0 (Pagel & Meade 2014). One thousand randomly chosen trees from the Bayesian analyses, after discarding the burnin and outgroup species, were selected to account for phylogenetic uncertainty.

Throughout the analyses in BayesTraits, model testing was used to test whether more complex models better fitted the data than simpler models. Three different model tests were performed: likelihood ratio tests were used for Maximum Likelihood (ML) analyses for nested models, AIC relative likelihoods were used for Maximum Likelihood (ML) analyses of non-nested models and Bayes factors for Markov Chain Monte Carlo (MCMC) methods. The likelihood ratio tests were performed for each of the one thousand input trees based on the complex and simpler models and for each tree was tested if the p-value of the likelihood ratio statistic was below 0.05. For the AIC-test, the AIC values were calculated for each of the one thousand input trees of the complex and simpler model. Next, the relative likelihood of the simpler model was calculated and values less than 0.05 were considered evidence that the complex model better fitted the data than the simpler model. For the MCMC analyses Bayes factors were calculated from the marginal likelihoods using a stepping stone sampler (Xie et al. 2011), as marginal likelihoods estimated by a stepping stone sampler have been shown to be more robust than the harmonic mean marginal likelihoods (Baele et al. 2012). One hundred

stones were used to calculate an estimate of the marginal likelihood and each stone was run for 10,000 iterations. Bayes factors higher than 2 were considered positive evidence, higher than 5 strong evidence and higher than 10 as very strong evidence for selection of the more complex model compared to the simpler model with less parameters.

To infer the ancestral states of the discrete characters, a continuous-time Markov model using MCMC methods (Pagel et al. 2004) was applied. Hyper-priors were used to seed the mean of the exponential priors from a uniform distribution ranging from 0 to 100. Model tests using Bayes factors were applied to test whether different transition rates from one state to another state better fitted the data than both rates set equal. For the character of uni- or bisexual flowers, the Bayes factors did not reject the hypothesis that the transition rates are equal, this was accommodated in the prior settings. While equal rates were significantly rejected ($P < 0.05$) for the ancestral states of the staminodes presence and those were inferred using reversible-jump Markov Chain Monte Carlo (Pagel & Meade 2006).

A two-step process was run to infer the ancestral states of the continuous characters. First an MCMC with a continuous random walk model (Pagel 2002) was run to estimate a distribution of models from the available data and subsequently these models were used to infer the ancestral states. Bayes factors of initial analyses indicated that the trait 'number of stamens' does not evolve along the phylogeny following a Brownian motion model of evolution. Therefore, the lambda parameter was set to be estimated in analyses with the number of stamens character. Finally, after discarding the burnin, the mean and standard deviation of the ancestral state inferences were calculated for each node.

For both the discrete and continuous characters five runs using MCMC methods were performed for each trait to infer the ancestral nodes. The runs consisted of 10 million generations with a burnin of 100,000 generations and sampling every 10,000 generations. Convergence was checked by calculating the ESS-values with the R-package coda version 0.19-1 and by verifying if the acceptance rate for proposed changes to the chain lies between 20 and 40 %.

To test for correlated evolution between 2 character traits, both 5 MCMC and 2 ML analyses were run for each model. The binary traits were first run with the discrete independent model in BayesTraits in which the traits are assumed to have evolved independently. Then the traits were run with the discrete dependent model which assumes that the traits are correlated. For the continuous characters they were first run with the continuous random walk model and subsequently those analyses were rerun, but with the correlation between the two traits being forced to be zero. Both Bayes Factors and likelihood ratio tests were performed to test if the models that assume correlation between the traits better fitted the data than the models without such correlation.

We tested whether the four continuous morphological characters evolved along the phylogeny following a pulsed or a gradual mode of trait evolution. In the same analyses we also tested if morphological changes concentrate around speciation events. First, analyses were run with the kappa scaling parameter set to be estimated and subsequently run with the kappa parameter fixed to 0 and additionally run with the kappa parameter fixed to 1. A kappa close to 0 indicates a pulsed mode of evolution for the involved trait, while a kappa of 1 indicates a gradual mode of evolution. Values lower than 1 indicate that shorter branches contribute more to the character evolution, while values higher than 1 indicate that longer branches contribute more. Model testing as described for the correlation tests were used to test if the kappa parameter significantly differed from 1 and/or from 0.

5.3 Results

5.3.1 Phylogenetic analyses

The dataset used for the phylogenetic analyses comprised 6649 bp of sequence data that has been gathered for 88 specimens, including 80 specimens of *Monanthotaxis* representing 77% of the species of this genus. The best partitioning scheme found by Partitionfinder divided the nuclear and chloroplast markers in separate partitions and rendered the HKY + gamma substitution model best fitting in both cases. The analyses using CodeML did not find evidence for positive selection in the *matK* gene, while an indication for positive selection was found in 5 sites in the *rbcL* gene. Removing those five sites slightly improved the support values for a few nodes (Supplementary information Fig. S1 and S2). Excluding the nine species for which less than half of the DNA sequences were available did not change the principle topology, but did improve the support values of seven nodes (Fig. 2 and Supplementary information Fig. S1 and S3). As the absence of these nine species would result in the exclusion of some of the relevant morphological character variation, all subsequent analyses were done using all species, but without the five codons of *rbcL* with possible positive selection.

The genus *Monanthotaxis* was highly supported to be monophyletic in both the Bayesian and maximum likelihood analyses, with *Monanthotaxis obovata* highly supported as sister to the rest of the genus. Most backbone nodes are not well supported, in contrast to more recent nodes, notably clades A, B, C, E and H (Fig. 2 and Supplementary information Fig. S1).

Analyzing chloroplast and nuclear loci separately revealed a well-supported incongruent pattern within clade A (Supplementary information Fig. S4 and S5). The nuclear data reveal a sistergroup relationship between *M. ferruginea* and *M. bokoli*, whereas the chloroplast data show that *M. ferruginea* is sister to *M. orophila* with strong support. All three species involved are closely related and differ only slightly in floral morphological characters. Therefore, we consider the effect of this incongruence on the ancestral state analyses negligible and performed all analyses after concatenation of the chloroplast and nuclear data.

5.3.2 Morphological characters and analyses

The results clearly show that simplification has taken place in *Monanthotaxis* with strong correlations between number of stamens, petal size and number of carpels (Table 1). Furthermore, the outgroups and clades J and K of *Monanthotaxis* have many more stamens and larger petal sizes than the remaining *Monanthotaxis* species. The number of stamens ranged from 105 to 346 in the outgroups, and from 125 in *Monanthotaxis gracilis* to as few as three in *M. bidaultii.* Maximum petal size in *Monanthotaxis* ranged from 2.2 mm in *M. tripetala* to 50 mm in *M. hirsuta*, while reaching 130 mm in the outgroup species *Dasymaschalon dasymaschalum* (Fig. 3). Due to the low support for some of the backbone nodes, it is unclear along which branch the reduction in number of stamen and petal size occurred, and whether it occurred multiple times. A general reduction in number of carpels was inferred, a trend that is reversed by an increase in carpel number in species with unisexual flowers (clade I). Some of the latter have up to 150 carpels per flower, while in some other clades the number has been reduced to a single carpel per flower. The number of ovules per carpel ranged from 1 to 16 in *Monanthotaxis* (Fig. 4). Staminodes were present in species scattered across five different clades of *Monanthotaxis* and have arisen or disappeared multiple times. Unisexual flowers were confined to a single clade (Fig. 5).

The ancestor of *Monanthotaxis* most probably had bisexual flowers and lacked staminodes (Fig. 5 and Supplementary Information Table S1). The ancestral state inferences of the continuous traits should be interpreted with caution, but suggest that the ancestor of *Monanthotaxis* had petals of 10 mm long, 31 stamens, 21 carpels and 3 ovules per carpel (Fig. 3 and 4 and Supplementary information Table S1).



Fig. 2 Phylogeny of *Monanthotaxis*. *** = strong node support, ** = moderate node support, * = weak node support. Nodes indicated with black and white dots are strongly and moderately supported, respectively, after removing species for which only a few markers were available.

Table 1. Results of model tests of correlation between morphological characters. BF = results of 5 Bayes Factor tests, percentage of significant trees = percentage of trees with significant correlation using likelihood ratio test for continuous characters ($p < 0.05$) and using relative likelihood of AIC for the binary characters . Bin = Binary characters, cont = continuous characters. Nr of par. cor. = Number of rate parameters of model with correlation, nr of par. ind. = number of rate parameters of model without correlation. MLh cor. = Best marginal likelihood of the stepping stone sampler of the five MCMC runs of the model with correlation, MLh ind. = Best marginal likelihood of the stepping stone sampler of the five MCMC runs of the model without correlation. V = very strong indication of correlation, S = strong indication of correlation, P = positive indication of correlation, N = no or weak indication of correlation. In bold are the results which show a correlation for both types of test.

Morphological characters	Bin/Cont	Nr of par. cor.	Nr of par. ind.	MLh cor.	MLh ind.	BF	Percentage of significant trees
Stamen number vs carpel number	Continuous	**2**	**1**	**−38.2665**	**−44.1576**	**5x V**	**76.1%**
Stamen number vs ovule number	Continuous	2	1	−34.5393	−37.3479	4x S, 1x P	55.4%
Stamen number vs petal size	Continuous	**2**	**1**	**−18.0604**	**−30.9199**	**5x V**	**100%**
Carpel number vs ovule number	Continuous	2	1	−31.3965	−32.111	1x S, 4x N	0.7%
Carpel number vs petal size	Continuous	2	1	−23.5816	−26.7138	5x S	48.4%
Ovule number vs petal size	Continuous	**2**	**1**	**−8.1434**	**−14.5965**	**4x V, 1x S**	**100%**
Staminodes vs uni/bisexual flowers	Binary	8	4	−48.167	−49.4281	5x N	0.7%

Strong to very strong correlations were found between number of stamen, petal size and the number of ovules per carpel, indicating that the simplification of flowers has occurred jointly for different parts of the flowers. The number of carpels is only strongly correlated with the number of stamens when considering Bayes factors, and less strong after the likelihood ratio test (in only 76% of the input trees). The correlation between petal size and number of carpels was strong considering Bayes factors and weak between number of ovules and number of carpels, while the likelihood ratio tests found no significant correlations between these

variables in the majority of input trees. The discrete tests of correlation did not retrieve evidence for a correlation between presence of staminodes and flower sexuality (Table 1).

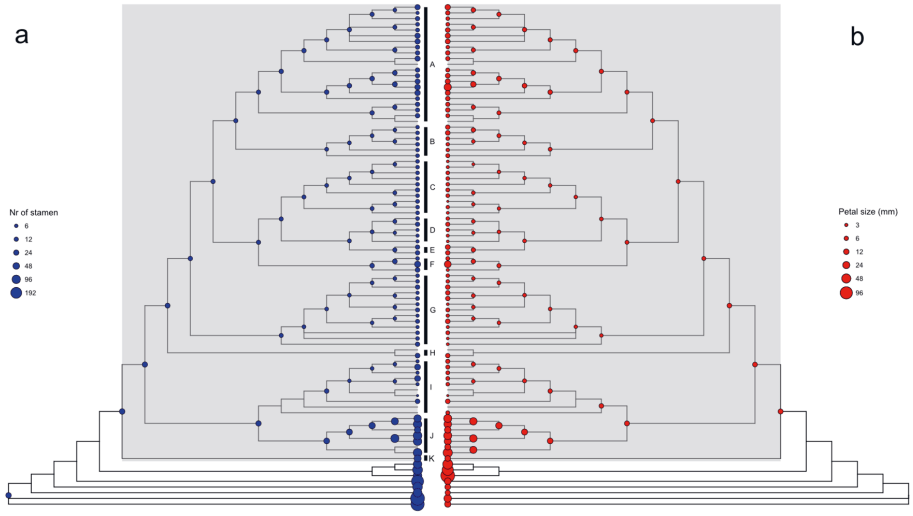

Fig. 3 Number of stamens (a) and petal size in mm (b) plotted onto the *Monanthotaxis* phylogeny, with internal nodes showing Bayesian estimation of mean values.

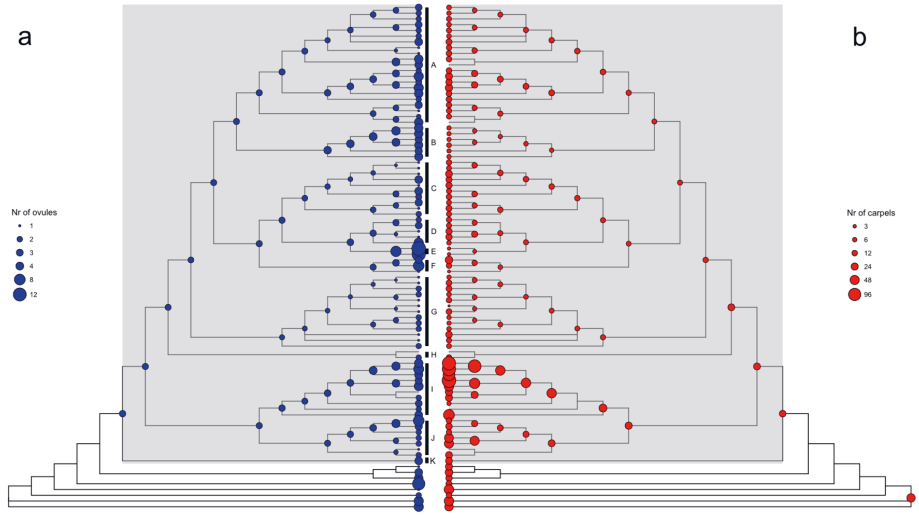

Fig. 4 Number of ovules (a) and carpels (b) plotted on the *Monanthotaxis* phylogeny, with internal nodes showing Bayesian estimation of mean values.

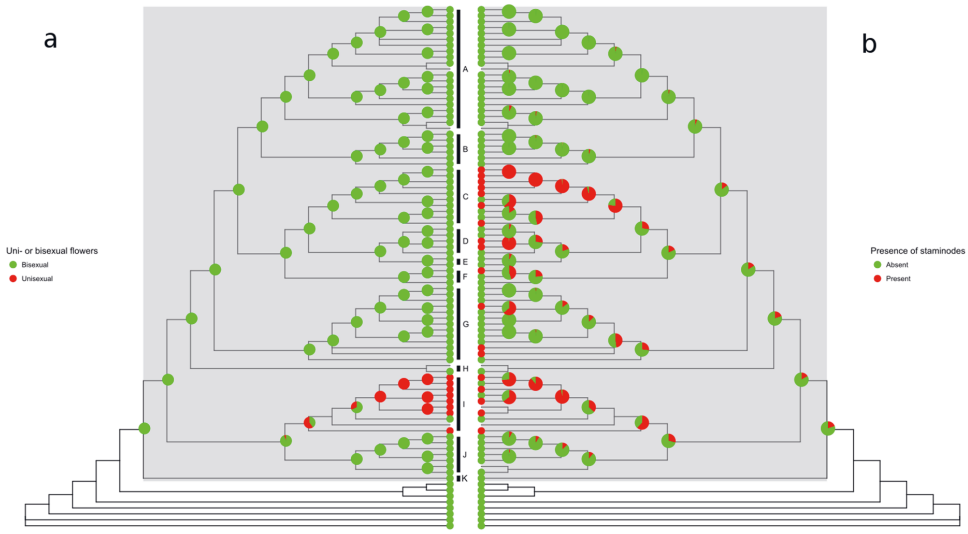

Fig. 5 Presence of uni- or bisexual flowers (a) and presence of staminodes (b) plotted on the *Monanthotaxis* phylogeny. Pie charts show inferred states.

The tests for mode of evolution significantly favoured a pulsed mode for the number of stamens and the number of carpels, indicated by kappa estimates of 0.01 and 0.1 respectively. No evidence for a significant deviation from a gradual mode of evolution was found for the number of ovules per carpel, while evidence for a deviation from a gradual mode of evolution was found using likelihood ratio tests for the petal length. The kappa estimate for petal length of 1.9 indicates that long branches contribute more to the evolution of petal length than would be expected under a gradual mode of evolution. However the Bayes factors did not indicate a deviation from a gradual mode of evolution for the petal length, suggesting that the signal is very weak if present (Table 2).

Table 2. Results of test for significant deviation from a Brownian motion model of evolution. MLh kappa = Best marginal likelihood of the stepping stone sampler of the model with the estimation of kappa, MLh kappa 1 = Best marginal likelihood of the stepping stone sampler of the model with kappa set to 1. BF = Bayes factor tests, V = very strong indication, P = positive indication and N = no indication for a deviation of kappa from 1.0. In bold are the results which show a significant deviation from a Brownian motion model of evolution.

Continuous trait	MLh kappa	MLh, kappa 1	BF	Percentage of significant trees	Kappa estimate
Carpels	**−18.7002**	**−20.3879**	**5x P**	**99.3%**	0.1
Stamens	**−19.0699**	**−27.2545**	**5x V**	**100%**	0.01
Ovules	−12.1765	−10.7361	5x N	5.6%	0.9
Petal length	−4.31857	−4.6971	5x N	92.7%	1.9

5.4 Discussion

In this study the majority of the *Monanthotaxis* species were included in phylogenetic analyses and data of the floral characters were acquired for all species of which flowers are known. The results demonstrate that a reduction in flower size and number of floral parts has occurred in most species of *Monanthotaxis*. The methods also proved useful for the generation of new insights into the evolution of a group for which hardly any ecological information is available. In a previous study the monophyly and generic delimitation of *Monanthotaxis* were resolved (Guo et al. 2017), based on a sample of 40% of the species of *Monanthotaxis* that still lacked some crucial species, such as those with unisexual flowers. In this study, the monophyly of *Monanthotaxis* is reaffirmed and although some nodes along the backbone of the tree receive weak support, most nodes within the genus are well supported (Fig. 2). Morphologically similar species are consistently closely related. As a result, the majority of the clades are easily recognizable by the combination of a few morphological characters. For example, the species of the well-supported clade A are distinct by the extra-axillary inflorescences, rounded flower buds, six petals in two whorls, and 30 or fewer stamens. The well-supported clade C is distinguishable by axillary inflorescences, ovate flower buds and petals in a single whorl at the base, with the outer petals overlapping the inner petals distally.

There is a trend across the phylogeny towards a reduction of stamen number and petal length in *Monanthotaxis (*Fig. 3). Indeed, all outgroup species have more than 100 stamens per flower (e.g. Fig. 1a), while the only clades of *Monanthotaxis* with more than 40 stamens per flower are the early diverging clades J and K. There are some other genera of Annonaceae which show only a few stamens, such as *Orophea*, *Bocagea* and *Miliusa* (Van Heusden 1992). Within the tribe Uvarieae, *Monanthotaxis* is the only genus in which species with a low number of stamens occur. Consequently, the low number of stamens in most *Monanthotaxis* species is

considered a reduction. Note, however, that the ancestral state for the genus *Monanthotaxis* was inferred as 31 stamen and petals of 10 mm, which is fewer than the number of stamens and a smaller petal size than the species in clades J and K, suggesting an increase has occurred in those clades. The species of these two clades were previously assigned to the genus *Friesodielsia* based on their superficial resemblance with that genus (Guo et al. 2017).

The very strong correlation between number of stamens and petal length, and between number of stamens and number of carpels within the genus *Monanthotaxis* is consistent with the general notion that the number of floral structures depends on available space (Endress 1994). However, the reduction in flower size apparently did involve all floral parts of the species with unisexual flowers. Despite the consistent small petals, most of the unisexual flowers contain many carpels. *Monanthotaxis wieringae*, for example, has a maximum petal length of 5 mm, but has around 130 carpels. This discrepancy probably explains the weak correlation between carpel number and petal length in most of the likelihood ratio tests. However, the male flowers do follow the general reduction trend with fewer stamens in species with smaller flowers.

Pollen-ovule ratio is an indicator of the breeding system in angiosperms (Cruden 1977). A high ratio indicates cross-pollination, while low pollen-ovule ratios generally are found in self-pollinating species. In view of this, the strong correlation between number of ovules per carpel and number of stamen, and between number of carpels and number of stamen, may suggest that no differences in breeding system exist within the genus *Monanthotaxis*. This is a tentative hypothesis, since the diversity in stamen forms (Fig. 1b,c,e) as well as the presence of species with unisexual flowers and bisexual flowers could indicate that different breeding systems occur in *Monanthotaxis* (Charlesworth 1993). Moreover, it is questionable whether number of stamen can directly be linked to the number of pollen grains as there is considerable variation in anther cell size within the genus *Monanthotaxis*.

The presence of non-functional staminodes is often thought to be an intermediate stage in the reduction of stamens (Walker-Larsen & Harder 2000). In the genus *Monanthotaxis* the staminodes do not have an apparent function; they form an outer whorl of reduced stamens which are often only visible as very tiny appendages less than half a millimeter in length, such as in *M. zenkeri* (Hoekstra et al. 2016). The fact that the presence of staminodes occurs on multiple independent branches on the phylogeny could indicate that the process of reduction is still ongoing in *Monanthotaxis*. *Monanthotaxis whytei* (Fig. 1d) is the only species on which an ontogenetic study has been performed (Ronse Decraene & Smets 1990). First an outer whorl of 6 staminodes is formed; this is followed by an inner whorl of 9 staminodes then a further inner whorl of 9 stamens. The outer whorl of staminodes already stops developing early in the floral development and is not visible in the mature flowers, while the whorl of 9 staminodes is only visible as very small appendages (Fig. 1d). This could indicate that the reduction of stamens in the genus *Monanthotaxis* takes place centripetally, i.e. from the outer

to the inner whorls and that the stamen whorl in species with only one whorl is homologous with the inner whorl in species with multiple whorls. It is interesting to note that the presence of staminodes in species with unisexual flowers (clade I, Fig. 1b,f,g) only occurs in male flowers and not in the female flowers a characteristic rarely reported in plants with unisexual flowers (Walker-Larsen & Harder 2000).

Reduction trends can follow a gradual mode of evolution or the slightly controversial (Pennell et al. 2014, Theißen 2009) pulsed mode of evolution, in which rapid change is followed by periods of stasis or little changes. Genome reductions and duplications, for example, by their nature have been demonstrated to follow a pulsed mode of evolution (Adams et al. 2002, Wolf & Koonin 2013), but this mode of evolution has rarely been established for morphological characters. The strong indication for a pulsed mode of evolution of the number of carpels and stamens may suggest that sudden events, such as changes in environment or pollination shifts, have triggered the floral reduction in *Monanthotaxis*. It must be noted that a limitation of the test used in this study is the simultaneous inference of the mode of evolution and of the amount of morphological change associated with speciation events (Pennell et al. 2014). Currently, methods are being developed which can disentangle these questions (Landis & Schraiber 2017). Alternatively, the inference of a pulsed mode of evolution for the number of stamens and carpels could be explained by the reduction of entire whorls. A gradual loss of whorls will be discernable as saltational changes in numbers of individual stamens and carpels, given the high number of floral parts per whorl. The irregular pattern of stamens and carpels in some species hampered the observation of the number of whorls in this study. Ontogenetic studies are needed for *Monanthotaxis* species with higher numbers of stamens and carpels to assess the exact number of whorls and assess the mode of evolution of those characteristics.

In general, we demonstrate an evolutionary reduction of flowers with a high number of floral parts to reduced flowers with as few as three petals and three stamens in the genus *Monanthotaxis* (Fig. 1b). The question remains whether a shift in pollination regime has triggered this reduction. In most species of Annonaceae the flowers are pollinated by beetles. Self-pollination is generally prevented by protogyny, viz. flowers entering the pistillate phase first, with a subsequent non-sexual phase and finally the staminate phase (Saunders 2012). This is also the case in the genera *Desmos*, *Dasymaschalon* and *Friesodielsia*, the genera most closely related with *Monanthotaxis* for which pollination studies exist (Saunders 2012). Protogyny also occurs in *Monanthotaxis* as in herbarium specimens only flowers in the pistillate phase or staminate phase have been observed. Flowers with overlapping staminate and pistillate functional phases have not been observed. The pollinators of *Monanthotaxis* however are unknown. Despite great differences in petal morphology in the tribe Uvarieae, most species are reported to be pollinated by beetles. However, pollination by cockroaches as well as bees has been reported in the genus *Uvaria* and flies and thrips have been reported as pollinators in some other genera outside the Uvarieae (Saunders 2012). Small unisexual flowers, as those of most *Monanthotaxis* species in clade I, have been correlated with fly as

well as wind pollination (Charlesworth 1993). However, without further studies the question remains if the great diversity in stamen forms and number in *Monanthotaxis* also reflect a diversity in pollination syndromes in this genus.

Monanthotaxis is the second-most diverse genus of Annonaceae in Africa, especially in central Africa as many as 10 species can occur sympatrically. The majority of these sympatric species belong to different subclades, with most pairs of sister species showing allopatric distributions. Therefore, the diversification of *Monanthotaxis* may have been promoted by floral adaptations of different subclades. This enabled them to occupy different ecological microniches and consequently species of different clades are able to co-occur. Dispersal limitation could have promoted subsequent diversification. The pattern of allopatric and sympatric distributions can only be tested directly if more accurate distribution data become available. Recent expeditions have shown that the known distributions of species are larger than previously thought and these also uncovered many undescribed species (Hoekstra et al. 2016) showing that the genus is undersampled in some areas of Africa. Finally, follow-up studies on the ontogeny, pollination and ecology are needed to understand more about the diversification of the genus *Monanthotaxis* and to answer questions on biodiversity of tropical rain forests.

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Chapter 6

General Discussion

6.1 Introduction

The goal of this thesis is to better understand the evolution of Annonaceae with a special focus on the systematics and evolution of *Monanthotaxis*. In this discussion three general themes connected with this goal will be discussed: Accelerated rates of evolution, species diversification, including processes of speciation, and taxonomy and taxonomists. In each of these themes the findings of this thesis and current knowledge in connection with the family Annonaceae and/or the genus *Monanthotaxis* will be discussed and future prospects of research on these subjects will be pinpointed.

6.2 Accelerated rates of Evolution

Most phylogenetic inference methods follow the molecular clock. They have the assumption that there is a constant rate of evolution. However, there are many deviations from a constant rate of evolution. Already in the first molecular phylogenies of the family Annonaceae such a deviation from a constant rate of evolution became apparent. One of the major clades, now the subfamily Annonoideae, had long branches, while the other major clade, the subfamily Malmeoideae, had short branches (Chatrou et al. 2012, Richardson et al. 2004). There are many mechanisms which could have generated these different rates of evolution. To study the evolution of a group it is important to understand why there are any deviations from a molecular clock. In chapter 2 (Hoekstra et al. 2017) an important step in diminishing the number of plausible hypotheses was set.

Deviations from a constant rate of evolution occur widely at all levels of evolution. Within genes 3rd codon positions mutate faster than 1st and 2nd positions, and in animals mitochondrial DNA mutates faster than the nuclear genome, while in plants it is the other way around, i.e. the nuclear genome mutates faster than the mitochondrial genome (Smith & Keeling 2015, Wolfe et al. 1987).

The rate of mutations and how often these mutations get fixed in a population are important factors driving the rate of evolution. The DNA in cells of organisms is under continuous threat of mutations caused by exogenous factors such as UV-light and heat, as well as endogenous factors such as oxidative stress and errors in DNA replication. Several repair mechanisms have been uncovered which repair these lesions in the DNA (Boesch et al. 2011). In 2015 the Nobel prize for chemistry was awarded to three pioneers in uncovering these mechanisms. One of these mechanisms is called mismatch repair. During DNA replication a wrong nucleotide is sometimes inserted. DNA polymerases have a 3' to 5' exonuclease activity which can correct these mistakes (Brutlag & Kornberg 1972), but still 5 out of each 100.000 base pairs gets wrongly inserted. The mismatch repair mechanism detects these errors and corrects them reducing the amount of mismatches during DNA replication to 1 in a hundred million per base

pair per generation in humans (Ségurel et al. 2014). Most details of the different repair mechanisms are known in the bacterium *Escherichia coli* and in humans, but DNA repair mechanisms appear to occur in all organisms and most of these mechanisms have been found in plants. The majority of information on plants comes from comparative analyses instead of direct observations (Britt 1996, Spampinato 2017). This field of science is rapidly developing, but still many questions remain open, particularly which repair mechanisms work in the organelles and especially in the chloroplasts. As the genes which encode the proteins of these mechanisms are not present in the mitochondrial and chloroplast DNA, the proteins must be actively transported into the organelles (Oldenburg & Bendich 2015). It appears that not all repair mechanisms are present in the organelles. Some parts of the repair mechanisms are shared between the nuclear genome and the organelles, but there are also many differences and even some pathways are specific for DNA repair in organelles (Boesch et al. 2011, Britt 1996). If a mutation in any of the repair mechanisms would change the substitution rate between different species this would most probably only be apparent in the nuclear genome or one of the organellar genomes but not all together. As demonstrated in chapter 2, the accelerated rate of evolution in Annonoideae as compared to Malmeoideae occurs both in the nuclear and chloroplast genome. Therefore, it is highly unlikely that a difference in repair mechanisms between the two subfamilies would have caused this difference (Hoekstra et al. 2017).

Fixation of a mutation in a population depends on many factors. If the generation time of the involved species is shorter, the rate of evolution is generally higher. This was first shown in mammals (Li et al. 1987, Ohta 1993). In plants a significant difference in rate of evolution was found between annual and perennial plants (Andreasen & Baldwin 2001) and between woody and herbaceous plants (Kay et al. 2006, Smith & Donoghue 2008, Yang et al. 2015). However, in a study on many different groups of plants no effect of the generation time on the rate of evolution has been found (Jobson & Albert 2002, Whittle & Johnston 2003). In contrast to animals, plants do not maintain a separate germ line, the reproductive organs are formed from the apical meristem of somatic cells and therefore they accumulate mutations during their life. This could be the reason why no clear correlation between generation time and the rate of evolution has been found in plants (Lanfear et al. 2013). It would be interesting to test if for example fruits of one individual tree would contain more mutations compared to fruit from the same individual but 10 years in the past. With current sequencing techniques this would be easily testable. To my knowledge, this has not been tested within one individual spanning multiple years, but has been tested between different generations of self-pollinating *Arabidopsis thaliana* and the number of mutations per base pair per generation also depended on the temperature in which the plants were grown (Belfield et al. 2021). Within Annonaceae hardly anything is known about generation time. From a few cultivated species some data is known, for example *Annona muricata* can set its first fruit around 3 years after germination (Lemos & Blake 1996), but for species from tropical forests, such as *Monanthotaxis*, nothing

is known. All species of Annonaceae are woody. Within the subfamily Annonoideae both lianas and trees occur, while the subfamily Malmeoideae contains tree species only (Chatrou et al. 2012). However, because of the previous argumentation it seems very unlikely that the growth habit has caused the difference in rate of evolution between the two subfamilies.

Another important factor for mutations to get fixed in a population is natural selection, viz. is a mutation under positive or negative selection or is it a neutral mutation. Neutral mutations such as synonymous substitutions are more common than non-synonymous substitutions. Variations in selective pressure on genes can cause accelerated rates of evolution in parts of the genome. For example, carnivorous and heterotrophic plants do not or hardly depend on the genes for acquisition of sugars or other resources and the lack of selective pressure increases the rate of evolution on those genes (Barrett & Freudenstein 2008, Bromham et al. 2013, Lemaire et al. 2011, Wicke et al. 2014). Selective pressure can also become less stringent by intracellular gene transfer, gene duplications and also by whole genome duplications. The mutation rate increases often in these transferred genes or duplicated parts (Brunet et al. 2006, Mower et al. 2004).

Any of these examples are unlikely to be the cause of the difference in the rate of evolution in Annonoideae and Malmeoideae as these differences are visible in both the chloroplast and the nuclear genome as well as in the introns and spacers (chapter 2, Hoekstra et al. 2017). However there is an indication of different levels of selection pressure between the Annonoideae and Malmeoideae as the ratio of nonsynonymous versus synonymous substitutions is higher in the Annonoideae than in the Malmeoideae (a pattern not found by Chatrou et al. 2014). Small effective population sizes could cause a pattern like this. According to the nearly neutral theory of evolution, slightly deleterious mutations have a higher chance of getting fixed in groups with a small effective population size (Ohta 1992). Therefore, the rate of evolution and the omega-ratio, i.e. nonsynonymous substitutions divided by the synonymous substitutions, is higher in groups with smaller effective population sizes.

It is difficult to test whether small effective population sizes have been the cause of evolutionary rate differences between the two major subfamilies of Annonaceae. The current population sizes of the different species of Annonaceae are hardly known. For example, the recently described *Monanthotaxis sterilis* is actually quite common within its range (Hoekstra et al. 2021), while several other species have only been collected once in history and it is unknown if they still exist and how big their populations are (e.g. Hoekstra et al. 2016, Hoekstra et al. 2021). Furthermore, even if the current population sizes would be known, the more important effective population sizes of the past would remain unknown. With phylogenetic methods and population genetics it is possible to estimate past population sizes and bottlenecks (Schrider & Kern 2018, Urquía et al. 2019), but this would be limited in detecting the most recent population bottleneck. In the evolutionary history of a subfamily

such as the Annonoideae there could as well have been multiple bottlenecks in any species and ancestral species during the millions of years of evolution.

Although it is generally not possible to test whether small population sizes have caused the elevated rate of evolution in a group, there are several ways to indirectly study this effect. In several groups with a small effective population size an elevated rate of evolution has been detected. For example, endosymbiotic bacteria go through a population bottleneck when switching host and therefore have a small effective population size. It was shown that their rate of evolution is higher than those of their nearest free-living species (Moran 1996, Woolfit & Bromham 2003). In a comparison between island species and their continental sister species also an elevated amount of non-synonymous substitutions compared to the synonymous substitutions was found, although the overall rate of evolution was not significant higher in the island species (Woolfit & Bromham 2005). A direct way to study the effect of small population sizes on the rate of evolution would be to use a long-term study of DNA-exchanging bacterial colonies or sexually reproducing fungi in which the colonies are regularly subdivided and the populations kept small. If from the beginning one subpopulation is kept on a huge and continuous size than this group should have a lower rate of evolution and a lower amount of non-synonymous substitutions compared to the small and regularly subdivided populations.

An unexpected and exciting finding of chapter 2 was that the subfamily Annonoideae had a wide range in chloroplast genome size while the Malmeoideae had a smaller range of sizes, chloroplast genome sizes similar to most other angiosperms. An interesting question is if this variance in chloroplast genome size has the same origin as the elevated rate of evolution in Annonoideae. In most angiosperms, chloroplast genome size is around 150 kb and consists of a large single copy, a short single copy and an inverted repeat (IR). Variations in the chloroplast genome size are generally caused by variations in the IR size. The exact function of the IR remains unknown, one of the hypotheses is that the IR plays a role in maintaining plastome structural integrity and in replication initiation. However targeted inactivation of the IR has proven that the IR is not essential for these functions (Scharff & Koop 2007). Both copies of the IR also are assumed to have identical sequences, the IR could therefore function in a DNA repair mechanism to homogenize the sequences. Generally the IR has a lower rate of evolution than the single copies (Perry & Wolfe 2002). It should therefore be expected that species with a larger IR should have a lower substitution rate, however in Annonaceae this is not the case, the Annonoideae with larger IRs have higher substitution rates than the Malmeoideae with normal IR sizes. To further study this pattern in Annonaceae it would be best to better understand the IR, its function and its role in the rate of mutations of the cpDNA. The chloroplast genome generally occurs in linear or branched patterns and rarely in a circular form (Oldenburg & Bendich 2015). It would be interesting to study the effect of these shapes and genome stability with artificially shortening or lengthening the IR. With current

developments in CRISPR/Cas techniques (Cui et al. 2018) this should be possible or at least in the near future.

6.3 Species diversification and speciation

Understanding species diversity is an important step in protecting biodiversity. Species diversity is correlated with many factors such as latitude, altitude and area. In general, effects of the past have caused current species diversity. Species diversification is one of the main processes that have shaped current species diversity and which will shape the species diversity of the future. There are many processes which affect species diversification, such as the rate of evolution, processes at the population level and ecological processes such as niche specialisation.

Species diversification has often been correlated with the rate of evolution (Barraclough et al. 1996, Bromham et al. 2015, Duchene & Bromham 2013). The potential underlying mechanisms for this correlation have been reviewed in Hua & Bromham (2017), but in short an increase in the substitution rate could reduce the time to form reproductive isolation between two populations. And a reduced time to reproductive isolation between populations will lead to an increased rate of speciation. Reproductive isolation could be formed by prezygotic isolation (e.g. Quinn et al. 2000) or by postzygotic isolation through Dobzhansky-Muller incompatibilities (Presgraves 2010).

A different possibility is that an increase in speciation causes an increase in the molecular rate of evolution (Venditti & Pagel 2010). However, evidence against this causation is that one would not expect a genome-wide increase in the rate of evolution, but only an increase in the rate of evolution in genes involved in speciation. Furthermore, an increase in speciation could generate smaller populations, but in smaller populations an increase in nearly neutral substitutions would be expected and an increase in non-synonymous substitutions compared to synonymous substitutions have been observed in smaller populations compared to larger populations (Woolfit & Bromham 2005), while the correlation between the rate of evolution and species diversification is genome-wide including in synonymous substitutions (Bromham et al. 2015, Duchene & Bromham 2013, Lanfear et al. 2010).

A third possibility could be that the correlation between the rate of evolution and species diversification is coincidental as both factors could be linked to a different factor. For example, both the rate of evolution and species diversification have been correlated to environmental energy, measured as temperature, evapotranspiration and UV radiation (Davies et al. 2004). Also it should be noted that the correlation between species diversity and the rate of evolution has not been found in all phylogenies and appears to be absent in mammals (Goldie et al. 2011, Webster et al. 2003).

The subfamily Annonoideae has a higher rate of evolution than the subfamily Malmeoideae (chapter 2) and indeed the subfamily Annonoideae contains almost twice as many species than the Malmeoideae, suggestive of the correlation between species diversification and rate of evolution. The genus *Monanthotaxis* is one of the more species-rich genera in the family Annonaceae and the second-most species-rich genus of the family in Tropical Africa (chapter 4). However, it is unclear whether the genus has a higher rate of evolution than less species-rich and closely-related genera such as *Sphaerocoryne*, *Afroguatteria* and Asiatic genera such as *Dasymaschalon* and *Desmos*. Actually the most species-rich genus of Annonaceae in Africa and Asia is the genus *Uvaria* which belongs to the same tribe as *Monanthotaxis* (chapter 4, Hoekstra et al. 2021). Only three species of the tribe Uvarieae were included in the study of the rate of evolution in the family Annonaceae (chapter 2, Hoekstra et al. 2017) which is insufficient to say anything about the rate of evolution within the tribe Uvarieae. In chapter 3 (Guo et al. 2017) a wider array of species of the tribe Uvarieae were included in a phylogeny. However, the rate of evolution was not studied in that chapter and also insufficient sequences per species were included to make better substantiated claims about rates of evolution. A quick glance on the phylogeny does not indicate an elevated rate of evolution for *Monanthotaxis* compared to its sister genera and there is even a slight indication that the smaller genus *Desmos* could have a higher rate of evolution as indicated by the slightly longer branch lengths of some taxa (chapter 3, Guo et al. 2017).

Species diversification rate is the rate of speciation minus the rate of extinction. Speciation occurs most often after geographic isolation, i.e. allopatric speciation, or after ecological divergence. Hernandez et al. (2021) checked for the geographic mode of speciation in 622 plant species sister pairs. They found that 30% of the sister pairs occur allopatrically, 18 fully sympatric and the rest partially sympatric, which might suggest that allopatric speciation is the most common mode in plants. In the African Annonaceae genera *Isolona* and *Monodora* most species sister pairs have an allopatric distribution and very little ecological divergence was found between the sister pairs, suggesting that a geographic mode of speciation is the most important in these genera (Couvreur et al. 2011).

In the genus *Monanthotaxis* the geographic mode of speciation has not been studied. However, this thesis provides the fundaments for the study of the evolution and diversification of this clade. In chapter 4 the taxonomy of the continental species of *Monanthotaxis* has been revised, and in chapter 3 and chapter 5 phylogenetic relationships of most species of *Monanthotaxis* were inferred. Phylogenetic hypotheses suggest that several sister species have disjunct distributions, for example *Monanthotaxis discrepantinervia* from Tanzania and *M. atewensis* from Ghana, however some other sister pairs occur at least in a part of their distribution in sympatry, of these *Monanthotaxis ferruginea* and *M. bokoli* have even been found in the same area. Most tropical rainforests in Africa contain multiple sympatric species of *Monanthotaxis*. It looks like in most places these sympatric species belong to different

clades of the genus. For example, the species of *Monanthotaxis* in Gabon belong to 9 of the 11 clades defined in chapter 5. Therefore, it appears that both sympatric and allopatric speciation could have been important in the diversification of *Monanthotaxis.*

In several parts of the world ecological divergence has been found in the majority of plant species sister pairs with as major differences between them shifts in habitat, pollinators, soil type and flower size (Anacker & Strauss 2014, Niet & Johnson 2009). Pollination is considered as very important in ecological speciation and plays an important role in creating reproductive isolation (Waser & Campbell 2004). Hernández-Hernández and Wiens (2020) found that biotically mediated pollination explained most variation in diversification rates in flowering plants. Considering all this, *Monanthotaxis* could potentially be a key model to study species diversification and speciation of tropical rain forests. In chapter 5 (Hoekstra et al. 2018) the floral evolution of *Monanthotaxis* was studied and the genus displays a wide variety in floral morphology with large flowers containing many stamens and carpels to small flowers with only 3 stamen. One possibility for this variation in floral morphology are shifts in pollination strategies.

Very little is known about pollination of Annonaceae in Africa and hardly anything is known about pollination of *Monanthotaxis*. To understand more about the evolution and diversification of the diverse tropical genus *Monanthotaxis*, the highest priority should be to study the pollination of the genus. It seems highly unlikely that a species such as *M. diclina*, which has male flowers on leafy branches in the canopy and female flowers on the trunks in the forest understorey, has the same pollination strategy as a species such as *M. obovata* which has bisexual flowers near the tip of the branches and occurs in open woodland. Like this there are many other issues, such as the occurrence of staminodes in some species, which could potentially be answered if observations and tests on pollination would be available for the genus *Monanthotaxis*.

6.4 Taxonomy and taxonomists

Taxonomy, the science of recognizing and delimiting species, is one of the corner stones in biology. Well-defined and taxonomic delimited species and the proper use of nomenclature are vital for the good communication and reproducibility of science (Bennett & Balick 2014). The malaria mosquitos (*Anopheles maculipennis* complex) are a well-known example of a species complex in which an improved taxonomy helped to understand the distribution and spread of malaria. The distribution of *Anopheles maculipennis* Meigen, 1818 did not match the distribution of malaria. Also in some areas of their distribution the mosquitos often attacked humans, while in other areas they only suck blood of animals. Several studies proved *A. maculipennis* is not a single species but consists of several cryptic species (Becker et al. 2010).

Several species of the genus *Monanthotaxis* are being used locally against malaria (Asase et al. 2005, Mungai 2015, Rasoanaivo et al. 1992) and extracts of the species of *M. kenyensis* indeed have antiplasmodial effects on malaria (Mungai et al. 2014, Mungai 2015). In recent years, the number of studies researching phytochemical constituents of *Monanthotaxis* has been increasing (see Hoekstra et al. 2021 and refs therein) showing the need of the revision of *Monanthotaxis*. For example in the study on the antiplasmodial effect of *Monanthotaxis kenyensis*, this species has been in that time correctly named *Monanthotaxis parvifolia* subsp. *kenyensis*. However, in the revision this subspecies has been raised to species level as it is not the closest relative of *Monanthotaxis parvifolia*. It is doubtful whether this species will be correctly cited in malaria research as *M. kenyensis* as researchers often refer to it as *Monanthotaxis parvifolia* instead of *M. parvifolia* subsp. *kenyensis* (e.g. Laryea & Borquaye 2019). Similarly a *Monanthotaxis* species is locally used against malaria in Ghana, but the specimens could first not be identified to species level (Asase et al. 2005) and afterwards have been referred to as *Monanthotaxis caffra* (Laryea & Borquaye 2019). However, *M. caffra* does not occur in Ghana, only in South Africa and Swaziland, and thus the correct identity of the medicinal *Monanthotaxis* from Ghana remains unknown. Hopefully in the future these identification errors will not occur anymore thanks to the revision of *Monanthotaxis* (Hoekstra et al. 2021).

Together with ecology, systematics is one of the fundamental sciences generating knowledge about biodiversity (Kim & Byrne 2006). To be able to protect biodiversity it must be known which species exist. Currently around 2 million species have been described (Bánki et al. 2021), and in this thesis 23 species have been added to that number (Hoekstra et al. 2014, Hoekstra et al. 2016, Hoekstra et al. 2021). The total number of species in the world remains unknown and estimates vary from slightly less than 2 million (Costello et al. 2011) to up to a trillion species (Locey & Lennon 2016). The higher estimates differ mostly from the lower estimates in the number of bacteria and microbes (Larsen et al. 2017, Locey & Lennon 2016). But even in more well-known groups as the higher plants still many species are waiting to be described. Even after the revision of *Monanthotaxis* there are still several specimens belonging to this genus which cannot be assigned to any of the known species (Hoekstra et al. 2021). More collections of flowering material from the tropical rainforests of Africa will most certainly lead to additional new species.

Extinction rates are rapidly accelerating (Ceballos et al. 2015) and many species will be extinct before even being described (Mora et al. 2013). Almost all countries in the world have signed the convention on biological diversity which acknowledges the importance of taxonomy for the protection and knowledge of biodiversity. They started the global taxonomy initiative, which makes plans to stop the taxonomic impediment or at least reduce it.

Technological advances in the last decades have greatly helped taxonomists. The digitalisation of herbarium specimens and online availability of literature and database with names and

synonyms have speeded up the work of taxonomists. The advancements in molecular technologies also are of great help in defining and delimiting taxa. For example, all collections of *Monanthotaxis sterilis* till now are sterile. These specimens could not have been ascribed with certainty to the genus *Monanthotaxis* without the DNA sequences (Hoekstra et al. 2021, Hoekstra et al. 2018).

Despite all these advances in technologies the number of annually described species has remained more or less constant over the last 20 years, while the number of authors describing new species has increased (Christenhusz & Byng 2016, Joppa et al. 2011). However it is generally agreed that this speed is not high enough to describe the majority before they get extinct.

In the Netherlands, a clear decline in the number of professional taxonomists can be seen in the last 20 years with circa 15 FTEs of plant taxonomists in three different universities in 2000 down to around 10 FTEs in 2010 and only ca 2.5 FTEs in one institute in 2021 (pers. comm. J. Wieringa & P. Maas). In many other countries a similar pattern can be seen. Fortunately there are several countries in biodiverse regions, such as Mexico, India and Brazil, in which the number of professional taxonomist is increasing (Zhang et al. 2014). Already in the nineties an unevenly distribution of taxonomists over the earth was reported with most taxonomists in Europe and North America (Gaston & May 1992). In my opinion, the number of taxonomists should be increased globally to battle the taxonomic impediment. Local endemic species groups for example a genus endemic to Brazil could best be revised in an institute in the country of origin. But continental or pantropical species groups could best be revised in institutes which have large collections of most species across countries and which have facilities for researchers to visit or loan specimens from other herbaria. For example, of the species of *Monanthotaxis* described new to science in this thesis, at least one specimen was present for 20 of the 23 species in the herbarium of Naturalis, making Naturalis the most cost-efficient herbarium in the world to revise the genus *Monanthotaxis*.

Herbaria around the world still contain many undescribed species on their shelves and some estimate that even a half of undescribed plant species already have been collected and are awaiting in herbaria to be described (Bebber et al. 2010). For the genus *Monanthotaxis* the newly described species in this thesis already had been collected for the first time approximately around 40 years ago. For more well-studied groups, such as amphibians, the limiting factor for describing new taxa is field work in the more remote areas (Dubois et al. 2021). Within plants there are many genera, especially the large more speciose genera which have not been revised in more than a 100 years, for which a revision with only herbarium material will suffice to learn much more about the worlds biodiversity. However in the recently revised taxa, such as *Monanthotaxis*, the limiting factor for describing new taxa is field work. Well-trained field botanist which have access to a herbaria with well-identified

specimens tend to collect much more rare, endangered and new plant taxa than unexperienced field botanists (Ahrends et al. 2011).

Besides the global taxonomy initiative there are several initiatives to battle the taxonomic impediment. The CETAF is a consortium of European museums, botanic gardens and biodiversity research centres which hold biological and geological collections. They have as their mission to explore and document the diversity in nature and make their collections available for research. They are developing taxonomic training and e-learning capacity (Price 2014). Another initiative is the World Flora Online, which is an effort to build an online flora of all known plants in the world (Borsch et al. 2020). Besides these there are many more projects which aim at disseminating taxonomic knowledge and improving technologies, but as Engel et al. (2021) state “the main problem of the taxonomic impediment is a shortage of taxonomists, not the lack of technical approaches”. Hopefully the tides will turn and new species will be described in an accelerated pace before they get extinct or potentially can even be protected and prevented from extinction.

References

Achenbach H, Hemrich H. 1991. Alkaloids, flavonoids and phenylpropanoids of the west African plant Oxymitra velutina. Phytochemistry 30: 1265–1267.

Adams KL, Qiu YL, Stoutemyer M, Palmer JD. 2002. Punctuated evolution of mitochondrial gene content: high and variable rates of mitochondrial gene loss and transfer during angiosperm evolution. Proc Natl Acad Sci USA 99.

Ahrends A, Rahbek C, Bulling MT, Burgess ND, Platts PJ, Lovett JC, Kindemba VW, Owen N, Sallu AN, Marshall AR, Mhoro BE, Fanning E, Marchant R. 2011. Conservation and the botanist effect. Biological Conservation 144: 131-140.

Aleman JC, Jarzyna MA, Staver AC. 2018. Forest extent and deforestation in tropical Africa since 1900. Nature Ecology & Evolution 2: 26-33.

Álvarez I, Wendel JF. 2003. Ribosomal ITS sequences and plant phylogenetic inference. Molecular Phylogenetics and Evolution 29: 417-434.

Anacker BL, Strauss SY. 2014. The geography and ecology of plant speciation: range overlap and niche divergence in sister species. Proceedings of the Royal Society B: Biological Sciences 281: 20132980.

Andreasen K, Baldwin BG. 2001. Unequal evolutionary rates between annual and perennial lineages of checker mallows (*Sidalcea*, Malvaceae): Evidence from 18S–26S rDNA internal and external transcribed spacers. Molecular Biology and Evolution 18: 936-944.

Appanah S, Gentry AH, LaFrankie JV. 1993. Liana diversity and species richness of Malaysian rain forests. Journal of Tropical Forest Science 6: 116-123.

Arber EAN, Parkin J. 1907. On the origin of angiosperms. Journal of the Linnean Society of London, Botany 38: 29-80.

Arroyo-Rodríguez V, Asensio N, Dunn JC, Cristóbal-Azkarate J, Gonzalez-Zamora A. 2015. Use of lianas by primates: more than a food source. In: Schnitzer SA, Bongers F, Burnham RJ, Putz FE (eds), Ecology of lianas: 407–426. John Wiley & Sons, Chichester.

Asase A, Oteng-Yeboah AA, Odamtten GT, Simmonds MSJ. 2005. Ethnobotanical study of some Ghanaian anti-malarial plants. Journal of Ethnopharmacology 99: 273–279.

Bachman S, Moat J, Hill A, de la Torre J, Scott B. 2011. Supporting Red List threat assessments with GeoCAT: geospatial conservation assessment tool. ZooKeys 150: 117–126.

Baele G, Lemey P, Bedford T, Rambaut A, Suchard MA, Alekseyenko AV. 2012. Improving the accuracy of demographic and molecular clock model comparison while accommodating phylogenetic uncertainty. Molecular Biology and Evolution 29: 2157-2167.

Bagshawe AG, Baker EG. 1908. Uganda Annonaceae. Journal of Botany 46: 219–222.

Baillon H. 1868. Mémoires sur la famille des Annonacées. Adansonia 8: 295–344.

Baillon H. 1890. Observations sur quelques nouveaux types du Congo. Bulletin Mensuel de la Société Linnéenne de Paris 1: 876–879.

Baker EG. 1913. Flowering plants Dicotyledons Polypetalae. Annonaceae. In: Rendle AB, Baker EG, Wernham HF (eds), Catalogue of the Plants collected by Mr. & Mrs. P. A. Talbot in the Oban District South Nigeria. Order of the Trustees of the British Museum, London.

Baker JG, Moore SM. 1877. Descriptive notes on a few of Hildebrandt's East African plants. Journal of Botany 15: 65–72.

Bakker FT, Lei D, Yu J, Mohammadin S, Wei Z, van de Kerke S, Gravendeel B, Nieuwenhuis M, Staats M, Alquezar-Planas DE, Holmer R. 2016. Herbarium genomics: plastome sequence assembly from a range of herbarium specimens using an Iterative Organelle Genome Assembly pipeline. Biological Journal of the Linnean Society of London 117: 33-43.

Ball HW, Exell AW, Harding JP, et al. 1962. Systematics association committee for descriptive biological terminology. II. Terminology of simple symmetrical plane shapes (Chart 1). Taxon 11(5): 145–156.

Bankevich A, Nurk S, Antipov D, Gurevich AA, Dvorkin M, Kulikov AS, Lesin VM, Nikolenko SI, Pham S, Prjibelski AD, Pyshkin AV, Sirotkin AV, Vyahhi N, Tesler G, Alekseyev MA, Pevzner PA. 2012. SPAdes: A new genome assembly algorithm and its applications to single-cell sequencing. Journal of Computational Biology 19: 455-477.

Bánki O, Roskov Y, Vandepitte L, DeWalt RE, Remsen D, Schalk P, Orrell T, Keping M, Miller J, Aalbu R, Adlard R, Adriaenssens E, Aedo C, Aescht E, Akkari N, Alonso-Zarazaga MA, Alvarez B, Alvarez F, Anderson G, et. al. 2021. Catalogue of Life Checklist (Version 2021-10-18). Catalogue of Life. Last accessed 2021-11-06 2021.

Barraclough TG, Harvey PH, Nee S. 1996. Rate of rbcL gene sequence evolution and species diversification in flowering plants (Angiosperms). Proceedings: Biological Sciences 263: 589-591.

Barrett CF, Freudenstein JV. 2008. Molecular evolution of rbcL in the mycoheterotrophic coralroot orchids (*Corallorhiza* Gagnebin, Orchidaceae). Molecular phylogenetics and evolution 47: 665-679.

Beaulieu JM, O'Meara BC, Crane P, Donoghue MJ. 2015. Heterogeneous rates of molecular evolution and diversification could explain the Triassic age estimate for angiosperms. Systematic Biology 64: 869-878.

Bebber DP, Carine MA, Wood JRI, Wortley AH, Harris DJ, Prance GT, Davidse G, Paige J, Pennington TD, Robson NKB, Scotland RW. 2010. Herbaria are a major frontier for species discovery. Proceedings of the National Academy of Sciences of the United States of America 107: 22169-22171.

Becker N, Petric D, Zgomba M, Boase C, Madon M, Dahl C, Kaiser A. 2010. Mosquitoes and their control. Springer Science & Business Media.

Belfield EJ, Brown C, Ding ZJ, Chapman L, Luo M, Hinde E, van Es SW, Johnson S, Ning Y, Zheng SJ, Mithani A, Harberd NP. 2021. Thermal stress accelerates *Arabidopsis thaliana* mutation rate. Genome Research 31: 40-50.

Bengtsson-Palme J, Ryberg M, Hartmann M, Branco S, Wang Z, Godhe A, De Wit P, Sánchez-García M, Ebersberger I, de Sousa F, Amend A, Jumpponen A, Unterseher M, Kristiansson E, Abarenkov K, Bertrand YJK, Sanli K, Eriksson KM, Vik U, Veldre V, Nilsson RH. 2013. Improved software detection and extraction of ITS1 and ITS2 from ribosomal ITS sequences of fungi and other eukaryotes for analysis of environmental sequencing data. Methods in Ecology and Evolution 4: 914-919.

Benjamini Y, Hochberg Y. 1995. Controlling the false discovery rate: A practical and powerful approach to multiple testing. Journal of the Royal Statistical Society. Series B (Methodological) 57: 289-300.

Bennett BC, Balick MJ. 2014. Does the name really matter? The importance of botanical nomenclature and plant taxonomy in biomedical research. Journal of Ethnopharmacology 152: 387-392.

Bentham G. 1862. On African Annonaceae. Transactions of the Linnean Society of London 23: 463–480.

Bentham G, Hooker JD. 1862. Genera plantarum 1. A. Black, Londini.

Birky CW, Walsh JB. 1992. Biased gene conversion, copy number, and apparent mutation rate differences within chloroplast and bacterial genomes. Genetics 130: 677-683.

Birky CWJ. 2001. The inheritance of genes in mitochondria and chloroplasts: laws, mechanisms, and models. Annual Review of Genetics 35: 125-148.

Blazier JC, Ruhlman TA, Weng M-L, Rehman SK, Sabir JSM, Jansen RK. 2016. Divergence of RNA polymerase α subunits in angiosperm plastid genomes is mediated by genomic rearrangement. Scientific Reports 6: 24595.

Boesch P, Weber-Lotfi F, Ibrahim N, Tarasenko V, Cosset A, Paulus F, Lightowlers RN, Dietrich A. 2011. DNA repair in organelles: Pathways, organization, regulation, relevance in disease and aging. Biochimica et Biophysica Acta (BBA) - Molecular Cell Research 1813: 186-200.

Bofkin L, Goldman N. 2007. Variation in evolutionary processes at different codon positions. Molecular Biology and Evolution 24: 513-521.

Bolger AM, Lohse M, Usadel B. 2014. Trimmomatic: a flexible trimmer for Illumina sequence data. Bioinformatics 30: 2114-2120.

Bollen A. 2007. Fruit characteristics: fruit selection, animal seed dispersal and conservation matters in the Sainte Luce forests. In: Ganzhorn J, Goodman S, Vincelette M (eds.), Biodiversity, Ecology, and Conservation of Littoral Ecosystems in the Region of Tolagnaro (Fort Dauphin), Southeastern Madagascar: 127–145. Smithsonian Institute, Washington DC.

Borchsenius F. 2009. FastGap 1.2. Department of Biosciences, Aarhus University http://www.aubot.dk/FastGap_home.htm. Last.

Borsch T, Berendsohn W, Dalcin E, Delmas M, Demissew S, Elliott A, Fritsch P, Fuchs A, Geltman D, Güner A, Haevermans T, Knapp S, le Roux MM, Loizeau P-A, Miller C, Miller J, Miller JT, Palese R, Paton A, Parnell J, Pendry C, Qin H-N, Sosa V, Sosef M, von Raab-Straube E, Ranwashe F, Raz L, Salimov R, Smets E, Thiers B, Thomas W, Tulig M, Ulate W, Ung V, Watson M, Jackson PW, Zamora N. 2020. World Flora Online: Placing taxonomists at the heart of a definitive and comprehensive global resource on the world's plants. TAXON 69: 1311-1341.

Botermans M, Sosef MSM, Chatrou LW, Couvreur TLP. 2011. Revision of the African genus *Hexalobus* (Annonaceae). Systematic Botany 36: 33–48.

Boutique R. 1951a. Annonaceae. In: Robyns W, Staner P, Demaret F, Germain R, Gilbert G, Hauman L, Homès M, Jurion F, Lebrun J, Vanden Abeele M, Boutique Rs (eds.), Flore du Congo belge et du Ruanda-Urundi. Spermatophytes: 256–389. Bruxelles.

Boutique R. 1951b. Annonacées nouvelles de la flore du Congo Belge et du Ruanda-Urundi. Bulletin du Jardin botanique de l'Etat, Bruxelles/Bulletin van den Rijksplantentuin, Brussel 21: 95–126.

Britt AB. 1996. DNA damage and repair in plants. Annual Review of Plant Physiology and Plant Molecular Biology 47: 75-100.

Britten R. 1986. Rates of DNA sequence evolution differ between taxonomic groups. Science 231: 1393-1398.

Bromham L, Cowman PF, Lanfear R. 2013. Parasitic plants have increased rates of molecular evolution across all three genomes. BMC Evolutionary Biology 13: 126.

Bromham L, Hua X, Lanfear R, Cowman PF. 2015. Exploring the relationships between mutation rates, life history, genome size, environment, and species richness in flowering plants. The American Naturalist 185: 507-524.

Bromham L, Penny D. 2003. The modern molecular clock. Nature Reviews Genetics 4: 216-224.

Brooks DR, Bilewitch J, Condy C, Evans DC, Folinsbee KE, Fröbisch J, Halas D, Hill S, McLennan DA, Mattern M, Tsuji LA, Ward JL, Wahlberg N, Zamparo D, Zanatta D. 2007. Quantitative phylogenetic analysis in the 21st Century. Revista Mexicana de Biodiversidad 78: 225-252.

Brown JM, Hedtke SM, Lemmon AR, Lemmon EM. 2010. When trees grow too long: Investigating the causes of highly inaccurate bayesian branch-length estimates. Systematic Biology 59: 145-161.

Brunet FdrG, Crollius HR, Paris M, Aury J-M, Gibert P, Jaillon O, Laudet V, Robinson-Rechavi M. 2006. Gene loss and evolutionary rates following whole-genome duplication in teleost fishes. Molecular Biology and Evolution 23: 1808-1816.

Brutlag D, Kornberg A. 1972. Enzymatic synthesis of deoxyribonucleic acid: XXXVI. A proofreading function for the 3′ → 5′ exonuclease activity in deoxyribonucleic acid polymerases. Journal of Biological Chemistry 247: 241-248.

Buckler ES, IV, Ippolito A, Holtsford TP. 1997. The evolution of ribosomal DNA divergent paralogues and phylogenetic implications. Genetics 145: 821-832.

Buckley TR, Cordeiro M, Marshall DC, Simon C. 2006. Differentiating between hypotheses of lineage sorting and introgression in New Zealand Alpine Cicadas (*Maoricicada* Dugdale). Systematic Biology 55: 411-425.

Bygrave PC. 2000. Molecular systematics of the Annonaceae Juss. University of Reading Reading, UK.

Cai Z, Penaflor C, Kuehl JV, Leebens-Mack J, Carlson JE, dePamphilis CW, Boore JL, Jansen RK. 2006. Complete plastid genome sequences of *Drimys*, *Liriodendron*, and *Piper*: implications for the phylogenetic relationships of magnoliids. BMC Evolutionary Biology 6: 77.

Camus E-G, Camus A. 1913. Sur une plante a parfum de l'Afrique Occidentale: Le *Popowia Capea*. Bulletin Scientifique et Industriel de la maison Roure-Bertrand fils de grasse 3: 1–17.

Cardoso D, Särkinen T, Alexander S, Amorim AM, Bittrich V, Celis M, Daly DC, Fiaschi P, Funk VA, Giacomin LL, Goldenberg R, Heiden G, Iganci J, Kelloff CL, Knapp S, Cavalcante de Lima H, Machado AFP, dos Santos RM, Mello-Silva R, Michelangeli FA, Mitchell J, Moonlight P, de Moraes PLR, Mori SA, Nunes TS, Pennington TD, Pirani JR, Prance GT, de Queiroz LP, Rapini A, Riina R, Rincon CAV, Roque N, Shimizu G, Sobral M, Stehmann JR, Stevens WD, Taylor CM, Trovó M, van den Berg C, van der Werff H, Viana PL, Zartman CE, Forzza RC. 2017. Amazon plant diversity revealed by a taxonomically verified species list. Proceedings of the National Academy of Sciences 114: 10695-10700.

Castresana J. 2000. Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. Molecular Biology and Evolution 17: 540-552.

Cavaco A, Keraudren M. 1958. Famille - Annonacées. In: Humbert H (ed), Flore de Madagascar et des Comores 78: 1–109. Typographie Firmin-Didot et Cie., Paris.

Ceballos G, Ehrlich PR, Barnosky AD, García A, Pringle RM, Palmer TM. 2015. Accelerated modern human–induced species losses: Entering the sixth mass extinction. Science Advances 1: e1400253.

Chaowasku T, Johnson DM, Van der Ham RW, Chatrou LW. 2012. Characterization of *Hubera* (Annonaceae), a new genus segregated from *Polyalthia* and allied to *Miliusa*. Phytotaxa 69: 33–56.

Chaowasku T, Thomas DC, van der Ham RWJM, Smets EF, Mols JB, Chatrou LW. 2014. A plastid DNA phylogeny of tribe Miliuseae: Insights into relationships and character evolution in one of the most recalcitrant major clades of Annonaceae. American Journal of Botany 101: 691-709.

Charlesworth D. 1993. Why are unisexual flowers associated with wind pollination and unspecialized pollinators? The American Naturalist 141: 481-490.

Chatelain C, Gautier L, Spichiger R. 1996. A recent history of forest fragmentation in southwestern Ivory Coast. Biodiversity & Conservation 5: 37–53.

Chatrou LW. 1998. Changing genera. Systematic studies in Neotropical and West African Annonaceae. Utrecht Herbarium Division, Utrecht.

Chatrou LW, Escribano MP, Viruel MA, Maas JW, Richardson JE, Hormaza JI. 2009. Flanking regions of monomorphic microsatellite loci provide a new source of data for plant species-level phylogenetics. Molecular Phylogenetics and Evolution 53: 726–733.

Chatrou LW, Koek-Noorman J, Maas PJM. 2000. Studies in Annonaceae XXXVI. The *Duguetia* alliance: Where the ways part. Annals of the Missouri Botanical Garden 87: 234–245.

Chatrou LW, Pirie MD, Erkens RHJ, Couvreur TLP, Neubig KM, Abbott JR, Mols JB, Maas JW, Saunders RMK, Chase MW. 2012. A new subfamilial and tribal classification of the pantropical flowering plant family Annonaceae informed by molecular phylogenetics. Botanical Journal of the Linnean Society 169: 5–40.

Chatrou LW, Pirie MD, van Velzen R, Bakker FT. 2014. Annonaceae substitution rates: a codon model perspective. Revista Brasileira de Fruticultura 36: 108-117.

Chatrou LW, Turner IM, Klitgaard BB, Maas PJM, Utteridge TMA. 2018. A linear sequence to facilitate curation of herbarium specimens of Annonaceae. Kew Bulletin 73: 39.

Chevalier A. 1920. Exploration botanique de l'Afrique occidentale française: 5–16. P. Lechevallier, Paris.

Chipp TF. 1923. Diagnoses Africanae: LXXVII. Bulletin of Miscellaneous Information (Royal Gardens, Kew) 1923: 180–185.

Choi CW, Song SB, Oh JS, Kim YH. 2015. Antiproliferation effects of selected Tanzania plants. African Journal of Traditional, Complementary and Alternative Medicines 12: 96–102.

Christenhusz MJ, Byng JW. 2016. The number of known plants species in the world and its annual increase. Phytotaxa 261: 201-217.

Clara C, Matasyoh JC, Wagara IN, Nakavuma J. 2014. Antifungal activity of flavonoids isolated from *Monanthotaxis littoralis* against mycotoxigenic fungi from maize. American Journal of Chemistry and Application 1: 54–60.

Clark S, Egan R, Frazier PI, Wang Z. 2013. ALE: a generic assembly likelihood evaluation framework for assessing the accuracy of genome and metagenome assemblies. Bioinformatics 29: 435-443.

Costello MJ, Wilson S, Houlding B. 2011. Predicting total global species richness using rates of species description and estimates of taxonomic effort. Systematic Biology 61: 871-871.

Couvreur TLP. 2009. Monograph of the syncarpous African genera *Isolona* and *Monodora* (Annonaceae). Systematic Botany Monographs 87: 1–150.

Couvreur TLP. 2014. Revision of the African genus *Uvariastrum* (Annonaceae). PhytoKeys 33: 1–40.

Couvreur TLP, Chatrou LW, Sosef MS, Richardson JE. 2008. Molecular phylogenetics reveal multiple tertiary vicariance origins of the African rain forest trees. BMC Biology 6: 54, doi:10.1186/1741-7007-6-54.

Couvreur TLP, Helmstetter AJ, Koenen EJM, Bethune K, Brandão RD, Little SA, Sauquet H, Erkens RHJ. 2019. Phylogenomics of the major tropical plant family Annonaceae using targeted enrichment of nuclear genes. Frontiers in Plant Science 9.

Couvreur TLP, Maas PJM, Meinke S, Johnson DM, Keßler P. 2012. Keys to the genera of Annonaceae. Botanical Journal of the Linnean Society 169: 74–83.

Couvreur TLP, Niangadouma R, Sonké B, Sauquet H. 2015. *Sirdavidia*, an extraordinary new genus of Annonaceae from Gabon. PhytoKeys 46: 1–19.

Couvreur TLP, Pirie MD, Chatrou LW, Saunders RMK, Su YCF, Richardson JE, Erkens RHJ. 2011a. Early evolutionary history of the flowering plant family Annonaceae: steady diversification and boreotropical geodispersal. Journal of Biogeography 38: 664–680.

Couvreur TLP, Porter-Morgan H, Wieringa JJ, Chatrou LW. 2011b. Little ecological divergence associated with speciation in two African rain forest tree genera. BMC Evolutionary Biology 11: 296.

Couvreur TLP, Richardson JE, Sosef MSM, Erkens RHJ, Chatrou LW. 2008. Evolution of syncarpy and other morphological characters in African Annonaceae: A posterior mapping approach. Molecular Phylogenetics and Evolution 47: 302-318.

Cruden RW. 1977. Pollen-ovule ratios: A conservative indicator of breeding systems in flowering plants. Evolution 31: 32-46.

Cui Y, Xu J, Cheng M, Liao X, Peng S. 2018. Review of CRISPR/Cas9 sgRNA design tools. Interdisciplinary Sciences: Computational Life Sciences 10: 455-465.

Darling AE, Mau B, Perna NT. 2010. ProgressiveMauve: multiple genome alignment with gene gain, loss and rearrangement. PloS one 5: e11147.

Davies TJ, Savolainen V, Chase MW, Moat J, Barraclough TG. 2004. Environmental energy and evolutionary rates in flowering plants. Proceedings of the Royal Society of London. Series B: Biological Sciences 271: 2195-2200.

De Wildeman E. 1905a. Études de systématique et de géographie botaniques sur la flore du Bas- et du Moyen-Congo. Annales du Musée du Congo 1.: 213–329.

De Wildeman E. 1905b. Mission Émile Laurent. Imprimerie F. van Buggenhoudt, Bruxelles.

De Wildeman E. 1909. Études systématique et de géographie botaniques sur la flore du Bas- et du Moyen-Congo. Annales du Musée du Congo 3: 1–148.

De Wildeman E. 1911. Florule des districts politiques des Bangala et de l'Ubangi (Congo Belge). Plantae Thonnerianae Congolenses, serie 2. Misch & Thron, Libraires-Éditeurs, Bruxelles et Leipzig.

De Wildeman E. 1914. Decades novarum specierum Florae Congolensis. Bulletin du Jardin Botanique de l'État a Bruxelles 4: 359–429.

De Wildeman E. 1922. Études sur les récoltes botaniques du Dr J. Bequaert chargé de missions au Congo Belge (1913-1915). Plantae Bequaertianae 1: 453–593.

De Wildeman E, Durand T. 1900. Contributions à la flore du Congo. Annales du Musée du Congo Botanique série II, 1: 1–48.

Dedome S-LO, Alitonou GA, Yedomonhan H, Tchobo FP, Sessou P, Yovo M, Yessinou E, Farougou S, Avlessi F, Menut C. 2017. First report on chemical composition and acaricidal activity on the cattle tick *Rhipicephalus microplus* of essential oil from *Monanthotaxis parvifolia* (Oliv.) Verdc. American Journal of Applied Chemistry 5: 53–56.

DeRose-Wilson LJ, Gaut BS. 2007. Transcription-related mutations and GC content drive variation in nucleotide substitution rates across the genomes of *Arabidopsis thaliana* and *Arabidopsis lyrata*. BMC Evolutionary Biology 7: 66.

Dickerson RE. 1971. The structure of cytochromec and the rates of molecular evolution. Journal of Molecular Evolution 1: 26-45.

Diels L. 1907. Annonaceae africanae. Botanische Jahrbücher fur Systematik, Pflanzengeschichte und Pflanzengeographie 39: 469–486.

Diels L. 1908. Annonaceae africanae. II. Botanische Jahrbücher fur Systematik, Pflanzengeschichte und Pflanzengeographie 41: 328–329.

Diels L. 1912. Beiträge zur Flora von Papuasien. Serie I. 8. Die Anonaceen von Papuasien. Botanische Jahrbücher für Systematik 49: 113-167.

Diels L. 1915. Annonaceae africanae. III. Botanische Jahrbücher fur Systematik, Pflanzengeschichte und Pflanzengeographie 53: 434–448.

Dinsmore MP, Louis Jr EE, Randriamahazomanana D, Hachim A, Zaonarivelo JR, Strier KB. 2016. Variation in habitat and behavior of the Northern Sportive Lemur (*Lepilemur septentrionalis*) at Montagne des Français, Madagascar. Primate Conservation 30: 73–88.

Dirzo R, Raven PH. 2003. Global state of biodiversity and loss. Annual Review of Environment and Resources 28: 137-167.

Dodsworth S, Guignard MS, Christenhusz MJM, Cowan RS, Knapp S, Maurin O, Struebig M, Leitch AR, Chase MW, Forest F. 2018. Potential of herbariomics for studying repetitive DNA in Angiosperms. Frontiers in Ecology and Evolution 6.

Dornburg A, Brandley MC, McGowen MR, Near TJ. 2012. Relaxed clocks and inferences of heterogeneous patterns of nucleotide substitution and divergence time estimates across whales and dolphins (mammalia: cetacea). Molecular Biology and Evolution 29: 721-736.

Doyle JA, Le Thomas A. 2012. Evolution and phylogenetic significance of pollen in Annonaceae. Botanical Journal of the Linnean Society 169: 190-221.

Drouin G, Daoud H, Xia J. 2008. Relative rates of synonymous substitutions in the mitochondrial, chloroplast and nuclear genomes of seed plants. Molecular Phylogenetics and Evolution 49: 827-831.

Drummond A, Rambaut A. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. BMC Evol Biol 7: 214.

Drummond AJ, Suchard MA. 2010. Bayesian random local clocks, or one rate to rule them all. BMC Biology 8: 114.

Dubois A, Ohler A, Pyron RA. 2021. New concepts and methods for phylogenetic taxonomy and nomenclature in zoology, exemplified by a new ranked cladonomy of recent amphibians (Lissamphibia). Megataxa 5: 1-738.

Duchene D, Bromham L. 2013. Rates of molecular evolution and diversification in plants: chloroplast substitution rates correlate with species-richness in the Proteaceae. BMC Evolutionary Biology 13: 65.

Duraiappah AK, Naeem S, Agardy T, Ash NJ, Cooper HD, Diaz S, Faith DP, Mace G, McNeely JA, Mooney HA. 2005. Ecosystems and human well-being: biodiversity synthesis; a report of the Millennium Ecosystem Assessment. Island Press Washington, DC.

Emerson KJ, Merz CR, Catchen JM, Hohenlohe PA, Cresko WA, Bradshaw WE, Holzapfel CM. 2010. Resolving postglacial phylogeography using high-throughput sequencing. Proceedings of the National Academy of Sciences 107: 16196-16200.

Endress PK. 1994. Shapes, sizes and evolutionary trends in stamens of Magnoliidae. Botanische Jahrbücher für Systematik 115: 429-460.

Endress PK, Armstrong JE. 2011. Floral development and floral phyllotaxis in *Anaxagorea* (Annonaceae). Annals of Botany 108: 835-845.

Endress PK, Doyle JA. 2009. Reconstructing the ancestral angiosperm flower and its initial specializations. American Journal of Botany 96: 22-66.

Engel MS, Ceríaco LMP, Daniel GM, Dellapé PM, Löbl I, Marinov M, Reis RE, Young MT, Dubois A, Agarwal I, Lehmann A. P, Alvarado M, Alvarez N, Andreone F, Araujo-Vieira K, Ascher JS, Baêta D, Baldo D, Bandeira SA, Barden P, Barrasso DA, Bendifallah L, Bockmann FA, Böhme W, Borkent A, Brandão CRF, Busack SD, Bybee SM, Channing A, Chatzimanolis S, Christenhusz MJM, Crisci JV, D'elía G, Da Costa LM, Davis SR, De Lucena CAS, Deuve T, Fernandes Elizalde S, Faivovich J, Farooq H, Ferguson AW, Gippoliti S, Gonçalves FMP, Gonzalez VH, Greenbaum E, Hinojosa-Díaz IA, Ineich I, Jiang J, Kahono S, Kury AB, Lucinda PHF, Lynch JD, Malécot V, Marques MP, Marris JWM, Mckellar RC, Mendes LF, Nihei SS, Nishikawa K, Ohler A, Orrico VGD, Ota H, Paiva J, Parrinha D, Pauwels OSG, Pereyra MO, Pestana LB, Pinheiro PDP, Prendini L, Prokop J, Rasmussen C, Rödel M-O, Rodrigues MT, Rodríguez SM, Salatnaya H, Sampaio Í, Sánchez-García A, Shebl MA, Santos BS, Solórzano-Kraemer MM, Sousa ACA, Stoev P, Teta P, Trape J-F, Dos Santos CV-D, Vasudevan K, Vink CJ, Vogel G, Wagner P, Wappler T, Ware JL, Wedmann S, Zacharie CK. 2021. The taxonomic impediment: a shortage of taxonomists, not the lack of technical approaches. Zoological Journal of the Linnean Society 193: 381-387.

Engler A. 1895. Fam.: Anonaceae. In: Engler A (ed), Die Pflanzenwelt Ost-Afrikas und der Nachbargebiete: 178–179. Geographische Verlagshandlung Dietrich Reimer, Berlin.

Engler A, Diels L. 1899. Diagnosen neuer afrikanischer Pflanzenarten. 4. Anonaceae. Notizblatt des Königlichen botanischen Gartens und Museums zu Berlin 2: 292–302.

Engler A, Diels L. 1901. Monographien Afrikanischer Pflanzen-Familien und -Gattungen. VI. Anonaceae. Verlag von Wilhelm Engelmann, Leipzig.

Engler A, Harms HAT (eds). 1959. Die Natürlichen Pflanzenfamilien ed. 2, 17a(2). Duncker & Humblot, Berlin.

Eo SH, DeWoody JA. 2010. Evolutionary rates of mitochondrial genomes correspond to diversification rates and to contemporary species richness in birds and reptiles. Proceedings of the Royal Society of London. Series B: Biological Sciences 277: 3587-3592.

Erkens RHJ, Chatrou LW, Koek-Noorman J, Maas JW, Maas PJM. 2007. Classification of a large and widespread genus of Neotropical trees, *Guatteria* (Annonaceae) and its three satellite genera *Guatteriella*, *Guatteriopsis* and *Heteropetalum*. Taxon 56: 757–774.

Ewango CEN, Bongers F, Makana J-R, Poorter L, Sosef MSM. 2015. Structure and composition of the liana assemblage of a mixed rain forest in the Congo Basin. Plant Ecology and Evolution 148: 29-42.

Exell AW. 1932. Gossweller's Portuguese West African Plants. The Journal of Botany 70: 206–214.

Exell AW. 1934. Notes from the British Museum Herbarium. The Journal of Botany 72: 279–281.

Exell AW. 1937. New species from Tropical Africa. The Journal of Botany 75: 163–167.

Exell AW. 1939. Notes from the British Museum Herbarium. The Journal of Botany 77: 320–321.

Exell AW, Mendonça FA. 1937. Ranunculaceae-Aquifoliaceae. Conspectus Florae Angolensis: 1–176. Ministerio do ultramar junta de investigaçoes coloniais, Lisboa.

Facciola S. 1998. Cornucopia: a source book of edible plants, 2nd edition. Kampong Publications, Vista.

Farris JS, Albert VA, Källersjö M, Lipscomb D, Kluge AG. 1996. Parsimony jackknifing outperforms neighbor-joining. Cladistics 12: 99-124.

Feliner GN, Rosselló JA. 2007. Better the devil you know? Guidelines for insightful utilization of nrDNA ITS in species-level evolutionary studies in plants. Molecular phylogenetics and evolution 44: 911-919.

Felsenstein J. 1981. Evolutionary trees from DNA sequences: a maximum likelihood approach. Journal of Molecular Evolution 17.

Felsenstein J. 2004. Inferring Phylogenies. Sinauer Associates, Inc, Sunderland, MA.

Fero M, Aedo C, Cabezas F, Velayos M. 2014. Taxonomic revision of *Neostenanthera* (Annonaceae). Systematic Botany 39: 17–30.

Fitch WM. 1971. Toward defining the course of evolution: minimum change for a specific tree topology. Systematic Biology 20: 406-416.

Fleischer TC, Waigh RD, Waterman PG. 1997. Bisabolene sesquiterpenes and flavonoids from Friesodielsia enghiana. Phytochemistry 44: 315–318.

Foden W, Potter L. 2005. National Assessment: Red List of South African Plants version 2017.1. redlist.sanbi.org. Last accessed 2017/11/23.

Foerster S, Zhong Y, Pintea L, Murray CM, Wilson ML, Mjungu DC, Pusey AE. 2016. Feeding habitat quality and behavioral trade-offs in chimpanzees: a case for species distribution models. Behavioral Ecology 27: 1004–1016.

Fournier G, Hadjiakhoondi A, Leboeuf M, Cave A, Charles B. 1997. Essential oils of Annonaceae. Part VII. Essential oils of *Monanthotaxis diclina* (Sprague) Verdcourt and *Unonopsis guatterioides* R.E Fries. Flavour and Fragrance Journal 12: 95–98.

Friedman J, Barrett Spencer CH. 2008. A phylogenetic analysis of the evolution of wind pollination in the angiosperms. International Journal of Plant Sciences 169: 49-58.

Fries RE. 1953. Verstreute Beobachtungen hinsichtlich der Familie Annonaceae. Arkiv för Botanik Serie 2, band 3(2): 35–42.

Fries RE. 1959. Annonaceae. In: Melchior HS (ed), Die Natürlichen Pflanzenfamilien, ed 2, 17 a II.: 1–171. Duncker & Humblot, Berlin.

Fries RE, Fries TCE. 1925. Beiträge zur Kenntnis der Flora des Kenia, Mt. Aberdare und Mt. Elgon. VII. Notizblatt des Königlichen botanischen Gartens und Museums zu Berlin 9: 299–333.

Friis EM, Pedersen KR, Crane PR. 2006. Cretaceous angiosperm flowers: Innovation and evolution in plant reproduction. Palaeogeography, Palaeoclimatology, Palaeoecology 232: 251-293.

Gaston KJ, May RM. 1992. Taxonomy of taxonomists. Nature 356: 281-282.

Gautier-Hion A, Duplantier J-M, Quris R, Feer F, Sourd C, Decoux JP, Dubost G, Emmons L, Erard C, Hecketsweiler P, Moungazi A, Roussilhon C, Thiollay JM. 1985. Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. Oecologia 65: 324–337.

Gerwing JJ, Vidal E. 2002. Changes in liana abundance and species diversity eight years after liana cutting and logging in an Eastern Amazonian Forest. Conservation Biology 16: 544-548.

Ghesquière MJ. 1939. Notes synonymiques sur quelques Annonacées d'Afrique. Revue de Zoologie et de Botanique Africaines 32: 139–142.

Ghogue J-P, Sonké B, Couvreur TLP. 2017. Taxonomic revision of the African genera *Brieya* and *Piptostigma* (Annonaceae). Plant Ecology and Evolution 150: 173–216.

Glenn TC. 2011. Field guide to next-generation DNA sequencers. Molecular Ecology Resources 11: 759-769.

Goldie X, Lanfear R, Bromham L. 2011. Diversification and the rate of molecular evolution: no evidence of a link in mammals. BMC evolutionary biology 11: 1.

Goodwillie C, Ness JM. 2005. Correlated evolution in floral morphology and the timing of self-compatibility in *Leptosiphon jepsonii* (Polemoniaceae). International Journal of Plant Sciences 166: 741-751.

Goodwillie C, Sargent RD, Eckert CG, Elle E, Geber MA, Johnston MO, Kalisz S, Moeller DA, Ree RH, Vallejo-Marin M, Winn AA. 2010. Correlated evolution of mating system and floral display traits in flowering plants and its implications for the distribution of mating system variation. New Phytologist 185: 311-321.

Graham SW, Lam VKY, Merckx VSFT. 2017. Plastomes on the edge: the evolutionary breakdown of mycoheterotroph plastid genomes. New Phytologist 214: 48-55.

Gray A. 1852. *Richella*, nov. gen. Proceedings of the American Academy of Arts and Sciences 2: 325.

Guo X, Hoekstra PH, Tang CC, Thomas DC, Wieringa JJ, Chatrou LW, Saunders RMK. 2017a. Cutting up the climbers: Evidence for extensive polyphyly in *Friesodielsia* (Annonaceae) necessitates generic realignment across the tribe Uvarieae. Taxon 66: 3-19.

Guo X, Tang CC, Saunders RMK. 2017b. (2496) Proposal to conserve the name *Friesodielsia* against *Schefferomitra* (Annonaceae). TAXON 66: 204-205.

Guo X, Tang CC, Thomas DC, Couvreur TLP, Saunders RMK. 2017c. A mega-phylogeny of the Annonaceae: taxonomic placement of five enigmatic genera and support for a new tribe, Phoenicantheae. Scientific Reports 7: 7323.

Guo X, Wang J, Xue B, Thomas DC, Su YCF, Tan Y-H, Saunders RMK. 2014. Reassessing the taxonomic status of two enigmatic *Desmos* species (Annonaceae): Morphological and molecular phylogenetic support for a new genus, *Wangia*. Journal of Systematics and Evolution 52: 1-15.

Hall TA. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acids Symposium Series 41: 95-98.

Harcourt C, Nash L. 1986. Species differences in substrate use and diet between sympatric galagos in two Kenyan coastal forests. Primates 27: 41–52.

Harmon LJ, Weir JT, Brock CD, Glor RE, Challenger W. 2008. GEIGER: investigating evolutionary radiations. Bioinformatics 24: 129-131.

Harvey WH, Sonder OW. 1860. Flora Capensis: being a systematic description of the plants of the Cape colony, Caffraria & Port Natal. Hodges, Smith and Co., Dublin.

Hawthorne WD, Jongkind CCH. 2006. Woody plants of Western African forests. A guide to the forest trees, shrubs and lianes from Senegal to Ghana. Royal Botanic Gardens, Kew.

Hedberg I, Hedberg O, Madati PJ, Mshigeni KE, Mshiu EN, Samuelsson G. 1982. Inventory of plants used in traditional medicine in Tanzania. I. Plants of the families Acanthaceae-Cucurbitaceae. Journal of Ethnopharmacology 6: 29–60.

Hernández-Hernández T, Miller EC, Román-Palacios C, Wiens JJ. 2021. Speciation across the tree of life. Biological Reviews 96: 1205-1242.

Hernández-Hernández T, Wiens JJ. 2020. Why are there so many flowering plants? A multiscale analysis of plant diversification. The American Naturalist 195: 948-963.

Hickey LJ. 1979. A revised classification of the architecture of dicotyledonous leaves. In: Metcalfe C, Chalk Ls (eds.), Anatomy of the dicotyledons: 25-39. Clarendon Press, Oxford.

Hickey LJ, Wolfe JA. 1975. The bases of Angiosperm phylogeny: Vegetative morphology. Annals of the Missouri Botanical Garden 62: 538-589.

Hiern WP. 1896. Catalogue of the African plants collected by Dr. Friedrich Welwitsch: 5–13. Order of the Trustees, London.

Hillis DM, Moritz C, Porter CA, Baker RJ. 1991. Evidence for biased gene conversion in concerted evolution of ribosomal DNA. Science 251: 308-310.

Ho SYW. 2014. The changing face of the molecular evolutionary clock. Trends in Ecology & Evolution 29: 496-503.

Hoekstra PH, Chatrou LW, Wieringa JJ. 2014. A new species of *Monanthotaxis* from Gabon with a unique inflorescence type for Annonaceae. Phytotaxa 186: 106-112.

Hoekstra PH, Wieringa JJ, Chatrou LW. 2016. A nonet of novel species of *Monanthotaxis* (Annonaceae) from around Africa. PhytoKeys: 71-103.

Hoekstra PH, Wieringa JJ, Maas PJM, Chatrou LW. 2021. Revision of the African species of *Monanthotaxis* (Annonaceae). Blumea 66: 107-221.

Hoekstra PH, Wieringa JJ, Smets E, Brandão RD, Lopes JdC, Erkens RHJ, Chatrou LW. 2017. Correlated evolutionary rates across genomic compartments in Annonaceae. Molecular Phylogenetics and Evolution 114: 63-72.

Hoekstra PH, Wieringa JJ, Smets E, Chatrou LW. 2018. Floral evolution by simplification in *Monanthotaxis* (Annonaceae) and hypotheses for pollination system shifts. Scientific Reports 8: 12066.

Holland PWH. 2013. Evolution of homeobox genes. Wiley Interdisciplinary Reviews: Developmental Biology 2: 31-45.

Hooker JD, Bentham G. 1849. Flora Nigritiana: 204–212. Hippolyte Baillière, London.

Hooker JD, Thomson T 1855. Flora indica being a systematic account of the plants of British India 1: 1–285. W. Pamplin, London.

Hooker WJ. 1848. Icones Plantarum or figures, with brief descriptive characters and remarks, or new or rare plants, selected from the author's herbarium: tab DCCLXVII. Hippolyte Baillière, London.

Hua X, Bromham L. 2017. Darwinism for the genomic age: Connecting mutation to diversification. Frontiers in Genetics 8: 12.

Huelsenbeck JP, Hillis DM. 1993. Success of phylogenetic methods in the four-taxon case. Systematic Biology 42: 247-264.

Huelsenbeck JP, Larget B, Swofford D. 2000. A compound poisson process for relaxing the molecular clock. Genetics 154.

Hugall AF, Lee MSY. 2007. The likelihood node density effect and consequences for evolutionary studies of molecular rates. Evolution 61: 2293-2307.

Hutchinson J, Dalziel JM. 1927a. Flora of West Tropical Africa 1 (1): 1–125. Crown Agents for the Colonies, London.

Hutchinson J, Dalziel JM. 1927b. Tropical African Plants: I. Bulletin of Miscellaneous Information (Royal Gardens, Kew) 1927: 150–157.

IUCN Standards and Petitions Subcommittee. 2016. Guidelines for using the IUCN Red List categories and criteria. Version 11. IUCN http://www.iucnredlist.org/documents/RedListGuidelines.pdf. Last accessed 3 May 2016.

Jobson RW, Albert VA. 2002. Molecular rates parallel diversification contrasts between carnivorous plant sister lineages. Cladistics 18: 127-136.

Johnson DM, Luke Q, Goyder DJ, Murray NA. 2017. New species of *Xylopia* (Annonaceae) from East Africa. Kew Bulletin 72: 11.

Johnson DM, Murray NA. 2018. A revision of *Xylopia* L. (Annonaceae): the species of Tropical Africa. PhytoKeys 97: 1–252.

Joly S, McLenachan PA, Lockhart PJ. 2009. A statistical approach for distinguishing hybridization and incomplete lineage sorting. The American Naturalist 174: E54-E70.

Joppa LN, Roberts DL, Pimm SL. 2011. The population ecology and social behaviour of taxonomists. Trends in Ecology & Evolution 26: 551-553.

Joseph CC, Magadula JJ, Nkunya MHH. 2007. A novel antiplasmodial 3',5'-diformylchalcone and other constituents of *Friesodielsia obovata*. Natural Product Research 21: 1009–1015.

Jussieu ALd. 1789. Genera plantarum secundum ordines naturales disposita, juxta methodum in Horto Regio Parisiensi exaratum, anno M.DCC.LXXIV. Apud Viduam Herissant et Theophilum Barrois, Parisiis.

Kapralov MV, Filatov DA. 2007. Widespread positive selection in the photosynthetic Rubisco enzyme. BMC Evolutionary Biology 7.

Kass RE, Raftery AE. 1995. Bayes Factors. Journal of the American Statistical Association 90: 773-795.

Katoh K, Misawa K, Kuma Ki, Miyata T. 2002. MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. Nucleic Acids Research 30: 3059-3066.

Katoh K, Standley DM. 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. Molecular Biology and Evolution 30: 772-780.

Kay KM, Whittall JB, Hodges SA. 2006. A survey of nuclear ribosomal internal transcribed spacer substitution rates across angiosperms: an approximate molecular clock with life history effects. BMC Evolutionary Biology 6: 36.

Keay RWJ. 1953. Revision of the "Flora of West Tropical Africa": III. Kew Bulletin 8: 69–82.

Keay RWJ. 1954. Flora of West Tropical Africa, second edition. Vol. 1, part 1. Crown Agents for Oversea Governments an Administrations, London.

Keay RWJ, Boutique R. 1953. Proposal no. 43. Taxon 2: 178–179.

Kenfack D, Gosline G, Gereau RE, Schatz GE. 2003. The Genus *Uvariopsis* (Annonaceae) in Tropical Africa, with a recombination and one new species from Cameroon. Novon 13: 443–449.

Kenfack D, Thomas DW, Chuyong G, Condit R. 2007. Rarity and abundance in a diverse African forest. Biodiversity and Conservation 16: 2045-2074.

Keßler P. 1993. Annonaceae. In: Kubitzki K, Rohwer J, Bittrich Vs (eds.), Flowering Plants. Dicotyledons: Magnoliid, hamamelid and Caryophyllid Families.: 93-129. Springer-Verlag, Berlin.

Kim KC, Byrne LB. 2006. Biodiversity loss and the taxonomic bottleneck: emerging biodiversity science. Ecological Research 21: 794.

Kimaro J, Lulandala L. 2013. Contribution of non-timber forest products to poverty alleviation and forest conservation in Rufiji District Tanzania. Livestock Research for Rural Development 25.

Kimura M, Ohta T. 1971. Theoretical aspects of population genetics. Princeton University Press, Princeton, New Jersey.

Klucking E. 1986. Annonaceae. Cramer, Berlin & Stuttgart.

Kluge AG. 1989. A concern for evidence and a phylogenetic hypothesis of relationships among *Epicrates* (Boidae, Serpentes). Systematic Biology 38: 7-25.

Krehenwinkel H, Kennedy SR, Rueda A, Lam A, Gillespie RG. 2018. Scaling up DNA barcoding – Primer sets for simple and cost efficient arthropod systematics by multiplex PCR and Illumina amplicon sequencing. Methods in Ecology and Evolution 9: 2181-2193.

Kück P, Mayer C, Wägele J-W, Misof B. 2012. Long branch effects distort maximum likelihood phylogenies in simulations despite selection of the correct model. PLOS ONE 7: e36593.

Kurz S. 1875. Descriptions of new plants from the Nicobar Islands (including a few from the Andaman Islands). Journal of Botany, British and foreign 13: 321–333.

Kusimi JM. 2015. Characterizing land disturbance in Atewa Range Forest Reserve and Buffer Zone. Land Use Policy 49: 471–482.

Lagesen K, Hallin P, Rødland EA, Stærfeldt H-H, Rognes T, Ussery DW. 2007. RNAmmer: consistent and rapid annotation of ribosomal RNA genes. Nucleic Acids Research 35: 3100-3108.

Landis MJ, Schraiber JG. 2017. Pulsed evolution shaped modern vertebrate body sizes. Proceedings of the National Academy of Sciences 114: 13224-13229.

Lanfear R, Calcott B, Ho SYW, Guindon S. 2012. PartitionFinder: Combined selection of partitioning schemes and substitution models for phylogenetic analyses. Molecular Biology and Evolution 29: 1695-1701.

Lanfear R, Ho SY, Love D, Bromham L. 2010a. Mutation rate is linked to diversification in birds. Proceedings of the National Academy of Sciences of the United States of America 107: 20423-20428.

Lanfear R, Ho SYW, Davies TJ, Moles AT, Aarssen L, Swenson NG, Warman L, Zanne AE, Allen AP. 2013. Taller plants have lower rates of molecular evolution. Nature Communications 4: 1879.

Lanfear R, Hua X, Warren DL. 2016. Estimating the effective sample size of tree topologies from bayesian phylogenetic analyses. Genome Biology and Evolution 8: 2319-2332.

Lanfear R, Welch JJ, Bromham L. 2010b. Watching the clock: Studying variation in rates of molecular evolution between species. Trends in Ecology & Evolution 25: 495-503.

Langmead B, Salzberg SL. 2012. Fast gapped-read alignment with Bowtie 2. Nature Methods 9: 357-359.

Larget B, Simon DL. 1999. Markov chain Monte Carlo algorithms for the Bayesian analysis of phylogenetic trees. Molecular Biology and Evolution 16.

Larsen BB, Miller EC, Rhodes MK, Wiens JJ. 2017. Inordinate fondness multiplied and redistributed: the number of species on Earth and the new pie of life. The Quarterly Review of Biology 92: 229 - 265.

Laryea MK, Borquaye LS. 2019. Antimalarial efficacy and toxicological assessment of extracts of some Ghanaian medicinal plants. Journal of Parasitology Research 2019: 1630405.

Le Thomas A. 1963. Notes systématiques sur les Annonacées africaines et malgaches. Adansonia 3: 287–293.

Le Thomas A. 1965. Notes sur quelques Annonacées Ouest-Africaines. Adansonia sér 2, 5: 443–454.

Le Thomas A. 1968. Nouvelles Annonacées d'Afrique Équatoriale. Adansonia sér 2, 8: 241–247.

Le Thomas A. 1969. Annonacées. In: Aubréville As (ed.), Flore du Gabon Vol. 16: 1–371. Muséum National d'Histoire Naturelle, Paris.

Le Thomas A. 1980. Ultrastructural characters of the pollen grains of African Annonaceae and their significance for the phylogeny of primitive angiosperms: Part I. Pollen & Spores 22: 267-342.

Le Thomas A. 1981. Ultrastructural characters of the pollen grains of African Annonaceae and their significance for the phylogeny of primitive angiosperms: Part II. Pollen & Spores 23: 5-36.

Lemaire B, Huysmans S, Smets E, Merckx V. 2011. Rate accelerations in nuclear 18S rDNA of mycoheterotrophic and parasitic angiosperms. Journal of Plant Research 124: 561-576.

Lemey P, Salemi M, Vandamme A-M. 2009. The phylogenetic handbook: a practical approach to phylogenetic analysis and hypothesis testing. Cambridge University Press, New York.

Lemos EEP, Blake J. 1996. Micropropagation of juvenile and mature *Annona muricata* L. Journal of Horticultural Science 71: 395-403.

Li W-H, Ellsworth DL, Krushkal J, Chang BHJ, Hewett-Emmett D. 1996. Rates of nucleotide substitution in primates and rodents and the generation–Time effect hypothesis. Molecular Phylogenetics and Evolution 5: 182-187.

Li W-H, Tanimura M, Sharp PM. 1987. An evaluation of the molecular clock hypothesis using mammalian DNA sequences. Journal of Molecular Evolution 25: 330-342.

Liang G-Y, Gray AI, Thomas DW, Waterman PG. 1988. Polyoxygenated cyclohexane epoxide derivatives from the stem bark of *Monanthotaxis buchananii*. Phytochemistry 27: 3857-3860.

Linder CR, Rieseberg LH. 2004. Reconstructing patterns of reticulate evolution in plants. American Journal of Botany 91: 1700-1708.

Locey KJ, Lennon JT. 2016. Scaling laws predict global microbial diversity. Proceedings of the National Academy of Sciences of the United States of America 113: 5970-5975.

López-Giráldez F, Townsend JP. 2011. PhyDesign: an online application for profiling phylogenetic informativeness. BMC Evolutionary Biology 11: 152.

Lundell CL. 1974. Studies of American Plants. VI. Wrightia 5: 23-44.

Luo R, Liu B, Xie Y, Li Z, Huang W, Yuan J, He G, Chen Y, Pan Q, Liu Y, Tang J, Wu G, Zhang H, Shi Y, Liu Y, Yu C, Wang B, Lu Y, Han C, Cheung DW, Yiu S-M, Peng S, Xiaoqian Z, Liu G, Liao X, Li Y, Yang H, Wang J, Lam T-W, Wang J. 2012. SOAPdenovo2: an empirically improved memory-efficient short-read de novo assembler. GigaScience 1: 18.

Maas PJM, Westra LYT. 1992. *Rollinia*. Flora Neotropica 57: 1–188.

Maas PJM, Westra LYT, Chatrou LW., et al. 2003. *Duguetia* (Annonaceae). Flora Neotropica 88: 1–274.

Maas PJM, Westra LYT, Guerrero SA, Lobão AQ, Scharf U, Zamora NA, Erkens RHJ. 2015. Confronting a morphological nightmare: revision of the Neotropical genus *Guatteria* (Annonaceae). Blumea - Biodiversity, Evolution and Biogeography of Plants 60: 1-219.

Maddison WP, Maddison DR. 2016. Mesquite: a modular system for evolutionary analysis. Version 3.11. http://mesquiteproject.org. Last.

Marshall DC. 2009. Cryptic failure of partitioned Bayesian phylogenetic analyses: Lost in the land of long trees. Systematic Biology 59: 108-117.

Mayrose I, Friedman N, Pupko T. 2005. A gamma mixture model better accounts for among site rate heterogeneity. Bioinformatics 21: ii151-ii158.

McCormack JE, Hird SM, Zellmer AJ, Carstens BC, Brumfield RT. 2013. Applications of next-generation sequencing to phylogeography and phylogenetics. Molecular phylogenetics and evolution 66: 526-538.

McLennan MR. 2013. Diet and feeding ecology of Chimpanzees (*Pan troglodytes*) in Bulindi, Uganda: Foraging strategies at the forest-farm interface. International Journal of Primatology 34: 585–614.

Metzker ML. 2010. Sequencing technologies the next generation. Nature Reviews Genetics 11: 31-46.

Mevy J, Bessiere J, Pelissier Y, Masotti V, Ruzzier M, Rabier J, Viano J. 2004. Composition of the volatile constituents of the aerial parts of an endemic plant of Ivory Coast, *Monanthotaxis capea* (EG & A. Camus) Verdc. Flavour and fragrance journal 19: 526–528.

Mildbraed J. 1911. Wissenschaftliche Ergebnisse der Deutschen Zentral-Africa-Expedition, 1907–1908: unter Führung Adolf Friedrichs, Herzogs zu Mecklenburg. Bd. 2: 177–270. Klinkhardt & Biermann, Leipzig.

Mildbraed J. 1932. Neue und seltene Arten aus dem südlichen Ostafrika (Tanganyika-Territ. Mandat) leg. H. J. Schlieben. Notizblatt des Königlichen botanischen Gartens und Museums zu Berlin 11: 393–417.

Mildbraed J. 1933. Neue und seltene Arten aus dem südlichen Ostafrika (Tanganyika-Territ. Mandat) leg. H. J. Schlieben, III. Notizblatt des Königlichen botanischen Gartens und Museums zu Berlin 11: 802–826.

Mildbraed J. 1936. Neue und seltene Arten aus Ostafrika (Tanganyika-Territ. Mandat) leg. HJ Schlieben, XI. Notizblatt des Königlichen botanischen Gartens und Museums zu Berlin 13: 260–303.

Miller MA, Pfeiffer W, Schwartz T. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. Gateway Computing Environments Workshop (GCE). IEEE pp. 1-8.

Mitchell CH, Diggle PK. 2005. The evolution of unisexual flowers: morphological and functional convergence results from diverse developmental transitions. American Journal of Botany 92: 1068-1076.

Mols JB, Gravendeel B, Chatrou LW, Pirie MD, Bygrave PC, Chase MW, Keßler PJA. 2004. Identifying clades in Asian Annonaceae: monophyletic genera in the polyphyletic Miliuseae. American Journal of Botany 91: 590–600.

Mora C, Rollo A, Tittensor DP. 2013. Comment on "Can we name Earth's species before they go extinct?". Science 341: 237-237.

Moran NA. 1996. Accelerated evolution and Muller's rachet in endosymbiotic bacteria. Proceedings of the National Academy of Sciences of the United States of America 93: 2873-2878.

Morton BR. 2003. The role of context-dependent mutations in generating compositional and codon usage bias in grass chloroplast DNA. Journal of Molecular Evolution 56: 616-629.

Morton BR, Bi IV, McMullen MD, Gaut BS. 2006. Variation in mutation dynamics across the maize genome as a function of regional and flanking base composition. Genetics 172: 569-577.

Morton BR, Clegg MT. 1995. Neighboring base composition is strongly correlated with base substitution bias in a region of the chloroplast genome. Journal of Molecular Evolution 41: 597-603.

Mower JP, Stefanovic S, Young GJ, Palmer JD. 2004. Plant genetics: Gene transfer from parasitic to host plants. Nature 432: 165-166.

Mulholland D, Naidoo N, Hutchings A, Lavaud C, Massiot G. 2000. Crotepoxide, a cyclohexane diepoxide from *Monanthotaxis caffra*. Biochemical Systematics and Ecology 28: 595-597.

Mungai N, Kibwage I, Mwangi J, Guantai A, Njogu P, Ongarora D. 2014. Isolation, characterization and antiplasmodial activity of phytochemical constituents from *Monanthotaxis parvifolia* (Oliv.) Verdc ssp. *kenyensis* Verdc. East and Central African Journal of Pharmaceutical Sciences 17: 87-93.

Mungai NN. 2015. Antiplasmodial and phytochemical investigation of *Monanthotaxis parvifolia* (Oliv.) Verdc. ssp. *kenyensis* Verdc. (Annonaceae). Department of Pharmacology and Pharmacognosy. University of Nairobi Nairobi, Kenya.

Nakavuma JL, Matasyoh JC, Wagara IN, Kalema J, Alinaitwe L. 2016. Toxicity studies on anti-fungal essential oils extracted from selected aromatic plants from Mabira and Kakamega forests, East Africa. European Journal of Medicinal Plants 14: 1–14.

Niet Tvd, Johnson SD. 2009. Patterns of plant speciation in the Cape floristic region. Molecular Phylogenetics and Evolution 51: 85-93.

Nixon KC, Carpenter JM. 1996. On simultaneous analysis. Cladistics 12: 221-241.

Ntiamoa-Baidu Y, Asamoah SA, Owusu EH, Owusu-Boateng K. 2000. Avifauna of two upland evergreen forest reserves, the Atewa range and Tano Offin, in Ghana. Ostrich 71: 277–281.

Nylander J. 2004. MrModeltest, version 2 [online]. Program distributed by the author. Evolutionary Biology Centre, Uppsala University. http://www.abc.se/~nylander/mrmodeltest2/mrmodeltest2.html. Last.

Nylander JAA, Ronquist F, Huelsenbeck JP, Nieves-Aldrey J. 2004. Bayesian phylogenetic analysis of combined data. Systematic Biology 53: 47-67.

Nylander JAA, Wilgenbusch JC, Warren DL, Swofford DL. 2007. AWTY (are we there yet?): a system for graphical exploration of MCMC convergence in Bayesian phylogenetics. Bioinformatics 24: 581-583.

O'Malley MA, Wideman JG, Ruiz-Trillo I. 2016. Losing complexity: the role of simplification in macroevolution. Trends in Ecology & Evolution 31: 608-621.

Ohta T. 1992. The nearly neutral theory of molecular evolution. Annual Review of Ecology and Systematics 23: 263-286.

Ohta T. 1993. An examination of the generation-time effect on molecular evolution. Proceedings of the National Academy of Sciences of the United States of America 90: 10676-10680.

Oldenburg DJ, Bendich AJ. 2015. DNA maintenance in plastids and mitochondria of plants. Frontiers in Plant Science 6: 883-883.

Oliver D. 1868. Order III. Annonaceae. In: Oliver D (ed), Flora of Tropical Africa. 1. Ranunculaceae to Connaraceae: 13–39. J.E. Taylor and Co., London.

Ossowski S, Schneeberger K, Lucas-Lledó JI, Warthmann N, Clark RM, Shaw RG, Weigel D, Lynch M. 2010. The rate and molecular spectrum of spontaneous mutations in *Arabidopsis thaliana*. Science 327: 92-94.

Pagel M. 2002. Modelling the evolution of continuously varying characters on phylogenetic trees. In: MacLeod N, Forey PLs (eds.), Morphology, shape and phylogeny: 269-286. CRC Press, Boca Raton.

Pagel M, Meade A. 2006. Bayesian analysis of correlated evolution of discrete characters by reversible-jump markov chain monte carlo. The American Naturalist 167: 808-825.

Pagel M, Meade A. 2014. BayesTraits V2.0. http://www.evolution.rdg.ac.uk/BayesTraits.html. Last.

Pagel M, Meade A, Barker D, Thorne J. 2004. Bayesian estimation of ancestral character states on phylogenies. Systematic Biology 53: 673-684.

Paiva JAR. 1966. Revisão das Annonaceae de Angola. In: Fernandes A, Neves JB (eds), Memórias da Sociedade Broteriana: 1–128. Oficinas da Tip. Alcobacense, LT, Alcobaça.

Panichpol K, Waterman PG. 1978. Novel flavonoids from the stem of *Popowia cauliflora*. Phytochemistry 17: 1363–1367.

Paradis E, Claude J, Strimmer K. 2004. APE: Analyses of phylogenetics and evolution in R language. Bioinformatics 20: 289-290.

Parmena D, Mgina C, Joseph C. 2012. Composition of non volatile oils and antimicrobial activities of extracts from *Monanthotaxis discolor*, and an undescribed *Uvariondedron* species. Tanzania Journal of Science 38: 221–231.

Pellegrin F. 1949. *Popowia* (Annonacées) d'Afrique. Bulletin de la Société Botanique de France 96: 212–213.

Pellegrin F. 1950. Annonacées nouvelles africaines. Notulae Systematicae 14: 75–76.

Pennell MW, Harmon LJ, Uyeda JC. 2014. Is there room for punctuated equilibrium in macroevolution? Trends in Ecology & Evolution 29: 23-32.

Perry AS, Wolfe KH. 2002. Nucleotide substitution rates in legume chloroplast DNA depend on the presence of the inverted repeat. Journal of Molecular Evolution 55: 501-508.

Philippe H, Zhou Y, Brinkmann H, Rodrigue N, Delsuc F. 2005. Heterotachy and long-branch attraction in phylogenetics. BMC Evolutionary Biology 5: 50.

Phillips O, Miller J. 2002. Global patterns of forest diversity: the dataset of Alwyn H. Gentry. Monographs in systematic botany 89: 1-319.

Pichi-Sermolli REG. 1954. Nomenclature committees: Special committee for Pteridophyta and Phanerogamae: Subcommittee for Phanerogamae. Taxon 3: 112–123.

Pimm SL, Joppa LN. 2015. How many plant species are there, where are they, and at what rate are they going extinct? Annals of the Missouri Botanical Garden 100: 170-176.

Pirie MD, Chatrou LW, Mols JB, Erkens RHJ, Oosterhof J. 2006. 'Andean-centred' genera in the short-branch clade of Annonaceae: testing biogeographical hypotheses using phylogeny reconstruction and molecular dating. Journal of Biogeography 33: 31-46.

Pirie MD, Doyle JA. 2012. Dating clades with fossils and molecules: the case of Annonaceae. Botanical Journal of the Linnean Society 169: 84-116.

Poczai P, Hyvönen J. 2010. Nuclear ribosomal spacer regions in plant phylogenetics: problems and prospects. Molecular Biology Reports 37: 1897-1912.

Posluszny U, Fisher JB. 2000. Thorn and hook ontogeny in *Artabotrys hexapetalus* (Annonaceae). American Journal of Botany 87: 1561-1570.

Presgraves DC. 2010. The molecular evolutionary basis of species formation. Nature Reviews Genetics 11: 175-180.

Price MJ. 2014. The Consortium of European Taxonomic Facilities (CETAF): Exploring and documenting diversity in nature. TAXON 63: 1161-1163.

Quinn TP, Unwin MJ, Kinnison MT. 2000. Evolution of temporal isolation in the wild: Genetic divergence in timing of migration and breeding by introduced chinook salmon populations. Evolution 54: 1372-1385.

Rainer H, Chatrou LW. 2006. AnnonBase: world species list of Annonaceae. http://www.sp2000.org and http://www.annonaceae.org. Last accessed 9 January 2020.

Rambaut A, Drummond A. 2009. Tracer: MCMC trace analysis tool, version 1.5.

Rasoanaivo P, Petitjean A, Ratsimamanga-Urverg S, Rakoto-Ratsimamanga A. 1992. Medicinal plants used to treat malaria in Madagascar. Journal of Ethnopharmacology 37: 117-127.

Richardson JE, Chatrou LW, Mols JB, Erkens RHJ, Pirie MD. 2004. Historical biogeography of two cosmopolitan families of flowering plants: Annonaceae and Rhamnaceae. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences 359: 1495-1508.

Rickett HW. 1958. Report of the committee for Spermatophyta, conservation of generic names 1. Taxon 7: 184–193.

Rickett HW. 1961. Report of the committee for Spermatophyta, conservation of generic names III. Taxon 10: 122–126.

Riginos C, Buckley YM, Blomberg SP, Treml EA, Associate Editor: Stephen BH, Editor: Judith LB. 2014. Dispersal capacity predicts both population genetic structure and species richness in reef fishes. The American Naturalist 184: 52-64.

Robson N. 1958. New and little known species from the Flora Zambesiaca area, VI. Boletim da Sociedade Broteriana sér 2, 32: 151–173.

Robson N. 1960. Annonaceae. In: Exell AW, Wild H (eds), Flora Zambesiaca 1(1): 104–149. Crown agents for oversea governments and administrations, London.

Robyns W, Ghesquière MJ. 1933. Sur la présence des genres *Enneastemon* Exell et *Monanthotaxis* Baill. (Annonacées) au Congo Belge. Annales de la Société scientifique de Bruxelles série B, 53: 161–169.

Robyns W, Ghesquière MJ. 1934. Une espèce nouvelle du genre *Enneastemon* Exell (Annonaceae) du Gabon. Bulletin du Museum National d'Histoire Naturelle Série 2, 6: 90–91.

Rogers ME, Abernethy KA, Fontaine B, Wickings EJ, White LJT, Tutin CEG. 1996. Ten days in the life of a mandrill horde in the Lope Reserve, Gabon. American Journal of Primatology 40: 297–313.

Rogers ME, Maisels F, Williamson EA, Fernandez M, Tutin CEG. 1990. Gorilla diet in the Lopé Reserve, Gabon. Oecologia 84: 326–339.

Ronquist F, Huelsenbeck JP. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19: 1572-1574.

Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP. 2012. MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61: 539-542.

Ronse Decraene LP, Smets E. 1990. The floral development of *Popowia whitei* (Annonaceae). Nordic Journal of Botany 10: 411-420.

Rousseau-Gueutin M, Huang X, Higginson E, Ayliffe M, Day A, Timmis JN. 2013. Potential functional replacement of the plastidic acetyl-coA carboxylase subunit (accD) gene by recent transfers to the nucleus in some angiosperm lineages. Plant Physiology 161: 1918-1929.

Ruffo CK, Birnie A, Tengnäs B. 2002. Edible wild plants of Tanzania. Regional Land Management Unit, RELMA/Sida, Nairobi.

Sanger F, Nicklen S, Coulson AR. 1977. DNA sequencing with chain-terminating inhibitors. Proceedings of the National Academy of Sciences 74: 5463-5467.

Sassen M, Jum C. 2007. Assessing local perspectives in a forested landscape of central Cameroon. Forests, Trees and Livelihoods 17: 23–42.

Saunders RMK. 2010. Floral evolution in the Annonaceae: hypotheses of homeotic mutations and functional convergence. Biological Reviews 85: 571-591.

Saunders RMK. 2012. The diversity and evolution of pollination systems in Annonaceae. Botanical Journal of the Linnean Society 169: 222-244.

Sauquet H, Doyle JA, Scharaschkin T, Borsch T, Hilu KW, Chatrou LW, Le Thomas A. 2003. Phylogenetic analysis of Magnoliales and Myristicaceae based on multiple data sets: implications for character evolution. Botanical Journal of the Linnean Society 142: 125-186.

Sauquet H, von Balthazar M, Magallón S, Doyle JA, Endress PK, Bailes EJ, Barroso de Morais E, Bull-Hereñu K, Carrive L, Chartier M, Chomicki G, Coiro M, Cornette R, El Ottra JHL, Epicoco C, Foster CSP, Jabbour F, Haevermans A, Haevermans T, Hernández R, Little SA, Löfstrand S, Luna JA, Massoni J, Nadot S, Pamperl S, Prieu C, Reyes E, dos Santos P, Schoonderwoerd KM, Sontag S, Soulebeau A, Staedler Y, Tschan GF, Wing-Sze Leung A, Schönenberger J. 2017. The ancestral flower of angiosperms and its early diversification. Nature Communications 8: 16047.

Scarcelli N, Mariac C, Couvreur TLP, Faye A, Richard D, Sabot F, Berthouly-Salazar C, Vigouroux Y. 2016. Intra-individual polymorphism in chloroplasts from NGS data: where does it come from and how to handle it? Molecular Ecology Resources 16: 434-445.

Scharff LB, Koop H-U. 2007. Targeted inactivation of the tobacco plastome origins of replication A and B. The Plant Journal 50: 782-794.

Scheffer RHCC. 1885. Sur quelques plantes nouvelles ou peu connues de l'archipel Indien. Annales du Jardin botanique de Buitenzorg 2: 1–31.

Schnell R. 1953. Plantes nouvelles ou peu connues d'Afrique occidentale française (Guinée et Côte d'Ivoire). Bulletin de l'institut Français d'Afrique Noire 15: 93–94.

Schrempf D, Szöllősi G. 2020. The Sources of Phylogenetic Conflicts. In: Scornavacca C, Delsuc F, Galtier Ns (eds.), Phylogenetics in the Genomic Era: 3.1:1--3.1:23. No commercial publisher | Authors open access book.

Schrider DR, Kern AD. 2018. Supervised machine learning for population genetics: A new paradigm. Trends in Genetics 34: 301-312.

Scott Elliot GF. 1894. On the botanical results of the Sierra Leone boundary commission. The Journal of the Linnean Society, Botany 30: 64–100.

Ségurel L, Wyman MJ, Przeworski M. 2014. Determinants of mutation rate variation in the human germline. Annual Review of Genomics and Human Genetics 15: 47-70.

Shapiro B, Rambaut A, Drummond AJ. 2006. Choosing appropriate substitution models for the phylogenetic analysis of protein-coding sequences. Molecular Biology and Evolution 23: 7-9.

Sillans R. 1953. Plantes ligneuses nouvelles d'Afrique tropicale. Revue internationale de botanique appliquée et d'agriculture tropicale 33: 545–561.

Simmons MP, Ochoterena H. 2000. Gaps as characters in sequence-based phylogenetic analyses. Systematic Biology 49: 369-381.

Simmons MP, Zhang L-B, Webb CT, Reeves A. 2006. How can third codon positions outperform first and second codon positions in phylogenetic inference? An empirical example from the seed plants. Systematic Biology 55: 245-258.

Sloan DB, Alverson AJ, Wu M, Palmer JD, Taylor DR. 2012. Recent acceleration of plastid sequence and structural evolution coincides with extreme mitochondrial divergence in the angiosperm genus *Silene*. Genome Biology and Evolution 4: 294-306.

Slowinski JB, Roderic DMP. 1999. How should species phylogenies be inferred from sequence data? Systematic Biology 48: 814-825.

Smith DR, Keeling PJ. 2015. Mitochondrial and plastid genome architecture: Reoccurring themes, but significant differences at the extremes. Proceedings of the National Academy of Sciences of the United States of America 112: 10177-10184.

Smith LM, Sanders JZ, Kaiser RJ, Hughes P, Dodd C, Connell CR, Heiner C, Kent SBH, Hood LE. 1986. Fluorescence detection in automated DNA sequence analysis. Nature 321: 674-679.

Smith SA, Donoghue MJ. 2008. Rates of molecular evolution are linked to life history in flowering plants. Science 322: 86 - 89.

Soltis PS, Soltis DE, Chase MW. 1999. Angiosperm phylogeny inferred from multiple genes as a tool for comparative biology. Nature 402: 402-404.

Sonké B, Couvreur TLP. 2014. Tree diversity of the Dja Faunal Reserve, southeastern Cameroon. Biodiversity Data Journal 2.

Sosef MSM, Dauby G, Blach-Overgaard A, van der Burgt X, Catarino L, Damen T, Deblauwe V, Dessein S, Dransfield J, Droissart V, Duarte MC, Engledow H, Fadeur G, Figueira R, Gereau RE, Hardy OJ, Harris DJ, de Heij J, Janssens S, Klomberg Y, Ley AC, Mackinder BA, Meerts P, van de Poel JL, Sonké B, Stévart T, Stoffelen P, Svenning J-C, Sepulchre P, Zaiss R, Wieringa JJ, Couvreur TLP. 2017. Exploring the floristic diversity of tropical Africa. BMC Biology 15: 15.

Sourd C, Gautier-Hion A. 1986. Fruit selection by a Forest Guenon. Journal of Animal Ecology 55: 235–244.

Spampinato CP. 2017. Protecting DNA from errors and damage: an overview of DNA repair mechanisms in plants compared to mammals. Cellular and Molecular Life Sciences 74: 1693-1709.

Sprague TA. 1908. Diagnoses africanae: XXI. Bulletin of Miscellaneous Information (Royal Gardens, Kew) 1908: 52–59.

Sprague TA, Hutchinson J. 1916. XXVII. African Anonaceae. Bulletin of Miscellaneous Information (Royal Gardens, Kew) 1916: 145-161.

Staats M, Cuenca A, Richardson JE, Vrielink-van Ginkel R, Petersen G, Seberg O, Bakker FT. 2011. DNA damage in plant herbarium tissue. PloS one 6: e28448.

Stamatakis A. 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics 22.

Stamatakis A. 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30: 1312-1313.

Stapf O. 1905. Contributions to the flora of Liberia. Journal of the Linnean Society Botany 37: 79–115.

Starks CM, Williams RB, Rice SM, Norman VL, Lawrence JA, Goering MG, O'Neil-Johnson M, Hu J-F, Eldridge GR. 2012. Polyoxygenated cyclohexene derivatives from *Monanthotaxis congoensis*. Phytochemistry 74: 185-189.

Steenis CGGJv. 1948. Remarks on some generic names used for Malaysian phanerogams I. Bulletin du Jardin Botanique de Buitenzorg, Buitenzorg séries 3: 457.

Stévart T, Dauby G, Lowry PP, Blach-Overgaard A, Droissart V, Harris DJ, Mackinder BA, Schatz GE, Sonké B, Sosef MSM, Svenning J-C, Wieringa JJ, Couvreur TLP. 2019. A third of the tropical African flora is potentially threatened with extinction. Science Advances 5: eaax9444.

Straub SCK, Parks M, Weitemier K, Fishbein M, Cronn RC, Liston A. 2012. Navigating the tip of the genomic iceberg: Next-generation sequencing for plant systematics. American Journal of Botany 99: 349-364.

Sukumaran J, Holder MT. 2010. DendroPy: A Python library for phylogenetic computing. Bioinformatics 26: 1569-1571.

Sullivan J, Swofford DL. 2001. Should we use model-based methods for phylogenetic inference when we know that assumptions about among-site rate variation and nucleotide substitution pattern are violated? Systematic Biology 50: 723-729.

Susko E. 2014. Bayesian long branch attraction bias and corrections. Systematic Biology 64: 243-255.

Svennblad B, Erixon P, Oxelman B, Britton T. 2006. Fundamental differences between the methods of maximum likelihood and maximum posterior probability in phylogenetics. Systematic Biology 55: 116-121.

Swofford DL. 2002a. PAUP*. Phylogenetic analysis using parsimony (* and other methods), version 4. Sunderland, Massachusetts: Sinauer Associates http://paup.sc.fsu.edu/. Last accessed 11 November 2016.

Swofford DL, Olsen GJ, Waddell PJ, Hillis DM. 1996. Phylogenetic inference. In: Hillis DM, Moritz C, Mable Bs (eds.), Molecular systematics: 407-514. Sinauer, Sunderland, Massachusetts.

Swofford DL, Waddell PJ, Huelsenbeck JP, Foster PG, Lewis PO, Rogers JS. 2001. Bias in Phylogenetic estimation and its relevance to the choice between parsimony and likelihood methods. Systematic Biology 50: 525-539.

Talavera G, Castresana J. 2007. Improvement of phylogenies after removing divergent and ambiguously aligned blocks from protein sequence alignments. Systematic Biology 56: 564-577.

Tchouto MGP, Yemefack M, De Boer WF, De Wilde JJFE, Van Der Maesen LJG, Cleef AM. 2006. Biodiversity hotspots and conservation priorities in the Campo-Ma'an rain forests, Cameroon. Biodiversity & Conservation 15: 1219-1252.

Theißen G. 2009. Saltational evolution: hopeful monsters are here to stay. Theory in Biosciences 128: 43-51.

Thiers B. Continuously updated. Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. http://sweetgum.nybg.org/science/ih/.

Thomas DC, Surveswaran S, Xue B, Sankowsky G, Mols JB, Keßler PJA, Saunders RMK. 2012. Molecular phylogenetics and historical biogeography of the *Meiogyne-Fitzalania* clade (Annonaceae): Generic paraphyly and late Miocene-Pliocene diversification in Australasia and the Pacific. Taxon 61: 559-575.

Thorne JL, Kishino H, Painter IS. 1998. Estimating the rate of evolution of the rate of molecular evolution. Molecular Biology and Evolution 15: 1647-1657.

Thwaites GHK, Hooker JD. 1864. Enumeratio plantarum Zeylaniae Dulau, London.

Turland NJ, Wiersema JH, Barrie FR, et al. (eds). 2018. *International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017.* Regnum Vegetabile 159. DOI https://doi.org/10.12705/Code.2018.

Turner I. 2012. Annonaceae of Borneo: A review of the climbing species. Gardens' Bulletin Singapore 64: 371-479.

Urquía D, Gutierrez B, Pozo G, Pozo MJ, Espín A, Torres MdL. 2019. *Psidium guajava* in the Galapagos Islands: Population genetics and history of an invasive species. PLOS ONE 14: e0203737.

Valenta K, Brown KA, Rafaliarison RR, Styler SA, Jackson D, Lehman SM, Chapman CA, Melin AD. 2015. Sensory integration during foraging: the importance of fruit hardness, colour, and odour to brown lemurs. Behavioral Ecology and Sociobiology 69: 1855–1865.

van 't Padje A. 2013. The evolution of lianas in the tropical plant family Annonaceae. Wageningen University, Biosystematics Group, Bachelor Thesis, Wageningen.

Van Eck H, Ham C, van Wyk G. 1997. Survey of indigenous tree uses and preferences in the Eastern Cape Province. Southern African Forestry Journal 180: 61–64.

van Gemerden BS, Olff H, Parren MPE, Bongers F. 2003. The pristine rain forest? Remnants of historical human impacts on current tree species composition and diversity. Journal of Biogeography 30: 1381-1390.

Van Heusden E. 1992. Flowers of annonaceae. Blumea Supplement 7: 1-218.

van Marle EJ. 2003. Leaf anatomy of *Pseudoxandra*. In: Maas PJM, Westra LYT, Revision of the neotropical genus *Pseudoxandra* (Annonaceae). Blumea 48: 206–211.

van Setten AK, Koek-Noorman J. 1986. Studies in Annonaceae. VI. A leaf-anatomical survey of genera of Annonaceae in the Neotropics. Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 108: 17–50.

Van Setten AK, Koek-Noorman J. 1992. Fruits and seeds of Annonaceae: Morphology and its significance for classification and identification. Studies in Annonaceae XVII. Bibliotheca Botanica 142: 1-101.

van Steenis CGGJ. 1964. An account of the genera *Richella* A. Gray and *Oxymitra* (Bl.) Hook.f. & Th. (Annonaceae). Blumea 12: 353–361.

Van Wyk BE. 2011. The potential of South African plants in the development of new food and beverage products. South African Journal of Botany 77: 857–868.

Venditti C, Pagel M. 2010. Speciation as an active force in promoting genetic evolution. Trends in Ecology & Evolution 25: 14-20.

Verdcourt B. 1971a. Annonaceae. In: Milne-Redhead E, Polhill RMs (eds.), Flora of tropical East Africa: 1–132. East African Community by the Crown Agents for Oversea Governments and Administrations, London.

Verdcourt B. 1971b. Notes on east African Annonaceae. Kew Bulletin 25: 1–34.

Verdcourt B. 1986. New taxa of East African Annonaceae. Kew bulletin 41: 287–297.

Versteegh CPC, Sosef MSM. 2007. Revision of the African genus *Annickia* (Annonaceae). Systematics and Geography of Plants 77: 91–118.

Walker-Larsen J, Harder LD. 2000. The evolution of staminodes in angiosperms: patterns of stamen reduction, loss, and functional re-invention. American Journal of Botany 87: 1367-1384.

Walker JW. 1971a. Contributions to the pollen morphology and phylogeny of the Annonaceae. I. Grana 11: 45-54.

Walker JW. 1971b. Pollen morphology, phytogeography, and phylogeny of the Annonaceae. Contributions from the Gray Herbarium of Harvard University: 1-130.

Wang J, Chalermglin P, Saunders RMK. 2009. The genus *Dasymaschalon* (Annonaceae) in Thailand. Systematic Botany 34: 252-265.

Wang J, Thomas DC, Su YCF, Meinke S, Chatrou LW, Saunders RMK. 2012. A plastid DNA phylogeny of *Dasymaschalon* (Annonaceae) and allied genera: Evidence for generic non-monophyly and the parallel evolutionary loss of inner petals. Taxon 61: 545–558.

Warren D, Geneva A, Swofford D, Lanfear R. 2016. rwty: R We There Yet. https://CRAN.R-project.org/package=rwty. Last.

Waser NM, Campbell DR. 2004. Ecological speciation in flowering plants. In: Tautz D, Metz JAJ, Doebeli M, Dieckmann Us (eds.), Adaptive Speciation: 264-277. Cambridge University Press, Cambridge.

Waterman PG, Pootakahm K. 1979a. Chemical studies on the Annonaceae–V. The Flavonoids of the Fruit of *Popowia cauliflora* Chipp. Planta Medica 35: 366–369.

Waterman PG, Pootakahm K. 1979b. Chemical studies on the annonaceae. VI. The alkaloids of the stem and fruit of *Monanthotaxis cauliflora*. Planta Medica 37: 247-252.

Weberling F, Hoppe JR. 1996. Comparative morphological evaluation of inflorescence characters in Annonaceae. In: Morawetz W, Winkler H (eds), Reproductive morphology in Annonaceae: 29–53. Österreichische Akademie der Wissenschaften, Vienna.

Webster AJ, Payne RJH, Pagel M. 2003. Molecular phylogenies link rates of evolution and speciation. Science 301: 478-478.

Wekesa C, Ndalilo L, Ongugo P, Leley N, Swiderska K. 2015. Traditional knowledge based innovations for adaptation and resilience to climate change: the case of coastal Kenya. XIV World Forestry Congress, Durban.

Wendel J, Doyle J. 1998. Phylogenetic incongruence: Window into genome history and molecular evolution. In: Soltis P, Soltis D, Doyle Js (eds.), Molecular Systematics of Plants II: 265 - 296. Kluwer Academic Press, Dordrecht.

Wertheim JO, Fourment M, Kosakovsky Pond SL. 2012. Inconsistencies in estimating the age of HIV-1 subtypes due to heterotachy. Molecular Biology and Evolution 29: 451-456.

Whittle C-A, Johnston MO. 2003. Broad-scale analysis contradicts the theory that generation time affects molecular evolutionary rates in plants. Journal of Molecular Evolution 56: 223-233.

Wicke S, Müller KF, de Pamphilis CW, Quandt D, Wickett NJ, Zhang Y, Renner SS, Schneeweiss GM. 2013. Mechanisms of functional and physical genome reduction in photosynthetic and nonphotosynthetic parasitic plants of the broomrape family. The Plant Cell 25: 3711-3725.

Wicke S, Schäferhoff B, dePamphilis CW, Müller KF. 2014. Disproportional plastome-wide increase of substitution rates and relaxed purifying selection in genes of carnivorous Lentibulariaceae. Molecular Biology and Evolution 31: 529-545.

Wicke S, Schneeweiss GM, dePamphilis CW, Müller KF, Quandt D. 2011. The evolution of the plastid chromosome in land plants: gene content, gene order, gene function. Plant Molecular Biology 76: 273-297.

Wild H. 1959. (61) *Enneastemon* Exell (1932) versus *Clathrospermum* Planchon ex Bentham (1862). Taxon 8: 30.

Wolf YI, Koonin EV. 2013. Genome reduction as the dominant mode of evolution. BioEssays 35: 829-837.

Wolfe KH, Li WH, Sharp PM. 1987. Rates of nucleotide substitution vary greatly among plant mitochondrial, chloroplast, and nuclear DNAs. Proceedings of the National Academy of Sciences of the United States of America 84: 9054-9058.

Woolfit M, Bromham L. 2003. Increased rates of sequence evolution in endosymbiotic bacteria and fungi with small effective population sizes. Molecular Biology and Evolution 20: 1545-1555.

Woolfit M, Bromham L. 2005. Population size and molecular evolution on islands. Proceedings of the Royal Society of London. Series B: Biological Sciences 272: 2277-2282.

Wyman SK, Jansen RK, Boore JL. 2004. Automatic annotation of organellar genomes with DOGMA. Bioinformatics 20: 3252-3255.

Xie W, Lewis PO, Fan Y, Kuo L, Chen M-H. 2011. Improving marginal likelihood estimation for bayesian phylogenetic model selection. Systematic Biology 60: 150-160.

Xue B, Su YCF, Thomas DC, Saunders RMK. 2012. Pruning the polyphyletic genus *Polyalthia* (Annonaceae) and resurrecting the genus *Monoon*. TAXON 61: 1021-1039.

Yang Y, Moore MJ, Brockington SF, Soltis DE, Wong GK-S, Carpenter EJ, Zhang Y, Chen L, Yan Z, Xie Y, Sage RF, Covshoff S, Hibberd JM, Nelson MN, Smith SA. 2015. Dissecting

molecular evolution in the highly diverse plant clade Caryophyllales using transcriptome sequencing. Molecular Biology and Evolution 32: 2001-2014.

Yang Z. 2007a. PAML 4: a program package for phylogenetic analysis by maximum likelihood. Molecular Biology and Evolution 24.

Yang Z. 2007b. PAML 4: Phylogenetic analysis by maximum likelihood. Molecular Biology and Evolution 24: 1586-1591.

Yang Z, Rannala B. 1997. Bayesian phylogenetic inference using DNA sequences: a Markov Chain Monte Carlo Method. Molecular Biology and Evolution 14: 717-724.

Yang Z, Wong WSW, Nielsen R. 2005. Bayes empirical bayes inference of amino acid sites under positive selection. Molecular Biology and Evolution 22: 1107-1118.

Zhang Z-Q, Christenhusz MJ, Esser H-J, Chase MW, Vorontsova MS, Lindon H, Monro A, Lumbsch HT. 2014. The making of world's largest journal in systematic botany. Phytotaxa 191: 1-9.

Zheng T, Ichiba T, Morton BR. 2007. Assessing substitution variation across sites in grass chloroplast DNA. Journal of Molecular Evolution 64: 605-613.

Zhong B, Deusch O, Goremykin VV, Penny D, Biggs PJ, Atherton RA, Nikiforova SV, Lockhart PJ. 2011. Systematic error in seed plant phylogenomics. Genome Biology and Evolution 3: 1340-1348.

Zhou L, Su YC, Saunders RM. 2009. Molecular phylogenetic support for a broader delimitation of *Uvaria* (Annonaceae), inclusive of *Anomianthus*, *Cyathostemma*, *Ellipeia*, *Ellipeiopsis* and *Rauwenhoffia*. Systematics and Biodiversity 7: 249–258.

Zhu A, Guo W, Jain K, Mower JP. 2014. Unprecedented heterogeneity in the synonymous substitution rate within a plant genome. Molecular Biology and Evolution 31: 1228-1236.

Zuckerkandl E, Pauling L. 1965. Evolutionary divergence and convergence in proteins. In: Bryson V, Vogel HJs (eds.), Evolving genes and proteins: 97-166. Academic Press, New York.

Summary

The family Annonaceae consists of woody plants and are mostly restricted to tropical rain forests. In these forests it is one of the most speciose and abundant plant families, making it an important family for understanding the diversity, ecology and evolution of tropical plants.

The two most important subfamilies of the Annonaceae are the Annonoideae and the Malmeoideae. These subfamilies are sister groups and together contain over 95% of Annonaceae species. Already in the first phylogenies published a remarkable difference between the branch lengths of these subfamilies became apparent. This suggests a difference in the rate of evolution between these subfamilies. Lineage-specific rate heterogeneity could mislead phylogenetic inferences with currently available models. In chapter 2 these differences in the molecular rate of evolution within the family Annonaceae were studied. Using high-throughput sequencing data 72 genes, 99 spacers and 16 introns from 24 chloroplast genomes and nuclear ribosomal DNA of 23 species were used to compare the rate of evolution between the two major sister subfamilies of the Annonaceae, the Annonoideae and Malmeoideae. In all analyses we found higher substitution rates for the Annonoideae compared to the Malmeoideae. Also the size of the chloroplast genome varied widely, with larger sizes for the Annonoideae compared to the Malmeoideae. Furthermore, values for omega (dN/dS)-ratios were higher for Annonoideae than the Malmeoideae. This could indicate less stringent purifying (negative) selection in the Annonoideae, a pattern that occurs in groups with small population sizes.

The genus *Monanthotaxis* belongs to the faster evolving subfamily Annonoideae. It is the second most species rich genus of Annonaceae in Africa. Before studying the evolution of the genus a firm taxonomic foundation is needed. This is realised in chapter 3 and 4.

The generic boundaries and phylogenetic relationships of *Monanthotaxis* and related genera were not clear with the genus *Friesodielsia* even being polyphyletic. In chapter 3 this was studied using two nuclear and five chloroplast DNA regions of 101 taxa. Bayesian, maximum likelihood and maximum parsimony analyses revealed that the species of *Friesodielsia* formed five distinct clades. To ensure strict monophyly of the genera, the name *Friesodielsia* was restricted to the Asian clade, while one of the African species formerly assigned to *Friesodielsia* was transferred to the genus *Afroguatteria*, one other to the genus Sphaerocoryne and the other 8 African species to the genus *Monanthotaxis*. Further, two monospecific genera, *Exellia* and *Gilbertiella*, were synonymised with *Monanthotaxis*, rendering the genus *Monanthotaxis* monophyletic.

In chapter 4 the continental African species of *Monanthotaxis* were revised. This includes 79 species and one variety of which 13 species were newly described. Ten additional species were described previously in this PhD project. In this chapter a key for flowering material was provided and a synoptic key including 45 characters. Topics included in the revision are the history of the taxonomy of *Monanthotaxis*, morphology, leaf anatomy, floral biology, distribution and habitat, phylogeny and finally ethnobotany and phytochemistry. Each species was fully described including synonymy, notes on distribution, habitat & ecology, vernacular names, uses and a preliminary IUCN conservation status.

Based on this taxonomic foundation, the floral evolution of *Monanthotaxis* was studied in chapter 5. In the plant family Annonaceae, flowers generally have six petals and many stamens and carpels. In the genus *Monanthotaxis* several deviations from this pattern have been observed, some flowers only contain three petals and three stamens. Five chloroplast and two nuclear DNA regions were used of 72 out of 94 *Monanthotaxis* species to reconstruct a phylogeny of the genus. Four quantitative and two qualitative floral characters were mapped onto this phylogeny. A strong correlation between petal size, stamen and carpel number showed a reduction in flower size and number of floral parts within the genus *Monanthotaxis.* The large variation in stamen shape and numbers combined with a non-gradual mode of evolution and sympatric co-occurrence of *Monanthotaxis* species from different clades suggest that the high diversity in the African rainforest of this genus is caused by switches in pollination systems.

Samenvatting

De plantenfamilie Annonaceae bestaat uit houtige planten en komt voornamelijk voor in tropische regenwouden. In deze bossen is het een van de meest soortenrijke en abundante plantenfamilies, waardoor het een belangrijke familie is voor het begrijpen van de diversiteit, ecologie en evolutie van tropische planten.

De twee belangrijkste onderfamilies van de Annonaceae zijn de Annonoideae en de Malmeoideae. Deze onderfamilies zijn zustergroepen die samen meer dan 95% van de soorten van Annonaceae bevatten . Al in de eerste gepubliceerde fylogenieën was een opmerkelijk verschil tussen de taklengtes van deze onderfamilies duidelijk. Dit suggereert een verschil in de snelheid van evolutie tussen deze subfamilies. Variatie in de evolutiesnelheid van verschillende takken zouden tot foutieve fylogenetische reconstructies kunnen leiden met de huidig beschikbare modellen. In hoofdstuk 2 werden deze verschillen in de moleculaire evolutiesnelheid binnen de familie Annonaceae bestudeerd. Met behulp van data van 'high-throughput sequencing' werden 72 genen, 99 spacers en 16 introns van 24 chloroplastgenomen en nucleair ribosomaal DNA van 23 soorten gebruikt om de evolutiesnelheid te vergelijken tussen de Annonoideae en Malmeoideae. In alle analyses vonden we hogere substitutiesnelheden voor de Annonoideae in vergelijking met de Malmeoideae. Ook de grootte van het chloroplast genoom varieerde sterk, met grotere lengtes voor de Annonoideae in vergelijking met de Malmeoideae en de Annonoideae hadden hogere omega (dN/dS)-ratio's dan de Malmeoideae. Dit zou kunnen wijzen op een minder sterke zuiverende (negatieve) selectie in de Annonoideae, een patroon dat voorkomt in groepen met kleine populatiegroottes.

Het genus *Monanthotaxis* behoort tot de sneller evoluerende onderfamilie Annonoideae. Het is het op één na meest soortenrijke genus van Annonaceae in Afrika. Voordat de evolutie van het genus kan worden bestudeerd, is een stevige taxonomische basis nodig. Dit is gerealiseerd in hoofdstuk 3 en 4.

De grenzen van de genera en fylogenetische relaties van *Monanthotaxis* en verwante geslachten waren niet duidelijk en het genus *Friesodielsia* was zelfs polyfyletisch. In hoofdstuk 3 werd dit bestudeerd met behulp van twee nucleaire en vijf chloroplast-DNA-regio's van 101 taxa. Bayesiaanse, 'maximum likelihood' en maximum parsimonie analyses onthulden dat de soorten van *Friesodielsia* vijf verschillende clades vormden. Om monofylie van de genera te bewerkstelligen, werd de naam *Friesodielsia* beperkt tot de Aziatische clade. Eén van de Afrikaanse soorten die voorheen tot *Friesodielsia* behoorde, hoort nu tot het genus *Afroguatteria*, een tweede soort tot het genus *Sphaerocoryne*, en de overige acht Afrikaanse soorten behoren nu tot het genus *Monanthotaxis*. Verder werden twee monospecifieke

genera, *Exellia* en *Gilbertiella*, gesynonimiseerd met *Monanthotaxis*, waardoor het genus *Monanthotaxis* nu monofyletisch is.

In hoofdstuk 4 werden de continentale Afrikaanse soorten van *Monanthotaxis* gereviseerd. Dit genus bevat 79 soorten (en één variëteit), waarvan er 13 nieuw zijn beschreven. Eerder in dit PhD-project werden tien bijkomende soorten beschreven. In dit hoofdstuk staan een determinatiesleutel voor bloeiend materiaal en een synoptische sleutel met 45 kenmerken. Onderwerpen die in deze revisie zijn opgenomen zijn de geschiedenis van de taxonomie van *Monanthotaxis*, de morfologie, de bladanatomie, de bloembiologie, de verspreiding en habitat, de fylogenie, ethnobotanie en fytochemie van *Monanthotaxis*. Elke soort wordt volledig beschreven, inclusief synoniemen, opmerkingen over verspreiding, habitat en ecologie, lokale namen, gebruik en een voorlopige IUCN-beschermingsstatus.

Gebruik makend van deze taxonomische basis werd de bloemenevolutie van *Monanthotaxis* bestudeerd in hoofdstuk 5. In de plantenfamilie Annonaceae hebben bloemen over het algemeen zes kroonbladen en veel meeldraden en vruchtbladen. In het genus *Monanthotaxis* komen verschillende variaties op dit patroon voor, sommige soorten hebben bloemen met maar drie kroonbladen en drie meeldraden per bloem. Vijf chloroplast en twee nucleaire DNA-regio's werden gesequeneerd voor 72 van de 94 *Monanthotaxis* soorten om een fylogenie van het genus te reconstrueren. Vier kwantitatieve en twee kwalitatieve kenmerken van de bloemen werden in kaart gebracht op deze fylogenie. Een sterke correlatie tussen de grootte van het kroonblad, aantal meeldraden en vruchtbladen toonde een afname in bloemgrootte en aantal bloemdelen binnen het genus *Monanthotaxis*. De grote variatie in vormen en aantallen meeldraden, in combinatie met een niet-graduele wijze van evolutie en het sympatrisch voorkomen van *Monanthotaxis*-soorten uit verschillende clades, suggereert dat de grote diversiteit in het Afrikaanse regenwoud van dit genus wordt veroorzaakt door veranderingen in bestuivingstypes.

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About the author



Paul was born on 20 January 1986 in Linschoten and he grew up in Beusichem. At the age of 8 he became very interested in nature, especially birds and soon his interests expanded to butterflies, plants and mushrooms. At the age of 16 he joined the Dutch youth society for Nature studies (NJN) and later on he started to search and identify almost everything in nature for which he could get literature. In 2004 he started his bachelor in Biology with a specialization in Ecology at the University of Wageningen, followed by his MSc at the same university. For his first Master thesis he studied the performance of biodiversity assessment methods and estimates of biodiversity using a rapid collection assessment applied to Gabon at the department of Biosystematics under supervision of Dr. Jan Wieringa. For his second master thesis he studied the effects of habitat fragmentation on bird species composition and configuration in Yucatan, Mexico at the Resource Ecology group under the supervision of Dr. Fred de Boer and at CICY in Mérida, Mexico under the supervision of Dr. Eurídice Leyequién. He also did an internship during his MSc at Naturalis Biodiversity Center in Leiden under the supervision of Prof. Dr. Menno Schilthuizen studying the phylogenetics of the microsnail *Gyliotrachela hungerfordiana*. After finishing his MSc he first did some plant inventories for Ekoza and Aquasense before heading to Mexico where he worked as a database manager for the seed bank of useful and rare plants of Southeast Mexico. Returning to the Netherlands he started his PhD at the Naturalis Biodiversity Center and the Biosystematics group of the Wageningen University. Currently he is working on insects and acari as a taxonomist at Eurofins MITOX and as a freelancer he does plant inventories.

List of publications

Hoekstra PH, Wieringa JJ, Maas PJM, Chatrou LW. 2021. Revision of the African species of *Monanthotaxis* (Annonaceae). Blumea 66: 107-221.

Verheyde F, **Hoekstra P**, Libert P-N, Meijer H, De Ketelaere A, Vandaudenard T, Belgers D, Brosens E. 2021. Two hundred and five ichneumonid wasps reported for the first time in Belgium and the Netherlands (Hymenoptera: Ichneumonidae). Belgian Journal of Entomology 122: 1-142.

Faraji F, **Hoekstra PH**. 2021. Some new species records of the predatory mite family Phytoseiidae (Acari: Mesostigmata) from the Netherlands. Soil Organisms 93: 35-57.

Faraji F, **Hoekstra PH**. 2021. Discovery of two phytoseiid species (Acari: Mesostigmata): First records for Germany and Spain with the proposal of a synonymy. Revista ibérica de aracnología 38: 31-35.

Bieman CFM, **Hoekstra PH**. 2021. The Psyllid *Agonoscena succincta* new to the Netherlands (Hemiptera, Aphalaridae). Entomologische berichten 81: 52-54.

Hoekstra PH, Wieringa JJ, Smets E, Chatrou LW. 2018. Floral evolution by simplification in *Monanthotaxis* (Annonaceae) and hypotheses for pollination system shifts. Scientific Reports 8: 12066.

Hoekstra PH, Wieringa JJ, Smets E, Brandão RD, Lopes JdC, Erkens RHJ, Chatrou LW. 2017. Correlated evolutionary rates across genomic compartments in Annonaceae. Molecular Phylogenetics and Evolution 114: 63-72.

Guo X*, **Hoekstra PH***, Tang CC, Thomas DC, Wieringa JJ, Chatrou LW, Saunders RMK. 2017. Cutting up the climbers: Evidence for extensive polyphyly in *Friesodielsia* (Annonaceae) necessitates generic realignment across the tribe Uvarieae. Taxon 66: 3-19. *These authors contributed equally to this work.

Tetetla-Rangel E, Dupuy JM, Hernández-Stefanoni JL, **Hoekstra PH**. 2017. Patterns and correlates of plant diversity differ between common and rare species in a Neotropical dry forest. Biodiversity and Conservation 26: 1705-1721.

Hoekstra PH, Wieringa JJ, Chatrou LW. 2016. A nonet of novel species of *Monanthotaxis* (Annonaceae) from around Africa. PhytoKeys: 71-103.

Hoekstra PH, Chatrou LW, Wieringa JJ. 2014. A new species of *Monanthotaxis* from Gabon with a unique inflorescence type for Annonaceae. Phytotaxa 186: 106-112.

Hoekstra P, Schilthuizen M. 2011. Phylogenetic relationships among isolated populations of the limestone-dwelling microsnail Gyliotrachela hungerfordiana (Gastropoda: Vertiginidae). Journal of zoological systematic and evolutionary research 49: 266-

PE&RC Training and Education Statement

With the training and education activities listed below the PhD candidate has complied with the requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)

Review of literature (6 ECTS)

- The evolution of niches, a case study in *Annonaceae*

Post-graduate courses (5.5 ECTS)

- Current trends in phylogenetics; Biosystematics group, WUR (2013)
- The Science of conservation; PE&RC (2016)

Laboratory training and working visits (5.1 ECTS)

- Herbarium visits and morphological and taxonomic work; Muséum National d'histoire naturelle Paris & Royal Botanic Gardens Kew, British Museum London, Herbarium Meise (2013)
- Herbarium visits and morphological and taxonomic work; Muséum National d'histoire naturelle Paris & Université Libre de Bruxelles Herbarium (2016)

Invited review of journal manuscripts (2 ECTS)

- Taxon: species delimitation in the genus *Greenwayodendron* (2018)
- European journal of Taxonomy: phylogeny and taxonomy of genus *Winitia* (2019)

Deficiency, refresh, brush-up courses (3 ECTS)

- Plant families of the tropics; Leiden University/Naturalis (2013)

Competence strengthening / skills courses (3.3 ECTS)

- Competence assessment; WGS (2013)
- Improve your writing; WGS (2013)
- General research skills for PhDs'; Leiden University/Naturalis (2015)

PE&RC Annual meetings, seminars and the PE&RC weekend (1.2 ECTS)

- PE&RC First year weekend (2014)
- PE&RC Day (2014)

Discussion groups / local seminars or scientific meetings (7.5 ECTS)

- Journal club biosystematics (2013)
- Naturalis seminars (2014-2016)
- Understanding evolution (2015-2016)

International symposia, workshops and conferences (7.5 ECTS)

- AETFAT Congress; South Africa (2014)
- JSTP Annonaceae workshop; China (2015)
- Botany congress; Georgia (2016)

Lecturing / supervision of practicals / tutorials (3 ECTS)

- European flora and fauna
- Webs of terrestrial diversity

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