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Léo-Paul Dagallier

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# THÈSE POUR OBTENIR LE GRADE DE DOCTEUR DE L'UNIVERSITÉ DE MONTPELLIER

En Sciences de l'évolution et de la Biodiversité

École doctorale GAIA

Unité de recherche DIADE

## DIVERSIFICATION OF THE TROPICAL AFRICAN FLORA: SPATIAL AND TEMPORAL APPROACHES

Présentée par Léo-Paul DAGALLIER  
Le 9 décembre 2021

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UNIVERSITÉ  
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# Diversification of the tropical African flora: spatial and temporal approaches



Léo-Paul M. J. Dagallier

2018 – 2021

# Abstract

This thesis investigates the diversification of the tropical African flora, through different spatial and temporal approaches. The current patterns of distribution of the species across the continent are the result of various environmental changes, and we investigated how these changes affected the flora using the geographical distribution of the species, molecular phylogenies, and several various biogeographic and diversification models. The thesis can be divided in 2 great parts of different spatial and taxonomic scales.

The first part is at large geographical and taxonomic scale, and focuses on the whole flora across the continent. In the Chapter 2, we described the patterns of plant endemism in tropical Africa, and identified ‘cradles’ (regions with significantly more recently diverged taxa) and ‘museums’ (regions with significantly more anciently diverged taxa) of angiosperm diversity at the generic level. We show that the montane areas of the biogeographically complex region of Eastern Africa are both cradles and museums of diversity, underlining the important role played by mountains in the diversification of the flora. In contrast, the Guineo-Congolian lowland rain forest region is characterised by widespread and old lineages.

The second part of the thesis reduces the geographical and taxonomic scales. It focuses on the species rich African tropical rain forests (TRF) and their evolution, informed by the study of the Monodoreae tribe (Annonaceae), a clade of 92 plant species restricted to the TRF. To do so, the systematic and taxonomy of the Monodoreae need to be well resolved, especially for the two genera *Uvariadendron* and *Uvariopsis* that lack a recent revision. Thus, the Chapter 3 is dedicated to the systematic of the Monodoreae, for which we reconstructed a robust phylogenetic tree using more than 300 nuclear genes. Our results support systematic changes, such as the erection of the Ophryptealeae tribe, the reinstatement of the monotypic genus *Dennettia* Baker f., and several species description and name synonymies in *Uvariadendron* and *Uvariopsis*. In addition, the Chapter 4 is dedicated to the taxonomic revision of the aforementioned *Uvariadendron* and *Uvariopsis* genera. Based on the examination of more than 800 herbarium specimens, we provide a description for every species, including several newly described species. We also discuss their morphology, pollination biology, seed dispersal and uses, and provide maps of their geographical distributions. Finally, the Chapter 5 investigates the biogeography and the diversification of the African TRF, focusing on the Monodoreae. We reconstructed a fossil-calibrated molecular phylogeny of the tribe in a Bayesian framework, and applied several models of biogeography and diversification to test the impact of past environmental changes on the evolution of the tribe. We found that the Monodoreae originated in East African TRF ca. 25 million years ago (Ma), and

expanded toward Central-Africa during the early to middle Miocene, supporting the existence of an African TRF extending from East to West until ca. 13.5 Ma. We found no evidence for discrete and synchronous vicariance events in the TRF during the middle Miocene, but we inferred range contractions possibly due to aridification in Africa, but with TRF blocks more connected than previously thought during the middle Miocene. The Monodoreae likely experienced a sudden extinction during the late Miocene, supporting that aridification of tropical Africa led to drastic reduction of the TRF. Just after the sudden extinction, we inferred high speciation rates, suggesting that both the fragmentation and the following re-connection of the TRF in the early Pliocene stimulated diversification. Such a high diversification was likely associated with the increasing African paleo-elevation during the late Miocene and Pliocene, supporting the idea that the uplift of East Africa was a factor that promoted diversification.

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# Chapter 1 | Introduction

## 1. Context

Biodiversity, or ‘biological diversity’, is the concept that represents all the living organisms, from genes to ecosystems, and encompasses their variability and complexity (McNeely *et al.*, 1990). Biodiversity is undergoing a critical crisis due to climate change and human activities, leading to the scientific consensus that biodiversity is facing its sixth mass extinction (Barnosky *et al.*, 2011; Pimm *et al.*, 2014). Managing this crisis to avoid biodiversity and humanity collapse is probably one of the most important challenge the humans will have to face (Ceballos & Ehrlich, 2018).

### 1.1. The present and the future

To face this challenge, the biodiversity sciences are continuously expanding our knowledge’s boundaries. Studies that describe the present day biodiversity are paramount for establishing the state of the art of biodiversity. Species unknown to science<sup>1</sup> are continuously discovered and described (e.g. Dagallier *et al.*, 2021; Sharkey *et al.*, 2021; Zhurbenko *et al.*, 2021), and the estimates of undescribed species are around 15% for flowering plants (Joppa *et al.*, 2011) and range from 21 to 86% for the whole terrestrial biodiversity (Mora *et al.*, 2011; Costello *et al.*, 2012). Beyond describing species, assessing the degree to which they are threatened with extinction is important in order to implement adequate conservation policies (Margules & Pressey, 2000). To date, 28% of the described and assessed species are threatened with extinction (IUCN, 2020). Similarly, some regions of the world, mainly in tropical regions, are considered as ‘biodiversity hotspots’ as they harbor a great amount of threatened and irreplaceable biodiversity (Myers *et al.*, 2000; Sechrest *et al.*, 2002).

Predictive studies that infer how biodiversity might respond to climate changes in the future are also of great importance to anticipate and prepare to the global changes (e.g. Bellard *et al.*, 2012; Réjou-Méchain *et al.*, 2021; Saatchi *et al.*, 2021). It has been suggested that in order to preserve the adaptive potential of biodiversity (to preserve the ‘evolutionary potential’), we should not only consider the species as simple units of biodiversity, but we should also focus on their evolutionary history and preserve regions with species representing a lot of the Earth’s evolutionary history (i.e. with high phylogenetic diversity) (Sechrest *et al.*, 2002; Mace *et al.*, 2003; Forest *et al.*, 2007).

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<sup>1</sup> By ‘unknown to science’, I mean unknown to the science driven by Western institutions (Trisos *et al.*, 2021). Indeed, some species (if not many) might be known from the local communities (i.e. being part of the local science) (e.g. Whaanga *et al.*, 2013), but not described following the international standards (Turland *et al.*, 2018), and thus not being recognized as ‘known’ by the Western scientific community, although they are clearly locally ‘known’.

## 1.2. The past

Focusing on evolutionary history means looking into the past. Put in a broader context, we can say that our abilities to understand the present and forecast the future rely on our knowledge of the past. Indeed, current biodiversity is the result of millions of years of evolutionary history, that led to the variability and complexity of forms and functioning we observe now. Furthermore, it also led the biodiversity to be unevenly distributed on the planet, a feature that questioned the biogeographers since a long time (von Humboldt & Bonpland, 1805; de Candolle, 1820; Prichard, 1836; Sclater, 1858; Wallace, 1876). The distribution of biodiversity forms different biogeographical regions, i.e. regions of relative homogeneous species composition, also termed bioregions or ecoregions (Olson *et al.*, 2001; Kreft & Jetz, 2010). Some regions of the world, such as the tropics, harbor a greater number of species than in other parts of the world (Stevens, 1989; Barthlott *et al.*, 1996; Gaston, 2000; Mutke & Barthlott, 2005). Similarly, some regions such as the mountains or the islands, harbor a great number of species with restricted geographical distribution found nowhere else (i.e. endemic species) (Burgess *et al.*, 1998; Lamoreux *et al.*, 2006; Kier *et al.*, 2009; López-Pujol *et al.*, 2011; Rosauer & Jetz, 2015).

The current diversity patterns are the result of both biotic and abiotic factors that impacted the evolutionary history of the species (Benton, 2009; Ezard *et al.*, 2011; Smith *et al.*, 2014; Couvreur *et al.*, 2021). Biotic factors that influence speciation or extinction are related to the interaction between species (e.g. competition, mutualism) or to the intrinsic features of species (e.g. dispersal abilities to colonize new isolated regions, acquisition of characters leading to reproductive isolation) (Van Valen, 1973). The abiotic factors that influence speciation or extinction are related to the physical processes occurring on Earth such as geological movements and climate changes across the time (Benton, 2009).

When taking into account the temporal scale, some regions can be identified as ‘cradles’ of diversity, that is areas harboring significantly more recently diverged species than other regions. In contrast, ‘museums’ of diversity are defined as places where significantly more species have diverged anciently and persisted over time (López-Pujol *et al.*, 2011; Rangel *et al.*, 2018). For example, montane regions have been suggested to be both ‘cradles’ and ‘museums’ of diversity (López-Pujol *et al.*, 2011). They act as ‘cradles’ of diversity in having fragmented habitats that promote divergence by isolation of small populations (Hughes & Eastwood, 2006; Wen *et al.*, 2014; Schwery *et al.*, 2014; Merckx *et al.*, 2015), and as ‘museums’ of diversity as their complex topography supports relatively stable habitats that allow the persistence of the species over long periods of time (Peterson *et al.*, 1997; Fjeldså & Lovett, 1997; Hewitt, 2000; Tzedakis *et al.*, 2002; Loarie *et al.*, 2009; López-Pujol *et al.*, 2011; Tolley *et al.*, 2011).

### 1.3. Tropical Africa

Tropical Africa is a mosaic of several different bioregions, composed mainly of forested areas (lowland rain forests, montane rain forests) around the equator, surrounded by non-forested areas like grasslands, savannas or shrublands (White, 1983; Olson *et al.*, 2001; Mayaux *et al.*, 2004; Linder *et al.*, 2005; Sayre *et al.*, 2013; Droissart *et al.*, 2018). High species richness and centres of taxonomic endemism are found in Cameroon, Gabon, eastern Democratic Republic of the Congo (DRC), and eastern Tanzania (Linder, 2001; Küper *et al.*, 2004; Sosef *et al.*, 2017). It harbors some of the world's biodiversity hotspots, in coastal West and Central Africa around the Guinean gulf, in coastal East Africa and around the Great Lakes (Myers *et al.*, 2000; Küper *et al.*, 2004), and a third of its flora has been preliminary assessed as threatened with extinction (Stévant *et al.*, 2019). Geologically, tropical Africa is heterogeneous, with a great topographic variability in East Africa, and West and Central Africa relatively low in altitude, although presenting some montane regions like the Cameroon Volcanic Line (Guillocheau *et al.*, 2018). The second largest extent of tropical rain forest (TRF) in the world is found in the Guineo-Congolian region (Malhi *et al.*, 2013). In Africa, the TRF are divided in two major forested blocks of floristic affinities: West-Central and East TRFs (Couvreur *et al.*, 2008; Droissart *et al.*, 2018; Brée *et al.*, 2020).

### 1.4. Tropical rain forests and Annonaceae

TRF are evergreen tree dominated formations, with a closed and generally high canopy, under which grow numerous strata of understorey trees, shrubs and herbs, but also lianas and epiphytes (Whitmore, 1998; Corlett & Primack, 2011; Eiserhardt *et al.*, 2017). They grow under warm and humid climates with minimum 2000 mm of annual precipitations and 24°C of average annual temperature, and with generally no or very short dry season (less than four months with less than 100 mm of precipitation) (Morley, 2000; Hill & Hill, 2001). TRF harbor a great diversity of tree species from various emblematic plant families, such as the Arecaceae (Palms), Apocynaceae, Malvaceae, Melastomataceae, Moraceae, or Rubiaceae, just to name a few (Turner, 2001).

The Annonaceae is one of these emblematic tropical families (Chatrou *et al.*, 2012a). This family is mainly known for some of its species producing edible fruits (paw paw, soursop, custard apple, cherimoya; several *Annona* L. species), and for the ylang-ylang (*Cananga odorata* (Lam.) Hook.f. & Thomson) essential oil, widely used in aromatherapy and as a fragrance made famous by several luxury perfumeries (Couic-Marinier & Laurain-Mattar, 2019). Some other Annonaceae also show pharmacological properties (Takahashi *et al.*, 2006) and are used by the local communities for medicine, food and crafts (Focho *et al.*, 2010; Bele *et al.*, 2011). The Annonaceae is composed of ca. 2500 species and ca.

111 genera of trees, shrubs and lianas, and are mainly restricted to TRF (Chatrou *et al.*, 2012b; Guo *et al.*, 2017), which makes them a good model for studying the evolutionary history in the TRF (Couvreur *et al.*, 2008; Chatrou *et al.*, 2012a; Brée *et al.*, 2020). Several previous molecular analyses, have inferred the relationships within the family that helped to clarify the higher level systematics with several subfamilies and tribes (Richardson *et al.*, 2004; Pirie *et al.*, 2006; Couvreur *et al.*, 2011a, 2019; Chatrou *et al.*, 2012b; Guo *et al.*, 2017). Within the subfamily Annonoideae, the tribe Monodoreae (previously referred as “African long branch clade”) is composed of 11 genera and 92 species restricted to Africa and Madagascar (Guo *et al.*, 2017, Chapter 3). Monodoreae species are mainly TRF restricted with limited opportunities for long distance dispersal (see the introduction in Chapter 5), and the two species rich genera *Isolona* and *Monodora* were inferred to have mainly undergone geographical speciation (Couvreur *et al.*, 2011b). The Monodoreae can thus be viewed as a good proxy for understanding the geographical evolution and diversification of the TRF in Africa (Couvreur *et al.*, 2008). But proxies are debatable. Particularly, making extrapolations from studies on single clades to the whole flora, or from local scale process to continent scale processes might be a shortcut in our understanding of the evolution of the biodiversity. Indeed, in the African TRF, it has been shown that at the population level, instead of having a common response to environmental changes, the species have various and specific responses (Helmstetter *et al.*, 2020a).

## 2. The tools

### 2.1. Herbarium specimens as a base unit

Botanical exploration of the world over the past centuries brought back millions of dried plant specimens now archived in herbaria (James *et al.*, 2018). Herbarium specimens are highly valuable as they provide important data on the morphology of the plant, its collection history, geography, habitat and ecology, and vernacular names and uses. They are the base material for writing the taxonomic monographs, which are the gold standards for documenting the biodiversity (Grace *et al.*, 2021). Several institutions undertook to digitize the herbarium specimens and their associated data, and this is a step forward in biodiversity sciences as it greatly eases the access to such data (Le Bras *et al.*, 2017; Soltis, 2017). Data aggregators, such as the Global Biodiversity Information Facility (GBIF), also greatly help the data accessibility through centralization of the data, although such database should be used with extreme care (Maldonado *et al.*, 2015). In addition to such wide data sources, comprehensive geo-referenced and taxonomically checked databases bring ready-to-use high quality geographical datasets. For tropical Africa, this is the case of the RAINBIO database (Dauby *et al.*, 2016). This database contains more than 600'000 checked geo-referenced records representing more than 25'000 plant species, and

served as a basis for the enhancing our knowledge of tropical African plant biodiversity (Sosef *et al.*, 2017; Veranso-Libalah *et al.*, 2018; Droissart *et al.*, 2018; Cosiaux *et al.*, 2018; Demenou *et al.*, 2018; Pironon *et al.*, 2019; Stévant *et al.*, 2019). In the Chapter 2, we used this dataset to infer the patterns of angiosperm generic diversity and endemism accross Africa, and combined it to a ‘mega-phylogeny’ (see below) to infer the patterns of phylogenetic diversity and to identify cradles and museums of plant diversity (Chapter 2).

## 2.2. Molecular phylogenetics

Plant herbarium specimens are also source of another type of valuable data: the plants’ DNA. Although DNA contained in the dried herbarium plant specimen can be degraded (Staats *et al.*, 2011), quality extractions from herbarium specimens can be achieved thanks to optimized DNA extraction protocols (Taylor & Swann, 1994; Särkinen *et al.*, 2012), and short DNA fragments sequencing technologies (Metzker, 2010). The use of DNA in biodiversity sciences found enthusiasts for the identification of taxa, the so-called DNA-barcoding (Moritz & Cicero, 2004; Vijayan & Tsou, 2010), and also for reconstructing the evolutionary history of the species, via molecular evolution models (Fitch & Margoliash, 1967). The basic idea of molecular phylogenetic is that the degree of evolutionary divergence between two species is proportional with the differences in molecular sequences. From there, the field of phylogenetic grew up, and plenty of methods and tools were developed to infer the evolutionary history of the species (e.g. Sanderson, 2002; Posada, 2008; Smith & O’Meara, 2012; Stamatakis, 2014; Nguyen *et al.*, 2015; Bouckaert *et al.*, 2019; Bromham, 2019). Initially, the phylogenetic reconstruction were focused on a few taxa and used a few number of genes. The increase in sequence data availability -but also to the increase in computing performances- allowed the reconstruction of ‘mega-phylogenies’, i.e. phylogenetic trees containing thousands of species (Chase *et al.*, 1993; Hilu *et al.*, 2003), and an increasing number of genes (Hinchliff & Smith, 2014; Zanne *et al.*, 2014; Magallón *et al.*, 2015; Smith & Brown, 2018; Janssens *et al.*, 2020).

## 2.3. Phylogenomics

Advances in sequencing technologies (Mardis, 2008, 2013, 2017; Shendure & Ji, 2008; Metzker, 2010; Rohland & Reich, 2012; Hu *et al.*, 2021) allowed to sequence more and more genes, even complete genomes (Ng & Kirkness, 2010). This triggered great advances in phylogenetic studies with the rise of phylogenomics, i.e. phylogenetics with genome-scale sequence data (Eisen & Fraser, 2003; Scornavacca *et al.*, 2020). Thanks to the increasing availability of large-scale sequencing data for a wide array of non-model organisms (Ekblom & Galindo, 2011), phylogenomic approaches enhance our knowledge about the evolution of the tree (or trees) of life, bringing clarifications and asking new both biological

and methodological questions (e.g. Delsuc *et al.*, 2005; Pease *et al.*, 2018; Allio *et al.*, 2020; Smith *et al.*, 2020; Pavón-Vázquez *et al.*, 2021; Redmond & McLysaght, 2021; Valencia-Montoya *et al.*, 2021). In plants, several family specific phylogenomic tools, such as baiting kits for targeted sequencing, were developed to answer family specific questions (Barrett *et al.*, 2016; Heyduk *et al.*, 2016; Reginato *et al.*, 2016; Pease *et al.*, 2016; Morales-Briones *et al.*, 2018; Helmstetter *et al.*, 2020b; Koenen *et al.*, 2020; Stull *et al.*, 2020; Meleshko *et al.*, 2021). In the Chapter 3, we used such a kit developed specifically for the Annonaceae family (Couvreur *et al.*, 2019) to reconstruct a robust phylogenetic tree of the Monodoreae tribe based on more than 300 nuclear genes, to test the limits between the genera and the species. An angiosperm-specific baiting kit was also designed to allow targeted sequencing in any flowering plant clade (Johnson *et al.*, 2019), and it was shown that combining both angiosperm-specific and family-specific kits is a good strategy for bias mitigation in phylogeny reconstruction (Shah *et al.*, 2021; Yardeni *et al.*, 2021).

## 2.4. Molecular dating

A phylogenetic tree represents the evolutionary relationships between the species. However, in order to represent the evolutionary history of the clade in focus, the phylogenetic tree needs to be anchored in time. This is done with molecular dating and uses fossil calibration. The basic idea subtending molecular dating is that the divergence time between two species can be measured with the differences between two molecular sequences (DNA, protein), like a ‘molecular evolutionary clock’ (Zuckerkandl & Pauling, 1965). Though, the rates of molecule evolution are not constant through time, between the taxa, or between the genes, so ‘relaxed’ molecular clocks were developed to account this rate heterogeneity (Sanderson *et al.*, 2004; Drummond *et al.*, 2006; Rutschmann, 2006). The molecular clocks are then generally calibrated by geologically dated fossils to have a phylogenetic tree dated in a multi-million years timescale (Ho & Phillips, 2009; Sauquet, 2013).

## 2.5. Diversification models

A dated phylogenetic tree is a phylogram, basically a graph linking the species with their relationships and tempo of divergence from their ancestral node. From such graph, it is possible to infer the diversification dynamics of the clade represented. The diversification is the balance between the speciation (divergence of a new species) and extinction (disappearance of an extent species). A wealth of models has been developed to infer the diversification dynamics with a phylogenetic tree (Morlon, 2014), such as to model the variations in diversification rates between the species (Rabosky, 2014; Höhna *et al.*, 2019; Maliet *et al.*, 2019), to model the variation with time (Morlon *et al.*, 2011), with environmental variables (Condamine *et al.*, 2013), with species-specific morphological or geographical states

(Maddison *et al.*, 2007; FitzJohn, 2010, 2012; Goldberg *et al.*, 2011; Goldberg & Igić, 2012; Beaulieu & O’Meara, 2016; Caetano *et al.*, 2018; Nakov *et al.*, 2019), or to model tree-wide sudden changes in diversification rates (Stadler, 2011; May *et al.*, 2016). A common approach used in diversification modeling is to fit an array of different models on the estimated dated tree, and to infer to which model the observed data fit the best, in order to have an idea of under which of the modeled processes the data were likely generated (e.g. Condamine *et al.*, 2013).

Recently, it has been suggested that an infinity of diversification dynamics can be modeled from phylogenetic trees of extant taxa, due to unidentifiability of parameters in the models (Louca & Pennell, 2020). This led to be interpreted such as we should abandon such modeling (Pagel, 2020). However, Helmstetter *et al.* (2021) suggested that the unidentifiability issue might only apply for time-dependent, clade-independent models for which the exact values of the speciation and extinction rates cannot be estimated, but this might not apply for clade-specific or character-specific models, concluding we should continue exploring the use of these models, being aware of their limits (Helmstetter *et al.*, 2021). Moreover, in a hypotheses-driven framework, one is more interested about the relative fit of different scenarios than about the exact values of the parameters (Morlon *et al.*, 2020; Helmstetter *et al.*, 2021).

## 2.6. ‘All models are wrong, but some are useful’

From phylogenetic reconstruction to diversification models, several tools presented above rely on mathematical modeling. It is important to keep in mind that “all models are wrong, but some models are useful” (Box, 1979). The first part of this aphorism, “all models are wrong”, tells that given the complexity of biological systems, precisely modeling the ‘true’ process is impossible. The second part, “some models are useful”, tells that despite this complexity, some models can resolve concerns about the biological process in question, in being as close as possible of the ‘true’ process. The challenging matters are thus to inform as much as possible the model with our prior knowledge of the process, in order to build realistic and plausible models. For example, the development of the relaxed clock models for phylogenetic dating mentioned above (Drummond *et al.*, 2006), were designed upon the constant clock models (Zuckermandl & Pauling, 1965), integrating the prior knowledge that the rates of molecular evolution were not constant between the clades (Britten, 1986; Hasegawa & Kishino, 1989). Similarly, in the diversification models framework exposed above, the fitted models are likely oversimplifying the reality, and some unconsidered models might be closer to the ‘true’ process than the considered models (Louca & Pennell, 2020). However, our prior belief on the diversification dynamics reduces the range of fitted models (e.g. the models with negative speciation or extinction rates are

discarded as they are biologically impossible, even if they have a better fit), and as we build the compared models based on the prior hypotheses, we evaluate the relative fit (and not the absolute fit) of the different models, which ultimately inform on the most likely hypothesis (Morlon *et al.*, 2020).

The various models used and fitted along this thesis might not be modeling the exact ‘true’ biological processes in focus, but they reflect the ‘truth’ as much as possible in incorporating the best of our prior knowledge.

### 3. Thesis outline

In this thesis, I explored the past in order to understand the present, using different spatial and temporal scales. I do not pretend to present ‘the’ story about the tropical African flora, but instead ‘a’ story about its diversification. The thesis can be divided in 2 great parts. The first part is at large geographical and taxonomic scale, focusing on the whole flora across the continent. We described the patterns of plant endemism in tropical Africa, and identify what region act as ‘cradles’ and ‘museums’ of angiosperm diversity at the generic level (Chapter 2). The second part reduces the geographical and taxonomic scales, and focuses on the species rich African TRF and their evolution, informed by the study of the Monodoreae tribe. To do so, the systematic and taxonomy of the Monodoreae need to be well resolved, especially for the two genera *Uvariadendron* and *Uvariopsis* that lack a recent revision. Thus, the Chapter 3 is dedicated to the systematic of the Monodoreae, for which we reconstructed a robust phylogenetic tree using targeted sequencing data and explored the relationships between the species and genera. In addition, the Chapter 4 is dedicated to the taxonomic revision of the aforementioned *Uvariadendron* and *Uvariopsis* genera, with the description of all the species, including several newly described species. Finally, the Chapter 5 investigates the biogeography and the diversification of the African TRF, focusing on the Monodoreae. We reconstructed a time-calibrated molecular phylogeny of the tribe, and applied several models of biogeography and diversification to test the impact of past environmental changes on the evolution of the tribe.



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# Chapter 2 | Cradles and museums of generic plant diversity across tropical Africa\*

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**Abstract.** Determining where species diversify (cradles) and persist (museums) over evolutionary time is fundamental to understanding the distribution of biodiversity and for conservation prioritization. Here, we identify cradles and museums of angiosperm generic diversity across tropical Africa, one of the most biodiverse regions on Earth. Regions containing non-random concentrations of young (neo-) and old (paleo-) endemic taxa were identified using distribution data of 1719 genera combined with a newly generated time-calibrated mega-phylogenetic tree. We then compared the identified regions with the current network of African protected areas (PAs). At the generic level, phylogenetic diversity and endemism are mainly concentrated in the biogeographically complex region of Eastern Africa. We show that mountainous areas are centres of both neo- and paleo-endemism. In contrast, the Guineo-Congolian lowland rain forest region is characterised by widespread and old lineages. We found that overlap between centres of phylogenetic endemism and PAs is high (> 85%). We show the vital role played by mountains acting simultaneously as cradles and museums of tropical African plant biodiversity. In contrast, lowland rain forests act mainly as museums for generic diversity. Our study shows that incorporating large-scale taxonomically verified distribution datasets and mega-phylogenies lead to an improved understanding of tropical plant biodiversity evolution.

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# 1. Introduction

Understanding the ecological and evolutionary processes that shape biodiversity is crucial to establish conservation priorities (McNeely *et al.*, 1990; Myers *et al.*, 2000). Endemic taxa are defined as being geographically restricted and their spatial concentration often highlights evolutionary processes. Traditional methods have mainly focused on using taxonomic diversity, i.e. taxon richness, to depict biodiversity patterns. However, adding the evolutionary history allows a more detailed picture of such patterns (Faith, 1992; Forest *et al.*, 2007). Combining data from phylogenetic trees and taxon diversity enables the calculation of phylogenetic diversity (PD), i.e. the total length of branches of a phylogenetic tree connecting taxa in a particular area (Faith, 1992). Regions with high PD contain important

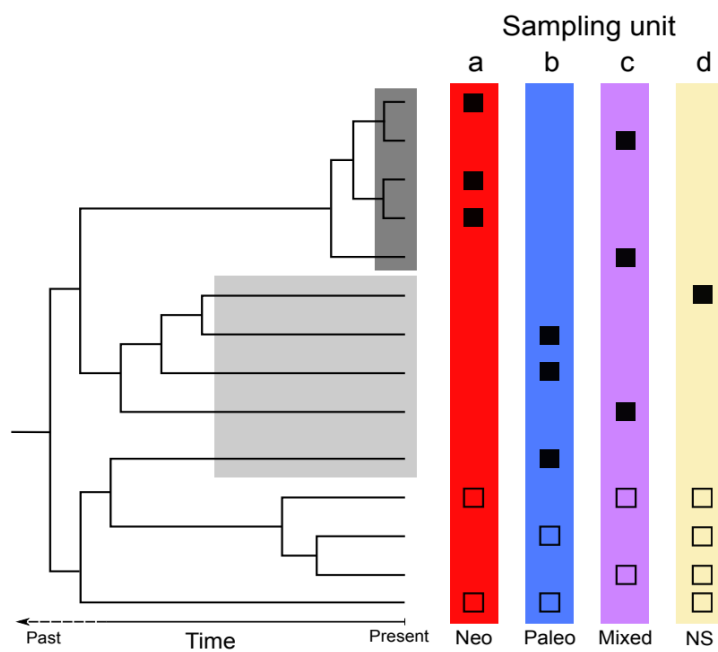


Figure 1: Theoretical framework for identifying the four categories of phylogenetic endemism based on a phylogenetic tree with branch lengths calibrated in units of time and the distribution of 14 taxa across four sites of equal taxonomic richness. Neo-endemic: endemic taxon sustained by a relatively short branch (highlighted in the dark grey box); paleo-endemic: endemic taxon sustained by a relatively long branch (highlighted in the light grey box). Site a): centre of neo-endemism with an over-representation of neo-endemics; site b): centre of paleo-endemism with an over-representation of paleo-endemics; site c): centre of mixed-endemism with an over-representation of both neo- and paleo-endemics; site d): non significant site. Black filled squares: endemic taxon (i.e. present in a relatively low number of sites). Unfilled squares: non-endemic taxon (i.e. present in a relatively high number of sites). Colours of CANAPE categories same as in Figure 6, see methods.

levels of evolutionary history (Sechrest *et al.*, 2002; Forest *et al.*, 2007). Phylogenetic endemism (PE) is the spatial restriction of phylogenetic lineages, i.e. the degree to which a part of the evolutionary history is range-restricted (Rosauer *et al.*, 2009). In this context, two types of endemic taxa can be distinguished (Kruckeberg & Rabinowitz, 1985; Nekola, 1999; Ferreira & Boldrini, 2011; Mishler *et al.*, 2014). Neo-endemics are taxa that diverged recently (i.e. sustained by short phylogenetic branches) and whose narrow range is generally linked to a lack of time to disperse and expand. In contrast, paleo-endemics are taxa that diverged much earlier and which are also range-restricted, either because of range reduction or dispersal opportunities. Spatial concentrations of neo- or paleo-endemic taxa are referred to as centres of neo-endemism or paleo-endemism, respect-

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ively (Figures 1a and 1b), and concentrations of both neo- and paleo-endemic taxa are called centres of mixed-endemism (Figure 1c) (Mishler *et al.*, 2014). Centres of neo-endemism can be viewed as ‘cradles of diversity’, that is regions with high speciation rates, and are centres of diversification, whereas centres of paleo-endemism can be viewed as ‘museums of diversity’, where taxa have persisted over time. By studying the distribution of endemic taxa together with their evolutionary history, we can generate hypotheses about historical processes that shaped biodiversity (Mishler *et al.*, 2014; Thornhill *et al.*, 2016, 2017; Scherson *et al.*, 2017). Such knowledge is crucial for the improvement of conservation management in the context of an unprecedented biodiversity decline (Humphreys *et al.*, 2019).

Tropical Africa contains some of the most biologically diverse regions of the world (Myers *et al.*, 2000; Linder, 2001; Küper *et al.*, 2004). Although it has lower species diversity when compared to the Neotropics and South-East Asia, tropical Africa still harbours an estimated 30 000 to 35 000 species of plants (Couvreur, 2015). High species richness and centres of taxonomic endemism are found in Cameroon, Gabon, eastern Democratic Republic of the Congo (DRC), and eastern Tanzania (Linder, 2001; Küper *et al.*, 2004; Sosef *et al.*, 2017). Furthermore, Africa contains the second largest continuous tropical rain forest block after the Amazon basin (Malhi *et al.*, 2013). Heterogeneous topography and climate across the continent gave rise to intricate biogeographical patterns forming numerous bioregions and transition zones (White, 1983; Linder *et al.*, 2012; Fayolle *et al.*, 2014; Droissart *et al.*, 2018). Tropical African plant diversity patterns have been relatively well explored by taxonomic approaches (Brenan, 1978; White, 1983; Lovett *et al.*, 2000; Linder, 2001; Küper *et al.*, 2004; Klopper *et al.*, 2007; Droissart *et al.*, 2018). However, in an evolutionary context our understanding about where diversity originated and where it is maintained is limited.

The lowland rain forests of the Guineo-Congolian region have been suggested to be Pleistocene cradles of diversity (Table 1) with glacial forest refugia triggering speciation (Diamond & Hamilton, 1980; Maley, 1996; Robbrecht, 1996; Sosef, 1996; Huntley & Voelker, 2016). However, molecular dating estimates in several plant and animal clades have shown that many species originated before the start of the Pleistocene, suggesting that forest refugia patterns reflect mainly Pliocene climatic fluctuation (Plana *et al.*, 2004; Voelker *et al.*, 2010). This led to the idea that lowland rain forests are museums of diversity (Table 1, Muriene *et al.*, 2013). In other studies, these lowland regions have been found to be concentrations of old and widespread lineages, especially in birds (Table 1, Fjeldså, 1994; Fjeldså & Lovett, 1997; Fjeldså & Bowie, 2008; Fjeldså *et al.*, 2012).

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Cradles of diversity have also been suggested in montane regions of Africa (Table 1), such as the Albertine Rift and the Eastern Arc Mountains (Fjeldså & Lovett, 1997; Roy, 1997; Dimitrov *et al.*, 2012), thereby supporting a ‘montane speciation model’ (Roy, 1997). Indeed, mountains are important centres of global diversification that represent heterogeneous and dynamic landscapes as well as to isolation and reconnection processes that are linked with past climate changes (Peterson *et al.*, 1997; Fjeldså *et al.*, 2012; Hoorn *et al.*, 2013; Antonelli *et al.*, 2018; Muellner-Riehl, 2019). This diversification is the consequence of different mechanisms, e.g. fragmented habitats promoting allopatric divergence

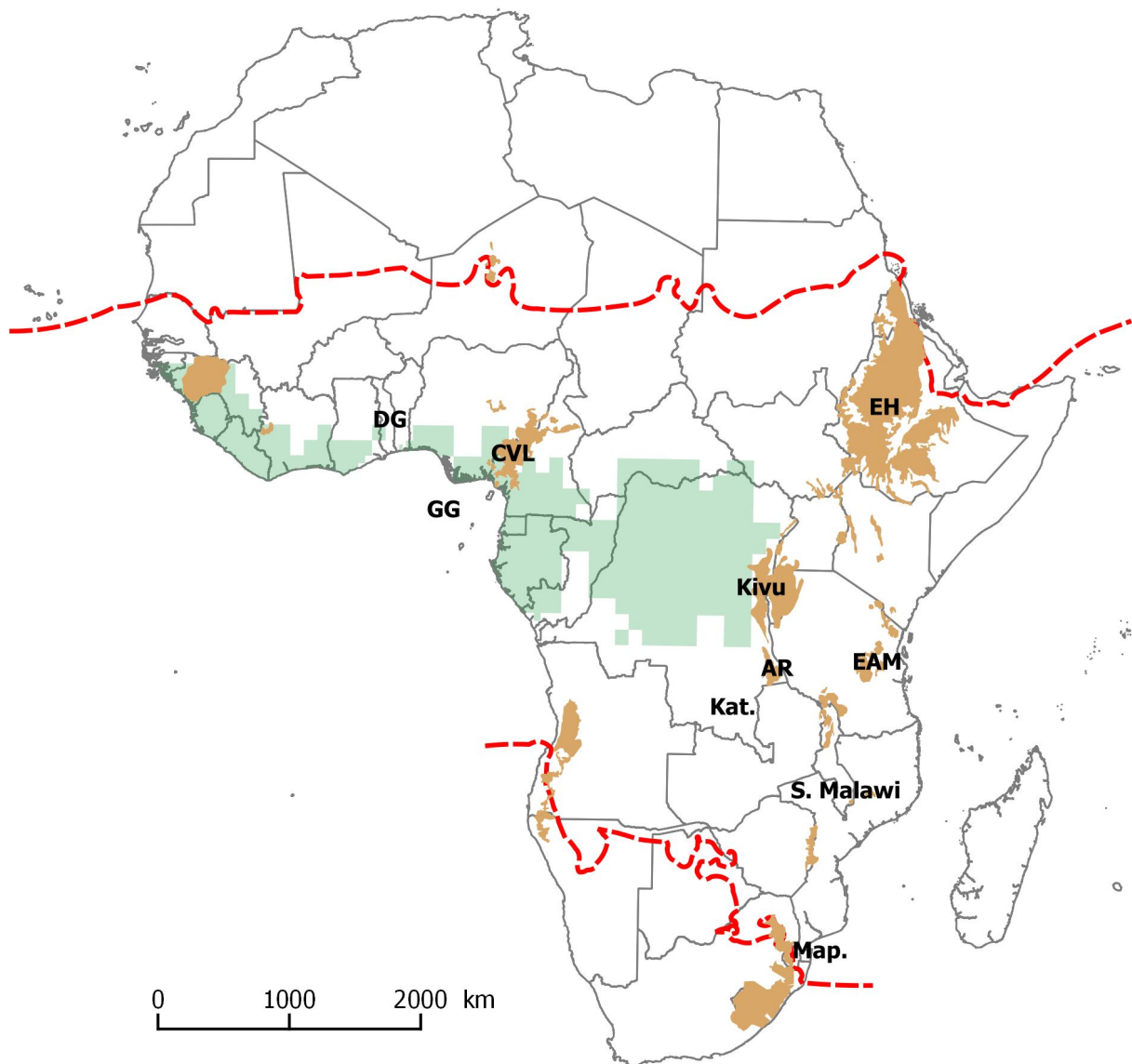


Figure 2: Map of Africa. Red dotted line delineates the study zone. Green shading delineates the Guineo-Congolian bioregion as defined by Droissart *et al.* (2018). Brown shadings delineate ‘montane regions’ (GMBA mountain inventory\_V1.2; Körner *et al.*, 2017). Locations cited in the main text: AR: Albertine Rift; CVL: Cameroon Volcanic Line; DG: Dahomey Gap; EAM: Eastern Arc Mountains; EH: Ethiopian Highlands; GG: Guinean Gulf; Kat.: Katanga; Map.: Maputaland; S.Malawi: South Malawi. The map is projected in the Africa Albers Equal Area Conic coordinate reference system (ESRI:102022).

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by isolation of small populations (Hughes & Eastwood, 2006; Schwery *et al.*, 2014; Merckx *et al.*, 2015; see Wen *et al.*, 2014 for a review of all the mechanisms). Mountains have also been acknowledged as museums of diversity as their complex topography supports relatively stable habitats by buffering climatic fluctuations and by allowing the movement of habitats over relatively short altitudinal distances to respond to temperature shifts, and thereby allowing their persistence over long periods of time (Peterson *et al.*, 1997; Fjelds  & Lovett, 1997; Hewitt, 2000; Tzedakis *et al.*, 2002; Loarie *et al.*, 2009; L pez-Pujol *et al.*, 2011; Tolley *et al.*, 2011). However, studies focusing on bird and few plant clade distributions have identified co-occurrence of neo- and paleo-endemic taxa in African mountain areas (Wasser & Lovett, 1993; Fjelds  & Lovett, 1997; L pez-Pujol *et al.*, 2011), suggesting that mountains are both cradles and museums of diversity (Fjelds  & Lovett, 1997) (Table 1).

For plants, these hypotheses have not yet been tested using both large distribution datasets and dated molecular phylogenies. Botanical datasets recording African plant distribution information are becoming increasingly comprehensive (Stropp *et al.*, 2016; Dauby *et al.*, 2016) and are significantly improving our understanding of biodiversity and phytogeographical patterns across tropical Africa (Sosef *et al.*, 2017; Droissart *et al.*, 2018). In parallel, the incorporation of evolutionary history information is now possible thanks to the generation of large phylogenies using existing data available on Genbank (Hinchliff & Smith, 2014; Smith & Brown, 2018). Together, this allows us to test the above hypotheses at new levels of precision.

Table 1: Hypotheses and ‘Categorical Analysis of Neo- And Paleo-Endemism’ (CANAPE) predictions tested across the tropical African angiosperm flora. SU: sampling unit (100 km<sup>2</sup>).

Hypotheses	CANAPE predictions	References
Lowland rain forests are museums of diversity	Significant concentration of old and range restricted (paleo-endemics) or old and wide-spread in lowland rain forest SUs.	Fjelds� (1994); Fjelds� & Lovett (1997); Fjelds� & Bowie (2008); Fjelds� <i>et al.</i> (2012)
Lowland rain forests are cradles of diversity (past refugia as ‘species pump’)	Significant concentration of young and range restricted taxa (neo-endemic) in lowland rain forest SUs.	Maley (1996); Sosef (1996); Huntley & Voelker (2016)
Montane regions are centres of diversification (‘montane speciation model’), i.e. cradles of diversity	Significant concentrations of neo-endemic taxa (centres of neo-endemism) in montane SUs.	Roy (1997); Dimitrov <i>et al.</i> (2012); Schwery <i>et al.</i> (2014)
Montane regions are centres of persistence of the lineages, i.e. museums of diversity	Significant concentration of paleo-endemic taxa (centres of paleo-endemism) in montane SUs.	Fjelds� & Lovett (1997); L�pez-Pujol <i>et al.</i> (2011); Tolley <i>et al.</i> (2011)
Montane regions are centres of both diversification and persistence of the lineages	Significant concentration of both paleo- and neo-endemic taxa (centres of mixed-endemism) in montane SUs.	Wasser & Lovett (1993); Fjelds� & Lovett (1997); L�pez-Pujol <i>et al.</i> (2011)

Here, we evaluate five main hypotheses (Table 1) related to the evolutionary and historical processes shaping tropical African biodiversity. We identify significant centres of neo- and paleo- endemism across the entire tropical African angiosperm flora at generic level based on a taxonomically verified distribution dataset and a newly generated mega-phylogeny of angiosperms. At the generic level, we identified areas of significant phylogenetic diversity (PD), phylogenetic endemism (PE) and centres of neo-, paleo- or mixed-endemism across tropical Africa to answer the following questions: Do previously identified areas of high taxon diversity display more PD and PE than expected by chance? Are African mountains centres of diversification, centres of lineage persistence, or both? Are African lowlands rain forests museums or cradles of diversity? Finally, as centres of phylogenetic endemism are of high conservation interest, we explored the overlap between the protected areas network across tropical Africa and the different centres of endemism identified.

## 2. Material and methods

### 2.1. Study area

Here, tropical Africa is defined by the ecoregions characterized by Olson *et al.* (2001) with the ‘south Saharan steppe and woodlands’ ecoregion and Mauritania as northern limit and the ‘Drakensberg montane grassland’, ‘Highveld grassland’, ‘Kalahari Acacia Baikiaea woodland’, ‘Kalahari xeric savannah’ and ‘Namibian savannah woodlands’ ecoregions as southern limits (Sosef *et al.*, 2017; Droisart *et al.*, 2018). This study includes continental Africa and the Guinean Gulf islands (Bioko, Sao Tomé and Príncipe), but excludes Madagascar (Figure 2).

### 2.2. Taxonomic level

We conducted this study on tropical African plants at the genus level. This taxonomic level presents advantages and drawbacks. Conceptually, genera should represent clear morphological differences of the flora and older evolutionary events than species, which is the main focus of this study. From a methodological point of view, generic names are comparatively stable taxonomic entities, which circumvent biases due to taxonomic uncertainties and potential mis-identifications of species (but see discussion). Moreover, mega-phylogenies are better resolved at the genus than at the species level (Hinchliff & Smith, 2014; Smith & Brown, 2018). Finally, genus-level studies are useful for addressing broad scale biodiversity patterns (Forest *et al.*, 2007; Thornhill *et al.*, 2016; Scherson *et al.*, 2017). A drawback is that really recent species cradles will be missed by this approach (see discussion).



## 2.3. Datasets

### 2.3.1. Plant occurrence data

We used the RAINBIO dataset (Dauby *et al.*, 2016), a database of geo-referenced occurrences of African vascular plants with comparatively high taxonomic quality. It represents a compilation of 614 022 botanical records collected from 1782 to 2015 providing distribution information for 25 356 species and 3 158 genera within 273 families. This represents ~89% of all known tropical African plant species.

Species occurrence data was projected using the Africa Albers Equal Area Conic coordinate reference system (ESRI:102022, <http://spatialreference.org/>). For that, we transformed coordinates from decimal degrees into metres, the base unit of this coordinate reference system. The study area was divided into  $100 \times 100$  kilometres (km) equal-area square sampling units (SU).

Using the RAINBIO dataset, we applied three filters, leading to the RAINBIO<sub>filtered</sub> dataset we used for all our analyses:

- Angiosperm filter. As our study and phylogeny focused on Angiospermae, Pteridophyta and Gymnospermae were excluded.
- Edge effect filter. When considering patterns of relative endemism in a delimited zone, bias toward over-representation of artificial endemic taxa at the boundaries, is frequent. This artefact is due to the rough cut within the geographic distribution of the taxa occurring both in and outside the study area, thereby artificially leading to identify these taxa as endemics although some of them may occur on both sides of the boundary. In order to avoid this edge effect, we kept only genera with more than 90% of their occurrences falling within our study area.
- Occurrence filter. Specimen density in RAINBIO is heterogeneous across tropical Africa. Poorly sampled SUs occur in poorly known regions and thus are more likely to include taxa that were collected only once (Sosef *et al.*, 2017). This can artificially increase the endemism of these SUs. To avoid potential bias caused by poorly sampled SUs, we included in our analyses only SUs in which at least 100 recorded occurrences are present. A threshold of at least 100 occurrences per SU was selected after testing different threshold values (results not presented here).

### 2.3.2. Phylogenetic data

We used a newly generated dated angiosperm phylogenetic tree (see Janssens *et al.*, 2019 for details). Briefly, phylogenetic inference was conducted based on a sampling of two plastid markers (matK and

rbcl) retrieved from GenBank for 36 234 plant species distributed across 8 357 genera. The alignment was conducted with MAFFT (Katoh *et al.*, 2002) and refined with Geneious 7.0 (Auckland, New Zealand). The final topology results from maximum likelihood tree inference with RAxML 7.4.2 (Stamatakis, 2006), constrained at the family level, under the general time reversible substitution model with gamma rate heterogeneity. Divergence time was estimated using 52 fossil calibration points scattered among the angiosperms and dated using the penalized likelihood algorithm implemented in treePL (Smith & O’Meara, 2012). The hard maximum and minimum age constraint of the angiosperms were set at 220 and 140 million years, respectively (Soltis *et al.*, 2002; Bell *et al.*, 2005; Moore *et al.*, 2007; Bell *et al.*, 2010; Magallón *et al.*, 2015). Finally, generic names in the RAINBIO dataset and in the phylogenetic tree were standardized using the Taxonomic Name Resolution Service (TNRS) tool (Boyle *et al.*, 2013).

## 2.4. Data analyses

### 2.4.1. Biodiversity analyses

To explore the diversity, distribution and evolutionary history of the angiosperm in tropical Africa, we used the RAINBIO<sub>filtered</sub> dataset and the resulting dated phylogenetic tree to calculate a set of taxonomic and phylogenetic indices for each SU across our study area. All metrics were calculated using Biodiverse version 2.0 (Laffan *et al.*, 2010). We used the ‘Biodiverse pipeline’ to run Biodiverse directly from R ([https://github.com/NunzioKnerr/biodiverse\\_pipeline](https://github.com/NunzioKnerr/biodiverse_pipeline)).

#### Taxonomic indices

Genus richness (GR): number of distinct genera ( $g$ ) present in each SU.

$$GR = \sum_g 1$$

Weighted endemism (WE): Sum of the inverse of each genus’ ( $g$ ) geographical range ( $R_g$ ).  $R_g$  is measured as the number of SUs in which the genus occurs (Crisp *et al.*, 2001).

$$WE = \sum_g \frac{1}{R_g}$$

#### Phylogenetic indices

Phylogenetic diversity (PD): Sum of branch lengths connecting the root of the phylogenetic tree to all genera (tips of the phylogeny) within each SU (Faith, 1992). In the following formulas,  $C$  is the total

number of branches connecting all genera within a SU,  $c$  a branch (a single segment between two nodes, representing a clade), and  $L_c$  the branch length.

$$PD = \sum_{c \in C} L_c$$

Relative Phylogenetic Diversity (RPD): Ratio of the PD measured on the original phylogenetic tree ( $PD_{orig}$ ) divided by the PD measured on a theoretical tree ( $PD_{theor}$ ). The theoretical tree has the same topology as the original tree but all branches are of equal length. The RPD index thus measures the relative branch length within a SU: high RPD indicates an over-representation of long-branched genera whereas low RPD indicates over-representation of short-branched genera (Mishler *et al.*, 2014).

$$RPD = \frac{PD_{orig}}{PD_{theor}}$$

Phylogenetic Endemism (PE): Sum of branch lengths, weighted by the inverse of the branch's range ( $R_c$ ), for each branch ( $c$ ) connecting the roots of the phylogenetic tree to the genera (tips of the phylogeny) within a SU (Rosauer *et al.*, 2009).  $R_c$  is measured as the number of SUs in which the branch  $c$  occurs.

$$PE = \sum_{c \in C} \frac{L_c}{R_g}$$

Relative Phylogenetic Endemism (RPE): ratio of the PE measured on the original phylogenetic tree ( $PE_{orig}$ ) divided by the PE measured on a theoretical tree ( $PE_{theor}$ ). The theoretical tree has the same topology as the original but all branches are of equal length (Mishler *et al.*, 2014). This index is the base for the Categorical Analyses of Neo- And Paleo-Endemism (see later).

$$RPE = \frac{PE_{orig}}{PE_{theor}}$$

#### 2.4.2. Null model – Randomisations

To test which SUs had significantly higher or lower observed values than expected given the genus richness of the SU and the geographical range of all genera, we ran 999 randomisations using Biodiverse version 2.0 (Laffan *et al.*, 2010). For every run, the algorithm randomly re-assigns all the genera to each SU without replacement. In order to respect both genus richness patterns and the geographical range of taxa, we constrained the procedure to keep the original number of genera in each SU and to keep the original number of SUs in which each genus occurs ('rand\_struct' option in Biodiverse).

Then, for each metric, the observed value is compared to the 999 randomisation values. Significantly greater or lower than expected was defined as being greater than 97,5% or lower than 2,5% of the random values, respectively (two-tailed test,  $\alpha = 0.05$ ). High levels of significance were established for observed values above the 99% or below the 1% of the random values.

This randomisation test was carried out for WE, PD, PE and RPD, resulting in the assignment of a significance class for each of these metrics for each SU: significantly very low ( $<0.01$ ), significantly low ( $<0.025$ ), ‘not significant’, significantly high ( $>0.975$ ) or significantly very high ( $>0.99$ ).

### 2.4.3. Categorical Analyses of Neo- And Paleo-Endemism (CANAPE)

The Categorical Analyses of Neo- And Paleo-Endemism (CANAPE) discriminates SUs with significantly high phylogenetic endemism (PE) in neo- or paleo-endemism based on taxon occurrences and the dated phylogenetic tree (Mishler *et al.*, 2014). First, we calculate the PE based on the original phylogenetic tree ( $PE_{orig}$ ) and the PE based on the theoretical tree ( $PE_{theor}$ , branches of equal length) for each randomisation of genera composition and subsequently compare those to the observed values. This allows us to select SUs that are centres of high phylogenetic endemism, *i.e.* showing either significantly high  $PE_{orig}$ ,  $PE_{theor}$  or both (observed values of  $PE_{orig}$  and  $PE_{theor}$  greater than 95% of the random values; one-tailed test,  $\alpha = 0.05$ ). Second, significant SUs are categorized into four non-overlapping categories. If the RPE ratio ( $PE_{orig}/PE_{theor}$ ) is higher than expected (two-tailed test,  $\alpha = 0.05$ ), the SU contains significantly more endemic genera on long-branches and is identified as a centre of ‘paleo-endemism’. If the RPE ratio is lower than expected (two-tailed test,  $\alpha = 0.05$ ), the SU contains significantly more endemic genera on short branches and is identified as a centre of ‘neo-endemism’. If the RPE is not significantly high or low, but both  $PE_{orig}$  and  $PE_{theor}$  are significantly high at the level of  $\alpha = 0.05$ , SU is tagged as centre of ‘mixed-endemism’ (*i.e.* a mix of endemic genera with both long and short branches). Finally, if a ‘mixed-endemism’ SU presents both high  $PE_{orig}$  and  $PE_{theor}$  at level of  $\alpha = 0.01$ , the SU is tagged as a centre of ‘super-endemism’ (*i.e.* highly significant concentration of endemic long and short branches).

As CANAPE results might be sensitive to the SU size, CANAPE was also carried out with four different SUs size across the study zone: 50, 75, 200 and 300 km square. The SUs contain at least 50, 75, 200 and 300 occurrences, respectively.

### 2.4.4. Overlap with montane regions

A ‘montane’ region can be defined according to differences in elevation, relief or steepness. We adopted the montane definition of Körner *et al.* (2011) based on the concept of steepness, the basic

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and consistent feature that reflects landscape heterogeneity found in mountains. Indeed, a definition based solely on elevation would consider highlands plateau as mountains (*e.g.* Tibetan Plateau, Altiplano) even if they are relatively flat landscapes. For continental scale purposes, steepness is estimated with the ruggedness, *i.e.* the elevation range between a grid cell and the 8 adjacent cells in the grid (Körner *et al.*, 2011). A cell is then considered as ‘mountain’ if its ruggedness exceeds 200 m. Global Mountain Biodiversity Assessment (GMBA) provides ruggedness data for 2.5 Arc minute (*c.a.*  $4.6 \times 4.6$  km at the equator) plots across the globe (GMBA mountain definition\_V1.0 database; Körner *et al.*, 2011) and shapefiles delineating ‘montane areas’ (GMBA mountain inventory\_V1.2; Körner *et al.*, 2017). For each SU, we calculated the mean ruggedness, the percentage of montane plots (*i.e.* percentage of  $4.6 \times 4.6$  km plots whose ruggedness exceed 200 m) and the percentage of overlap with ‘montane areas’ defined by GMBA.

In contrast, we defined ‘lowlands’ on the elevation feature to avoid considering a highland plateau as a lowland area. Elevation data were retrieved from the Digital Elevation Modelling (DEM) data produced by the NASA Shuttle Radar Topographic Mission (SRTM, <http://srtm.csi.cgiar.org/>). We downloaded the 250 m resolution (SRTM version 4.1) data in GeoTiff raster format, and extracted a raster file of the tropical Africa region using QGIS 2.18. From this raster file, we calculated the mean elevation for each SU.

We compared the distribution of the mean ruggedness, the percentage of montane plots and the percentage of overlap with ‘montane areas’ of the SUs across:

- the three categories of the PD results (significantly high or very high PD; not significant; significantly low or very low PD), and
- the five categories of the CANAPE results (neo-endemism; paleo-endemism; mixed-endemism; super-endemism, not significant).

We compared the distribution of the mean elevation of the SUs across:

- the three categories of the RPD results (significantly high or very high RPD; not significant; significantly low or very low RPD)

As normality of the residuals (one of the fundamental assumptions for analyses of variance) was not fulfilled for the three comparisons (results not shown), we used a non-parametric Kruskal-Wallis test. If at least one of the distributions was significantly different from the others ( $p$ -value  $< 0.05$ ), then Wilcoxon pairwise comparison (two-tailed tests with Holm’s correction) was performed to disentangle which category was significantly different from which other ( $p$ -value  $< 0.05$ ).

### 2.4.5. CANAPE and protected areas network overlap

CANAPE results were overlapped with the African protected areas network retrieved from the World Database on Protected Areas (WDPA, <https://protectedplanet.net/>, accessed June 2018). Protected areas exclusively related to marine or faunal protection (e.g: "Bird Reserve", "Hunting Reserve", "Faunal Reserve") were excluded. The number of SUs that contained protected areas (PA) were counted for any PA and for the most restrictive PAs in terms of conservation (reported as Ia, Ib and II IUCN categories; PAs whose main focus is on biodiversity) (IUCN, 2008).

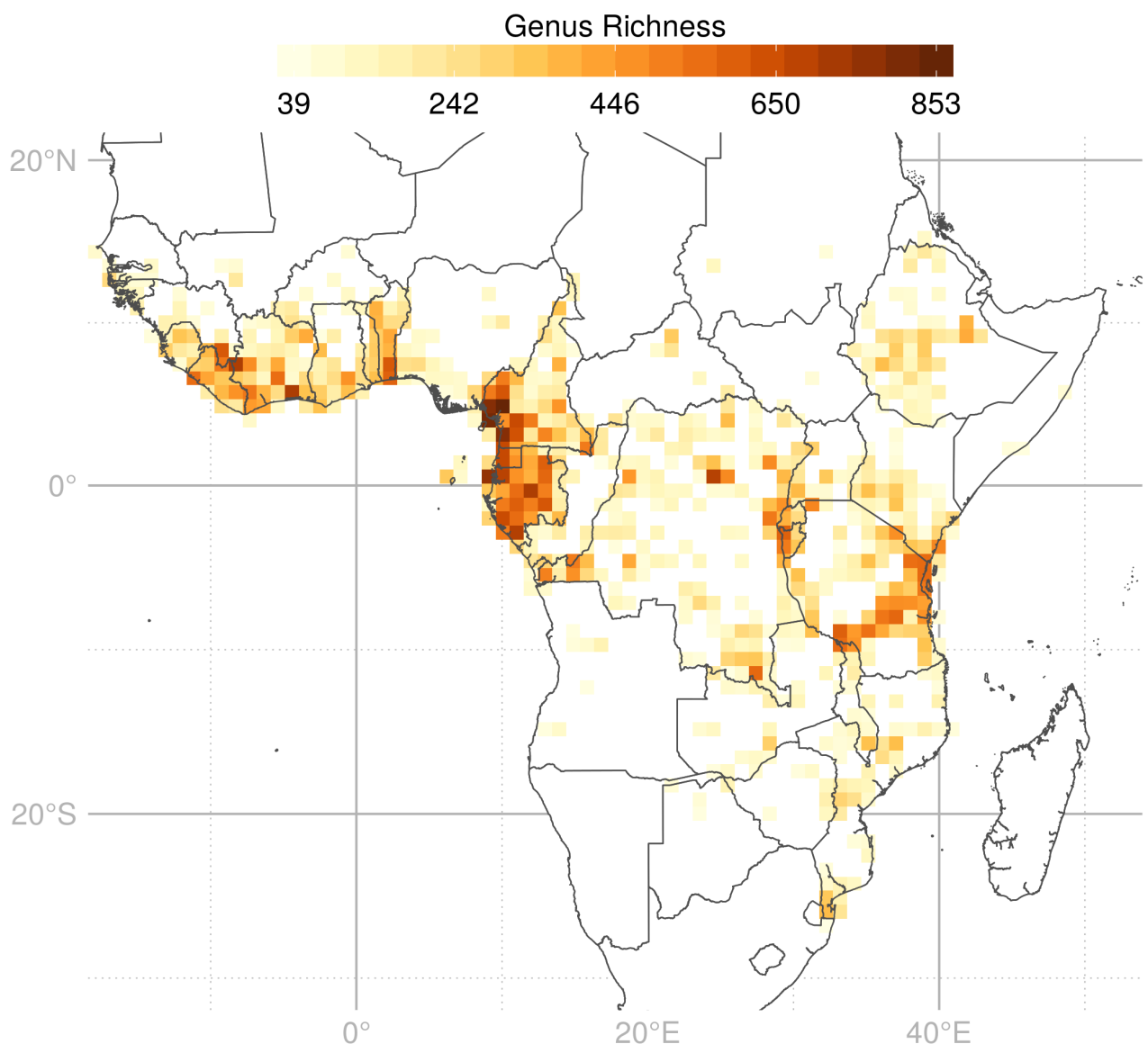


Figure 3: Genus richness map of the tropical African angiosperms, based on the distribution of 547 273 occurrences of 2 345 genera across 638 equal area (100 × 100 km) sampling units. White regions contain less than 100 records.

## 3. Results

### 3.1. Datasets

#### 3.1.1. Plant occurrence

The RAINBIO<sub>filtered</sub> dataset contained 547 273 occurrences of 2 345 genera distributed across 638 equal-area square sampling units (SUs). Genus Richness (GR) is unevenly distributed across tropical Africa, ranging from 39 to 853 genera per SU (Figure 3). The most diverse SUs are found around the Guinean Gulf, particularly in Gabon, western Cameroon, in the Dahomey Gap, the Eastern Arc Mountains and the Albertine Rift region, and to a lesser extent isolated SUs in the Democratic Republic of the Congo (DRC) and the Ethiopian Highlands.

#### 3.1.2. Phylogeny

The unfiltered phylogenetic tree contained 36 234 species and 8 357 genera. Based on the RAINBIO<sub>filtered</sub> dataset, this phylogenetic tree was pruned and included a final total of 1 719 genera. Of these, 36% (618/1719) were not monophyletic in the unfiltered phylogenetic tree. In this case, we randomly sampled one of the branches of the non-monophyletic genera. The tropical African flora at generic level represents 113 687 million years (My) of cumulative evolutionary history (*i.e.* the cumulative age of the taxa, estimated by the sum of all branch lengths on the tree).

## 3.2. Biodiversity analyses

### 3.2.1. Weighted endemism

Raw values of Weighted Endemism (WE) (Figure 4a) followed a similar pattern to GR (Figure 3) ( $R^2 = 0.764$ , Figure SI.1). Significantly high WE SUs (Figure 4b) are located in the eastern parts of tropical Africa, in Ethiopia, Kenya-Tanzania, Katanga (southeast DRC), Maputaland and scattered in southeast Africa. This indicated that these regions harbour more endemic genera than expected from random. In contrast, regions in Central and West Africa (*i.e.* the Guineo-Congolian region) are characterized by a significantly less WE than expected at random (Figure 4b).

### 3.2.2. Randomisation tests for phylogenetic diversity

Calculations of phylogenetic metrics were conducted on the 1 719 genera found both in the phylogenetic tree and in the RAINBIO<sub>filtered</sub> dataset. Phylogenetic diversity (PD) is highly correlated with genus richness ( $R^2 = 0.992$ , Figure SI.2, Figure SI.3). Higher PD than expected was found in 22 SUs (Figure 5a), located in mountainous areas (Figure SI.4, Table SI.1) around Lake Victoria, near the Eastern Arc

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Mountains, in northern Kivu, in Central Ethiopia and in the Cameroon Volcanic Line (Figure 5a). Conversely, 230 SUs presented lower PD than expected. These are distributed broadly across the study zone, with the main centres occurring in the Dahomey Gap and to the west, in northern Cameroon, central Gabon and coastal Congo, and across eastern Africa (Figure 5a).

SUs of significantly high Relative Phylogenetic Diversity (RPD), representing concentrations of long-branched (i.e. old) genera are clustered in the Guineo-Congolian region, western African forests and scattered in eastern Africa (Figure 5b). SUs of significant low RPD, representing concentrations of short-branched (i.e. young) genera, are scattered in the north of the Guineo-Congolian region and in eastern Africa (Figure 5b).



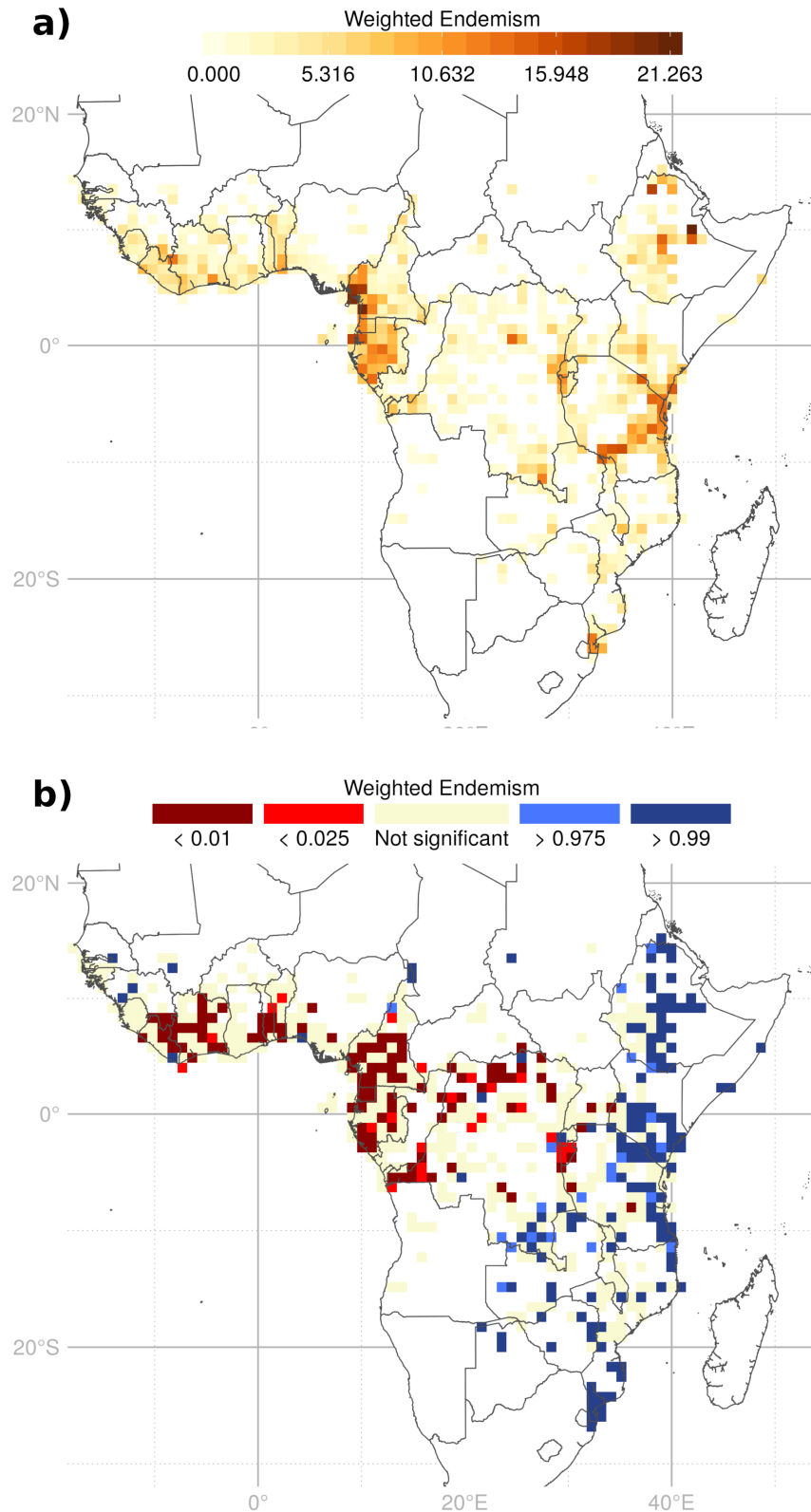


Figure 4: Weighted endemism (WE) maps of 2 345 tropical African angiosperm genera. (a) Observed values of WE. (b) Significant WE results from the randomisation test. Sampling units (SUs):  $100 \times 100$  km. Red SUs contain less WE than expected; blue SUs contain more WE than expected. Beige SUs are not significant. White regions contain less than 100 records and were not included in the analyses.

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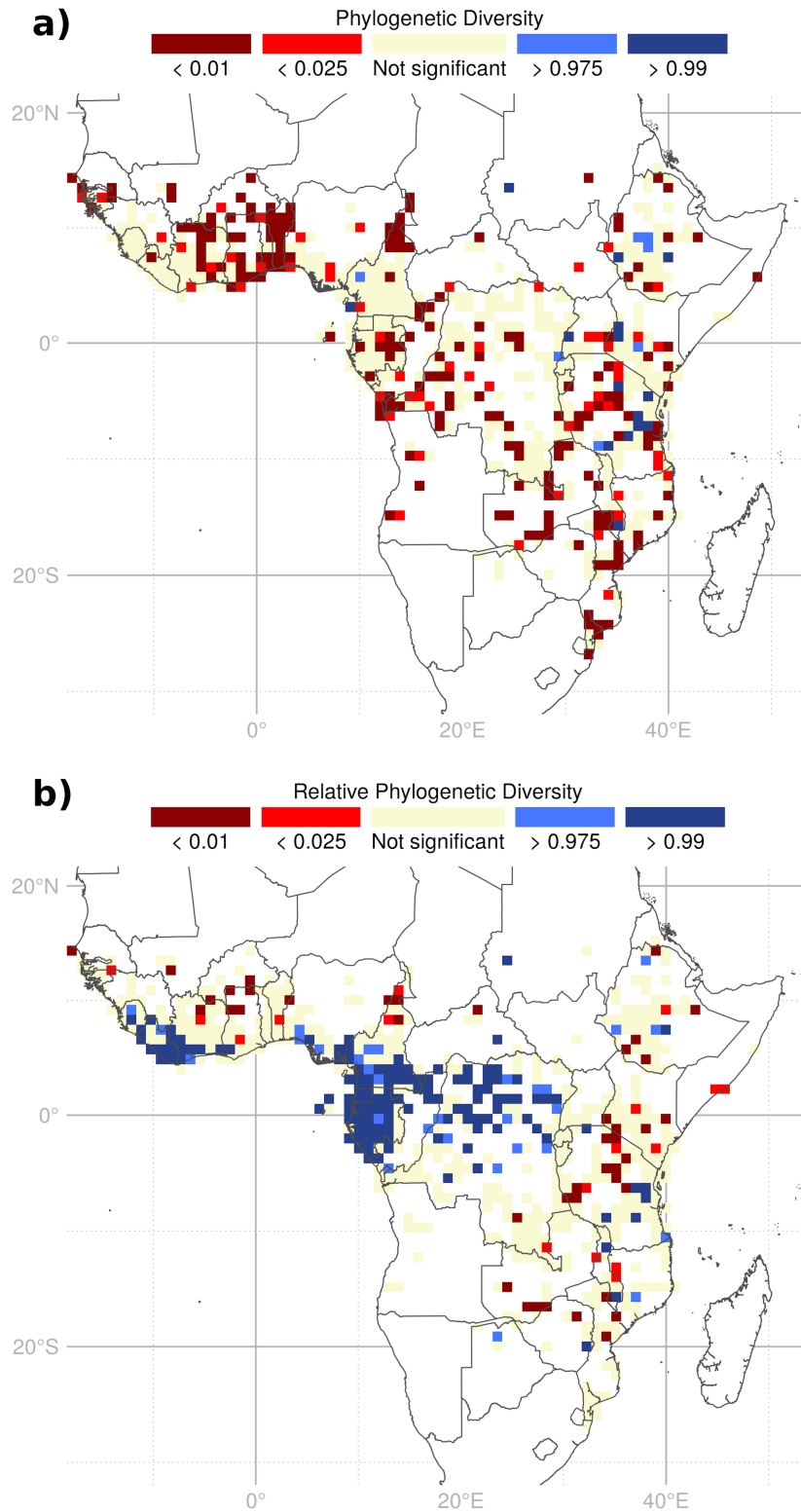


Figure 5: Maps of significant (a) Phylogenetic diversity (PD) and (b) Relative phylogenetic (RPD) resulting from the randomisation tests for 1 719 tropical African angiosperm genera. Sampling units (SUs) are  $100 \times 100$  km squares. Red SUs contain less PD or RPD than expected; blue SUs contain more PD or RPD than expected. Beige SUs are not significant. White regions contain less than 100 records and were not included in the analyses.

### 3.2.3. Categorical Analyses of Neo- And Paleo-Endemism

As for PD and GR, Phylogenetic Endemism (PE) is highly correlated with WE ( $R^2 = 0.985$ , Figure SI.5) and present a similar pattern of significance compared to the WE's (Figure SI.6). A total of 155 SUs were revealed by the CANAPE analyses as containing significantly more PE than expected (red,

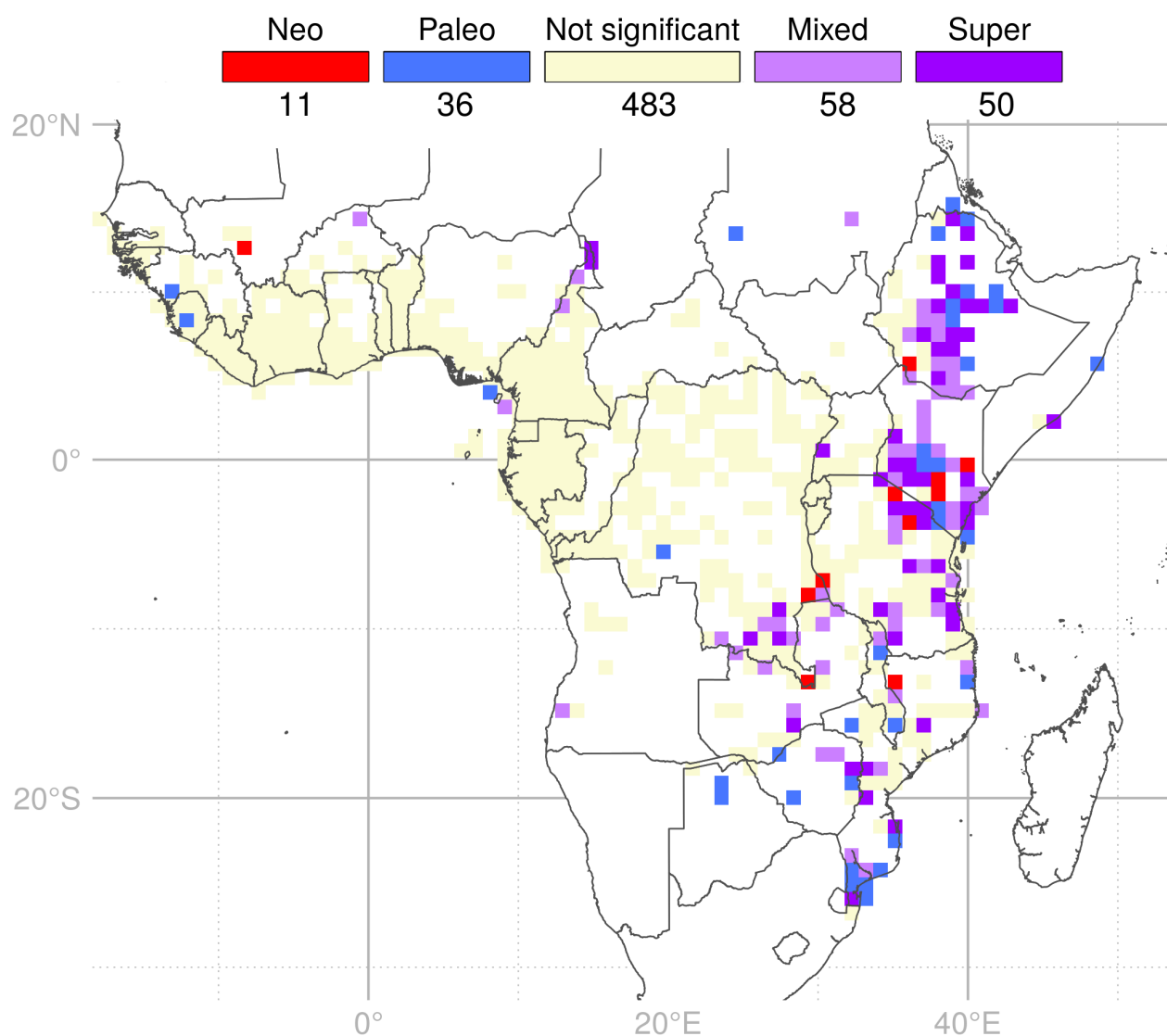


Figure 6: Map of significant phylogenetic endemism (PE) identified by the Categorical Analysis of Neo- And Paleo-Endemism (CANAPE) analyse for 1 719 tropical African angiosperm genera. Sampling units (SUs) are 100 × 100 km squares. Coloured SUs present significantly high PE: red SUs indicate centres of neo-endemism; blue SUs indicate centre of paleo-endemism; violet SUs are centres of mixed-endemism (i.e. mix of neo- and paleo-endemism), with darker violet indicating centres of super-endemism. Beige SUs are not significant. White regions contain less than 100 records and were not included in the analyses. Figures below the legend indicate the number of SUs included in each category.

blue and purple SUs in Figure 6). These are concentrated mainly in the eastern part of Africa. Areas of mixed- and super-endemism are the most common significant CANAPE SUs (58 and 50, respectively). Only 11 SUs are classified as areas of neo-endemism and these are generally surrounded by areas of mixed-, super- or paleo-endemism. As for neo-endemism, we found the 36 SUs of paleo-endemism surrounded by mixed- and super-endemism SUs. The Ethiopian Highlands show a concentration of mixed, super and paleo-endemic SUs. From central Kenya towards northern Tanzania, a similar cluster is found, with some neo-endemic SUs. Maputaland also concentrates phylogenetic endemism (mostly paleo-). Smaller clusters occurred across eastern Africa, such as in coastal and southwestern Tanzania, Katanga and other scattered areas in southeast Africa. Concentrations of significant PE in West and Central Africa are very low and mainly located in northern Cameroon, Bioko Island (Equatorial Guinea, Guinean Gulf), Guinea and Sierra Leone. Different SU sizes give a similar overall CANAPE results, with higher coverage of the study zone with large SUs (200 and 300 km square) and lower coverage with small SUs (50 and 75 km square) ().

### 3.2.4. Montane and lowland regions

The mean elevation (Figure 7) differs significantly between the RPD randomisation categories (Kruskal-Wallis test,  $p$ -value  $< 0.05$ , Table SI.2). The high RPD SUs are significantly lower in elevation than not significant and low RPD SUs (Wilcoxon pairwise comparison,  $p$ -value  $< 0.05$ , Table SI.2). Some SUs are outliers of high RPD distribution (solid dots), meaning these few SUs are occurring at high elevation.

The distribution of the mean ruggedness (Figure 8), the percentage of montane plots (Figure SI.9) and the percentage of overlap with 'montane areas' (Figure SI.8) differ significantly between the CANAPE categories

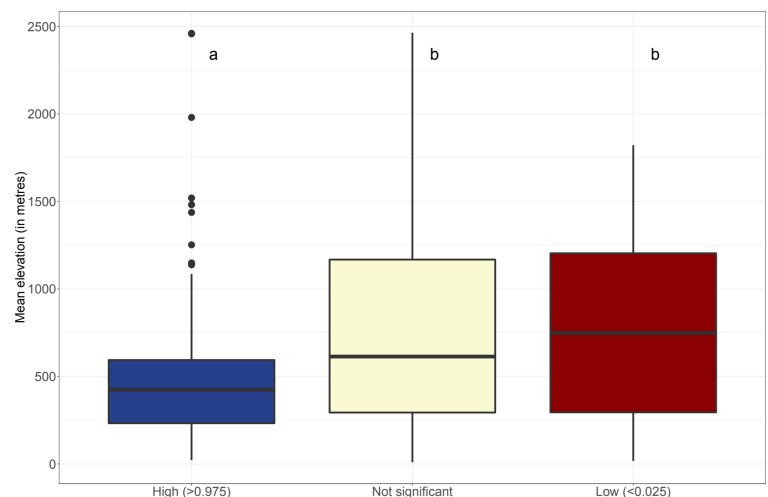


Figure 7: Boxplot of the distribution of the mean elevation (in metres) of the sampling units (SU) depending on their RPD significance class. Distributions of the mean elevation of the SUs are significantly different (Kruskal-Wallis test,  $p$ value  $< 0.05$ ). Different letters indicate significant differences ( $p$ value  $< 0.05$ ; pairwise comparison using Wilcoxon test with Holm's correction, see Table SI.2). For each box: the bold horizontal line corresponds to the median; the lower and upper bounds of the box correspond to first and third quartiles, respectively; the upper vertical line extends from the upper bound of the box to the highest value of the distribution, no further than  $1.5 \times$  IQR (Inter Quartile Range, or the distance between the first and third quartile); the lower vertical line extends from the lower bound of the box to the lowest value of the distribution, no further than  $1.5 \times$  IQR; black dots are values beyond IQR ('outlier' values).

( $p$ -values  $< 0.05$ , Table SI.3, Table SI.4 and Table SI.5). The mean ruggedness of mixed- and super-endemic SUs is significantly higher than the ruggedness of non-significant SUs (Figure 8) (Wilcoxon pairwise comparison,  $p$ -value  $< 0.05$ , Table SI.3). The mean ruggedness of neo- and paleo-endemic SUs is not different from all the others (Wilcoxon pairwise comparison,  $p$ -value  $< 0.05$ , Table SI.3).

The distribution of the percentage of montane plots and of the overlap with ‘montane areas’ of the SUs show similar differences across the five CANAPE categories, except for paleo-endemic SUs that are significantly different from non-significant SUs (Figure SI.9, Table SI.4, Figure SI.8, Table SI.5).

### 3.2.5. Protected areas network overlap

The overlap between the African protected areas (PA) network and centres of significant phylogenetic endemism detected by CANAPE is partial (Figure 9). More than 85% of the CANAPE cells contain at least a part of a PA, and more than 42% of the CANAPE cells partially overlap with one of the most restrictive PA IUCN category (Ia, Ib or II). The whole PA network covers 18.7% of the CANAPE cells surface, and 5.9% when considering only IA, Ib and II PA categories (Table SI.6 and Table SI.7).

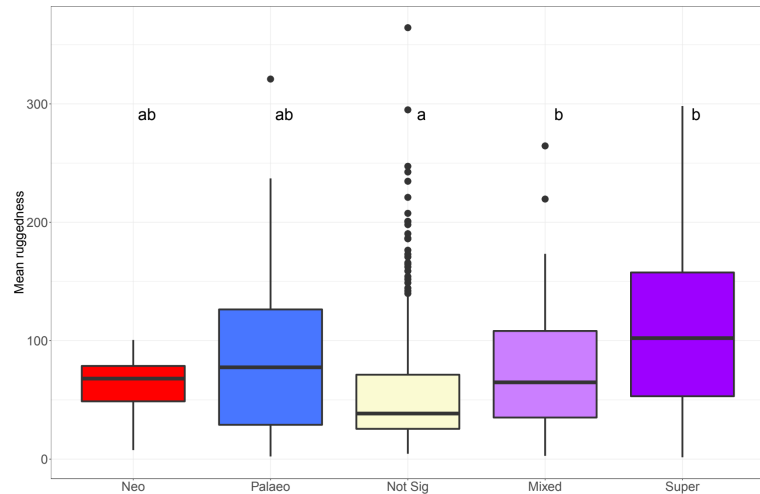


Figure 8: Boxplot of the distribution of the mean ruggedness (in metres) of the sampling units depending on their CANAPE category. Distributions of the mean ruggedness of the SUs are significantly different (Kruskal-Wallis test,  $p$ value  $< 0.05$ ). Different letters indicate significant difference ( $p$ value  $< 0.05$ ; pairwise comparison using Wilcoxon test with Holm’s correction, see Table SI.3). For each box: the bold horizontal line corresponds to the median; the lower and upper bounds of the box correspond to first and third quartiles, respectively; the upper vertical line extends from the upper bound of the box to the highest value of the distribution, no further than  $1.5 \times$  IQR (Inter Quartile Range, or the distance between the first and third quartile); the lower vertical line extends from the lower bound of the box to the lowest value of the distribution, no further than  $1.5 \times$  IQR; black dots are values beyond IQR (‘outlier’ values).

## 4. Discussion

### 4.1. Significant concentrations of evolutionary history and taxonomic endemism

In this study, we combined for the first time at the near continental level a large floristic dataset within a phylogenetic framework to examine more than 113 000 My of evolutionary history of tropical African angiosperms. Our generic richness (GR) map (Figure 3) corroborates previous studies highlighting Cameroon, Gabon, the Albertine Rift, the Eastern Arc Mountains and coastal Tanzania as containing

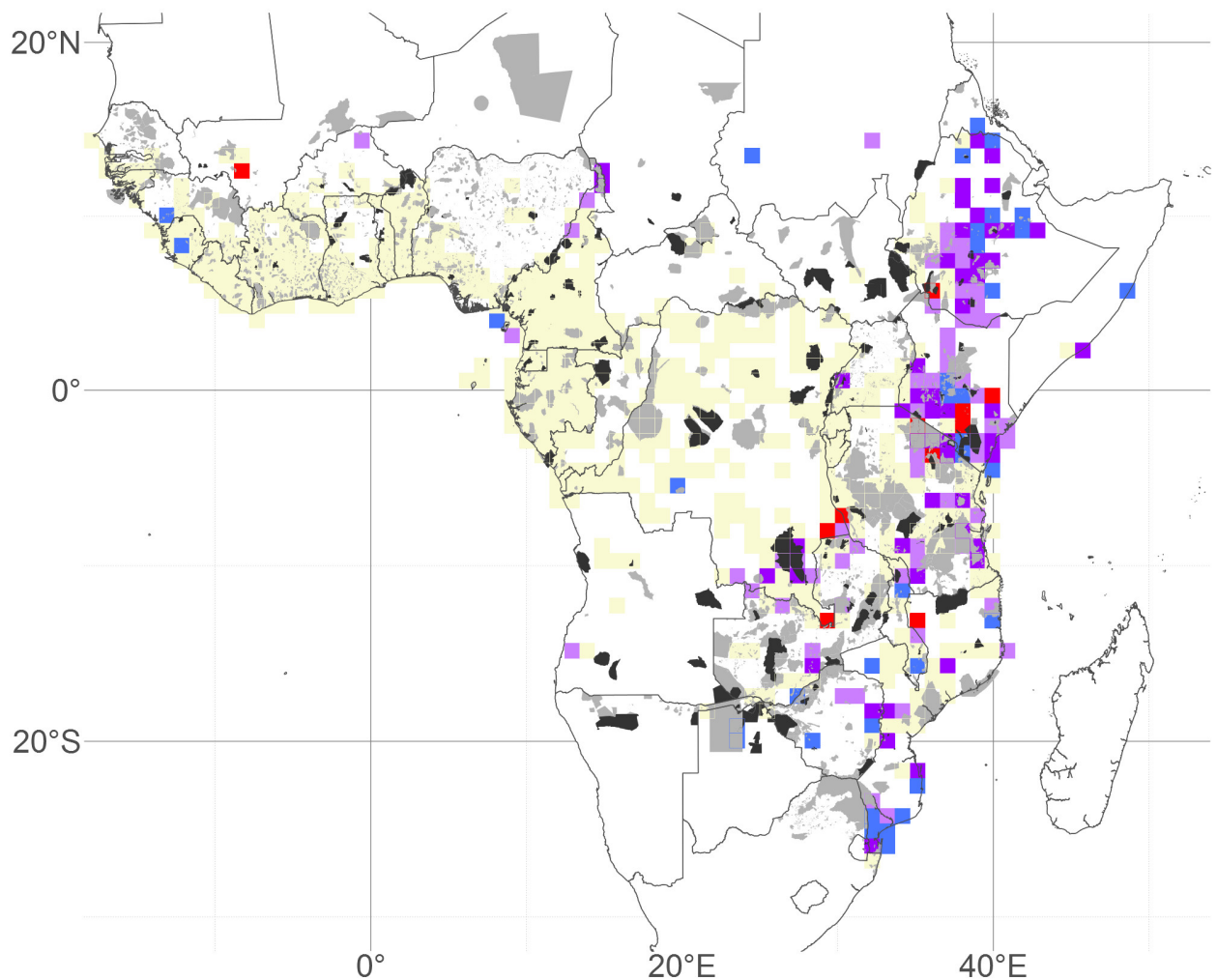


Figure 9: Map of the protected areas of Africa overlaid onto CANAPE results. Dark grey areas are the most restrictive PAs (Ia, Ib or II IUCN categories). Light grey are other PAs (III, IV, V or VI IUCN categories, or with no category assigned). Data retrieved from the World Database on Protected Areas (WDPA, <https://protectedplanet.net/>, accessed June 2018). Sampling units (SUs) are  $100 \times 100$  km squares. Coloured SUs present significantly high phylogenetic endemism: red SUs indicate centres of neo-endemism; blue SUs indicate centre of paleo-endemism; violet SUs are centres of mixed-endemism (i.e. mix of neo- and paleo-endemism), with darker violet indicating centres of super-endemism. Beige SUs are not significant. White SUs contain less than 100 records.

high taxon richness (Linder, 2001; Küper *et al.*, 2004; Lovett *et al.*, 2005; Plumptre *et al.*, 2007; Sosef *et al.*, 2017).

Despite the correlation between GR and Phylogenetic Diversity (PD, Figure SI.2), our randomization procedure reveals that in some regions, PD is higher or lower than expected by chance (Figure 5a). A decoupled pattern between GR and PD was also observed in South Africa (Forest *et al.*, 2007). Across tropical Africa, 230 out of 638 SUs showed significantly lower PD than expected by chance (phylogenetic clustering). These are located in a lowland rain forest in Gabon and central Democratic Republic of the Congo (DRC), but also in drier regions such as the Dahomey Gap, northern Cameroon, savannah regions in western DRC and in eastern Africa (Figure 5a). In the savannah (*i.e.* wooded grassland) regions, phylogenetic clustering is likely caused by the dominance of Poaceae and Fabaceae (Jacobs, 2004). In lowland tropical rain forest regions, phylogenetic clustering suggests evolutionary conservatism in tropical forest adaptations. Analogous phylogenetic clustering has been observed in some tropical forest and arid regions in Borneo, Central America, Australia and Chile (Webb, 2000; Swenson *et al.*, 2007; Thornhill *et al.*, 2016; Scherson *et al.*, 2017). In contrast, only six SUs had significantly higher PD than expected by chance (phylogenetic over-dispersion). These are mainly located in montane areas (Figure SI.5) of the Cameroon Volcanic Line, Ethiopian Highlands, northern Kivu, central Kenya, the Eastern Arc Mountains and in southern Malawi (Figure 5a). Phylogenetic over-dispersion may be related to competitive exclusion of closely related genera whose niches show a large overlap (Webb *et al.*, 2002), extinction (Kissling *et al.*, 2012; Couvreur, 2015), or colonization of phylogenetically distinct lineages. Another reason for this pattern could be linked to the complex topography of montane areas containing heterogeneous habitats and various soil types harbouring distinctly adapted plant lineages (Peterson *et al.*, 1997; Hoorn *et al.*, 2010, 2013; Antonelli *et al.*, 2018). Phylogenetically over-dispersed SUs have also been observed in ecotone regions in the Cape region (Forest *et al.*, 2007) and were argued to be of high conservation importance as they represent an important amount of evolutionary history (Faith, 1992; Swenson *et al.*, 2007; Forest *et al.*, 2015).

The regions of high taxonomic diversity mentioned above (Cameroon, Gabon, the Albertine Rift, the Eastern Arc Mountains and coastal Tanzania) are also known to contain a high number of endemic species (Linder, 2001; Küper *et al.*, 2004; Plumptre *et al.*, 2007). We indeed found a similar pattern between GR and observed Weighted Endemism (WE, Figure 4a, Figure SI.1). However, our randomisation procedure revealed that these regions present lower levels of generic endemism than expected (Figure 4b) - except for southern coastal Tanzania. This does not mean however that Cameroon, Gabon, the Albertine Rift and the Eastern Arc Mountains are not rich in endemic genera, but that given the high taxonomic richness, the concentration of endemic genera they harbour is not excep-



tional. Instead, generic level distribution ranges are wider than expected indicating an over-representation of widespread genera in the Guineo-Congolian region (Figure 4b). In contrast, East Africa, particularly Ethiopia, Kenya, Tanzania, Katanga (DRC), Maputaland and other SUs in southeast Africa, harbour more endemic genera than expected (high WE, Figure 4b). These represent important endemic portions of evolutionary history (high PE, Figure 6) possibly related to the topographic and edaphic complexity of East Africa. Indeed, East Africa has a greater elevation range than West or Central Africa (Guillocheau *et al.*, 2018) and the tectonic activity that occurred in East Africa generated places that differ edaphically from surrounding areas. Edaphic complexity plays a great role in generating endemism (Bruchmann & Hobohm, 2014, Rahbek *et al.*, 2019) and the habitat heterogeneity and fragmentation of montane regions is often associated with range-restricted taxa (Moritz *et al.*, 2002; Hughes & Eastwood, 2006; Kier *et al.*, 2009; Fjeldså *et al.*, 2012). Moreover, East Africa is acknowledged to be a ‘complex biogeographical mixture’ containing distinct taxa adapted to various localized environmental gradients generated by the complex topography and climate (Linder *et al.*, 2012; Droisart *et al.*, 2018). Endemic lineages are thus more likely to occur in greater proportion in the regions that are topographically and edaphically complex than in regions of low habitat heterogeneity (such as lowlands) or low edaphic complexity (such as, *inter alia*, the Eastern Arc Mountains). Finally, endemism in eastern Africa seems to have been undervalued in previous continental scale studies (Fjeldså & Lovett, 1997; Linder, 2001; but see Küper *et al.*, 2004). Our incorporation of evolutionary history and randomisation procedures allowed the identification of new regions of high evolutionary and conservation interests (Figure 6).

## 4.2. Cradles and museums of diversity

In our study, most SUs identified as containing significantly high phylogenetic endemism (PE) are centres of mixed- or super-endemism, concentrating both neo- and paleo-endemic genera (Figure 6). These mixed-endemism and super-endemism SUs occur significantly more in montane regions than non-significant SUs (Figure 8). In addition, neo-endemism SUs also show a non-significant tendency to mainly occur in montane areas (Figure 8). Thus, even though mountains have been suggested to act as cradles of diversity (Roy, 1997; Jetz *et al.*, 2004; Fjeldså & Rahbek, 2006; Schwery *et al.*, 2014; Merckx *et al.*, 2015), our results support the hypothesis that montane regions, particularly in East Africa, are both museums and cradles of diversity (Wasser & Lovett, 1993; Fjeldså & Lovett, 1997; López-Pujol *et al.*, 2011). Our results also suggest that the montane speciation model, where mountain ‘cradles’ are considered to feed surrounding (generally lowland) regions in species (Roy, 1997; Jetz *et al.*, 2004; Fjeldså & Rahbek, 2006; Hoorn *et al.*, 2013), is hard to support at genus level across tropical Africa. This hypothesis appears reductive as mountains can also act as ‘museums’, and centres of diversifica-



tion may also occur elsewhere, such as around river networks or in lowland ecotonal zones (e.g. transitions between forests and savannah) (Fjeldså, 1994; Plana, 2004).

Furthermore, by identifying Ethiopian highlands, Kenya, Tanzania, Katanga, southeast Africa and Maputaland as centres of mixed-endemism, we demonstrate that within these regions, processes of recent diversification occur together with favourable conditions for lineage persistence leading to a greater accumulation of evolutionary history than expected by chance. Several studies also found areas of mixed-endemism in other montane regions, such as in South America (Fjeldså, 1994; Fjeldså & Lovett, 1997; Bitencourt & Rapini, 2013), and China (López-Pujol *et al.*, 2011). In tropical Africa, previous identification of centres of neo- and paleo-endemism in plants focused on only two plant clades *a priori* assumed to be neo- or paleo-endemics, because of a lack of dated plant phylogenetic trees (Fjeldså & Lovett, 1997). Fjeldså and Lovett (1997) reported co-occurrences of neo- and paleo-endemics in some mountains, such as the Cameroon Volcanic Line or the Albertine Rift, but they did not detect the same East African regions to act both as museums and cradles as reported here (Figure 6). This underlines the importance of integrating randomisation and categorisation procedures together with a comprehensive phylogeny and angiosperm wide datasets to detect patterns of significant neo-, paleo- and mixed-endemism (Mishler *et al.*, 2014; Thornhill *et al.*, 2016).

In contrast, most parts of West and Central Africa present non-significant CANAPE SUs, indicating these regions harbour no more endemic genera than expected. Randomisation of the RPD revealed concentrations of old genera in lowland rain forests of Guineo-Congolia (Figure 5b, Figure 7). As mentioned above, these genera also appear to be widespread (low WE, Figure 4b). Several local museums of biodiversity have been proposed to occur within this region (Fjeldså & Lovett, 1997; Murienne *et al.*, 2013) which, according to Linder (2014) contain the oldest flora of tropical Africa, and here appears to be a museum of diversity as a whole.

Our study highlights the importance of incorporating large-scale taxonomically verified distribution datasets with mega-phylogenies, which lead to an improved understanding of tropical plant biodiversity evolution. Similar studies in other megadiverse regions such as the Amazon basin will allow comparison of tropical biodiversity origins and maintenance processes across the tropics.

### 4.3. Taxonomic and geographic resolution effects

Biodiversity and phylogenetic analysis at genus level have already demonstrated their relevance in understanding patterns of biodiversity evolution (Forest *et al.*, 2007; Thornhill *et al.*, 2016; Scherson *et al.*, 2017). However, interpretation must not be extrapolated to other taxonomic levels. This is particularly the case for analyses that are focused on species endemism, as different species within a genus may

show various geographic distribution patterns. For example, the genus *Impatiens* (Balsaminaceae) is widespread in the Old World tropics and subtropics, but the majority (ca. 80%) of its African species are range-restricted in regions such as the Eastern Arc Mountains (Grey-Wilson, 1980; Lovett *et al.*, 2000). Another drawback is that it is harder to detect centres of neo-endemism when using generic level data (Thornhill *et al.*, 2016). This makes the 11 SUs detected as centres of neo-endemism (Figure 6) strong cradles of diversity. The completeness of the plant distribution dataset as well as the resolution of the phylogeny may also affect our estimate of phylogenetic endemism. Here, even if RAINBIO dataset represents ca. 89% of the known diversity in tropical Africa, it is the best quality data that is available to date (Dauby *et al.*, 2016). The relatively high proportion of non-monophyletic genera (36%) that is present in the unfiltered angiosperm tree is inherent and unavoidable when making use of large-scale phylogenetic approaches. On one hand, this is caused by the compromise between the amount of markers used and the number of species included in the dataset (see *e.g.* Qian & Jin, 2016; Smith & Brown, 2018). On the other hand, there are still some taxonomical uncertainties regarding the generic status of certain angiosperm African genera (*e.g.* Rubiaceae, Convolvulaceae, Cyperaceae) in which several genera have not been taxonomically revised (Muasya *et al.*, 2009; De Block *et al.*, 2015; Simões & Staples, 2017). Despite this, we are confident that given the broad scale of our analysis our results will be robust to improved phylogenetic studies at the genus level.

In tropical Africa, documented regions with high levels of diversity and endemism, and postulated to act both as cradles and museums of species diversity are predominantly mountainous (*e.g.* Cameroon Volcanic Line, the Albertine Rift and the Eastern Arc Mountains) (Fjeldså & Lovett, 1997; Lovett *et al.*, 2005; Burgess *et al.*, 2007; Plumptre *et al.*, 2007). These mountain blocks are generally small in terms of size (*e.g.* less than  $70 \times 70$  km for the Eastern Arc Mountains; Burgess *et al.*, 2007). Thus, the resolution of our analyses ( $100 \times 100$  km SUs) may have diluted the montane endemism effect with the high diversity and potentially widespread genera of adjacent lowlands regions. Using smaller SUs gave a similar overall CANAPE result, but with less coverage of the study zone because of a higher number of poorly-sampled SUs that were excluded from the analyses (Figure SI.7). Moreover, in mixed-endemism regions, neo-endemics and paleo-endemics may be locally concentrated in different places within a mountain block (Bitencourt & Rapini, 2013).

#### 4.4. Conservation implications

Identifying and conserving areas of evolutionary potential, harbouring important processes leading to diversification and/or lineage persistence is of crucial conservation importance (Fjeldså, 1994; Mace *et al.*, 2003; Kraft *et al.*, 2010; Faith *et al.*, 2010). In eastern Africa, most of the centres of phylogenetic

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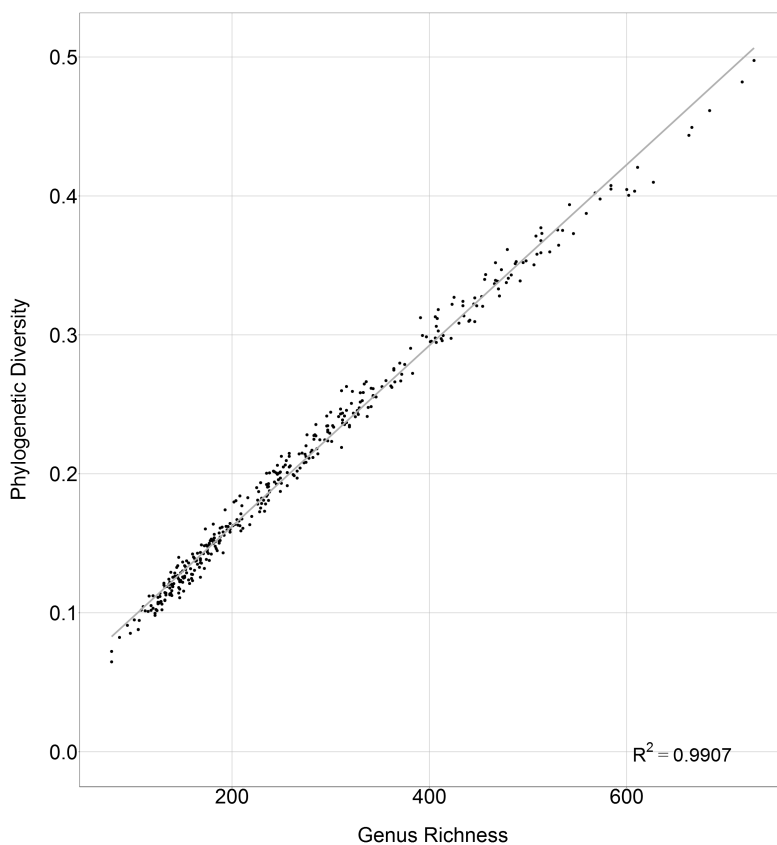
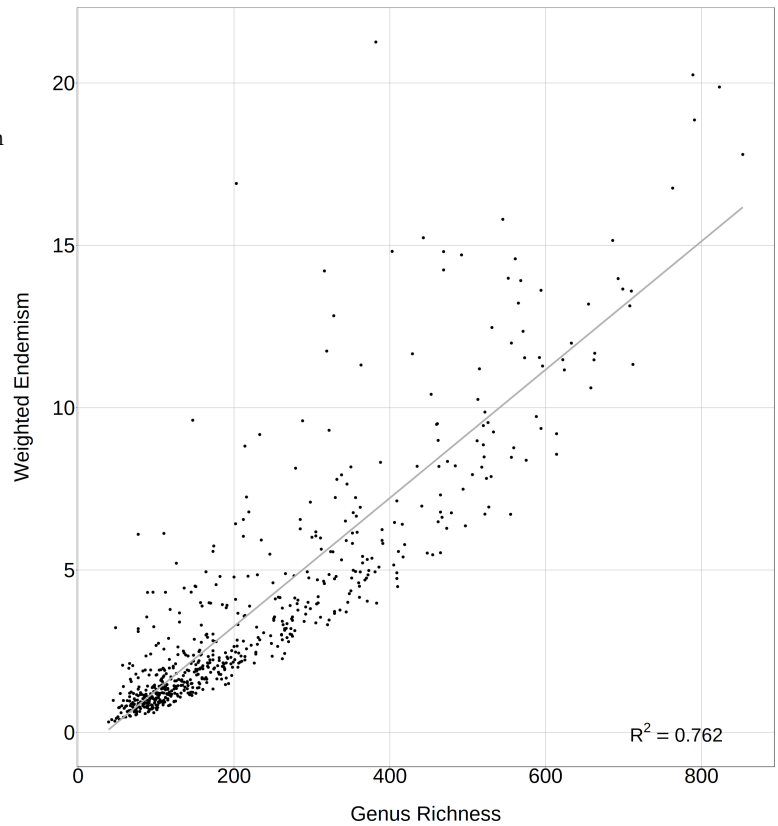
endemism are centres of mixed-endemism (Figure 6), somewhat bypassing the need to choose between conserving regions of active diversification or persistence (Cowling & Pressey, 2001).

The coverage of the identified centres of phylogenetic endemism by the protected areas (PA) network is high, as 85% of the CANAPE SUs contain at least a portion of PA, and 42% contain at least a portion of the most restrictive PAs (Ia, Ib or II types). This means that important regions of diversification and of persistence are already represented in the tropical African PA network. In terms of surface, only 18% of the CANAPE SUs' surface is covered by PAs (Figure 9, Table SI.6 and Table SI.7). That is expected as PAs are generally small areas and are unlikely to cover a complete 100 × 100 km SUs. Significant CANAPE areas that are not well represented by PAs are mainly situated in South Malawi and to a lesser extent in Ethiopia (Figure 9). Still, it is possible that the actual occurrences of endemics and the PAs within a SU do not coincide, so it might be worthwhile to analyse diversity patterns at a fine scale when adapting or adding PAs.

The regions containing significant high PE, particularly regions of mixed-endemism that are simultaneously 'cradles' and 'museums' of diversity, should be considered in future conservation planning or PA extension. Considerable increases in the coverage of multiple facets of biodiversity (taxonomic, phylogenetic and functional) are possible with small expansions of protected areas, if the planning is achieved thoroughly and with an explicit consideration of these multiple facets (Pollock *et al.*, 2015, 2017).

## 5. Supporting Information

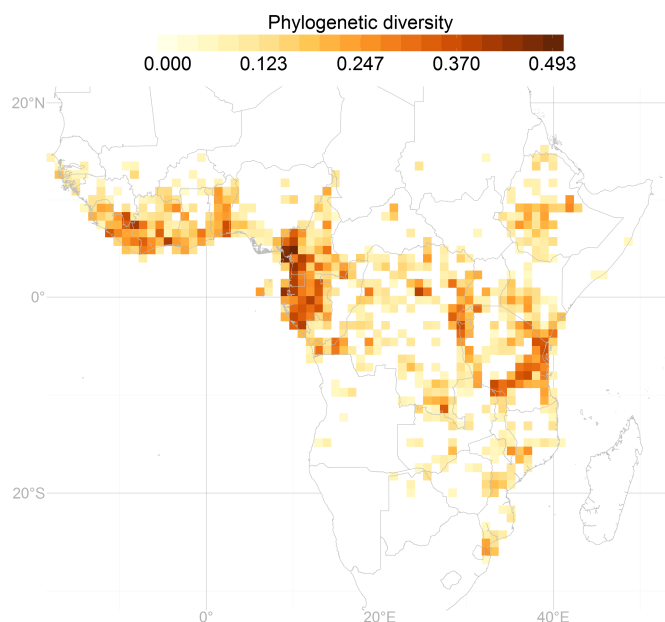
**Figure SI.1** Relationship between weighted endemism (WE) and genus richness (GR). WE and GR were calculated for each of the 638 sampling units (SUs) using 2 345 tropical African angiosperms genera and the phylogenetic tree. SUs are  $100 \times 100$  km squares.  $R^2$ : adjusted R-square resulting from the linear regression of WE on GR.



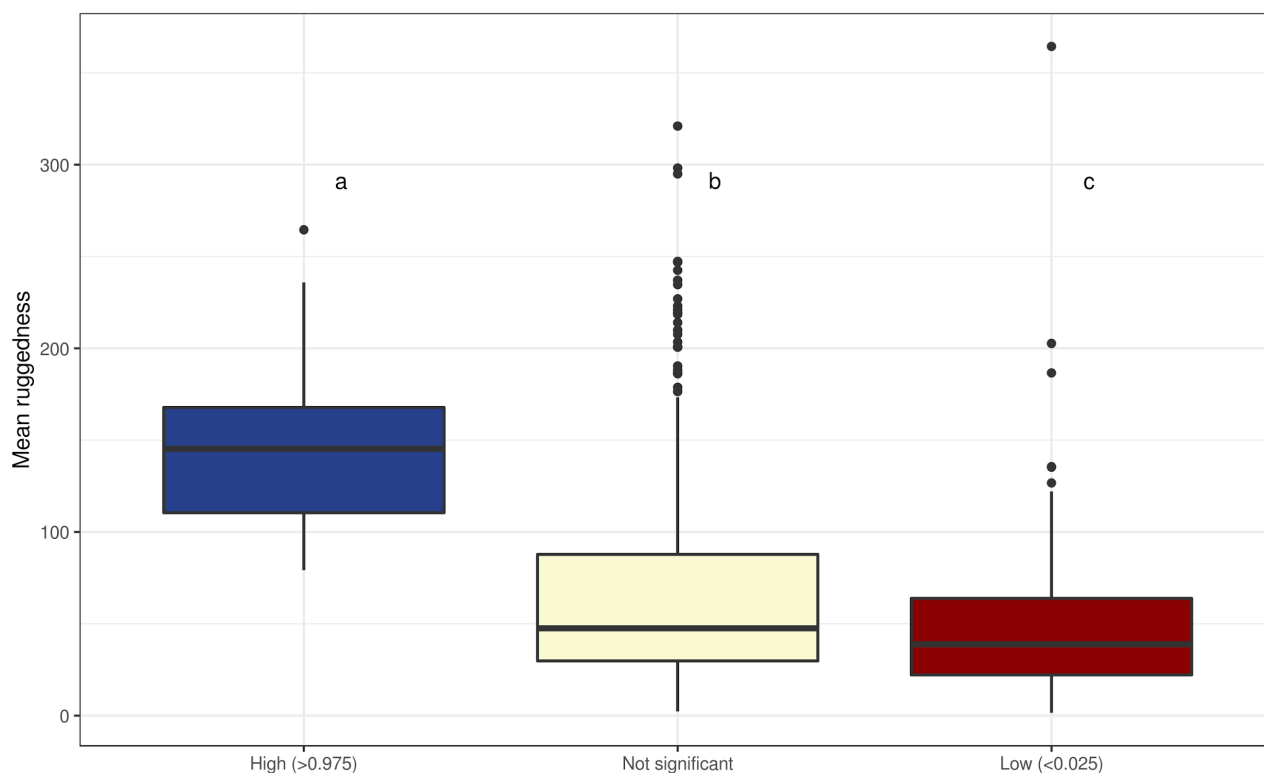
**Figure SI.2** Relationship between phylogenetic diversity (PD) and genus richness (GR). PD and GR were calculated for each of the 638 sampling units (SUs) using 1 719 tropical African angiosperms genera and the phylogenetic tree. SUs are  $100 \times 100$  km squares.  $R^2$ : adjusted R-square resulting from the linear regression of PD on GR.

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**Figure SI.3** Map of observed phylogenetic diversity. PD was calculated for each of the 638 sampling units (SUs) using 1 719 tropical African angiosperms genera and the phylogenetic tree. SUs are  $100 \times 100$  km squares. White SUs contain less than 100 records.

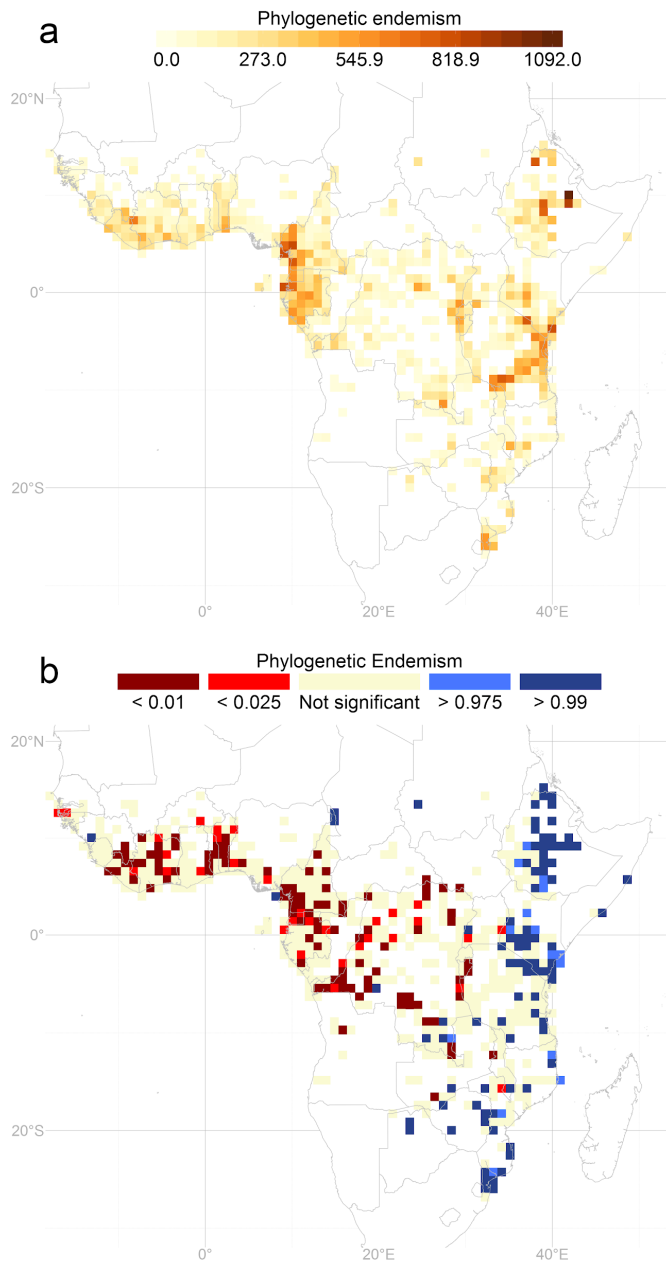
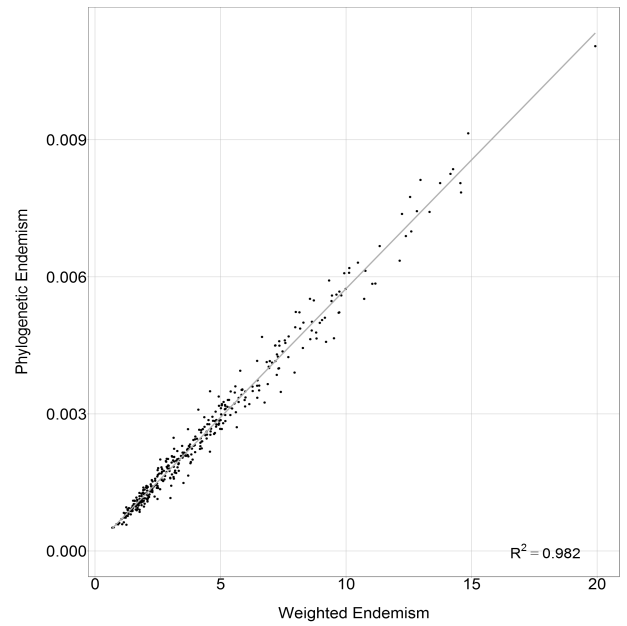


**Figure SI.4** Boxplot of the distributions of the mean ruggedness (in metres) of the SUs depending on their phylogenetic diversity (PD) significance class. Distributions are different (Kruskal-Wallis test,  $p$ -value =  $2.87 \times 10^{-14}$ ). Different letters indicates pairwise significant difference ( $p$  value < 0.05; pairwise comparison using Wilcoxon test with Holm's correction, see  $p$ -values in Table SI.1). For each box: the bold horizontal line corresponds to the median; the lower and upper bounds of the box correspond to first and third quartiles, respectively; the upper vertical line extends from the upper bound of the box to the highest value of the distribution, no further than  $1.5 \times$  IQR (Inter Quartile Range, or the distance between the first and third quartile); the lower vertical line extends from the lower bound of the box to the lowest value of the distribution, no further than  $1.5 \times$  IQR; black dots are values beyond IQR ('outlier' values).



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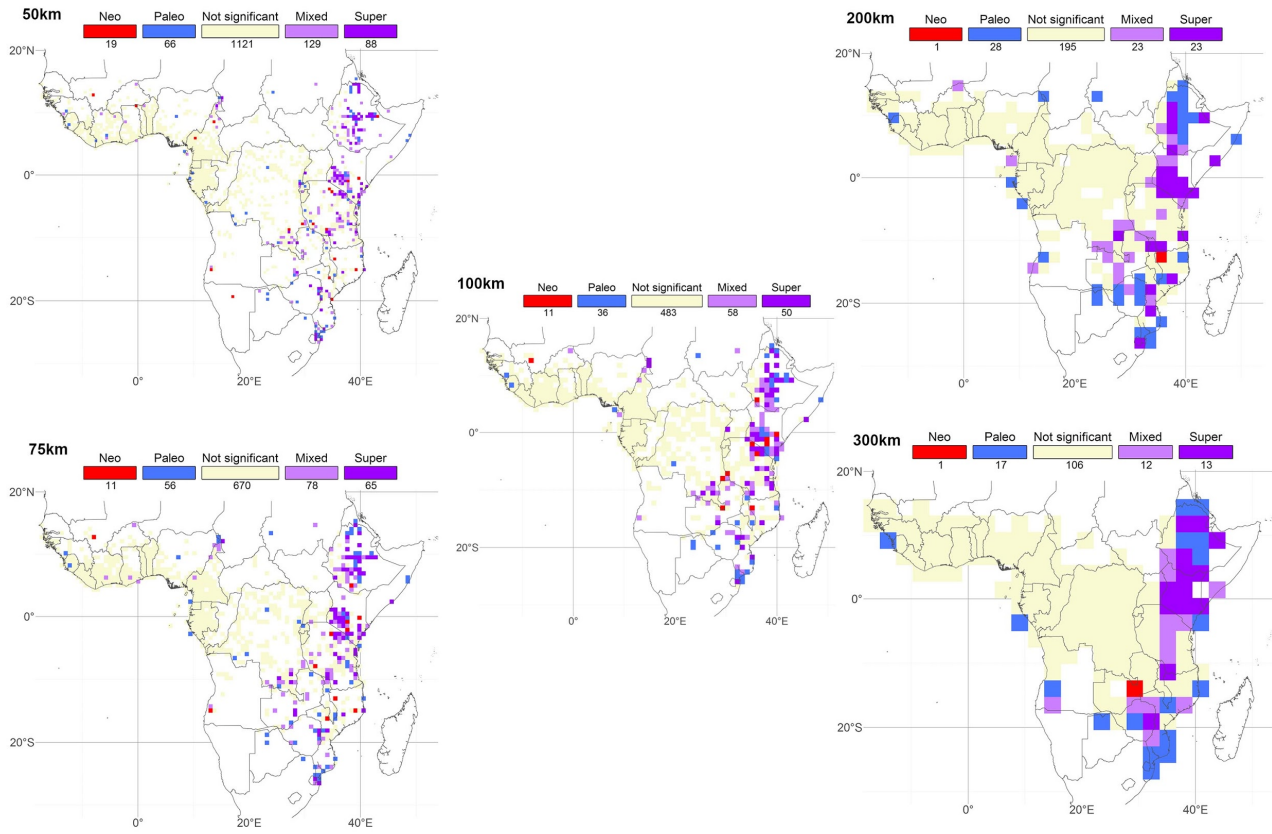
**Figure SI.5** Relationship between phylogenetic endemism (PE) and weighted endemism (WE). PE and WE were calculated for each of the 638 sampling units (SUs) using 1 719 tropical African angiosperms genera and the phylogenetic tree. SUs are  $100 \times 100$  km squares.  $R^2$ : adjusted R-square resulting from the regression of PE on WE.



**Figure SI.6** Maps of phylogenetic endemism: (a) Observed values, (b) Significant values from the randomisation test. PE was calculated for each of the 638 sampling units (SUs) using 1 719 tropical African angiosperms genera and the phylogenetic tree. SUs are  $100 \times 100$  km squares. Red SUs contain less PE than expected; blue SUs contain more PE than expected. Beige SUs are not significant. White SUs contain less than 100 records.

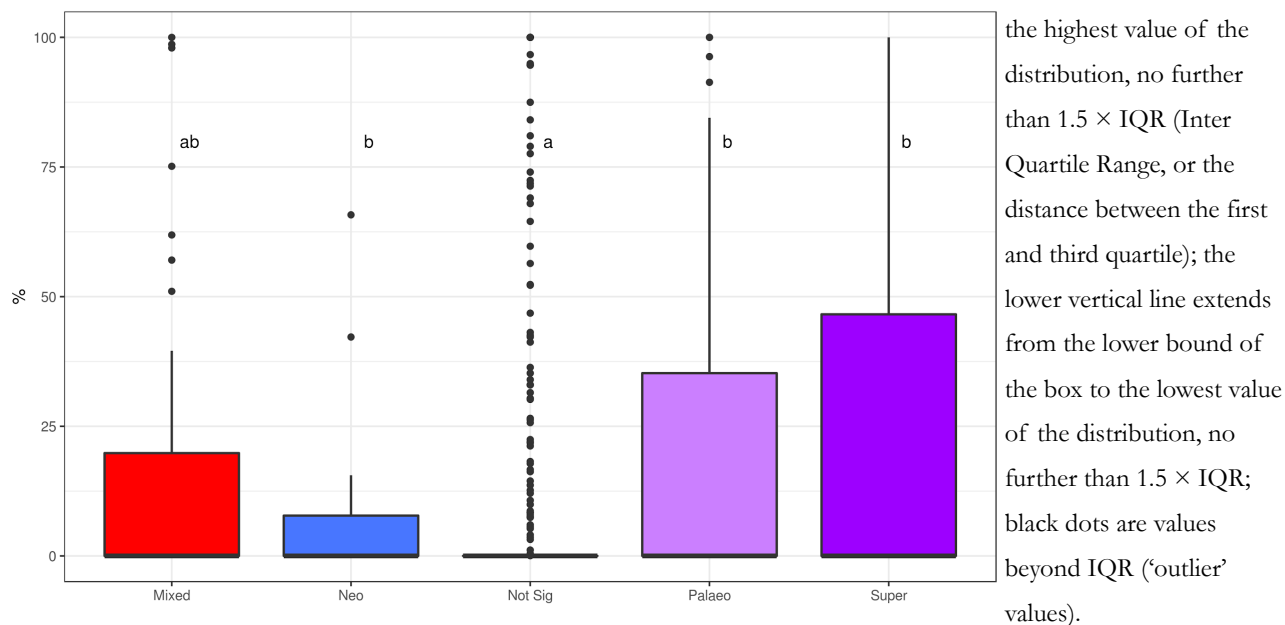
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**Figure SI.7** Maps of CANAPE results with different SU sizes. The  $50 \times 50$  km SUs contain at least 50 occurrences, the  $75 \times 75$  km SUs contain at least 75 occurrences, the  $100 \times 100$  km SUs contain at least 100 occurrences (that is the results interpreted in the main text), the  $200 \times 200$  km SUs contain at least 200 occurrences, and the  $300 \times 300$  km SUs contain at least 300 occurrences.

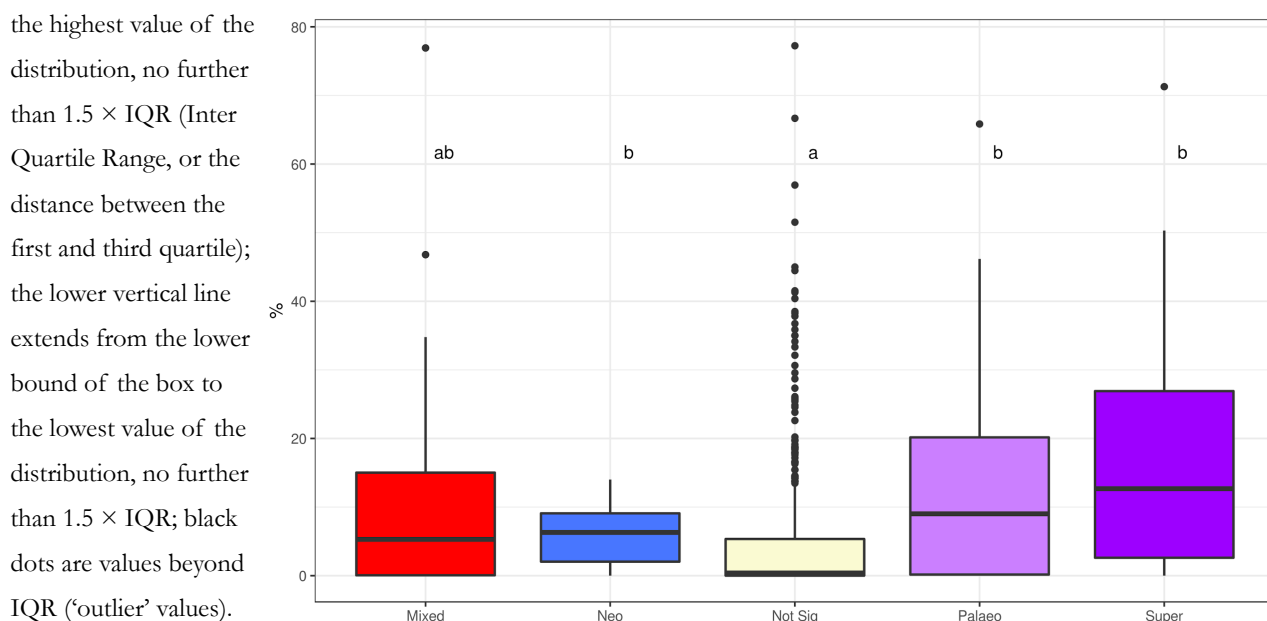


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**Figure SI.8** Boxplot of the distribution of the percentage of overlap of the SUs with ‘montane areas’ depending on their CANAPE category. Distributions are different (Kruskal-Wallis test,  $p$ -value =  $1.12 \times 10^{-9}$ ). Different letters indicates pairwise significant difference ( $p$  value < 0.05; pairwise comparison using Wilcoxon test with Holm’s correction, see  $p$ -values in Table SI.4). For each box: the bold horizontal line corresponds to the median; the lower and upper bounds of the box correspond to first and third quartiles, respectively; the upper vertical line extends from the upper bound of the box to



**Figure SI.9** Boxplot of the distribution of the percentage of montane plots of the sampling units depending on their CANAPE category. Distributions are different (Kruskal-Wallis test,  $p$ -value =  $1.91 \times 10^{-12}$ ). Different letters indicates pairwise significant difference ( $p$  value < 0.05; pairwise comparison using Wilcoxon test with Holm’s correction, see  $p$ -values in Table SI.3). For each box: the bold horizontal line corresponds to the median; the lower and upper bounds of the box correspond to first and third quartiles, respectively; the upper vertical line extends from the upper bound of the box to





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**Table SI.1** P-values resulting from the pairwise comparisons of mean ruggedness per sampling unit in each PD significance class (Wilcoxon test with Holm's correction). See Figure SI.5 for boxplot of the distributions.

<b>Mean ruggedness</b>	<b>High PD</b>	<b>Not significant</b>
<b>Not significant</b>	$7.2 \times 10^{-9}$	-
<b>Low PD</b>	$1.2 \times 10^{-12}$	$8.1 \times 10^{-6}$

**Table SI.2** P-values resulting from the pairwise comparisons of mean elevation per sampling unit in each RPD significance class. Kruskal-Wallis test rejected the null hypothesis of similar distribution between the three classes ( $p$  value =  $5.99 \times 10^{-6}$ ). Thus, pairwise comparisons were achieved using Wilcoxon rank sum test with Holm's correction of  $p$ -values. See Figure 7 in main text for boxplot of the distributions.

<b>Mean elevation</b>	<b>High RPD</b>	<b>Not significant</b>
<b>Not significant</b>	$1.20 \times 10^{-5}$	-
<b>Low RPD</b>	<b>0.00045</b>	$8.1 \times 10^{-6}$

**Table SI.3** P-values resulting from the pairwise comparisons of mean ruggedness per sampling unit in each CANAPE significance class. Kruskal-Wallis test rejected the null hypothesis of similar distribution between the five classes ( $p$ -value =  $3.51 \times 10^{-9}$ ). Thus, pairwise comparisons were achieved using Wilcoxon rank sum test with Holm's correction of  $p$ -values. See Figure 8 in main text for boxplot of the distributions.

	<b>Mixed</b>	<b>Neo</b>	<b>Not significant</b>	<b>Paleo</b>
<b>Neo</b>	1	-	-	-
<b>Not significant</b>	<b>0.027</b>	0.369	-	-
<b>Paleo</b>	1	1	0.055	-
<b>Super</b>	0.057	0.240	$9.60 \times 10^{-8}$	0.542

**Table SI.4** P-values resulting from the pairwise comparison of the percentage of montane plots of the sampling units depending on their CANAPE category (Wilcoxon test with Holm's correction). See boxplot on Figure SI.8 for boxplots of the distributions.

	<b>Mixed</b>	<b>Neo</b>	<b>Not Significant</b>	<b>Paleo</b>
<b>Neo</b>	1	-	-	-
<b>Not Significant</b>	0.002	0.143	-	-
<b>Paleo</b>	1	1	0.004	-
<b>Super</b>	0.057	0.465	$1.10 \times 10^{-9}$	0.561

**Table SI.5** P-values resulting from the pairwise comparison of the distribution of the percentage of overlap of the SUs with 'montane areas' depending on their CANAPE category (Wilcoxon test with Holm's correction). See boxplot on Figure SI.9 for boxplot of the distributions.

	<b>Mixed</b>	<b>Neo</b>	<b>Not significant</b>	<b>Paleo</b>
<b>Neo</b>	1	-	-	-
<b>Not significant</b>	$4.2 \times 10^{-4}$	1	-	-
<b>Paleo</b>	1	1	$1.22 \times 10^{-3}$	-
<b>Super</b>	0.811	1	$1.10 \times 10^{-9}$	1

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**Table SI.6** Number of significant CANAPE SUs overlaid by at least one protected area (all protected areas or only Ia, Ib or II types)

	Neo	Paleo	Mixed	Super	All	% of the total (155) significant CANAPE SUs
<b>All PAs</b>	9	30	52	42	133	85.81
<b>Ia, Ib, II PAs</b>	5	12	26	23	66	42.58

**Table SI.7** Surface intersection (in km<sup>2</sup>) between significant CANAPE SUs and protected areas (all protected areas or only Ia, Ib or II types)

	Neo	Paleo	Mixed	Super	All	% of the 155 SUs surface
<b>All PAs</b>	24 900	56 700	104 000	104 000	289 000	18.66
<b>Ia, Ib, II PAs</b>	11 500	15 600	37 500	27 200	91 800	5.92

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# Chapter 3 | Systematics of the Monodoreae tribe, with a focus on the *Uvariodendron* and *Uvariopsis* genera\*

**Abstract.** Monodoreae (Annonaceae, Annonoideae) is a tribe composed of 11 genera and 92 species mainly restricted to the tropical African rain forests. They have morphologically variable flowers, but can be characterized by a tree or shrub habit, indumentum of simple hairs, and sessile or shortly stipitate monocarp. All the genera are taxonomically well circumscribed except the species rich genera *Uvariodendron* and *Uvariopsis* that lack a recent taxonomic revision. The Monodoreae tribe is phylogenetically well supported by previous work that inferred the phylogenetic relationships of the Annonaceae family, or that focused on particular genera. However, the phylogenetic relationships of the Monodoreae have only been inferred using few data regarding the taxonomic sampling and the number of molecular markers used. Here, we generated a robust phylogenomic tree of the Monodoreae, including 95% of the species, with several specimens per species, based on more than 300 nuclear genes. We used two approaches, the concatenation approach and the gene trees approach, to infer the phylogenetic tree of the Monodoreae and test the limits between the genera and species. Given the species rich *Uvariodendron* and *Uvariopsis* have never been fully assessed phylogenetically, we give a particular focus on these two genera. All the genera were recovered monophyletic, except the genus *Uvariopsis* for which the species *Uvariopsis tripetala* (Baker f.) Schatz was excluded. We thus reinstated the monotypic genus *Dennettia* and its single species *Dennettia tripetala* Baker f. The genera *Ophrypetalum* and *Sanrafaelia* were excluded from the Monodoreae tribe, and we erect a new tribe, Ophrypetaleae, to accommodate these two sister genera. Below the genus level, the genera *Isolona*, *Monodora*, *Uvariastrum*, *Uvariodendron* and *Uvariopsis* show weakly supported nodes and phylogenetic conflict between the two approaches, suggesting that population level processes of evolution might occur in these taxa. Our result also support, at the molecular level, the description of several new species of *Uvariodendron* and *Uvariopsis*, as well as several name synonymies.

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\* Manuscript in preparation

## 1. Introduction

The Annonaceae is a diverse family of trees, shrubs and lianas, having a pantropical distribution, with most of the species restricted to the tropical rain forests. Recent work based on molecular phylogenetics have classified Annonaceae into four subfamilies and several tribes (Chatrou *et al.*, 2012; Guo *et al.*, 2017b; Couvreur *et al.*, 2019). Within the Annonoideae subfamily, the tribe Monodoreae -previously referred to as the “African long-branch clade” (Couvreur *et al.*, 2008a)- is composed of species distributed exclusively in tropical Africa and Madagascar. The tribe is composed of 11 genera and with the new species described here it includes 92 species.

Monodoreae is morphologically very variable, with several genera exhibiting characteristics unusual for the Annonaceae family as a whole (van Heusden, 1992). The genus *Uvariopsis* has dimerous and unisexual flowers, whereas most of the Annonaceae have trimerous and bisexual flowers (van Heusden, 1992). In contrast to the typical Annonaceae flower with six free petals arranged in two whorls, the genera *Asteranthe*, *Hexalobus*, *Isolona*, *Monodora*, *Sanrafaelia*, and some species of *Uvariopsis* have fused inner and outer petals forming a single whorl of petals. The genus *Isolona* and *Monodora* have prezygotic fused carpels, i.e. syncarpous gynoecia, which is unique in the Annonaceae (Deroin, 1985; Couvreur *et al.*, 2008b; Couvreur, 2009). This important diversity renders a clear morphological circumscription of the Monodoreae tribe complicated. To date it has however been recognized by the combination of the tree or shrub habit, indumentum of simple hairs, and especially sessile or shortly stipitate monocarps (Couvreur *et al.*, 2008b; Chatrou *et al.*, 2012). Taxonomically, most of the 11 genera have been taxonomically revised (Couvreur, 2009, 2014; Botermans *et al.*, 2011; Gosline *et al.*, 2019) except for the monotypic genera *Monocyclanthus*, *Ophrypetalum* and *Sanrafaelia*, and the genus *Asteranthe* with two species (Vollesen, 1980). Recently, the new genus *Lukea* was described with two species, and was suggested to be close to *Mischogyne* and *Monocyclanthus* based on morphological characters (Cheek *et al.*, 2021).

In contrast, for the more species rich genera, *Uvari dendron* and *Uvariopsis*, the latest revisions are more than 80 years old (Fries, 1930; Robyns & Ghesquière, 1933). However, several species have been described since then (Verdcourt, 1971b; Gereau & Kenfack, 2000; Kenfack *et al.*, 2003; Couvreur & Luke, 2010; Dagallier *et al.*, 2021; Gosline *et al.*, 2022; Couvreur *et al.*, in press). Morphologically, *Uvari dendron* has the typical Annonaceae hermaphroditic flowers with one whorl of three sepals and two whorls of three petals. In contrast, *Uvariopsis* has flowers with one whorl of two sepals and one whorl of three or four petals, and most of the species having unisexual flowers. Phylogenetically, *Uvariopsis* and *Monocyclanthus* are sister genera, and *Uvari dendron* is the sister genera to *Uvariopsis*

– *Monocyclanthus* (Couvreur *et al.*, 2008a). The taxonomic history of *Uvariopsis* is complex with several expansions of the concept of the genus (see Discussion and the taxonomic history section of Chapter 4). For example, Kenfack *et al.* (2003) combined the monotypic genus *Dennettia* Baker f. into *Uvariopsis*, expanding the concept of this genus to trimerous flowers. This was supported by a molecular phylogeny based on few plastid markers, but was recently contested based on morphological grounds (Cheek *et al.*, 2021).

The exploration of the phylogenetic relationships of species rich clades such as the Annonaceae is a challenge. Several studies previously explored the Annonaceae focusing on the whole family (Johnson, 2003; Doyle *et al.*, 2004; Richardson *et al.*, 2004; Guo *et al.*, 2017b; Xue *et al.*, 2020) or on particular tribes or genera (Couvreur *et al.*, 2008b,a; Couvreur, 2009; Thomas *et al.*, 2012; Tang *et al.*, 2015; Guo *et al.*, 2017a; Ortiz-Rodriguez *et al.*, 2018). These phylogenies were reconstructed using a few number of genes (generally less than 10 chloroplastic markers), but as technologies advances, recent work tend to include more and more genes (Lopes *et al.*, 2018; Guo *et al.*, 2018). In the Monodoreae tribe, phylogenetic relationships between the genera have been inferred with relatively strong statistical support in several molecular phylogenetic studies based on a few chloroplastic markers (Couvreur *et al.*, 2008a; Guo *et al.*, 2017b; Xue *et al.*, 2020). These studies inferred three main clades, referred to here as: the “*Isolona* clade”, (containing the genera (*Asteranthe*, (*Hexalobus*, *Uvariastrum*)), (*Isolona*, *Monodora*)); the “*Uvariopsis* clade” (containing the genera ((*Uvariopsis*, *Monocyclanthus*), *Uvarioidendron*), *Mischogyne*); and the *Sanrafaelia* – *Ophrypetalum* clade. This later clade was recovered as sister to rest of the *Monodoreae* tribe with moderate to strong support based on phylogenetic analyses of plastid markers. The development of phylogenomics in Annonaceae (Couvreur *et al.*, 2019) not only brought new insights in the understanding of the evolution of the family and of the tropical rain forests (Brée *et al.*, 2020; Helmstetter *et al.*, 2020a,b), but also clarified the systematics of the family. Indeed, among other results, using hundreds of nuclear markers, Couvreur *et al.* (2019) found the African genus *Annickia* to be excluded from the Piptostigmateteae tribe, and erected the new tribe Annickieae. Some Monodoreae genera were also included in this study and in contrast to previous analyses (Couvreur *et al.*, 2008b,a; Guo *et al.*, 2017b), they found a strong phylogenetic affinity of *Sanrafaelia* to another tribe of Annonaceae, namely Uvarieae (Couvreur *et al.*, 2019). However, this relationship was based on few species sampled across the family, but this suggests that phylogenomic could bring new insights to the Monodoreae tribe systematic

In Monodoreae, the relationships between species have only been inferred, based on few chloroplastic markers, within *Isolona*, *Monodora* and more recently *Mischogyne* (Couvreur, 2009; Gosline *et al.*, 2019) providing support to species and generic delimitation within the tribe. Moreover, the placement

of *Lukea* within Monodoreae and the relationships in the species rich *Uvari dendron* and *Uvariopsis* genera have never been assessed with a complete taxon sampling. Examining *Uvariopsis* in a phylogenetic context could confirm or in firm the previously established combinations in the genus.

The aim of the present study is to generate a robust phylogenomic tree of the Monodoreae and test the limits between the genera and species. Given the species rich *Uvari dendron* and *Uvariopsis* have never been fully assessed phylogenetically, and the taxonomic complexities of *Uvariopsis*, we give a particular focus on these two genera. We discuss species delineation based on both molecular and morphological evidences. In parallel to the present systematic work, we publish the taxonomic revision of *Uvari dendron* and *Uvariopsis* (Chapter 4).

## 2. Material & methods

### 2.1. Morphology

We examined the morphological characters of the Monodoreae species based on the protologues of the species and on the taxonomic revisions of the different genera (Diels, 1936; Keay, 1953; Verdcourt, 1960, 1996; Vollesen, 1980; Couvreur, 2009, 2014; Botermans *et al.*, 2011; Gosline *et al.*, 2019; Cheek *et al.*, 2021). In addition, we examined as many specimens of *Uvari dendron* and *Uvariopsis* as possible, as well as several specimens of *Monocyclanthus*. The specimens come from B, DSM, EA, K, M, MO, MPU, P, WAG and YA herbaria (Thiers, 2016). The high quality scans of some additional specimens or sheets from BR, COI and MA were also examined, as well as pictures taken in the field or personal fieldwork observations.

### 2.2. Phylogenomics

#### 2.2.1. Taxon sampling

We sampled at least one specimen per species of the Monodoreae tribe, except for the species *Lukea quentini* Gosline & Cheek (Cheek *et al.*, 2021), *Uvariopsis sessiliflora* (Mildbr. & Diels) Robyns & Ghesq., *Uvariopsis bisexualis* Verdc., and *Uvariopsis dicaprio* Cheek & Gosline (Gosline *et al.*, 2022) for which no material was available. We also included several specimens from the Uvarieae tribe representing different genera, as well as several other Annonaceae outgroups (Chatrou *et al.*, 2012, Table SI.8). Within Monodoreae, we sampled, when possible, more than one specimen per species following these cases: one specimen per subspecies or variety; one specimens per major geographic region for widespread species (between East Africa, West Africa, Central Africa); several specimens for morphologically variable species representing that variability (Table SI.8).

## CHAPTER 3

For all specimens, DNA was extracted from either silicagel dried leaf samples or leaf material taken from herbarium specimens. Details about specimens and vouchers are available in Table SI.8.

For the downstream analyses, every sample was assigned a unique identifier as follow: RUN\_###\_I###\_T###\_Genus\_species-COL\_NUM. “RUN\_###\_I###\_T###” is the identifier used for the sequencing process and bioinformatics analyses. “Genus\_species” is the most up to date taxonomic identification of the specimen (i.e. after applying the taxonomic changes treated in this paper). To ease the reading of updated names, some of the specimens have their old identification in parentheses like “Genus\_species\_(ex\_old name)”. “COL\_NUM” is the three first letters of the name of the collector and the number of collection of the specimen (e.g. “VAL\_2540” stands for the specimen n°2540 collected by J.L.C.H van Valkenburg). The details about every sample can be found in the Table SI.8.

### 2.2.2. DNA extraction, library preparation and sequencing

DNA extraction and NGS library preparations for nuclear exon capture followed Couvreur *et al.* (2019). Libraries were sequenced using an Illumina HiSeq 2000 platform using paired-end sequencing of length 150bp by Novogene Co. Ltd.

### 2.2.3. Raw sequence bioinformatics

Raw read sequences were demultiplexed using the demultadapt script (<https://github.com/Maillol/demultadapt>). Adapters were removed from the reads using cutadapt 1.18 (Martin, 2011) with the “-b” option and the “-O 7 -m 35 -q 20 -e 0.1” parameters. Low quality reads were then filtered (mean quality phred score below 30 and read less than 35 bp long) using a script modified from [https://github.com/SouthGreenPlatform/arcad-hts/blob/master/scripts/arcad\\_hts\\_2\\_Filter\\_Fastq\\_On\\_Mean\\_Quality.pl](https://github.com/SouthGreenPlatform/arcad-hts/blob/master/scripts/arcad_hts_2_Filter_Fastq_On_Mean_Quality.pl). Reverse and forward reads were paired according to their names in the fastq files using a custom script ([https://github.com/SouthGreenPlatform/arcad-hts/blob/master/scripts/arcad\\_hts\\_3\\_synchronized\\_paired\\_fastq.pl](https://github.com/SouthGreenPlatform/arcad-hts/blob/master/scripts/arcad_hts_3_synchronized_paired_fastq.pl)). A final step of 6 bp trimming was performed on the reverse reads using FASTX-Toolkit ([https://github.com/agordon/fastx\\_toolkit](https://github.com/agordon/fastx_toolkit)).

### 2.2.4. Contig assembly and alignment

To process the clean reads, we used the HybPiper pipeline (Johnson *et al.*, 2016) following Couvreur *et al.* (2019). This pipeline mapped the reads on to the targetted nuclear exons using BWA v0.7.12 (Li & Durbin, 2009). The mapped reads were assembled into contigs using SPAdes v3.11.1 (Bankevich *et al.*, 2012). Overlapping contigs were then assembled into ‘supercontigs’ containing both targetted sequence (i.e. exon) and off-target sequence data (i.e. partial intron). The pipeline ends up with one file per gene (supercontig) containing the alignment of the sequence for every individual.

### 2.2.5. Phylogenetic reconstruction

We used two different approaches for the phylogenetic reconstruction: the concatenation approach and the gene tree approach. For each approach, we first removed the supercontigs that were putatively identified as paralogs within the HybPiper pipeline, and then filtered our dataset to select only the supercontigs that are present in 75% of the individuals and for which the sequence contains at least 75% of the length of the target sequence (75/75 filter, following Couvreur *et al.*, 2019).

#### Concatenation approach

For each supercontig, the alignments were filled with gaps and missing individuals so that every sequence in the alignment has the same length and every alignment contains all the individuals. The alignments were then concatenated into a single “supermatrix” using the *pxcat* function in the *phyx* program (Brown *et al.*, 2017). Phylogenetic tree was inferred from the supermatrix using an optimized maximum likelihood (ML) tree search implemented in RAxML 8.2.9 with the GTRGAMMA model after a rapid bootstrap analysis (Stamatakis, 2014). We specified *Anaxagorea crassipetala* as an outgroup (“-o” option) and constrained the ML search on a backbone topology (“-g” option), in order to avoid long branches attraction due to the scarce sampling of the outgroups. The topology only includes the outgroup species and follows the results of Couvreur *et al.* (2019): (Anaxagorea\_crassipetala-MAA\_9408, (((((Uvarioidendron\_kirkii-DAG\_09, Uvaria\_grandiflora-COU\_838), Annona\_glabra-CHA\_467), Duguetia\_staudtii-COU\_1014), Guatteria\_jefensis-MAA\_9553), Greenwayodendron\_suaveolens-COU\_746)).

#### Gene trees approach

Gene trees we inferred a phylogenetic tree for every supercontig using RAxML 8.2.9 (Stamatakis, 2014) under the GTRGAMMA model and 100 bootstrap replicates. For every tree obtained, we removed the branches with a bootstrap support less than 10% using the Newick Utilities program ([https://github.com/tjunier/newick\\_utils](https://github.com/tjunier/newick_utils)), in order to improve the accuracy of the inferred species tree (Zhang *et al.*, 2018). We then inferred the summary species tree from all the (unrooted) genes trees using ASTRAL-III 5.7.5 under the multi-species coalescent model (Zhang *et al.*, 2018). The support at the branches was estimated both with the quartet support (QS) values (“-t 1” option) and with the local posterior probabilities (LPP) (default parameters). The species tree was then rooted on *Anaxagorea crassipetala* (Anaxagorea\_crassipetala-MAA\_9408).

The phylogenetic trees obtained were then plotted and annotated using the *ggtree*, *ggplot* and *treeio* packages (Wickham, 2016; Yu *et al.*, 2017; Wang *et al.*, 2020).

CHAPTER 3

Table 2: Morphological comparison of the Monodoreae genera. In bold, the combination of morphological characters diagnostic to each specific genus. H:w, height:width ratio.

	Leaves length	Tertiary vein- ation	Sepals	Petals	Receptacle H:w	Flower sexuality	Carpels
<i>Asteranthe</i>	40 – 165 (180) mm	reticulate	3, free to shortly con- nate at base	2 whorls of 3, <b>fused at base</b> , inner and outer petals subequal	ca. 1	bisexual	<b>free</b>
<i>Dennettia</i>	<b>&lt; 150 mm long</b>	reticulate	<b>3, fused at base, form- ing a persistent ring with the 3 lobes gener- ally clearly distinct, curved downward on the fruiting pedicel</b>	1 whorl of 3, free	< 1	bisexual	free
<i>Hexalobus</i>	36 – 360 mm long	reticulate	3, free to shortly con- nate at base	<b>1 whorl of 6, fused at base, folded in bud</b>	ca. 1	bisexual	<b>free</b>
<i>Isolona</i>	<b>50 – 280 mm long</b>	between reticulate and percurrent	<b>3, free, valvate</b>	1 whorl of 6, <b>fused at base</b>	< 1	bisexual	fused (true syn- carpy)
<i>Lukea</i>	68 – 210 mm long	prominent reticulate	<b>3, fused, forming a bowl-shaped</b> recept- acle, persistent on the fruiting pedicel	1 whorl of 3, free	> 1	bisexual	<b>free</b>
<i>Mischogyne</i>	<b>70 – 320 mm long</b>	prominent reticulate	<b>3, free, reduplicate- valvate in bud</b>	2 whorls of 3, free	> 1	bisexual	free, <b>connivent at base and separ- ated and slightly curved outwards at apex</b>
<i>Monocyclanthus</i>	> 150 mm long	reticulate	<b>3, fused at base, form- ing a ring</b> with the lobes <b>generally uncon- spicuous, persistent on the fruiting pedicel</b>	1 whorl of 6, free	> 1	bisexual	<b>free</b>
<i>Monodora</i>	<b>40 – 500 mm long</b>	between reticulate and percurrent	<b>3, free, valvate</b>	<b>2 whorls of 3, fused at base</b> , outer petals longer than inner petals, inner petals connivent at apex	<b>&lt;1 to 1</b>	bisexual	fused (true syn- carpy)
<i>Uvariastrum</i>	60 – 220 mm long	reticulate	3, free, <b>reduplicate- valvate</b> in bud, enclos- ing the petals in bud	2 whorls of 3, free	ca. 1	bisexual	<b>free, connivent all along their length</b>
<i>Uvariadendron</i>	<b>65 – 750 mm long</b>	reticulate	<b>3, connivent to fused at base</b>	<b>2 whorls of 3, free, in- ner and outer subequal in length, inner petals connivent</b> at apex	<b>ca. 1</b>	bisexual	free
<i>Uvariopsis</i>	70 – 615 mm long	reticulate	<b>2, free to fused at base</b>	<b>1 whorl of 4</b> (1 whorl of 3 in <i>Uvariopsis congolana</i> ), free to fused	1 – 1.2	<b>unisexual</b> (except for <i>Uvariopsis bisexualis</i> )	free

### 3. Results

#### 3.1. Specimens examined

In total, we examined 961 herbarium specimens, including 496 of *Uvariadendron*, 419 of *Uvariopsis*, 37 of *Dennettia*, seven *Monocyclanthus* and two *Lukea*. In addition, we examined the morphological characters of the Monodoreae genera based on the taxonomic revisions and on the protologues (Diels, 1936; Keay, 1953; Verdcourt, 1960, 1996; Vollesen, 1980; Couvreur, 2009, 2014; Botermans *et al.*, 2011; Gosline *et al.*, 2019; Cheek *et al.*, 2021). We compiled the morphological characters of the Monodoreae genera in the Table 2.

#### 3.2. Phylogenomics

A total of 466 exon regions were recovered out of the 469 contained by the Annonaceae baiting kit (Couvreur *et al.*, 2019). Of these, 63 exon regions were identified as potential paralogs using HybPiper. After discarding the potential paralogs and applying the 75/75 filter (see Methods), the dataset comprised 315 supercontigs. This subset of 315 supercontigs was used for the downstream phylogenetic analyses with both the concatenation (after concatenation to a supermatrix) and gene trees approaches. After alignment, the supercontigs ranged in length between 307 and 9506 distinct sites (mean: 1400, median: 981). After concatenation of the 315 supercontigs, the supermatrix totalled 440\*998 distinct sites.

#### 3.3. Phylogenetic relationships

At the genus level and above, we recovered the same topology with both the concatenation (RAxML) and the gene tree (ASTRAL) approaches (Figures 10 and 11) with high levels of statistical support. The bootstrap (BS) values were all 100%, the local posterior probabilities (LPP) were all above 0.9, and the quartet support (QS) were generally high. The clade *Sanrafaelia* – *Ophrypetalum* is retrieved as sister to the Uvarieae (rather than to Monodoreae) with maximum BS and LPP support but with relatively low QS (44%) (Figures 10 and 11). All the genera were retrieved as monophyletic, except *Uvariopsis* for which the species *Uvariopsis tripetala* clustered as sister to *Monocyclanthus* (Figures 10 and 11). The two specimens of the species *Lukea triciae* were recovered as sister to *Mischogyne* with strong support. However, the branch leading to the crown node of *Mischogyne* was relatively long (Figures 10 and 11).

Species monophyly within the genera *Asteranthe*, *Hexalobus*, *Lukea*, *Mischogyne*, and *Monocyclanthus* received strong support, and the relationships between species were generally strong (BS > 90%, LPP > 0.9) and similar between both phylogenetic approaches (Figures 10 and 11). In *Hexalobus*, the three



specimens of *Hexalobus monopetalus* sampled from different countries (from Senegal, Mozambique and Angola) clustered together (Figures 10 and 11, Table SI.8) despite the species been widespread.

In *Isolona*, *Monodora*, *Uvariastrum*, *Uvariadendron* and *Uvariopsis*, there are incongruences in topologies between the RAxML and the ASTRAL trees, and the node support is generally strong (BS > 90%, LPP > 0.9), but some nodes are weakly (BS < 70%, LPP < 0.7) to moderately supported (70% < BS < 90%, 0.7 < LPP < 0.9) (Figures 10 and 11).

In *Uvariastrum*, *U. pierreanum* and *U. insculptum* are strongly supported as monophyletic, but *U. zenkeri* is found monophyletic only with the concatenation approach and with weak support (Figure 10). The species *U. germainii* is retrieved as sister to *U. pierreanum* with weak to strong support in both approaches. In contrast, the position of *U. hexaloboides* is uncertain, either as sister to *U. insculptum* (Figure 11) or as sister to all the other species in the genus (Figure 11).

In *Uvariadendron* and *Uvariopsis*, most species were recovered as monophyletic (Figures 10 and 11), but in some cases we appear to have species complex, that is either a cluster of closely related individuals from more than one species, or separate clusters of individuals from a single species (Sigovini *et al.*, 2016). In *Uvariadendron*, the specimens identified as *U. giganteum* (*Couvreur 1057* and *Couvreur 1206*) and *U. magnificum* (*Hamilton 676*) are nested within the specimens identified as *U. fuscum*, and most of the nodes subtending *U. fuscum* specimens are weakly supported in both RAxML and ASTRAL trees (Figures 10 and 11). The specimens previously identified as *U. molundense* clustered together, but formed three genetically distinct and strongly supported groups: one including the single specimen *Sosef 2219*, previously identified as *U. molundense* var. *citrata*, sister to the other two groups, another one composed of specimens *Sosef 2261* and *Valkenburg 2540*, and a final group composed of the remaining sampled specimens. The three groups are separated by relatively long branches, especially the group formed by the specimens *Sosef 2261* and *Valkenburg 2540* (Figures 10 and 11).

In *Uvariopsis*, the group formed by *U. bakeriana*, *U. citrata*, *U. korupensis*, *U. submontana* (« large leaves » group on Figure 10) is strongly supported at the crown node, but forms a species complex: while *U. bakeriana* is retrieved as monophyletic with strong support (Figures 10 and 11), *U. korupensis* is retrieved as paraphyletic in both phylogenetic approaches (Figures 10 and 11), while *U. citrata* is retrieved as monophyletic with moderate support in the gene tree approach only (QS < 50%, LPP < 0.7).

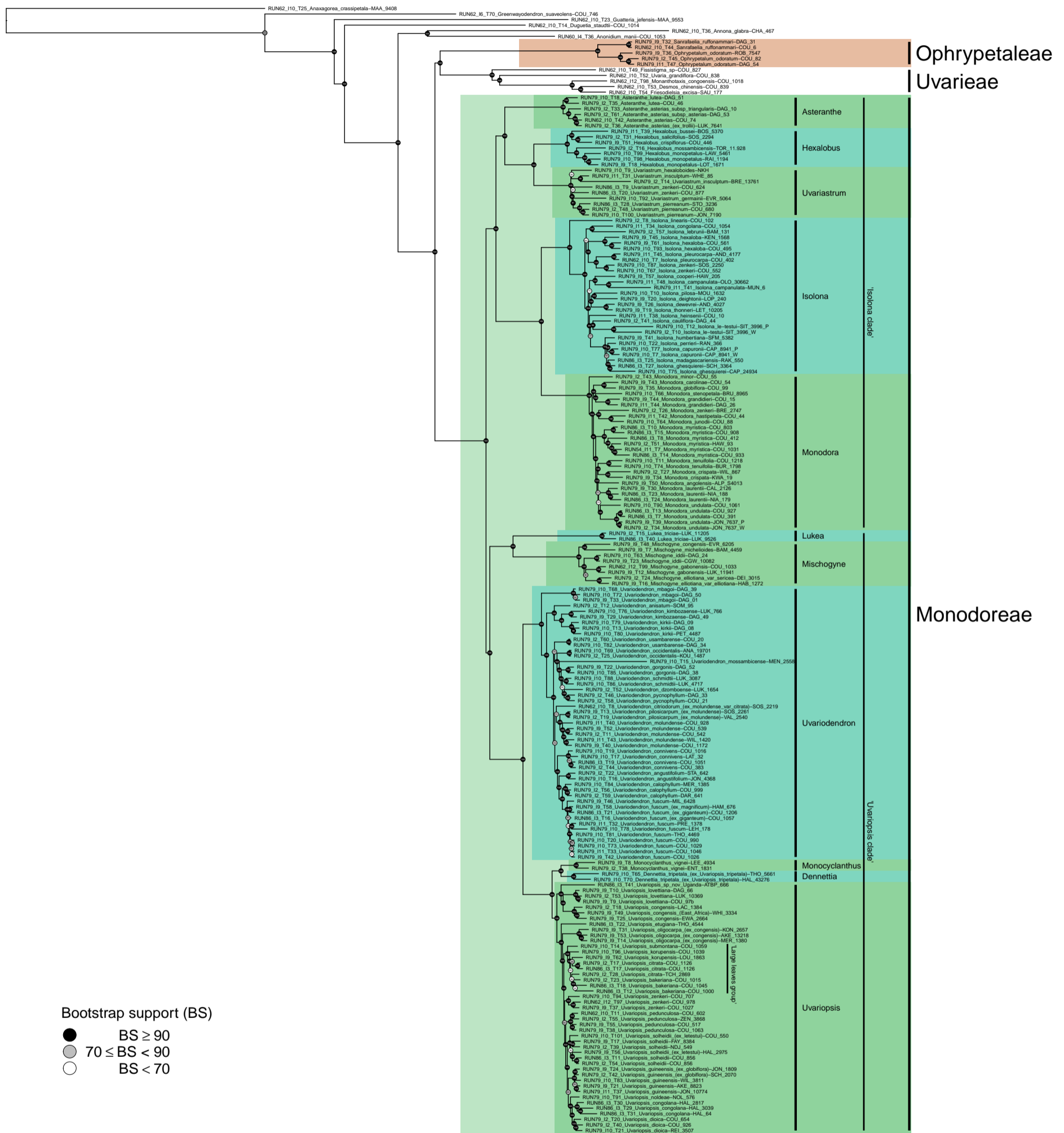


Figure 10: RAxML maximum likelihood tree of the Monodoreae, based on a concatenated supermatrix of 315 nuclear genes. Bootstrap support values (in %) are given at the nodes. The name of the specimens is composed of a unique identifier, followed by the species (or variety/subspecies) name, followed by the 3 first letters of the name of the collector and the collection number. The identification of the specimens follow the taxonomic changes treated in this study. For the details on the specimens see Table SI.8.

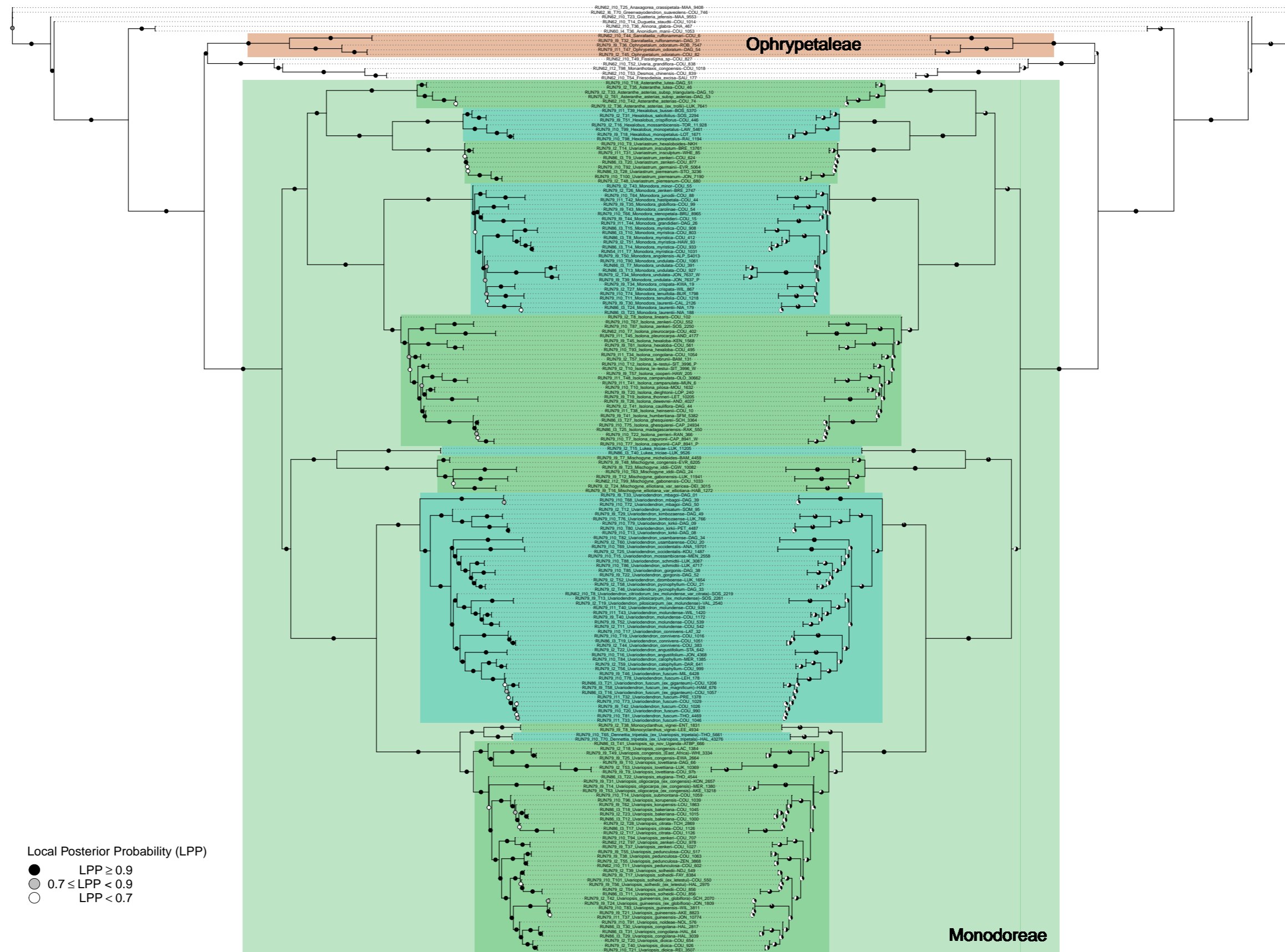


Figure 11: Phylogenetic trees of the Monodoreae reconstructed using ASTRAL, based on 315 nuclear genes trees. On the left, the branch support is given as local posterior probability (LPP) in three shades of greys. On the right, the branch support is given as pie charts of the quartet support (QS) such as the black proportion represents the percentage of quartets in the gene trees agreeing with the branch in the species tree. Names of the specimens identical to Figure 10. For the details on the specimens see Table SI.8.

## 4. Discussion

Here, for the first time, we reconstructed phylogenetic trees of the Monodoreae tribe based on 315 nuclear loci, using an Annonaceae specific targeted sequencing protocol (Couvreur *et al.*, 2019). Our analyses included all known genera of the tribe and 88 species out of the 92 described species. All genera, except for the paraphyletic *Uvariopsis*, were covered as monophyletic with strong support in both phylogenetic approaches (Figures 10 and 11). Relationships between genera are similar to those previously inferred using plastid markers (Couvreur *et al.*, 2008a; Guo *et al.*, 2017b), except for the placement of *Uvariopsis tripetala* sister to *Monocyclanthus*, rather than nested within *Uvariopsis* (Couvreur *et al.*, 2008a) and the *Ophrypetalum* – *Sanrafaelia* clade sister to Uvarieae, rather than sister to *Monodoreae* (see below). Below the genus level, most of the nodes are strongly supported. Some nodes, however, in the genera *Isolona*, *Monodora*, *Uvariastrum*, *Uvari dendron* and *Uvariopsis* are weakly to moderately supported in both concatenation and gene trees approaches. This generally coincides with incongruence in the species relationships between the two phylogenetic reconstruction approaches used here (Figures 10 and 11). In addition, in *Isolona* and *Monodora*, our results are conflicting with previous analyses based on chloroplastic loci (Couvreur *et al.*, 2008a, 2011).

Phylogenetic conflicts are common in plants phylogenomics: incongruences can occur between concatenation and gene tree approaches (Shen *et al.*, 2021) and between reconstructions based on nuclear loci or chloroplast loci (Morales-Briones *et al.*, 2018). Such incongruence are often attributed to reticulate processes of evolution occurring at the population level, like horizontal gene transfer, hybridizations or incomplete lineage sorting (ILS) (Maddison, 1997; Naciri & Linder, 2015; Morales-Briones *et al.*, 2018; Schrepf & Szöllősi, 2020). Phylogenetic conflict, associated with little divergence between species, is also known to coincide with rapidly evolving taxa in case of adaptative radiations (Meyer *et al.*, 2017) and morphological innovations (Parins-Fukuchi *et al.*, 2021). Widespread species can also be retrieved as nonmonophyletic, with diverging range-restricted species embedded within them. This is due to the retention of ancestral polymorphism in the widespread species where both the population size and the generation time are too high to achieve complete lineage sorting from the divergence time until the present day (Pennington & Lavin, 2016). This has been documented in Amazonia where tree species restricted to seasonally drought forests are retrieved embedded in rainforests tree species (Pennington & Lavin, 2016). These processes at the population level might be the cause of the observed phylogenetic conflicts in *Isolona*, *Monodora*, *Uvariastrum*, *Uvari dendron*, and *Uvariopsis*, and likely explain the species complex in the two later genera (see below).

#### 4.1. *Ophrypetaleae*: a new tribe

The two, monotypic East African genera *Ophrypetalum* Diels (Kenya and Tanzania) and *Sanrafaelia* Verdc. (Tanzania) (Diels, 1936; Verdcourt, 1960, 1996) are recovered with maximum support as sister genera confirming previous analyses (Couvreur *et al.*, 2008a) (Figures 10 and 11). This clade has previously been recovered as sister to all the other Monodoreae genera in several studies based on a few chloroplastic markers, with moderate to strong support (Couvreur *et al.*, 2008a; Chatrou *et al.*, 2012; Guo *et al.*, 2017b; Xue *et al.*, 2020). Here, with more than 300 nuclear loci and a much denser species sampling, we retrieved the *Ophrypetalum* – *Sanrafaelia* clade as sister to the Uvarieae tribe, with strong support (Figures 10 and 11). Our analyses thus confirm the result of Couvreur *et al.* (2019) using the same baiting kit, but only sampling *Sanrafaelia* and fewer species within Monodoreae. The discrepancy between the relationships inferred in the previous studies and here can be attributed to the higher number of loci sequenced, but also to the use of nuclear loci (vs. chloroplastic loci).

The Monodoreae exhibits a great morphological diversity and it is thus difficult to characterise it with a single synapomorphy for all species. Despite this difficulty, the Monodoreae tribe is characterized by sessile or shortly stipitate monocarps (less than 10 mm), even though this character is found in several other genera across the family (e.g. the African monotypic genus *Meiocarpidium*). Both *Ophrypetalum* and *Sanrafaelia* present shortly stipitate monocarps, which previously suggested their placement within the Monodoreae tribe, in addition of being African (Couvreur *et al.*, 2008b). The Uvarieae tribe is mainly comprised of lianas (although some genera are trees, e.g. *Dasymachalon*, Wang *et al.*, 2009, 2012) with indumentum of stellate or simple hairs, and stipitate monocarps (Couvreur *et al.*, 2008b; Chatrou *et al.*, 2012). This precludes *Ophrypetalum* and *Sanrafaelia* as being part of Uvarieae on morphological bases. This is also supported genetically by the long branches separating it from the crown node of the Uvarieae tribe (Figure 10). We thus propose the erection of a new tribe to accommodate these two genera.

***Ophrypetaleae*** Dagallier & Couvreur, **tribus nov.** – TYPE: *Ophrypetalum* Diels

Shrubs to trees; indumentum of simple hairs. Carpels 1 – 15. Monocarps 1 – 10, sessile to shortly stipitate, 5 cm long or more, narrowly cylindrical, length:width ratio more than 5.

Included genera: *Ophrypetalum* Diels, *Sanrafaelia* Verdc.

#### 4.2. *Asteranthe*

*Asteranthe* is an East African genus characterised by basally fused petals (Verdcourt, 1971b). The monophyly of the genus *Asteranthe* receives strong support (Figures 10 and 11), and is sister to the

*Hexalobus* – *Uvariastrum* clade confirming previous analyses (Couvreur *et al.*, 2008a). *Asteranthe trollii* Diels was described in 1936 (Diels, 1936) but the name was synonymized by Verdcourt with *Asteranthe asterias* (S. Moore) Engl. & Diels. Verdcourt argued that the type species of *A. trollii* was very similar to *A. asterias* (Verdcourt, 1971b). Here, we sequenced the specimen *Luke 7641*, originally identified as *A. trollii* which clustered with the other sampled specimens of *A. asterias* (Figures 10 and 11). Even though the specimen we sequenced is not the type specimen, our result supports the synonymy proposed by Verdcourt (Verdcourt, 1971a,b).

In addition, Verdcourt (1971b) described the subspecies *Asteranthe asterias* subsp. *triangularis* based on the petals being narrowly triangular (vs. linear-oblong to linear in *Asteranthe asterias* subsp. *asterias*). Here we find the two subspecies to be genetically separated (Figures 10 and 11) supporting Verdcourt's proposal. However, sampling more specimens of *A. asterias* subsp. *triangularis* would be necessary to decide whether the subspecies should be erected to the species level.

### 4.3. *Hexalobus*

The genus *Hexalobus* currently contains five accepted species (Botermans *et al.*, 2011). This genus is characterized by basely fused petals which are longitudinally folded (wrinkled) in bud, a character unique within the family (van Heusden, 1992; Botermans *et al.*, 2011). The species *H. monopetalus* has a very widespread “ring” type distribution, from Senegal to the north of South Africa (and parts of Angola). It occurs in drier woodland savannah or gallery forests (Botermans *et al.*, 2011). This is unique among the Monodoreae species, that generally have ecological affinities with wetter areas and have a more restricted geographical distribution. We retrieved *H. monopetalus* as monophyletic (Figures 10 and 11), confirming that despite its widespread distribution, it is a single species. *H. monopetalus* forms a clade with *H. mosambicensis* which is also dry adapted (Botermans *et al.*, 2011).

The widespread central African species *H. crispiflorus* is recovered as sister to the more narrower *H. salicifolius* (Cameroon and Gabon) with maximum support in both analyses (Figures 10 and 11). This confirms they are closely related as suggested by Le Thomas (1969). They do however differ by several morphological characters such as smaller leaves and smoother monocarps in *H. salicifolius*. Monophyly, however, needs to be confirmed by a denser sampling within each species.

### 4.4. *Uvariastrum*

*Uvariastrum* is a genus containing five species that are characterized by reduplicate-valvate (*i.e.* curved outwards) sepals margins (Couvreur, 2014). Morphologically, the five species are clearly differentiable on several characters such as the indumentum and leaf morphology. Our results however, underline

some level of phylogenetic conflict (Figures 10 and 11). The geographical distributions of all the species overlap, at least partially, in central Africa, except for *U. hexaloboides* that is distributed in Zambia and in Katanga region (south Democratic Republic of the Congo) (Couvreur, 2014). The lack of support for the nodes subtending *U. zenkeri* and *U. germainii* could be caused by old or occasional hybridization between the species but the inter-fertility has never been accounted for any of the *Uvari-*  
*astrum* species.

#### 4.5. The case of the newly described genus *Lukea*

Recently, the genus *Lukea* Gosline & Cheek was described, endemic to East Africa with two species: *Lukea quentinii* Cheek & Gosline and *Lukea triciae* Cheek & Gosline (Cheek *et al.*, 2021). Morphologically, *Lukea* resembles *Mischogyne* by the finely reticulate tertiary venation of the leaves and the absence of connective shield on the stamens (Gosline *et al.*, 2019). *Lukea* presents a bowl-shape calyx persisting in fruit, a character unique within the Monodoreae tribe, although resembling the fused sepals found in *Monocyclanthus* (Cheek *et al.*, 2021). Our results found the specimens of *Lukea triciae* as sister to *Mischogyne* but with great genetic divergence (Figures 10 and 11). This supports the description of the *Lukea* taxon as a new genus. However, future analyses should include specimens of *Lukea quentinii* in order to confirm the delimitation of this genus. This is particularly important, as this later species is the type of the genus.

#### 4.6. *Mischogyne*

*Mischogyne* is a genus of five species characterized by the combination of different morphological features such as prominent reticulate tertiary veins and carpels touching each other at their base but separated at their apex (Gosline *et al.*, 2019). The clade formed by *M. congensis* and *M. micheloides* is consistent in both our analyses (Figures 10 and 11) and with previous phylogenetic work on the genus based on a few plastid locus (Gosline *et al.*, 2019). The position of the East African species *M. idii* remains however uncertain, either retrieved as sister to the clade *M. congensis* – *M. micheloides* (Gosline *et al.*, 2019) or sister to the clade *M. elliotiana* – *M. gabonensis* (Figures 10 and 11).

#### 4.7. *Uvariopsis*

*Uvariopsis* Engl. is one of the most diverse genera of the Monodoreae tribe with 18 currently accepted species (and 3 potential additional species, see Chapter 4), and until recently, several species were unknown to science (Couvreur & Luke, 2010; Couvreur & Niangadouma, 2016). The thorough examination of the 419 specimens greatly enhanced the delineation of the species within the genus and lead to the discovery of new ones.

Morphologically, *Uvariopsis* is characterised by monoecious individuals (separate male and female flowers on a single individual) and by exhibiting a type of flower uncommon in Annonaceae, composed of two sepals and four petals (Robyns & Ghesquière, 1933). *Uvariopsis congolana* (De Wild.) Fries however has two sepals and three petals (De Wildeman, 1909). *Uvariopsis congolana* was previously described as a different genus *Thonnera*, but was later recombined into *Uvariopsis* (Fries, 1953). Both our molecular phylogenetic analyses retrieved *U. congolana* as sister species of *U. dioica* with strong support (Figures 10 and 11), confirming its placement in *Uvariopsis*. In 1986, Verdcourt described the species *U. bisexualis* from Tanzania, having the typical *Uvariopsis* flower with two sepals and four petals (and other typical pollen microscopic characters, see Verdcourt, 1986), but with bisexual flowers, thus extending the concept of the genus as also having bisexual flowers (Verdcourt, 1986). Unfortunately, we were not able to sample this species here.

#### 4.7.1. *Dennettia*, *Monocyclanthus* and flower variations in *Uvariopsis*

In 1913, Baker described the monotypic genus *Dennettia* Baker f., with a single species *Dennettia tripetala* Baker f. having bisexual flowers described as composed of “2 rarely 3 sepals” and three petals (Baker, 1913). In 2003, Kenfack *et al.* recombined the genus *Dennettia* into the genus *Uvariopsis* as *Uvariopsis tripetala* (Baker f.) G.E. Schatz, based on four main arguments (Kenfack *et al.*, 2003). First, the morphological description of *Uvariopsis* was expanded to include bisexual flowers by Verdcourt (1986, *U. bisexualis*); second, Kenfack *et al.* (2003), observed specimens of *D. tripetala* exhibiting flowers with 2 sepals and 4 petals; third, they considered that because *U. congolana* has 3 petals, the number of perianth segments is unreliable as a generic distinction for *Uvariopsis*; and fourth, the pollen microscopic features of *D. tripetala* are very close to those of *Uvariopsis* (Kenfack *et al.*, 2003; Doyle *et al.*, 2004). This was initially confirmed based on molecular phylogenetic analyses using few plastid regions, recovering *Uvariopsis tripetala* as nested within *Uvariopsis* but based on just two species sampled (Couvreur *et al.*, 2008a; Chatrou *et al.*, 2012).

After the careful examination of 16 flowering specimens identified as *Uvariopsis tripetala* (including the type *Dennett 44*), we found that this species invariably exhibits 3 sepals and 3 petals. The sepals are fused at base over up to more than half of their length, forming a ring persisting and curved downward on the fruiting pedicel. For some rare calyxes (mainly remaining on the fruiting pedicels), the lobes (i.e. the free parts at the apices of the basally fused sepals) are sometimes almost inconspicuous, making the confusion with a two-sepals calyx possible. We haven't seen any flowers of *U. tripetala* with four petals, contrary to the affirmation of Kenfack *et al.* (2003). If such flower arrangements exist, it must remain extremely rare. It is also possible that the four-petals flowers observed by Kenfack *et al.* (2003) were actually flower buds of the new species, *Uvariopsis oligocarpa* Dagallier & Couvreur (see below), as



their geographic ranges overlap and leaves are quite similar (but *U. oligocarpa* is unisexual). In contrast to the previous phylogenetic analyses, we did not recover *Uvariopsis tripetala* as nested within *Uvariopsis*, but as sister to the monotypic West African genus *Monocyclanthus vignei* Keay, with strong support in both phylogenetic approaches (Figures 10 and 11). *Uvariopsis tripetala* differs from *Monocyclanthus vignei* (Keay, 1953) by having three petals in one whorl (vs. six petals in one whorl), the lobes of the calyx generally well distinct (vs. generally inconspicuous), and a receptacle height:width ratio less than 1, i.e. wider than tall (vs. a receptacle height:width ratio greater than 1, i.e. taller than wide) (see Table 2).

All these morphological and phylogenetic elements suggest that *U. tripetala* is part of neither the genus *Uvariopsis*, nor the genus *Monocyclanthus*. We thus reinstate the monotypic genus *Dennettia*, with its single species *Dennettia tripetala* Baker f.. The updated description of *Dennettia tripetala* is given in the Taxonomic treatment section below.

#### 4.7.2. Monophyly of *Uvariopsis* and synoptic characters

*U. congolana* differs from all the other *Uvariopsis* species by having flowers with 3 petals instead of 4. The number of petals is not consistently reliable for the distinction of the genus *Uvariopsis* with the other genera, as highlighted by Kenfack *et al.* (2003). However, *U. congolana* has 2 sepals, similarly to all the other *Uvariopsis* species, making the number of sepals a reliable character for the genus circumscription. The synoptic characters of the genus *Uvariopsis* Engl. are thus given as follow:

##### *Uvariopsis* Engl.

Shrubs to trees with flowers exhibiting invariably two sepals, in combination with at least one of the two following characters (and generally with both of them): flowers unisexual (plant monoecious) and flowers exhibiting one whorl of four petals.

Molecularly, we find that the monophyly of *Uvariopsis* (excluding “*U. tripetala*”) is strongly supported and that the monophyly of most of the species is strongly supported in both phylogenetic approaches (Figures 10 and 11).

#### 4.7.3. The “large leaves” group:

Morphologically, the species *U. bakeriana*, *U. citrata*, *U. korupensis* and *U. submontana* show similarities, and form the group we refer to here as the “large leaves” group (see Figure 10). They are all trees with large obovate leaves (up to 30 – 60 cm long) having rounded to cordate bases, and display flowers borne along the trunk with varying degrees on density (from highly packed in *U. submontana* to sparse in *U. citrata*). In addition, flowering pedicels are shorter than 7 cm and petals generally 3 to 10 times

longer than wide. Despite these similarities, they differ between them by several marked characters. *U. bakeriana* has narrowly ovate to linear and bright pinkish to deep red petals (Hutchinson & Dalziel, 1927). *U. citrata* has sessile flowers and has leaves, young branches and flowers emitting a strong lemon scent when crushed (Couvreur & Niangadouma, 2016). *U. korupensis* and *U. submontana* have similar flowers with pedicels generally 20 – 70 mm long and ovate to narrowly ovate petals slightly fused at base, but are differentiated on the sepals being smaller in *U. korupensis* (1 – 5 (7) mm long) than in *U. submontana* (5 – 11 mm long) (Gereau & Kenfack, 2000; Kenfack *et al.*, 2003).

Phylogenetically, the “large leaves” group is monophyletic with strong support, but shows weak to moderate support at the internal nodes. Based solely on the phylogeny, one would consider the whole group as a single species. However, given the morphological differences of each species we choose to keep the taxonomy of this group as it is. Phylogenetic conflict is known to be coincident with morphological innovations (Parins-Fukuchi *et al.*, 2021), as observed in recent and fast diverging groups (Meyer *et al.*, 2017). Here we retrieve such a pattern, with substantial morphological differentiation between *U. citrata*, *U. bakeriana* and *U. korupensis*, but a lack of support at nodes subtending them. *U. korupensis* is retrieved as paraphyletic and the two specimens of this species sampled here (*Couvreur 1039* and *Louis 1863*) come from very different localities stretching its currently known distribution. They are likely from different isolated relictual populations failing to coalesce due to the persistence of ancestral polymorphism (Pennington & Lavin, 2016). The species *U. bakeriana* and *U. citrata* likely emerged from two populations that diverged from the ancestral *U. korupensis* population. This remains to be clarified with the sampling of more specimens (in particular of *U. submontana*) or with a phylogeographic and adapted population genomics approaches (Hardy *et al.*, 2013; Migliore *et al.*, 2019; Helmstetter *et al.*, 2020b).

#### 4.7.4. New and under collected species

Recently, we described *Uvariopsis etugiana* Dagallier & Couvreur, a rare species known from only two localities in Cameroon (Couvreur *et al.*, in press) which is phylogenetically confirmed here (Figures 10 and 11).

*Uvariopsis noldeae* Exell & Mendonça is a species from Angola (Exell & Mendonça, 1951). It is only known from the type specimen (*Nolde 576*) and is morphologically similar to *Uvariopsis solheidii* (De Wild.) Robyns & Ghesq., except for the young branches that are sparsely pubescent to glabrous whereas young branches of *U. solheidii* are tomentose to shortly tomentose. We thus suspected these two names to be synonyms, but our phylogenetic analyses revealed with strong support that *U. noldeae*

is genetically different from *U. solheidii*, and retrieved as sister to several other species (Figures 10 and 11).

*Uvariopsis congensis* differs from the other *Uvariopsis* species by its relatively small to medium sized leaves (less than 180 mm long), globose flower buds (vs. conical), and short flowering pedicels (less than 12 mm long). It is a widespread species distributed from Central Africa (Cameron, Gabon) to East Africa (Uganda, Kenya) (Robyns & Ghesquière, 1933; Verdcourt, 1971b). Interestingly, some of the specimens we identified as *U. congensis* were from West Africa, (Sierra Leone to Ghana), thus outside of its suggested range. A thorough examination of these West African specimens showed they differed by the morphology of their fruits. Moreover our molecular phylogenetic analyses retrieved these West African specimens (“*Uvariopsis oligocarpa*” on the Figures 10 and 11) as monophyletic with strong support, and clearly separated from the Central and East African specimens of *Uvariopsis congensis* (Figures 10 and 11). We thus describe these specimens under a new species *Uvariopsis oligocarpa* Dagallier & Couvreur (see Chapter 4 – Taxonomic treatment section). Morphologically, the sterile specimens of *U. oligocarpa* are similar to *U. congensis* and *Dennettia tripetala*. However, they are easily differentiated when female flowers or fruits are available (see Chapter 4 – Taxonomic treatment section).

Finally, the specimens of *Uvariopsis congensis* from East Africa (Verdcourt, 1971b) are also morphologically different from the specimens distributed in Central Africa. The East African specimens represent trees from 7 to 15 meters tall (vs. shrubs to trees from 2 to 7 meters tall for the Central African specimens) and they have narrowly elliptic laminas with a length:width ratio between 3 and 4 (vs. elliptic to obovate with a length:width ratio comprised between 2.1 and 3.1). Interestingly, the morphological differences between the two morphotypes are not supported by our phylogenetic analyses (Figures 10 and 11). Thus given our sampling we shall refrain from splitting *U. congensis* in two different species. However, to account for the morphological differences between the two morphotypes, we create the new variety *Uvariopsis congensis* var. *angustifolia* corresponding to the East African morphotype (see the Chapter 4 – Taxonomic treatment section).

The specimen *ATBP 666* (African Tropical Biodiversity Programme, MO04937010) collected from the Budongo Forest Reserve in Uganda, is a sterile specimen tentatively identified as *Uvariopsis congensis*. This specimen resembles this species except for its longer petioles when compared to typical *U. congensis* (ca. 6 mm vs. 2.5 – 5 mm in *U. congensis*). Interestingly, our results recovered this specimen as sister to the clade formed by *U. lovettiana* and *U. congensis*, with strong support (Figures 10 and 11). This result could suggest a possible undescribed species. Unfortunately, the available material is too poor for a proper new species description. We thus refer to this species as “*Uvariopsis* sp. nov.

Uganda” (see also Chapter 4). This species might be rare occurring only in the Budongo Forest Reserve. Plant surveys of this locality are relatively old (Synnott, 1985) and it has recently been assessed as a key biodiversity area (Plumptre *et al.*, 2019). This potentially new species underlies once again the great diversity of the East African region, with locations (forest remnants) containing numerous endemic species or genera (e.g. Scharff, 1992; Couvreur *et al.*, 2009; Gosline *et al.*, 2019; Dagallier *et al.*, 2021).

#### 4.7.5. Synonymies

In the Revision of the Flora of West Tropical Africa, Keay (1952) synonymised *Uvariopsis pedunculosa* (Diels) Robyns & Ghesq. with *U. dioica* (Diels) Robyns & Ghesq. Based on the examination of many herbarium specimens (including the type specimen), we found that the specimens previously identified with the name *U. pedunculosa* were morphologically very different from *U. dioica*. Indeed, *U. dioica* has free petals whereas *U. pedunculosa* has basely fused petals. Instead, we found that *U. pedunculosa* exhibits the same morphology than the specimens identified as *U. vanderystii* Robyns & Ghesq. Thus, in the Annonaceae Flora of Cameroon (Couvreur *et al.* in press), we synonymized *Uvariopsis vanderystii* Robyns & Ghesq. with *Uvariopsis pedunculosa* (Diels) Robyns & Ghesq. Phylogenetically, our results show that the holotype of *U. pedunculosa* (Zenker 3868) did not cluster with *U. dioica*, but with the specimens previously identified as *U. vanderystii* (e.g. Couvreur 602) (Figures 10 and 11) confirming the synonymisation of the name *U. vanderystii* with *U. pedunculosa*.

*Uvariopsis solheidii* (De Wild.) Robyns & Ghesq. and *Uvariopsis letestui* Pellegr. are two morphologically very similar species characterized by tomentose young branches, flowering pedicels up to 200 mm long, ovate to narrowly ovate petals and ridged bright-red monocarps (Robyns & Ghesquière, 1933; Pellegrin, 1948; Le Thomas, 1965). They have usually been distinguished based on the shape of their petals (narrowly ovate petals in *U. solheidii* vs. elliptic-ovate petals in *U. letestui*), the position of the bracts along the flowering pedicel, and the length of the flower pedicels (longer in *U. solheidii* than in *U. letestui*, but with an overlap) (Le Thomas, 1969). Our observations indicate a high overlap between these distinctive characters, and difficulties to place some specimens in one or the other species. Our molecular phylogenies retrieve the specimens of *U. solheidii* as paraphyletic with the specimens of *U. letestui*. Together, they form a strongly supported monophyletic group (Figures 10 and 11). We thus make the two names synonyms. Given the anteriority rule (Turland *et al.*, 2018), the name *Uvariopsis solheidii* prevails. We also collapse the morphological variation of *U. letestui* as a variety of the species. The full descriptions of the species and variety is given in the Chapter 4 – Taxonomic treatment below.

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*Uvariopsis globiflora* Keay and *Uvariopsis guineensis* Keay are distributed in West Africa, from Guinea to Ghana. They have traditionally been discriminated based on the position of their flowers and the fusion of the petals, with *U. globiflora* having axillary or terminal flowers and free petals and *U. guineensis* having flowers borne on trunk (cauliflory) and fused petals (Keay, 1952). The reliability of the position of the flowers is a character that has been previously discussed in the genus *Uvarioidendron* and has been concluded as being an unreliable character (Le Thomas, 1967, 1969). Keay himself, who described *U. globiflora*, already noticed that “it is [...] possible that cauliflory may occur in *U. globiflora*” (Keay, 1952). Indeed, among the specimens we observed, we found specimens with flowers both on trunk and axillary (e.g. notes on *Morton A 4247*, identified as *U. globiflora*, say “flowers on trunks, branches and amongst leaves”), or with characters of both *U. globiflora* and *U. guineensis* (e.g. *Schmidt 2070*, identified as *U. globiflora*, has both axillary flowers and fused petals), rendering their placement in one or the other species equivocal. Hawthorne and Jongkind (2006) also underlined this and treated the names *U. guineensis* and *U. globiflora* as synonyms. Our results support this, as specimens named as *U. guineensis* and *U. globiflora* clustered together with strong support (Figures 10 and 11). To account for a morphotype with free petals, we recombine *U. globiflora* to a variety of *U. guineensis* as *U. guineensis* var. *globiflora*. The full and updated descriptions of the species and variety is given in the Chapter 4 – Taxonomic treatment section.

Flower position in *U. guineensis* is not a reliable character for species delineation (Le Thomas, 1967, 1969). Interestingly, the unreliability of sympetaly for clearly distinguish *U. guineensis* s.s. (that is excluding the var. *globiflora*) and *U. guineensis* var. *globiflora* as two different phylogenetic species suggests that the fusion of the petals is a labile character in this species. In the Monodoreae, all genera and species of the “*Uvariopsis* clade” (Figure 10) have free petals, except for *U. pedunculosa*, *U. zenkeri* and *U. guineensis* s.s. that have fused petals. These two species are both branching at the stem of the clade composed of *U. solheidii*, *U. guineensis*, *U. noldeae*, *U. congolana* and *U. dioica*, that all exhibit free petals, except *U. guineensis* s.s.. This suggests that free petals was the ancestral state of the “*Uvariopsis* clade”. Then *U. pedunculosa* and *U. zenkeri* evolved to sympetaly, and then the clade composed of *U. solheidii*, *U. guineensis*, *U. noldeae*, *U. congolana* and *U. dioica* secondarily returned to a free petals state, except *U. guineensis* s.s.. All the genera in the “*Isolona* clade” (*Asteranthe*, *Hexalobus*, *Isolona*, and *Monodora*) have fused petals, except *Uvariastrum*. This would favour the hypothesis that sympetaly is the ancestral state for the “*Isolona* clade”, with a secondary loss in *Uvariastrum* (Couvreur *et al.*, 2008b). At a broader taxonomic scale, sympetaly has been recognized as a strong synapomorphy for one of the major clades of Angiosperms, the Asterid (Soltis & Soltis, 2004). But recently, it has been shown that sympetaly is a more labile character than expected and that it

cannot longer be used as a synapomorphy for the Asterids as several transition between free and fused petals might have occurred (Stull *et al.*, 2018). In the Monodoreae tribe, it seems to be similar, with sympetaly being likely synapomorphous to some genera or clades (e.g. the “*Isolona* clade”), but being labile in some other clades (e.g. *Uvariopsis guineensis*). Similar transitions between free to fused petals states also occurred in other clades in the Annonaceae, like for example in *Sanrafaelia* (Ophrypetaleae tribe) or some species of *Disepalum*, *Fusaea*, *Annona* and *Polyalthia* (Couvreur *et al.*, 2008b; Xue *et al.*, 2012).

#### 4.8. *Uvariodendron*

Morphologically, the genus *Uvariodendron* R.E.Fr. represents the typical Annonaceae flower. The species of this genus don't share any common character that makes the genus peculiar, but they can be recognized by the combination of the following characters. They are shrub or trees, with generally sessile or sometimes pedicellate (but pedicel less than 7 cm) bisexual flowers composed of one whorl of 3 sepals, and two whorls of 3 free and sub-equal petals. The flower bud is globose, and in buds, the petals of the outer whorl are valvate all along their margins, whereas the petals of the inner whorl are valvate only at the apex. The stamens are numerous (ca. 200 to 3000) and the carpels (between 5 and 160 in number) generally have coiled stigma covered with an exudate at anthesis. The monocarps are sessile to shortly stipitate (with stipe up to 12 mm). Phylogenetically, the genus is retrieved monophyletic with strong support (Figures 10 and 11).

##### 4.8.1. East Africa: an endless source of botanical discoveries

East Africa is a region that harbours a great plant diversity, with several species being endemic to the whole region or to small localities (Scharff, 1992; Burgess *et al.*, 1998, 2007; Couvreur *et al.*, 2009; Gosline *et al.*, 2019; Dagallier *et al.*, 2021). This pattern is known to be the result of the topographic heterogeneity of this region (Guillocheau *et al.*, 2018) that promotes both recent divergence and persistence of more anciently diverged lineages (Chapter 2, Fjeldså & Lovett, 1997; Rahbek *et al.*, 2019).

Recently, we described three new *Uvariodendron* species from the East African coastal forests based on their morphology: *Uvariodendron dzomboense* Dagallier, W.R.Q. Luke & Couvreur, *Uvariodendron mbagoi* Dagallier & Couvreur, and *Uvariodendron schmidtii* W.R.Q. Luke, Dagallier & Couvreur (Dagallier *et al.*, 2021). Here, our phylogenetic analyses retrieve these species as monophyletic and phylogenetically different, confirming their species status (Figures 10 and 11). *Uvariodendron mbagoi* is retrieved as the sister species to all the other *Uvariodendron* species, suggesting an East African origin of the genus.

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In addition to these recently described species, our results reveal another undescribed species. It is represented by four specimens previously identified as *Uvariodendron kirkii*, restricted from the Kimboza Forest Reserve in Tanzania (newly described here as *Uvariodendron kimbozaense* Dagallier). Phylogenetically, it is retrieved as sister to *U. kirkii* although clearly divergent at the molecular level (Figures 10 and 11). Morphologically, it is also close to *U. kirkii*, but differs by having larger flowers and different leaves dimensions (see Chapter 4). The flower of *U. kimbozaense* has imbricate sepals at the base (vs. connivent at base in *U. kirkii*), petals 16 – 39 mm long and 9 – 19 mm wide (vs. 10 – 20 mm long and 6 – 13 mm wide in *U. kirkii*), and the inner petals have a soft transversal curvature (vs. strong “boat-shaped” transversal curvature in *U. kirkii*). The leaves of *U. kimbozaense* have an acute to rounded base (vs. acute to decurrent base in *U. kirkii*), and on the upper side of the lamina, the mid rib is slightly raised with a tiny central depression (vs. slightly sunken in *U. kirkii*). The full description is given in the Chapter 4 – Taxonomic treatment section.

In the Flora Zambesiaca (Robson, 1960), a potential new species of *Uvariodendron* was documented without being named because of the scarcity of the material. It is only known from a single specimen (*Mendonça 2558A*) collected in 1944 in Mozambique. Phylogenetically, the specimens appears distinct from the other *Uvariodendron* species as it is retrieved as sister species to the group of East African species composed of *U. gorgonis*, *U. schmidtii*, *U. dzomboense* and *U. pycnophyllum* with strong support (see *Uvariodendron mossambicense* in Figures 10 and 11). Our results thus confirm that is specimen represents a new species. Morphologically, it is very similar to *U. dzomboense* by the short leaves (less than 130 mm long), narrowly elliptic and acute to slightly decurrent laminae, and the globose, ca. 5 mm in diameter and sessile flower buds. It differs by the number of carpels (ca. 5 vs. 50 – 75 in *U. dzomboense*). The description from the Flora Zambesiaca was based on a sheet from LISC. Our examination of this species is based on a sheet from WAG that contains a single monocarp, thus slightly enhancing the description of the species. The monocarp has a short stipe (ca. 12 mm long) which also differentiates it from *U. dzomboense* that has sessile monocarps. Even if the material remains scarce for a complete description, we provide evidences from both phylogeny and morphology that this species is distinct from the other known *Uvariodendron* species. We thus name this species *Uvariodendron mossambicense* Robson ex Dagallier and provide a description as complete as possible (see the Chapter 4 – Taxonomic treatment section).

East Africa has been relatively well explored botanically, as shown by the completion of the Flora of Tropical East Africa (Beentje, 2015) and the publication of several parts of the Flora Zambesiaca (Exell & Wild, 1960). However, our descriptions of several new species suggests that other botanical discov-

eries might arise from further exploration. This stresses out the importance of local botanical initiatives (e.g. Binggeli, 2019; Bingham *et al.*, 2021; Hyde *et al.*, 2021).

#### 4.8.2. The morphological continuum of *Uvariodendron fuscum*.

In the Flora of Cameroon (Couvreur *et al.*, in press), the name *Uvariodendron mirabile* R.E.Fr. was synonymized with *Uvariodendron fuscum* (Benth.) R.E.Fr. In our phylogenetic analyses, the sequenced type (*Preuss 1378*) and paratype (*Lehmbach 178*) of the name *U. mirabile*, clustered both with the other specimens identified as *U. fuscum* (e.g. *Mildbraed 6428*, one paratype of the name *U. fuscum*) (Figures 10 and 11), confirming they are conspecific.

Morphologically, *Uvariodendron fuscum* (Benth.) R.E.Fr., *Uvariodendron giganteum* (Engl.) R.E.Fr. and *Uvariodendron magnificum* Verdc. share morphological similarities and differences. They mainly diverge along a morphological continuum by the size of their leaves (lamina length) and the size of their flowers (sepals and petals dimensions, number of carpels), with *U. magnificum* having larger leaves and flowers than *U. giganteum*, with the latter having larger leaves and flowers than *U. fuscum*. In addition, *U. magnificum* flowers have apically imbricate inner petals while the other *Uvariodendron*'s have apically connate inner petals (Verdcourt, 1969). In terms of similarities, they all present elliptic to obovate leaves. *Uvariodendron fuscum* and *U. giganteum* have similar sepals (fused over up to half of their length), inner petals (free, obovate) and outer petals (free, ovate). *Uvariodendron giganteum* and *U. magnificum* have young branches covered with long and soft hairs producing a whitish appearance quickly falling off with age, whereas the young branches of *U. fuscum* vary from being sparsely pubescent to glabrous. Some of the characters that discriminate the species overlap (e.g. lamina length), particularly for *U. fuscum* and *U. giganteum*, and some of the specimens we observed were hard to place in one or the other species (e.g. *Couvreur 1029*).

Phylogenetically, the specimens of the three species clustered together, with strong support at the crown node and a weak to moderate support at the internal nodes (Figures 10 and 11). The phylogenetic branches are short (Figure 10) indicating a low divergence between the specimens and both *U. fuscum* and *U. giganteum* are retrieved as paraphyletic. This suggests that the speciation process is still taking place with gene flow still occurring between populations. We thus propose that the three described species are actually three different morphotypes of the same species. *Uvariodendron fuscum* represents the smaller morphotype (small leaves and flowers relatively to the others), *U. magnificum* represents the greater morphotype (great leaves and flowers relatively to the others), and *U. giganteum* represents the intermediate morphotype. The imbrication of inner petals of *U. magnificum* that Verdcourt (1969) described as a synapomorphy for the species should be considered as a developmental



constraint imposed by the size of the petals. Indeed, in bud, we can imagine that the only way for such long (50 – 53 mm long) and wide (36 – 38 mm wide) petals to arrange with the other floral elements is to overlap.

We thus synonymize the names *U. giganteum* and *U. magnificum* with *U. fuscum*. The first mention of *U. fuscum* dates back to 1862, as *Uvaria fusca* (Bentham, 1862), whereas the name *U. giganteum* dates back to 1899, as *Uvaria gigantea* (Engler & Diels, 1899) and the name *U. magnificum* to 1969 (Verdcourt, 1969). Given the anteriority rule, the name *Uvari dendron fuscum* prevails. The description of the species is given in the Chapter 4 – Taxonomic treatment section.

### 4.8.3. The complexity of *Uvari dendron molundense*.

The species *Uvari dendron molundense* (Engler & Diels) R.E.Fr. is distributed in Cameroon and Gabon. In 1969, Le Thomas synonymized the names *Uvari dendron mayumbense* and *Uvari dendron letestui* with *U. molundense*. Indeed, the position of the flowers along the trunk and branches, previously used to discriminate these species (Fries, 1930), was no longer valid as some specimens are both cauliflorous and ramiflorous (Le Thomas, 1969). Le Thomas (1969) also described the variety *Uvari dendron molundense* var. *citrata* from some specimens from Gabon exhibiting a strong lemon scent. The examination of 106 specimens identified as *U. molundense* revealed that this species shows a great morphological variability, especially for the leaf shape. For example, some specimens show young leaves with decurrent bases, whereas older leaves have a rounded base. The specimens identified as *U. molundense* form three phylogenetically supported groups separated by relatively high molecular divergence (Figures 10 and 11), at least as much molecular divergence as between other clearly morphologically divergent species (e.g. between *U. dzombense* and *U. pycnophyllum*). Although the three groups have morphological similarities, we were able to distinguish them and we thus propose to separate them in three distinct species: *U. molundense*, *U. citriodorum* Dagallier sp. nov, and *U. pilosicarpum* Dagallier sp. nov. A key morphologically separating the three species is given in the Taxonomic treatment section, as well as the full description of *U. citriodorum* and *U. pilosicarpum*.

## 5. Taxonomic treatment

### 5.1. *Dennettia*

*Dennettia tripetala* Bak. f.

**Type.** NIGERIA – Edo State • R.E. Dennett 44 (holotype: K (K000040961) sheet designated here, isotypes: K (K000040959)); Benin city; ca. 6°20' N, 5°38' E; 1 Jan. 1907.

## SYSTEMATICS OF THE MONODOREAE

**Description.** Shrub to tree 1 – 5 m tall, D.B.H unknown; young branches sparsely pubescent to glabrous, old branches glabrous. Leaves distichous, simple, pinnately veined, margins entire and flat. Petiole 2 – 5 mm long, 1 – 1.5 mm wide, glabrous. Leaf lamina 72 – 155 mm long, 30 – 68 mm wide, length:width ratio 1.9 – 3.25, elliptic, papyraceous to coriaceous, base acute to decurrent, apex attenuate, acumen 6 – 13 mm long, above glabrous when young and old, below glabrous when young and old; mid rib sunken above, raised below, above glabrous, below glabrous; secondary veins 5 – 10 pairs, brochidodromous to weakly brochidodromous, impressed above, raised below; tertiary veins reticulate. Flowers actinomorphic, bisexual. Inflorescences borne on branches or axillary, composed of 1 to 6 flowers. Peduncle ca. 0 – 1 mm long, ca. 1 mm in diameter. Flower pedicel 3.5 – 10 mm long, 1 – 2.5 mm in diameter, pubescent to sparsely pubescent. Bracts 1 to 3 at base, upper bract 0.5 – 2 mm long, 1.5 – 2 mm wide, broadly ovate, pubescent outside, glabrous inside. Sepals 3, 1 – 3 mm long, 1.5 – 4 mm wide, broadly ovate, fused on up to more than 50% of their length, forming a persistent ring with the 3 lobes generally clearly distinct, curved downward on fruit pedicel, pubescent outside, glabrous inside, color unknown. Petals 3, 5 – 14 mm long, 4.5 – 10 mm wide, length:width ratio 1 – 1.7, broadly ovate to ovate, connivent in bud, free at anthesis, pubescent to sparsely pubescent outside, glabrate inside, light brown to dark red outside, purple pink inside. Stamens ca. 1200, 0.5 – 1 mm long, 0.3 – 0.5 mm wide, anthers linear, connective truncate. Carpels 8 – 30, 2 – 4.5 mm long, 0.5 – 2 mm wide, pubescent, free; stigma 0.5 – 1 mm long, 0.5 – 1 mm wide, coiled, pubescent. Fruiting pedicel 5 – 14 mm long, 1 – 2.5 mm in diameter, pubescent to glabrous. Monocarps, 1 – 7, 11 – 32 mm long, 5 – 18 mm wide, length:width ratio 1.5 – 2.3, cylindrical, slightly constricted between the seeds when dried, sparsely pubescent to glabrous, greyish green (when unripe?), subsessile; stipe 0.1 – 3 mm long, 1 – 2 mm wide, pubescent. Seeds 4 – 12 per monocarp, biseriate, 7.5 – 10 mm long, 2 – 5 mm wide, ellipsoid.

**Specimens examined.** BENIN – Mono • J.-P. Essou 1443 (BENIN, MO, WAG); Aplahoué, Kpédjihoundéhoué; 7°21'N, 1°44'E; 17 Feb. 1999 – Ouémé • A. Akoègninou 2201 (BENIN, WAG); Kétou, Ewè; 7°28'N, 2°35'E; 01 Feb. 1999 – Zou • K. Küppers 2059 (FR, WAG), Noyau Central forêt classée de Lama; 6°57'N, 2°07'E; 28 Feb. 1998. CAMEROON – South-West Region • D.W. Thomas 5661 (K, MO, P, WAG), Nganjo. West bank of Meme River on Kumba Mbonge road; 4°33'N, 9°24'E; alt. 50 m; 25 Feb. 1986 • E. Westphal 9932 (WAG), Victoria; 4°01'N, 9°12'E; 04 Apr. 1978 • G.W.J. Mildbraed 10515 (K), Likomba - Pflanzung, 15 - 35 km NE of Victoria; 4°06'N, 9°20'E; alt. 50 m; 18 Oct. 1928 • T.D. Maitland 626 (K); Fako, Victoria (= Limbe), Bonjongo; 4°06'N, 9°08'E; alt. 600 m; Apr. 1929 • T.D. Maitland 627 (P), Victoria (= Limbe), Bonjongo; 4°06'N, 9°08'E; 1929 • T.D. Maitland s.n (K), Mt Cameroon; 4°15'N, 9°13'E; alt. 920 m; 1930. GHANA – Ashanti Region • J.K. Morton A 3394 (K), Nyinahin range, W of Kunasi; 6°36'N, 2°07'W; alt. 700 m; 07 Jun. 1958 – Central Region • J.B. Hall GC 43611 (K, WAG), Ojobi near Awutu; 5°29'N, 0°32'E; 29 Feb. 1972 • J.K. Morton s.n (K), About 1 mile N of Ojobi, Senya Beraku; 5°23'N, 0°29'E; 24 May. 1953 – Unknown major area • J.B. Hall GC 43276 (K), Yaugwu FR; alt. 460 m; 19 Mar. 1972. GUINEA – Kindia • D. Molmou 603 (P), Layah, Sousoude. Just avant Tonkoyah; 9°43'39.3"N, 13°12'26.6"W; alt. 12 m; 06 Jul. 2013. IVORY COAST – Bouaflé • C.C.H. Jongkind 4356 (MO, WAG), Parc National de la Marahoue. Near south border; 6°59'N, 6°10'W; alt. 250 m; 11 Feb. 1998 – Bouaké • L. Aké Assi 18031 (G), Forêt de Bamoro; 7°48'N, 5°05'W; 07 Jun. 1989 – Bouna • C. Geerling 2222 (K, WAG), Iringou (Gawi-Bania confl. Bamago); 8°58'N, 3°39'W; 15 Mar. 1968 • P.P. Poilecot 1224 (G), P.N. Comoé Sud; 8°45'N, 3°35'W; 13 Apr. 1986 • P.P. Poilecot 4164 (G, MO), P.N. Comoé Sud; 8°45'N, 3°35'W; 13 Apr. 1986 – Danané • A.J.M. Leeuwenberg 2999 (K, L, MO, P, WAG, WAG), 2 km E of Danané; 7°16'N, 8°07'W; alt. 410 m; 06 Mar. 1959 – Oumé • A. Le Thomas 27 (P), Lamto-Station,

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Fleuve Bandama; 6°13'N, 5°01'30"W; 07 Jul. 1985 • A. Le Thomas 97 (P), Lamto-Station, Bandama; 6°13'N, 5°01'30"W; 26 Jul. 1985 – Sassandra • A. Aubréville 163 (BR, K, P); 4°59'N, 6°08'W; 07 Mar. 1957 – Soubré • L. Aké Assi 9490 (G, P), Forêt du Bassin de la Lobo; 6°07'N, 6°48'W; 22 Feb. 1967 – Vavoua • F.N. Kouamé 1470 (CSRS, G), F.C. du Haut-Sassandra, Centre. forêt très dégradée, relevé FNK20; 7°07'N, 7°00'W; 07 Apr. 1995 – Unknown major area • A. Aubréville 145 (K, P); 7°37'26.4"N, 5°33'14.4"W; 28 Feb. 1957 • L. Aké Assi 13255 (G), Mont Niénokoué; 5°23'N, 7°10'W; 19 Jan. 1976 • L. Aké Assi 9543 (G, K, P), Mount Mafa; 5°52'N, 4°04'W; 14 Mar. 1967. NIGERIA – Anambra State • J.C. Okafor FHI 35869 (K), Onitsha; Nnwei; Ukpok - Nzagha village; 6°50'N, 6°50'E; 22 Oct. 1956 – Cross River State • C.F.A. Onochie FHI 36331 (K), Calabar, Ikot Efanga, c. 12 miles from Calabar on the Oban road; 4°58'N, 8°29'E; 09 Feb. 1957 – Oyo State • C.E. Darter 41837 (K), Olokemeji Forest Reserve; agbola pool, Ogun River; 7°25'N, 3°32'E; 06 Apr. 1958 – Unknown major area • J.O. Ariwaodo ARS 1184 (K), Munta Village. SIERRA LEONE – Western Area • J.K. Morton SL 2013 (FHI, IFAN, K, SL, WAG); Western Area, near York by Whale Bay, Peninsula; 8°17'N, 13°11'W; 02 May. 1965.

## 5.2. Key to *Uvariadendron molundense*, *U. citriodorum* and *U. pilosicarpum*

1. - Longest leaves with a lamina smaller than 25 cm long, obovate with base decurrent, apex acuminate; monocarps ellipsoid, curved, acuminate and densely pubescent. *Uvariadendron pilosicarpum*
  - Longest leaves with a lamina generally greater than 25 cm long, elliptic to oblong to obovate, with base rounded to convex (sometimes minutely decurrent at the very base, and decurrent on young leaves), apex attenuate to acuminate; monocarps cylindrical, straight and pubescent to glabrate.....2
2. - Crushed leaves emitting a strong lemon scent.....*Uvariadendron citriodorum*
  - Crushed leaves not emitting a strong lemon scent.....*Uvariadendron molundense*

## 6. Supporting Information

**Table SI.8** Taxon sampling and voucher information for every specimen sampled in this study

Custom database identifier	Bioinformatic identifier	Collector name	Collector number	Year collected	Country of origin	Ingroup/outgroup	Family	Tribe	Species name	Old identification	Tip label in Figures 10 and 11
TC-S1147	RUN62_I10_T42	Couvreur, T.L.P.	74	2006	Tanzania	Ingroup	Annonaceae	Monodoreae	<i>Asteranthe asterias</i>	<i>Asteranthe asterias</i>	RUN62_I10_T42_Asteranthe_asterias-COU_74
TC-S1601	RUN79_I2_T36	Luke, Q.W.R.	7641	2001	Tanzania	Ingroup	Annonaceae	Monodoreae	<i>Asteranthe asterias</i>	<i>Asteranthe trollii</i>	RUN79_I2_T36_Asteranthe_asterias_(ex_trollii)-LUK_7641
TC-S1585	RUN79_I2_T61	Dagallier, L-P. M.J.	53	2019	Tanzania	Ingroup	Annonaceae	Monodoreae	<i>Asteranthe asterias</i> subsp <i>asterias</i>	<i>Asteranthe asterias</i> subsp <i>asterias</i>	RUN79_I2_T61_Asteranthe_asterias_subsp_asterias-DAG_53
TC-S1544	RUN79_I2_T33	Dagallier, L-P. M.J.	10	2019	Tanzania	Ingroup	Annonaceae	Monodoreae	<i>Asteranthe asterias</i> subsp <i>triangularis</i>	<i>Asteranthe asterias</i> subsp <i>triangularis</i>	RUN79_I2_T33_Asteranthe_asterias_subsp_triangularis-DAG_10
TC-S1583	RUN79_I10_T18	Dagallier, L-P. M.J.	51	2019	Tanzania	Ingroup	Annonaceae	Monodoreae	<i>Asteranthe lutea</i>	<i>Asteranthe lutea</i>	RUN79_I10_T18_Asteranthe_lutea-DAG_51
TC-S1645	RUN79_I2_T35	Couvreur, T.L.P.	46	2006	Tanzania	Ingroup	Annonaceae	Monodoreae	<i>Asteranthe lutea</i>	<i>Asteranthe lutea</i>	RUN79_I2_T35_Asteranthe_lutea-COU_46
TC-S1632	RUN79_I10_T65	Thomas, D.W.	5661	1986	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Dennettia tripetala</i>	<i>Uvariopsis tripetala</i>	RUN79_I10_T65_Dennettia_tripetala_(ex_Uvariopsis_tripetala)-THO_5661
TC-S1633	RUN79_I10_T70	Hall, J.B.	GC43276	1972	Ghana	Ingroup	Annonaceae	Monodoreae	<i>Dennettia tripetala</i>	<i>Uvariopsis tripetala</i>	RUN79_I10_T70_Dennettia_tripetala_(ex_Uvariopsis_tripetala)-HAL_43276
TC-S1600	RUN79_I11_T39	Bos, J.J.	5370	1969	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Hexalobus bussei</i>	<i>Hexalobus bussei</i>	RUN79_I11_T39_Hexalobus_bussei-BOS_5370
TC-S0180	RUN79_I9_T51	Couvreur, T.L.P.	446	2013	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Hexalobus crispiflorus</i>	<i>Hexalobus crispiflorus</i>	RUN79_I9_T51_Hexalobus_crispiflorus-COU_446
TC-S0081	RUN79_I10_T98	Raimundo, s.c.	1194	NA	Angola	Ingroup	Annonaceae	Monodoreae	<i>Hexalobus monopetalus</i>	<i>Hexalobus monopetalus</i>	RUN79_I10_T98_Hexalobus_monopetalus-RAI_1194
TC-S1604	RUN79_I10_T99	Lawesson, J.E.	5461	1989	Senegal	Ingroup	Annonaceae	Monodoreae	<i>Hexalobus monopetalus</i>	<i>Hexalobus monopetalus</i>	RUN79_I10_T99_Hexalobus_monopetalus-LAW_5461
TC-S1603	RUN79_I9_T18	Lotter, n.c.	1671	1985	Mozambique	Ingroup	Annonaceae	Monodoreae	<i>Hexalobus monopetalus</i>	<i>Hexalobus monopetalus</i>	RUN79_I9_T18_Hexalobus_monopetalus-LOT_1671
TC-S1602	RUN79_I2_T16	Torre, A.R.	11928	1964	Mozambique	Ingroup	Annonaceae	Monodoreae	<i>Hexalobus mossambicensis</i>	<i>Hexalobus mossambicensis</i>	RUN79_I2_T16_Hexalobus_mossambicensis-TOR_11.928
TC-S1658	RUN79_I2_T31	Sosef, M.S.M.	2294	2005	Gabon	Ingroup	Annonaceae	Monodoreae	<i>Hexalobus salicifolius</i>	<i>Hexalobus salicifolius</i>	RUN79_I2_T31_Hexalobus_salicifolius-SOS_2294
TC-S1642	RUN79_I11_T41	Munzinger, J.	63	1997	Ivory Coast	Ingroup	Annonaceae	Monodoreae	<i>Isolona campanulata</i>	<i>Isolona campanulata</i>	RUN79_I11_T41_Isolona_campanulata-MUN_6
TC-S1610	RUN79_I11_T48	Olorunfemi, J.	FHI 30662	1951	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Isolona campanulata</i>	<i>Isolona campanulata</i>	RUN79_I11_T48_Isolona_campanulata-OLO_30662
TC-S1656	RUN79_I10_T7	Capuron, R.	SF 8942	1954	Madagascar	Ingroup	Annonaceae	Monodoreae	<i>Isolona capuronii</i>	<i>Isolona capuronii</i>	RUN79_I10_T7_Isolona_capuronii-CAP_8941_W
TC-S1641	RUN79_I10_T77	Capuron, R.	SF 8941	1954	Madagascar	Ingroup	Annonaceae	Monodoreae	<i>Isolona capuronii</i>	<i>Isolona capuronii</i>	RUN79_I10_T77_Isolona_capuronii-CAP_8941_P
TC-S1576	RUN79_I2_T41	Dagallier, L-P. M.J.	44	2019	Tanzania	Ingroup	Annonaceae	Monodoreae	<i>Isolona cauliflora</i>	<i>Isolona cauliflora</i>	RUN79_I2_T41_Isolona_cauliflora-DAG_44
TC-S0740	RUN79_I11_T34	Couvreur, T.L.P.	1054	2016	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Isolona congolana</i>	<i>Isolona congolana</i>	RUN79_I11_T34_Isolona_congolana-COU_1054

Custom database identifier	Bioinformatic identifier	Collector name	Collector number	Year collected	Country of origin	Ingroup/outgroup	Family	Tribe	Species name	Old identification	Tip label in Figures 10 and 11
TC-S1072	RUN79_I9_T57	Hawthorne, W.D.	205	NA	Ghana	Ingroup	Annonaceae	Monodoreae	<i>Isolona cooperi</i>	<i>Isolona cooperi</i>	RUN79_I9_T57_Isolona_cooperi-HAW_205
TC-S1609	RUN79_I9_T20	Lopez Poveda, L.	240	2013	Sierra Leone	Ingroup	Annonaceae	Monodoreae	<i>Isolona deightonii</i>	<i>Isolona deightonii</i>	RUN79_I9_T20_Isolona_deightonii-LOP_240
TC-S1659	RUN79_I9_T26	Andel, T. R. van	4027	2001	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Isolona dewevrei</i>	<i>Isolona dewevrei</i>	RUN79_I9_T26_Isolona_dewevrei-AND_4027
TC-S1655	RUN79_I10_T75	Capuron, R.	24934 SF	1966	Madagascar	Ingroup	Annonaceae	Monodoreae	<i>Isolona ghesquierei</i>	<i>Isolona ghesquierei</i>	RUN79_I10_T75_Isolona_ghesquierei-CAP_24934
TC-S2183	RUN86_I3_T27	Schatz, G. E.	3364	1992	Madagascar	Ingroup	Annonaceae	Monodoreae	<i>Isolona ghesquierei</i>	<i>Isolona ghesquierei</i>	RUN86_I3_T27_Isolona_ghesquierei-SCH_3364
TC-S1643	RUN79_I11_T38	Couvreur, T.L.P.	10	2006	Tanzania	Ingroup	Annonaceae	Monodoreae	<i>Isolona heinsenii</i>	<i>Isolona heinsenii</i>	RUN79_I11_T38_Isolona_heinsenii-COU_10
TC-S0234	RUN79_I10_T93	Couvreur, T.L.P.	495	2013	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Isolona hexaloba</i>	<i>Isolona hexaloba</i>	RUN79_I10_T93_Isolona_hexaloba-COU_495
TC-S1608	RUN79_I9_T45	Kennedy, J.D.	1568	NA	Nigeria	Ingroup	Annonaceae	Monodoreae	<i>Isolona hexaloba</i>	<i>Isolona hexaloba</i>	RUN79_I9_T45_Isolona_hexaloba-KEN_1568
TC-S0284	RUN79_I9_T61	Couvreur, T.L.P.	561	2013	Gabon	Ingroup	Annonaceae	Monodoreae	<i>Isolona hexaloba</i>	<i>Isolona hexaloba</i>	RUN79_I9_T61_Isolona_hexaloba-COU_561
TC-S1640	RUN79_I9_T41	Service Forestier de Madagascar	5382 SF	1951	Madagascar	Ingroup	Annonaceae	Monodoreae	<i>Isolona humbertiana</i>	<i>Isolona humbertiana</i>	RUN79_I9_T41_Isolona_humbertiana-SFM_5382
TC-S1638	RUN79_I10_T12	Sita, P.	3996	1975	Republic of Congo	Ingroup	Annonaceae	Monodoreae	<i>Isolona le-testui</i>	<i>Isolona le-testui</i>	RUN79_I10_T12_Isolona_le-testui-SIT_3996_P
TC-S1661	RUN79_I2_T10	Sita, P.	3996	1975	Republic of Congo	Ingroup	Annonaceae	Monodoreae	<i>Isolona le-testui</i>	<i>Isolona le-testui</i>	RUN79_I2_T10_Isolona_le-testui-SIT_3996_W
TC-S1611	RUN79_I2_T57	Bamps, P.	131	1958	Democratic Republic of the Congo	Ingroup	Annonaceae	Monodoreae	<i>Isolona lebrunii</i>	<i>Isolona lebrunii</i>	RUN79_I2_T57_Isolona_lebrunii-BAM_131
TC-S1652	RUN79_I2_T8	Couvreur, T.L.P.	102	2006	Tanzania	Ingroup	Annonaceae	Monodoreae	<i>Isolona linearis</i>	<i>Isolona linearis</i>	RUN79_I2_T8_Isolona_linearis-COU_102
TC-S2181	RUN86_I3_T25	Rakotonirina, C. Z.	550	2014	Madagascar	Ingroup	Annonaceae	Monodoreae	<i>Isolona madagascariensis</i>	<i>Isolona madagascariensis</i>	RUN86_I3_T25_Isolona_madagascariensis-RAK_550
TC-S1605	RUN79_I10_T22	Randriamampionona, B.	366	1993	Madagascar	Ingroup	Annonaceae	Monodoreae	<i>Isolona perrieri</i>	<i>Isolona perrieri</i>	RUN79_I10_T22_Isolona_perrieri-RAN_366
TC-S1662	RUN79_I10_T10	Moungazi, A.	1632	2004	Gabon	Ingroup	Annonaceae	Monodoreae	<i>Isolona pilosa</i>	<i>Isolona pilosa</i>	RUN79_I10_T10_Isolona_pilosa-MOU_1632
TC-S0028	RUN62_I10_T7	Couvreur, T.L.P.	402	2012	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Isolona pleurocarpa</i>	<i>Isolona pleurocarpa</i>	RUN62_I10_T7_Isolona_pleurocarpa-COU_402
TC-S1660	RUN79_I11_T45	Andel, T. R. van	4177	2001	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Isolona pleurocarpa</i>	<i>Isolona pleurocarpa</i>	RUN79_I11_T45_Isolona_pleurocarpa-AND_4177
TC-S1612	RUN79_I9_T19	Letouzey, R.	10205	1970	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Isolona thonneri</i>	<i>Isolona thonneri</i>	RUN79_I9_T19_Isolona_thonneri-LET_10205
TC-S0278	RUN79_I10_T67	Couvreur, T.L.P.	552	2013	Gabon	Ingroup	Annonaceae	Monodoreae	<i>Isolona zenkeri</i>	<i>Isolona zenkeri</i>	RUN79_I10_T67_Isolona_zenkeri-COU_552
TC-S1657	RUN79_I10_T87	Sosef, M.S.M.	2250	2005	Gabon	Ingroup	Annonaceae	Monodoreae	<i>Isolona zenkeri</i>	<i>Isolona zenkeri</i>	RUN79_I10_T87_Isolona_zenkeri-SOS_2250
TC-S1693	RUN79_I2_T15	Luke, Q.W.R.	11205	2005	Tanzania	Ingroup	Annonaceae	Monodoreae	<i>Lukea triciae</i>	<i>Lukea triciae</i>	RUN79_I2_T15_Lukea_triciae-LUK_11205
TC-S2245	RUN86_I3_T40	Luke, Q.W.R.	9526	2003	Tanzania	Ingroup	Annonaceae	Monodoreae	<i>Lukea triciae</i>	<i>Lukea triciae</i>	RUN86_I3_T40_Lukea_triciae-

Custom database identifier	Bioinformatic identifier	Collector name	Collector number	Year collected	Country of origin	Ingroup/outgroup	Family	Tribe	Species name	Old identification	Tip label in Figures 10 and 11
TC-S1613	RUN79_I9_T48	Evrard, C.	6205	1959	Democratic Republic of the Congo	Ingroup	Annonaceae	Monodoreae	<i>Mischogyne congensis</i>	<i>Mischogyne congensis</i>	LUK_9526 RUN79_I9_T48_Mischogyne_congensis-EVR_6205
TC-S1614	RUN79_I9_T16	Haba, P.M.	1272	2019	Guinea	Ingroup	Annonaceae	Monodoreae	<i>Mischogyne elliotiana</i> var <i>elliotiana</i>	<i>Mischogyne elliotiana</i> var <i>elliotiana</i>	RUN79_I9_T16_Mischogyne_elliotiana_var_elliotiana-HAB_1272
TC-S1615	RUN79_I2_T24	Deighton, F.C.	3015	1935	Sierra Leone	Ingroup	Annonaceae	Monodoreae	<i>Mischogyne elliotiana</i> var <i>sericea</i>	<i>Mischogyne elliotiana</i> var <i>sericea</i>	RUN79_I2_T24_Mischogyne_elliotiana_var_sericea-DEI_3015
TC-S0729	RUN62_I12_T99	Couvreur, T.L.P.	1033	2016	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Mischogyne gabonensis</i>	<i>Mischogyne gabonensis</i>	RUN62_I12_T99_Mischogyne_gabonensis-COU_1033
TC-S1616	RUN79_I9_T12	Luke, Q.W.R.	11941	2007	Equatorial Guinea	Ingroup	Annonaceae	Monodoreae	<i>Mischogyne gabonensis</i>	<i>Mischogyne gabonensis</i>	RUN79_I9_T12_Mischogyne_gabonensis-LUK_11941
TC-S1556	RUN79_I10_T63	Dagallier, L-P. M.J.	24	2019	Tanzania	Ingroup	Annonaceae	Monodoreae	<i>Mischogyne iddii</i>	<i>Mischogyne iddii</i>	RUN79_I10_T63_Mischogyne_iddii-DAG_24
TC-S1617	RUN79_I9_T23	Cribb, P.	10082	1976	Tanzania	Ingroup	Annonaceae	Monodoreae	<i>Mischogyne iddii</i>	<i>Mischogyne iddii</i>	RUN79_I9_T23_Mischogyne_iddii-CGW_10082
TC-S1664	RUN79_I9_T7	Bamps, P.	4459	1973	Angola	Ingroup	Annonaceae	Monodoreae	<i>Mischogyne michelioides</i>	<i>Mischogyne michelioides</i>	RUN79_I9_T7_Mischogyne_michelioides-BAM_4459
TC-S1685	RUN79_I2_T38	Enti, A.A.	1831	1978	Ghana	Ingroup	Annonaceae	Monodoreae	<i>Monocyclanthus vignei</i>	<i>Monocyclanthus vignei</i>	RUN79_I2_T38_Monocyclanthus_vignei-ENT_1831
TC-S1669	RUN79_I9_T8	Leeuwenberg, A.J.M.	4934	1962	Liberia	Ingroup	Annonaceae	Monodoreae	<i>Monocyclanthus vignei</i>	<i>Monocyclanthus vignei</i>	RUN79_I9_T8_Monocyclanthus_vignei-LEE_4934
TC-S1665	RUN79_I9_T50	Alpin, D.	S4013	2005	no locality	Ingroup	Annonaceae	Monodoreae	<i>Monodora angolensis</i>	<i>Monodora angolensis</i>	RUN79_I9_T50_Monodora_angolensis-ALP_S4013
TC-S1646	RUN79_I9_T43	Couvreur, T.L.P.	54	2006	Tanzania	Ingroup	Annonaceae	Monodoreae	<i>Monodora carolinae</i>	<i>Monodora carolinae</i>	RUN79_I9_T43_Monodora_carolinae-COU_54
TC-S1618	RUN79_I2_T27	de Wilde, W.J.J.O.	867	1963	Ivory Coast	Ingroup	Annonaceae	Monodoreae	<i>Monodora crispata</i>	<i>Monodora crispata</i>	RUN79_I2_T27_Monodora_crispata-WIL_867
TC-S1619	RUN79_I9_T34	Kwangue, A.T.	19	1992	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Monodora crispata</i>	<i>Monodora crispata</i>	RUN79_I9_T34_Monodora_crispata-KWA_19
TC-S1651	RUN79_I9_T35	Couvreur, T.L.P.	99	2006	Tanzania	Ingroup	Annonaceae	Monodoreae	<i>Monodora globiflora</i>	<i>Monodora globiflora</i>	RUN79_I9_T35_Monodora_globiflora-COU_99
TC-S1558	RUN79_I11_T44	Dagallier, L-P. M.J.	26	2019	Tanzania	Ingroup	Annonaceae	Monodoreae	<i>Monodora grandidieri</i>	<i>Monodora grandidieri</i>	RUN79_I11_T44_Monodora_grandidieri-DAG_26
TC-S0362	RUN79_I9_T44	Couvreur, T.L.P.	15	2006	Tanzania	Ingroup	Annonaceae	Monodoreae	<i>Monodora grandidieri</i>	<i>Monodora grandidieri</i>	RUN79_I9_T44_Monodora_grandidieri-COU_15
TC-S1644	RUN79_I11_T42	Couvreur, T.L.P.	44	2006	Tanzania	Ingroup	Annonaceae	Monodoreae	<i>Monodora hastipetala</i>	<i>Monodora hastipetala</i>	RUN79_I11_T42_Monodora_hastipetala-COU_44
TC-S1649	RUN79_I10_T64	Couvreur, T.L.P.	88	2006	Tanzania	Ingroup	Annonaceae	Monodoreae	<i>Monodora junodii</i>	<i>Monodora junodii</i>	RUN79_I10_T64_Monodora_junodii-COU_88
TC-S1620	RUN79_I9_T30	Callens, H.	2126	1949	Democratic Republic of the Congo	Ingroup	Annonaceae	Monodoreae	<i>Monodora laurentii</i>	<i>Monodora laurentii</i>	RUN79_I9_T30_Monodora_laurentii-CAL_2126
TC-S2175	RUN86_I3_T23	Niangadouma, R. N.	188	2003	Gabon	Ingroup	Annonaceae	Monodoreae	<i>Monodora laurentii</i>	<i>Monodora laurentii</i>	RUN86_I3_T23_Monodora_laurentii-NIA_188
TC-S2176	RUN86_I3_T24	Niangadouma, R. N.	179	2003	Gabon	Ingroup	Annonaceae	Monodoreae	<i>Monodora laurentii</i>	<i>Monodora laurentii</i>	RUN86_I3_T24_Monodora_laurentii-NIA_179
TC-S1647	RUN79_I2_T43	Couvreur, T.L.P.	55	2006	Tanzania	Ingroup	Annonaceae	Monodoreae	<i>Monodora minor</i>	<i>Monodora minor</i>	RUN79_I2_T43_Monodora_minor-

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TC-S0727	RUN54_I11_T7	Couvreur, T.L.P.	1031	2016	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Monodora myristica</i>	<i>Monodora myristica</i>	COU_55 RUN54_I11_T7_Monodora_myristica-COU_1031
TC-S1067	RUN79_I2_T51	Hawthorne, W.D.	93	NA	Ghana	Ingroup	Annonaceae	Monodoreae	<i>Monodora myristica</i>	<i>Monodora myristica</i>	RUN79_I2_T51_Monodora_myristica-HAW_93
TC-S0543	RUN86_I3_T10	Couvreur, T.L.P.	803	2015	Republic of Congo	Ingroup	Annonaceae	Monodoreae	<i>Monodora myristica</i>	<i>Monodora myristica</i>	RUN86_I3_T10_Monodora_myristica-COU_803
TC-S0632	RUN86_I3_T14	Couvreur, T.L.P.	933	2016	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Monodora myristica</i>	<i>Monodora myristica</i>	RUN86_I3_T14_Monodora_myristica-COU_933
TC-S0608	RUN86_I3_T15	Couvreur, T.L.P.	908	2015	Gabon	Ingroup	Annonaceae	Monodoreae	<i>Monodora myristica</i>	<i>Monodora myristica</i>	RUN86_I3_T15_Monodora_myristica-COU_908
TC-S0042	RUN86_I3_T8	Couvreur, T.L.P.	412	2013	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Monodora myristica</i>	<i>Monodora myristica</i>	RUN86_I3_T8_Monodora_myristica-COU_412
TC-S1621	RUN79_I10_T66	Brummitt, D.	8965	1970	Malawi	Ingroup	Annonaceae	Monodoreae	<i>Monodora stenopetala</i>	<i>Monodora stenopetala</i>	RUN79_I10_T66_Monodora_stenopetala-BRU_8965
TC-S1454	RUN79_I10_T11	Couvreur, T.L.P.	1218	2019	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Monodora tenuifolia</i>	<i>Monodora tenuifolia</i>	RUN79_I10_T11_Monodora_tenuifolia-COU_1218
TC-S1622	RUN79_I10_T74	Burgt, X.M van der	1798	2014	Ghana	Ingroup	Annonaceae	Monodoreae	<i>Monodora tenuifolia</i>	<i>Monodora tenuifolia</i>	RUN79_I10_T74_Monodora_tenuifolia-BUR_1798
TC-S0747	RUN79_I10_T90	Couvreur, T.L.P.	1061	2016	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Monodora undulata</i>	<i>Monodora undulata</i>	RUN79_I10_T90_Monodora_undulata-COU_1061
TC-S1653	RUN79_I2_T34	Jongkind, C.C.H.	7637	2006	Guinea	Ingroup	Annonaceae	Monodoreae	<i>Monodora undulata</i>	<i>Monodora undulata</i>	RUN79_I2_T34_Monodora_undulata-JON_7637_W
TC-S1637	RUN79_I9_T39	Jongkind, C.C.H.	7637	2006	Guinea	Ingroup	Annonaceae	Monodoreae	<i>Monodora undulata</i>	<i>Monodora undulata</i>	RUN79_I9_T39_Monodora_undulata-JON_7637_P
TC-S0626	RUN86_I3_T13	Couvreur, T.L.P.	927	2015	Gabon	Ingroup	Annonaceae	Monodoreae	<i>Monodora undulata</i>	<i>Monodora undulata</i>	RUN86_I3_T13_Monodora_undulata-COU_927
TC-S0041	RUN86_I3_T7	Couvreur, T.L.P.	391	2012	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Monodora undulata</i>	<i>Monodora undulata</i>	RUN86_I3_T7_Monodora_undulata-COU_391
TC-S1623	RUN79_I2_T26	Breteler, F.J.	2747	1962	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Monodora zenkeri</i>	<i>Monodora zenkeri</i>	RUN79_I2_T26_Monodora_zenkeri-BRE_2747
TC-S1624	RUN79_I10_T92	Evrard, C.	5064	1958	Democratic Republic of the Congo	Ingroup	Annonaceae	Monodoreae	<i>Uvariastrum germainii</i>	<i>Uvariastrum germainii</i>	RUN79_I10_T92_Uvariastrum_germainii-EVR_5064
TC-S0068	RUN79_I10_T9	Nkhoma, C.N.	80	1993	Zambia	Ingroup	Annonaceae	Monodoreae	<i>Uvariastrum hexaloboides</i>	<i>Uvariastrum hexaloboides</i>	RUN79_I10_T9_Uvariastrum_hexaloboides-NKH
TC-S1625	RUN79_I11_T31	Wheatley, J.	85	1992	F	Ingroup	Annonaceae	Monodoreae	<i>Uvariastrum insculptum</i>	<i>Uvariastrum insculptum</i>	RUN79_I11_T31_Uvariastrum_insculptum-WHE_85
TC-S0001	RUN79_I2_T14	Breteler, F.J.	13761	2005	Ivory Coast	Ingroup	Annonaceae	Monodoreae	<i>Uvariastrum insculptum</i>	<i>Uvariastrum insculptum</i>	RUN79_I2_T14_Uvariastrum_insculptum-BRE_13761
TC-S0062	RUN79_I10_T10	Jongkind, C.C.H.	7190	2005	Guinea	Ingroup	Annonaceae	Monodoreae	<i>Uvariastrum pierreanum</i>	<i>Uvariastrum pierreanum</i>	RUN79_I10_T10_Uvariastrum_pierreanum-JON_7190
TC-S0461	RUN79_I2_T48	Couvreur, T.L.P.	680	2015	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Uvariastrum pierreanum</i>	<i>Uvariastrum pierreanum</i>	RUN79_I2_T48_Uvariastrum_pierreanum-COU_680
TC-S2205	RUN86_I3_T28	Stone, J. R.	3236	2001	Gabon	Ingroup	Annonaceae	Monodoreae	<i>Uvariastrum pierreanum</i>	<i>Uvariastrum pierreanum</i>	RUN86_I3_T28_Uvariastrum_pierreanum-STO_3236
TC-S1304	RUN86_I3_T20	Couvreur, T.L.P.	877	2015	Gabon	Ingroup	Annonaceae	Monodoreae	<i>Uvariastrum zenkeri</i>	<i>Uvariastrum zenkeri</i>	RUN86_I3_T20_Uvariastrum_zenkeri-COU_877

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TC-S0402	RUN86_I3_T9	Couvreur, T.L.P.	624	2014	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Uvariastrum zenkeri</i>	<i>Uvariastrum zenkeri</i>	RUN86_I3_T9_Uvariastrum_zenkeri-COU_624
TC-S1689	RUN79_I10_T16	Jongkind, C.C.H.	4368	1998	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Uvari dendron angustifolium</i>	<i>Uvari dendron angustifolium</i>	RUN79_I10_T16_Uvari dendron_angustifolium-JON_4368
TC-S1680	RUN79_I2_T22	Staudt, A.	642	NA	Ivory Coast	Ingroup	Annonaceae	Monodoreae	<i>Uvari dendron angustifolium</i>	<i>Uvari dendron angustifolium</i>	RUN79_I2_T22_Uvari dendron_angustifolium-STA_642
TC-S1681	RUN79_I2_T12	Someren, V.L.G. van	95	NA	Kenya	Ingroup	Annonaceae	Monodoreae	<i>Uvari dendron anisatum</i>	<i>Uvari dendron anisatum</i>	RUN79_I2_T12_Uvari dendron_anisatum-SOM_95
TC-S1695	RUN79_I10_T84	Merello, M. C.	1385	1996	Ghana	Ingroup	Annonaceae	Monodoreae	<i>Uvari dendron calophyllum</i>	<i>Uvari dendron calophyllum</i>	RUN79_I10_T84_Uvari dendron_calophyllum-MER_1385
TC-S0696	RUN79_I2_T56	Couvreur, T.L.P.	999	2016	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Uvari dendron calophyllum</i>	<i>Uvari dendron calophyllum</i>	RUN79_I2_T56_Uvari dendron_calophyllum-COU_999
TC-S1682	RUN79_I2_T59	Daramola, B.O.	641	1995	Nigeria	Ingroup	Annonaceae	Monodoreae	<i>Uvari dendron calophyllum</i>	<i>Uvari dendron calophyllum</i>	RUN79_I2_T59_Uvari dendron_calophyllum-DAR_641
TC-S0088	RUN62_I10_T8	Sosef, M.S.M.	2219	2005	Gabon	Ingroup	Annonaceae	Monodoreae	<i>Uvari dendron citriodorum</i>	<i>Uvari dendron molundense var citrata</i>	RUN62_I10_T8_Uvari dendron_citriodorum_(ex_molundense_var_citrata)-SOS_2219
TC-S1692	RUN79_I10_T17	Latilo, M.G.	32	1959	Nigeria	Ingroup	Annonaceae	Monodoreae	<i>Uvari dendron connivens</i>	<i>Uvari dendron connivens</i>	RUN79_I10_T17_Uvari dendron_connivens-LAT_32
TC-S0713	RUN79_I10_T19	Couvreur, T.L.P.	1016	2016	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Uvari dendron connivens</i>	<i>Uvari dendron connivens</i>	RUN79_I10_T19_Uvari dendron_connivens-COU_1016
TC-S0054	RUN79_I2_T44	Couvreur, T.L.P.	383	2012	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Uvari dendron connivens</i>	<i>Uvari dendron connivens</i>	RUN79_I2_T44_Uvari dendron_connivens-COU_383
TC-S1051	RUN86_I3_T19	Couvreur, T.L.P.	1051	2016	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Uvari dendron connivens</i>	<i>Uvari dendron connivens</i>	RUN86_I3_T19_Uvari dendron_connivens-COU_1051
TC-S1674	RUN79_I2_T52	Luke, Q.W.R.	1654	NA	Kenya	Ingroup	Annonaceae	Monodoreae	<i>Uvari dendron dzomboense</i>	<i>Uvari dendron dzomboense</i>	RUN79_I2_T52_Uvari dendron_dzomboense-LUK_1654
TC-S0687	RUN79_I10_T20	Couvreur, T.L.P.	990	2016	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Uvari dendron fuscum</i>	<i>Uvari dendron fuscum</i>	RUN79_I10_T20_Uvari dendron_fuscum-COU_990
TC-S0725	RUN79_I10_T73	Couvreur, T.L.P.	1029	2016	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Uvari dendron fuscum</i>	<i>Uvari dendron fuscum</i>	RUN79_I10_T73_Uvari dendron_fuscum-COU_1029
TC-S1670	RUN79_I10_T78	Lehmbach, n.c.	178	NA	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Uvari dendron fuscum</i>	<i>Uvari dendron fuscum</i>	RUN79_I10_T78_Uvari dendron_fuscum-LEH_178
TC-S1699	RUN79_I10_T81	Thomas, D.W.	4469	1985	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Uvari dendron fuscum</i>	<i>Uvari dendron fuscum</i>	RUN79_I10_T81_Uvari dendron_fuscum-THO_4469
TC-S1636	RUN79_I11_T32	Preuss, P.R.	1378	1898	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Uvari dendron fuscum</i>	<i>Uvari dendron fuscum</i>	RUN79_I11_T32_Uvari dendron_fuscum-PRE_1378
TC-S1046	RUN79_I11_T33	Couvreur, T.L.P.	1046	2016	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Uvari dendron fuscum</i>	<i>Uvari dendron fuscum</i>	RUN79_I11_T33_Uvari dendron_fuscum-COU_1046
TC-S0722	RUN79_I9_T42	Couvreur, T.L.P.	1026	2016	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Uvari dendron fuscum</i>	<i>Uvari dendron fuscum</i>	RUN79_I9_T42_Uvari dendron_fuscum-COU_1026
TC-S1671	RUN79_I9_T46	Mildbraed, J.	6428	1900	Equatorial Guinea	Ingroup	Annonaceae	Monodoreae	<i>Uvari dendron fuscum</i>	<i>Uvari dendron fuscum</i>	RUN79_I9_T46_Uvari dendron_fuscum-MIL_6428
TC-S1634	RUN79_I9_T58	Hamilton, B.	676	1968	Uganda	Ingroup	Annonaceae	Monodoreae	<i>Uvari dendron fuscum</i>	<i>Uvari dendron magnificum</i>	RUN79_I9_T58_Uvari dendron_fuscum_(ex_magnificum)-HAM_676
TC-S0743	RUN86_I3_T16	Couvreur, T.L.P.	1057	2016	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Uvari dendron fuscum</i>	<i>Uvari dendron giganteum</i>	RUN86_I3_T16_Uvari dendron_fuscum_(ex_giganteum)-COU_1057
TC-S1442	RUN86_I3_T21	Couvreur, T.L.P.	1206	2019	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Uvari dendron fuscum</i>	<i>Uvari dendron giganteum</i>	RUN86_I3_T21_Uvari dendron_fusc-



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TC-S1570	RUN79_I10_T85	Dagallier, L-P. M.J.	38	2019	Tanzania	Ingroup	Annonaceae	Monodoreae	<i>Uvariodendron gorgonis</i>	<i>Uvariodendron gorgonis</i>	cum_(ex_giganteum)-COU_1206 RUN79_I10_T85_Uvariodendron_gorgonis-DAG_38
TC-S1584	RUN79_I9_T22	Dagallier, L-P. M.J.	52	2019	Tanzania	Ingroup	Annonaceae	Monodoreae	<i>Uvariodendron gorgonis</i>	<i>Uvariodendron gorgonis</i>	RUN79_I9_T22_Uvariodendron_gorgonis-DAG_52
TC-S1673	RUN79_I10_T76	Luke, Q.W.R.	766	NA	Tanzania	Ingroup	Annonaceae	Monodoreae	<i>Uvariodendron kimbozaense</i>	<i>Uvariodendron kirkii</i>	RUN79_I10_T76_Uvariodendron_kimbozaense-LUK_766
TC-S1581	RUN79_I9_T29	Dagallier, L-P. M.J.	49	2019	Tanzania	Ingroup	Annonaceae	Monodoreae	<i>Uvariodendron kimbozaense</i>	<i>Uvariodendron kirkii</i>	RUN79_I9_T29_Uvariodendron_kimbozaense-DAG_49
TC-S1542	RUN79_I10_T13	Dagallier, L-P. M.J.	8	2019	Tanzania	Ingroup	Annonaceae	Monodoreae	<i>Uvariodendron kirkii</i>	<i>Uvariodendron kirkii</i>	RUN79_I10_T13_Uvariodendron_kirkii-DAG_08
TC-S1543	RUN79_I10_T79	Dagallier, L-P. M.J.	9	2019	Tanzania	Ingroup	Annonaceae	Monodoreae	<i>Uvariodendron kirkii</i>	<i>Uvariodendron kirkii</i>	RUN79_I10_T79_Uvariodendron_kirkii-DAG_09
TC-S1672	RUN79_I10_T80	Peter, G.A.	4487	NA	Tanzania	Ingroup	Annonaceae	Monodoreae	<i>Uvariodendron kirkii</i>	<i>Uvariodendron kirkii</i>	RUN79_I10_T80_Uvariodendron_kirkii-PET_4487
TC-S1571	RUN79_I10_T68	Dagallier, L-P. M.J.	39	2019	Tanzania	Ingroup	Annonaceae	Monodoreae	<i>Uvariodendron mbagoi</i>	<i>Uvariodendron mbagoi</i>	RUN79_I10_T68_Uvariodendron_mbagoi-DAG_39
TC-S1582	RUN79_I10_T72	Dagallier, L-P. M.J.	50	2019	Tanzania	Ingroup	Annonaceae	Monodoreae	<i>Uvariodendron mbagoi</i>	<i>Uvariodendron mbagoi</i>	RUN79_I10_T72_Uvariodendron_mbagoi-DAG_50
TC-S1538	RUN79_I9_T33	Dagallier, L-P. M.J.	1	2019	Tanzania	Ingroup	Annonaceae	Monodoreae	<i>Uvariodendron mbagoi</i>	<i>Uvariodendron mbagoi</i>	RUN79_I9_T33_Uvariodendron_mbagoi-DAG_01
TC-S0627	RUN79_I11_T40	Couvreur, T.L.P.	928	2015	Gabon	Ingroup	Annonaceae	Monodoreae	<i>Uvariodendron molundense</i>	<i>Uvariodendron molundense</i>	RUN79_I11_T40_Uvariodendron_molundense-COU_928
TC-S1683	RUN79_I11_T43	de Wilde, W.J.J.O	1420	1963	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Uvariodendron molundense</i>	<i>Uvariodendron molundense</i>	RUN79_I11_T43_Uvariodendron_molundense-WIL_1420
TC-S0269	RUN79_I2_T11	Couvreur, T.L.P.	542	2013	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Uvariodendron molundense</i>	<i>Uvariodendron molundense</i>	RUN79_I2_T11_Uvariodendron_molundense-COU_542
TC-S1377	RUN79_I9_T40	Couvreur, T.L.P.	1172	2018	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Uvariodendron molundense</i>	<i>Uvariodendron molundense</i>	RUN79_I9_T40_Uvariodendron_molundense-COU_1172
TC-S0266	RUN79_I9_T52	Couvreur, T.L.P.	539	2013	Gabon	Ingroup	Annonaceae	Monodoreae	<i>Uvariodendron molundense</i>	<i>Uvariodendron molundense</i>	RUN79_I9_T52_Uvariodendron_molundense-COU_539
TC-S1667	RUN79_I10_T15	Mendonça, F.A.	2558A	1944	Mozambique	Ingroup	Annonaceae	Monodoreae	<i>Uvariodendron mossambicense</i>	<i>Uvariodendron sp nov</i>	RUN79_I10_T15_Uvariodendron_mossambicense-MEN_2558
TC-S1626	RUN79_I10_T69	Anakwense, F.	FHI 19701	1950	Nigeria	Ingroup	Annonaceae	Monodoreae	<i>Uvariodendron occidentalis</i>	<i>Uvariodendron occidentalis</i>	RUN79_I10_T69_Uvariodendron occidentalis-ANA_19701
TC-S1679	RUN79_I2_T25	Kouamé, FN'G.	1487	NA	Ivory Coast	Ingroup	Annonaceae	Monodoreae	<i>Uvariodendron occidentalis</i>	<i>Uvariodendron occidentalis</i>	RUN79_I2_T25_Uvariodendron occidentalis-KOU_1487
TC-S0144	RUN79_I2_T19	Valkenburg, J.L.C.H van	2540	2003	Gabon	Ingroup	Annonaceae	Monodoreae	<i>Uvariodendron pilosicarpum</i>	<i>Uvariodendron molundense</i>	RUN79_I2_T19_Uvariodendron_pilosicarpum_(ex_molundense)-VAL_2540
TC-S1698	RUN79_I9_T13	Sosef, M.S.M.	2261	2005	Gabon	Ingroup	Annonaceae	Monodoreae	<i>Uvariodendron pilosicarpum</i>	<i>Uvariodendron molundense</i>	RUN79_I9_T13_Uvariodendron_pilosicarpum_(ex_molundense)-SOS_2261
TC-S1565	RUN79_I2_T46	Dagallier, L-P. M.J.	33	2019	Tanzania	Ingroup	Annonaceae	Monodoreae	<i>Uvariodendron pycnophyllum</i>	<i>Uvariodendron pycnophyllum</i>	RUN79_I2_T46_Uvariodendron_pycnophyllum-DAG_33
TC-S0052	RUN79_I2_T58	Couvreur, T.L.P.	21	2006	Tanzania	Ingroup	Annonaceae	Monodoreae	<i>Uvariodendron pycnophyllum</i>	<i>Uvariodendron pycnophyllum</i>	RUN79_I2_T58_Uvariodendron_pycnophyllum-COU_21
TC-S1635	RUN79_I10_T86	Luke, Q.W.R.	4717	1997	Kenya	Ingroup	Annonaceae	Monodoreae	<i>Uvariodendron schmidtii</i>	<i>Uvariodendron schmidtii</i>	RUN79_I10_T86_Uvariodendron_schmidtii-LUK_4717
TC-S1675	RUN79_I10_T88	Luke, Q.W.R.	3087	NA	Kenya	Ingroup	Annonaceae	Monodoreae	<i>Uvariodendron schmidtii</i>	<i>Uvariodendron schmidtii</i>	RUN79_I10_T88_Uvariodendron_schmidtii

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TC-S1566	RUN79_I10_T82	Dagallier, L-P. M.J.	34	2019	Tanzania	Ingroup	Annonaceae	Monodoreae	<i>Uvari dendron usambarensis</i>	<i>Uvari dendron usambarensis</i>	iii-LUK_3087 RUN79_I10_T82_Uvari dendron_usambarensis-DAG_34
TC-S0053	RUN79_I2_T60	Couvreur, T.L.P.	20	2006	Tanzania	Ingroup	Annonaceae	Monodoreae	<i>Uvari dendron usambarensis</i>	<i>Uvari dendron usambarensis</i>	RUN79_I2_T60_Uvari dendron_usambarensis-COU_20
TC-S0712	RUN79_I2_T23	Couvreur, T.L.P.	1015	2016	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Uvariopsis bakeriana</i>	<i>Uvariopsis bakeriana</i>	RUN79_I2_T23_Uvariopsis_bakeriana-COU_1015
TC-S0697	RUN86_I3_T12	Couvreur, T.L.P.	1000	2016	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Uvariopsis bakeriana</i>	<i>Uvariopsis bakeriana</i>	RUN86_I3_T12_Uvariopsis_bakeriana-COU_1000
TC-S1045	RUN86_I3_T18	Couvreur, T.L.P.	1045	2016	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Uvariopsis bakeriana</i>	<i>Uvariopsis bakeriana</i>	RUN86_I3_T18_Uvariopsis_bakeriana-COU_1045
TC-S0825	RUN79_I2_T17	Couvreur, T.L.P.	1126	2016	Gabon	Ingroup	Annonaceae	Monodoreae	<i>Uvariopsis citrata</i>	<i>Uvariopsis citrata</i>	RUN79_I2_T17_Uvariopsis_citrata-COU_1126
TC-S1663	RUN79_I2_T28	Tchouto, P.	2869	2000	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Uvariopsis citrata</i>	<i>Uvariopsis citrata</i>	RUN79_I2_T28_Uvariopsis_citrata-TCH_2869
TC-S0825	RUN86_I3_T17	Couvreur, T.L.P.	1126	2016	Gabon	Ingroup	Annonaceae	Monodoreae	<i>Uvariopsis citrata</i>	<i>Uvariopsis citrata</i>	RUN86_I3_T17_Uvariopsis_citrata-COU_1126
TC-S1691	RUN79_I2_T18	Lachenaud, O.	1384	2013	Gabon	Ingroup	Annonaceae	Monodoreae	<i>Uvariopsis congensis</i>	<i>Uvariopsis congensis</i>	RUN79_I2_T18_Uvariopsis_congensis-LAC_1384
TC-S1686	RUN79_I9_T25	Ewango, C.E.N.	2664	2015	Democratic Republic of the Congo	Ingroup	Annonaceae	Monodoreae	<i>Uvariopsis congensis</i>	<i>Uvariopsis congensis</i>	RUN79_I9_T25_Uvariopsis_congensis-EWA_2664
TC-S1700	RUN79_I9_T49	White, F.	3334	1952	Zambia	Ingroup	Annonaceae	Monodoreae	<i>Uvariopsis congensis</i>	<i>Uvariopsis congensis</i>	RUN79_I9_T49_Uvariopsis_congensis_(East_Africa)-WHI_3334
TC-S2234	RUN86_I3_T29	Hallé, N.	3039	1964	Gabon	Ingroup	Annonaceae	Monodoreae	<i>Uvariopsis congolana</i>	<i>Uvariopsis congolana</i>	RUN86_I3_T29_Uvariopsis_congolana-HAL_3039
TC-S2235	RUN86_I3_T30	Hallé, N.	2817	1964	Gabon	Ingroup	Annonaceae	Monodoreae	<i>Uvariopsis congolana</i>	<i>Uvariopsis congolana</i>	RUN86_I3_T30_Uvariopsis_congolana-HAL_2817
TC-S2236	RUN86_I3_T31	Hallé, N.	64	1966	Gabon	Ingroup	Annonaceae	Monodoreae	<i>Uvariopsis congolana</i>	<i>Uvariopsis congolana</i>	RUN86_I3_T31_Uvariopsis_congolana-HAL_64
TC-S1696	RUN79_I10_T21	Reitsma, J.M.	3507	1987	Gabon	Ingroup	Annonaceae	Monodoreae	<i>Uvariopsis dioica</i>	<i>Uvariopsis dioica</i>	RUN79_I10_T21_Uvariopsis_dioica-REI_3507
TC-S0625	RUN79_I2_T20	Couvreur, T.L.P.	926	2015	Gabon	Ingroup	Annonaceae	Monodoreae	<i>Uvariopsis dioica</i>	<i>Uvariopsis dioica</i>	RUN79_I2_T20_Uvariopsis_dioica-COU_654
TC-S0625	RUN79_I2_T40	Couvreur, T.L.P.	654	2015	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Uvariopsis dioica</i>	<i>Uvariopsis dioica</i>	RUN79_I2_T40_Uvariopsis_dioica-COU_926
TC-S1712	RUN86_I3_T22	Thomas, D.W.	4544	1985	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Uvariopsis etugiana</i>	<i>Uvariopsis etugiana</i>	RUN86_I3_T22_Uvariopsis_etugiana-THO_4544
TC-S1684	RUN79_I10_T83	de Wilde, J.J.F.E.	3811	1962	Liberia	Ingroup	Annonaceae	Monodoreae	<i>Uvariopsis guineensis</i>	<i>Uvariopsis guineensis</i>	RUN79_I10_T83_Uvariopsis_guineensis-WIL_3811
TC-S1654	RUN79_I11_T37	Jongkind, C.C.H.	10774	2011	Guinea	Ingroup	Annonaceae	Monodoreae	<i>Uvariopsis guineensis</i>	<i>Uvariopsis guineensis</i>	RUN79_I11_T37_Uvariopsis_guineensis-JON_10774
TC-S1697	RUN79_I2_T42	Schmidt, H.H.	2070	1996	Ghana	Ingroup	Annonaceae	Monodoreae	<i>Uvariopsis guineensis</i>	<i>Uvariopsis globiflora</i>	RUN79_I2_T42_Uvariopsis_guineensis_(ex_globiflora)-SCH_2070
TC-S1678	RUN79_I9_T21	Aké Assi, L.	8823	1966	Ivory Coast	Ingroup	Annonaceae	Monodoreae	<i>Uvariopsis guineensis</i>	<i>Uvariopsis guineensis</i>	RUN79_I9_T21_Uvariopsis_guineensis-AKE_8823
TC-S1688	RUN79_I9_T24	Jongkind, C.C.H.	1809	1994	Ghana	Ingroup	Annonaceae	Monodoreae	<i>Uvariopsis guineensis</i>	<i>Uvariopsis globiflora</i>	RUN79_I9_T24_Uvariopsis_guineensis_(ex_globiflora)-JON_1809

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TC-S0735	RUN79_H10_T96	Couvreur, T.L.P.	1039	2016	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Uvariopsis korupensis</i>	<i>Uvariopsis korupensis</i>	RUN79_H10_T96_Uvariopsis_korupensis-COU_1039
TC-S1630	RUN79_I9_T62	Louis, A.M.	1863	1985	Gabon	Ingroup	Annonaceae	Monodoreae	<i>Uvariopsis korupensis</i>	<i>Uvariopsis korupensis</i>	RUN79_I9_T62_Uvariopsis_korupensis-LOU_1863
TC-S1628	RUN79_I2_T53	Luke, Q.W.R.	10369	2004	Tanzania	Ingroup	Annonaceae	Monodoreae	<i>Uvariopsis lovettiana</i>	<i>Uvariopsis lovettiana</i>	RUN79_I2_T53_Uvariopsis_lovettiana-LUK_10369
TC-S1598	RUN79_I9_T10	Dagallier, L-P. M.J.	66	2019	Tanzania	Ingroup	Annonaceae	Monodoreae	<i>Uvariopsis lovettiana</i>	<i>Uvariopsis lovettiana</i>	RUN79_I9_T10_Uvariopsis_lovettiana-DAG_66
TC-S1650	RUN79_I9_T9	Couvreur, T.L.P.	97b	2006	Tanzania	Ingroup	Annonaceae	Monodoreae	<i>Uvariopsis lovettiana</i>	<i>Uvariopsis lovettiana</i>	RUN79_I9_T9_Uvariopsis_lovettiana-COU_97b
TC-S1599	RUN79_H10_T91	Nolde, I. von	576	1938	Angola	Ingroup	Annonaceae	Monodoreae	<i>Uvariopsis noldeae</i>	<i>Uvariopsis noldeae</i>	RUN79_H10_T91_Uvariopsis_noldeae-NOL_576
TC-S1694	RUN79_I9_T14	Merello, M. C.	1380	1996	Ghana	Ingroup	Annonaceae	Monodoreae	<i>Uvariopsis oligocarpa</i>	<i>Uvariopsis congensis</i>	RUN79_I9_T14_Uvariopsis_oligocarpa_(ex_congensis)-MER_1380
TC-S1690	RUN79_I9_T31	de Koning, J.	2657	1973	Ivory Coast	Ingroup	Annonaceae	Monodoreae	<i>Uvariopsis oligocarpa</i>	<i>Uvariopsis congensis</i>	RUN79_I9_T31_Uvariopsis_oligocarpa_(ex_congensis)-KON_2657
TC-S1676	RUN79_I9_T53	Aké Assi, L.	13218	1976	Ivory Coast	Ingroup	Annonaceae	Monodoreae	<i>Uvariopsis oligocarpa</i>	<i>Uvariopsis congensis</i>	RUN79_I9_T53_Uvariopsis_oligocarpa_(ex_congensis)-AKE_13218
TC-S0318	RUN62_H10_T11	Couvreur, T.L.P.	602	2013	Gabon	Ingroup	Annonaceae	Monodoreae	<i>Uvariopsis pedunculosa</i>	<i>Uvariopsis pedunculosa</i>	RUN62_H10_T11_Uvariopsis_pedunculosa-COU_602
TC-S1701	RUN79_I2_T55	Zenker, G.	3868	1910	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Uvariopsis pedunculosa</i>	<i>Uvariopsis pedunculosa</i>	RUN79_I2_T55_Uvariopsis_pedunculosa-ZEN_3868
TC-S0749	RUN79_I9_T38	Couvreur, T.L.P.	1063	2016	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Uvariopsis pedunculosa</i>	<i>Uvariopsis pedunculosa</i>	RUN79_I9_T38_Uvariopsis_pedunculosa-COU_1063
TC-S0428	RUN79_I9_T55	Couvreur, T.L.P.	517	2013	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Uvariopsis pedunculosa</i>	<i>Uvariopsis pedunculosa</i>	RUN79_I9_T55_Uvariopsis_pedunculosa-COU_517
TC-S0276	RUN79_H10_T10	Couvreur, T.L.P.	550	2013	Gabon	Ingroup	Annonaceae	Monodoreae	<i>Uvariopsis solheidii</i>	<i>Uvariopsis letestui</i>	RUN79_H10_T10_Uvariopsis_solheidii_(ex_letestui)-COU_550
TC-S1629	RUN79_I2_T39	Ndjangou, J.B.	549	2011	Democratic Republic of the Congo	Ingroup	Annonaceae	Monodoreae	<i>Uvariopsis solheidii</i>	<i>Uvariopsis solheidii</i>	RUN79_I2_T39_Uvariopsis_solheidii-NDJ_549
TC-S0573	RUN79_I2_T54	Couvreur, T.L.P.	856	2015	Gabon	Ingroup	Annonaceae	Monodoreae	<i>Uvariopsis solheidii</i>	<i>Uvariopsis solheidii</i>	RUN79_I2_T54_Uvariopsis_solheidii-COU_856
TC-S1687	RUN79_I9_T17	Fay, J.M.	8384	1988	Central African Republic	Ingroup	Annonaceae	Monodoreae	<i>Uvariopsis solheidii</i>	<i>Uvariopsis solheidii</i>	RUN79_I9_T17_Uvariopsis_solheidii-FAY_8384
TC-S1631	RUN79_I9_T56	Hallé, N.	2975	1964	Gabon	Ingroup	Annonaceae	Monodoreae	<i>Uvariopsis solheidii</i>	<i>Uvariopsis letestui</i>	RUN79_I9_T56_Uvariopsis_solheidii_(ex_letestui)-HAL_2975
TC-S0573	RUN86_I3_T11	Couvreur, T.L.P.	856	2015	Gabon	Ingroup	Annonaceae	Monodoreae	<i>Uvariopsis solheidii</i>	<i>Uvariopsis solheidii</i>	RUN86_I3_T11_Uvariopsis_solheidii-COU_856
TC-S2246	RUN86_I3_T41	African Tropical Biodiversity Programme	666	1998	Uganda	Ingroup	Annonaceae	Monodoreae	<i>Uvariopsis sp nov Uganda</i>	<i>Uvariopsis sp</i>	RUN86_I3_T41_Uvariopsis_sp_nov_Uganda-ATBP_666
TC-S0745	RUN79_H10_T14	Couvreur, T.L.P.	1059	2016	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Uvariopsis submontana</i>	<i>Uvariopsis submontana</i>	RUN79_H10_T14_Uvariopsis_submontana-COU_1059
TC-S0674	RUN62_H12_T97	Couvreur, T.L.P.	978	2016	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Uvariopsis zenkeri</i>	<i>Uvariopsis zenkeri</i>	RUN62_H12_T97_Uvariopsis_zenkeri-COU_978
TC-S0485	RUN79_H10_T94	Couvreur, T.L.P.	707	2015	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Uvariopsis zenkeri</i>	<i>Uvariopsis zenkeri</i>	RUN79_H10_T94_Uvariopsis_zenkeri-

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TC-S0723	RUN79_I9_T37	Couvreur, T.L.P.	1027	2016	Cameroon	Ingroup	Annonaceae	Monodoreae	<i>Uvariopsis zenkeri</i>	<i>Uvariopsis zenkeri</i>	COU_707 RUN79_I9_T37_Uvariopsis_zenkeri-COU_1027
TC-S1586	RUN79_I11_T47	Dagallier, L.-P. M.J.	54	2019	Tanzania	Ingroup	Annonaceae	Ophrypetaleae	<i>Ophrypetalum odoratum</i>	<i>Ophrypetalum odoratum</i>	RUN79_I11_T47_Ophrypetalum_odoratum-DAG_54
TC-S1648	RUN79_I2_T45	Couvreur, T.L.P.	82	2006	Tanzania	Ingroup	Annonaceae	Ophrypetaleae	<i>Ophrypetalum odoratum</i>	<i>Ophrypetalum odoratum</i>	RUN79_I2_T45_Ophrypetalum_odoratum-COU_82
TC-S1666	RUN79_I9_T36	Robertson, S.A.	7547	2005	Tanzania	Ingroup	Annonaceae	Ophrypetaleae	<i>Ophrypetalum odoratum</i>	<i>Ophrypetalum odoratum</i>	RUN79_I9_T36_Ophrypetalum_odoratum-ROB_7547
TC-S1151	RUN62_I10_T44	Couvreur, T.L.P.	6	2006	Tanzania	Ingroup	Annonaceae	Ophrypetaleae	<i>Sanrafaelia ruffonammari</i>	<i>Sanrafaelia ruffonammari</i>	RUN62_I10_T44_Sanrafaelia_ruffonammari-COU_6
TC-S1563	RUN79_I9_T32	Dagallier, L.-P. M.J.	31	2019	Tanzania	Ingroup	Annonaceae	Ophrypetaleae	<i>Sanrafaelia ruffonammari</i>	<i>Sanrafaelia ruffonammari</i>	RUN79_I9_T32_Sanrafaelia_ruffonammari-DAG_31
TC-S1100	RUN62_I10_T25	Maas, P.J.M. <i>et al.</i>	9408	2004	Costa Rica	Outgroup	Annonaceae	Anaxagoreoideae	<i>Anaxagorea crassipetala</i>	<i>Anaxagorea crassipetala</i>	RUN62_I10_T25_Anaxagorea_crassipetala-MAA_9408
TC-S1131	RUN62_I10_T36	Chatrou, L.W.	467	2000		Outgroup	Annonaceae	Annoneae	<i>Annona glabra</i>	<i>Annona glabra</i>	RUN62_I10_T36_Annona_glabra-CHA_467
TC-S0739	RUN60_I4_T36	Couvreur, T.L.P.	1053	2016	Cameroon	Outgroup	Annonaceae	Annoneae	<i>Anonidium manii</i>	<i>Anonidium manii</i>	RUN60_I4_T36_Anonidium_manii-COU_1053
TC-S0711	RUN62_I10_T14	Couvreur, T.L.P.	1014	2016	Cameroon	Outgroup	Annonaceae	Duguetieae	<i>Duguetia staudtii</i>	<i>Duguetia staudtii</i>	RUN62_I10_T14_Duguetia_staudtii-COU_1014
TC-S1098	RUN62_I10_T23	Maas, P. J. M.	9553	2004	Panama	Outgroup	Annonaceae	Guatterieae	<i>Guatteria jefensis</i>	<i>Guatteria jefensis</i>	RUN62_I10_T23_Guatteria_jefensis-MAA_9553
TC-S1292	RUN62_I6_T70	Couvreur, T.L.P.	746	2015	Gabon	Outgroup	Annonaceae	Piptostigmateae	<i>Greenwayodendron suaveolens</i>	<i>Greenwayodendron suaveolens</i>	RUN62_I6_T70_Greenwayodendron_suaevolens-COU_746
TC-S1174	RUN62_I10_T53	Couvreur, T.L.P.	839	2015	Malaysia	Outgroup	Annonaceae	Uvarieae	<i>Desmos chinensis</i>	<i>Desmos chinensis</i>	RUN62_I10_T53_Desmos_chinensis-COU_839
TC-S1164	RUN62_I10_T49	Couvreur, T.L.P.	827	2015	Malaysia	Outgroup	Annonaceae	Uvarieae	<i>Fissistigma sp</i>	<i>Fissistigma sp</i>	RUN62_I10_T49_Fissistigma_sp-COU_827
TC-S1187	RUN62_I10_T54	Sauquet, H.	177	2015	Malaysia	Outgroup	Annonaceae	Uvarieae	<i>Friesodielsia excisa</i>	<i>Friesodielsia excisa</i>	RUN62_I10_T54_Friesodielsia_excisa-SAU_177
TC-S0715	RUN62_I12_T98	Couvreur, T.L.P.	1018	2016	Cameroon	Outgroup	Annonaceae	Uvarieae	<i>Monanthotaxis congoensis</i>	<i>Monanthotaxis congoensis</i>	RUN62_I12_T98_Monanthotaxis_congoensis-COU_1018
TC-S1173	RUN62_I10_T52	Couvreur, T.L.P.	838	2015	Malaysia	Outgroup	Annonaceae	Uvarieae	<i>Uvaria grandiflora</i>	<i>Uvaria grandiflora</i>	RUN62_I10_T52_Uvaria_grandiflora-COU_838

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# Chapter 4 | Taxonomic revision of the tropical African genera *Uvariodendron* and *Uvariopsis*\*

**Abstract.** *Uvariodendron* and *Uvariopsis* (tribe Monodoreae, Annonaceae) are two tropical rain forests genera from Africa, comprising 18 described species each. Morphologically, *Uvariodendron* represents the typical Annonaceae flower being hermaphroditic with three sepals and two whorls of three petals, whereas *Uvariopsis* has two sepals and four petals (except *Up. congolana* that has three petals) and unisexual flowers (except *Up. bisexualis*). Four new species of *Uvariodendron* are described: *Ud. citriodorum* Dagallier **nom. nov.**, *Ud. kimbozaense* Dagallier **sp. nov.**, *Ud. mossambicense* Dagallier **sp. nov.** and *Ud. pilosicarpum* Dagallier **sp. nov.** The names *Ud. giganteum* and *Ud. magnificum* are reduced into synonymy with *Ud. fuscum* as two new varieties *Ud. fuscum* var. *giganteum* **comb. nov.** and *Ud. fuscum* var. *magnificum* **comb. nov.**. In *Uvariopsis*, one new species is fully described, *Up. oligocarpa* Dagallier & Couvreur **sp. nov.**, and three potentially new species are preliminarily described. The name *Up. globiflora* is reduced in synonymy with *Up. guineensis* and collapsed as the variety *Up. guineensis* var. *globiflora* **comb. nov.** and the name *Up. letestui* is reduced in synonymy with *Up. solheidii* as the new variety *Up. solheidii* var. *letestui* **comb. nov.** The new variety of *Up. congensis* var. *angustifolia* **var. nov.** is also described. This taxonomic revision provides an updated taxonomy of *Uvariodendron* and *Uvariopsis* together with a discussion about their morphology, pollination biology, seed dispersal and uses. Finally, all the species are mapped.

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\* Manuscript in preparation

## 1. Introduction

Annonaceae is the most diverse family within the Magnoliales, with ca. 2500 species within 109 genera (Chatrou *et al.*, 2012; Guo *et al.*, 2017, Chaowasku *et al.*, 2018b,a; Chatrou *et al.*, 2018). The family has a pantropical distribution and is composed of trees, shrubs and lianas. The tribe Monodoreae Baill. is part of the sub-family Annonoideae Raf. (Couvreur *et al.*, 2008; Chatrou *et al.*, 2012; Guo *et al.*, 2017). Including the species described here, it is composed of 92 species within 11 genera. The species are mainly restricted to tropical Africa within one genus reaching into Madagascar. The taxonomy within the tribe is well known for most of the genera. Recent works and updates include the revision of the syncarpous genera *Monodora* and *Isolona* (Couvreur, 2009), the synpetalous genus *Hexalobus* (Botermans *et al.*, 2011), the genus *Uvariastrum* (Couvreur, 2014) and of the genus *Mischogyne* (Gosline *et al.*, 2019). The genus *Asteranthe* is known by two species (Verdcourt, 1971; Vollesen, 1980). However, for the genera *Uvariadendron* and *Uvariopsis*, the taxonomic revisions including all the species are relatively old and several new species and regional revisions were published since then. The aim of the present work is to revise the taxonomy of these two genera. This will complete the systematic work on the Monodoreae presented in Chapter 3.

## 2. Material & methods

Measurements and observation were made on dried herbarium specimens from the following herbaria B, BM, DSM, EA, G, K, M, MO, MPU, P, WAG, YA (Thiers, 2016). Additional scans of herbarium specimens from BR, COI, FHO, MA, MHU and MO were also examined. In total, ca. 1,500 herbarium sheets, representing 857 specimens, were studied for this revision. Some additional duplicates from other herbaria might appear in the lists of specimens, but these were not seen and are cited for information. The format for the list of specimens is adapted from Bénichou *et al.* (2018).

Morphological descriptions followed terminologies from Hickey *et al.* (1999) and the Systematics Association Committee for Descriptive Biological Terminology (1962) for leaf and plane shapes, Payne (1978) for the indumentum, and Harris and Harris (2001) for the other terms.

To avoid ambiguities, when necessary, the names *Uvariadendron* and *Uvariopsis* will be abbreviated to *Ud.* and *Up.*, respectively.

### 3. Taxonomic history

#### 3.1. *Uvariodendron*

The first species names referring to what will later become *Uvariodendron* were first described by Bentham (1862) as *Uvaria connivens* and *Uvaria fusca* and by Engler (1899) as *Uvaria angustifolia* and *Uvaria gigantea* (Engler, 1899). These four species have flowers superficially similar to other *Uvaria* L. species, but they are trees, whereas *Uvaria* s.s. are lianas. Based on this character, Engler and Diels grouped them into the new section within *Uvaria* (Engler & Diels, 1901): *Uvariodendron* (literally meaning “tree *Uvaria*’s”). For the next 30 years, several new tree species from Central and East Africa were described within this section: *Uvaria megalantha* Diels and *Uvaria winkleri* Diels (Diels, 1907); *Uvaria molundensis* Diels and *Uvaria pycnophylla* Diels (Diels, 1915); *Uvaria letestui* Pellegrin (Pellegrin, 1920); *Uvaria gossweileri* Exell and *Uvaria mayumbensis* Exell (Exell, 1926) and finally *Uvaria manii* Hutch. & Dalziel (Hutchinson & Dalziel, 1927a).

In 1930, Fries (1930) revised several Annonaceae genera, and erected *Uvaria* L. section *Uvariodendron* Engl. & Diels to the level of genus. The morphological characters that distinguished *Uvariodendron* Engl. & Diels from the *Uvaria* L. were the tree habit (vs. liana in *Uvaria*), the indumentum of simple hairs (vs. generally stellate hairs) and flowers borne on trunk or axillary (vs. terminal). Fries thus combined the “tree *Uvaria*” names cited above as: *Uvariodendron angustifolium* (Engl. & Diels) R.E.Fr., *Uvariodendron connivens* (Benth.) R.E.Fr., *Uvariodendron fuscum* (Benth.) R.E.Fr., *Uvariodendron giganteum* (Engl.) R.E.Fr., *Uvariodendron letestui* (Pellegrin) R. E. FR., *Uvariodendron mayumbense* (Exell) R. E. Fr., *Uvariodendron molundense* (Diels) R. E. Fr. and *Uvariodendron pycnophyllum* (Diels) R. E. Fr.. Fries (1930) also synonymised the name *Uvaria megalantha* Diels and *Uvaria winkleri* Diels with *Uvariodendron connivens* (Benth.) R.E.Fr.. He also described three new species: *Uvariodendron calophyllum* R.E.Fr., *Uvariodendron mirabile* R.E.Fr. and *Uvariodendron usambarensis* R.E.Fr. (Fries, 1930). A few years later, Exell and Mendonça combined the Angolan *Uvaria gossweileri* into *Uvariodendron gossweileri* (Exell & Mendonça, 1937). After that, we have to wait 1955 to see a new species published: *Uvariodendron anisatum* Verdc. from Kenya (Verdcourt, 1955). Then it is at the end of the 1960’s that several new species were described. Le Thomas described the new *Uvariodendron occidentale* Le Thomas previously described as part of *Uvariodendron mirabile* R.E.Fr. (Le Thomas, 1967). In her *Flore du Gabon*, she also described a new variety *Uvariodendron molundense* var. *citrata* Le Thomas, and synonymised *Uvariodendron letestui* Pellegrin and *Uvariodendron mayumbense* (Exell) R.E.Fr. with *Uvariodendron molundense* (Diels) R.E.Fr. (Le Thomas, 1969). The same year, Verdcourt described three new species from East Africa: *Uvariodendron gorgonis* Verdc., *Uvario-*

*dendron kirkii* Verdc., and *Uvari dendron magnificum* Verdc. (Verdcourt, 1969). Later, he also described *Uvari dendron oligocarpum* Verdc. (Verdcourt, 1986), a species that was recently (Dagallier *et al.*, 2021) combined into *Polyceratocarpus oligocarpus* (Verdc.) Dagallier. In that same publication, an additional three new species were published from Kenyan and Tanzanian coastal forests: *Uvari dendron dzomboense* Dagallier, W.R.Q. Luke & Couvreur, *Uvari dendron mbagoi* Dagallier & Couvreur, and *Uvari dendron schmidtii* W.R.Q. Luke, Dagallier & Couvreur. In the Flora of Cameroon, the name *Uvari dendron mirabile* R.E.Fr. was synonymized with *Uvari dendron fuscum* (Benth.) R.E.Fr. (Couvreur *et al.*, in press). Here, based on molecular and morphological analysis (Chapter 3 and 4), we reassess the name *Uvari dendron molundense* into three species: *Ud. molundense*, *Ud. citriodorum* **nom. nov.** (ex. *Ud. molundense* var. *citrata*) and *Ud. pilosicarpum* **sp. nov.** and describe *Ud. kimbozaense* **sp. nov.** and *Ud. mossambicense* **sp. nov.** from East Africa. We also recombine the names *Ud. giganteum* and *Ud. magnificum* within *Ud. fuscum* as varieties: *Ud. fuscum* var. *giganteum* **comb. nov.** and *Ud. fuscum* var. *magnificum* **comb. nov.** Thus to date, and after this taxonomic work, *Uvari dendron* contains 18 species.

Note: According to Kuntze, who undertook nomenclatural work between the end of the 19<sup>th</sup> and the beginning of the 20<sup>th</sup> centuries, the generic name *Uva* should be used instead of *Uvaria* (Kuntze, 1891). Indeed, Burman was the first to use the name *Uva* in its Thesaurus Zelanica (Burman, 1736), but Linné changed the name to *Uvaria* while citing the same specimen and describing the same species (Linné, 1747). Kuntze underlines that no nomenclatural rule precludes the use of the name *Uva* and favors its use over the name *Uvaria* (Kuntze, 1891). Among other invalid *Uvaria* names, he corrects the names *Uvaria gigantea* Engler to *Uva gigantea* Engler, *Uvaria angustifolia* Engler & Diels to *Uva angustifolia* Engler & Diels (Kuntze, 1891), *Uvaria connivens* Benth. to *Uva connivens* Benth. and *Uvaria fusca* Benth. to *Uva fusca* Benth. (Kuntze, 1903). Although this nomenclatural standardisation work was published, the use of *Uva* was apparently not followed by the scientific community even today as the name *Uvaria* continues to be used (Diels 1907, Meade *et al.*, 2018).

### 3.2. *Uvariopsis*

The genus *Uvariopsis* Engler was erected in 1899 with the description of *Uvariopsis zenkeri* Engler (Engler, 1899). As circumscribed by Engler at the time, the genus was distinguished by its mainly unisexual flowers, two sepals and four fused petals. A few years later, Diels erected the genus *Tetrastemma* Diels with the description of *Tetrastemma dioicum* Diels (Diels, 1907). *Tetrastemma* was also characterised by unisexual flowers with two sepals and four petals, but differed from *Uvariopsis* by being dioecious and cauliflorous (vs. monoecious and ramiflorous), and by having free petals (vs. fused

at base). Based on the free petals character, four other *Tetrastemma* species were described in the following years: *Tetrastemma solheidii* De Wild. in 1909 (De Wildeman, 1909), *Tetrastemma pedunculatum* Diels and *Tetrastemma sessiliflorum* Mildbr. & Diels in 1915 (Diels, 1915), and *Tetrastemma bakerianum* Hutch. & Dalziel in 1927 (Hutchinson & Dalziel, 1927a).

In parallel, two other genera, morphologically closed to *Uvariopsis* and *Tetrastemma* were described: *Thonnera* De Wild. and *Denettia* Baker f.. The genus *Thonnera* De Wild. included a single species *Thonnera congolana* De Wild. differing from *Tetrastemma* by flowers having three petals (De Wildeman, 1909). In 1953, however, Fries combined this name into *Uvariopsis* as *Uvariopsis congolana* (De Wild.) Fries without further justification (Fries, 1953). The genus *Denettia* Baker f. was characterised by having bisexual flowers with three sepals and three petals, which differed from *Tetrastemma*, *Thonnera*, and *Uvariopsis*. It included a single species *Denettia tripetala* Baker f. (Baker, 1913).

In 1933, Robyns & Ghesquière described *Uvariopsis vanderystii* Robyns & Ghesq., and suggested it was a kind of intermediate species showing characters of *Tetrastemma*, e.g. cauliflory, and of *Uvariopsis*, e.g. fused petals (Robyns & Ghesquière, 1933a). The same year, they revised the two genera with their “Essai de révision des genres *Uvariopsis* Engl. & Diels et *Tetrastemma* Diels (Annonacées)” (Robyns & Ghesquière, 1933b). In this publication, they described several new species: *Uvariopsis batesii* Robyns & Ghesq., *Uvariopsis chevalieri* Robyns & Ghesq. and *Uvariopsis congensis* Robyns & Ghesq.. The later species is ramiflorous and has free petals, which is again showed characters of both *Uvariopsis* and *Tetrastemma* characters. Because several species shared characters of both *Uvariopsis* Engler and *Tetrastemma* Diels, they extend the concept of *Uvariopsis* and combined the name *Tetrastemma* with *Uvariopsis*. The new species combinations were: *Uvariopsis bakeriana* (Hutch. & Daltz.) Robyns & Ghesq., *Uvariopsis dioica* (Diels) Robyns & Ghesq., *Uvariopsis pedunculosa* (Diels) Robyns & Ghesq., *Uvariopsis sessiliflora* (Mildb. & Diels) Robyns & Ghesq., *Uvariopsis solheidii* (De Wild.) Robyns & Ghesq.. In 1948, Pellegrin described *Uvariopsis letestui* Pellegrin, a new species from Gabon (Pellegrin, 1948), and 3 years later Exell and Mendonça described a new species from Angola: *Uvariopsis noldeae* Exell & Mendonça (Exell & Mendonça, 1951). In 1952, Keay published the new species *Uvariopsis globilora* Keay (Keay, 1952). He also combined a species previously described by Chevalier under the name *Uvaria spectabilis* Chev. (Chevalier, 1920) and cited in the Flora of Tropical West Africa as *Uvaria spectabilis* Chev. ex Hutch. & Dalziel (Hutchinson & Dalziel, 1927b) into *Uvariopsis guineensis* (Chev. ex Hutch. & Dalziel) Keay (Keay, 1952). More than 30 years later, Verdcourt described *Uvariopsis bisexualis* Verdc. from Tanzania. Although this species has bisexual flowers, Verdcourt placed it in *Uvariopsis* based on pollen morphology that was very close to *Uvariopsis* species (Verdcourt, 1986). The concept of *Uvariopsis* Engler was thus enlarged to include bisexual species.

In the early 2000's, Gereau & Kenfack published a key to the genus, as well as describing the new species *Uvariopsis korupensis* Gereau & Kenfack (Gereau & Kenfack, 2000). This publication was followed by the description of *Uvariopsis submontana* Kenfack, Gosline & Gereau (Kenfack *et al.*, 2003). In that later publication, the name *Denettia tripetala* Baker f. was recombined into *Uvariopsis tripetala* (Baker f.) G.E. Schatz. based on the fact that the concept of *Uvariopsis* was expanded to bisexual flowers (Kenfack *et al.*, 2003). More recently, the Tanzanian species *Uvariopsis lovettiana* Couvreur & W.R.Q. Luke (Couvreur & Luke, 2010) and the Gabonese species *Uvariopsis citrata* Couvreur & Niangadouma (Couvreur & Niangadouma, 2016) were described. In the Flora of Cameroon, the new species *Uvariopsis etugiana* Dagallier & Couvreur was described and the name *Uvariopsis vanderystii* Robyns & Ghesq. was synonymized into *Uvariopsis pedunculosa* (Diels) Robyns & Ghesq. (Couvreur *et al.*, in press). Finally, the species *Uvariopsis dicaprio* Gosline & Cheek was described from Cameroon (Gosline *et al.*, in press). In the present work, based on molecular and morphological analyses (Chapter 3 and 4), we retain the name *Dennettia tripetala* and thus the genus *Dennettia*. We also describe a new species, *Up. oligocarpa* **sp. nov.**, and synonymize the names *Up. globiflora* with *Up. guineensis* and *Up. letestui* with *Up. solheidii*, collapsing them to varieties as *Up. guineensis* var. *globiflora* **comb. nov.** and *Up. solheidii* var. *letestui* **comb. nov.**, respectively. We also describe a new variety of *Up. congensis*, *Up. congensis* var. *angustifolia* **var. nov.** and provide a preliminary description of potentially three new species which lack sufficient material to be formally described. This brings the total number of *Uvariopsis* species to 21 (18 of which are formally described).

#### 4. Morphology and informative characters

Like many Annonaceae, *Uvariodendron* and *Uvariopsis* are trees or shrubs with plagiotropic branches on an orthotropic axis, with indumentum of simple hairs and with no latex or exudate. A distichous phyllotaxis of the primary axis (the trunk) was reported for *Ud. pycnopyllum* (Johnson 2003), but no information was reported for the other species and for *Uvariopsis*. The trunks are generally cylindrical and straight, with no buttresses. The base of the trunk of some *Uvariopsis* species (*Up. dioica*, *Up. submonana*, *Up. korupensis*) can be thickened by the growth of numerous inflorescences clumped on the trunk between the ground to generally ca. 50 cm (up to 4 m).

The branches of *Uvariodendron* and *Uvariopsis* can be sparsely pubescent when young, but the hairs generally quickly fall off. The pubescence distinguishes *Ud. calophyllum* from the other species as it has a thick brown tomentum on its young branches that can remain on older branches. The species *Ud. fuscum* (var. *giganteum* and var. *magnificum*) also have a characteristic indumentum of long soft



## CHAPTER 4

hairs producing a whitish appearance on the younger branches, but that quickly disappear in older branches.

In both genera, the leaves are distichous, simple, entire, exstipulate, with the midrib sunken above, raised below, the secondary veins weakly brochidodromous to brochidodromous and the tertiary veins reticulate. The two genera show different forms of leaves, from elliptic to obovate to oblong, ranging from 65 to 750 mm long. In contrast to other smaller genera (e.g. *Uvariastrum*, Couvreur 2014) leaf base shape can hardly be used to distinguish species because several different shapes (e.g. from acute to rounded) can occur within species. However, it should be mentioned that subcordate leaf bases are generally found in *Up. bakeriana*, *Up. citrata*, *Up. korupensis*, and *Up. submontana*, and decurrent leaf bases in *Ud. pilosicarpum*, *Up. bisexualis*, *Up. congensis*, *Up. lovettiana*, *Up. oligocarpa* and *Up. zenkeri*. It is also worth mentioning that some species have complex leaf bases, like rounded in shape but minutely decurrent when looking at the very base (*Ud. citriodorum*, *Ud. gorgonis*, *Ud. molundense*). The petiole in *Uvariopsis* are generally short and thick, less than 6 mm long with a length:width ratio less than 2, whereas in *Uvari dendron* the petiole are generally greater than 4 mm with a length:width ratio comprised between 2 and 5.

The smell of the plant (crushed leaves and/or bark) is a particular feature of some of the *Uvari dendron* and *Uvariopsis* species. Crushed leaves of *Ud. citriodorum* and *Up. citrata* have a strong lemon scent, a feature also shared by some specimens of *Ud. gorgonis*. Crushed leaves and bark of *Ud. mbagoi* have a strong bergamot scent (between orange and lemon), and all parts of *Ud. anisatum* smell of anise. *Ud. angustifolium* is also described as having a strong aromatic scent.

In contrast to sterile parts, *Uvari dendron* and *Uvariopsis* have very different fertile parts. Flowers and fruits of *Uvari dendron* and *Uvariopsis* are axillary or on the trunk (cauliflorous), depending on the species. The position of the flower was regarded as an important character to discriminate some species like *Ud. molundense* and *Up. guineensis* (Keay, 1952; Le Thomas, 1967, 1969) but as discussed in the Chapter 3 it is considered unreliable in *Uvari dendron* and *Uvariopsis* (see also Le Thomas, 1969).

Inflorescences in *Uvari dendron* are borne on trunk, old branches or axillary. In Annonaceae, the inflorescence is a rhipidium, i.e. determinate inflorescence with a terminal flower and lateral cymose and monochasial partial inflorescences (Weberling and Hoppe 1996). In *Uvari dendron*, the inflorescences are borne on the trunk, old branches or axillary to the leaf. The axis of the inflorescences (peduncle and partial peduncles) are contracted, rendering their interpretation difficult without a detailed study. They appear to be rhipidia composed of one to two flowers (most of the species), up to

three (*Ud. calophyllum*, *Ud. gorgonis*, *Ud. mbagoi*) or rarely up to 11 (*Ud. kimbozaense*) flowers. Generally, in multi-flowered rhipidia, the flower in terminal position is fully developed while the lower flowers on the axis are buds.

Flowers in *Uvariodesdron* are hermaphroditic with one whorl of three sepals and two whorls of three petals, as usually found in Annonaceae (van Heusden, 1992). The fusion and arrangement of the sepals can be used to distinguish between species: always fused (*Ud. angustifolium*, *Ud. dzomboense*, *Ud. fuscum*, *Ud. mossambicense*, *Ud. occidentale*, *Ud. pycnophyllum*, *Ud. schmidtii*), always imbricate (*Ud. citriodorum*, *Ud. kimbozaense*, *Ud. mbagoi*, *Ud. pilosicarpum*), or from free to fused to imbricate (*Ud. anisatum*, *Ud. calophyllum*, *Ud. connivens*, *Ud. gorgonis*, *Ud. kirki*, *Ud. molundense*). The sepals are smaller than, and morphologically different to, the petals. The outer and inner petals are subequal in length, from 10 to 40 mm at anthesis. In bud, the outer petals are valvate (adpressed against each other all along the margin) whereas inner petals are valvate only at the apex. In mature flowers, the outer and inner petals are free, but the inner petals can remain valvate at apex. In most species, the petals are cream to yellow in color, with a red to purple streak at the base of the inner side of the petals, except in *Ud. connivens* that has petals pink to red on both sides at anthesis, and in *Ud. calophyllum* that has outer petals covered with a brown tomentum. The stamens are numerous (more than 200), with linear anthers and truncate connective. The carpels vary from five to 160, they are free, linear, with a coiled stigma. The monocarps are sessile or subsessile and cylindrical.

*Uvariopsis* has inflorescences borne on trunk in most of the species, but can be cauliflorous (*Up. congensis*, *Up. guineensis*, *Up. lovettiana*, *Up. oligocarpa*, *Up. zenkeri*). They are generally composed of one to three flowers. Like in *Uvariodesdron*, the peduncle and partial peduncle are contracted, rendering their interpretation as rhipidium difficult. In particular, *Up. dioica*, *Up. submonana* and *Up. korupensis* have flowers in clumps of up to 50 flowers on the trunk and it is impossible to distinguish if they are clumps of inflorescences or single inflorescence of up to 50 flowers.

The flowers of *Uvariopsis* have one whorl of two sepals and one whorl of four petals (except *Up. congolana* that has three petals). In Annonaceae, flowers with two sepals and four petals are rare and can be found in only a few other genera such as *Disepalum* or *Tridimeris* (van Heusden, 1992). The petals are usually free, but fused in some species (*Up. congolana*, *Up. guineensis*, *Up. korupensis*, *Up. pedunculosa*, *Up. submontana*, and *Up. zenkeri*). Another rare character in Annonaceae exhibited by *Uvariopsis* is its exclusively unisexual flowers (except for *Up. bisexualis* that has hermaphroditic flowers). In Annonaceae, unisexual flowers are found in several androdioecious species, e.g. in *Polyacarpus* (Couvreur *et al.* 2009) or *Diclinanona* (Erkens *et al.*, 2014). Species with exclusively unisexual

flowers are more rare and found only in a few genera: *Monanthotaxis*, *Pseuduvaria*, *Stelechocarpus* and *Winitia* (van Heusden, 1992; Chaowasku & Van Der Ham, 2013; Hoekstra et al., 2021). Unisexual *Uvariopsis* species are monoecious, i.e. have male and female flowers on the same individual, even the species *Up. dioica* that has a misleading specific epithet. The length of the flower pedicels in *Uvariopsis* varies greatly, from less than 11 mm (*Up. bakeriana*, *Up. citrata*, *Up. congensis*, *Up. etugiana*, *Up. oligocarpa*, *Up. sessiliflora* and *Up. zenkeri*) to more than 100 mm up to 400 mm (*Up. congolana*, *Up. pedunculosa*). Fruit of *Uvariopsis* are sessile to subsessile cylindrical monocarps. Their texture and pubescence can be informative: either smooth (*Up. congensis*, *Up. dioica*, *Up. guineensis*, *Up. korpensis*, *Up. lovettiana*, *Up. sessiliflora*, *Up. oligocarpa*) or wrinkled to verrucose (*Up. bakeriana*, *Up. congolana*, *Up. pedunculosa*, *Up. solheidii*), and either pubescent to tomentose (*Up. pedunculosa*, *Up. oligocarpa*, *Up. zenkeri*) or sparsely pubescent to glabrous.

## 5. Pollination and seed dispersal

The pollination biology of *Uvarioidendron* and *Uvariopsis* is poorly known for most of the species, except for *Ud. connivens*, *Ud. calophyllum*, *Up. bakeriana* and *Up. pedunculosa* (Gottsberger *et al.*, 2011, note that the species identified as *Up. congolana* in this reference is actually *Up. pedunculosa*), and also *Up. dioica* (Mertens *et al.* 2018). *Uvarioidendron* are mainly pollinated by beetles (Coleoptera, Scarabaeidae and Curculionidae). The inner petals remain connate at apex until anthesis, forming a semi-closed pollination chamber in which the pollinators feed on pollen and mate (e.g. Figure 21D). The pollinators are attracted by the aromatic scent emitted by the flowers. Flowers of *Ud. connivens* and *Ud. calophyllum* were found to be thermogenetic, which could enhance the scent diffusion and the pollinator attraction (Gottsberger *et al.*, 2011). However, rather than active thermogenesis, it is possible that the pollination chamber buffers the air temperature from outside. The petals of *Uvarioidendron* flowers are thick and the pollinators feed on the petals and deposit their eggs in the petal tissue, which is testified by the gnaw marks on the petals (e.g. Figure 21D), similarly to other Annonaceae species having thick petals (Gottsberger & Webber, 2018). Although this probably doesn't play a role in pollination, we have seen completely eaten petals on flowers of *Ud. kimbozaense* (Figure 21E), with animal hairs stuck on the stigma exudate (Figure 21C), suggesting that small mammals like rodents may feed on the petals. Direct observation of such feeding on petals should however confirm this hypothesis.

In *Uvariopsis*, the species *Up. bakeriana* and *Up. pedunculosa* have been reported as emitting a strong pungent scent, and to be pollinated by flies (Diptera) (Gottsberger *et al.*, 2011). *Up. dioica* has been reported to be pollinated by flies cockroaches and orthopterans (Mertens *et al.* 2018), and pictures of living specimens of *Up. dioica* (Bidault 1558) and *Up. guineensis* (Bidault 4798) show flies visiting the

flowers. Petals of *Up. bakeriana* are dark red to dark pink and verrucose, which looks like body flesh. This is characteristic of the sapromiophylous pollination syndrome (Gottsberger *et al.*, 2011). Most of the *Uvariopsis* species present petals with flesh-like colors and texture. This suggests that sapromiophyly is the dominant pollination syndrome in *Uvariopsis*. In contrast, the species *Up. dicaprio* present pale yellow-green flowers, suggesting nocturnal pollinators such as moths (Gosline *et al.*, 2022).

Similarly to pollination biology, data on seed and fruit dispersal of *Uvariodendron* and *Uvariopsis* remain scarce. Fruits of *Uvariodendron* are part of gorillas' diet (Rogers *et al.*, 2004), as well as fruits of *Up. congolana* (Yamagiwa *et al.*, 1994) and *Up. solheidii* (notes of specimen J.M. Fay 8384). Fruits of *Up. solheidii* are also eaten by small rodents and squirrels (Gautier-Hion *et al.*, 1985). Chimpanzees (*Pan*) and guenons (*Cercopithecus*) consume the fruits of *Up. congensis* (Lambert, 2011; Watts *et al.*, 2012; Kagoro-Rugunda & Hashimoto, 2015).

## 6. Ethnobotany

*Uvariodendron* and *Uvariopsis* species are used for food. The ripe fruits of *Ud. angustifolium* (Jones 3490) and *Ud. fuscum* (van Andel 3761) are eaten, as well as the young leaves of *Ud. connivens* (Cheek 5180) and *Ud. fuscum* (Cheek 5145) that are boiled and used in soup. The bark of *Ud. mbagoi* (Dagallier 39) is used as infusion for tea or as spice in meat meals. The leaves of *Up. citrata* (Letouzey 9017) are used to wrap the fish during the cooking to give it an aromatic taste.

*Uvariodendron* and *Uvariopsis* species are also part of the pharmacopoeia of several local communities, such as in Benin and Cameroon where *Ud. angustifolium*, *Ud. connivens*, *Ud. fuscum*, *Up. bakeriana*, *Up. dioica* and *Up. korupensis* are used to cure various conditions (Jiofack *et al.*, 2009; Bele *et al.*, 2011; Bada Amouzoun *et al.*, 2019) or in Kenya where *Ud. kirkii* is used as contraceptive (Kaingu *et al.*, 2017).

Other usages such as firewood and craft were reported for *Ud. angustifolium*, *Up. bakeriana*, *Up. dioica*, and *Up. korupensis* (Bele *et al.*, 2011; Bada Amouzoun *et al.*, 2019), as well as dye with fruits of *Ud. connivens* (Mbani 14).

## 7. Taxonomic treatment

### 7.1. *Uvariodendron* (Engl. & Diels) R.E.Fr., Acta Horti Berg. x. 51 (1930)

*Uvaria* L. section **Uvariodendron**, Engl. & Diels in Engl. Afr. Pfl. VI 8 (1901)

**Description.** Shrub to trees 2 – 30 m tall, D.B.H. 1 – 35 cm; young branches pubescent to tomentose to glabrous, old branches slightly tomentose to glabrous. Leaves distichous, simple, pinnately veined, margins entire, flat to slightly revolute. Petiole 2.5 – 35 mm long, 1 – 9 mm wide, pubescent to tomentose to glabrous. Leaf lamina 65 – 750 mm long, 20 – 250 mm wide, length:width ratio 2.1 – 6.2, elliptic to obovate to oblong, coriaceous, base acute to decurrent to rounded to subcordate, apex acute to acuminate, acumen 0.5 – 38 mm long; glabrous when young and old above, pubescent to glabrous when young, glabrous when old below; mid rib sunken above, raised below, glabrous above, pubescent to glabrous below; secondary veins 8 – 41 pairs, brochidodromous to weakly brochidodromous, impressed above, raised below; tertiary veins reticulate. Inflorescences borne on trunk, on branches or axillary, composed of 1 – 11 sessile to pedicellate flowers. Flower pedicel 0 – 65 mm long, 1 – 9 mm in diameter, pubescent to glabrous. Flowers actinomorphic, hermaphroditic, buds globose to ovoid, sessile to pedicellate, 2 – 22 mm high, 4 – 30 mm in diameter, pubescent. Bracts 1 to 6, upper bract 1 – 35 mm long, 1 – 50 mm wide, depressed ovate to ovate, generally adpressed, enclosing the bud or semi-clasping the pedicel, pubescent outside, glabrous to pubescent inside. Sepals 3, 3 – 55 mm long, 2.5 – 43 mm wide, valvate, imbricate or fused, pubescent outside, glabrous inside, green to brown. Outer petals 3, 10 – 70 mm long, 9 – 47 mm wide, length:width ratio 0.9 – 2.5, ovate to elliptic, pubescent outside, puberulent to glabrous inside, cream to brown to wine red outside, cream with dark red at base to wine red inside. Inner petals 3, 10 – 53 mm long, 5 – 38 mm wide, length:width ratio 0.9 – 2.4, elliptic to obovate, pubescent outside, puberulent to glabrous inside, cream to brown to wine red outside, cream with dark red at base to wine red inside. Stamen 200 – 3000, 1 – 5 mm long, 0.1 – 0.7 mm wide, anthers linear, connective truncate. Carpels 5 to 160, 1 – 7 mm long, 0.5 – 2.2 mm wide, pubescent, free; stigma 0 – 2 mm long, 0.5 – 2 mm wide, coiled, pubescent, generally covered with an exudate at anthesis. Fruiting pedicel 0 – 31 mm long, 2 – 8 mm in diameter, pubescent. Monocarps 1 to 80, 17 – 90 mm long, 4.5 – 32 mm wide, length:width ratio 1.3 – 11, generally cylindrical, pubescent to glabrous, green to orange to red to dark-blue black; sessile to stipitate; stipe 0 – 12 mm long, 1 – 10 mm wide, pubescent to glabrous. Seeds 1 – 18 per monocarp, uniseriate to biseriate, 3 to 29 mm long, 2 – 11 mm wide, ellipsoid to semicircular.

7.1.1. Key to *Uvariodendron* species

1. - Largest leaves with lamina  $\leq$  35 cm long.....2
- Largest leaves with lamina  $>$  35 cm long.....13
2. - Largest leaves with lamina  $<$  16 cm long.....3
- Largest leaves with lamina  $>$  16 cm long.....5
3. - Plant with strong bergamot scent (bark and crushed leaves), leaves stiff, between coriaceous and cartilaginous, apex acute to shortly acuminate; monocarps cylindrical and tomentose with regular tufts of higher hair density..... *Ud. mbagoi*
- Plant without bergamot scent, leaves coriaceous, apex attenuate; monocarps cylindrical and glabrous or ovoid and densely pubescent.....4
4. - Flower buds ca. 4 mm in diameter, covered by ca. 6 velutinous bracts 5 – 6 mm long; flowers with ca. 50 – 75 carpels; monocarps ovoid, densely pubescent, sessile . *Ud. dzomboense*
- Flower buds ca. 6 mm in diameter, covered by 2 – 5 velutinous bracts ca. 4 mm long; flowers with ca. 5 carpels; monocarps cylindrical, glabrous, with stipe ca. 12 mm long.....  
..... *Ud. mossambicense*
5. - Sepals fused at base over  $>$  10% of their length.....6
- Sepals free or fused at base over  $\leq$  10% of their length, connivent or imbricate.....9
6. - Plant with a strong lemon scent; leaves narrowly elliptic, base acute to cuneate, flower sessile with petals 15 – 25 mm long and 5 – 15 mm wide..... *Ud. angustifolium*
- Plants with no lemon scent; leaves elliptic to oblong to obovate, base acute to decurrent; flower pedicellate, or flower sessile with petals 20 – 36 mm long and 15 – 19 mm wide.....7
7. - Plant with bark reddish peeling off; flower bud globose to ovoid, sessile,  $>$  6 mm high; flower with sepals  $\geq$  10 mm long and wide.....  
..... *Ud. pycnophyllum*
- Plant with bark not reddish and not peeling off; flower bud globose, subsessile to pedicellate,  $\leq$  6 mm high; flower with sepals  $<$  8 mm long.....8
8. - Leaves 17 – 35 cm long; flowers with sepals 3 – 5 mm long, outer petals elliptic 15 – 25 mm long, carpels 20 to 40; fruits with 6 to 11 stipitate (stipe 5 – 12 mm) monocarps.....  
..... *Ud. occidentale*
- Leaves 15.9 – 18.8 cm long, flowers with sepals 5.5 – 7 mm long, outer petals broadly obovate 11 – 12 mm long, carpels ca. 7; fruits with 3 to 5 sessile monocarps..... *Ud. schmidtii*
9. - Leaves obovate, base decurrent, apex acuminate; flowers with bract ca. 10 mm long, ca. 30 carpels..... *Ud. pilosicarpum*
- Leaves elliptic to oblong to obovate, base acute to decurrent or acute to rounded, apex acute to attenuate; flowers with bract  $\leq$  6 mm long,  $<$  20 carpels .....10
10. - Plant with a strong aniseed smell; flowering pedicels 15 – 65 mm..... *Ud. anisatum*
- Plant with no aniseed smell; flowering pedicels  $\leq$  28 mm.....11
11. - Leaves with strong lemon scent when crushed, leaves  $\geq$  25 cm..... *Ud. citriodorum*
- Leaves with no lemon scent when crushed, leaves  $<$  22 cm.....12
12. - Leaves 14 – 22 cm long with a mid rib slightly raised above with a tiny central depression all along the length; flower with imbricate sepals 6 – 12 mm long, and elliptic petals 16 – 39 mm long with a slight transversal curvature..... *Ud. kimbozaense*
- Leaves 7 – 19 cm long with a mid rib slightly sunken above; flower with connivent sepals 3 – 6.5 mm long, ovate petals 10 – 20 mm long with a strong transversal curvature..... *Ud. kirkii*
13. - Young branches, petioles, and mid rib below the lamina covered with a brown tomentum, generally persisting on older branches..... *Ud. calophyllum*
- Young branches, petioles, and mid rib below the lamina pubescent to glabrous or covered with long soft hairs quickly falling off.....14
14. - Leaves with rounded to subcordate base..... *Ud. usambarensis*
- Leaves with acute to rounded base.....15

15. - Monocarps with l:w ratio  $\geq 5$ , very narrowly cylindrical, torulose to torose (i.e. very strongly constricted between the seeds); seeds  $< 10$  mm long.....*Ud. gorgonis*  
 - Monocarps with l:w ratio  $< 3.5$ , cylindrical, not constricted between the seeds; seeds  $> 10$  mm long.....16
16. - Young branches glabrous; flowering pedicel  $\geq 10$  mm, petals wine red outside and inside; monocarps sparsely pubescent to glabrous.....*Ud. connivens*  
 - Young branches pubescent to glabrous; flower pedicel  $\leq 15$  mm, petals wine red cream to light yellow outside, cream with dark red steak inside; monocarps pubescent to sparsely pubescent 17
17. - Bracts 3 – 8 mm long and 3 – 10 mm wide; sepals imbricate, 5 – 9 mm long and 5 – 10 mm wide .....*Ud. molundense*  
 - Bracts 8 – 35 mm long and 10 – 50 mm wide; sepals fused at base over 20 – 50% of their length, 11 – 55 mm long and 13 – 43 mm wide .....*Ud. fuscum* (18)
18. - Young branches sparsely pubescent to glabrous; sepals 11 – 23 mm long and 13 – 26 mm wide; carpels 20 to 70; fruiting pedicel ca. 5 mm long.....*Ud. fuscum* var. *fuscum*  
 - Young branches with long soft hairs producing a whitish appearance quickly falling off; sepals 20 – 55 mm long and 16 – 43 mm wide; carpels 50 to 160; fruiting pedicel  $\geq 9$  mm long. .  
 .....19
19. - Flowering pedicels 0 – 7.5 mm long, sepals 20 – 30 mm long and 16 – 26 mm wide, petals 21 – 40 mm long and 17 – 29 mm wide, carpels 50 to 100.....*Ud. fuscum* var. *giganteum*  
 - Flowering pedicels 10 – 15 mm long, sepals 30 – 55 mm long and 30 – 43 mm wide, petals 50 – 70 mm long and 36 – 47 mm wide, carpels 150 to 160.....*Ud. fuscum* var. *magnificum*

### 7.1.2. Species descriptions

*Uvariadendron angustifolium* (Engl. & Diels) R.E.Fr., Acta Horti Berg. x. 58 (1930)

*Uvaria angustifolia* Engl. & Diels, Notizbl. Königl. Bot. Gart. Berlin 2: 295 (1899)

*Uva angustifolia* Kuntze, Deutsche Bot. Monatschr. xxi. 173 (1903)

**TYPE.** CAMEROON – South-West Region • A. Staudt 742a (holotype: B), Johann - Albrechtshöhe; 4°10'N, 9°12'E; alt. 400 m; 20 Mar. 1896.

**Description.** Shrub to tree 3 – 12 m tall, D.B.H. unknown; young branches sparsely pubescent to glabrous, old branches glabrous; plant with strong aromatic smell. Leaves distichous, simple, pinnately veined, with strong lemon smell when crushed, margins entire, flat. Petiole 3 – 7.5 mm long, 1 – 2 mm wide, pubescent to glabrous. Leaf lamina 100 – 199 mm long, 30 – 58 mm wide, length:width ratio 3 – 4, narrowly elliptic, coriaceous, base acute to cuneate, apex acute to broadly acuminate, acumen 11 – 14 mm long; glabrous when young and old above, pubescent to glabrous when young, pubescent at base to glabrous when old below; mid rib slightly sunken above, raised below, glabrous above, pubescent to glabrous below; secondary veins 8 – 14 pairs, weakly brochidodromous, slightly impressed above, raised below; tertiary veins reticulate. Inflorescences borne on trunk and branches, composed of 1 (sub)sessile flower. Flower pedicel 0 – 6 mm long, 2 – 3 mm in diameter, velutinous. Flowers actinomorphic, hermaphroditic, buds globose, sessile to shortly pedicellate, 5 – 8 mm high, 6 – 8 mm in diameter, sericeous.

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Bracts 1 to 6, upper bract 6 – 11 mm long, 9 – 15 mm wide, ovate, appressed, enclosing the bud, sericeous outside, glabrous inside. Sepals 3, 9 – 13 mm long, 9 – 13 mm wide, fused at base, slightly imbricate at mid-length, sericeous outside, glabrous inside, color unknown. Outer petals 3, 15 – 25 mm long, 9 – 15 mm wide, length:width ratio 1.13 – 1.78, elliptic to oblong, velutinous outside, glabrous inside, yellowish brown outside, crimson with cream margins inside. Inner petals 3, 15 – 22 mm long, 5 – 10 mm wide, length:width ratio 1.9 – 3, obovate, velutinous outside, glabrous inside, yellowish brown outside, crimson with cream margins inside. Stamen more than 200, 3 – 3.5 mm long, 0.1 – 0.5 mm wide, anthers linear, connective truncate. Carpels 7 to 30, 3 – 4.5 mm long, 1 – 1.5 mm wide, pubescent, free; stigma 1 – 2 mm long, 0.8 – 1.5 mm wide, coiled, pubescent, covered with an exudate at anthesis. Fruiting pedicel ca. 5 mm long, 3.5 mm in diameter, pubescent. Monocarps 2 to 10, 23 – 40 mm long, 17 – 30 mm wide, length:width ratio ca 1.3, ellipsoid, smooth, sparsely pubescent to glabrous, yellow, with strong lemon smell; shortly stipitate, stipe 1 – 3.5 mm long, 1 – 2.5 mm wide, pubescent. Seeds 9 to 18 per monocarp, biseriate, 21 to 28 mm long, ca. 10 mm wide, semicircular.

**Distribution.** Cameroon, Ghana, Ivory Coast, Nigeria.

**Notes.** This species can be easily distinguished from the other *Uvariadendron* species by its narrowly elliptic leaves. It also emits a strong citrus scent, a characteristic shared with other Annonaceae species: *Uvariadendron citriodorum* Le Thomas and *Uvariopsis citrata* Couvreur & Niangadouma.

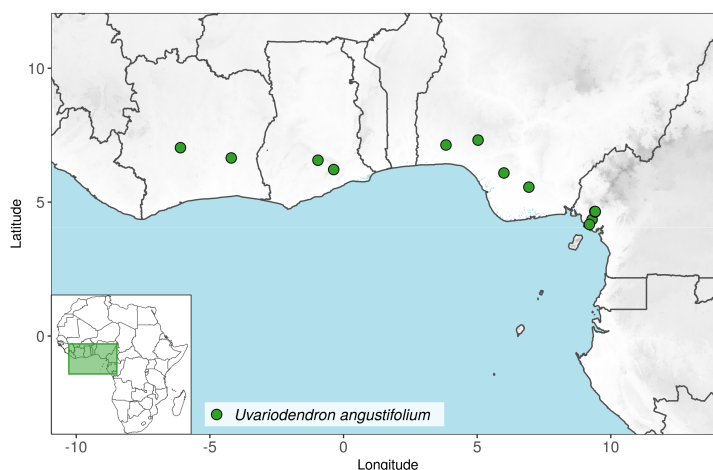


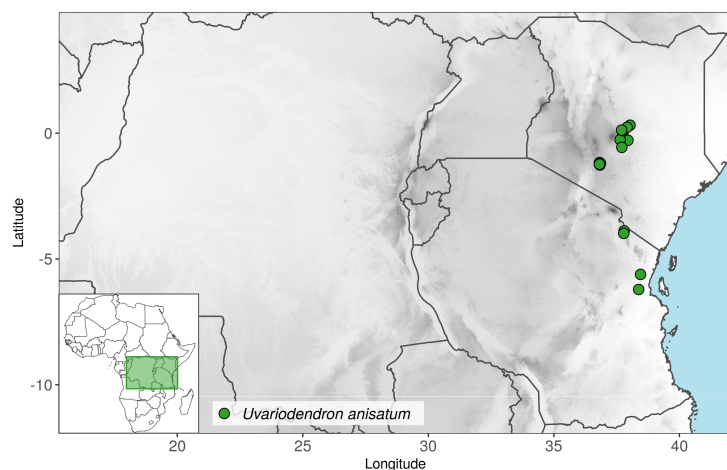
Figure 12: Distribution of *Uvariadendron angustifolium*

**Specimens examined.** CAMEROON – Central Region • R.W.J. Keay FHI 37524 (FHI, K), between Bafia and Likoko; 4°21'N, 9°18'E; 05 Feb. 1958 – South-West Region • D.W. Thomas 6087 (MO, YA); Meme, Vicinity of Lake Barombi, Kumba; 4°39'N, 9°24'E; alt. 300 m; Apr. 1986 • D.W. Thomas 7018 (YA), Cocoa farms along the road between Konye and Bakole; 4°39'N, 9°25'E; alt. 300 m; 25 May. 1987 – Unknown major area • A. Staudt 642 (BM, G, K), Kumba; 4°38'N, 9°25'E; 1896. GHANA – Ashanti Region • C. Vigne 1610 (K, P), Pra River, ashanti; 6°33'54.36"N, 0°57'21.6"E; alt. 152 m; Feb. 1929 – Western Region • N.K. Lovi 3964 (K, P), New Tafo E.P; 6°13'N, 0°22'E; 03 Dec. 1954. IVORY COAST – Bouaflé • C.C.H. Jongkind 4368 (IAGB, MO, WAG, WAG), Parc National de la Marahoue; 7°02'N, 6°06'W; alt. 270 m; 13 Feb. 1998 – Daoukro • A.J.B. Chevalier s.n (P), Moréno: environs du poste de Bangouanou; 6°39'N, 4°12'W; 26 Nov. 1909. NIGERIA – Edo State • B.O. Daramola 94/ 337 (K, MO), Iyekorionwon, Edo State, about 35 kilometers from Uyo (Ugo ?); 6°05'19.05"N, 6°00'04.46"E; 09 Jan. 1994 – Ondo State • A.P.D. Jones FHI 3480 (K); Owo District, Owo forest reserve about 4 miles North of Igbatoro crossing; 5°33'36.36"N, 6°56'06"E; 19 Apr. 1943 • Anakwense, F FHI 19702 (K); Akure, Akure Forest Reserve; 7°19'N, 5°02'E; 11 Dec. 1950 – Oyo State • D. Gledhill 817 (K); Ibadan District, Gambari Forest Reserve; 7°08'N, 3°50'E; 02 Feb. 1968.



*Uvariodendron anisatum* Verdc., Kew Bull. 10(4):596 (1956)

**TYPE.** KENYA – Nairobi • B. Verdcourt 526 (holotype: EA; isotypes: K, PRE); Nairobi District, in Karura Forest and Thika Gorge; 1°14'S, 36°49'E; 24 Jun. 1951.



**Description.** Shrub to tree 3.5 – 15 (22) m tall, D.B.H. up to 10 cm; young branches sparsely pubescent to glabrous, old branches glabrous; plant with aniseed smell. Leaves distichous, simple, pinnately veined, reddish pink when young, dark green when old, margins entire, flat. Petiole 3 – 9 mm long, 1.5 – 4 mm wide, sparsely pubescent to glabrous. Leaf lamina 80 – 313 mm long, 45

Figure 13: Distribution of *Uvariodendron anisatum*

– 187 mm wide, length:width ratio 2.3 – 3.1, elliptic to obovate, coriaceous, base acute to decurrent, apex acute to attenuate, glabrous when young and old above, sparsely pubescent to glabrate when young, glabrous when old below; mid rib sunken above, raised below, glabrous above, sparsely pubescent to glabrous below; secondary veins 12 – 21 pairs, weakly brochidodromous, impressed above, raised below; tertiary veins reticulate. Inflorescences clustered on the trunk or borne on branches, composed of 1 – 3 flowers. Flower pedicel 15 – 65 mm long, 1 – 2 mm in diameter, pubescent. Flowers actinomorphic, hermaphroditic, buds globose, pedicellate, 3.5 – 6 mm high, 4.5 – 6 mm in diameter, sericeous. Bracts 1 to 2 at base and 1 towards the upper half of the pedicel, upper bract 2 – 4.5 mm long, 3 – 8 mm wide, clasping the pedicel, velutinous outside, glabrous inside. Sepals 3, 3.5 – 6 mm long, 4 – 8 mm wide, valvate to fused at base over 10 % of their length, velutinous outside, glabrous inside, color unknown. Outer petals 3, 10 – 23 mm long, 9 – 16 mm wide, length:width ratio 1 – 1.6, broadly ovate to ovate, velutinous outside, glabrous inside, cream outside, cream inside. Inner petals 3, 12.5 – 15 mm long, 5 – 9 mm wide, length:width ratio 1.5 – 2, obovate, shortly velutinous outside, glabrous inside, cream outside, cream inside. Stamen more than 400, 1.5 – 2.5 mm long, 0.1 – 0.5 mm wide, anthers linear, connective truncate. Carpels 7 to 12, 2 – 5 mm long, 1 – 1.5 mm wide, pubescent, free; stigma 1 – 2 mm long, 1 – 1.5 mm wide, coiled, pubescent. Fruiting pedicel 21 – 59 mm long, 2 – 3 mm in diameter, sparsely pubescent to glabrous. Monocarps 3 to 14, 38 – 70 mm long, 13 – 20 mm wide, length:width ratio 2.3 – 3.5, cylindrical, longitudinally ridged, slightly constricted between the seeds, slightly acuminate, sparsely pubescent, dark olive green to dark-blue black; sessile to shortly stipitate,

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stipe 0 – 2 mm long, 3 – 4.5 mm wide, sparsely pubescent. Seeds 8 – 18 per monocarp, biseriata, 10 to 12 mm long, 5 – 8 mm wide, ellipsoid to semicircular.

**Distribution.** Kenya and Tanzania.

**Notes.** This species is characterized by a strong aniseed smell, a character unique in the Annonaceae family to my knowledge. Apart from the smell, it closely resembles *Uvariadendron kirkii* and can hardly be differentiated on dry sterile material. In flowers, it can be differentiated from *Ud. kirkii* by its flower pedicel generally longer (15 – 65 mm, vs. 5 – 28 mm), its relatively flat petals with a slight transversal curvature (vs. “boat-shaped” petals, i.e. with a strong transversal curvature). Note that the petals curvature is not easy to rely on dry specimen. In fruits, it can be differentiated with a greater fruit pedicel than *Ud. kirkii* (21 – 59 mm long, vs. 7 – 22 mm long). Verdcourt also used the monocarps to differentiate the 2 species, the monocarps of *Ud. anisatum* being dark blue and with a slight longitudinal ridge, and the monocarps of *Ud. kirkii* being dull-orange and without any pseudosuture (Verdcourt, 1969). However, these 2 characters are no longer valid for a clear differentiation of the 2 species as the specimen Robertson MDE 293, which is *Ud. kirkii* (no aniseed smell reported, flower pedicel length of ca. 11 mm), has dark blue grey fruits, and several specimens of *Ud. kirkii* (e.g. Drummond 3983, Gilbert 4967, Greenway 2681) present a slight longitudinal ridge.

**Specimens examined.** KENYA – Central • E. Battiscombe 1285 (EA, K); Kiambu District, Kiambu Forest; 1°10'S, 36°49'E; alt. 1700 m; 17 Jun. 1924 • Moon, J.L. 811 (K); Kiambu District, Kyambu; 1°11'48.48"S, 36°51'32.76"E; alt. 1737 m; 29 Jul. 1913 – Eastern • H.J. Beentje 4089 (EA); Meru, Kijegge Hill; 0°17'N, 37°57'E; alt. 1400 m; 08 Mar. 1989 • I. Malombe 1368 (EA), Ngaia Forest, Kiegoi village, NE border; 0°14'N, 37°55'E; alt. 1170 m; 22 May. 2008 • M.A. Brunt 1546 (K), Embu Meru road; 0°15'43.26"N, 37°38'23.43"E; 16 Feb. 1964 • Parnell, L.E. EA 13340 (K); Meru, Lower Imenti Foest Reserve; 0°07'14.88"N, 37°41'52.08"E; 24 Aug. 1965 • R.B. Faden 70/ 120 (EA, K); Meru District, Lower Imenti Forest, 6 miles from Meru along Meru - Mikinduri Road; 0°06'N, 37°45'E; alt. 1190 m; 01 Mar. 1970 • S.A.L. Smith 287 (K); Embu District, Kiangombe, northern slopes; 0°33'52.56"N, 37°42'27.72"E; alt. 1550 m; 30 Nov. 2000 • W.R.Q. Luke 7123 (EA); Meru, Ngaia Forest, camp 142; 0°19'N, 38°02'E; alt. 1080 m; 22 Nov. 2000 – K4 Central • H.J. Beentje 1830 (EA, WAG, WAG), Nairobi, E. Karura forest near Kiambu R; 1°14'30"S, 36°49'30"E; alt. 1600 m; 13 Jan. 1985 • R.B. Faden 74/ 886 (K, WAG), Meru District, Lower Imenti Forest, on Meru-Mikinduri Road; 0°04'N, 37°45'E; alt. 1190 m; 26 Jun. 1974 – Nairobi • B. Verdcourt 3689 (K); Nairobi District, Karura Forest, by Ruaraka R. to W. of main Thika highway; 1°14'S, 36°49'E; 21 Jul. 1963 • B. Verdcourt 406 (B, K, K); Nairobi District, Thika Road House; 1°15'59.57"S, 36°50'04.08"E; alt. 1676 m; 24 Dec. 1950 • B. Verdcourt 674 (K); Nairobi District, Karura Forest; 1°14'S, 36°49'E; 29 Jun. 1952 • E. Polhill 324 (K); Nairobi District, Karura Forest; 1°14'S, 36°49'E; 10 Jan. 1961 • Someren, V.G.L. van 95 (G, K); Nairobi District, Karura Forest; 1°14'S, 36°49'E; 13 Mar. 1940. TANZANIA – Kilimanjaro • K.B. Vollesen 96/ 15 (K), Mkomazi Game Reserve, Ibaya Hill; 3°59'S, 37°47'E; alt. 1350 m; 03 Jun. 1996 • R.A. Abdallah 96/ 86 (K), Mkomazi National Park, Mkomazi Game Reserve, Maji Kununua Ridge; 3°53'S, 37°48'E; alt. 1500 m; 07 Jun. 1996 – Pwani • Sacleux, R.P. 212 (P), Mandéra (Zanguebar); 6°12'51.22"S, 38°22'37.73"E; Jan. 1889 – Tanga • R.C. Wingfield 2880 (K), Msangasi Forest Reserve, 50km S of Korogwe; 5°36'55.14"S, 38°27'06.26"E; alt. 300 m; 31 Mar. 1975.

*Uvariadendron calophyllum* R.E.Fr., Acta Horti Berg. x. 63 (1930)

*Uvaria gigantea* Engl., Notizbl. Königl. Bot. Gart. Berlin 2: 292. (1899) (pro parte: Zenker 1738)

**TYPE.** CAMEROON – South Region • G.A. Zenker 2344 (holotype: B; isotypes: BM, G, K, K, L, M, P, WAG), Bipindi; 3°05'N, 10°25'E; 1901.

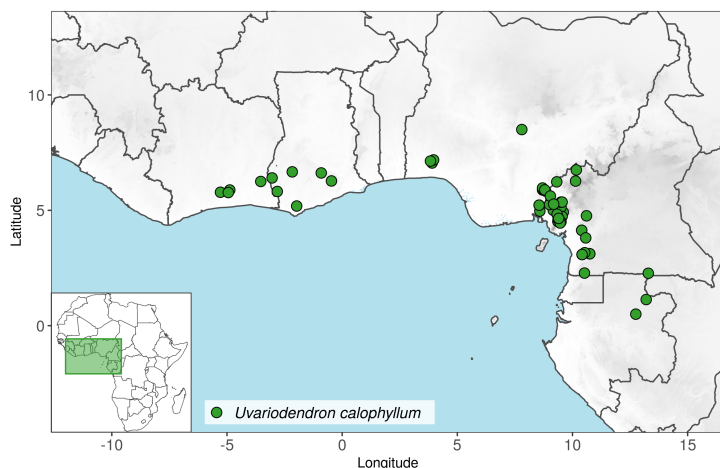


Figure 14: Distribution of *Uvariadendron calophyllum*

**Description.** Tree 2 – 20 m tall, D.B.H. 1 – 32.1 cm; young branches tomentose, old branches slightly tomentose to glabrous. Leaves distichous, simple, pinnately veined, reddish when young, dark green when old, margins entire, flat. Petiole 4 – 25 mm long, 2 – 9 mm wide, tomentose. Leaf lamina 258 – 765 mm long, 61 – 248 mm wide, length:width ratio 2.2 –

4.9, obovate, coriaceous, base rounded to slightly truncate, apex acuminate, acumen 6 – 32 mm long; glabrous when young and old above, pubescent to glabrous when young and old below; mid rib sunken above, raised below, glabrous above, tomentose below; secondary veins 20 – 41 pairs, brochidodromous to weakly brochidodromous, impressed above, raised below; tertiary veins reticulate. Inflorescences borne on trunk and branches, composed of 2 – 3 (sub)sessile flowers. Flower pedicel 0 – 11 mm long, 4 – 9 mm in diameter, tomentose. Flowers actinomorphic, hermaphroditic, buds globose, sessile, 7 – 17 mm high, 7 – 30 mm in diameter, tomentose. Bracts 1 to 6, upper bract 10 – 23 mm long, 10 – 40 mm wide, ovate, appressed, enclosing the bud, tomentose outside, glabrous inside. Sepals 3, 10 – 27 mm long, 10 – 26 mm wide, imbricate to fused at base, tomentulose outside, glabrous inside, dark brown outside, reddish inside. Outer petals 3, 15 – 46 mm long, 10 – 33 mm wide, length:width ratio 0.9 – 1.5, broadly elliptic to elliptic, tomentulose outside, glabrous inside, cream outside, cream with dark red at base inside. Inner petals 3, 14 – 41 mm long, 11 – 32 mm wide, length:width ratio 1.2 – 1.9, obovate, shortly tomentulose outside, glabrous inside, cream outside, dark red with cream margins inside. Stamen more than 3000, 3.5 – 4.9 mm long, 0.1 – 0.5 mm wide, anthers linear, connective truncate. Carpels 35 to ca. 150, 2 – 5 mm long, 0.5 – 2 mm wide, pubescent, free; stigma 1 – 2 mm long, 0.5 – 2 mm wide, coiled, velutinous, covered with an exudate at anthesis. Fruiting pedicel 1 – 7 mm long, 4 – 7 mm in diameter, densely pubescent. Monocarps 3 to 35, 27 – 55 mm long, 9 – 25 mm wide, length:width ratio 1.8 – 3.7, ellipsoid to obovoid, tomentose, brown; sessile to shortly stipitate, stipe 0 –

TAXONOMIC REVISION OF UVARIODENDRON AND UVARIOPSIS

10 mm long, 1.5 – 3 mm wide, tomentose. Seeds 7 – 13 per monocarp, biseriate, ca. 13 mm long, 8 – 9 mm wide, semicircular.

**Distribution.** Cameroon, Gabon, Ghana, Ivory Coast, Nigeria

**Notes.** This species is close to *Uvariadendron connivens* and *Ud. fuscum* var. *giganteum* by having great obovate leaves (more than 25 cm long). However it can easily be distinguished from these three other species as it presents a tomentum of short hairs particularly dense on the young parts (branches, petioles and lower midrib), producing a brown appearance with whitish reflections. The flower buds and outer petals are also covered outside with a similar brown and dense tomentum. The older parts of the plant are generally glabrous but can also present remnants of the tomentum.

**Specimens examined.** CAMEROON – Central Region • J.N. Asonganyi 421 (P, YA), Ndikiniméki, at Sonossi 26km W. of Ndikinimeki. Map 1/200 000; 4°45'44.24"N, 10°36'29.26"E; 29 Mar. 1982 – Littoral • A.J.M. Leeuwenberg 5282 (BR, K, MO, P, PRE, WAG, WAG), 8 km W of Masok; 4°08'N, 10°24'E; alt. 400 m; 31 Mar. 1965 • A.J.M. Leeuwenberg 5282 a (K, P, WAG), 8 km W. of Masok; 4°08'N, 10°24'E; alt. 400 m; 31 Mar. 1965 • R.G. Letouzey 12352 (P, YA), colline entre Tchirikoy et Sokelle II(30km NW Eseka) - feuille IGN 1/200 000 EDEA; 3°48'18.03"N, 10°34'32.35"E; 14 Dec. 1973 – North-West Region • E.U. Ujor FHI 29281 (FHI, K); Mentchum, Nkom-Wum, Bamenda Prov., Wum Distr., Nkom - Wum F.R. on German old road leading to Timber Camp by the left; 6°16'N, 10°08'E; 03 Jul. 1951 • R.G. Letouzey 14020 (P, WAG, YA), Piste Baji-Tumbo, entre Baji et rivière Chonogbonbon, 55 km NNE Wum; 6°45'N, 10°10'E; 12 Jul. 1975 – South Region • G.A. Zenker 1738 (B, BM, G, K, M, P, P, WAG), Bipindi; 3°05'N, 10°25'E; 1898 • G.A. Zenker s.n (P), Bipinde, Bipindi; 3°05'N, 10°25'E; Apr. 1903 • M.P.E. Parren 223 (KRIBI, WAG, WAG), About 7 km NE of Ebom. Plot 13, subplot 84, tree 6, coordinates: X = 7, Y = 3 m; 3°07'N, 10°45'E; alt. 500 m; Aug. 1996 • M.P.E. Parren 68 (KRIBI, WAG, WAG), About 7 km NE of Ebom. Plot 4, subplot 53, tree 9, coordinates: X = 7.5, Y = 8.5 m; 3°07'N, 10°45'E; alt. 500 m; Aug. 1996 • R.G. Letouzey 15272 (P, YA), Piste Meyo Ntem-Evouzok, 75 Km W Ambam, entre 1er et 3e bras du Ntem; 2°16'48"N, 10°31'12"E; 28 Nov. 1979 • T.L.P. Couvreur 1157 (K, MPU, P, WAG, YA), on road Lolodorf-Bipindi, about half way, near Mbiguiligui village (Mbikiliki); 3°09'41.51"N, 10°31'52.18"E; alt. 250 m; 26 Feb. 2018 • T.L.P. Couvreur 486 (YA), 15 km east from Lélé village; 2°16'17.2"N, 13°17'30.35"E; alt. 578 m; 09 Sep. 2013 – South-West Region • A. Binuyo FHI 35564 (FHI, K, WAG), Kumba Distr. Along the path from Pete to Bopo at the right handside of the road in Southern Bakundu Forest Reserve; 4°31'N, 9°22'E; 23 Feb. 1956 • A.H. Gentry 62407 (MO), Banyong, Batanga area, between Awong and Banyu, ca 15 km W of Manyemen. TRANSECT 2; 5°00'N, 9°10'E; alt. 420 m; 02 May. 1988 • B. Sonké 5610 (MO); Meme, Nguti, Sanctuaire Mbanyang Mbo; 5°21'24"N, 9°32'57"E; alt. 239 m; 14 Apr. 2011 • C.F.A. Onochie FHI 30860 (FHI, K), S.Bakundu, S. Bakundu F.R., between Bombe Rest House and Mbalange; 4°27'N, 9°28'E; 19 Mar. 1953 • D.W. Thomas 3322 (K, MO, P, YA), North-eastern corner of Korup National Park; near Baro village; 5°16'N, 9°11'E; alt. 200 m; 24 Mar. 1984 • D.W. Thomas 4549 (MO, YA), Takamanda Forest Reserve; 6°14'N, 9°19'E; alt. 170 m; 21 Mar. 1985 • D.W. Thomas 5965 (K, MO, WAG, WAG, YA), 30 km W of Kumba on Mbonge Road; 4°31'N, 9°22'E; alt. 50 m; 26 Mar. 1986 • D.W. Thomas 6090 (P, YA); Meme, from the vicinity of Lake Barombi, Kumba; 4°39'N, 9°24'E; alt. 300 m; Apr. 1986 • D.W. Thomas 7499 (MO, P, WAG, YA); Ndian, Between Baro and Ikenge villages, along foot path, in the Korup National Park; 5°15'N, 9°00'E; alt. 250 m; 01 Apr. 1988 • G.K. Gottsberger 210307/ 12 (ULM, WAG), c. 20 m from Banyang Mbo Research Station; 5°08'N, 9°30'E; 21 Mar. 2007 • J. Dundas FHI 13898 (K), Southern Bakundu Forest Reserve; 4°30'N, 9°30'E; 19 Feb. 1946 • J. Nemba 64 (K, MO, P, WAG, YA, YA), Bolo Forest, 5 kms W of Kumba - Mamfe road near Konye; 4°55'N, 9°36'E; alt. 300 m; 25 Mar. 1986 • J. Olorunfemi FHI 30561 (FHI, K), Mungo River F.R., Kumba Distr.: Mumbo - Southern Bakossi; 4°50'N, 9°20'E; 09 May. 1951 • M.R. Cheek 9337 (K, YA), Mungo River F.R., Mungo river forest reserve. c. 1Km East of bridge, Chained road to S; 4°44'N, 9°33'E; alt. 200 m; 24 Oct. 1998 • R.G. Letouzey 13673 (P, YA), entre Babong et Okurikang, 35km WSW. Mamfe (feuille IGN 1/200 000 Mamfe); 5°37'02.16"N, 9°02'22.7"E; 29 May. 1994 • T.L.P. Couvreur 1013 (MPU, WAG, YA), Bayang Mbo Wildlife Sanctuary, after Mbu river; 5°21'19.19"N, 9°30'01.69"E; alt. 242 m; 26 Mar. 2016 • T.L.P. Couvreur 980 (WAG, YA), on top of hill, near Small Ekombe village, 3 km after Kumba on road to Ekondo Titi town; 4°37'22.48"N, 9°22'37.12"E; alt. 615 m; 13 Jan. 2016 • T.L.P. Couvreur 999 (MPU, WAG, YA), Bayang Mbo Wildlife Sanctuary, after Mbu river; 5°21'04.06"N, 9°30'01.78"E; alt. 251 m;

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25 Mar. 2016. GABON – Ogooué-Ivindo • J. Florence 1005 (P), Station d'Ipassa, 10km S de Makokou; 0°30'N, 12°45'E; alt. 500 m; 17 Apr. 1978 • N. Hallé; A. Le Thomas 548 (P), Bélinga, mines de fer; 1°08'N, 13°12'E; alt. 700 m; 16 Aug. 1966. GHANA – Ashanti Region • C. Vigne 1611 (K, P), Kwahu Prasu; 6°37'10.2"N, 0°54'27.72"E; Feb. 1929 • H. Abbin GC 43343 (K), Tano Ofin Forest Reserve, Tano Ofni F.R.; 6°40'N, 2°10'W; 16 Aug. 1972 – Eastern Region • F.R. Irvine 3016 (K), Bunsu; 6°16'21.42"N, 0°27'52.93"E; May. 1938 – Western Region • A.A. Enti FE- 2169 (B), Neung Forest Reserve, Takoradi-Tarkwa Road; 5°11'07.08"N, 1°58'23.52"W; May. 1982 • A.A. Enti FH 6705 (K, P, WAG, WAG), Enchi Distr., Enchi - Nyankamam; 5°49'N, 2°49'W; May. 1957 • M.C. Merello 1385 (MO), Bia National Park, Bia National Forest and Production Reserve. Secondary logging roads west from MIM Timber Company Camp; 6°24'15"N, 3°02'30"W; alt. 140 m; 04 Mar. 1996. IVORY COAST – Adzopé • L. Aké Assi 11501 (G), Forêt d'Abongoua; 6°15'N, 3°32'W; 19 Mar. 1971 – Divo • C. Chatelain 679 (G), Forêt de l'IRCC de Divo; 5°47'N, 5°17'W; 19 Dec. 1990 • L. Aké Assi 8469 (G), Forêt de Mopri; 5°46'10.5"N, 4°56'34.87"W; 22 Jan. 1966 – Tiassalé • L. Aké Assi 4290 (G, P), Forêt d'Amitioro; 5°52'50.13"N, 4°52'46.45"W; 07 May. 1957. NIGERIA – Cross River State • B.O. Daramola 641 (MO), Ikom Forest Reserve; 5°58'N, 8°42'E; 06 May. 1995 • J.O. Ariwaodo 447 (FHI, WAG); Ikom District, Efraya; 5°53'N, 8°42'E; 25 Mar. 1977 • M.G. Latilo FHI 43924 (K); Ikom District, Cross River North Forest Res., between miles 156 & 157 on Ikom-Namfe road; 5°53'08.13"N, 8°47'51.41"E; 10 May. 1961 • P.A. Talbot 123 (K), Oban; 5°13'23.28"N, 8°33'06.9"E; 1911 • P.A. Talbot s.n (BM); Calabar, Oban; 5°13'23.28"N, 8°33'06.9"E; 1912 • P.P.C. van Meer 1490 (WAG), Ekinta River Forest Reserve, Northern part. Near and between pillar 18 and 19; 4°58'N, 8°35'E; 26 Apr. 1971 • P.P.C. van Meer 1664 (WAG); Ikom District, Cross River North Forest Reserve. Compt 1 and 2. 15 km SE of Ikom; 5°52'N, 8°46'E; 18 May. 1971 • P.P.C. van Meer 1736 (WAG); Ikom District, Cross River North Forest Reserve. Compt 1 and 2. 15 km SE of Ikom; 5°52'N, 8°46'E; 20 May. 1971 • R.W.J. Keay FHI 28683 (K, P); Ikom District, Cross River North Forest Res.; 5°50'N, 8°50'E; 19 Jan. 1951 – Nassarawa State • A.P.D. Jones FHI 16965 (P), Khaya HF nr. Onda enclave; 8°30'N, 7°48'E; 18 Feb. 1946 – Oyo State • C.F.A. Onochie FHI 31539 (K); Ibadan District, c. 14 miles south of Ibadan on the Ijebu-Ode road; 7°11'00.66"N, 3°58'13.92"E; 19 Mar. 1958 • D.P. Stanfield FHI 44949 (K, MO); Ibadan District, Gambari Forest Reserve; 7°07'59.88"N, 3°49'59.88"E; alt. 80 m; 11 Mar. 1964 • R.W.J. Keay FHI 22812 (K); Ibadan District, Ibadan Forest Reserve, c. 22 miles south of Ibadan. School Enumeration area 1948; 7°03'02.43"N, 3°54'20.56"E; 22 Apr. 1948.

### *Uvariadendron citriodorum* Dagallier, **nom. nov.**

*Uvariadendron molundense* var. *citrata* Le Thomas, Fl. Gabon No. 16, 283 (1969)

**TYPE.** GABON – Ogooué-Ivindo • N. Hallé; A. Le Thomas 525 (sheets here designated, holotype: P (P00363400), isotypes: K, MO, P (P00363398), WAG), Bélinga, mines de fer, sommet de Belvédère; 1°08'N, 13°12'E; alt. 800 m; 15 Aug. 1966.

**Description.** Tree to shrub 4 – 5 m tall, D.B.H. unknown; young branches glabrous, old branches glabrous. Leaves distichous, simple, pinnately veined, with strong lemon smell when crushed, margins entire, flat. Petiole 6 – 10 mm long, 1.5 – 3.5 mm wide, sparsely pubescent to glabrous. Leaf lamina (183) 250 – 337 mm long, 72 – 97 mm wide, length:width ratio 2.3 – 4.2, elliptic to oblong, coriaceous, base acute to rounded (sometimes minutely decurrent at the very base, and decurrent on young leaves), apex attenuate, glabrous when young and old above, glabrous when young and old below; mid rib sunken above, raised below, glabrous above, sparsely pubescent to glabrous below; secondary veins 12 – 18 pairs, weakly brochidodromous, impressed above, raised below; tertiary veins reticulate. Inflorescences borne on branches or axillary, composed of 1 sessile flower. Flowers actinomorphic, hermaphroditic, buds globose, sessile, 5 – 6 mm high, 5 – 7 mm in diameter, velutinous. Mature flower unknown, measures taken from flower buds or fruits. Bracts 1 to 4, upper bract ca. 5 mm long, ca. 7

## TAXONOMIC REVISION OF UVARIODENDRON AND UVARIOPSIS

mm wide, broadly ovate, semi clasping the pedicel, velutinous outside, glabrous inside. Sepals 3, ca. 7 mm long, ca. 6 mm wide (measures taken from bud), imbricate, velutinous outside, glabrous inside, color unknown. Outer petals 3, length, shape, indumentum and color unknown. Inner petals 3, length, shape, indumentum and color unknown. Stamen number unknown, ca. 1 mm long, ca. 0.2 mm wide, anthers linear, connective truncate. Carpels 10 to 20, ca. 2 mm long, ca. 0.4 mm wide, sparsely pubescent, free; stigma 0.5 mm long, 0.5 mm wide, pubescent. Fruiting pedicel 10 – 12 mm long, 2 – 5 mm in diameter, pubescent to glabrous. Monocarps 5 to 20, 25 – 40 mm long, 9 – 20 mm wide, length:width ratio 1.9 – 2.9, cylindrical, oblong, straight, truncate or rounded at apex, pubescent to glabrate, pale greyish green to red; sessile to shortly stipitate, stipe 0 – 5 mm long, 3 – 5 mm wide, pubescent to glabrous. Seeds 9 – 14 per monocarp, biseriate, 13 to 15 mm long, ca. 11 mm wide, semi-circular.

**Distribution.** Known from one locality in Gabon: Bélinga, mines de fer, and one locality in Republic of the Congo: Les Saras.

**Etymology.** The specific epithet refers to the strong lemon smell of the plant. The epithet ‘*citrata*’ would prevail as it is the one given by Le Thomas for the variety. However, this specific epithet is already taken by *Uvariopsis citrata*

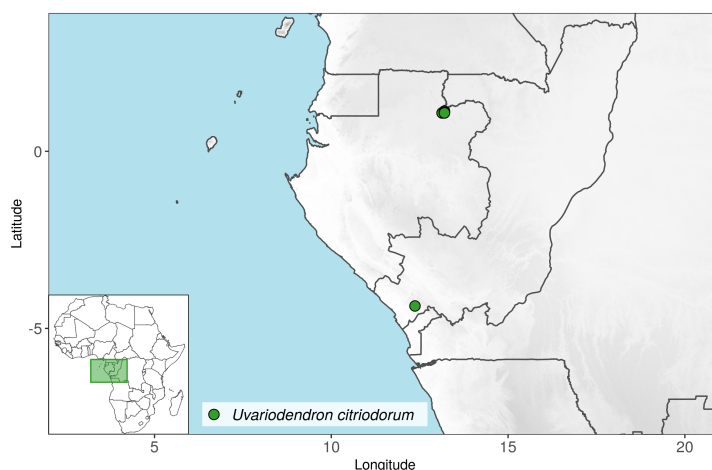


Figure 15: Distribution of *Uvariodendron citriodorum*

Couvreur & Niangadouma, from the genus *Uvariopsis*, which is closely related to *Uvariodendron*. Following the recommendation 23.A.3.h from the code of nomenclature (“Avoid [the specific epithets] that have been used before in any closely allied genus”), we choose the specific epithet ‘*citriodorum*’.

**Notes.** This species differs from the other species, and particularly from *Ud. molundense*, in having leaves emitting a strong lemon scent when crushed. Apart for this character, this species is morphologically very similar to *Ud. molundense*. However, as *Ud. citriodorum* and *Ud. molundense* don’t form a monophyletic group together (see Chapter 3), they can’t be considered the same species following the phylogenetic species concept.

**Specimens examined.** GABON – Ogooué-Ivindo • M.S.M. Sosef 2219 (BR, K, LBV, MO, WAG), Bélinga, Mines de Fer, 4 km on the road to Mvadi; 1°05’N, 13°12’E; alt. 900 m; 05 Nov. 2005 • N. Hallé 2896 (P), Bélinga; 1°05’N, 13°08’E; alt. 900 m; 29 Oct. 1964 • N. Hallé 3082 (P), Bélinga; 1°05’N, 13°08’E; alt. 950 m; 07 Nov. 1964 • N. Hallé; A. Le Thomas 13 (P), Bélinga, mines de fer, route du Belvédère; 1°05’N, 13°12’E; alt. 950 m; 08 Jul. 1966 • N. Hallé; A. Le Thomas 152 (P), Bélinga, mines de fer, route du pt. B3; 1°06’N, 13°12’E; 25 Jul. 1966 • N. Hallé; A. Le Thomas 47 (K, MO, P), Bélinga,

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mines de fer; 1°08'N, 13°12'E; alt. 950 m; 16 Jul. 1966. REPUBLIC OF THE CONGO – Kouilou • H. de Foresta 1759 (P), Les Saras, piste Cofibois, environs de la plantation Coobama de 1987; 4°22'S, 12°22'E; 25 Nov. 1988.

*Uvariadendron connivens* (Benth.) R.E.Fr., Acta Horti Berg. x. 55 (1930)

*Uvaria connivens* Benth., Trans. Linn. Soc. London 23(3): 465 (1862)

*Uvaria winkleri* Diels, Bot. Jahrb. Syst. 38(3): 240 (1907)

*Uvaria megalantha* Diels, Bot. Jahrb. Syst. 39(3-4): 472 (1907)

*Uva connivens* Kuntze, Revis. Gen. Pl. 1: 8. (1891)

**TYPE.** EQUATORIAL GUINEA – Bioko Sur • G. Mann 1159 (holotype: K; isotype: P), Fernando Po; 3°30'N, 8°40'E; 1861.

**Description.** Tree 3 – 20 m tall, D.B.H. 2 – 25 cm; young branches glabrous, old branches glabrous. Leaves distichous, simple, pinnately veined, margins entire, flat. Petiole 5 – 21 mm long, 2 – 6 mm wide, glabrous. Leaf lamina 254 – 636 mm long, 66 – 177 mm wide, length:width ratio 2.3 – 6.2, elliptic to oblong to obovate, coriaceous, base acute to rounded, sometimes truncate or subcordate, apex acute to acuminate, acumen 5 – 24 mm long; glabrous when young and old above, glabrous when young and old below; mid rib sunken above, raised below, glabrous above, glabrous below; secondary veins 16 – 28 pairs, weakly brochidodromous, impressed above, raised below; tertiary veins reticulate. Inflorescences borne on trunk and branches or axillary, composed of 1 flower. Flower pedicel (5) 10 – 40 mm long, 1.4 – 4 mm, increasing toward the apex up to 10 mm in diameter, pubescent to glabrous. Flowers actinomorphic, hermaphroditic, buds ovoid to globose, pedicellate, 9 – 22 mm high, 8 – 30 mm in diameter, pubescent. Bracts 1 to 6, upper bract 4 – 13 mm long, 6 – 17 mm wide, ovate, appressed, enclosing the bud, pubescent outside, glabrous inside. Sepals 3, 5 – 14 mm long, 7 – 17 mm wide, imbricate to fused at base, puberulent outside, glabrous inside, dull green. Outer petals 3, 14 – 32 mm long, 12 – 29 mm wide, length:width ratio 0.95 – 1.5, broadly ovate to ovate, pubescent to puberulent outside, puberulent to glabrous inside, wine red (cream in immature flowers) outside, wine red (cream in immature flowers) inside. Inner petals 3, 9.5 – 30 mm long, 8 – 23 mm wide, length:width ratio 0.9 – 1.9, broadly ovate to ovate, pubescent to puberulent outside, puberulent to glabrous inside, wine red (cream in immature flowers) outside, wine red (cream in immature flowers) inside. Stamen 1900 – 2500, 2 – 3.8 mm long, 0.3 – 0.5 mm wide, anthers linear, connective truncate. Carpels 5 to 33, 2 – 6.5 mm long, 0.8 – 1.5 mm wide, pubescent, free; stigma 0 – 2 mm long, 1 – 1.8 mm wide, coiled, pubescent, covered with an exudate at anthesis. Fruiting pedicel 13 – 31 mm long, 3 – 8 mm in diameter, glabrous. Monocarps 1 to 10, 22 – 55 mm long, 17 – 32 mm wide, length:width ratio 1.3 – 2, cylindrical to ovoid, longitudinally ridged, sparsely pubescent to glabrous, red to orange when ripe, green when immature; stipe 0 – 8 mm

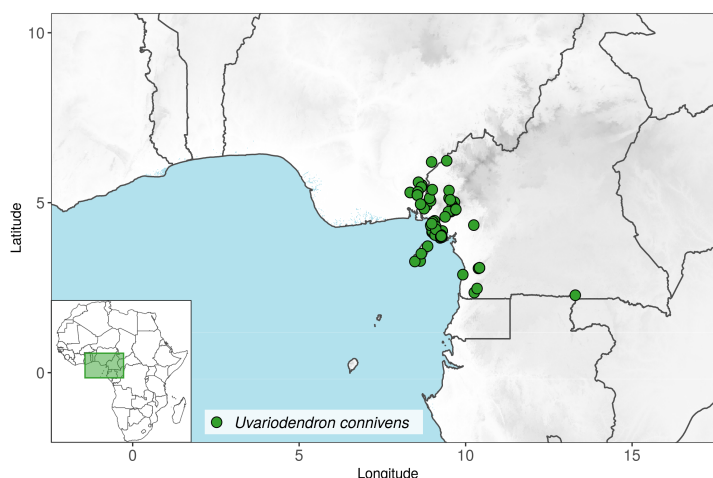


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long, 3 – 10 mm wide, slightly pubescent to glabrous. Seeds 8 – 23 per monocarp, biseriate, 13 to 29 mm long, 3 – 14 mm wide, semicircular.

**Distribution.** Cameroon, Equatorial Guinea (Bioko Island) and Nigeria.

**Notes.** This species is easily differentiated from the other species by its petals being wine red both outside and inside in mature flowers. Apart from this character, *Ud. connivens* resemble *Ud. calophyllum* and *Ud. fuscum* in having great leaves (more than 25 cm



long). It can be distinguished from Figure 16: Distribution of *Uvariodendron connivens*

these species by being glabrous when young and old, and by having a distinct flower pedicel 10 – 40 mm long, whereas *Ud. calophyllum* and *Ud. fuscum* flowers are sessile (flower pedicel 10 – 15 mm maximum in *Ud. fuscum* var. *magnificum*).

**Specimens examined.** CAMEROON – Littoral • T.L.P. Couvreur 620 (MPU, YA), Ebo Wildlife Reserve, Djuma permanent camp. On Djuma-Djuma trail; 4°20'23.59"N, 10°14'41.58"E; alt. 335 m; 14 Feb. 2014 – South Region • G.A. Zenker 2624 (B, BM, G, K, L, M, MA, P, P, WAG), Bipindi; 3°05'N, 10°25'E; 1903 • G.A. Zenker 3204 (BM, G, K, L, M, P, WAG), Kamerun. Bipinde; 3°05'N, 10°25'E; 1904 • G.A. Zenker 3401 (BM, G, K), Bipinde; 3°05'N, 10°25'E; 1907 • G.A. Zenker 3487 (BM, G, K), Bipinde; 3°05'N, 10°25'E; 1908 • G.A. Zenker 358 (B, G, M, P, P, U, WAG), Mimfia; 3°04'N, 10°23'E; Sep. 1913 • G.A. Zenker 3845 (BM, K), Bipindi; 3°05'N, 10°25'E; 1909 • J.J. Bos 5412 (P, WAG, WAG), 6 km S. of Kribi, 2 - 4 km E. of Grand Batanga road; 2°53'N, 9°55'E; 26 Sep. 1969 • T.L.P. Couvreur 383 (MPU, WAG, YA); Océan, Campo Ma'an National Park, 5 km after main entrance; 2°21'19.48"N, 10°15'33.59"E; alt. 300 m; 15 Feb. 2012 • T.L.P. Couvreur 484 (MPU, YA), 15 km east from Lélé village; 2°16'39.39"N, 13°17'37.19"E; alt. 549 m; 09 Sep. 2013 • T.L.P. Couvreur 706 (MPU, WAG, YA), Campo Ma'an National Park, 11 km on trail from Ebinanemeyong village, on road, 7 km from Nyabessan to Campo town; 2°28'25.42"N, 10°20'39.1"E; 14 Feb. 2015 – South-West Region • B.-A. Nkongmeneck 959 (YA); Fako, Idenau, Mt Cameroun, versabt de Idenao. Feuille IGN 1/200 000 Buea/Douala; 4°12'N, 9°05'E; alt. 300 m; 23 Feb. 1985 • Baker, WJ 294 (K, SCA, YA); Fako, Mabeta, 6km SE Limbe SBL; 3°59'N, 9°17'E; 10 Aug. 1993 • Bongyu, J 73 (K); Fako, Mabeta-Moliwe Reserve; 3°58'N, 9°14'E; 06 Apr. 1992 • C.F. Tekwe 87 (K, SCA, YA), Isobi, above Isobe; 4°10'N, 9°00'E; alt. 40 m; 10 Jun. 1992 • D. Kenfack 1507 (MO), Mokoko; 4°27'N, 9°04'00.12"E; 24 Apr. 2001 • D. Kenfack 879 (MO); Ndian, Korup National Park, 11km from Mundemba, along Fabe road; 5°05'03.43"N, 9°32'20.63"E; alt. 9 m; 11 Jul. 1997 • D.W. Thomas 2264 (K, MO, P, WAG, YA); Ndian, Map NB 32 IV Buea-Douala. South Korup Reserve; 4°55'N, 8°50'E; alt. 50 m; Jul. 1983 • D.W. Thomas 4447 (K, MO, P, YA), forest and meadows on the gently sloping side of Mount Cameroun above small Koto village; 4°18'N, 9°06'E; alt. 550 m; 06 Mar. 1985 • D.W. Thomas 5533 (P, YA), forest between Kindonge and small Ekombe, Southern Bakundu Forest Reserve; 4°35'N, 9°23'E; alt. 200 m; 10 Feb. 1986 • D.W. Thomas 5537 (P, YA), at Bonenza, 2 km N of Limbe-Idenao road; 4°03'N, 9°05'E; alt. 300 m; 10 Feb. 1986 • D.W. Thomas 6928 (P, YA), footpath toward Matene from Mbilishe; 6°14'N, 9°26'E; alt. 400 m; 1987 • D.W. Thomas 7961 (MO, P, YA), Steep hillside south of Esukutang village; 5°23'N, 9°00'E; alt. 300 m; 25 May. 1988 • D.W. Thomas 9875 (K, SCA, YA), West of the Onge River and ridges on 'Thump Mount'; 4°20'N, 8°57'E; alt. 200 m; 09 Nov. 1993 • F. Nguembock 76 (K); Fako, Mabeta-Moliwe Reserve; 3°58'N, 9°14'E; 10 Mar. 1992 • G. Mann 763 (BM, K), Ambas Bay; 4°01'N, 9°12'E; Feb. 1861 • G.K. Gottsberger 130307/ 21 (ULM, WAG), c. 300 m from Banyang Mbo Research Station; 5°08'N, 9°30'E; 13 Mar. 2007 • G.P. Tchouto Mbatchou 685 (K, SCA, YA), Bomana secondary forest. Transect OA, Plot OA0Z; 4°15'N, 9°01'E; alt. 200 m; 05 Oct. 1993 • I. von Rege 87 (K, SCA, YA); Fako, Mabeta, 6km SE Limbe SBL; 3°59'N, 9°17'E; alt. 60



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m; 11 Aug. 1993 • J. Nemba 550 (MO, P, YA), Secondary growth and old growth forest along Kumba-Mamfe road at mile 14 Lkiliwindi; 4°44'N, 9°29'E; alt. 200 m; 15 Jun. 1987 • J. Nemba 56 (L, P, U, YA), 5 kms west of Kumba-Mamfe road near Konye; 4°55'N, 9°36'E; alt. 300 m; 25 Mar. 1986 • J.-P. Ghogue 1551 (YA), Bimbia Bonadikombo (former Mabeta Moliwe), 18km SE Limbe; 3°59'36"N, 9°15'43"E; alt. 50 m; 10 Apr. 2003 • J.F. Villiers 2483 (P, YA), 4km E Bomana, 34 NW limbé; 4°12'55.22"N, 9°06'11.21"E; 14 Dec. 1984 • J.I. Wheatley 194 (K, SCA, YA); Fako, Mabeta-Moliwe TC 10; 4°01'N, 9°16'E; alt. 50 m; 20 Apr. 1992 • J.I. Wheatley 326 (K, SCA, YA); Fako, Mabeta-Moliwe TD 5835m; 4°01'N, 9°16'E; alt. 100 m; 24 Jun. 1992 • J.J. Wieringa 45 (WAG); Fako, Limbe, Bakingini, forest above 'mile 11 village'; 4°04'10"N, 9°03'50"E; alt. 160 m; 20 Jan. 1994 • J.J. Wieringa 5839 (BR, FHO, MO, WAG), Bakingini, at edge of plantation area above Mile 11; 4°04'10.8"N, 9°03'27.6"E; alt. 150 m; 06 Mar. 2007 • J.M. Dalziel 8243 (K), Buea1, Buea to Mayuko; 4°09'N, 9°14'E; 13 Feb. 1927 • J.M. Mbani 14 (K, SCA, YA), Njonji; 4°08'11.04"N, 8°59'22.56"E; alt. 100 m; 13 Feb. 1992 • J.M. Mbani 382 (K, SCA, YA), Ekumbe Mofako, Plot M19; 4°28'N, 9°04'E; 21 May. 1994 • J.P. Watts 245 (K, YA), Moliwe, Makota River watershed.TD 5832m; 4°00'N, 9°15'E; alt. 100 m; 29 Apr. 1992 • J.P. Watts 394 (K, SCA, YA), c.5km South East of Moliwe, TF +4000m; 4°02'N, 9°17'E; alt. 100 m; 09 Jun. 1992 • J.P. Watts 782 (K, SCA, YA), forest to the West of Onge River, about 4km West of Liwenyi village (c 14km North of Idenau); 4°23'N, 8°59'E; alt. 260 m; 28 Oct. 1993 • M. Etuge 156 (MA, MO, P, WAG, YA), Bakolle Bakossi, on Kumba - Mamfe road; 5°01'N, 9°40'E; alt. 350 m; 24 May. 1986 • M. Etuge 2390 (K, YA), Max's trail, Nyasoso; 4°49'39.72"N, 9°40'51.96"E; alt. 1100 m; 24 Jun. 1996 • M. Etuge 2396 (K, YA), Max's trail, Nyasoso; 4°49'39.72"N, 9°40'51.96"E; alt. 1100 m; 24 Jun. 1996 • M. Etuge 6506 (YA), Mungo River F.R., Mungo F.R; 4°44'17"N, 9°33'38"E; 22 Feb. 2006 • M.R. Cheek 5180 (K, P, SCA, YA), Liwenyi, Low altitude forest on the West bank of the Onge river above the first set of rapids, that is about 1-2 hours walk inland from Enyenge. Grid ref. and alt. approx. Local names and uses from Clement Offu (Enyenge); 4°17'N, 8°58'E; alt. 50 m; 28 Oct. 1993 • M.R. Cheek 5462 (K, SCA, YA), Low altitude forest above oil palm plantation. Reached after c. 40 minutes walk N then E from Njonji. Hunters path to 'Lake Njonji'. Little farming, but many gaps and fallen trees at low altitude, c. 150-300m, crossing and running alongside substantial seasonal stream. At c. 400 m, *Hypselodelphys-Aframomum* thicket dominates; 4°08'N, 9°01'E; alt. 300 m; 18 Nov. 1993 • M.R. Cheek 8164 (K, YA); Ndian, Korup National Park, Ekundu Kundu, Transect 10, c. 1100m; 5°08'N, 8°55'E; alt. 170 m; 25 Apr. 1996 • N. Ndam 1076 (K, SCA), Bonjare, Plot 09; 4°26'N, 9°01'E; alt. 220 m; 30 Apr. 1994 • N. Ndam 1118 (K, SCA), Bonjare, Plot 10; 4°26'N, 9°01'E; alt. 270 m; 01 May. 1994 • N. Ndam 708 (K, YA), Bomana-Koto Rd c 500m Bearing 305deg towards Onge river 3 hr walk from the rd; 4°13'N, 9°04'E; alt. 400 m; 18 Oct. 1993 • P. Nkeng 37 (K, SCA, YA), Etome; 4°03'N, 9°07'E; alt. 300 m; 02 Mar. 1992 • R.G. Letouzey 15175 (P, YA); Ndian, Rivières Mosongosele et de Ndian depuis Mosongosele jusqu'à l'entrée amont de la mangroce, env. 20km au SW de Mundemba (feuille IGN 1/200 000 Buea-Douala); 4°49'27.3"N, 8°45'15.72"E; 13 Jun. 1976 • R.G. Letouzey 15177 (MO, P, P, WAG, YA), Au SW de Mosongosele, 20 km WSW Mendumba; 4°54'N, 8°45'E; 14 Jun. 1976 • S. Cable 2329 (K, YA); Ndian, Korup National Park, Ekundu Kundu, path to Esoki about 4km from Ekundu-Kundu (as on 27th); 5°03'16.8"N, 8°56'58.5"E; alt. 350 m; 29 Apr. 1996 • S. Cable 611 (K, SCA, YA), Dikulu, Coastal lowland rain forest along Mangrove stream; 3°59'N, 9°14'E; alt. 50 m; 17 Dec. 1993 • S.N. Ekema 1078 (K, YA), Mokoko Forest Reserve, Boa/Likingé; 4°24'N, 9°00'E; alt. 150 m; 31 May. 1994 • T.C.H. Sunderland 1264 (K, SCA, YA), Mabeta-Moliwe: TB 6000m; 4°03'N, 9°16'E; alt. 40 m; 22 Apr. 1992 • T.C.H. Sunderland 1536 (K, K, SCA, YA), Nyasoso, Mt Kupe: Max's Trail; 4°48'05.04"N, 9°42'29.16"E; alt. 1600 m; 09 Jul. 1992 • T.D. Maitland 537 (K, P), Buea area, at Balifamba; 4°10'N, 9°18'E; alt. 731 m; 1929 • T.L.P. Couvreur 1016 (MPU, WAG, YA), Bayang Mbo Wildlife Sanctuary, after Mbu river; 5°21'26.28"N, 9°30'05.88"E; alt. 253 m; 26 Mar. 2016 • T.L.P. Couvreur 1051 (MPU, WAG, YA), Mount Cameroon National Park, on the Bomona trail, behind Bomona village, 10 km NW from Idenau; 4°17'48.27"N, 9°04'43.77"E; alt. 690 m; 03 Apr. 2016 • W.G. Gosline 235 (K, YA), Kupe Village, trail to Kupe rock saddle; 4°47'10"N, 9°41'30"E; alt. 950 m; 28 Nov. 1999 – Unknown major area • W.G. Gosline 209 (K, WAG, YA), Meme Division, Mahole-Bintulu road; 4°47'30"N, 9°36'12"E; alt. 300 m; 24 Nov. 1999. EQUATORIAL GUINEA – Bioko Norte • Carvalho, M.G 4220 (K, MA), BIOCO: Malabo - Cupapa, km 22-23, margenes del rio Ejoa, 32NMK9005, 200m; 3°43'12"N, 8°51'36"E; 06 Jul. 1989 – Bioko Sur • W.R.Q. Luke 11955 (EA, K, MA), Moaba - Moka trail, Biadyi River Camp Pt 140; 3°17'06.4"N, 8°38'17.81"E; alt. 650 m; 16 Mar. 2007 • W.R.Q. Luke 13184 (K, MA), Moraka pt 340 to 342; 3°16'13.8"N, 8°28'29.64"E; alt. 3 m; 28 Jan. 2009. NIGERIA – Cross River State • C.F.A. Onochie FHI 36080 X (K); Calabar, Oban Group Forest Reserve, between Akor and Orem; 5°36'N, 8°35'E; 21 Jan. 1957 • E.U. Ujor FHI 31636 (K); Calabar, Ikot Ewa; 4°57'24.84"N, 8°38'44.88"E; 05 Jul. 1952 • H.D. Onyechusim FHI 54055 (K); Calabar, between miles 57-58 Osomba village on Calabar-Mamfe road; 5°27'23.32"N, 8°39'55.34"E; 21 Feb. 1964 • M.C. Ejiofor FHI 21898 (K); Calabar, Oban Group Forest Reserve; 5°36'N, 8°35'E; 07 May. 1952 • M.G. Latilo 23 (K); Calabar, Akamkpa Rubber Estate. Calabar River Division; 5°18'N, 8°20'E; 21 Mar. 1959 • M.G. Latilo 32 (K, MO); Calabar, Akamkpa Rubber Estate. Dukwe felling area. Calabar River Division; 5°18'N, 8°20'E; 23 Mar. 1959 • P.A. Talbot 1254 (BM, K), Oban; 5°13'23.28"N, 8°33'06.9"E; 1911 • P.A. Talbot 158 (BM); Calabar, Oban; 5°19'N, 8°34'E; 1911 • P.A. Talbot 402

## TAXONOMIC REVISION OF UVARIODENDRON AND UVARIOPSIS

(BM), Oban; 5°13'23.28"N, 8°33'06.9"E; 1911 • P.A. Talbot 404 (BM, K), Oban; 5°13'23.28"N, 8°33'06.9"E; 1911 • P.A. Talbot 433 (BM), Oban; 5°13'23.28"N, 8°33'06.9"E; 1911 • P.A. Talbot 434 (BM), Oban; 5°13'23.28"N, 8°33'06.9"E; 1911 • P.A. Talbot 82 (BM, K), Oban; 5°13'23.28"N, 8°33'06.9"E; 1911 • P.A. Talbot s.n (BM); Calabar, Oban; 5°13'23.28"N, 8°33'06.9"E; 1912 • P.P.C. van Meer 1412 (WAG); Calabar, Oban Group Forest Reserve, East Block; 5°31'N, 8°41'E; alt. 200 m; 21 Apr. 1971 • P.P.C. van Meer 1430 (U); Calabar, Oban Group Forest Reserve, East Block; 5°31'N, 8°41'E; alt. 200 m; 22 Apr. 1971 • P.P.C. van Meer 1430 (WAG); Calabar, Oban Group Forest Reserve, East Block; 5°31'N, 8°41'E; alt. 200 m; 22 Apr. 1971 • R.W.J. Keay FHI 28191 (K); Ikom District, Afi River Forest Reserve, near Aboabam, forest by river Nkem; 6°11'52.16"N, 8°58'40.48"E; 09 Dec. 1950.

***Uvari dendron dzomboense*** Dagallier, W.R.Q.Luke & Couvreur, *PhytoKeys* 174: 114 (2021)

**TYPE.** KENYA – Coast • S.A. Robertson MDE 207 (holotype: K; isotypes: EA, MO, WAG), Kwale District - Dzombo Hill; 4°26'S, 39°13'E; alt. 300 m; 07 Feb. 1989.

**Description.** Tree 4 – 7 m tall, D.B.H. unknown; young branches sparsely pubescent to glabrous, old branches glabrous; leaf bud 'eragrostiform', composed of 5, distichous, longitudinally folded, velutinous scales. Leaves distichous, simple, pinnately veined, margins entire, slightly revolute. Petiole 3 – 4 mm long, 1 – 1.5 mm wide, sparsely pubescent to glabrous. Leaf

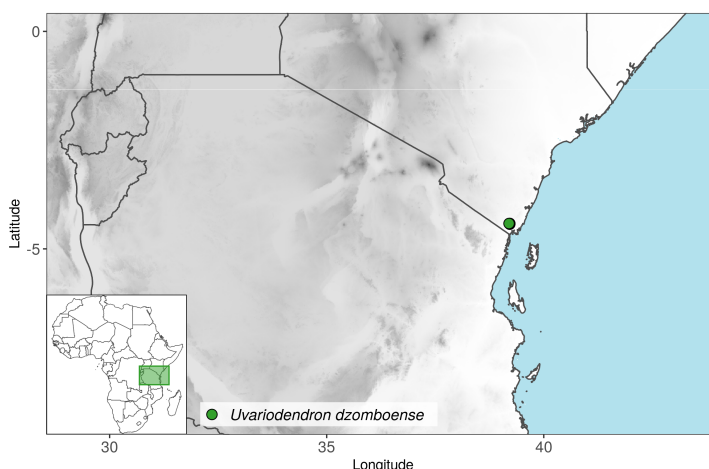


Figure 17: Distribution of *Uvari dendron dzomboense*

lamina 65 – 132 mm long, 20 – 45 mm wide, length:width ratio 2.9 – 3.6, elliptic to narrowly elliptic, coriaceous, base acute to slightly decurrent, apex attenuate, glabrous when young and old above, sparsely pubescent to glabrous when young, glabrous when old below; mid rib sunken above, raised below, glabrous above, slightly pubescent to glabrous below; secondary veins 12 – 13 pairs, weakly brochidodromous, impressed above, raised below; tertiary veins reticulate. Inflorescences borne on trunk and branches, composed of 1 flower. Flower pedicel 8 – 30 mm long, 2 – 2.5 mm in diameter, densely pubescent. Flowers actinomorphic, hermaphroditic, buds globose, sessile, ca. 4 mm high, ca. 4.5 mm in diameter, sparsely pubescent. Bracts 6 at base of the pedicel in flower bud, 1 on mature flower towards the lower half of the pedicel, upper bract 5 – 6 mm long, 5 – 8 mm wide, ovate, pubescent to shortly pubescent outside, glabrous inside. Sepals 3, 5 – 7 mm long, 4.5 – 7 mm wide, fused at base, pubescent to shortly pubescent outside, glabrous inside, color unknown. Outer petals 3, ca. 16 mm long, ca. 9 mm wide, length:width ratio ca. 1.8, ovate, shortly velutinous outside, glabrous inside, color unknown. Inner petals 3, ca. 18 mm long, ca. 8 mm wide, length:width ratio ca. 2.3, obovate, shortly velutinous outside, glabrous inside, color unknown. Stamen more than 700, 2 mm long, 0.5 mm wide, anthers linear, connective truncate. Carpels 50 to 75, ca. 2 mm long, 1 – 1.5 mm wide, densely

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pubescent, free; stigma unknown. Fruiting pedicel ca. 14 mm long, ca. 4 mm in diameter, pubescent. Monocarps (unripe?) ca. 35, ca. 15 mm long, ca. 10 mm wide, length:width ratio ca 1.5, ovoid, densely pubescent, golden brown; sessile mm long. Seeds (unripe?) ca. 5 per monocarp, uniseriate, ca. 4.5 mm long, ca. 10 mm wide.

**Distribution.** Only known from one locality in Kenya: Dzombo Hill.

**Notes.** This species differs from the other *Uvariodendron* species by the combination of small (i.e. less than 150 mm long) narrowly elliptic to elliptic leaves and 50–75 densely pubescent carpels. It differs from *Ud. kirkii* by its smaller leaves (132 mm maximum versus 210 mm maximum) and higher number of carpels (50–75 versus 7–20).

**Specimens examined.** KENYA – Coast • W.R.Q. Luke 1654 (EA, K); Kwale District, Dzombo Forest Reserve; 4°25'S, 39°13'E; alt. 270 m; 06 Jan. 1989 • W.R.Q. Luke 2884 (EA, K); Kwale District, Dzombo Forest Reserve; 4°25'S, 39°13'E; alt. 271 m; 04 Oct. 1991 • W.R.Q. Luke 3370 (EA); Kwale District, Dzombo Forest Reserve; 4°25'S, 39°13'E; alt. 272 m; 12 Nov. 1992 • W.R.Q. Luke 7443 (EA); Kwale District, Dzombo; 4°25'S, 39°12'E; alt. 270 m; 28 Jun. 2001.

*Uvariodendron fuscum* (Benth.) R.E.Fr., Acta Horti Berg. x. 61 (1930)

*Uvaria fusca* Benth., Trans. Linn. Soc. London 23(3): 466 (1862)

*Uva fusca* Kuntze, Revis. Gen. Pl. 1: 8 (1891)

*Uvariodendron mirabile* R.E.Fr., Acta Horti Berg. x. 59 (1930)

*Uvaria connivens* Benth., Trans. Linn. Soc. London 23(3): 465 (1862) (pro parte *Lehmbach* 57 and 178)

*Uvariodendron giganteum* (Engl.) R.E.Fr. **syn. nov.**, Acta Horti Berg. x. 62 (1930)

*Uvaria gigantea* Engl., Notizbl. Königl. Bot. Gart. Berlin 2: 292. 1899 (pro parte *Zenker & Staudt* 108 and 698)

*Uva gigantea* Kuntze, Deutsche Bot. Monatsschr. xxi. 173 (1903)

*Uvariodendron magnificum* Verdc. **syn. nov.**, Kew Bull. 23(3): 515 (1969)

**TYPE.** EQUATORIAL GUINEA – Bioko Sur • G. Mann 308 (holotype: K; isotype: P); 3°30'N, 8°40'E; alt. 396 m; 1860.

**Description.** Tree 3 – 15 m tall, D.B.H. 5 – 35 cm; young branches with long soft hairs producing a whitish appearance quickly falling off to glabrous, old branches glabrous. Leaves distichous, simple, pinnately veined, margins entire, flat. Petiole 4 – 35 mm long, 2 – 8 mm wide, pilose to glabrous. Leaf lamina 160 – 750 mm long, 43 – 225 (250) mm wide, length:width ratio (2.1) 2.5 – 4, narrowly elliptic to elliptic to narrowly obovate, coriaceous, base acute to cuneate to rounded, apex rounded to acuminate, acumen 1 – 23 mm long; glabrous when young and old above, pilose to glabrous when young, glabrous when old below; mid rib sunken above, raised below, glabrous above, pilose to glabrous below; secondary veins 15 – 33 pairs, weakly brochidodromous, impressed above, raised below; tertiary

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veins reticulate. Inflorescences borne on trunk and branches, composed of 1 – 2 (sub)sessile to pedicellate flowers. Flower pedicel 0 – 15 mm long, 3 – 6 mm in diameter, velutinous. Flowers actinomorphic, hermaphroditic, buds globose, sessile, 6 – 15 mm high, 6.5 – 15 mm in diameter, velutinous. Bracts 1 to 6, upper bract 8 – 35 mm long, 10 – 50 mm wide, broadly ovate, clasping the pedicel, enclosing the sepals, pubescent outside, glabrous inside. Sepals 3, 11 – 55 mm long, 13 – 43 mm wide, ovate, fused at base over 20 – 50 % of their length, velutinous outside, glabrous inside, brown. Outer petals 3, 20 – 70 mm long, 17 – 47 mm wide, length:width ratio 1.1 – 1.7, elliptic to broadly ovate, velutinous outside, glabrous inside, cream outside, cream with a dark red streak from base up to 75% of the petal length inside. Inner petals 3, 20 – 53 mm long, 15 – 38 mm wide, length:width ratio 1.1 – 2.1, elliptic to broadly obovate to obovate, puberulent outside, glabrous inside, cream outside, dark red with cream margins inside. Stamen more than 2400, 3.5 – 5 mm long, 0.1 – 0.5 mm wide, anthers linear, connective truncate, pale yellow. Carpels 20 to 160, 4 – 7 mm long, 0.5 – 2.2 mm wide, velutinous, free; stigma 1 – 2 mm long, 0.8 – 1.1 mm wide, coiled, glabrous to velutinous, covered with an exudate at anthesis. Fruiting pedicel 5 – 18 mm long, 5 – 8 mm in diameter, pubescent. Monocarps 6 to 80, 20 – 60 mm long, 11 – 32 mm wide, length:width ratio 1.7 – 2.5, cylindrical, curved, acuminate, puberulent, green to brown; sessile to shortly stipitate, stipe 0 – 4 mm long, 2 – 5 mm wide, pubescent to glabrate. Seeds 1 – 16 per monocarp, biseriate, 14 to 23 mm long, 7 – 11 mm wide, semicircular, orange-brown.

**Distribution.** Cameroon, Democratic Republic of the Congo, Gabon, Equatorial Guinea (Bioko Island), Nigeria Uganda.

**Notes.** *Ud. fuscum* encompasses a large morphological variation along a continuum of the leaf and flower size, with the var. *magnificum* being the larger, followed by the var. *giganteum* and then the type variety being the

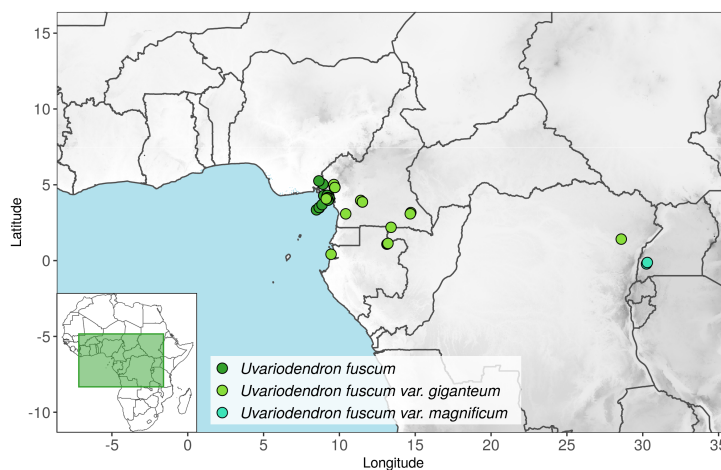


Figure 18: Distribution of *Uvariodendron fuscum*

smaller. It resembles *Ud. calophyllum*, *Ud. connivens* and *Ud. usambarensis* in having large elliptic to obovate leaves. It differs from *Ud. calophyllum* and *Ud. connivens* in having pilose to glabrous young branches and petioles (vs. tomentose in *Ud. calophyllum* and completely glabrous in *Ud. connivens*). It differs from *Ud. connivens* in having flower pedicels between 0 and 15 mm long (vs. between 10 and 40 mm long) and in having cream petals with dark red streak within the flower (vs. wine red petals both inside and outside).

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**Specimens examined.** CAMEROON – South-West Region • B.-A. Nkongmeneck 891 (YA), Mt Cameroun, flanc d'Ekona Lelu, feuille IGN: 1/200 000 Buea-Douala; 4°16'N, 9°18'E; alt. 1300 m; 14 Jan. 1985 • D.W. Thomas 4469 (K, MO, P, P, YA), forest and meadows on the gently sloping side of Mount Cameroun above small Koto village; 4°18'N, 9°06'E; alt. 550 m; 06 Mar. 1985 • Dahl, A 622 (K), trail north of Likombe village; 4°14'N, 9°11'E; alt. 1060 m; 02 Mar. 1995 • E.W.G. Kalbreyer 41 (K); 4°01'N, 9°12'E; 1877 • G.W.J. Mildbraed 10720 (K), Likomba - Pflanzung, 15 - 35 km NE of Victoria; 4°06'N, 9°20'E; alt. 50 m; Nov. 1928 • H. Lehmbach 178 (B), Buea; 4°09'N, 9°14'E; alt. 1800 m; 16 Jan. 1898 • H. Lehmbach 57 (B, K), Buea1, Buea; 4°09'N, 9°14'E; alt. 1000 m; 26 Apr. 1897 • J.J. Wieringa 2058 (WAG); Fako, Mt Etinde (=Small Mt. Cameroon), near and at summit; 4°05'N, 9°07'E; alt. 1400 m; 29 Jan. 1994 • M. Groves 122 (K, SCA, YA), trail north of Likombe Village; 4°14'N, 9°11'E; alt. 1000 m; 21 Feb. 1995 • M.R. Cheek 5145 (K, SCA, YA), Liwenyi, on the West bank of the Onge river above the first set of rapids, that is about 1-2 hours walk inland from Enyenge; 4°17'N, 8°58'E; alt. 50 m; 27 Oct. 1993 • P. Lane 142 (K, SCA, YA), Mount Kupé, within Permanent Sample Plot on Shrike Trail leading from Nyasoso to summit; 4°50'N, 9°40'E; alt. 1200 m; 20 Jun. 1994 • P.R. Preuss 1378 (P), zwischen Victoria und Bimbia; 3°58'58.55"N, 9°15'19.17"E; 15 Mar. 1898 • R.W.J. Keay FHI 37485 (FHI, K), Kumba Distr., eastern boundary of Bambuko F.R., about 11 miles SSW. of Musome. Northern slopes of Cameroon Mt; 4°18'18.11"N, 9°11'55.75"E; alt. 1000 m; 01 Feb. 1958 • S. Cable 1353 (K, SCA, YA), path towards grassland and top of Mount Cameroon from Likombe; 4°07'N, 9°11'E; alt. 1060 m; 22 Feb. 1995 • S. Cable 1524 (K, SCA, YA), Upper Boando, logging path that becomes trail to summit; 4°04'N, 9°09'E; alt. 900 m; 14 Mar. 1995 • S. Cable 1626 (K, YA), path to summit of Etinde from Upper Boando; 4°04'N, 9°09'E; alt. 1000 m; 16 Mar. 1995 • S. Cable 2187 (K, YA); Ndian, Korup National Park, Ekundu Kundu, path from Ekundu-Kundu to about 1km; 5°02'14.24"N, 8°54'58.14"E; alt. 300 m; 26 Apr. 1996 • T.D. Maitland 453 (K), Buea, above upper farm; 4°09'N, 9°14'E; alt. 1219 m; 1924 • T.D. Maitland s.n 9 (K), Cameroon mountain, Buea area; 4°09'N, 9°14'E; alt. 1219 m; 1930 • T.D. Maitland s.n 10 (K), Cameroon mountain, Buea; 4°09'N, 9°14'E; alt. 975 m; 1930 • T.L.P. Couvreur 1026 (WAG, YA), on trail leading to top of Mt Etinde, after Ekonjo village; 4°04'02.27"N, 9°09'10.16"E; alt. 749 m; 01 Apr. 2016 • T.L.P. Couvreur 1029 (MPU, WAG, YA), on trail leading to top of Mt Etinde, after Ekonjo village; 4°04'04.83"N, 9°09'11.43"E; alt. 781 m; 01 Apr. 2016 • T.L.P. Couvreur 1040 (MPU, WAG, YA), Mount Cameroon National Park, Bakinguili trail, above Bakinguili village; 4°05'48.05"N, 9°03'24.71"E; alt. 563 m; 02 Apr. 2016 • T.L.P. Couvreur 1046 (MPU, WAG, YA), Mount Cameroon National Park, on the Bomona trail, behind Bomona village, 10 km NW from Idenau; 4°17'46.46"N, 9°06'06.31"E; alt. 859 m; 03 Apr. 2016 • T.L.P. Couvreur 990 (MPU, WAG, YA), slopes of Mount Cameroon, on the Bokwango trail, near Bokwango village, 4 km south west of Buea; 4°07'25.26"N, 9°11'11.28"E; alt. 1227 m; 23 Mar. 2016 • T.L.P. Couvreur 992 (MPU, WAG, YA), slopes of Mount Cameroon, on the Bokwango trail, near Bokwango village, 4 km south west of Buea; 4°07'27.06"N, 9°10'13.93"E; alt. 1560 m; 23 Mar. 2016. EQUATORIAL GUINEA – Bioco (Fernando Poo) • G.W.J. Mildbraed 6428 (B), Pico Basilé, Fernando Poo: Nordseite d. Pics v. Sta. Isabel oberhalb Basilé, Wald über der Kakao-Region 6-800m, viel Allanblackia, (oberer Tropenwald); 3°41'24.72"N, 8°51'27.72"E; alt. 800 m; 16 Aug. 1911 – Bioko Sur • W.R.Q. Luke 12203 (MA), Moeri: Camp1 to Camp2; 3°28'09.84"N, 8°40'06.96"E; alt. 704 m • W.R.Q. Luke 13279 (K), Hormiga Camp pt 346 to North camp pt 347; 3°20'51"N, 8°29'23.64"E; alt. 800 m; 01 Feb. 2009. NIGERIA – Cross River State • K. Schmitt 323 (MO), Cross River National Park. Oban Hills. SW facing slope ca 5km E of Neghe; 5°15'20"N, 8°38'50"E; 07 Feb. 1995.

*Uvariadendron fuscum* var. *giganteum* (R.E.Fr.) Dagallier, **comb. nov.**

*Uvariadendron giganteum* (Engl.) R.E.Fr., Acta Horti Berg. x. 62 (1930)

*Uvaria gigantea* Engl., Notizbl. Königl. Bot. Gart. Berlin 2: 292. 1899 (pro parte Zenker 108 and 698)

*Uva gigantea* Kuntze, Deutsche Bot. Monatsschr. xxi. 173 (1903)

**TYPE.** CAMEROON – Central Region • G.A. Zenker; A. Staudt 108 (lectotype, here designated: P (P00362654); isolectotype: COI (COI00004926)), Yaoundé, Yaunde; 3°52'N, 11°31'E; alt. 800 m; 1895.

**Description.** Tree 3 – 12 m tall, D.B.H. 5 – 30 cm; young branches with long soft hairs producing a whitish appearance quickly falling off, old branches glabrous. Leaves distichous, simple, pinnately veined, margins entire, flat. Petiole 8 – 35 mm long, 3.5 – 8 mm wide, pilose to glabrous. Leaf lamina

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357 – 676 mm long, 84 – 225 mm wide, length:width ratio 2.5 – 4, narrowly elliptic to elliptic to narrowly obovate, coriaceous, base acute to rounded, apex acute to acuminate, acumen 1 – 15 mm long; glabrous when young and old above, pilose to glabrous when young, glabrous when old below; mid rib sunken above, raised below, glabrous above, pilose to glabrous below; secondary veins 22 – 33 pairs, weakly brochidodromous, impressed above, raised below; tertiary veins reticulate. Inflorescences borne on trunk and branches, composed of 1 – 2 (sub)sessile flowers. Flower pedicel 0 – 7.5 mm long, 3 – 6 mm in diameter, velutinous. Flowers actinomorphic, hermaphroditic, buds globose, sessile, 7 – 9 mm high, 8.5 – 10 mm in diameter, velutinous. Bracts 1 to 6, upper bract 16 – 22 mm long, 20 – 50 mm wide, broadly ovate, clasping the pedicel, enclosing the sepals, velutinous outside, glabrous inside. Sepals 3, 20 – 30 mm long, 16 – 26 mm wide, ovate, fused at base over 20 – 50 % of their length, velutinous outside, glabrous inside, brown. Outer petals 3, 25 – 40 mm long, 17 – 30 mm wide, length:width ratio 1.1 – 1.4, broadly ovate, velutinous outside, glabrous inside, cream to greenish outside, cream with a dark red to deep purple-red streak from base up to 75% of the petal length inside. Inner petals 3, 21 – 40 mm long, 17 – 29 mm wide, length:width ratio 1.1 – 1.5, broadly obovate to obovate, velutinous outside, glabrous inside, cream outside, dark red to dark purplish red with cream margins inside. Stamen more than 2400, 3.5 mm long, 0.3 – 0.5 mm wide, anthers linear, connective truncate, pale yellow. Carpels 50 to 100, 4 – 7 mm long, 1 mm wide, velutinous, free; stigma 1 – 2 mm long, 1 mm wide, coiled, velutinous, covered with an exudate at anthesis. Fruiting pedicel 9 – 15 mm long, 7 – 8 mm in diameter, pubescent. Monocarps 6 to 24, 20 – 50 mm long, 11 – 25 mm wide, length:width ratio 1.7 – 3.8, cylindrical, curved, acuminate, slightly constricted between the seeds, puberulent, green to brown; shortly stipitate, stipe 0 – 4 mm long, 2 – 5 mm wide, pubescent. Seeds 8 – 14 per monocarp, biseriate, ca. 14 mm long, ca. 7 mm wide, semicircular, orange-brown.

**Distribution.** Cameroon, Democratic Republic of the Congo, Gabon.

**Notes.** *Ud. fuscum* var. *giganteum* differs from the type variety in having young branches and petiole covered with long soft hairs producing a whitish appearance quickly falling off (vs. young branches and petiole sparsely pubescent to glabrous). Compared to the type variety, it has larger leaves (35.7 – 67.6 cm long and 8.4 – 22.5 cm wide, vs. 16 – 45 cm long and 4.3 – 11.8 cm wide), with generally more secondary veins (22 to 33 vs. 15 to 24), and flowers with generally greater sepals (20 – 30 mm long vs. 11 – 23 mm long) and more carpels (50 to 100 vs. 20 to 70). Most of these characters overlap and without the young branches covered with long soft hairs it can be hard to place some specimens in the var. *giganteum* with certainty. The specimen G.A. Zenker & A. Staudt 108, defined to be the type specimen by Fries (1930), was not found in B (lost or destroyed), so we make the duplicate from P as the lectotype and the duplicate from COI as the isolectotype.

## CHAPTER 4

**Specimens examined.** CAMEROON – Central Region • G.A. Zenker; A. Staudt 698 (B), Yaoundé, Yaunde; 3°52'N, 11°31'E; alt. 800 m; 04 Feb. 1895 • T.L.P. Couvreur 419 (MPU, WAG, YA), Mont Mbam Minkon, on trail, 5 km from Nkol Nyada village; 3°58'04.91"N, 11°24'08.64"E; alt. 1000 m; 21 Mar. 2013 – East Region • T.L.P. Couvreur 1206 (MPU, WAG, YA), 60 km south of Yokadouma, 30 km after Ngato, 15 km after river. ALPICAM 'base de vie', then on forestry road starting 4 km before Maséa village; 3°09'55.18"N, 14°42'25.64"E; alt. 587 m; 05 Mar. 2019 • T.L.P. Couvreur 1229 (MPU, WAG, YA), 60 km south of Yokadouma, 30 km after Ngato, 15 km after river. ALPICAM 'base de vie', then 40 km on forestry road starting 4 km before Maséa village. Coupe 4-4 of UFA 023; 3°05'08.17"N, 14°40'18.2"E; alt. 622 m; 08 Mar. 2019 – South Region • G.A. Zenker 1438 (L), Bipinde, Urwaldgebiet; 3°05'N, 10°25'E; 1898 • M. Biholong 279 (P, YA), près d'Alati. Ancienne piste Alati - Mintom II; 2°11'44.45"N, 13°24'17.61"E; 17 Jan. 1975 – South-West Region • C. Doumenge 473 (L, MO, P), Cameroon. Bakossi Mountains 1-8 Km NNE of Menyum Village; 5°01'N, 9°38'E; alt. 1000 m; 22 May. 1987 • P. Lane 501 (K, SCA, WAG, YA), Mount Kupe Division. Ndum. Forest trail 2 km south from Etube-Tape village; 4°51'N, 9°42'E; alt. 1200 m; 02 Feb. 1995 • T.L.P. Couvreur 1057 (MPU, WAG, YA), Nyasoso village, on max's trail to Mt Kupe; 4°49'27.88"N, 9°41'59.42"E; alt. 1227 m; 05 Apr. 2016 • T.L.P. Couvreur 512 (MPU, YA); Fako, on trail from Ekongo village, located 5 km before the entrance to Limbe, 7 km on secondary road. On flank of Mt Etinde. 100 m in Mont Cameroon National Park; 4°04'19.23"N, 9°08'00.76"E; alt. 959 m; 16 Oct. 2013 • T.R. van Andel 3761 (MO, SCA, U, WAG, WAG), Bokwango. Trail to Mann's spring; 4°07'44"N, 9°11'26"E; alt. 1130 m; 21 Jun. 2001. DEMOCRATIC REPUBLIC OF THE CONGO – Orientale • T.B. Hart 910 (WAG); Mambasa, Epulu, Zaire, Zone de Mambasa (Ituri); 1°25'N, 28°35'E; alt. 750 m; 23 Mar. 1989. GABON – Estuaire • T.-J. Klaine 1690 (P), Environs de Libreville; 0°25'N, 9°27'E; 18 Oct. 1899 – Ogooué-Ivindo • N. Hallé 3156 (P), Bélinga; 1°05'N, 13°08'E; 12 Nov. 1964 • N. Hallé; A. Le Thomas 430 (K, P), Bélinga, mines de fer, le long de la rivière Folley; 1°07'N, 13°11'E; 12 Aug. 1966 • N. Hallé; A. Le Thomas 549 (K, P), Bélinga, mines de fer; 1°08'N, 13°12'E; alt. 700 m; 16 Aug. 1966.

***Uvari dendron fuscum* var. *magnificum* (Verdc.) Dagallier, **comb. nov.****

*Uvari dendron magnificum* Verdc., Kew Bull. 23(3): 515 (1969)

**TYPE.** UGANDA – Western Province • Hamilton 696 (holotype: K; isotypes: ENT, MHU); Ankole District, Kashoya – Kitomi CFR; 0°13'N, 30°15'E; alt. 1050 m; 15 Jun. 1968.

**Description.** Tree 7.5 – 15 m tall, D.B.H. unknown; young branches with long soft hairs producing a whitish appearance quickly falling off, old branches glabrous. Leaves distichous, simple, pinnately veined, margins entire, flat. Petiole 6 – 20 mm long, ca. 5 mm wide, pilose to glabrous. Leaf lamina 210 – 750 mm long, 57 – 215 (250) mm wide, length:width ratio 3 – 4, narrowly obovate, coriaceous, base acute to cuneate, apex rounded to acuminate, acumen 9 – 12 mm long; glabrous when young and old above, pilose to glabrous when young, glabrous when old below; mid rib sunken above, raised below, glabrous above, pilose to glabrous below; secondary veins 23 – 30 pairs, weakly brochidodromous, impressed above, raised below; tertiary veins reticulate. Inflorescences borne on trunk and old branches, composed of 1 flower. Flower pedicel 10 – 15 mm long, unknown. Flowers actinomorphic, hermaphroditic, buds globose, sessile. Flower not seen, description from verdcourt (1969). Bracts 5 to 6, upper bract 8 – 35 mm long, 10 – 40 mm wide, ovate, pubescent outside, glabrous inside. Sepals 3, 30 – 55 mm long, 30 – 43 mm wide, ovate, fused at base, pubescent outside, glabrous inside. Outer petals 3, 60 – 70 mm long, 43 – 47 mm wide, length:width ratio 1.4 – 1.5, elliptic, valvate, pubescent outside, glabrous inside, white outside, purple red inside. Inner petals 3, 50 – 53 mm long, 36 – 38 mm wide, length:width ratio ca. 1.4, elliptic, imbricate at apex, puberulent at base outside, glabrous inside,

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white outside, purple red inside. Stamen very numerous, 5 mm long, anthers linear. Carpels 150 to 160, 6 mm long, 2.2 mm wide, pubescent, free; stigma coiled, pubescent. Fruiting pedicel 13 – 18 mm long, unknown, pubescent. Monocarps 10 to 80, 28 – 60 mm long, 13 – 32 mm wide, length:width ratio 1.9 – 2.5, cylindrical, curved, acuminate, pubescent, brownish, fruits not seen, data from Verdcourt (1969); shortly stipitate mm long. Seeds 1 – 16 per monocarp, biseriate, 18 to 23 mm long, 10 – 11 mm wide, semicircular.

**Distribution.** Known from only one locality in the Western Province in Uganda.

**Notes.** *Ud. fuscum* var. *magnificum* differs from the type variety in having young branches and petiole covered with long soft hairs producing a whitish appearance quickly falling off (vs. young branches and petiole sparsely pubescent to glabrous). Compared to the type variety, it has larger leaves (21. – 75 cm long and 5.7 – 21.5 (25) cm wide, vs. 16 – 45 cm long and 4.3 – 11.8 cm wide), with more secondary veins (23 to 30 vs. 15 to 24). It differs from the type variety and from the var. *giganteum* by its flowers having longer pedicels 10 – 15 mm long (vs. 0 – 7.5 mm long), larger sepals (30 – 55 mm long and 30 – 43 mm wide, vs. 11 – 30 mm long and 13 – 26 mm wide), larger petals (50 – 70 mm long and 36 – 47 mm wide, vs. 20 – 40 mm long and 15 – 30 mm wide) and more carpels (150 to 160 vs. 20 to 100).

*Uvari dendron gorgonis* Verdc., Kew Bull. 23(3): 512 (1969)

**TYPE.** KENYA – Coast • B. Verdcourt 3940 (sheets here designated, holotype: K (K000198902); isotype: EA, K (K000198901)); Kwale District, Mrima hill (about halfway up road to Lungalunga from Mwambweni); 4°29'06.81"S, 39°15'47.19"E; alt. 182 m; 16 Jan. 1964.

**Description.** Tree 3 – 27 m tall, D.B.H. 3 – 50 cm; young branches pubescent to glabrous, old branches glabrous; plant with lemon smell. Leaf bud 'eragrostiform', composed of 6 – 12, distichous, longitudinally folded, velutinous scales. Leaves distichous, simple, pinnately veined, margins entire, flat. Petiole 4 – 18 mm long, 1.5 – 5 mm wide, sparsely pubescent to glabrous. Leaf lamina 153 – 410 mm long, 36 – 127 mm wide, length:width ratio 2.3 – 4.3, elliptic to oblong to obovate, coriaceous, base generally acute to rounded, and minutely decurrent at the extreme base, apex generally acute to acuminate but can also appear rounded or retuse, acumen 0.5 – 12 mm long; glabrous when young and old above, sparsely pubescent to glabrous when young, glabrous when old below; mid rib sunken above, raised below, glabrous above, sparsely pubescent to glabrous below; secondary veins 13 – 22 pairs, weakly brochidodromous, impressed above, raised below; tertiary veins reticulate. Inflorescences borne on trunk and branches, composed of 1 – 3 flowers. Flower pedicel 8 – 18 mm long, 3 – 8 mm in diameter, velutinous. Flowers actinomorphic, hermaphroditic, buds globose, sessile, 7 – 15 mm high, 9 – 14 mm in diameter, velutinous. Bracts 1 to 8, upper bract 3 – 12 mm long, 9 – 25 mm wide, broadly ovate,



clasping the pedicel, enclosing the bud, velutinous outside, glabrous inside. Sepals 3, 8 – 13 mm long, 8 – 24 mm wide, imbricate to fused over up to ca. 30 % of their length, velutinous outside, glabrous inside, clear brown. Outer petals 3, 15 – 35 mm long, 13 – 23 mm wide, length:width ratio 1.1 – 2.2, broadly elliptic to elliptic, velutinous outside, glabrous inside, cream outside, cream with a dark purplish red streak from base up to 75% of the petal length inside. Inner petals 3, 15 – 40 mm long, 9 – 16 mm wide, length:width ratio 1.5 – 2.7, obovate, valvate at apex, velutinous outside, glabrous inside, cream to cream with a dark purplish red streak at base up to 15% of their length outside, dark purplish red with cream apex inside. Stamen more than 1400, 2.5 – 3 mm long, 0.4 – 1 mm wide, anthers linear, connective truncate. Carpels 40 to 80, 3 – 4.5 mm long, 0.8 – 1.5 mm wide, pubescent, free; stigma 0.5 mm long, 0.8 – 1.1 mm wide, coiled, velutinous. Fruiting pedicel 10 – 20 mm long, 3 – 5 mm in diameter, velutinous. Monocarps 20 to 60, 24 – 90 mm long, 4.5 – 11 mm wide, length:width ratio 5 – 11, very narrowly cylindrical, torulose to torose, velutinous, greyish green; stipe 5 – 11 mm long, 1.5 – 3 mm wide, velutinous. Seeds 3 – 14 per monocarp, uniseriate, 3 to 9 mm long, 2 – 7 mm wide, ellipsoid.

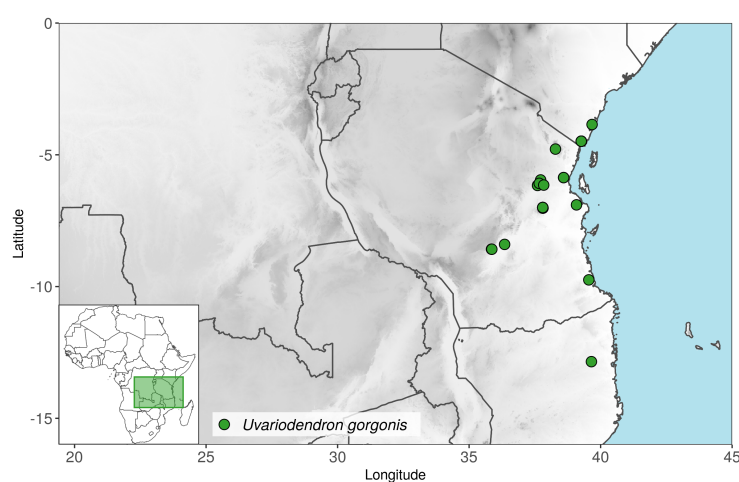


Figure 19: Distribution of *Uvariodendron gorgonis*

**Distribution.** Kenya, Mozambique and Tanzania.

**Notes.** This species can be differentiated from all other species by its fruits, unique in the genus. The fruits of *Ud. gorgonis* are composed of 20 to 60 monocarps, while most of the *Uvariodendron* species have fruits composed of 1 to 20 monocarps (except *Ud. calophyllum* and *Ud. fuscum* var.

*giganteum* that have fruits composed of up to 35 monocarps). Moreover, the monocarps are 5 to 10 times longer than wide (vs. 1.3 to 4.5 times longer than wide in the other species). They are torulose to torose, i.e. very strongly constricted between the seeds. The ovules (and seeds) are uniseriate. The combination of these characters confers the fruits the aspect of a hairy head. This feature probably inspired Verdcourt to name this species after the Gorgons, these creatures from ancient Greek mythology described as having hair made of snakes, although he didn't mention it in the protologue.

Vegetatively, this species is harder to differentiate as its leaves have dimensions that overlap with most of the other species. However, the bases of the leaves are quite peculiar: they appear generally acute to rounded but a closer look actually detects them as minutely decurrent at the extreme base. Similarly, the

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apices of the leaves are generally acute to acuminate, but can appear rounded to slightly retuse with a minute acumen.

The leaves of *Ud. gorgonis* also present a citrus smell, as in *Ud. angustifolium*, *Ud. citriodorum* and *Uvariopsis citrata*.

**Specimens examined.** KENYA – Coast • B. Verdcourt 1890 (K); Kwale District, Mrima Forest, Mrima Hill; 4°29'06.81"S, 39°15'47.19"E; 06 Sep. 1957 • B. Verdcourt 1911 (B, EA, K); Kwale District, Mrima Forest, Mrima Hill; 4°29'06.81"S, 39°15'47.19"E; 07 Sep. 1951 • J.P.M. Brenan 14601 (EA, K, P); Kilifi District, K7, Kilifi District. Pangani 'Kaya' Forest; 3°51'S, 39°40'30"E; alt. 170 m; 19 Nov. 1978 • R.B. Faden 70/ 253 (K); Kwale District, Mrima Hill, about halfway between Mgambweni and Lungalunga; 4°29'S, 39°16'E; alt. 70 m; 25 Jun. 1970 • S.A. Robertson MDE 78 (K); Kwale District, Mrima Hill; 4°29'S, 39°16'E; alt. 270 m; 04 Feb. 1989. MOZAMBIQUE – Cabo Delgado • W.R.Q. Luke 9983 (MO), Quirimba NP, Ngura Inselberg; 12°51'S, 39°39'E; alt. 420 m; 10 Dec. 2003. TANZANIA – Lindi • F.M. Mbago 2148 (K), Ruawa Forest; 9°44'46.58"S, 39°33'04.77"E; alt. 250 m; 01 Sep. 2001 – Morogoro • B.J. Harris 3223 (DSM, EA); Morogoro Rural District, Kimboza Forest Reserve, KFR near Matombo, Uluguru Mts; 7°00'S, 37°48'E; 06 Sep. 1969 • C.D. Mgaza 323 (K), Luzunguru forest reserve; 6°05'S, 37°40'E; 19 Sep. 1959 • F.C. Magogo 2171 (K); Morogoro Rural District, Kimboza Forest Reserve, Kibungo Forest Reserve (Kimboza); 7°00'S, 37°48'E; alt. 600 m; 31 Aug. 1981 • F.M. Mbago 1616 (DSM); Kilombero District, Lower Kihansi Hydropower Project; 8°24'S, 36°21'E; 30 Aug. 1997 • F.M. Mbago 1734 (K), T7: Udzungwa scarp, Upper Kihansi Gorge, forest opposite the spray zone; 8°34'54.77"S, 35°51'05.9"E; alt. 950 m; 15 Jul. 1998 • L.-P.M.J. Dagallier 47 (DSM, MPU, P, WAG); Morogoro Rural District, Kimboza forest; 7°01'16.89"S, 37°48'17.38"E; alt. 278 m; 15 Nov. 2019 • L.-P.M.J. Dagallier 52 (DSM, K, MPU, P, WAG); Morogoro Rural District, Kimboza forest; 7°01'18.69"S, 37°48'31.63"E; alt. 262 m; 15 Nov. 2019 • L.-P.M.J. Dagallier 57 (DSM, MPU, P, WAG); Mvomero District, Turiani village; 6°09'36.19"S, 37°36'17.72"E; alt. 377 m; 18 Nov. 2019 • L.-P.M.J. Dagallier 61 (DSM, MPU, P, WAG); Mvomero District, Turiani village; 6°09'46.83"S, 37°36'12.66"E; alt. 373 m; 18 Nov. 2019 • L.B. Mwasumbi 19144 (MO); Kilombero District, Kihansi gorge; 8°35'S, 35°51'50"E; alt. 800 m; 04 Sep. 1998 • Pócs, A 6061 B (DSM); Morogoro Rural District, Kimboza Forest Reserve, between Mkuyuni and Matombo; 7°00'S, 37°48'E; alt. 300 m; 19 Nov. 1969 • Pócs, A 6280 F (DSM); Morogoro Rural District, Kimboza Forest Reserve; 7°00'S, 37°48'E; alt. 300 m; 05 Nov. 1970 • R.B. Drummond 1954 (K); Morogoro Rural District, 6.4 km N of Turiani, Lusunguru Forest Reserve, near Mtibwa sawmill; 6°05'S, 37°41'E; 31 Mar. 1953 • S. Paulo 163 (EA, K); Morogoro Rural District, Kimboza Forest Reserve; 7°00'S, 37°48'E; Nov. 1953 • S.R. Semsei 1498 (K), Mtibwa Forest Reserve; 6°08'56.76"S, 37°50'10.32"E; Nov. 1953 • S.R. Semsei 773 (K); Morogoro Rural District, Kimboza Forest Reserve; 7°00'S, 37°48'E; Jul. 1952 • S.R. Semsei 852 (K); Morogoro Rural District, Mtibwa Forest Reserve; 6°07'S, 37°39'E; Aug. 1952 • T.L.P. Couvreur 69 (DSM, MO, WAG, WAG); Kilombero District, Kimboza Forest reserve, 2 km after Kimboza village, 45 km from Morogoro; 7°01'19.2"S, 37°48'16.8"E; alt. 250 m; 25 Nov. 2006 • Y.S. Abeid 2651 (EA, MO); Mvomero District, Kanga Forest Reserve, near Kwa Beku subvillage; 5°57'15"S, 37°43'11.4"E; alt. 500 m; 11 Mar. 2006 – Pwani • L.B. Mwasumbi 113377 (DSM); Kisarawe District, Pugu hills Forest Reserve; 6°54'S, 39°05'E; 28 May. 2002 – Tanga • F.M. Mbago 3756 (DSM); Handeni District, T3: Handeni Kwansisi Mgulwi stream; 5°51'55.64"S, 38°35'39.34"E; alt. 203 m; 16 Aug. 2016 • G.A. Peter 13872 (B, K, WAG); Lushoto District, O. Usambara, Mashewa; 4°47'S, 38°17'E; alt. 400 m; Sep. 1915 • L.-P.M.J. Dagallier 38 (BR, DSM, K, MO, MPU, P, WAG); Handeni District, Kwansisi village; 5°51'50.36"S, 38°35'31.77"E; alt. 196 m; 13 Nov. 2019.

### *Uvarioidendron kimbozaense* Dagallier, sp. nov.

**TYPE.** TANZANIA – Morogoro • L.-P.M.J. Dagallier 49 (holotype: MPU; isotypes: DSM, K, P, WAG); Morogoro Rural District, Kimboza forest; 7°01'16.69"S, 37°48'35.24"E; alt. 279 m; 15 Nov. 2019.

**Diagnosis.** This species can be distinguished from other species by the combination of the following characters: leaves with a mid rib slightly raised above with a tiny central depression all along the length, flower pedicel with up to 4 bracts 6 – 12 mm long, flower with imbricate sepals and 16 – 39 mm long, elliptic, and almost flat petals.

## CHAPTER 4

**Description.** Tree 5 – 7 m tall, D.B.H. 15 – 20 cm; young branches sparsely pubescent to glabrous, old branches glabrous. Leaves distichous, simple, pinnately veined, margins entire, flat. Petiole 4 – 5 mm long, 1.5 – 2 mm wide, glabrous. Leaf lamina 147 – 215 mm long, 44 – 68 mm wide, length:width ratio 2.5 – 3.6, elliptic to oblong, coriaceous, base acute to rounded, apex attenuate, glabrous when young and old above, glabrous when young and old below; mid rib slightly sunken on a raised surface/ slightly raised with a tiny central depression all along the length above, raised below, glabrous above, glabrous below; secondary veins 12 – 17 pairs, weakly brochidodromous, impressed above, raised below; tertiary veins reticulate. Inflorescences borne on growth of the trunk and on old branches, composed of 1 – 11 flowers. Flower pedicel 10 – 14 mm long, 2 – 3 mm in diameter, pubescent. Flowers actinomorphic, hermaphroditic, buds globose to oblate, pedicellate, 5 – 10 mm high, 7 – 16 mm in diameter, pubescent. Bracts 1 at base and from 1 to 4 along the pedicel, upper bract 3 – 6 mm long, 6 – 14 mm wide, broadly ovate, adpressed, clasping the pedicel, pubescent outside, glabrous inside. Sepals 3, 6 – 12 mm long, 12 – 21 mm wide, depressed ovate, imbricate, pubescent outside, glabrous inside, green to brownish-green. Outer petals 3, 16 – 28 mm long, 13 – 19 mm wide, length:width ratio 1.2 – 1.8, broadly elliptic to elliptic, puberulent outside, puberulent at apex to glabrous inside, cream outside, cream with a purple-red to reddish black streak from base up to 50% of the petal length inside. Inner petals 3, 18 – 39 mm long, 9 – 18 mm wide, length:width ratio 2 – 2.2, obovate, softly transversally curved, puberulent outside, glabrous inside, cream to cream with a slight purplish red streak at base outside, purple-red at base to reddish black toward the apex inside. Stamen more than 600, 2 – 3.5 mm long, 0.5 – 0.7 mm wide, anthers linear, connective truncate. Carpels 11 to 16, 4 – 5 mm long, 1.8 – 2 mm wide, densely pubescent, free; stigma 1 – 1.5 mm long, 1.5 – 2 mm wide, coiled, densely pubescent, covered with an exudate at anthesis. Fruits unknown.

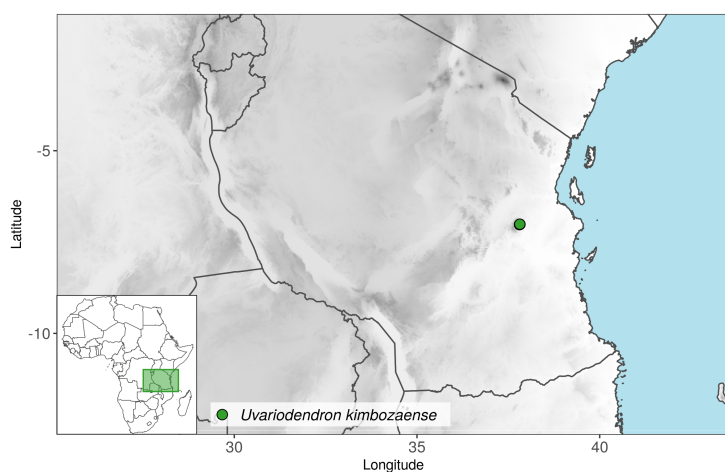


Figure 20: Distribution of *Uvariodendron kimbozaense*

**Distribution.** Known from only one locality in Tanzania: the Kimboza Forest Reserve.

**Etymology.** The specific epithet comes from Kimboza Forest Reserve (Tanzania), from where the species is endemic.

**Notes.** *Ud. kimbozaense* is very close to *Ud. kirkii* and has been previously identified as such in all the specimens

examined. It differs from *Ud. kirkii* by having slightly greater leaves (140 – 220 mm, vs. 70 – 190 mm

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long) with a mid rib slightly raised above with a tiny central depression all along the length (vs. slightly sunken above). It also has more bracts on the flower pedicel (1 to 4, vs. 1 maximum), greater (6 – 12 mm long, vs. 3 – 6.5 mm long) and imbricate (vs. connivent) sepals, and greater (16 – 39 mm long, vs. 10 – 20 mm long), elliptic (vs. ovate), and almost flat petals (with a slight transversal curvature vs. “boat-shaped” petals, with a strong transversal curvature) (Figure 21, Table 3).

**Specimens examined.** TANZANIA – Morogoro • C.J. Kayombo 5357 (MO); Morogoro Rural District, Kimboza Forest Reserve; 7°00'43"S, 37°48'50"E; alt. 400 m; 21 Mar. 2006 • T.L.P. Couvreur 71 (DSM, MO, WAG, WAG); Kilombero District, Kimboza Forest reserve, 2 km after Kimboza village, 45 km from Morogoro; 7°01'19.2"S, 37°48'16.8"E; alt. 250 m; 25 Nov. 2006 • W.R.Q. Luke 766 (EA), Uluguru Mts nr Ruvu bridge; 7°01'S, 37°49'E; alt. 450 m; 04 Nov. 1987.

Table 3: Morphological comparison between *Ud. kimbozaense* and *Ud. kirkii* (see also Figure 21)

	Lamina base	Mid rib relief above	Flower bud	Bracts	Sepals	Petals size	Inner petals shape
<i>Ud. kirkii</i>	acute to <b>decurrent</b>	slightly sunken (Figure 21K)	globose, <b>1.3 – 6 mm diameter</b>	1 at base of the pedicel and sometimes 1 on the upper half of the pedicel	3 – 6.5 mm long, 4 – 8 mm wide, very broadly to broadly ovate, <b>connivent</b> (Figure 21B)	10 – 20 mm long, 6 – 13 mm wide	<b>strongly</b> transversally curved (“boat-shape”) (Figure 21H)
<i>Ud. kimbozaense</i>	acute to <b>rounded</b>	slightly raised with a tiny central depression all along the length (Figure 21I)	globose to oblate, <b>7 – 16 mm diameter</b>	1 at base of the pedicel and from <b>1 to 4 along the pedicel</b> (Figure 21A)	6 – 12 mm long, 12 – 21 mm wide, depressed ovate, <b>imbricate</b> (Figure 21A)	16 – 39 mm long, 9 – 19 mm wide	<b>softly</b> transversally curved (Figure 21G)

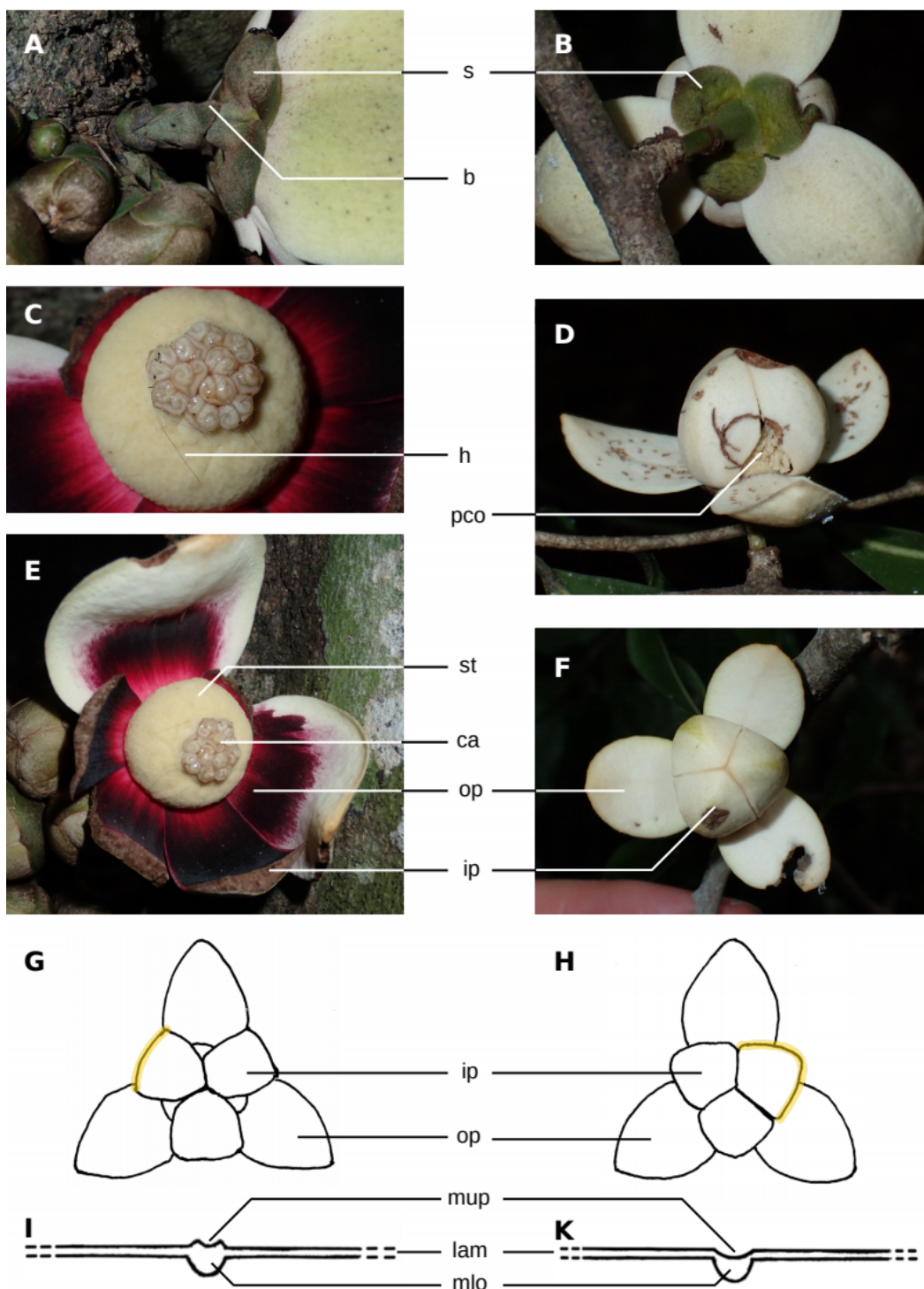


Figure 21: Morphological characters differentiating *Uvariodendron kimbozaense* Dagallier (A, C, E, G and I) and *Uvariodendron kirkii* Verdc. (B, D, F, H and J). A – B Detail of the flowering pedicel. C Detail of the carpels with hairs (h) stuck on the exudate. D Flowers from side showing the pollination chamber opening (pco). E – F Flowers from above. G – H Simplified representations of the flowers, from above; yellow marking underlines the soft (G) or strong “boat-shaped” (H) transversal curvature of the petals. I – J Simplified representation of the transversal cut of the leaf, by the midrib. Pictures from the specimens Dagallier 49 (A, C, E, G and I) and Dagallier 23 (B, D, F, H and J). b bract or bract scar, ca carpel, h hair possibly of petal consumer, ip inner petal, lam lamina, mlo lower (abaxial) side of the midrib, mup upper (adaxial) side of the midrib, op outer petal, pco pollination chamber opening, s sepal, st stamens.

*Uvariodendron kirkii* Verdc., Kew Bull. 23(3): 518 (1969)

**TYPE.** KENYA – Coast • B. Verdcourt 3939 (holotype: K; isotype: EA); Kwale District, Mrima hill (about halfway up road to Lungalunga from Mwambweni); 4°29'06.81"S, 39°15'47.19"E; alt. 182 m; 16 Jan. 1964.

**Description.** Shrub to tree 1.5 – 6 (10 – 15) m tall, D.B.H. 3 – 20 cm; young branches sparsely pubescent to glabrous, old branches glabrous. Leaves distichous, simple, pinnately veined, margins entire, flat. Petiole 2.5 – 8 mm long, 1 – 2 mm wide, glabrous. Leaf lamina 70 – 188 mm long, 22 – 75 mm wide, length:width ratio 2.1 – 3.5, elliptic, coriaceous, base acute to decurrent, apex attenuate, glabrous when young and old above, glabrous when young and old below; mid rib slightly sunken above, raised below, glabrous above, glabrous below; secondary veins 8 – 16 pairs, weakly brochidodromous, impressed above, raised below; tertiary veins reticulate. Inflorescences mostly axillary or borne on old branches, sometimes borne on trunk, composed of 1 – 2 flowers. Flower pedicel 5 – 28 mm long, 1 – 4 mm in diameter, pubescent. Flowers actinomorphic, hermaphroditic, buds globose, pedicellate, 2 – 5.5 mm high, 1.3 – 6 mm in diameter, pubescent. Bracts 1 at base and sometimes 1 on the upper half of the pedicel, upper bract 1 – 5 mm long, 1 – 8 mm wide, broadly ovate, adpressed, semi-clasping the pedicel, pubescent outside, glabrous inside. Sepals 3, 3 – 6.5 mm long, 4 – 8 mm wide, very broadly to broadly ovate, connivent, pubescent outside, glabrous inside, green to brownish-green. Outer petals 3, 10 – 17 mm long, 6 – 13 mm wide, length:width ratio 1.2 – 1.7, broadly ovate to ovate, pubescent to puberulent outside, puberulent to glabrous inside, cream to greenish pale yellow outside, cream to cream with a purple streak from base up to 50% of the petal length inside. Inner petals 3, 12 – 20 mm long, 7 – 8 mm wide, length:width ratio 1.3 – 1.9, obovate, strongly transversally curved (“boat-shape”), valvate at apex, puberulent outside, glabrous inside, white to cream outside, cream to cream with purple streak at base inside. Stamen more than 1000, 1.5 – 1.8 mm long, 0.2 – 0.3 mm wide, anthers linear, connective truncate. Carpels 8 to 16 (20), 2 – 3 mm long, 1 – 1.5 mm wide, pubescent, free; stigma 0 – 1.5 mm long, 1 – 1.3 mm wide, coiled, pubescent. Fruiting pedicel 7 – 22 mm long, 2 – 4 mm in diameter, pubescent. Monocarps 1 to 6, 23 – 36 mm long, 10 – 16 mm wide, length:width ratio 1.4 – 2.4, cylindrical, longitudinally ridged, slightly constricted between the seeds, minutely acuminate, puberulent, green to dull orange to greyish dark blue; sessile to shortly stipitate, stipe 0 – 3 mm long, 2 – 5 mm wide, pubescent. Seeds 12 – 15 per monocarp, biseriate, 11 to 15 mm long, 8 – 10 mm wide.

**Distribution.** Kenya and Tanzania.

**Notes.** This species is quite variable morphologically with leaves from 70 mm to almost 200 mm long. It can be distinguished from the other species with its pedicellate flowers growing mainly on leafy



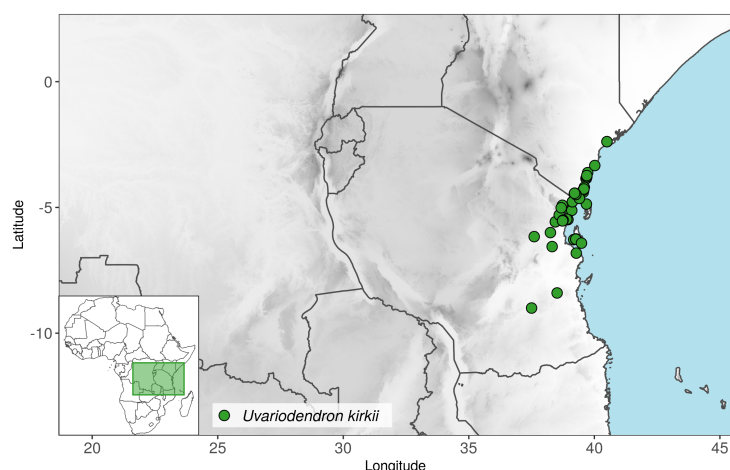


Figure 22: Distribution of *Uvariodendron kirkii*

branches and sometimes on the trunk. The pedicel is lower than in *Ud. anisatum* (5 – 28 mm vs. 15 – 65 mm long in *Ud. anisatum*). At anthesis the flowers generally present spread outer petals and inner petals connivent at apex (Figure 21D). At anthesis, the inner petals are “boat shaped”, that is the transversal curvature is strong (this character is not detectable on flower buds and on dried specimens). Some of the oldest specimens of this species were collected by Gustav Albert Peter under the name “*Uvariodendron crassum* (Peter)” (e.g. *Peter 4487*, *Peter 24366* in B). He died in 1937, before publishing this species. Verdcourt described and named this species in 1969, apparently before seeing Peter’s specimens.

**Specimens examined.** KENYA – Coast • B. Verdcourt 1891 (K); Kwale District, Mrima Forest, Mrima Hill; 4°29'06.81"S, 39°15'47.19"E; 06 Sep. 1957 • B. Verdcourt 5280 (K); Kwale District, Jombo Mt (near bottom); 4°26'08.11"S, 39°12'42.61"E; 11 Apr. 1978 • F.C. Magogo 768 (K); Kwale District, Shimba Hills, Dzombo Mountain; 4°26'09.4"S, 39°12'46.1"E; alt. 305 m; 08 Apr. 1968 • I.R. Dale 3836 (K), Witu Forest Reserve, Gongoni Forest, Witu; 2°23'07"S, 40°30'09"E; Oct. 1937 • J.B. Gillett 19901 (K); Kwale District, Diani forest. Areas NW & NE within 1km N of turn off from new road for Jadini hotel, W & E of this road. Areas SW & SE within 1.5km s of this point; 4°19'S, 39°33'E; alt. 12 m; 11 Jul. 1972 • J.B. Gillett 19906 (EA, K); Kwale District, Diani forest. Areas NW & NE within 1km N of turn off from new road for Jadini hotel, W & E of this road. Areas SW & SE within 1.5km s of this point; 4°19'S, 39°33'E; alt. 12 m; 11 Jul. 1972 • J.B. Gillett 24009 (B, EA); Kwale District, Kenya: K7: Kwale District Waa Kaya forest near coast N. of Tiwi ruined Mosque; 4°12'S, 39°36'E; alt. 30 m; 30 Dec. 1982 • J.P.M. Brenan 14592 (K); Kilifi District, K7, Kilifi District. Pangani 'Kaya' Forest; 3°51'S, 39°40'50"E; alt. 170 m; 19 Nov. 1978 • L.J. Lap 112 (MO, WAG); Kilifi District, Kaya Kauma. Mapsheet K198/1. Along the path extending westwards from the Kaya cementary. Western hill slope forest of Kaya Kauma; 3°37'S, 39°44'E; 22 Dec. 1981 • M.G. Gilbert 4967 (EA, K, WAG), Kwale District. Jombo Hill; 4°28'S, 39°12'E; alt. 300 m; 07 Jan. 1978 • M.G. Gilbert 5334 (K); Kilifi District, Cha Simba rocks on Mariakani - Kilifi Road; 3°44'S, 39°42'E; alt. 200 m; 16 Feb. 1979 • Mwadime, N 204 (EA); Kwale District, Shimoni, mwamba-wanga area; 4°38'30.17"S, 39°24'12.97"E; alt. 2 m; 13 Dec. 2012 • R.B. Drummond 3983 (K); Kwale District, Jardini Beach, 18 miles south of Mombasa, sea level; 4°19'30"S, 39°34'20"E; 26 Aug. 1953 • R.B. Drummond 4029 (K, U); Kwale District, Mwasangombe Forest, 15 miles S.W. of Kwale; alt. 230 m; 27 Aug. 1953 • R.B. Faden 77/ 397 (K); Kwale District, Kinondo (Ngalani Kaya) Forest; 4°23'30"S, 39°33'30"E; alt. 5 m; 15 Feb. 1977 • R.B. Faden 77/ 437 (K); Kilifi District, just north of Mwarakaya on Chonyi - Ribe road; 3°47'S, 39°42'E; alt. 140 m; 16 Feb. 1977 • S. Rawlins EAH 11275 (K), Witu; 2°23'05.64"S, 40°30'04.68"E; alt. 24 m; Jun. 1957 • S.A. Robertson MDE 293 (EA, K, WAG), Kwale Distr., Dzombo Hill; 4°26'S, 39°13'E; alt. 400 m; 09 Feb. 1989 • S.A. Robertson MDE 46 (K); Kwale District, Mrima hill; 4°29'S, 39°16'E; 03 Feb. 1989 • S.A. Robertson 5929 (K); Kwale District, Kaya Diani; 4°16'S, 39°35'E; alt. 10 m; 10 Nov. 1989 • S.A. Robertson 6465 (EA); Kilifi District, Watamu, Ashe plot; 3°20'S, 40°01'E; alt. 10 m; 28 May. 1991 • S.A. Robertson 7550 (EA, K, WAG, WAG); Kilifi District, Kambe Rocks; 3°51'S, 39°40'E; alt. 120 m; 13 May. 2005. TANZANIA – Dar es Salaam • J. Kirk s.n (K), Dar es Salaam; 6°48'57.96"S, 39°16'49.44"E; Mar. 1860 – Kaskazini Pemba (North Pemba) • P.J. Greenway 2681 (K); Micheweni District, Ras Kigomasha; 4°52'S, 39°41'E; 10 Dec. 1930 – Lindi • K.B. Vollesen 3150 (EA), c. 7km NWN of Kingupina; 8°24'S, 38°31'E; alt. 125 m; 25 Dec. 1975 • R.I. Ludanga 1369 (EA), Selous, Likandage (Utunge); 9°00'S, 37°30'E; 28 Jan. 1972 – Morogoro • L.-P.M.J. Dagallier 60 (DSM, MPU, P, WAG); Mvomero District, Turiani village; 6°09'40.59"S, 37°36'14.48"E; alt. 384 m; 18 Nov. 2019 – Pwani • B.J. Harris 6209 (EA), Approx 6 mls north of Chalinze on

## TAXONOMIC REVISION OF UVARIODENDRON AND UVARIOPSIS

road D'Salaam-Chalinze-Segera; 6°33'23.93"S, 38°19'08.14"E; alt. 274 m; 04 Apr. 1972 • G.A. Peter 24366 (B, K), Useguha; Aug. 1918 – Tanga • G.A. Peter 40249 (B), Usaguha: Hale in Pangani; 5°18'S, 38°36'E; alt. 330 m; 14 May. 1926 • G.A. Peter 52280 (B); Usambara, O Usambara; 5°00'45.96"S, 38°40'43.59"E; 05 Aug. 1915 • H.G. Faulkner 1961 (B, K); Tanga District, Sawa Creek; 5°07'S, 39°06'E; 17 Feb. 1957 • J. Procter 3592 (K); Pangani District, Msumbugwe Forest Reserve; 5°30'15.12"S, 38°45'23.76"E; Apr. 1967 • L.-P.M.J. Dagallier 23 (DSM, MPU, P, WAG), Kilulu Hill, 50km North of Tanga; 4°46'21.58"S, 39°07'33.48"E; alt. 247 m; 08 Nov. 2019 • L.-P.M.J. Dagallier 8 (DSM, K, MPU, P, WAG), forest patch near Msangazi river, along the road from Chalinze to Korogwe-Tanga; 5°34'16.18"S, 38°26'47.01"E; alt. 306 m; 06 Nov. 2019 • L.-P.M.J. Dagallier 9 (DSM, MPU, P, WAG), Kilulu Hill, 50km North of Tanga; 4°46'23.64"S, 39°07'29.07"E; alt. 263 m; 07 Nov. 2019 • M.A. Mwangoka 1356 (MO); Muheza District, Kuze Kibago village. NW part of Kwemnyese public forest patch; 4°54'51"S, 38°43'35"E; alt. 100 m; 01 Jun. 2000 • R.E.S. Tanner 12 (K); Pangani District, Msubugwe Forest; 5°31'59.88"S, 38°43'59.88"E; alt. 100 m; 1955 • R.E.S. Tanner 29 (K); Pangani District, Msubugwe Forest; 5°31'59.88"S, 38°43'59.88"E; alt. 100 m; 1955 • R.E.S. Tanner 3467 (B, K); Pangani District, Mwera, Kwa Besa, Mwanamgaru; 5°29'S, 38°57'E; 28 Mar. 1957 • R.E.S. Tanner 6 (K); Pangani District, Msubugwe Forest; 5°31'59.88"S, 38°43'59.88"E; alt. 100 m; 1955 • T.L.P. Couvreur 34 (DSM, FHO, MO, NHT, WAG, WAG); Handeni District, road 3 km before arriving to Kwedikwazu coming from Dar Es Salaam. At Msangazi river; 5°34'21.6"S, 38°26'46.8"E; alt. 300 m; 14 Nov. 2006 • W.D. Hawthorne 776 (K), Nr Langoni village; 5°28'S, 38°54'E; 27 May. 1982 – Zanzibar Central/South • Vaughan, J 2318 (BM), Kufile cave; 6°25'08.1"S, 39°29'15.85"E; 23 Feb. 1936 – Zanzibar West • Aplin, D 1 (K), Zanzibar: Chumbe I; 6°16'44"S, 39°10'37"E; alt. 5 m; Feb. 1988 • J.H. Vaughan 1689 (K); Magharibi (West) District, Kombeni Cave Well; 6°15'S, 39°16'E; 22 Nov. 1930 • P.J. Greenway 2654 (K); Magharibi (West) District, Haitajwa Hill; 6°16'S, 39°16'E; 04 Dec. 1930 • Vaughan, J 1689 (K), Kombeni caves; 6°15'39.2"S, 39°15'39.95"E; 22 Nov. 1930 • Vaughan, J 1715 (K), Kombeni caves; 6°15'39.2"S, 39°15'39.95"E; 04 Dec. 1930 • Vaughan, J 1731 (EA, K), Kombeni caves; 6°15'39.2"S, 39°15'39.95"E; Dec. 1930 – Unknown major area • Botany Students DSM 1394 (DSM, K, WAG, WAG), Steinbruch Forest Reserve near Maweni, W of Tanga; 5°06'S, 39°01'E; alt. 80 m; 31 Dec. 1969 • G.A. Peter 4487 (B, K, WAG, WAG), Useguha; 6°00'S, 38°15'E; 10 Jun. 1914.

*Uvari dendron mbagoi* Dagallier & Couvreur, PhytoKeys 174: 109 (2021)

**TYPE.** TANZANIA – Tanga • L.-P.M.J. Dagallier 39 (holotype: MPU (MPU1375316); isotypes: DSM, K, MO, MPU (MPU1375317), P, WAG); Handeni District, Kwedijela forest, ~8km Kwamsisi village; 5°54'50.12"S, 38°36'12.35"E; alt. 156 m; 13 Nov. 2019.

**Description.** Tall shrubs to trees 3 – 6 m tall, D.B.H. 5 – 10 cm; young branches sparsely pubescent to glabrous, old branches glabrous; slash with strong bergamot smell (the citrusy smell of *Citrus bergamia* Risso). Leaves distichous, simple, pinnately veined, stiff, greyish green, margins entire, slightly revolute. Petiole 3 – 6.5 mm long, 1.2 – 3 mm wide, sparsely pubescent to glabrous. Leaf lamina 76 – 157 mm long, 31 – 59 mm wide, length:width ratio 2.2 – 3.5, narrowly elliptic to elliptic to obovate, between coriaceous and cartilaginous, base acute to slightly decurrent (sometimes cuneate), apex acute to shortly acuminate, acumen 5 – 10 mm long; glabrous when young and old above, sparsely pubescent to glabrous when young, glabrous when old below; mid rib sunken above, raised below, glabrous above, sparsely pubescent to glabrous when young, glabrous when old below; secondary veins 10 – 13 pairs, weakly brochidodromous, indistinct to slightly impressed above, slightly raised to raised below; tertiary veins reticulate. Inflorescences borne on trunk and old branches, composed of 1 – 2 (3) sessile flowers. Flower pedicel 0 – 0.6 mm long, ca 2 mm in diameter, velutinous. Flowers actinomorphic, hermaphroditic, buds globose, 5 – 9 mm high, 5 – 9 mm in diameter, velutinous, falling off very easily. Only flower



## CHAPTER 4

buds and old fallen flowers seen. Bracts 2 to 5 at base of the pedicel, upper bract 4 – 8 mm long, 10 – 15 mm wide, appressed, enclosing the bud, pubescent outside, glabrous inside. Sepals 3, ca. 7 – 8 mm long, ca. 7 – 12 mm wide (measures taken from bud), imbricate, enclosing the petals in bud, velutinous outside, glabrous inside, brown. Outer petals 3, 4.5 – 5.5 mm long, 4.5 – 5 mm wide (measures taken from bud), length:width ratio ca. 1, ovate, shortly velutinous outside, glabrous inside, color unknown. Inner petals 3, 3.5 – 4.5 mm long, 4 – 4.5 mm wide (measures taken from bud), length:width ratio ca. 1, ovate, glabrous outside, glabrous inside, color unknown. Stamen more than 400, mature length unknown, anthers linear, connective truncate. Carpels 12 to 16, ca. 1.5 mm long, ca. 1 mm wide (measures taken from old flower), velutinous, free; stigma mature length unknown, coiled. Fruiting pedicel 0 – 6 mm long, ca. 4 mm in diameter, pubescent. Monocarps 1 to 7, 20 – 50 mm long, 10 – 12 mm wide, length:width ratio 2 – 4.5, cylindrical, generally curved, longitudinally ridged and slightly constricted between the seeds, tomentose with regular tufts of higher hair density, green-grey; sessile to shortly stipitate, stipe 0 – 1.5 mm long, ca. 5 mm wide, tomentose. Seeds 4 – 17 per monocarp, uniseriate to biseriata, 8 to 8.5 mm long, 5.5 – 6 mm wide, ellipsoid.

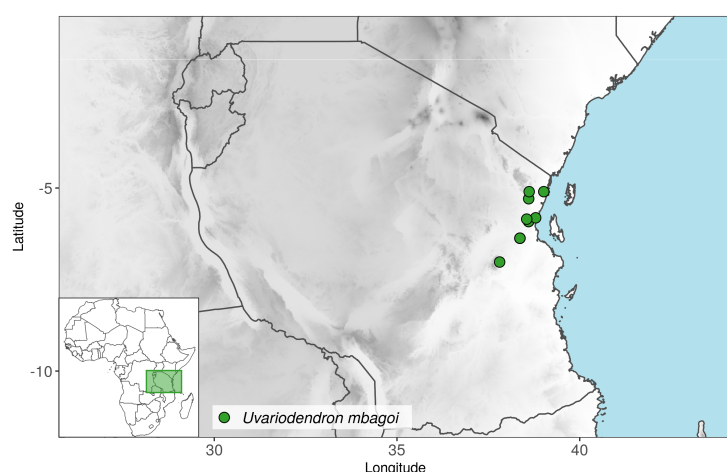


Figure 23: Distribution of *Uvarioidendron mbagoi*

**Distribution.** Tanzania.

**Notes.** This species differs from the other *Uvarioidendron* species by the strong bergamot scent of crushed leaves and bark, by having stiff greyish-green leaves with slightly revolute margins, and by its globose flower buds easily falling off and its tomentose fruits having regular tufts of higher hair density.

**Specimens examined.** TANZANIA – Morogoro • L.-P.M.J. Dagallier 50 (DSM, K, MPU, P, WAG); Morogoro Rural District, Kimboza forest; 7°01'18.38"S, 37°48'32.13"E; alt. 267 m; 15 Nov. 2019 – Pwani • L.-P.M.J. Dagallier 1 (DSM, K, MPU, P, WAG), Msata Hill, 30km North of Chalinze; 6°22'17.78"S, 38°21'49.97"E; alt. 317 m; 06 Nov. 2019 • L.-P.M.J. Dagallier 3 (WAG), Msata Hill, 30km North of Chalinze; 6°22'17.09"S, 38°21'50.23"E; alt. 328 m; 06 Nov. 2019 • L.-P.M.J. Dagallier 6 (WAG), Msata Hill, 30km North of Chalinze; 6°22'17.93"S, 38°21'49.94"E; alt. 323 m; 06 Nov. 2019 • T.L.P. Couvreur 3 (DSM, WAG, WAG); Bagamoyo District, Mazizi hill, on road between Chilinze and Wami River; 6°22'14.4"S, 38°21'51"E; alt. 100 m; 09 Nov. 2006 • U. Bloesch s.n (WAG), Kwedijela Coastal Forest, T3; 5°55'S, 38°36'E; 18 Sep. 2004 – Tanga • C.M. Kisena 3039 (MO); Handeni District, T3; Collected from Kwedivikilo sacred forest near Manga Village; 5°06'S, 38°37'E; 17 Nov. 1997 • F.M. Mbago 3323 (DSM, K); Handeni District, Kwedijela forest, 8km Kwamsisi village; 5°51'S, 38°33'E; 07 Oct. 2004 • G.A. Peter 52283 (B, K, WAG); Pangani District, Useguha. Inseln des Pangani bei Hale; 5°17'34.8"S, 38°36'14.06"E; alt. 340 m; 31 Jan. 1915 • L.-P.M.J. Dagallier 40 (DSM, K, MO, MPU, P, WAG); Handeni District, Kwedijela forest, ~8km Kwamsisi village; 5°54'50.77"S, 38°36'13.27"E; alt. 155 m; 13 Nov. 2019 • T.C.E. Congdon

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532 (K); Pangani District, Mkwaja Ranch; 5°48'50.76"S, 38°47'40.92"E; alt. 90 m; 04 Dec. 1998 • W.D. Hawthorne 1420 A (K), Mkulumuzi river, karst river valley, Steinbruch reserve; 5°06'S, 39°01'00.12"E; 12 Aug. 1982.

*Uvari dendron molundense* (Diels) R.E.Fr., Acta Horti Berg. x. 61 (1930)

*Uvaria molundensis* Diels, Bot. Jahrb. Syst. 53(3-5): 435 (1915)

*Uvaria letestui* Pellegr., Bull. Mus. Natl. Hist. Nat. xxvi. 658 (1920).

*Uvaria gossweileri* Exell, J. Bot. 64 (Suppl. 1): 3 (1926)

*Uvaria mannii* Hutch. & Dalziel, Fl. W. Trop. Afr. I. 50 (1927); Kew Bull 150 (1927)

*Uvaria mayumbense* Exell, J. Bot. 64 (Suppl. 1): 3 (1926)

*Uvari dendron mayumbense* (Exell) R.E.Fr., Acta Horti Berg. x. 57 (1930)

*Uvari dendron letestui* (Pellegr.) R.E.Fr., Acta Horti Berg. x. 60 (1930)

**TYPE.** CAMEROON – East Region • G.W.J. Mildbraed 4373 (holotype: B), Südkameruner Waldgebiet: Bezirk Molundu, 'Bange Busch', unbewohnter Urwald zwischen Lokomo, Bumba und Bange; 2°50'N, 15°15'E; 29 Jan. 1911.

**Description.** Tree to shrub 1.2 – 10 m tall, D.B.H. 1.5 – 20 cm; young branches sparsely pubescent to glabrous, old branches glabrous. Leaves distichous, simple, pinnately veined, margins entire, flat. Petiole 4 – 17 mm long, 1.5 – 5 mm wide, sparsely pubescent to glabrous. Leaf lamina (180) 200 – 460 mm long, 51 – 160 mm wide, length:width ratio 2.2 – 4.8, elliptic to oblong to obovate, coriaceous, base acute to rounded (sometimes minutely decurrent at the very base), apex attenuate to acuminate, acumen 2 – 38 mm long; glabrous when young and old above, sparsely pubescent to glabrous when young, glabrous when old below; mid rib sunken above, raised below, glabrous above, sparsely pubescent to glabrous below; secondary veins 12 – 22 pairs, brochidodromous to weakly brochidodromous, impressed above, raised below; tertiary veins reticulate. Inflorescences borne on trunk and branches or axillary, composed of 1 flower. Flower pedicel 2 – 14 mm long, 1 – 4 mm in diameter, pubescent. Flowers actinomorphic, hermaphroditic, buds globose, sessile, 3.5 – 9 mm high, 4 – 14 mm in diameter, velutinous. Bracts 1 to 6, upper bract 3 – 8 mm long, 3 – 10 mm wide, broadly ovate, clasping the pedicel, velutinous outside, glabrous inside. Sepals 3, 5 – 9 (14) mm long, 5 – 10 mm wide, imbricate (sometime fused at base), velutinous outside, glabrous inside, green to brown. Outer petals 3, 12 – 30 mm long, 9 – 22.5 mm wide, length:width ratio 1.1 – 2.5, elliptic, pubescent outside, pubescent at apex to glabrous inside, light yellow to cream outside, purple with cream margins inside. Inner petals 3, 11 – 27 mm long, 8 – 20 mm wide, length:width ratio 1.2 – 2.4, obovate, pubescent outside, glabrous inside, light yellow to cream outside, purple with cream margins inside. Stamen more than 1000, 0.8 – 2.5 mm long, 0.1 – 1 mm wide, anthers linear, connective truncate. Carpels 8 to 40, 1 – 5 mm long, 0.5 – 2 mm wide, pubescent, free; stigma 0 – 2 mm long, 1 – 1.5 mm wide, coiled, densely pubescent, covered with

an exudate at anthesis. Fruiting pedicel 3 – 15 mm long, 2.5 – 6 mm in diameter, pubescent to glabrous. Monocarps 2 to 10, 21 – 60 mm long, 9 – 30 mm wide, length:width ratio 1.3 – 3.4, cylindrical, generally straight, truncate or rounded at apex, pubescent to glabrate, greyish green to orange; sessile to shortly stipitate, stipe 0 – 4 mm long, 2 – 4 mm wide, pubescent to glabrate. Seeds 3 – 10 per monocarp, biseriate, 12 to 14 mm long, 7 – 10 mm wide, semicircular, pale brown to pinkish brown.

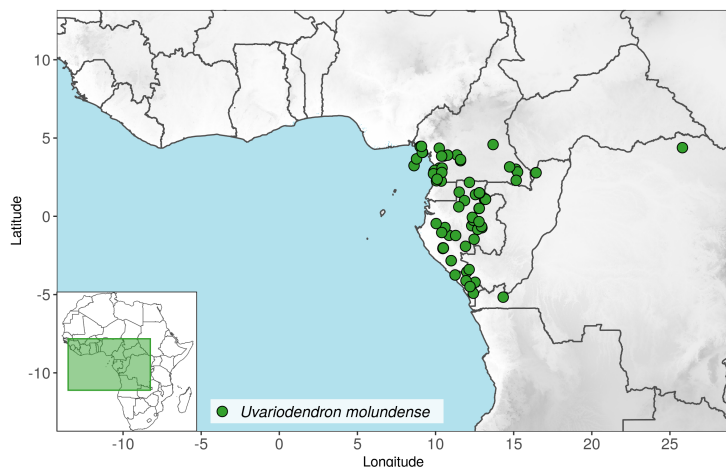


Figure 24: Distribution of *Uvariodendron molundense*

Mariga [Maringa?]; 4°55'S, 12°25'E; 17 Jan. 1916. CAMEROON – Central Region • D. Dang 643 (P, YA), colline 'ZOABISSIM' dans l'appellation locale, 4km environ N du village EKEKAM; 3°55'N, 11°22'E; alt. 1085 m; 09 Mar. 1978 • F. Tadjouteu 566 (K, YA), Ndanan 1, Mefou National park, 18km from MFOU; 3°33'N, 11°36'02.47"E; alt. 700 m; 22 Mar. 2004 • M.R. Cheek 11839 (YA), Ndanan 1, Eastern part of the park, West of Ndangan 1; 3°37'19"N, 11°36'03"E; alt. 710 m; 18 Mar. 2004 – East Region • J.F. Villiers 625 (P, YA), Camp CFA Bango I, bord de la riv. Bango 36km SE Bateka Malen, village situé à 21km N de Molundou (Feuille IGN Molundou 1/200.000); 2°17'49.56"N, 15°09'41.81"E; 08 Nov. 1971 • R.G. Letouzey 3117 (P, YA), Bertoua, Kap; 4°35'N, 13°40'50"E; 23 Feb. 1960 • R.G. Letouzey 5142 (P, YA), a 30km au NE de Bangé (km75 route Yokadouma - Molundu) feuille IGN 1/200 000. Yokadouma; 3°00'25.8"N, 15°08'13.99"E; 25 May. 1963 • T.L.P. Couvreur 1195 (MPU, WAG, YA), 60 km south of Yokadouma, 30 km after Ngato, 15 km after river. ALPICAM 'base de vie', then on forestry road starting 4 km before Maséa village; 3°09'19"N, 14°44'16.87"E; alt. 613 m; 04 Mar. 2019 – Littoral • T.L.P. Couvreur 1172 (MPU, P, WAG, YA), Mapubi, 30 km before Edea on Yaoundé-Edea road. On forestry road, 5 km direction to Sanaga river; 3°50'39.26"N, 10°23'22.88"E; alt. 164 m; 28 Feb. 2018 • T.L.P. Couvreur 613 (MPU, YA), Ebo Wildlife Reserve, Djuma permanent camp. On Djashaka trail; 4°21'06.18"N, 10°14'12.1"E; alt. 378 m; 13 Feb. 2014 • T.L.P. Couvreur 652 (WAG, YA), Mambe Massif, above Boga village, 100 km along road from Yaoundé to Edea; 3°54'36.26"N, 10°46'31.86"E; alt. 637 m; 19 Jun. 2014 • T.L.P. Couvreur 655 (MPU, WAG, YA), Mambe Massif, above Boga village, 100 km along road from Yaoundé to Edea; 3°54'29.55"N, 10°46'20.29"E; alt. 657 m; 19 Jun. 2014 • T.L.P. Couvreur 656 (WAG, YA), Mambe Massif, above Boga village, 100 km along road from Yaoundé to Edea; 3°54'24.79"N, 10°46'17.82"E; alt. 653 m; 20 Jun. 2014 • W.J.J.O. de Wilde 1420 (K, MO, P, WAG, WAG), 40 km NW. of Eséka, W. of Yaoundé; 3°51'N, 10°32'E; 12 Dec. 1963 – South Region • B.-A. Nkongmeneck 800 (YA); Océan, environs de Mvini, à 34km E de Campo. Feuille IGN 1/200 000 Kribi-Nyabessa; 2°22'18.12"N, 10°06'15.48"E; 24 Oct. 1984 • G.A. Zenker 3511 (BM, K, L, P), Kamerun, Bipinde; 3°05'N, 10°25'E; 1908 • G.P. Tchouto Mbatchou T8X 70 (WAG), Campo Ma'an area, Bibabimvoto, Dipikar island, in the Campo area along transect T8; 2°16'16"N, 10°03'35"E; alt. 60 m; 26 Aug. 2000 • G.W.J. Mildbraed 5936 (B, K), S. Cameroon: Kribi; 2°48'N, 10°24'E; 1911 • J.J. Bos 3259 (P, WAG, YA), About 13 km from Kribi, Ebolowa road; 2°51'N, 10°00'E; 13 Nov. 1968 • J.J. Bos 5474 (BR, MO, P, WAG, WAG, YA), S. bank of Lobé river, SE. of Gr. Batanga ferry; 2°52'N, 9°54'E; 11 Oct. 1969 • J.J. Bos 6521 (WAG), 6 km N. of km 46 Kribi - Lolodorf; 3°05'N, 10°15'E; 12 Mar. 1970 • J.J. Bos 7075 (P, WAG, WAG), 5 km N. of km 7 Kribi - Ebolowa road, behind Pygmeé village; 2°56'N, 9°57'E; 10 Jul. 1970 • M.E. Elad 1270 (KRIBI, WAG), Campo-Ma'an area, Bibabimvoto, along transect T4; 2°15'03"N, 10°21'51"E; alt. 40 m; 01 Feb. 2000 • T.R. van Andel 4228 (KRIBI, U, WAG, WAG, YA), Campo Ma'an area, Boussebeliga. Trail to Bimvoa chute; 2°43'N, 9°52'E; alt. 40 m; 26 Oct. 2001 – South-West Region • B. Sonké

**Distribution.** Cameroon, Democratic Republic of the Congo, Gabon, Equatorial Guinea (Bioko Island), Republic of the Congo.

**Notes.** This species present a great morphological variability and has no specific character that clearly differentiate it from the other species.

**Specimens examined.** ANGOLA – Cabinda

• J. Gossweiler 6159 (BM), Mayombe Pango

## TAXONOMIC REVISION OF UVARIODENDRON AND UVARIOPSIS

1226 (K, SCA); Ndian, Dikome; 4°27'N, 9°01'E; 05 May. 1994 • B.N. Khayota 537 (K, SCA, YA), Upper Boando, footpath to south of village; 4°05'N, 9°10'E; alt. 650 m; 14 Mar. 1995 • D. Kenfack 1509 (MO), Mokoko, at the center base forest; 4°27'N, 9°04'00.12"E; 25 Apr. 2001 • G.P. Tchouto Mbatchou 136 (K, SCA, YA), Mapanja; 4°05'N, 9°09'E; alt. 1040 m; 20 Apr. 1992 • G.P. Tchouto Mbatchou 611 (K, SCA, YA), Mokoko, forest above Bonja village; 4°28'N, 9°06'E; alt. 240 m; 23 Mar. 1993 • M. Akogo 234 (K, SCA, YA), Ekumbe Mofako, Mokoko Forest Reserve, Ekumbe-Mofako; 4°28'N, 9°03'E; alt. 140 m; 21 Apr. 1994. CENTRAL AFRICAN REPUBLIC – Sangha-Mbaéré • D.J. Harris 5112 (E, MO), Kongana research camp, 25 km SE of Bayanga; 2°47'N, 16°25'E; 08 Jun. 1994 • D.J. Harris 5504 (E, MO), Kongana camp, 22 km SE of Bayanga; 2°47'N, 16°26'E; 11 Feb. 1996. DEMOCRATIC REPUBLIC OF THE CONGO – Bas-Congo • P. Compère 1112 (K), vallée de la Quinongo. Territ: Songololo. Province: Léopoldville; 5°09'57.72"S, 14°19'37.82"E; 21 Dec. 1959 – Orientale • P. Gérard 5604 (K, WAG); Ango, Digba, Forêt de Akare entre rivière Bili et Ase; 4°23'N, 25°48'E; 05 Nov. 1963. EQUATORIAL GUINEA – Bioko Norte • G. Mann 257 (K, P); 3°40'N, 8°47'E; 1860 – Bioko Sur • W.R.Q. Luke 11889 (EA), Moaba. Pt 140; 3°14'06"N, 8°37'22"E; alt. 8 m; 15 Mar. 2007. GABON – Moyen-Ogooué • T.L.P. Couvreur 928 (LBV, WAG, YA), 27 km after Lambaréné, on road to Bifoum (N1), then around 20 km on road to Lake Azingo; 0°27'52.7"N, 10°02'18.45"E; alt. 95 m; 24 Nov. 2015 • T.L.P. Couvreur 932 (LBV, WAG, YA), 33 km south of Lambaréné, then 18 km on dirt road just after Mimongo village, in Morel petrol concession; 1°02'10.4"S, 10°23'39.95"E; alt. 185 m; 25 Nov. 2015 – Ngounié • G.M.P.C. Le Testu 5762 (BM, P), Mbigou, Mboumi riverside; 1°55'S, 11°55'E; 18 Nov. 1925 • G.V. Dauby 574 (LBV, MO), Est du Parc National de Waka, à ± 5 km au Sud de la rivière Mayi; 1°13'36.73"S, 11°17'09.31"E; alt. 604 m; 17 Feb. 2008 • J.C. Arends 450 (LBV, WAG, WAG), Waka River; 1°13'S, 10°52'E; alt. 330 m; 25 Nov. 1984 • O.L.S. Lachenaud 1444 (BRLU, LBV, MO), Mabounié, piste du nord-est; 0°43'02"N, 10°36'05"E; 17 Nov. 2013 • P.J.M. Maas 10207 (LBV, WAG), side roads of road Pény-Mouila, in CBG concession; 2°00'45.1"S, 10°28'52.7"E; alt. 115 m; 10 Nov. 2011 – Nyanga • G.M.P.C. Le Testu 1211 (BM), Tchibanga area, Nganda; 2°50'S, 11°00'E; 31 Oct. 1907 • G.M.P.C. Le Testu 1234 (BM, P, P), Tchibanga; 2°50'S, 11°00'E; Nov. 1907 – Ogooué-Ivindo • A. Mougazi 1631 (LBV, MO, P, WAG), Ivindo National Park, route Langoué, rivière Niadou; 0°15'N, 12°25'E; 05 May. 2004 • A. Mougazi 223 (P), Makokou, 10km S de Makokou; 0°30'30.82"N, 12°47'45.59"E; alt. 500 m • E. Bidault 2248 (BR, BRLU, LBV, MO, MO, P, WAG), concession forestière Rougier-Ivindo; 0°04'05"N, 12°21'15"E; alt. 460 m; 28 Oct. 2015 • J. Florence 930 (P), Station d'Ipasa, 10 Km S de Makokou; 0°30'N, 12°47'E; alt. 500 m; 14 Apr. 1978 • N. Hallé 3264 (L, P, U), Bélinga; 1°05'N, 13°08'E; 19 Nov. 1964 • N. Hallé 3332 (P), Bélinga; 1°05'N, 13°08'E; 25 Nov. 1964 • N. Hallé; A. Le Thomas 431 (MO, P, WAG), Bélinga, mines de fer, le long de la rivière Folley; 1°07'N, 13°11'E; 12 Aug. 1966 • N. Hallé; A. Le Thomas 451 (MO, P), Bélinga, mines de fer, route du Belvédère; 1°05'N, 13°12'E; alt. 900 m; 12 Aug. 1966 • T.L.P. Couvreur 564 (YA), along main trail departing from behind the herbarium at the Research station of Ipasa, in Ivindo National Park; 0°30'13.77"N, 12°47'36.4"E; alt. 519 m; 11 Nov. 2013 – Ogooué-Lolo • A.M. Louis 648 (WAG), ± 70 km N.W. of Lastoursville, along rd. to Achouka, old forest along Lolo R. near Wagny settlement; 0°36'N, 12°19'E; alt. 250 m; 13 Nov. 1983 • F.J. Breteler 13331 (WAG), near Bambidie, E of Lastoursville; 0°44'N, 12°58'E; alt. 300 m; 16 Oct. 1994 • G.M.P.C. Le Testu 8437 (BM, P), region de Lastoursville, Nzocou; 1°28'S, 12°28'E; 12 Oct. 1930 • G.M.P.C. Le Testu 9649 (P), region de Lastoursville, Lastoursville; 0°50'N, 12°42'E; 1934 • J.J. Wieringa 6223 (LBV, MO, WAG, WAG), c.55 km N of Lastoursville, CEB forestry concession 'Milolé' (UFA2-UFG2-lot2), foothills of Ngota Mountain; 0°20'24"N, 12°46'48"E; alt. 330 m; 28 Jan. 2008 • J.J. Wieringa 6263 (LBV, MO, WAG, WAG), c.30 km ENE of Lastoursville, 15 km on forestry road from Bambidie to Akieni; 0°39'11.4"N, 12°56'36.6"E; alt. 320 m; 29 Jan. 2008 • T.L.P. Couvreur 1110 (LBV, WAG), Lastoursville, in Precious Woods concession (CEB). 30 km east of Bambidie village, 55 km from Lastoursville; 0°39'46.04"N, 12°45'55.58"E; 07 Jun. 2016 – Ogooué-Maritime • M.S.M. Sosef 2270 (LBV, WAG), Doudou Mountains National Parc, c. 5 km S of Camp Peny (CBG); 2°03'30"S, 10°28'12"E; alt. 100 m; 14 Nov. 2005 • T.L.P. Couvreur 539 (MPU, YA), 5 km on loggers road from Peny (CGB) village; 2°01'55.92"S, 10°29'59.48"E; alt. 188 m; 07 Nov. 2013 • T.L.P. Couvreur 542 (MPU, YA), 5 km on loggers road from Peny (CGB) village; 2°01'53.63"S, 10°29'45.29"E; alt. 200 m; 07 Nov. 2013 – Woleu-Ntem • G.M.P.C. Le Testu 9064 (P), region de Minvoul, Minvoul; 2°10'N, 12°10'E; Mar. 1933 • L. Ngok Banak 1570 (LBV, LBV, MO, P, WAG), Minkébé National Park, southern inselberg area; 1°23'10.2"N, 12°33'17.4"E; alt. 620 m; 02 May. 2003 • M.S.M. Sosef 1894 (WAG), forestry concession Bordamur, c. 40 km NE of Mitzic; 1°00'06"N, 11°51'12"E; alt. 500 m; 06 Feb. 2003 • MINKÉbé Series W 15 (WAG), Minkébé area, near base camp number 1; 1°29'N, 12°49'E; 08 Feb. 1990 • MINKÉbé Series V 150 (WAG), Minkébé area, 10 x 10 m inventory plot V, placed 3.5-13.5 m north at 200-210 m on transect A; 1°30'N, 12°48'E; 04 Mar. 1990 • MINKÉbé Series W 403 (WAG), Minkébé area, 800 m on transect B (to the south); 1°30'N, 12°48'E; 20 May. 1990 • MINKÉbé Series AM 60 (WAG), Minkébé area, at 2000 m from the camp; 1°30'N, 12°48'E; 25 Mar. 1990 • T.L.P. Couvreur 853 (LBV, WAG, YA), Oyem, on road to Mbolonzok (off main road to Mongono and Equatorial Guinea); 1°32'39.18"N, 11°30'43.04"E; alt. 660 m; 13 Nov. 2015 • T.L.P. Couvreur 876 (LBV, WAG, YA), on road from Mitzic to Lalara (N2), just after the bridge over the Lara, c.500 m in forest; 0°36'12.83"N, 11°29'11.53"E; alt. 580 m; 15 Nov. 2015.

## CHAPTER 4

REPUBLIC OF THE CONGO – Kouilou • C. Farron 4882 (P), Pointe Noire, route du chantier de Boungolo (Pointe-Noire); 4°07'S, 11°57'E; 31 Jan. 1966 • Mianga N'Bissy 183 (P), Moyen Congo, Mayombe central, vers km 57 chemin de fer Pointe Noire – Brazzaville; 4°29'27"S, 12°12'15"E; Sep. 1947 • P. Sita 3759 (P), route du nouveau campement Maamar sur 18 km après l'ancien; 3°45'S, 11°15'E; 09 May. 1974 • T.L.P. Couvreur 789 (IEC, WAG), 30 km on Dolisie-Mvouti road, just behind the telephone antenna; 4°12'49.31"S, 12°31'44.71"E; alt. 710 m; 21 Sep. 2015 – Niari • P. Cabalion 153 (P), 3km O Banga Route Vounda-Banda; 3°33'18.97"S, 11°59'56.48"E; 06 Feb. 1976 • P. Sita 3995 (P), Niari-ouest, region Banda, Vallé de la Ngouanga; 3°24'S, 12°09'E; 05 Nov. 1975.

### *Uvariodendron mossambicense* Robson ex Dagallier, **sp. nov.**

**TYPE.** MOZAMBIQUE – Manica • F. de A. Mendonça 2558 A (holotype: WAG (WAG.1418614); isotypes: LISC, COI), Chimoio, Cataratas do Rio Revué; 19°37'S, 33°31'E; 23 Oct. 1944.

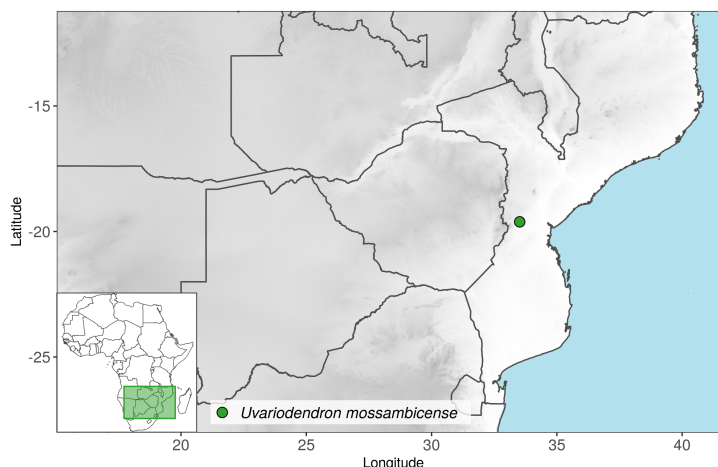
**Diagnosis.** This species can be differentiated from other species by the combination of the following characters: narrowly elliptic leaves less than 140 mm long with acute to slightly decurrent base, flowers with ca. 5 carpels and monocarps with stipe ca. 12 mm long.

**Description.** Small tree height unknown, D.B.H. unknown; young branches pubescent to glabrous, old branches glabrous; leaf bud 'eragrostiform', composed of 7, distichous, longitudinally folded, velutinous scales. Leaves distichous, simple, pinnately veined, margins entire, flat. Petiole 3 – 5 mm long, ca. 1.5 mm wide, glabrous. Leaf lamina 80 – 135 mm long, 30 – 50 mm wide, length:width ratio ca. 3, narrowly elliptic, coriaceous, base acute to slightly decurrent, apex attenuate, glabrous when young and old above, glabrous when young and old below; mid rib sunken above, raised below, glabrous above, glabrous below; secondary veins 10 – 16 pairs, brochidodromous, impressed above, raised below; tertiary veins reticulate. Inflorescences borne on branches, composed of 1 flower. Flowers actinomorphic, hermaphroditic, buds globose, sessile, ca. 6 mm high, ca. 6.5 mm in diameter, velutinous. Only flower bud seen. Bracts 2 to 5, upper bract ca. 4 mm long, ca. 7 mm wide, broadly ovate, appressed, half-enclosing the flower bud, velutinous outside. Sepals 3, 4 – 5 mm long, ca. 6 mm wide (measures taken from bud), broadly ovate, fused at base on almost 50 % of their length, forming a 3-lobed cupule, velutinous outside, glabrous inside. Outer petals 3, ca. 5 mm long, ca. 5 mm wide (measures taken from bud), length:width ratio ovate, velutinous outside. Inner petals 3, length, shape, indumentum and color unknown. Stamen numerous, length unknown, anthers linear. Carpels ca. 5, unknown, glabrous, free; stigma unknown, pubescent. Fruiting pedicel unknown. Monocarp 1 seen, ca. 37 mm long, ca. 9 mm wide, length:width ratio ca. 4.1, cylindrical, curved, slightly acuminate, glabrous, (monocarp found in the pocket of the specimen); stipitate, stipe ca. 12 mm long, ca. 3 mm wide, glabrate. Seeds 4 per monocarp, uniseriate, size and shape unknown.

**Distribution.** Only known from one locality in Mozambique: Chimoio, near the falls of Revué river.

**Etymology.** The specific epithet comes from the country where the single specimen of this species was found.

**Notes.** This species closely resembles *Ud. dzomboense* by its narrowly elliptic and small (less than 14 cm) leaves with acute to slightly decurrent base. However, *Ud. mossambicense* has flower buds ca. 6 mm in diameter (vs



ca. 4 mm in *Ud. dzomboense*), covered by 2 – 5 velutinous bracts ca. 4 mm long (vs. 6 sparsely pubescent bracts 5 – 6 mm long). *Ud. mossambicense* has ca. 5 carpels (vs. 50 – 75 in *Ud. dzomboense*) and monocarps with stipe ca. 12 mm long (vs. sessile monocarps).

***Uvari dendron occidentale*** Le Thomas, *Adansonia sér.* 2, 7: 251 (1967)

**TYPE.** IVORY COAST – Oumé • A. Aubréville 4140 (P), Oume, région d'Oumé; 6°23'N, 5°25'W; 28 Feb. 1957.

**Description.** Tree 5 – 10 m tall, D.B.H. up to 15 cm; young branches glabrous, old branches glabrous. Leaves distichous, simple, pinnately veined, margins entire, flat. Petiole 5 – 10 mm long, 1 – 3 mm wide, sparsely pubescent to glabrous. Leaf lamina 170 – 350 mm long, 55 – 95 mm wide, length:width ratio 2.5 – 3.7, elliptic to obovate, coriaceous, base acute to decurrent, apex acuminate, acumen 7 – 21 mm long; glabrous when young and old above, sparsely pubescent to glabrous when young, glabrous when old below; mid rib sunken above, raised below, glabrous above, glabrous below; secondary veins 10 – 18 pairs, weakly brochidodromous, impressed above, raised below; tertiary veins reticulate. Inflorescences borne on trunk, composed of 1 flower. Flower pedicel 6 – 16 mm long, 1 – 2 mm in diameter, pubescent. Flowers actinomorphic, hermaphroditic, buds globose, pedicellate, 4 – 6 mm high, 7 – 8 mm in diameter, pubescent. Bracts 1 to 3, upper bract 2.5 – 4 mm long, 4.5 – 5 mm wide, ovate, semi-clasping to clasping the pedicel, pubescent outside, pubescent inside. Sepals 3, 3 – 5 mm long, 2.5 – 6 mm wide, depressed ovate to broadly triangular, fused in a ring, pubescent outside, glabrous inside, color unknown. Outer petals 3, 15 – 25 mm long, 10 – 17 mm wide, length:width ratio 1.4 – 1.6, elliptic, pubescent outside, glabrous inside, yellow with purple marks on the margins outside, yellow with purple marks inside. Inner petals 3, 10 – 21 mm long, 6 – 10 mm wide, length:width ratio obovate, pubescent outside, glabrous inside, color unknown. Stamen more than 600, 2 – 2.5 mm long, 0.4 – 0.5 mm wide,



## CHAPTER 4

anthers linear, connective truncate and puberulent. Carpels 20 to 40, 3 – 4 mm long, 1 mm wide, pubescent, free; stigma 0.5 – 1 mm long, 1 mm wide, coiled, pubescent. Fruiting pedicel 15 – 22 mm long, 2 – 3.5 mm in diameter, pubescent to glabrous. Monocarps 6 to 11, 17 – 50 mm long, 7 – 20 mm wide, length:width ratio 1.6 – 2.7, cylindrical, curved, longitudinally ridged, acuminate, pubescent to glabrate, color unknown; stipitate, stipe 5 – 12 mm long, 1 – 2.5 mm wide, puberulent. Seeds 9 – 14 per monocarp, biseriata, 7 to 5 mm long, ca. 5 mm wide.

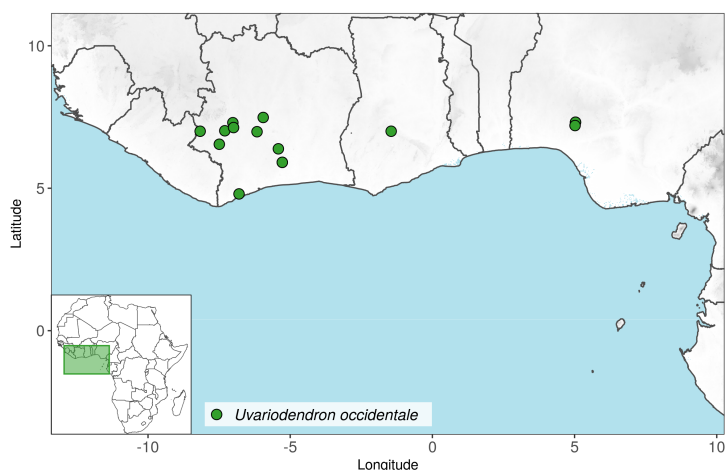


Figure 26: Distribution of *Uvariodendron occidentale*

**Distribution.** Ghana, Ivory Coast, Nigeria.

**Notes.** This species resembles *Ud. fuscum* and *Ud. molundense* but can be differentiated in having leaf bases acute to decurrent (vs. acute to rounded), flower slender flower pedicel 6 – 16 mm long and 1 – 2 mm wide (vs. flower subsessile in *Ud. fuscum* and flower pedicel rather short and thick 2 –

14 mm long and 2 – 4 mm wide in *Ud. molundense*), and sepals 3 – 5 mm long fused at base forming a ring (vs. 11 – 55 mm long and fused in *Ud. fuscum* and 5 – 9 mm long and free in *Ud. molundense*). A. Le Thomas initially named this species *Ud. occidentalis*. However, *Uvariodendron* is neutral (*dendron* -tree- is neutral in Greek), the termination of *occidental* -western- should be -e and not -is. It is thus corrected here as *Ud. occidentale*.

**Specimens examined.** GHANA – Ashanti Region • J.E. Andoh 4171 (K, P), Ofin Headwaters Reserve; 7°00'N, 1°27'W; Apr. 1936. IVORY COAST – Bouaflé • C.C.H. Jongkind 4349 (WAG), Parc National de la Marahoue. Near south border; 6°59'N, 6°10'W; alt. 250 m; 11 Feb. 1998 – Daloa • F.N. Kouamé 1443 (CSRS, G), F.C. du Haut-Sassandra, Nord. forêt dégradée, relevé FNK14; 7°01'N, 7°18'W; 04 Apr. 1995 • F.N. Kouamé 1486 (CSRS, G), F.C. du Haut-Sassandra, Centre. forêt dégradée de pente, relevé FNK14, entre layons 10 et 11; 7°00'N, 8°10'W; 13 Apr. 1995 • F.N. Kouamé 1487 (G), F.C. du Haut-Sassandra, Centre, forêt dégradée, relevé FNK14; 7°07'45.48"N, 6°59'29.4"W; 13 Apr. 1995 – Divo • L. Aké Assi 4633 (P), Divo, Forêt Classée de, Forêt de Divo; 5°54'30.6"N, 5°16'41.52"W; alt. 155 m; 11 Jun. 1958 • L. Aké Assi 6629 (G), Divo, Forêt Classée de, Forêt de Divo; 5°54'30.6"N, 5°16'41.52"W; alt. 155 m; Nov. 1962 – Guiglo • A. Aubréville 1224 (P), Guiglo, Debokun; 6°32'37.26"N, 7°29'36.58"W; 18 Apr. 1932 • A. Bakayoko 21 (G), Guiglo, Zaipobly, forêt sur colline; 7°29'N, 5°57'W; 27 Jan. 2001 – San-Pédro • L. Aké Assi 17192 (G), route de Tabou, forêt près de Para; 4°48'N, 6°48'W; 28 Dec. 1985 – Unknown major area • F.N. Kouamé 1623 (CSRS, G), Daloa F.C. du Haut-Sassandra, Nord. forêt très dégradée sur cuirasse, relevé FNK23; 7°18'N, 7°01'W; 07 Feb. 1995 • Unknown 1780 (P), Bords de l'Agnéby, Mudjika; Feb. 1933. NIGERIA – Ondo State • Anakwense, F FHI 19701 (K); Akure, Akure Forest Reserve; 7°19'N, 5°02'E; 11 Dec. 1950 • K. Obeng-Darko 182 (K); Akure, Owena Forest Reserve, Owena; 7°12'N, 5°01'E; 20 Feb. 1946 • R.W.J. Keay FHI 24604 (K); Akure, Akure Forest Reserve, Block 6C Akure FR; 7°19'N, 5°02'E; 28 Oct. 1948.

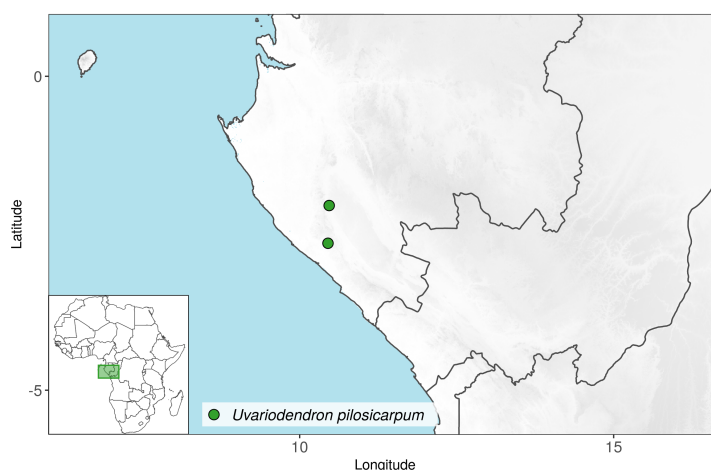
*Uvariodendron pilosicarpum* Dagallier, sp. nov.

**TYPE.** GABON – Nyanga • J.L.C.H. van Valkenburg 2540 (holotype: WAG (WAG.1418718); isotypes: BR (BR0000009320413), E, K, LBV, MO, P, WAG (WAG.1418719, WAG.1418720)), concession SFN; 2°39'34.2"S, 10°27'03"E; alt. 200 m; 01 Nov. 2003.

**Diagnosis.** This species can be differentiated from the other *Uvariodendron* species by the combination of the following characters: largest leaves smaller than 25 cm, obovate leaves with base decurrent, and monocarps ellipsoid, curved, acuminate and densely pubescent

**Description.** Tree 4 – 8 m tall, D.B.H.

ca. 8 cm; young branches sparsely pubescent to glabrous, old branches glabrous. Leaves distichous, simple, pinnately veined, margins entire, flat. Petiole 4 – 7 mm long, 1.5 – 2.5 mm wide, sparsely pubescent to glabrous. Leaf lamina 178 – 243 mm long, 60 – 87 mm wide, length:width ratio 2.3 –



3.6, obovate, coriaceous, base decurrent, apex acuminate, acumen 13 – 21 mm long; glabrous when young and old above, sparsely pubescent to glabrous when young, glabrous when old below; mid rib sunken above, raised below, glabrous above, glabrous below; secondary veins 12 – 19 pairs, weakly brochidodromous, impressed above, raised below; tertiary veins reticulate. Inflorescences borne on trunk and branches, composed of 1 flower. Flower pedicel unknown. Flowers actinomorphic, hermaphroditic, buds unknown. Mature flower unknown, measures taken from fruits. Bracts 1, upper bract ca. 10 mm long, ca. 12 mm wide, broadly ovate, semi clasping the pedicel, velutinous outside, glabrous inside. Sepals 3, 9 – 10 mm long, 12.5 – 18 mm wide (measures taken from young fruits), imbricate, pubescent outside, glabrous inside, color unknown. Outer petals unknown,. Inner petals unknown,. Stamen unknown. Carpels ca. 30,, free. Fruiting pedicel 8 – 13 mm long, 3.5 – 5.5 mm in diameter, pubescent to sparsely pubescent. Monocarps 6 to 30, 23 – 32 mm long, 10 – 15 mm wide, length:width ratio 2.2 – 2.3, ellipsoid, curved, acuminate at apex, densely velutinous, bright green with brown indumentum to glaucous with silvery indumentum, with resinous fragrance when cut; sessile to shortly stipitate, stipe 0 – 2 mm long, 2 – 3 mm wide, densely pubescent. Seeds unknown.

**Distribution.** Gabon.



**Etymology.** The specific epithet refers to the densely pubescent monocarps, characteristic of this species.

**Notes.** This species resembles *Ud. molundense* and *Ud. citriodorum* but can be differentiated in having the longest leaves smaller than 25 cm (vs longest leaves greater than 25 cm long), obovate leaves (vs. elliptic to oblong to obovate leaves), with base decurrent (vs. base rounded to convex) and monocarps ellipsoid, curved, acuminate and densely pubescent (vs. monocarps cylindrical, straight and pubescent to glabrate).

**Specimens examined.** GABON – Ogooué-Maritime • M.S.M. Sosef 2261 (BR, K, LBV, MO, WAG), Doudou Mountains National Parc, c. 5 km S of Camp Peny (CBG); 2°03'30"S, 10°28'12"E; alt. 100 m; 14 Nov. 2005.

*Uvariadendron pycnophyllum* (Diels) R.E.Fr., Acta Horti Berg. x. 58 (1930)

*Uvaria pycnophylla* Diels, Bot. Jahrb. Syst. 53(3-5): 434 (1915)

**TYPE.** TANZANIA – Tanga • Brönnle 1876 (lectotype, here designated: FHO (00060171); sheet from B lost or destroyed); Lushoto District, Amani; 5°06'S, 38°38'E; 20 Jul. 1908.

**Description.** Tree 3 – 10 m tall, D.B.H. 20 – 30 cm; young branches glabrous, old branches glabrous; bark of trunk and branches reddish, external thin layers peeling off. Leaves distichous, simple, pinnately veined, margins entire, flat. Petiole 8 – 11 mm long, 1.7 – 3 mm wide, glabrous. Leaf lamina 158 – 282 mm long, 43 – 83 mm wide, length:width ratio 3 – 4.5, elliptic to oblong, coriaceous, base acute to slightly decurrent, apex attenuate to acuminate, acumen 7 – 13 mm long; glabrous when young and old above, sparsely pubescent to glabrous when young, glabrous when old below; mid rib sunken above, raised below, glabrous above, glabrous below; secondary veins 11 – 17 pairs, weakly brochidodromous, impressed above, raised below; tertiary veins reticulate. Inflorescences borne on old branches or axillary, composed of 1 (sub)sessile flowers. Flower pedicel 0 – 10 mm long, ca. 4 mm in diameter, pubescent. Flowers actinomorphic, hermaphroditic, buds globose to ovoid, sessile, 7 – 10 mm high, 7.5 – 12 mm in diameter, pubescent. Bracts 2 to 6, up to 9 enclosing the bud, upper bract 10 – 13 mm long, 16 – 20 mm wide, depressed ovate to broadly ovate, adpressed, clasping the pedicel and sepals, pubescent outside, glabrous inside. Sepals 3, 10 – 12 mm long, ca 10 mm wide, fused at base, velutinous outside, glabrous inside, brown outside, yellow with red streak at base inside. Outer petals 3, 20 – 36 mm long, 16 – 19 mm wide, length:width ratio 1.1 – 2, elliptic to broadly obovate, free (valvate in bud), velutinous outside, glabrous inside, brownish to reddish-yellow outside, yellow with a pinkish-red streak from base up to 80% of the petal length inside. Inner petals 3, 20 – 31 mm long, ca. 15 mm wide, length:width ratio 1.9 – 2.1, obovate, valvate at apex (imbricate in bud), puberulent outside, glabrous inside, light yellow to cream, sometimes with a slight pinkish-red streak outside, pinkish-red to dark purplish-red

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with yellow margins inside. Stamen more than 1000, ca. 3 mm long, ca. 0.4 mm wide, anthers linear, connective truncate, yellow. Carpels 30 to 40, 4.5 mm long, 1.2 mm wide, velutinous, free; stigma 1.5 mm long, 1.2 mm wide, coiled, velutinous, covered with an exudate at anthesis. Fruiting pedicel 0 – 5 mm long, 3.5 mm in diameter, velutinous. Monocarps 3 to 7, 19 – 35 mm long, 14 – 22 mm wide, length:width ratio ca 1.6 – 2.2, ovoid to cylindrical, pubescent, red with brown pubescence, only unripe fruits seen; sessile, stipe 0 – 1 mm long, 2.2 mm wide, puberulent. Seeds ca. 4 per monocarp, uniseriate, unknown.

**Distribution.** Tanzania.

**Notes.** This species can be differentiated from the other species by its bark being reddish, with external thin layers peeling off. The specimen Brönnle 1876 in B, defined as the type by Fries (1930) was not found. We thus define the specimen Brönnle 1876 in FHO as the lectotype.

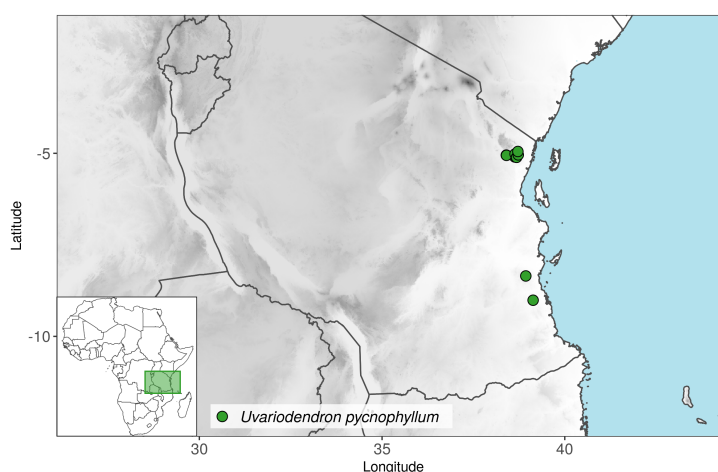


Figure 28: Distribution of *Uvariodendron pycnophyllum*

**Specimens examined.** TANZANIA – Lindi

- C.J. Kayombo 4558 (MO); Kilwa District, T8. NE end of Mbarawala Plateau, above valley running SE. Evergreen mixed dry rocky forest. Transect #3; 9°00'47"S, 39°07'59"E; alt. 280 m; 04 Nov. 2003 – Pwani • Frontier-Tanzania Coastal Forest Res. Prog 700 (K, MO); Rufiji District, Kiwengoma Forest. Northern edge of the Matumbi Highlands; 8°21'S, 38°56'E; alt. 365 m; 31 Jan. 1990 – Tanga • D.M. Johnson 1947 (DSM); Muheza District, along road Bombani-Kisiwani, ca 3km from Kisiwani; 5°01'S, 39°10'E; alt. 400 m; 05 Jun. 1996 • F.M. Mbago 3366 (DSM); Muheza District, 3 km from Kisiwani to Bombani along the road; 5°06'38.88"S, 38°40'49.08"E; alt. 150 m; 18 May. 2005 • L.-P.M.J. Dagallier 33 (BR, DSM, K, MO, MPU, P, WAG); Muheza District, along the road to Amani Nature Reserve; 5°06'04.09"S, 38°40'30.44"E; alt. 359 m; 11 Nov. 2019 • L.-P.M.J. Dagallier 37 (DSM, K, MO, MPU, P, WAG); Muheza District, along the road to Amani Nature Reserve; 5°06'07.83"S, 38°40'16.12"E; alt. 378 m; 12 Nov. 2019 • L.B. Mwasumbi 112474 (DSM); Muheza District, T3: Kwamngumi Forest Reserve; 4°57'S, 38°43'E; 12 Mar. 1999 • Langheinrich FHDS 2889 (B); Korogwe District, W Usambara Mts., Bungu; 5°03'S, 38°24'E; Jul. 1912 • M.A. Mwangoka 2966 (MO); Korogwe District, (T3) West Usambara Mountains, riverine forest patch in Kieti Village; 5°03'21"S, 38°24'17"E; alt. 1025 m; 31 May. 2002 • M.A. Mwangoka 6168 (MO); Muheza District, East Usambaras mountains, Kiwanda village Forest (Mpangamanyoka forest). W part of the forest; 5°02'32"S, 38°43'38"E; alt. 310 m; 05 Apr. 2009 • T.L.P. Couvreur 21 (DSM, K, MO, WAG, WAG); Muheza District, on road 200 m before arriving to Kisiwani village; 5°06'28.8"S, 38°40'55.2"E; alt. 300 m; 12 Nov. 2006.

*Uvariodendron schmidtii* W.R.Q.Luke, Dagallier & Couvreur, PhytoKeys 174: 116 (2021)

**TYPE.** KENYA – Coast • W.R.Q. Luke 3087 (holotype: EA (EA000008814), isotypes: K, MO, US); Kwale District, Shimba hills, Longo-Magandi; 4°14'S, 39°25'E; alt. 380 m; 20 Apr. 1992.

**Description.** Tree 10 – 12 m tall, D.B.H. unknown; young branches sparsely pubescent to glabrate, old branches glabrous; leaf bud 'eragrostiform', composed of 5 – 7, ca. 10 mm long, 10 mm wide,

## CHAPTER 4

distichous, longitudinally folded, velutinous scales.. Leaves distichous, simple, pinnately veined, margins entire, flat. Petiole 4.5 – 7 mm long, 1.5 – 2 mm wide, sparsely puberulent to glabrate. Leaf lamina 159 – 188 mm long, 49 – 71 mm wide, length:width ratio 2.4 – 3.3, narrowly elliptic to elliptic, coriaceous, base acute to decurrent, apex attenuate to acuminate, acumen 16 – 20 mm long; glabrous when young and old above, sparsely pubescent to glabrate when young, glabrous when old below; mid rib sunken above, raised below, glabrous above, pubescent to glabrous when young, glabrous when old below; secondary veins 10 – 14 pairs, brochidodromous to weakly brochidodromous, impressed above, raised below; tertiary veins reticulate. Inflorescences borne on trunk and branches, composed of 1 – 2 flowers. Flower pedicel 10 – 15 mm long, 2.5 mm in diameter, densely velutinous. Flowers actinomorphic, hermaphroditic, buds globose, sessile to pedicellate, ca. 6 mm high, ca. 7 mm in diameter, pubescent. Bracts 1 to 2 between the lower 20 – 70% of the length of the pedicel, upper bract ca. 5 mm long, ca. 10 mm wide, depressed ovate, adpressed, semi-clasping the pedicel, velutinous outside, glabrous inside. Sepals 3, 5.5 – 7 mm long, 7 – 9 mm wide, fused at base on more than 50 % of the length, forming a ring around the fruit pedicel, densely velutinous to velutinous outside, glabrous inside, brown outside, green inside. Outer petals 3, 11 – 12 mm long, 9 – 11 mm wide, length:width ratio 1.1 – 1.3, broadly obovate, velutinous to densely velutinous outside, glabrous inside, brown outside, cream with a bright reddish-pink streak at base inside. Inner petals 3, ca. 10 mm long, 8 – 9 mm wide, length:width ratio 1.1 – 1.3, broadly obovate, connivent at apex over ca. 50 % of the petal length, densely velutinous outside, glabrous inside, orangish-brown with cream margins and a bright reddish-pink streak at base outside, cream with a bright reddish-pink streak at base inside. Stamen more than 500, length and shape unknown. Carpels ca. 7, ca. 1.5 mm long, ca. 1 mm wide, velutinous, free; stigma coiled. Fruiting pedicel ca. 16 mm long, ca. 2.5 mm in diameter, pubescent. Monocarps 3 to 5, ca. 32 mm long, ca. 20 mm wide, length:width ratio ca. 1.6, rounded to ellipsoid, longitudinally ridged, sparsely pubescent, green turning orange; sessile, stipe ca. 0 mm long. Seeds unknown.

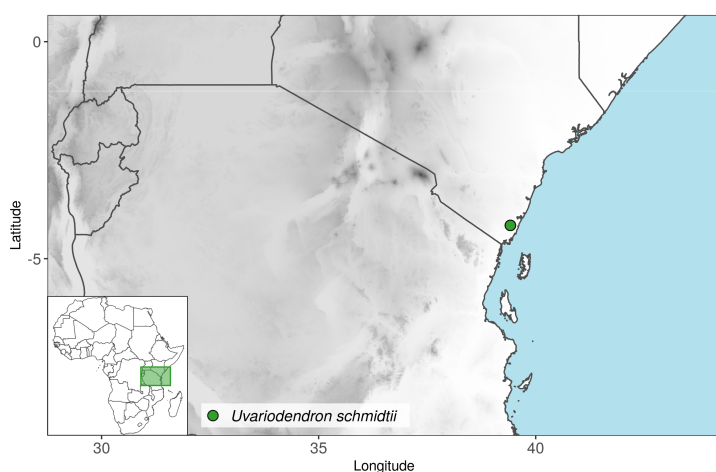


Figure 29: Distribution of *Uvariodendron schmidtii*

**Distribution.** Only known from one locality in Kenya: the Shimba Hills.

**Notes.** This species differs from other *Uvariodendron* species by its flowers that are small (petals < 13 mm long), velutinous, on a 10–15 mm long pedicel, with fused sepals forming a ring around the fruit pedicel, and fewer than 10 carpels.

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**Specimens examined.** KENYA – Coast • S.A. Robertson 7556 (EA, K, WAG, WAG); Kwale District, Shimba Hills NR, Longomandi forest; 4°14'S, 39°25'E; alt. 450 m; 04 Jun. 2005 • W.R.Q. Luke 2919 (EA); Kwale District, Shimba hills, Longo-Magandi; 4°14'S, 39°25'E; alt. 390 m; 15 Oct. 1991 • W.R.Q. Luke 4717 (EA, P); Kwale District, Shimba hills, Longo-Magandi; 4°14'S, 39°25'E; alt. 380 m; 12 Sep. 1997.

*Uvari dendron usambarens* R.E.Fr., Acta Horti Berg. x. 65 (1930)

**TYPE.** TANZANIA – Tanga • G. Scheffler 226 (holotype: B; isotypes: BM, EA, K, P), E Usambara Mts., Derema; 5°05'S, 38°38'E; 26 Mar. 1900.

**Description.** Tree 8 – 30 m tall, D.B.H. 17 – 30 cm; young branches pubescent to glabrous, old branches glabrous; the bark is dark on young individuals, peels on old individuals letting appear a pinkish-grey layer. Leaves distichous, simple, pinnately veined, margins entire, flat. Petiole 5 – 15 mm long, 1.5 – 6 mm wide, pubescent to glabrous. Leaf lamina 283 – 564 mm long, 79 – 180 mm wide, length:width ratio 2.4 – 3.9, obovate to oblong to elliptic, coriaceous, base rounded to subcordate, apex acuminate, acumen 5 – 18 mm long; glabrous when young and old above, sparsely pubescent to glabrous when young, glabrous when old below; mid rib sunken above, raised below, glabrous above, sparsely pubescent to glabrous below; secondary veins 18 – 30 pairs, weakly brochidodromous, impressed above, raised below; tertiary veins reticulate. Inflorescences borne on trunk and old branches, composed of 1 flower. Flower pedicel unknown. Flowers actinomorphic, hermaphroditic, buds ovoid, sessile, ca. 10 mm high, ca. 6 mm in diameter, pubescent. Only old rotten flower seen. Bracts unknown, 1 to 3 bracts scars observed on fruiting pedicel. Sepals 3, length, shape and indumentum unknown,. Outer petals 3, ca. 20 – 30 (?) mm long, ca. 10 – 20 (?) mm wide (measures taken on old and rotten flower), length:width ratio ovate, greenish yellow to brown with dark red streak from base up to 50% of the petal length inside. Inner petals 3, length, shape, indumentum and color unknown,. Stamen unknown. Carpels unknown,. Fruiting pedicel 12 – 22 mm long, 4 – 8 mm in diameter, pubescent to glabrous. Monocarps 1 to 17, 50 – 89 mm long, 18 – 27 mm wide, length:width ratio 1.8 – 3.6, cylindrical, pubescent to sparsely pubescent, pale yellowish green (unripe ?); stipe 1 – 5

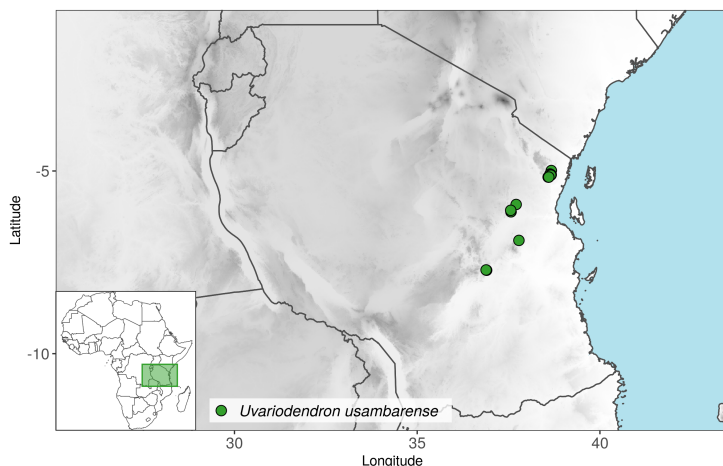


Figure 30: Distribution of *Uvari dendron usambarens*

mm long, 6 – 10 mm wide, pubescent to glabrous. Seeds 16 – 25 per monocarp, biseriate, 20 to 25 mm long, 12 – 14 mm wide.

**Distribution.** Tanzania: Usambaras mountains and Udzungwa mountains.

**Notes.** This species resemble *Ud. calophyllum*, *Ud. connivens*, *Ud. fuscum*

and *Ud. molundense* in having great obovate to elliptic to oblong leaves (28 – 57 cm), but can be differentiated in having rounded to subcordate leaf bases (vs. acute to rounded), and a dark bark when young, peeling of when old, letting appear a pinkish-grey layer.

**Specimens examined.** TANZANIA – Morogoro • A.R. Marshall 1100 (K), Msolwa - PSP9. Udzungwa National Park. Udzungwa Mountains; 7°42'30.24"S, 36°53'06.73"E; alt. 1124 m; 05 Aug. 2007 • B.J. Harris 4610 (DSM, K); Morogoro Rural District, Uluguru Mtns. near Kinole; 6°54'S, 37°47'E; alt. 900 m; 30 Apr. 1970 • C.F.M. Swynnerton 1110 (K); Morogoro Rural District, S Nguru Forest Reserve, Manyangu Forest, Liwale River; 6°07'S, 37°34'E; Feb. 1920 • M.A. Mwangoka 3272 (MA, MO); Morogoro Rural District, Nguru Mountains, Nguru South Forest Reserve, along valley between Mafuta and Ubili villages; 6°04'34"S, 37°33'33"E; alt. 555 m; 12 Aug. 2004 • P.J. Greenway 8628 (BM, K); Morogoro Rural District, S Nguru Forest Reserve, Manyangu Forest, Liwale River; 6°07'S, 37°34'E; alt. 760 m; 21 Aug. 1951 • W.R.Q. Luke 8737 (EA, K, NHT), Pt 303, Camp 244; 7°43'S, 36°54'E; alt. 900 m; 06 Jun. 2002 • Y.S. Abeid 2666 (EA, MO); Mvomero District, Kanga Forest Reserve, Submontane Forest, Work Unit 3, Base Camp; 5°55'S, 37°42'28"E; alt. 1140 m; 23 Mar. 2006 – Tanga • A.L. Borhidi 82031 (DSM, K); Lushoto District, Amani-Sigi Forest Reserve at the Sigi headwaters S of Amani near Kwamkoro sawmills; 5°10'S, 38°36'E; alt. 900 m; 19 Feb. 1982 • F.M. Mbago 3707 (DSM); Lushoto District, Amani, above Kisiwani village; 5°06'53.23"S, 38°39'16.51"E; alt. 961 m; 16 Oct. 2015 • I. Rajabu Hizza 185 (MO); Muheza District, T3. Amani Nature Reserve, phenology transect P-T 2, Kisiwani; 5°06'S, 38°40'E; alt. 400 m; 17 Nov. 1998 • J.C. Lovett 816 (DSM, K, MO); Muheza District, East Usambara mountains, Kwamkoro Forest Reserve. Area currently being logged by Sikh sawmills; 5°10'S, 38°35'E; alt. 950 m; 11 Jun. 1986 • L.-P.M.J. Dagallier 34 (BR, DSM, K, MO, MPU, P, WAG); Muheza District, Amani Nature Reserve; 5°06'31.52"S, 38°39'45.44"E; alt. 687 m; 12 Nov. 2019 • L.B. Mwasumbi 112429 (DSM), Kwamkoro N. R; 5°10'S, 38°36'E; 08 Nov. 1998 • M.A. Mwangoka 1593 (MO); Muheza District, Kwezitu public forest along path to peak between Mkalamo and Gonja Subvillages; 4°59'17"S, 38°40'12"E; alt. 825 m; 04 Aug. 2000 • T.L.P. Couvreur 20 (DSM, MO, WAG, WAG); Muheza District, c. 1 km straight up from Kisiwani village (just before Amani Nature Reserve); 5°05'55.2"S, 38°39'40.2"E; alt. 1000 m; 11 Nov. 2006.

## 7.2. *Uvariopsis* Engl., Notizbl. Königl. Bot. Gart. Berlin 2: 298 (1899)

*Tetrastemma* Diels, Bot. Jahrb. Syst. 38(3): 241 (1906)

*Thonnera* De Wild., Ann. Mus. Congo Belge, Bot. sér. 5, 3(1): 86 (1909)

**Description.** Shrub to tree 1.5 – 30 m tall, D.B.H 1.5 – 39 cm; young branches pubescent to glabrous, old branches sparsely pubescent to glabrous. Leaves distichous, simple, pinnately veined, margins entire and flat. Petiole 1 – 9 mm long, 1 – 6 mm wide, pubescent to glabrous. Leaf lamina 73 – 615 mm long, 22 – 165 mm wide, length:width ratio 2.1 – 5, elliptic to oblong to obovate, papyraceous to coriaceous, base acute to decurrent to rounded to subcordate, apex acute to acuminate, acumen 0.5 – 30 mm long, above glabrous when young and old, below sparsely pubescent at base to glabrous when young, glabrous when old; mid rib sunken above, raised below, above glabrous, below sparsely pubescent to glabrous; secondary veins 5 – 26 pairs, brochidodromous to weakly brochidodromous, impressed above, raised below; tertiary veins reticulate. Flowers actinomorphic, unisexual or hermaphroditic, male and female flowers similar or dimorphic, on same individuals (plant monoecious). Inflorescences borne in clumps of variable density on trunk, axillary or terminal, composed of 1 to 50 flowers. Peduncle inconspicuous to 2 mm long. Flower pedicel 0 – 430 mm long, 0.5 – 3 mm in diameter, pubescent to glabrous. Bracts 1 to 4, upper bract 0.5 – 4 mm long, 0.5 – 5 mm wide, triangular to broadly ovate, pubes-

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cent to sparsely pubescent outside, glabrous inside. Sepals 2, 0.7 – 18 mm long, 1 – 12 mm wide, triangular to broadly ovate, free to fused, pubescent to glabrous outside, glabrous inside, yellowish green to brown to dark red. Petals 3 to 4, 2.5 – 46 mm long, 1.5 – 22 mm wide, length:width ratio 0.9 – 5, elliptic to ovate, pubescent to glabrous outside, glabrous and soft to verrucose inside, cream to brown to dark red outside, cream to brown to dark red inside. Stamens 100 – 900, 0.1 – 2 mm long, 0.1 – 0.5 mm wide, anthers linear, connective truncate or absent. Carpels 3 – 280, 1 – 5 mm long, 0.5 – 3 mm wide, pubescent to glabrous, free; stigma 0.1 – 0.6 mm long, 0.2 – 1 mm wide, flat to coiled to globose, glabrous. Fruiting pedicel 2 – 400 mm long, 1 – 7 mm in diameter, pubescent to glabrous. Monocarps, 1 – 25, 10 – 85 mm long, 4.5 – 55 mm wide, length:width ratio 1.1 – 3.7, cylindrical, smooth to verrucose, straight to constricted between the seeds, pubescent to glabrous, dull olive green to red to brown, sessile to stipitate; stipe 0 – 14 mm long, 1 – 6 mm wide, pubescent to glabrous. Seeds 2 – 16 per monocarp, uniseriate to biseriate, 8 – 25 mm long, 5 – 15 mm wide, ellipsoid to semicircular.

7.2.1. Key to *Uvariopsis* species

1. - Largest leaves with lamina < 18 cm long, leaves with base acute to decurrent, flowers with petals < 16 mm long.....2
  - Largest leaves with lamina > 18 cm long, leaves with base acute or rounded or subcordate or decurrent, flowers with petals  $\geq$  or < 16 mm long.....7
2. - Leaves with base invariably acute, flowers sessile or flowering pedicel  $\leq$  2 mm, with sepals ca. 2 mm long and free petals.....*Up. sessiliflora*
  - Leaves with base acute to decurrent, flowers with flowering pedicel > 2 mm, or if pedicels  $\leq$  2 mm, flowers with sepals > 3 mm long and fused petals.....3
3. - Leaves with base invariably decurrent, flowers bisexual with 3 to 6 carpels.....*Up. bisexualis*
  - Leaves with base acute to decurrent, flowers unisexual with more than 13 carpels.....4
4. - Young branches and petioles densely to sparsely pubescent, petals ovate to triangular, fused at base over ca. 50% of their length .....*Up. zenkeri*
  - Young branches glabrous or very sparsely pubescent, petals broadly ovate to ovate, free at base .....5
5. - Flowers with 13 to 20 carpels, fruits composed of 1 to 3 monocarps, not constricted between the seeds and pubescent to sparsely pubescent.....*Up. oligocarpa*
  - Flowers with 20 to 40 carpels, fruits composed of 1 to 15 monocarps, strongly constricted between the seeds and glabrate to glabrous.....*Up. congensis* (6)
6. - Shrub to tree 2 – 6 m tall, leaves elliptic to obovate with a length:width ratio between 2.1 and 3.1 .....*Up. congensis* var. *congensis*
  - Shrub to tree 7 – 15 m tall, leaves narrowly elliptic with a length:width ratio between 3 and 4 .....*Up. congensis* var. *angustifolia*
7. - Larger leaves > 31 cm long, leaves with base rounded to subcordate or cordate .....8
  - Larger leaves  $\leq$  31 cm long, leaves with base acute to decurrent, or acute to rounded to subcordate.....11
8. - Leaves emitting a strong lemon scent when crushed, flowering pedicel  $\leq$  2 mm long.....*Up. citrata*
  - Leaves not emitting lemon scent when crushed, flowering pedicel > 2 mm long.....9
9. - Female and male flowers with flowering pedicel  $\leq$  8 mm, petals narrowly ovate to linear, always free.....*Up. bakeriana*
  - Female flowers with pedicel  $\geq$  20 mm, petals ovate to narrowly ovate, free to fused.....10
10. - Largest leaves with lamina  $\leq$  38 cm long, female flowers with sepals  $\geq$  6 mm long, female and male flowers with petals pinkish to dark red inside and outside.....*Up. submontana*
  - Largest leaves with lamina > 38 cm long, female flowers with sepals  $\leq$  5 mm long, female and male flowers with petals cream to brownish outside and cream to pinkish inside.....*Up. koropensis*
11. - Petals fused and female flowers with pedicel  $\geq$  8 cm.....12
  - Petals free and female flower with pedicels < 20 cm, or petals fused and female flowers with pedicels  $\leq$  6.5 cm.....13
12. - Flowers with 3 petals,  $\leq$  40 carpels, monocarps stipitate (stipe 3 – 4 mm long) sparsely pubescent to glabrous with ca. 4 longitudinal ridges.....*Up. congolana*
  - Flowers with 4 petals,  $\geq$  50 carpels, monocarps sessile pubescent and verrucose.....*Up. pedunculosa*
13. - Leaf base acute to decurrent.....14
  - Leaf base acute and minutely cordate or acute to rounded to subcordate.....15
14. - Flowering pedicel  $\leq$  10 mm, ca. 20 carpels.....*Up. etugiana*
  - Flowering pedicel  $\geq$  14 mm, > 30 carpels.....*Up. lovetiana*
15. - Leaf base acute and minutely cordate, inflorescence with peduncle ca. 2 mm long and 2 mm wide.....*Up. dicaprio*

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- Leaf base acute to rounded to subcordate, inflorescence with peduncle inconspicuous.....16
- 16. - Young branches and petiole tomentose to shortly tomentose..... *Up. solheidii* (17)
- Young branches and petiole pubescent to glabrous.....18
- 17. - Male flowers with petals 7 – 10 mm long, with a l:w ratio of ca. 3; female flowers with pedicel 63 – 198 mm long and petals 9 – 17 mm long with a l:w ratio > 1.8; petals curved outward at anthesis..... *Up. solheidii* var. *solheidii*
- Male flowers with petals 5 – 7 mm long, with a l:w ratio of ca. 2, female flowers with pedicel 20 – 110 mm long and petals 7.5 – 10 mm long with a l:w ratio > 1.8; petals straight at anthesis..... *Up. solheidii* var. *letestui*
- 18. - Flowers borne in clumps of 5 to 20 flowers on thickenings of the trunk, ≥ 100 carpels.....  
..... *Up. dioica*
- Flowers borne in inflorescences of 1 to 2 flowers on the trunk or axillary or terminal, ≤ 50 carpels.....19
- 19. - Petals ovate with a l:w ratio ≥ 1.8, brownish red outside, cream inside; male flowers with pedicel ≤ 4 mm; female flower pedicel ≥ 70 mm ..... *Up. noldeae*
- Petals broadly ovate with a l:w ratio ≤ 1.4, pale greenish to cream outside, cream with purplish base inside; male flowers with pedicel ≥ 5 mm; female flower pedicel ≤ 65 mm.....  
..... *Up. guineensis* (20)
- 20. - Flowers with petals fused at base over 30 – 50% of their length and 20 to 50 carpels; male flowers with petals 8 – 17 mm long and 9 – 17 mm wide..... *Up. guineensis* var. *guineensis*
- Flowers with petals free and 10 to 20 carpels; male flowers with petals 7 – 10 mm long and 5 – 9 mm wide ..... *Up. guineensis* var. *globiflora*

### 7.2.2. Species descriptions

*Uvariopsis bakeriana* (Hutch. & Daltz.) Robyns & Ghesq., Ann. Soc. Sci. Bruxelles, Ser. B liii. 320 (1933)

*Tetrastemma bakerianum* Hutch. & Dalziel, Kew Bull. 1927: 153 (1927) & Fl. W. Trop. Afr. I. 57 (1927)

**TYPE.** NIGERIA – Cross River State • P.A. Talbot 1517 (holotype: K; isotype: BM); Calabar, Oban; 5°19'N, 8°34'E; 1912.

**Description.** Tree 3 – 7 m tall, D.B.H 1.8 – 8 cm; young branches pubescent to puberulent, old branches sparsely pubescent to glabrous. Leaves distichous, simple, pinnately veined, margins entire and flat. Petiole 2 – 6 mm long, 2 – 4 mm wide, pubescent to glabrous. Leaf lamina 150 – 340 mm long, 40 – 90 mm wide, length:width ratio (2.27) 3.3 – 5, oblong to obovate, coriaceous, base rounded to subcordate, apex acuminate, acumen 6 – 32 mm long, above glabrous when young and old, below glabrous when young and old; mid rib sunken above, raised below, above glabrous, below sparsely pubescent to glabrous; secondary veins 10 – 26 pairs, brochidodromous to weakly brochidodromous, impressed above, raised below; tertiary veins reticulate. Flowers actinomorphic, unisexual, male and female flowers similar, on same individuals (plant monoecious). Male and female inflorescences borne on trunk, composed of 1 to 2 flowers. Peduncle inconspicuous. Flower pedicel 2 – 8 mm long, 0.5 – 2 mm in diameter, pubescent. Bracts 1 (2) at base of the pedicel, upper bract 1 – 2 mm long, 1 – 4 mm



wide, triangular, pubescent outside, glabrous inside. Sepals 2, 1 – 3.5 mm long, 1.5 – 3 mm wide, triangular, free, pubescent outside, glabrous inside, brown. Petals 4, 24 – 46 mm long, 3 – 8 mm wide, length:width ratio 4 – 10, narrowly ovate to linear, valvate, pubescent to sparsely pubescent outside, glabrous and highly verrucose inside, light red to dull yellowish brown outside, bright pink to dark pinkish red inside. Male flowers: stamens 400 – 600, 0.1 – 0.6 mm long, 0.1 – 0.3 mm wide, anthers linear, connective truncate or absent. Female flowers: carpels 15 – 40, 1.5 – 2.5 mm long, 1 – 1.5 mm wide, densely pubescent, free; stigma coiled. Fruiting pedicel 5 – 12 mm long, 2 – 2.5 mm in diameter, pubescent. Monocarps, 2 – 5, 21 – 50 mm long, 15 – 23 mm wide, length:width ratio 1.2 – 3.5, cylindrical, wrinkled, pubescent to glabrous, bright red, sessile to shortly stipitate; stipe up to 4 mm long, 1 – 3 mm wide, pubescent. Seeds 6 – 16 per monocarp, biseriate, 15 – 22 mm long, 8 – 12 mm wide, ellipsoid.

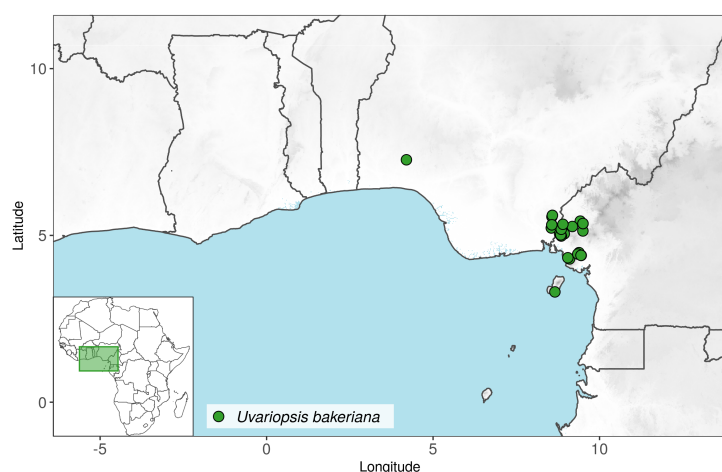


Figure 31: Distribution of *Uvariopsis bakeriana*

**Distribution.** Cameroon, Equatorial Guinea (Bioko island), Nigeria.

**Notes.** This species resembles *Up. citrata*, *Up. korupensis* and *Up. submontana* in having large obovate leaves (up to 35 cm long), with rounded to subcordate bases. *Up. bakeriana* differs in having short flower pedicel (2 – 8 mm, vs. 0 – 2 mm in *Up. citrata*, 6 – 70 mm in

*Up. korupensis* and 25 – 60 mm in *Up. submontana*), and with its petals being narrowly ovate to linear, with a length:width ratio comprised between 4 and 10 (vs. ca. less than 5 in *Up. citrata* and *Up. submontana*), free (vs. fused in *Up. korupensis*), and bright pinkish to deep red petals (vs. cream to brownish in *Up. citrata* and *Up. korupensis*).

**Specimens examined.** CAMEROON – Littoral • D.W. Thomas 4300 (K, MO), Korup National Park. Forest along footpath from Ndian River at PAMOL field 69 and transect P; 5°01'N, 8°50'E; alt. 50 m; 24 Jan. 1985 – South-West Region • C. Farron 7297 (P), South Bakundu Forest, Kendongi; 4°26'30.63"N, 9°20'43.88"E; 14 May. 1970 • C.F.A. Onochie 9305 (K), South Bakundu Forest; 4°24'06.26"N, 9°26'32.16"E; 12 Mar. 1948 • D.W. Thomas 1086 (K); Ndian, Korup Forest Reserve, Korup Reserve, path between transect P&Q; 4°59'N, 8°51'E; Mar. 1979 • D.W. Thomas 3210 (K, MO), forest in the Korup National Park; 5°03'N, 8°48'E; alt. 50 m; 28 Feb. 1984 • D.W. Thomas 3336 (MO), North-eastern corner of Korup National Park; near Baro village; 5°16'N, 9°11'E; alt. 200 m; 24 Mar. 1984 • D.W. Thomas 5606 (MO), along transect P, southern end of Korup National Park; 5°11'N, 8°51'E; alt. 50 m; 16 Feb. 1986 • D.W. Thomas 7835 (MO), Ajaman, near northern edge of Korup National Park; 5°20'N, 8°54'E; alt. 200 m; 22 May. 1988 • G.K. Gottsberger 100307/ 11 (ULM, WAG), c. 100 m from Banyang Mbo Research Station; 5°08'N, 9°30'E; 10 Mar. 2007 • J.P.M. Brenan 9305 (K), South Bakundu Forest; 4°29'N, 9°23'E; 12 Mar. 1948 • J.P.M. Brenan 9409 (BM, K), Banga, S. Bakundu FR; 4°24'N, 9°27'E; 13 Mar. 1948 • M.R. Cheek 7234 (K, SCA, YA); Ndian, Mundemba, Korup National Park, nature trail near suspension bridge;

## TAXONOMIC REVISION OF UVARIODENDRON AND UVARIOPSIS

4°59'N, 8°51'E; alt. 50 m; 01 Feb. 1995 • R.E. Gereau 5195 (MA, MO, WAG); Ndian, 2-2.5 km S of Six Cup Garri Creek; 5°02'N, 8°53'E; alt. 100 m; 06 Mar. 1993 • R.G. Letouzey 13841 (P), entre Etinkem et Nfaitok, 10km N Nguti; 5°25'39.72"N, 9°25'14.26"E; 15 Jun. 1975 • S. Cable 2150 (K, YA); Ndian, Korup National Park, Ekundu Kundu, path to Ekon 1, 5km from Ekundu-Kundu; 5°04'50.32"N, 8°54'29.81"E; alt. 300 m; 25 Apr. 1996 • S. Cable 2256 (K, YA); Ndian, Korup National Park, path from Ekundu Kundu to Faba, about 3km; 5°02'53.41"N, 8°56'25.12"E; alt. 300 m; 27 Apr. 1996 • T.L.P. Couvreur 1000 (MPU, WAG, YA), Bayang Mbo Wildlife Sanctuary, after Mbu river; 5°21'09.69"N, 9°30'09.23"E; alt. 259 m; 25 Mar. 2016 • T.L.P. Couvreur 1015 (MPU, WAG, YA), Bayang Mbo Wildlife Sanctuary, after Mbu river; 5°21'22.04"N, 9°30'05.8"E; alt. 250 m; 26 Mar. 2016 • T.L.P. Couvreur 1045 (MPU, WAG, YA), Mount Cameroon National Park, on the Bomona trail, behind Bomona village, 10 km NW from Idenau; 4°17'41.96"N, 9°05'53.93"E; alt. 856 m; 03 Apr. 2016 • W. Mukete 6 (K, MO, SCA, YA), Kosse, along the path to the Reserve; 4°19'48.72"N, 9°02'52.08"E; 24 Apr. 1996. EQUATORIAL GUINEA – Bioko Sur • W.R.Q. Luke 11907 (K, MA), Moaba. Pt 140-141; 3°18'20.6"N, 8°39'33.8"E; alt. 8 m; 15 Mar. 2007. NIGERIA – Cross River State • C.F.A. Onochie FHI 36140 X (K); Calabar, Oban Group Forest Reserve, Orem; 5°36'N, 8°35'E; 23 Jan. 1957 • J. Ntui 944 (MO), Oban Hills; 5°33'30"N, 8°34'12"E; alt. 600 m; 19 Dec. 1955 • M.C. Ejiofor FHI 21870 (K); Calabar, Oban Group Forest Reserve; 5°36'N, 8°35'E; 24 Apr. 1952 • P.A. Talbot 1516 (BM); Calabar, Oban; 5°19'N, 8°34'E; 1912 • P.A. Talbot 446 (BM), Oban; 5°13'23.28"N, 8°33'06.9"E; 1909 • P.W. Richards 5166 (K, K, P); Calabar, Oban; 5°13'27.54"N, 8°33'10.42"E; alt. 244 m; 13 Mar. 1955 – Ogun State • A.P.D. Jones FHI 12275 (P), c. 1/2 ml W. of Oaho Enclave, E.B. 34 Line 7. Road trace of U.A.C; 7°16'N, 4°12'E; 05 Apr. 1946.

*Uvariopsis bisexualis* Verdc., Kew Bull. 41(2): 289 (1986)

**TYPE.** TANZANIA – Iringa • J.C. Lovett 233 (holotype: K); Iringa Rural District, Udzungwa Mts., Sanje; 7°46'S, 36°54'E; alt. 1480 m; 02 Dec. 1983.

**Description.** Tree ca. 10 m tall, D.B.H unknown; young branches pubescent, old branches glabrous. Leaves distichous, simple, pinnately veined, margins entire and flat. Petiole 3.5 – 5 mm long, ca. 2 mm wide, sparsely pubescent to glabrous. Leaf lamina 135 – 152 mm long, 37 – 48 mm wide, length:width ratio ca. 3, elliptic to oblong, coriaceous, base decurrent, apex attenuate, above glabrous when young and old, below sparsely pubescent to glabrous when young, glabrous when old; mid rib sunken above, raised below, above glabrous, below sparsely pubescent to glabrous; secondary veins ca. 12 pairs, weakly brochidodromous, impressed above, raised below; tertiary veins reticulate. Flowers actinomorphic, hermaphroditic. Inflorescences borne on previous growth unit branches, composed of 1 flower. Peduncle inconspicuous. Flower pedicel 12 – 20 mm long, ca. 1 mm in diameter, pubescent. Bracts 1 at base to towards the lower half of the pedicel, upper bract ca. 1 mm long, ca. 1 mm wide. Sepals 2, 1.6 – 2.5 mm long, 2.2 – 2.5 mm wide, broadly ovate, free, pubescent outside, glabrous inside, color unknown. Petals 4, 12 – 14 mm long, 4 – 8 mm wide, length:width ratio 3 – 3.5, narrowly ovate, sparsely pubescent outside, glabrous inside, cream outside, cream with red base inside. Stamens numerous (exact number unknown), 0.5 – 0.7 mm long, ca. 0.5 mm wide, anthers linear, connective truncate or absent. Carpels 3 – 6, 2 – 4 mm long, 1 – 1.4 mm wide, glabrate at base to glabrous, free, ovules 22 – 24 per ovary, biseriate. Fruits unknown.

**Distribution.** Known from only one locality in Tanzania: Sanje in the Udzungwa mountains.

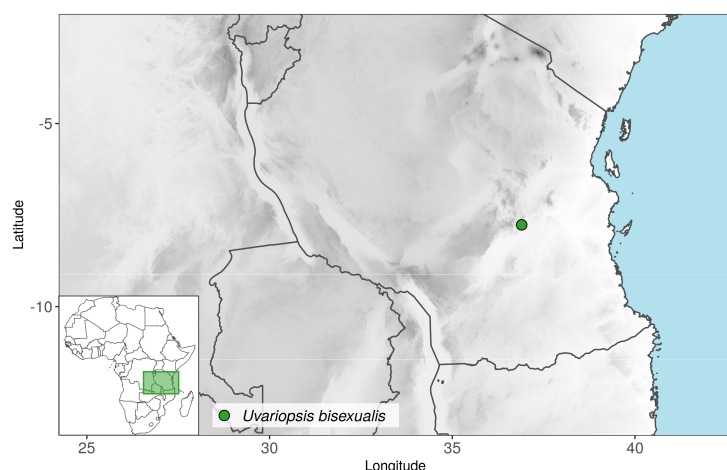


Figure 32: Distribution of *Uvariopsis bisexualis*

**Notes.** This species resembles *Up. congensis*, *Up. oligocarpa* and *Up. zenkeri* in having elliptic leaves generally less than 16 cm long with decurrent base. It differs from all the other *Uvariopsis* in having bisexual flowers and less than 6 carpels (vs. more than 10 carpels).

*Uvariopsis citrata* Couvreur & Niang., *PhytoKeys* 68: 3 (2016)

**TYPE.** GABON – Estuaire • T.L.P. Couvreur 1143 (holotype: WAG; isotypes: LBV, P), Monts de Cristal National Park, Mbé sector, 800 m from Kinguéle ANPN camp, near bridge; 0°27'50.18"N, 10°16'42.82"E; 14 Jun. 2016.

**Description.** Tree 4 – 10 m tall, D.B.H 3 – 10 cm; young branches pubescent, old branches glabrous. Leaves distichous, simple, pinnately veined, margins entire and flat, strong lemon scent when crushed. Petiole 4 – 8 mm long, 3 – 5 mm wide, pubescent to glabrous. Leaf lamina 312 – 500 mm long, 88 – 120 mm wide, length:width ratio 3.5 – 4.3, elliptic to obovate, coriaceous, base subcordate, apex acuminate, acumen 20 – 30 mm long, above glabrous when young and old, below glabrous when young and old; mid rib sunken above, raised below, above glabrous, below sparsely pubescent to glabrous; secondary veins 17 – 19 pairs, brochidodromous to weakly brochidodromous, impressed above, raised below; tertiary veins reticulate. Flowers actinomorphic, unisexual, male and female flowers similar, on same individuals (plant monoecious). Male and female inflorescences borne on trunk, sparsely spaced mostly towards the lower half of the trunk, composed of 1 to 2 sessile flowers. Peduncle inconspicuous. Flower pedicel 0 – 2 mm long, 1 – 2 mm in diameter, densely pubescent. Bracts up to 3 at base, upper bract 1 – 2 mm long, ca. 4 mm wide, broadly ovate, pubescent outside, glabrous inside. Sepals 2, 9 – 15 mm long, 4 – 6 mm wide, narrowly ovate, basely fused, enclosing the petals in bud, densely pubescent outside, densely pubescent to glabrous toward base inside, brown. Petals 4, 7 – 15 mm long, 5 – 8 mm wide, length:width ratio ca. 3.5, ovate, pubescent outside, glabrous inside, brownish to greenish yellow outside, greenish yellow inside. Male flowers: stamens number unknown, ca. 0.5 mm long, anthers linear, connective truncate. Female flowers: carpels 60, 4 – 5 mm long, ca. 0.5 mm wide, densely pubescent, free; stigma coiled. Fruits unknown.

**Distribution.** Cameroon, Gabon.

**Notes.** This species resembles *Up. bakeriana*, *Up. korupensis* and *Up. subomontana* in having large obovate leaves (more than 31 cm long), with rounded to subcordate bases. *Up. citrata* is unique within the genus by its leaves emitting a strong lemon scent when crushed. It also differs from all the other *Uvariopsis* species (except *Up. sessiliflora* and *Up. zenkeri*) in

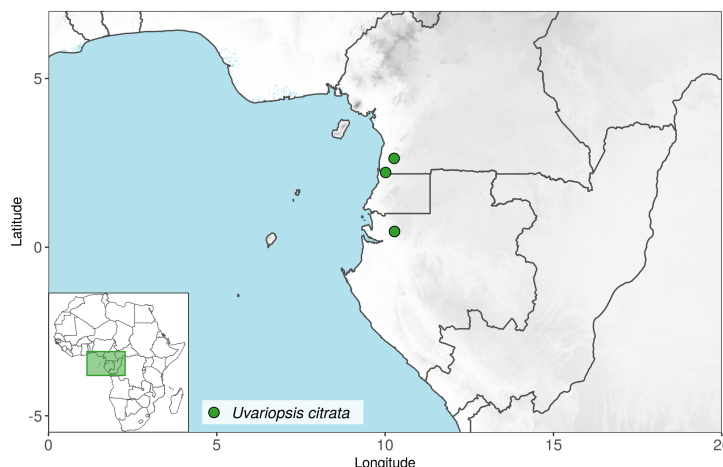


Figure 33: Distribution of *Uvariopsis citrata*

having subsessile flowers, with pedicel less than 2 mm. It differs from *Up. sessiliflora* and *Up. zenkeri* in having larger leaves (31 – 50 cm vs. less than 18 cm in *Up. sessiliflora* and *Up. zenkeri*).

**Specimens examined.** CAMEROON – South Region • G.P. Tchouto Mbatchou 2869 (KRIBI, WAG, WAG, YA), Campo-Ma'an area, Bibabimvoto; 2°12'48"N, 10°00'51"E; alt. 60 m; 13 May. 2000 • R.G. Letouzey 9017 (P), 15 km au SSE de Zingui (soit à 50km au SE de Kribi), feuille IGN 1/200000 Nyabessan; 2°37'52.24"N, 10°15'58.54"E; 14 Mar. 1968. GABON – Estuaire • T.L.P. Couvreur 1126 (LBV, WAG), Monts de Cristal National Park, 800 m from Kinguéle ANPN camp, near bridge; 0°27'50.18"N, 10°16'42.82"E; 11 Jun. 2016.

*Uvariopsis congensis* Robyns & Ghesq., Ann. Soc. Sci. Bruxelles, Ser. B liii. 317 (1933)

**TYPE.** DEMOCRATIC REPUBLIC OF THE CONGO – Kasai-Oriental • Kerkhoven, E. van der s.n (lectotype, here designated: BR (BR0000014588372)); Lusambo, Saint-Trudon [=Mombelaye]; 5°04'00.12"S, 23°28'59.88"E; alt. 475 m; 16 Aug. 1913.

**Description.** Shrub to tree 2 – 15 m tall, D.B.H 3 – 39 cm; young branches sparsely pubescent to glabrous, old branches glabrous. Leaves distichous, simple, pinnately veined, margins entire and flat. Petiole 2 – 5 mm long, 1 – 2.5 mm wide, glabrous. Leaf lamina 88 – 177 mm long, 30 – 77 mm wide, length:width ratio 2.1 – 3.1 (3.6), elliptic to narrowly elliptic to obovate, papyraceous to coriaceous, base acute to decurrent, apex attenuate to acuminate, acumen 5 – 18 mm long, above glabrous when young and old, below glabrous when young and old; mid rib sunken above, raised below, above glabrous, below glabrous; secondary veins 7 – 12 pairs, brochidodromous to weakly brochidodromous, impressed above, raised below; tertiary veins reticulate. Flowers actinomorphic, unisexual, male and female flowers similar, on same individuals (plant monoecious). Male and female inflorescences borne on old branches or axillary, composed of 1 to 2 flowers. Peduncle inconspicuous. Flower pedicel 3 – 11 mm long, 0.5 – 1 mm in diameter, pubescent to glabrous. Bracts 1 to 4 at base and one towards the lower half of pedicel, upper bract ca. 1 mm long, ca. 1 mm wide, triangular, pubescent outside, glabrous inside. Sepals 2, 0.7 – 1.5 mm long, 1.5 – 2 mm wide, broadly ovate, free, pubescent outside, glabrous inside, brown.

## CHAPTER 4

Petals 4, 2.5 – 8 mm long, 1.5 – 5 mm wide, length:width ratio 1 – 1.7, ovate, free, pubescent to glabrate outside, glabrous inside, cream to pale orange outside, cream to yellow inside. Male flowers: stamens 300 – 400, ca. 0.5 mm long, ca. 0.2 mm wide, anthers linear, connective truncate or absent. Female flowers: carpels 20 to 40, 1.5 – 2 mm long, 0.5 – 1 mm wide, pubescent, free; stigma 0.2 – 0.5 mm long, ca. 0.5 mm wide, globose to flat. Fruiting pedicel 5 – 15 mm long, 1 – 3 mm in diameter, pubescent to glabrous. Monocarps, 1 – 15, 13 – 45 mm long, 7 – 19 mm wide, length:width ratio 1.3 – 3.1, cylindrical, smooth to lumpy, strongly constricted between the seeds, apex rounded to slightly acuminate, glabrate to glabrous, green to orange to red when ripe (black when dry), stipitate; stipe 0 – 7 mm long, 1 – 3 mm wide, glabrous. Seeds 2 – 11 per monocarp, uniseriate to biseriate, 9.5 – 14 mm long, 7 – 10 mm wide, ellipsoid.

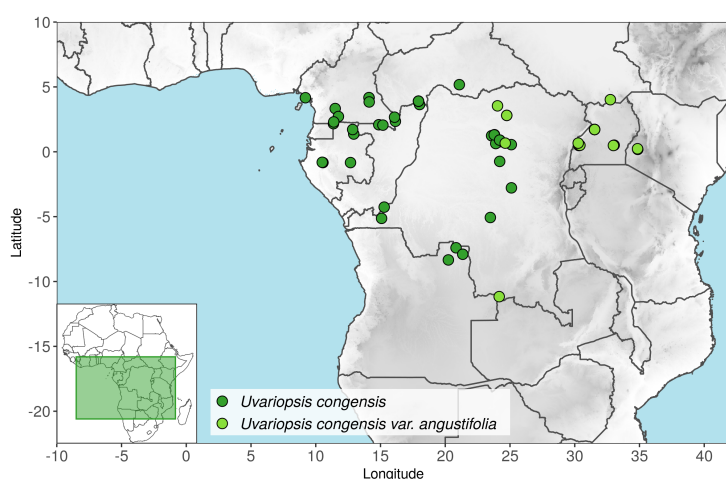


Figure 34: Distribution of *Uvariopsis congensis*

**Distribution.** Angola, Cameroon, Central African Republic, Democratic Republic of the Congo, Gabon, Kenya, Republic of the Congo, Uganda.

**Notes.** This species resembles *Up. oligocarpa* and *Up. zenkeri* in having elliptic leaves less than 18 cm long at maximum, with a decurrent base. It differs from *Up. oligocarpa* and *Up. zenkeri* in having more carpels (20

to 40 vs. 13 to 20 in *Up. oligocarpa* and 13 to 22 in *Up. zenkeri*) and glabrous monocarps strongly constricted between the seeds (vs. pubescent and not constricted in *Up. oligocarpa* and tomentose and slightly constricted in *Up. zenkeri*).

**Specimens examined.** ANGOLA – Lunda Norte • I.A. Darbyshire 759 (K), Lovue River near Capaia village; 8°20'17"S, 20°14'25"E; alt. 960 m; 30 Mar. 2013 • J. Gossweiler 13802 a (K), Sector fitocologico de Nordeste de Lunda, circunscricao de Chitato. Dundo, Luachimo; 7°24'S, 20°50'E; alt. 700 m; 05 Nov. 1946 • J. Gossweiler 14071 (B, P); 7°54'S, 21°21'E; alt. 700 m; 12 Jun. 1948. CAMEROON – Central Region • W.J.J.O. de Wilde 1914 (P, WAG, WAG), C. 30 km South of M'Balmayo; 3°20'N, 11°30'E; 13 Feb. 1964 – East Region • D.J. Harris 1512 (K, MO, P), West bank of Sangha River; 2°21'N, 16°09'E; alt. 350 m; 01 Nov. 1988 • F.J. Breteler 2812 (K, P, WAG, WAG), Near Bimba, bank of Doumé river, 40 km SW. of Batouri; 4°10'N, 14°07'E; alt. 580 m; 15 Apr. 1962 • J.F. Villiers 683 (P), 2 km N du confluent Ngoko-Malapa, 5km E de Moloundou; 2°03'17.9"N, 15°11'01.31"E; 21 Apr. 1971 • R.G. Letouzey 10641 (P), Bordure de la Sangha au Sud de Lidjombo (près ile Libongo) à 110 km au N. de Ouesso (feuilles IGN 1/200.000 Moloundou); 2°40'N, 16°05'E; 10 Apr. 1971 • R.G. Letouzey 12086 (K, P, WAG), près Ndongo, à 45 km WNW de Moloundou (Feuille IGN 1/200.000 SOUANKE); 2°05'N, 14°52'E; 15 Mar. 1973 • R.G. Letouzey 4755 (K, P), Rives de la Doumé près Bimba 40km SW de Batouri - feuille IGN 1/200.000 Batouri-Berberati; 4°10'32.91"N, 14°06'32.96"E; 15 Apr. 1962 • R.G. Letouzey 5491 (K, P), a 11 km au SSW de Koso (village situé à 60km au SSW de Batouri); 3°50'23.13"N, 14°07'33.62"E; 25 Jul. 1963 – South Region • R.G. Letouzey 10024 (P), Rives du Ntem près du confluent de la Kye, 16km ESE d'Ambam; 2°18'02.17"N, 11°23'15.84"E; 07 Feb. 1970 • R.G. Letouzey 9915 (P), Bord rivière Nlobo, près Ngomebae, 70km ESE d'Ebolowa sur

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route Mvangan; 2°43'N, 11°45'E; 24 Jan. 1970 – South-West Region • A. Staudt 556 (K), Johann - Albrechtshöhe, Johann - Albrechtshöhe, Kumba area; 4°10'N, 9°12'E; 1896. CENTRAL AFRICAN REPUBLIC – Basse-Kotto • C. Tisserant 1363 (P), Galerie Riv. Moku Sikumdu 10km N.O. Alindas; 5°10'24.36"N, 21°05'07.74"E; 19 Nov. 1927 – Lobaye • Équipe C. Tisserant 1504 (BM, BR, K, P); Mbaïki, Boukoko; 3°54'N, 17°56'E; 15 Jun. 1949 • Équipe C. Tisserant 2136 (BR, P); Mbaïki, Boukoko; 3°54'N, 17°56'E; 16 Jun. 1951 • Équipe C. Tisserant 2198 (BM, BR, P); Mbaïki, Boukoko; 3°54'N, 17°56'E; 17 Aug. 1951 • Équipe C. Tisserant 2241 (BM, BR, K, P, P); Mbaïki, Boukoko; 3°54'N, 17°56'E; 13 Sep. 1951 • F.J. Badré 239 (B, P); Mbaïki, Mbaïki, Bord de la Lobaye - Forêt 30km S de Mbaïki; 3°38'25.5"N, 18°00'57.02"E; 06 Nov. 1968. DEMOCRATIC REPUBLIC OF THE CONGO – Bas-Congo • J. Gillet 22 (BR); Madimba, Kisantu; 1899 • F.H.E.A.W. Robyns 233 (BR); Madimba, Kisantu, Station Rwé droite, Inkisi; 5°08'S, 15°05'E; 10 Jul. 1925 – Maniema • C.E.N. Ewango 2664 (MO), Territoire de Kailo, Parc National de la Lomami. Localité Katopa (Camp); 2°46'52"S, 25°06'34"E; alt. 458 m; 21 Mar. 2015 – Orientale • J. Bokdam 3388 (KIS, WAG, WAG); Kisangani, 10km W of Kisangani, near Lindi river; 0°33'N, 25°06'E; 19 Nov. 1971 • J.-P.A. Lebrun 2487 (P); Buta, Buta-Uele; 2°48'16.32"N, 24°44'59.68"E; Mar. 1931 • J.L.P. Louis 13423 (EA, K, MO, P); Isangi, Bassao (île), Un peu en aval de Liléko; 0°54'N, 24°12'E; alt. 470 m; 26 Jan. 1938 • M.D.J. Laurent 1618 (BR); Banalia, Bomaneh; 1°18'N, 23°47'E; 04 Mar. 1906 • R.G.A. Germain 4757 (K), à l'W de Basoko, embouchure de la Lombo; 1°14'14.83"N, 23°34'46.46"E; Feb. 1949 • R.G.A. Germain 4804 (P), Yankelili, près d'Isangi; 0°44'31"N, 24°12'15"E; Apr. 1949 • R.G.A. Germain 50 (B, K, P); Isangi, village de Yafolo, rives gauche en amont d'Isangi; 0°46'46"N, 24°16'13"E; alt. 470 m; 21 Dec. 1939 • R.G.A. Germain 8207 (K, M); Isangi, île Esali III (en aval d'Isangi); 0°53'34.91"N, 24°13'08.13"E; Feb. 1953 • R.G.A. Germain 8769 (K); Isangi, Yabwesu-Ogeto (Bas Lomami); 0°38'N, 23°54'E; 05 Apr. 1956 – Unknown major area • M.D.J. Laurent s.n (BR); 1°19'N, 23°48'E; 04 Mar. 1906. GABON – Moyen-Ogooué • T.O.B.E.B. Stévert 4523 (LBV, MO, P), Mabounié, along the Ngounié River; 0°49'59"N, 10°33'23"E; alt. 18 m; 11 May. 2012 – Ngounié • O.L.S. Lachenaud 1384 (BR, BRLU, LBV, MO, P, WAG), Mabounié, rive gauche de la Ngounié juste en aval du débarcadère; 0°48'40"N, 10°29'57"E; alt. 24 m; 15 Nov. 2013 – Ogooué-Lolo • F.J. Breteler 6647 (LBV, P, WAG, WAG), 4 km SW of Lastoursville, right side Ogooué R; 0°50'N, 12°41'E; 25 Sep. 1970 – Woleu-Ntem • G.M.P.C. Le Testu 9027 (BM, P), région de Bitam, Meyo kyè; 2°10'N, 11°22'E; Mar. 1933 • J.J. Wieringa 660 (WAG), c. 85 km N of Makokou, Minkébé district, Nsyé valley; 1°22'N, 12°56'E; alt. 505 m; 27 Feb. 1990 • MINKÉBÉ Series W 626 (K, LBV, MAKOK, MO, P, WAG), Minkébé area, river Nouna; 1°43'N, 12°51'E; 16 Dec. 1990. REPUBLIC OF THE CONGO – Pool • A.J.B. Chevalier 4176 (P), Brazzaville; 4°16'S, 15°17'E; Jul. 1902.

### *Uvariopsis congensis* var. *angustifolia* Dagallier, var. nov.

**TYPE.** SOUTH SUDAN – Unknown major area • I. Friis 735 (holotype: K), Talanga; 4°01'N, 32°45'E; alt. 1300 m; 07 Dec. 1980.

**Diagnosis.** *Up. congensis* var. *angustifolia* differs from the type variety in being trees 7 – 15 m high (vs. shrubs to trees 2 – 6 m high) and having narrowly elliptic leaves with a length:width ratio between 3 and 4 (vs. elliptic to obovate leaves with a length:width ratio between 2.1 and 3.1).

**Description.** Tree 7 – 15 m tall, D.B.H up to 39 cm; young branches glabrous, old branches glabrous. Leaves distichous, simple, pinnately veined, margins entire and flat. Petiole 2.5 – 5 mm long, 1 – 1.5 mm wide, glabrous. Leaf lamina 73 – 166 mm long, 22 – 46 mm wide, length:width ratio 3 – 4, narrowly elliptic, papyraceous to coriaceous, base decurrent, apex attenuate to slightly acuminate, acumen ca. 7 mm long, above glabrous when young and old, below glabrous when young and old; mid rib sunken above, raised below, above glabrous, below glabrous; secondary veins 8 – 12 pairs, weakly brochidodromous, impressed above, raised below; tertiary veins reticulate. Flowers actinomorphic, unisexual, male and female flowers similar, on same individuals (plant monoecious). Male and female inflorescences borne on old branches or axillary, composed of 1 to 2 flowers. Peduncle inconspicuous.



## CHAPTER 4

Flower pedicel 4 – 11 mm long, 0.5 – 1 mm in diameter, sparsely pubescent to glabrous. Bracts 1 to 4 at base of the pedicel, upper bract ca. 1 mm long, ca. 1 mm wide, triangular, pubescent outside, glabrous inside. Sepals 2, ca. 1 mm long, ca. 1 mm wide, broadly ovate, free, pubescent outside, glabrous inside, color unknown. Petals 4, 4 – 8 mm long, 3.5 – 4.5 mm wide, length:width ratio 1 – 1.4, ovate, free, puberulent to glabrate outside, glabrous inside, cream to pale orange outside, cream inside. Male flowers: stamens number unknown, ca. 0.5 mm long, ca. 0.2 mm wide, anthers linear, connective truncate or absent. Female flowers: carpels 20 to 40, ca. 1.5 mm long, c. 0.5 mm wide, pubescent, free; stigma unknown. Fruiting pedicel 6 – 10 mm long, 1 – 3 mm in diameter, pubescent to glabrous. Monocarps, 2 – 5, 18 – 30 mm long, 9 – 17 mm wide, length:width ratio 1.6 – 3.1, cylindrical, smooth to lumpy, strongly constricted between the seeds, apex rounded to slightly acuminate, glabrate to glabrous, red (black when dry), stipitate; stipe 3 – 7 mm long, 1.5 – 2 mm wide, glabrate. Seeds 2 – 11 per monocarp, uniseriate to biseriate, ca. 13 mm long, 9 – 10 mm wide, ellipsoid.

**Distribution.** Democratic Republic of the Congo, Kenya, Uganda.

**Notes.** The variety *Uvariopsis congensis* var. *angustifolia* was created to acknowledge the clear morphological variation exhibited by several specimens (mainly from East Africa), being taller trees and having narrower leaves than the other specimens (mainly from Central Africa), although these two morphotype show no phylogenetic divergence (see Chapter 3).

**Specimens examined.** DEMOCRATIC REPUBLIC OF THE CONGO – Orientale • J.-P.A. Lebrun 2463 (P), Likati Uele; 3°32'25"N, 24°02'11"E; Mar. 1931 • J.-P.A. Lebrun 2619 (P); Buta, Buta-Uele; 2°48'16.32"N, 24°44'59.68"E; Mar. 1931 • J.L.P. Louis 9562 (K); Isangi, Yalulia, à 20km à l'Est de Yangambi; 0°40'N, 24°38'E; alt. 470 m; 30 May. 1938. KENYA – Nyanza • B. Verdcourt 1695 (K); North Kavirondo, Kakamega Forest Station, By roadside leading to Yala River from Junction of main road with road leading to Forest House section. Kakamega Forest; 0°14'N, 34°51'E; 10 Dec. 1956 • R.B. Faden 70/ 34 (EA, K); North Kavirondo, Kakamega Forest, Kibiri Block, S. side of Yala River; 0°11'N, 34°52'E; alt. 1550 m; 21 Jan. 1970. UGANDA – Buganda • B.T. Styles 236 (K); Mengo, Mabira C.F.R., coupe 71; 0°29'03.48"N, 32°59'05.64"E; alt. 1100 m; 23 Nov. 1962 – Central • R.A. Dümmer 5591 (K), Mulange; 0°30'28.76"N, 33°02'39.79"E; Oct. 1922 – Western Province • B.T. Styles 122 (K); Masindi District, Budongo Forest Reserve, Waibira Block Compt. 19; 1°43'N, 31°32'E; alt. 1097 m; 04 Oct. 1962 • C.M. Harris 167 (K); Masindi District, Budongo Forest Reserve; 1°43'N, 31°32'E; Nov. 1932 • D.L.N. Hafashimana 13 (K); Masindi District, Budongo Forest Reserve, Kaniyo - Pabidi beat; 1°43'N, 31°32'E; alt. 1010 m; Feb. 1996 • J.G. Myers 13647 (K); Masindi District, Budongo Forest Reserve; 1°43'N, 31°32'E; 20 Dec. 1940 • Lindeman, H.A 534 (K); Masindi District, Budongo Forest Reserve; 1°43'N, 31°32'E; Mar. 1939 • M.T. Dawe 484 (K); Toro, Toro at Isungu; 0°28'59.88"N, 30°19'00.12"E; alt. 1500 m; 06 Sep. 1905 • S. Paulo 581 (K); Kabarole, Fort Portal Forest Reserve; 0°40'N, 30°16'E; 18 Jul. 1960 • W.J. Eggeling 2291 (EA, K); Masindi District, Budongo Forest Reserve; 1°43'N, 31°32'E; Nov. 1935 • W.J. Eggeling 3154 (K); Toro, Kibale Forest; 0°30'N, 30°24'E; Aug. 1936 • W.J. Eggeling 3357 (K); Masindi District, Budongo Forest Reserve; 1°43'N, 31°32'E; Jun. 1937. ZAMBIA – North-Western • F. White 3334 (BM, K, MO); Mwinilunga, west of Kalene Hill Mission; 11°10'02.16"S, 24°09'54.84"E; 22 Sep. 1952.

*Uvariopsis congolana* (De Wild.) Fries, Ark. Bot. ser. 2, 3: 42 (1953)

*Thonnera congolana* De Wild., Ann. Mus. Congo Belge, Bot. sér. 5, 3(1): 86 (1909)

**TYPE.** DEMOCRATIC REPUBLIC OF THE CONGO – Equateur • F. Thonner 100 (sheets here designated, lectotype: BR (BR0000008824394); isoelectotypes BR (BR0000008824202, BR0000008824219)), Libako près Ngali (Mongala); 2°39'N, 21°30'E; alt. 450 m; 22 Sep. 1896.

**Description.** Tree 1.5 – 10 m tall, D.B.H ca. 5 cm; young branches pubescent to glabrous, blackish when dry, old branches glabrous. Leaves distichous, simple, pinnately veined, margins entire and flat. Petiole 2 – 5 mm long, 1.5 – 4 mm wide, pubescent to glabrous. Leaf lamina 163 – 300 mm long, 44 – 110 mm wide, length:width ratio 2.4 – 4, (elliptic) oblong to obovate, papyraceous to coriaceous, base acute to rounded, apex attenuate to acuminate, acumen 2.5 – 22 mm long, above glabrous when young and old, below sparsely pubescent at base to glabrous when young, glabrous when old; mid rib sunken above, raised below, above glabrous, below sparsely pubescent to glabrous; secondary veins 8 – 17 pairs, brochidodromous to weakly brochidodromous, impressed above, raised below; tertiary veins reticulate. Flowers actinomorphic, unisexual, male and female flowers dimorphic, on same individuals (plant monoecious). Male inflorescences borne on trunk mainly at ground level, sometimes up to 1 m, composed of 1 to 3 flowers, clumped with other male or female inflorescences. Peduncle inconspicuous. Flower pedicel 95 – 200 mm long, 1 – 2 mm in diameter, sparsely pubescent. Bracts 1 to 3 from base towards the lower half of the pedicel, upper bract 1 – 3 mm long, 1 – 4 mm wide, depressed ovate, adpressed, semi clasping the pedicel, pubescent outside, glabrous inside. Sepals 2, 2 – 6.5 mm long, 2 – 10 mm wide, depressed ovate, free to basely fused, pubescent outside, glabrous inside, color unknown. Petals 3, 11 – 20 mm long, 9 – 22 mm wide, length:width ratio 0.8 – 2, broadly ovate to ovate, fused at base over ca. 30% of the petal length, pubescent to glabrate outside, glabrous inside, pinkish outside. Stamens numerous (exact number unknown), ca. 0.5 mm long, ca. 0.5 mm wide, anthers linear, connective truncate or absent. Female inflorescences borne on trunk mainly at ground level, sometimes up to 1 m, composed of 1 to 3 flowers, clumped with other male or female inflorescences. Flower pedicel 200 – 430 mm long, 1 – 2 mm in diameter, sparsely pubescent. Bracts 1 to 3 from base towards the lower half of the pedicel, upper bract 1 – 3 mm long, 1 – 4 mm wide, depressed ovate, adpressed, semi clasping the pedicel, pubescent outside, glabrous inside. Sepals 2, 2 – 6.5 mm long, 2 – 10 mm wide, depressed ovate, free to basely fused, pubescent outside, glabrous inside, color unknown. Petals 3, 11 – 20 mm long, 9 – 22 mm wide, length:width ratio 0.8 – 2, broadly ovate to ovate, fused at base over ca. 30% of the petal length, pubescent to glabrate outside, glabrous inside, pinkish outside. Carpels 20 to 40, 2 – 3.5 mm long, 0.6 – 1.5 mm wide, densely pubescent, free; stigma ca. 0.5 mm long, ca. 1 mm wide. Fruiting pedicel 200 – 400 mm long, 1 – 3 mm in diameter, sparsely pubescent to glab-



rous. Monocarps, 1 – 5, 50 – 80 mm long, 12 – 32 mm wide, length:width ratio 2.5 – 3.7, cylindrical, with ca. 4 longitudinal ridge, sparsely pubescent to glabrous, reddish, stipitate; stipe 3 – 4 mm long, 3 – 4 mm wide, sparsely pubescent to glabrous. Seeds (2) 6 – 16 per monocarp, uniseriate to biseriate, ca. 13 mm long, ca. 11 mm wide, ellipsoid, with a longitudinal ridge.

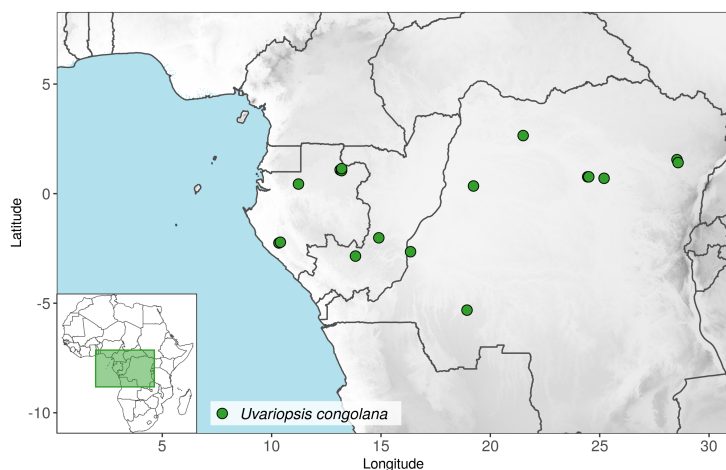


Figure 35: Distribution of *Uvariopsis congolana*

**Distribution.** Democratic Republic of the Congo, Gabon, Republic of the Congo.

**Notes.** Without any flower, this species resemble *Up. dioica*, *Up. guineensis*, *Up. pedunculosa* and *Up. solheidii* in having oblong to obovate leaves, with acute to rounded base and attenuate to acuminate apex. However, when flowering, *Up. congolana* differs from

all the other *Uvariopsis* species with flowers with 2 sepals and 3 petals (vs. 2 sepals and 4 petals in other *Uvariopsis* species). Its female flower pedicels and fruiting pedicels are longer comprised between 20 and 40 cm, which is longer than in the other *Uvariopsis* species (except *Up. pedunculosa* that has pedicels that can reach 33 cm). *Up. congolana* differs from *Up. pedunculosa* in having less 20 to 40 carpels (vs. 50 – 140 in *Up. pedunculosa*), and monocarps marked with longitudinal ridges (vs. monocarps verrucose in *Up. pedunculosa*).

**Specimens examined.** DEMOCRATIC REPUBLIC OF THE CONGO – Bandundu • A. Flamigni 10273 (K, M); Mushie, Bolobo; 2°39'03.24"S, 16°21'04.32"E; Mar. 1951 • R. Devred 2881 (K), Kwango, Kiyaka; 5°19'S, 18°56'E; 13 Mar. 1956 – Equateur • C.M. Evrard 5027 (K); Bolomba, Djoa; 0°20'53.88"N, 19°13'44.04"E; alt. 327 m; 15 Oct. 1958 – Orientale • C. Domis 3345 (K); Isangi, Yangambi; 0°46'N, 24°27'E; alt. 470 m; 09 Jan. 1952 • J. Bokdam 3733 (KIS, MO, WAG, WAG); Banalia, 20km along road from Kisangani to Bengamisa; 0°42'N, 25°12'E; 12 Dec. 1972 • J.L.P. Louis 5762 (B, K); Isangi, Yangambi, Isolove réserve flore; 0°46'N, 24°30'E; 12 Aug. 1937 • T.B. Hart 672 (MO); Mambasa, Epulu; 1°25'N, 28°35'E; alt. 750 m; 14 Aug. 1986 – Unknown major area • C.E.N. Ewango 617 (WAG), Epulu. Zone de Mambasa, Ituri Forest. Afarama; 1°33'N, 28°32'E; alt. 800 m. GABON – Ogooué-Ivindo • A. Mounrazi 234 (P), Bélinga; 1°08'27.49"N, 13°12'03.12"E; alt. 850 m • N. Hallé 2817 (K, P, P, U, WAG), Bélinga; 1°05'N, 13°08'E; alt. 850 m; 27 Oct. 1964 • N. Hallé 3039 (P), Bélinga; 1°05'N, 13°08'E; 06 Nov. 1964 • N. Hallé; A. Le Thomas 64 (K, P), Bélinga, mines de fer, route de Massaka; 1°03'N, 13°12'E; 17 Jul. 1966 – Ogooué-Maritime • J.C. Arends 696 (LBV, MO, P, WAG, WAG), Doudou Mountains; 2°15'S, 10°20'E; alt. 670 m; 08 Dec. 1984 • M.S.M. Sosef 1161 (LBV, MO, P, WAG), Monts Doudou, à ± 40km au Nord-Ouest de Doussala, autour du campement II; 2°13'S, 10°24'E; alt. 425 m; 08 Apr. 2000 – Woleu-Ntem • M.E. Leal 2335 (MO, WAG), Crystal Mountains National Park. Mt. Mekie; 0°26'16"N, 11°13'38"E; alt. 951 m; 20 Nov. 2008. REPUBLIC OF THE CONGO – Lékoumou • P. Sita 3209 (P), District de Zanaga, forêt de Mouoni; 2°51'S, 13°50'E; 08 Dec. 1971 – Plateaux • P. Sita 3351 (WAG), région de N'Gouala (Fort-Soufflay); 2°01'S, 14°54'E; 05 Jun. 1972.

*Uvariopsis dicaprio* Cheek & Gosline, PeerJ (2022)

**TYPE.** CAMEROON – Littoral • L. MacKinnon 51 (holotype K001381842; isotypes MO, YA); Yabassi, Ebo Forest, Dicam Trail 2000m from Bekop camp; 4°20'44"N, 10°24'33"E; alt. 849 m; 25 Mar. 2008.

**Description.** Tree 3 – 4 m tall, D.B.H 1.8 – 2.5 cm; young branches glabrous, old branches glabrous. Leaves distichous, simple, pinnately veined, margins entire and flat. Petiole 4 – 5 mm long, 1.9 – 2.1 mm wide, glabrous. Leaf lamina 177 – 230 mm long, 64 – 79 mm wide, length:width ratio 2.7 – 3, obovate, base acute, minutely cordate, apex acuminate, acumen 0.5 – 1.3 mm long, above glabrous when young and old, below glabrous when young and old; mid rib sunken above, raised below, above glabrous, below glabrous; secondary veins 5 – 9 pairs, brochidodromous, sunken above, raised below; tertiary veins reticulate. Flowers actinomorphic, unisexual. Male inflorescences borne on trunk from base towards 2.5 – 3 m, composed of 3 to 7 flowers. Peduncle ca. 2 mm long, ca. 2 mm in diameter, glabrous, bearing radiating 1-flowered partial peduncles 0.5 – 2 mm long, 0.9 – 1.2 mm wide. Flower pedicel 18 – 25 mm long, ca. 1 mm in diameter, glabrous. Bracts 0 to 2, upper bract ca. 1 mm long, ca. 1 mm wide, ovate, sparsely pubescent outside, glabrous inside. Sepals 2, 1 – 1.5 mm long, 2.1 – 2.5 mm wide, depressed ovate, glabrous outside, glabrous inside, green to pale brown. Petals 4, 14 – 16 mm long, 5.5 – 9 mm wide, length:width ratio 1.7 – 2.6, ovate to oblong, free, sparsely pubescent outside, glabrous inside, light yellow-green (black when dry) outside, light yellow-green with dark red base inside. Stamens ca. 0.5 mm long, ca. 0.1 mm wide, anthers linear, connective truncate. Female inflorescences unknown. Fruits unknown.

**Distribution.** Known from only one location in Cameroon: the Ebo Forest Reserve.

**Notes.** *Up. dicaprio* resembles *Up. solheidii* in having obovate leaves with acute to minutely cordate leaf base and acuminate apex. It differs from *Up. solheidii* in having young branches and petioles glabrous (vs. tomentose),

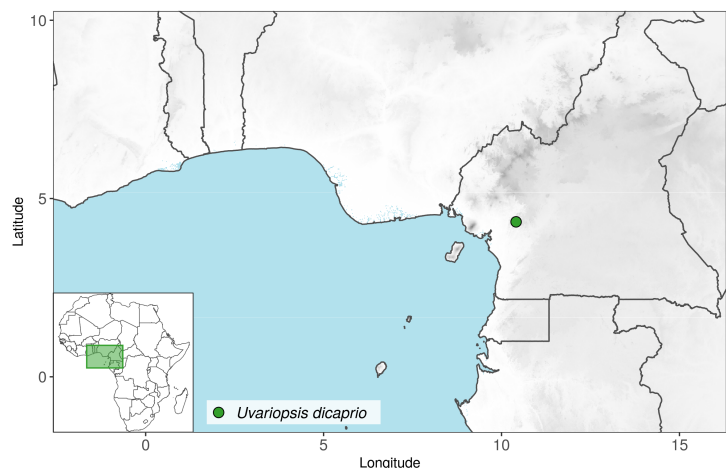


Figure 36: Distribution of *Uvariopsis dicaprio*

– 9 mm wide, vs. 5 – 10 mm long and 2.5 – 3.5 mm wide) and petals light yellow-green outside (vs. brown to light red outside). *Up. dicaprio* also differs from all the other *Uvariopsis* species in having and inflorescence peduncle ca. 2 mm long and 2 mm wide (vs. inconspicuous).

*Uvariopsis dioica* (Diels) Robyns & Ghesq., Ann. Soc. Sci. Bruxelles, Ser. B liii. 321 (1933)

*Tetrastemma dioicum* Diels, Bot. Jahrb. Syst. 38(3): 241 (1906)

**TYPE.** CAMEROON – Littoral • H.J.P. Winkler 909 (B), Edea; 3°47'50"N, 10°07'50"E; Nov. 1904.

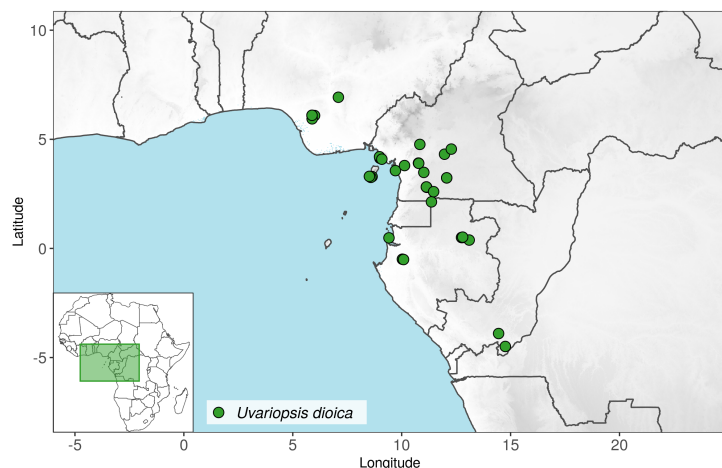


Figure 37: Distribution of *Uvariopsis dioica*

**Description.** Tree to shrub 3.6 – 20 m tall, D.B.H 8 – 40 cm; young branches pubescent to glabrous, old branches glabrous. Leaves distichous, simple, pinnately veined, margins entire and flat. Petiole 1.9 – 4 mm long, 1 – 2.5 mm wide, pubescent to glabrous. Leaf lamina 111 – 245 mm long, 38 – 92 mm wide, length:width ratio 3.5 – 3.7, elliptic to obovate, base acute to

rounded, apex acuminate, acumen 2 – 30 mm long, above glabrous when young and old, below glabrous when young and old; mid rib sunken above, raised below, above glabrous, below glabrous; secondary veins 8 – 14 pairs, brochidodromous, impressed above, raised below; tertiary veins reticulate. Flowers actinomorphic, unisexual, male and female flowers dimorphic, on same individuals (plant monoecious). Male inflorescences borne in clumps, on thickenings of the trunk, mainly between the base and the lower 3 m of the trunk (but up to ca. 5 m on large specimens), composed of 5 to 20 flowers. Peduncle inconspicuous. Flower pedicel (4) 9 – 55 mm long, 1 – 1.5 mm in diameter, pubescent to glabrate. Bracts 1 at base and 1 towards the lower half of the pedicel, upper bract ca. 1 mm long, ca. 1 mm wide, broadly ovate, adpressed, semi clasping the pedicel, pubescent outside, glabrous inside. Sepals 2, 1.5 – 3 mm long, 2.5 – 5 mm wide, circular to broadly ovate, sparsely pubescent outside, glabrous inside, purplish brown. Petals 4, 6 – 17 mm long, 3.5 – 9.5 mm wide, length:width ratio 1.6 – 2.5, ovate to elliptic, free, valvate, pubescent to glabrous outside, glabrous inside, red to brownish red outside, yellowish cream to reddish at base inside. Stamens ca. 300, 0.2 – 0.5 mm long, 0.1 – 0.5 mm wide, anthers linear, connective truncate. Female inflorescences less in number than the male inflorescences, borne in clumps, on thickenings of the trunk, between the base and the lower 25 – 50 (150 ?) cm of the trunk, composed of 6 to 10 flowers. Flower pedicel 20 – 77 (128) mm long, 1 – 2.5 mm in diameter, pubescent to glabrate. Bracts 1 to 3 at base and 1 to 2 towards the lower half of the pedicel, upper bract 1 – 3 mm long, 1 – 3 mm wide, broadly ovate, adpressed, semi clasping the pedicel, pubescent outside, glabrous inside. Sepals 2, 2 – 5 mm long, 4 – 11 mm wide, circular to broadly ovate, fused at base, sparsely pubescent outside, glabrous inside, purplish brown. Petals 4, 12 – 25 mm long, 6

TAXONOMIC REVISION OF UVARIODENDRON AND UVARIOPSIS

– 17 mm wide, length:width ratio 1.2 – 2.5, ovate to elliptic, free, valvate (rarely fused at base over 1 – 3 mm), pubescent to glabrous outside, glabrous inside, red to brownish red outside, yellowish cream to reddish at base inside. Carpels 100 – 280, 1.5 – 3.5 mm long, 0.7 – 1.5 mm wide, pubescent, free; stigma 0 – 0.6 mm long, 0.5 – 1 mm wide, coiled. Fruiting pedicel 33 – 97 mm long, 1 – 3.5 mm in diameter, sparsely pubescent to glabrous. Monocarps, 1 – 5, 17 – 85 mm long, 10 – 50 mm wide, length:width ratio 1.2 – 2.1, ellipsoid to cylindrical, smooth, not ridged, sparsely pubescent to glabrous, pale brownish grey to yellow to red, sessile to shortly stipitate; stipe up to 3 mm long, 4 – 5 mm wide, glabrate. Seeds 5 – 8 per monocarp, biseriate, 15 – 22 mm long, ca. 15 mm wide, ellipsoid, in a translucent slimy pulp.

**Distribution.** Cameroon, Equatorial Guinea (Bioko island), Gabon, Nigeria, Republic of the Congo.

**Notes.** *Up. dioica* resembles *Up. guineensis*, *Up. pedunculosa* and *Up. solheidii* in having elliptic to obovate leaves, with acute to rounded base and attenuate to acuminate apex. It differs from these species in having flowers borne in clumps of 5 to 20 flowers on thickenings of the trunk, lower than 3 m high (vs. inflorescences of 1 or 2 flowers). *Up. dioica* has 100 to 240 carpels, whereas all the other *Uvariopsis* species have less than 100 carpels. Only *Up. korupensis* and *Up. pedunculosa* can have up to 120 and 140 carpels, respectively, but *Up. dioica* has smaller leaves than *Up. korupensis* (11 – 25 cm long vs. 28 – 62 cm long) and smaller flower pedicels than *Up. pedunculosa* (20 – 77 mm long vs. 80 – 325 mm).

**Specimens examined.** CAMEROON – Central Region • G.W.J. Mildbraed 8260 (K), Übergangs - und Kampfgebiet gegen die Savanne an der Nord - grenze der Hylaea südlich des Sanaga zwischen Jaunde und Dengdeng unweit der vereinerung von Lom (Sanaga) und Djerem. Etwa 115 km N O Jaunde; 4°33'04.96"N, 12°16'43.94"E; Mar. 1914 • H. Jacques-Félix 2493 (P), Ndiki; 4°46'N, 10°50'E; Nov. 1938 • P.R.J. Bamps 1458 (P), Résèrve forestière de Makak; 3°29'N, 11°01'E; 14 Dec. 1967 • R.G. Letouzey 12290 (K, P), Mambe près de Boga, 30 km N. Eseka. (feuille IGN 1/200 000 Edea); 3°53'58.29"N, 10°46'58.4"E; 08 Dec. 1973 • R.G. Letouzey 9541 (MO, P, WAG, YA), Versant septentrional des Monts Mfiki au Sud de Ndo, 25 km NNE d'Esse; 4°19'N, 11°58'E; alt. 983 m; 09 Nov. 1969 – Littoral • R.G. Letouzey 12580 (P), Sude de Ngola (8km Est de l'embouchure de la Sanaga); 3°33'55"N, 9°42'46"E; 05 Jan. 1974 • T.L.P. Couvreur 654 (WAG, YA), Mambe Massif, above Boga village, 100 km along road from Yaoundé to Edea; 3°54'35.85"N, 10°46'25.97"E; alt. 686 m; 19 Jun. 2014 • T.L.P. Couvreur 659 (WAG, YA), Mambe Massif, above Boga village, 100 km along road from Yaoundé to Edea; 3°54'26.07"N, 10°46'21.27"E; alt. 654 m; 20 Jun. 2014 – South Region • J.J.F.E. de Wilde 7754 A (K, P, WAG, WAG), Roughly between the village of N'Kolandom and Station du Cacaoyer de N'Koemvone; 2°48'N, 11°09'E; 27 Nov. 1974 • J.J.F.E. de Wilde 8270 A (BR, MO, P, PRE, WAG, WAG), Station du Cacaoyer de N'koemvone, S. of Ebolowa, 14 km on the road to Ambam. On bank of the Seng river; 2°49'N, 11°08'E; alt. 500 m; 05 Jun. 1975 • J.J.F.E. de Wilde 8709 (BR, MO, P, PRE, WAG, WAG, YA), Station du Cacaoyer de N'koemvone, S. of Ebolowa, 14 km on the road to Ambam. On bank of the Seng River; 2°49'N, 11°08'E; alt. 550 m; 12 Dec. 1975 • R.G. Letouzey 4219 (K, P), Nkomo, près Ngoassé au S; de la rivière Lobo - feuille IGN 1/200000 Akonolinga; 3°14'N, 12°04'E; 13 Feb. 1962 • R.G. Letouzey 4230 (P), Nkomo, près Ngoassé au S; de la rivière Lobo - feuille IGN 1/200000 Akonolinga; 3°14'N, 12°04'E; 14 Feb. 1962 • R.G. Letouzey 9934 (K, P), près de la rivière Mboro, près Mevous, 50km SE d'Ebolowa sur piste d'Evindissi; 2°36'N, 11°28'E; 30 Jan. 1970 – South-West Region • G.W.J. Mildbraed 10647 (K), Bibundi-Pflanzung, Westlich des Kamerunberges; 4°12'N, 8°59'E; Nov. 1928 • J.F. Villiers 2429 (P), Pente SW Mt Cameroun, NE Bakingili, 20km WNW Limbé; 4°05'22.16"N, 9°05'21.91"E; alt. 800 m; 09 Dec. 1984 • J.J. Wieringa 2029 (BR, E, FHO, K, MO, SCA, WAG); Fako, Limbe, W of Njonji Lake; 4°08'N, 9°01'E; alt. 150 m; 27 Jan. 1994 • M.R. Cheek 5482 (K, SCA, YA), Low altitude forest above oil palm plantation. Reached

## CHAPTER 4

after c. 40 minutes walk N then E from Njonji. Hunters path to 'Lake Njonji'; 4°08'N, 9°01'E; alt. 300 m; 18 Nov. 1993 • M.R. Cheek 5501 (K, MO, SCA, YA), Low altitude forest above oil palm plantation. Reached after c. 40 minutes walk N then E from Njonji. Hunters path to 'Lake Njonji'; 4°08'N, 9°00'E; alt. 5 m; 19 Nov. 1993. EQUATORIAL GUINEA – Bioko Sur • W.R.Q. Luke 11970 (EA, MA), Moaba - Moka Trail Pt 139 - Pt 138; 3°17'26.92"N, 8°38'29.83"E; alt. 650 m; 16 Mar. 2007 • W.R.Q. Luke 13050 (MA), Ureka pt 330 to Moraka pt 339; 3°15'19.08"N, 8°35'04.56"E; alt. 141 m • W.R.Q. Luke 13113 (EA, MA, MO), Badja E Trail pt 338; 3°18'04.68"N, 8°31'01.2"E; alt. 700 m; 21 Jan. 2009. GABON – Moyen-Ogooué • E. Bidault 1558 (BR, BRLU, LBV, MO, P, WAG), Est du lac Azingo, à 30 km au Nord-Ouest de Lambaréné; 0°30'32.42"N, 10°05'08.01"E; alt. 48 m; 08 Jun. 2014 • T.L.P. Couvreur 926 (LBV, WAG, YA), 27 km after Lambaréné, on road to Bifoum (N1), then around 20 km on road to Lake Azingo; 0°29'38.73"N, 10°01'55.24"E; alt. 23 m; 24 Nov. 2015 • T.O.B.E.B. Stévant 4792 A (P, WAG), Okala, North of Libreville. Terrain de Montigny à Okala (Libreville); 0°29'N, 9°25'E; alt. 10 m; 12 Feb. 2014 – Ogooué-Ivindo • A. Hladik 1472 (BRUNOY, P, P, US), Ipassa, au croisement des layons J et VII; 0°30'N, 12°48'E; alt. 490 m; 29 Oct. 1971 • J.M. Reitsma 3507 (LBV, MO, WAG), Primary rain forest, near village Ekobakoba, 50 km SE of Makokou; inventory; 0°23'N, 13°06'E; 21 May. 1987 • L.J. Dorr 4248 (LBV, MO), Station I.R.E.T. (M'Passa Field Station). 10 km S de Makokou sur la riviere Ivindo; 0°30'N, 12°45'E; alt. 500 m; 13 May. 1985 • L.J. Dorr 4275 (LBV, MO, P), Station I.R.E.T. (M'Passa Field Station), 10 km S de Makokou sur la riviere Ivindo; 0°30'N, 12°45'E; alt. 500 m; 14 May. 1985 • M.S.M. Sosef 2210 (BR, LBV, MO, WAG), Ipassa Reserve, IRET Research Station, SW of Makokou; 0°31'N, 12°48'E; alt. 350 m; 04 Nov. 2005 – Woleu-Ntem • A.M. Louis 4098 (BR, LBV, MO, WAG), 25 km NE of Bitam, Nsimy; 2°08'N, 11°22'E; 02 May. 1995. NIGERIA – Edo State • A.F. Ross 2 / 6 (K); Benin, Sapoba Forest Reserve; 6°06'N, 5°53'E; 1934 • B.O. Daramola FHI 72315 (K, MO), Iyekoriowon. Forest Reserve. In P.S.P. 82 Ugo; 6°05'19.05"N, 6°00'04.46"E; 04 Oct. 1973 • R.D. Meikle 628 (K, P), Usonigbe Forest Reserve near Sapoba; 5°56'17.52"N, 5°53'20"E; 16 Nov. 1944 • R.W.J. Keay FHI 28066 (K, K, P); Benin, Sapoba Forest Reserve, Compté.9,S.S.I; 6°06'N, 5°53'E; 03 Nov. 1950 – Kogi State • M.G. Latilo FHI 47768 (K); Kabba, Southern Adoru Forest Reserve, Igala, bank of river Owe near Adoru; 6°55'38.49"N, 7°05'38.55"E; 01 Jul. 1963. REPUBLIC OF THE CONGO – Pool • J. Koechlin 4001 (P), Bangou, Forêt de; 3°54'S, 14°27'E; Dec. 1956 • P. Sita 3264 (P), Forêt de Bangou, Est de M'Passa; 4°29'34"S, 14°45'28"E; 18 Dec. 1971.

### *Uvariopsis etugiana* Dagallier & Couvreur, PhytoKeys (in press)

**TYPE.** CAMEROON – North-West Region • R.G. Letouzey 13414 (holotype: P), Rive droite de la Metchum, près Obang (18km S of Wum); 6°15'N, 10°01'59.99"E; alt. 600 m; 03 Dec. 1974.

**Description.** Tree 3 – 6 m tall, D.B.H unknown; young branches slightly pubescent, old branches glabrous. Leaves distichous, simple, pinnately veined, margins entire and flat, with minute pelucid punctuations. Petiole 3.5 – 4 mm long, 2.5 – 3.5 mm wide, glabrous. Leaf lamina 190 – 235 mm long, 70 – 85 mm wide, length:width ratio ca. 2.7, elliptic, coriaceous, base acute to slightly decurrent, apex attenuate to acuminate, acumen ca. 10 mm long, above glabrous when young and old, below glabrous when young and old; mid rib sunken above, raised below, above glabrous, below glabrous; secondary veins 8 – 10 pairs, brochidodromous, impressed above, raised below; tertiary veins reticulate. Flowers actinomorphic, unisexual, male and female flowers dimorphic, on same individuals (plant monoecious). Male inflorescences borne on trunk, composed of 1 to 2 flowers. Peduncle inconspicuous. Flower pedicel 8 – 10 mm long, 1 – 1.5 mm in diameter, glabrate to glabrous. Bracts 1 at base and 1 towards the middle or lower half of the pedicel, upper bract 1 – 1.5 mm long, 1 – 2.5 mm wide, broadly ovate, adpressed, semi clasping the pedicel, pubescent outside, glabrous inside. Sepals 2, ca. 2 mm long, ca. 4 mm wide, broadly ovate, basely fused, sparsely pubescent to glabrous outside, glabrous inside, color unknown. Petals 4, 6 – 11.5 mm long, 3.5 – 7 mm wide, length:width ratio 1.6 – 2.5, elliptic to ovate, sparsely

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pubescent to glabrous outside, glabrous inside, color unknown. Stamens numerous (exact number unknown), 0.5 – 1 mm long, ca. 0.2 mm wide, anthers linear, connective truncate. Female inflorescences borne on trunk, composed of 1 to 2 flowers. Flower pedicel ca. 4 mm long, ca. 2 mm in diameter, glabrate to glabrous. Bracts 1 at base and 1 towards the middle or lower half of the pedicel, upper bract ca. 1.5 mm long, ca. 2.5 mm wide, broadly ovate, adpressed, semi clasping the pedicel, pubescent outside, glabrous inside. Sepals 2, 1 – 1.5 mm long, 2 – 3.5 mm wide, broadly ovate, basely fused, sparsely pubescent to glabrous outside, glabrous inside, color unknown. Petals 4, ca. 14 mm long, ca. 8 mm wide, length:width ratio 1.6 – 2.5, elliptic, glabrous outside, glabrous inside, color unknown. Stamens ca. 5, ca. 1 mm long, sterile, seen on one female flower. Carpels ca. 20, ca. 3 mm long, ca. 1 mm wide, glabrate at base to glabrous, free; stigma coiled. Fruits unknown.

**Distribution.** Known from only two localities in the North-West and South-West Regions in Cameroon.

**Notes.** *Up. etugiana* resembles *Up. pedunculosa* in the shape of the leaves, and *Up. solheidii* in the shape of its flowers. However, *Up. etugiana* has a short flowering pedicel (4 – 10 mm vs. 14 – 325 mm in *Up. pedunculosa* and 9 – 198 mm in *Up. solheidii*) and

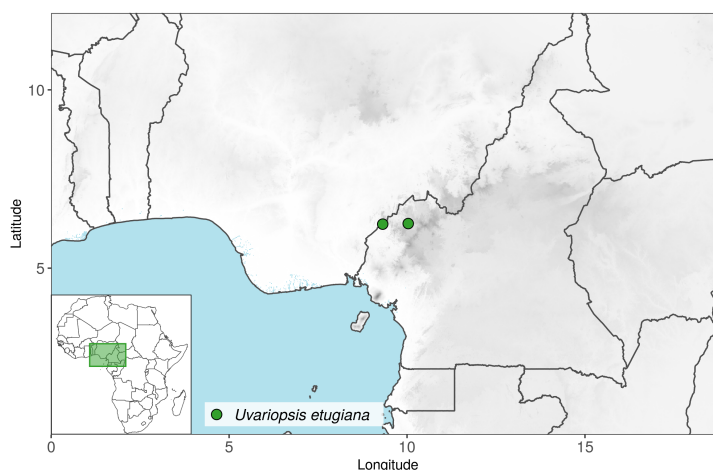


Figure 38: Distribution of *Uvariopsis etugiana*

petals which are glabrous outside (vs. pubescent in both *Up. pedunculosa* and *Up. solheidii*).

**Specimens examined.** CAMEROON – South-West Region • D.W. Thomas 4544 (MO), Takamanda Forest Reserve; 6°14'N, 9°19'E; alt. 170 m; 21 Mar. 1985.

*Uvariopsis guineensis* Keay, Kew Bull. 7(2): 152 (1952)

*Uvaria spectabilis* A.Chev., Explor. Bot. Afrique Occ. Franc. i. 7 (1920)

*Uvariopsis globiflora* Keay **syn. nov.**, Kew Bull. 7(2): 152 (1952)

**TYPE.** IVORY COAST – Danané • A.J.B. Chevalier 21305 (holotype: P), Haut Cavally, Pays des Byolas, entre Danané et Goutokouma; 7°16'N, 8°09'W; 25 Apr. 1909.

**Description.** Tree 2.5 – 9 m tall, D.B.H 4 – 12 cm; young branches sparsely pubescent to glabrous, old branches glabrous. Leaves distichous, simple, pinnately veined, margins entire and flat. Petiole 1.5 – 5 mm long, 1.5 – 3.5 mm wide, sparsely pubescent to glabrous. Leaf lamina 110 – 310 mm long, 45 – 108 mm wide, length:width ratio 2.3 – 4.2, elliptic to oblong to obovate, coriaceous, base acute to rounded,



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apex attenuate to acuminate, acumen 9 – 30 mm long, above glabrous when young and old, below glabrous when young and old; mid rib sunken above, raised below, above glabrous, below sparsely pubescent to glabrous; secondary veins 7 – 14 pairs, brochidodromous, impressed above, raised below; tertiary veins reticulate. Flowers actinomorphic, unisexual, male and female flowers dimorphic, on same individuals (plant monoecious). Male inflorescences borne on trunk, axillary or terminal, composed of 1 flower. Peduncle inconspicuous. Flower pedicel 5 – 16 mm long, 1 – 2 mm in diameter, sparsely pubescent. Bracts 1 at base and 1 towards the middle or lower half of the pedicel, upper bract 1 – 3.5 mm long, 1 – 3.5 mm wide, broadly ovate, adpressed, semi clasping the pedicel, pubescent outside, glabrous inside. Sepals 2, 1 – 3 mm long, 2 – 7 mm wide, broadly ovate, free to basely fused, pubescent to sparsely pubescent outside, glabrous inside, yellowish green. Petals 4, 7 – 17 mm long, 5 – 17 mm wide, length:width ratio 0.9 – 1.4, broadly ovate, free to fused at base over 30 – 50% of their length, pubescent to sparsely pubescent outside, glabrous inside, pale greenish to cream outside, greenish cream to cream with purplish base inside. Male flowers: stamens number unknown, 0.3 – 1 mm long, 0.2 – 0.3 mm wide, anthers linear, connective truncate. Female inflorescences borne on trunk, axillary or terminal, composed of 1 flower. Flower pedicel 10 – 65 mm long, 1 – 2 mm in diameter, sparsely pubescent. Bracts 1 to 3 at base and 1 towards the middle or lower half of the pedicel, upper bract 1 – 3.5 mm long, 1 – 3.5 mm wide, broadly ovate, adpressed, semi clasping the pedicel, pubescent outside, glabrous inside. Sepals 2, 1 – 6 mm long, 2 – 10 mm wide, broadly ovate, free to basely fused, sparsely pubescent to pubescent outside, glabrous inside, yellowish green. Petals 4, 9 – 24 mm long, 7 – 22 mm wide, length:width ratio 0.9 – 1.4, broadly ovate, free to fused at base over 30 – 50% of their length, pubescent to sparsely pubescent outside, glabrous inside, pale greenish to cream outside, greenish cream to cream with purplish base inside. Female flowers: carpels 10 – 50, 2 – 5 mm long, 0.6 – 1.1 mm wide, pubescent to velutinous, free; stigma ca. 0.5 mm long, 0.5 – 0.8 mm wide, coiled. Fruiting pedicel 17 – 69 mm long, 1.5 – 4.5 mm in diameter, sparsely pubescent to glabrous. Monocarps, 2 – 10, 20 – 70 (90) mm long, 12 – 25 mm wide, length:width ratio 1.7 – 3.3 (measures taken from both dried fruits and their associated specimen label, note that monocarps seem to sink when drying), cylindrical, smooth, straight to slightly curved, with a longitudinal ridge, sparsely pubescent to glabrous, dull olive green to red to brown, sessile to shortly stipitate; stipe up to 3 mm long, 2 – 6 mm wide, pubescent to glabrous. Seeds 2 – 22 per monocarp, biseriate, 12 – 17 mm long, 10 – 13 mm wide, in a yellow pulp with strong aniseed scent.

**Distribution.** Ghana, Guinea, Ivory Coast, Liberia, Sierra Leone.

**Notes.** *Up. guineensis* resembles *Up. dioica*, *Up. pedunculosa*, and *Up. solheidii* in having elliptic to oblong to obovate leaves, with acute to rounded base and attenuate to acuminate apex. Young branches

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and petioles of *Up. guineensis* are sparsely pubescent to glabrous (vs. pubescent to glabrous in *Up. dioica* and *Up. pedunculosa*, and tomentose to shortly tomentose in *Up. solhheidii*). *Up. guineensis* has less than 50 carpels (vs. more than 50 in *Up. dioica* and *Up. pedunculosa*), and its monocarpels are smooth with a single longitudinal ridge (vs. with longitudinal and trans-  
versal ridges in *Up. solhheidii* and verrucose in *Up. pedunculosa*).

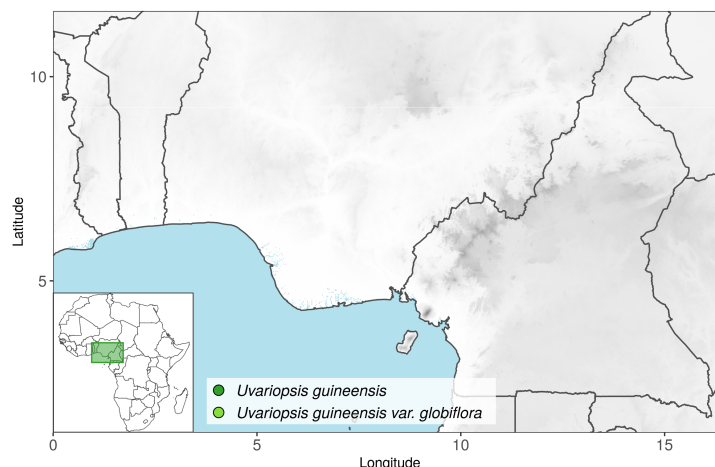


Figure 39: Distribution of *Uvariopsis guineensis*

**Specimens examined.** GHANA – Western Region • H.H. Schmidt 2070 (MO), Bia National Park and Production Reserve. From the town of Bankasa, Park Guard Camp 13, along foot trail to Park Guard Camp 11; 6°32'40"N, 3°08'20"W; alt. 180 m; 05 Mar. 1996. GUINEA – Nzérékoré • A.J.B. Chevalier 20797 (K, P); Macenta, Pays des Koniankéi, Fassakoïdou; 8°40'N, 9°17'W; 24 Feb. 1909 • C.C.H. Jongkind 10660 (WAG), Forêt Classée de Mt Yonon, not far from the Diane River; 7°58'58.8"N, 9°07'16.8"W; alt. 480 m; 07 May. 2011 • C.C.H. Jongkind 10774 (BR, MO, P, WAG), Forêt Classée de Mt Yonon, not far from the Diane River; 7°59'01.8"N, 9°07'17.4"W; alt. 445 m; 12 May. 2011 • C.C.H. Jongkind 11343 (MO, WAG, WAG), Nimba mountains. East side of main ridge; 7°38'56.4"N, 8°21'40.8"W; alt. 793 m; 30 Jun. 2012 • C.C.H. Jongkind 7767 (BR, K, P, WAG), Nimba Mountains, banks of Zié River close to reserve boundary; 7°42'58.2"N, 8°21'39.6"W; alt. 540 m; 21 Jun. 2007 • D. Bilivogui 4 (MO, P, WAG); Lola, Guinée Forestière, Nimba Mountains, SMFG iron ore mine concession. Gouan River valley, at its lowest point inside the reserve; 7°42'46"N, 8°23'40"W; alt. 535 m; 28 Sep. 2011 • E. Bidault 4798 (BRLU, MO, P, SERG), Monts Nimba, autour du camp Seringbara 2; 7°37'43.5"N, 8°25'39.72"W; alt. 1020 m; 09 Oct. 2019 • E. Bidault 632 (MO, P); Lola, Nimba Mountain, Guinée, Monts Nimba, site du patrimoine mondial, forêt de Gbié au nord de la grande savane; 7°56'38.37"N, 8°21'38"W; alt. 773 m; 26 Jun. 2012 • J.-G. Adam 3826 (WAG), Nzérékoré. Jomou; 24 Feb. 1949 • Nimba Botanic Team JR 1272 (WAG), Nimba Mountains, plot JRFM01, vallée de Gba; 7°40'34.8"N, 8°23'30"W; alt. 947 m; 05 Dec. 2007 • P.K. Haba 107 (K), Béro Mountains, Le sommet du Mont Thon dans les Monts Béro. Proche de la ville de Boola; 8°19'12"N, 8°41'47"W; alt. 1099 m; 03 Dec. 2007 • R.A.A. Schnell 3618 (P), Mt Nimba., Blanmbaya; 7°37'N, 8°25'W; Sep. 1947 • X.M. van der Burgt 1300 (K, WAG); Macenta, Guinée Forestière. Macenta + Beyla préfectures. Simandou Range. South of Pic de Fon, 1.4 km south and 900 m west of Fokou hill; 8°28'55"N, 8°54'05"W; alt. 855 m; 15 Sep. 2008. IVORY COAST – Abengourou • C. Versteegh 619 (U, WAG, WAG), Surroundings of Niablé, 30 km east of Abengourou; 6°39'40.63"N, 3°16'11.42"W; 31 Jul. 1969 – Abidjan • J. de Koning 4587 (WAG), Experimental Station ORSTOM, Adiopodoumé. Seedlings, seed source Banco Forest; 5°23'N, 4°03'W; 30 Oct. 1974 • J. de Koning 4905 (WAG), CULTA. Experimental Station ORSTOM, Adiopodoumé. Seedlings, seed source Banco Forest; 5°23'N, 4°03'W; 29 Nov. 1974 • J. de Koning 5170 (MO, WAG), Abidjan, Banco Forest; 5°23'N, 4°03'W; 16 Jan. 1975 • J. de Koning 5504 (BR, MO, WAG), Banco Forest; 5°23'N, 4°03'W; 08 Mar. 1975 – Daloa • L.P.G.A. Nusbaumer 36 (G), F.C. Scio., Pinhou, Lobykro à 5 Km, Bloc 28, Parcelle 141 de la Sodefor; 7°42'N, 6°50'W; 10 Sep. 2001 – Danané • L. Aké Assi 8823 (G), Forêt de Tiapleu 7.4197, -8.2116; 7°25'10.92"N, 8°12'57.6"W; 30 Apr. 1966 • L. Aké Assi 9131 (G), Momi Mont, Forêt Classée du, Forêt de Mont Momi; 7°24'N, 8°03'W; 28 Oct. 1966 – Soubré • A.J.B. Chevalier 19224 (P), entre le moyen Sassandra et le moyen Cavally; 5°55'59.75"N, 7°03'46.35"W; 06 Jul. 1907 – Vavoua • F.N. Kouamé 1445 (CSRS, G), F.C. du Haut-Sassandra, Nord. forêt dégradée, relevé FNK14; 7°18'N, 7°01'W; 04 Apr. 1995. LIBERIA – Bong • D.H. Linder 580 (K), Gbanga; 7°00'N, 9°29'W; 12 Sep. 1926 – Grand Gedeh • C.C.H. Jongkind 6667 (WAG), along Zwedru - Harper road, south of Tiama Town; 5°34'12.6"N, 8°09'16.2"W; alt. 260 m; 07 Jun. 2005 – Lofa • C.C.H. Jongkind 6691 (WAG), North Lorma National Forest; 8°03'N, 9°42'W; 19 Nov. 2005 • C.C.H. Jongkind 9478 (WAG), near Ziggida, rappid in Jèbèh River; 8°02'10.8"N, 9°28'55.8"W; alt. 455 m; 12 Feb. 2010 – Montserrado • J.J.F.E. de Wilde 3811 (MO, WAG), between Bomi hills and Lofa river, c. 15km N.N.W. of Bomi hills; 6°58'N, 10°52'W; 15 Apr. 1962 – Nimba • J.-G. Adam 20713 (IFAN, K, P, UPS), Nimba; 7°32'N, 8°32'W; alt. 450 m; 23 Jan. 1965 • J.-G. Adam 26362



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(MO), Granfield Mt Nimba; 7°34'N, 8°29'W; 17 Oct. 1971 • Nimba Botanic Team NS 74 (WAG), Valley between Mt Gangra and Mt Yuelliton, plot SNFR01; 7°33'22.2"N, 8°38'W; alt. 700 m; 14 Jan. 2009 • W.J. Harley 1556 (K), Bilimu; 7°24'N, 8°36'W; 06 Jan. 1948 – Sino • B. Senterre 7066 (MO), Dugbe hummingbird site (ca. 20km South of Sapo National Park, ca. 50 km East of Greenville), North of Money camp; 5°06'47"N, 8°32'18"W; alt. 107 m; 27 Mar. 2014 • C.C.H. Jongkind 8898 (WAG), Babooni road not too far from main road; 5°31'N, 8°37'36"W; alt. 140 m; 09 Mar. 2009. SIERRA LEONE – Eastern Province • D. Small 101 (K); Kenema, Dambayei Valley. Kenema, Kambui Hills F.R.; 7°48'N, 11°11'W; 25 May. 1951 • J. Momoh 37 (K, SL, WAG), Gola National Park, central block. 600 m N of Malimbe camp; 7°40'07"N, 10°53'22.7"W; alt. 320 m; 24 Oct. 2013 – Northern Province • J.-G. Adam 23345 (MO); Koinadugu, Loma Mountains, Kabala Mt Loma - Kamia; 9°22'37.15"N, 11°19'26.51"W; 26 Jan. 1966 • P. Jaeger 7488 (P); Koinadugu, Loma Mountains, Loma; 9°10'N, 11°07'W; 16 Sep. 1964 • P. Jaeger 7489 (G); Koinadugu, Loma Mountains, W Loma; 9°10'N, 11°07'W; alt. 300 m; 16 Sep. 1964 • P. Jaeger 8041 (G, K, P); Koinadugu, Mt Loma; 9°10'N, 11°07'W; alt. 600 m; 13 Oct. 1964 • P. Jaeger 8756 (K); Koinadugu, Mt Loma; 9°10'N, 11°07'W; alt. 800 m; 29 Dec. 1965 • P. Jaeger 9093 (K, P); Koinadugu, Mt Loma; 9°10'N, 11°07'W; 26 Jan. 1966 • P. Jaeger 9159 (G, K, P); Koinadugu, Mt W Loma; 9°10'N, 11°07'W; alt. 600 m; 29 Jan. 1966 – Southern Province • A.H. Unwin 51 (K); Pujehun, Gola Forest; 7°16'N, 11°18'W; 1909 • D. Small 593 (K, K, P); Pujehun, Gola forest; 7°40'N, 10°55'W; 08 Apr. 1952 • D. Small 655 (K); Pujehun, Gola Forest; 7°16'N, 11°18'W; 1952 • D. Small 676 (K, P); Pujehun, Gola forest, Bagbe Line 20n B.III; 7°16'N, 11°18'W; 19 May. 1952 • D. Small 678 (K); Pujehun, Gola forest, Bagbe Line 20n B.III; 7°16'N, 11°18'W; 15 May. 1952 • H.D. Jordan 2068 (B, K, P); Pujehun, Gola Forest, mile 44 (Tunkia); 7°39'N, 10°54'W; 14 May. 1955.

***Uvariopsis guineensis* var. *globiflora* (Keay) Dagallier, **comb. nov.****

*Uvariopsis globiflora* Keay, Kew Bull. 7(2): 152 (1952)

**TYPE.** GHANA – Eastern Region • C. Vigne FH 1877 (sheets here designated, holotype: K (K000041224); isotypes: K (K000041225, K000041226)), Amentia; 6°13'N, 1°10'W; alt. 160 m; Mar. 1930.

**Description.** Tree 2.5 – 9 m tall, D.B.H unknown; young branches sparsely pubescent to glabrous, old branches glabrous. Leaves distichous, simple, pinnately veined, margins entire and flat. Petiole 1.5 – 3.5 mm long, 1.5 – 3.5 mm wide, sparsely pubescent to glabrous. Leaf lamina 110 – 236 mm long, 45 – 80 mm wide, length:width ratio 2.3 – 3.1, elliptic to oblong, coriaceous, base rounded, apex attenuate to broadly acuminate, acumen 9 – 11 mm long, above glabrous when young and old, below glabrous when young and old; mid rib sunken above, raised below, above glabrous, below glabrous; secondary veins 8 – 12 pairs, brochidodromous, impressed above, raised below; tertiary veins reticulate. Flowers actinomorphic, unisexual, male and female flowers dimorphic, on same individuals (plant monoecious). Male inflorescences axillary or terminal (more rarely borne on trunk), composed of 1 flower. Peduncle inconspicuous. Flower pedicel 8 – 16 mm long, ca. 1 mm in diameter, sparsely pubescent. Bracts 1 at base and 1 towards the middle or lower half of the pedicel, upper bract 1 – 1.5 mm long, ca. 2 mm wide, broadly ovate, adpressed, semi clasping the pedicel, pubescent outside, glabrous inside. Sepals 2, 1 – 3 mm long, 2 – 4 mm wide, broadly ovate, free to basely fused, sparsely pubescent outside, glabrous inside, color unknown. Petals 4, 7 – 10 mm long, 5 – 9 mm wide, length:width ratio 1.1 – 1.4, broadly ovate, free, sparsely puberulent outside, glabrous inside, pale greenish to cream outside, cream with purplish base inside. Male flowers: stamens number unknown, 0.3 – 0.5 mm long, ca. 0.3 mm wide,

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anthers linear, connective truncate. Female inflorescences axillary or terminal (rarely borne on trunk), composed of 1 flower. Flower pedicel 15 – 33 mm long, 1 – 1.5 mm in diameter, sparsely pubescent. Bracts 1 at base and 1 towards the middle or lower half of the pedicel, upper bract 1 – 1.5 mm long, ca. 2 mm wide, broadly ovate, adpressed, semi clasping the pedicel, pubescent outside, glabrous inside. Sepals 2, 1 – 3 mm long, 2 – 4 mm wide, broadly ovate, free to basely fused, sparsely pubescent outside, glabrous inside, color unknown. Petals 4, 10 – 22 mm long, 9 – 17 mm wide, length:width ratio 1.1 – 1.4, broadly ovate, free, sparsely puberulent outside, glabrous inside, pale greenish to cream outside, cream with purplish base inside. Female flowers: carpels 10 – 20, 2 – 4 mm long, 1 – 1.1 mm wide, pubescent, free; stigma unknown. Fruiting pedicel 30 – 46 mm long, 1.5 – 4 mm in diameter, glabrate. Monocarps, 2 – 6, 20 – 52 mm long, 12 – 21 mm wide, length:width ratio 1.7 – 2.5, cylindrical, smooth, straight, with a slight longitudinal ridge, sparsely pubescent to glabrous, dull olive green, shortly stipitate; stipe 1 – 3 mm long, 2 – 3.5 mm wide, pubescent to sparsely pubescent. Seeds 2 – 8 per monocarp, biseriate.

**Distribution.** Ghana.

**Notes.** *Up. guineensis* var. *globiflora* differs from the type variety in having free petals (vs. fused at base over 30 – 50% of their length) and fewer carpels (10 – 20 carpels vs. 20 – 50 carpels). The male flowers have also smaller petals (7 – 10 mm long and 5 – 9 mm wide vs. 8 – 17 mm long and 9 – 17 mm wide).

**Specimens examined.** GHANA – Ashanti Region • J.E. Andoh FH 4246 (K, P), South Fomangsu Reserve; 6°36'N, 0°57'E; Oct. 1936 • J.E. Andoh 5096 (P), Bobiri Forest Reserve; 6°40'N, 1°20'W; Jan. 1948 – Brong-Ahafo Region • A.A. Enti FE 1220 (K, MO), Asukese F.R.; 7°09'07"N, 2°31'07"W; 02 Mar. 1973 – Eastern Region • A.A. Enti GC 37451 (K), Atewa Range F.R.; 6°09'N, 0°36'E; 14 Dec. 1967 • A.A. Enti R 698 (BR, MO), Aiyola Forest Reserve, Kade; 6°09'N, 0°57'E; 03 May. 1972 • C.C.H. Jongkind 1809 (MA, MO, WAG, WAG), Atewa Range Forest Reserve, along Old Geological Survey road; 6°14'06"N, 0°33'E; alt. 400 m; 26 Oct. 1994 • D.K. Harder 3325 (MO, WAG), Asiakwa District: Sagyimase Village; Atewa Range (Forest Reserve); between 6-8 km NW of intersection of Accra-Kumasi Road at Sagyimase along forest access road; 6°13'48"N, 0°32'42"E; alt. 810 m; 04 Jul. 1995 • J.K. Morton A 4247 (K, WAG), Kade Agric. Res. Station; 6°08'N, 0°55'E; 04 May. 1961 – Western Region • A. Foggie 4456 (K), Bia National Park, Bia F. Resrve; 6°29'55"N, 3°05'24"W; Apr. 1937.

*Uvariopsis korupensis* Gereau & Kenfack, *Adansonia* sér. 3, 22(1): 41 (2000)

**TYPE.** CAMEROON – South-West Region • D. Kenfack 1026 (holotype: YA; isotypes: MO, P, WAG); Ndian, Korup National Park, Chimpanzee Camp; 5°04'N, 8°52'E; alt. 160 m; 03 Feb. 1998.

**Description.** Tree 3 – 15 m tall, D.B.H 5 – 14 cm; young branches pubescent to glabrous, old branches glabrous. Leaves distichous, simple, pinnately veined, margins entire and flat. Petiole 2 – 7 mm long, 3 – 6 mm wide, pubescent to glabrous. Leaf lamina 280 – 615 mm long, 83 – 165 mm wide, length:width ratio 2.9 – 4.3, obovate, coriaceous, base rounded to cordate, apex acuminate, acumen 18 – 32 mm long, above glabrous when young and old, below glabrous when young and old; mid rib sunken above,

## CHAPTER 4

raised below, above glabrous, below glabrous; secondary veins 13 – 26 pairs, brochidodromous, impressed above, raised below; tertiary veins reticulate. Flowers actinomorphic, unisexual, male and female flowers dimorphic, on same individuals (plant monoecious, but individuals with only staminate flowers were also observed). Male inflorescences borne on thickenings of the trunk, mainly at the base of the trunk, towards up to 3.8 m, composed of 2 to 3 flowers. Peduncle inconspicuous. Flower pedicel 6 – 70 mm long, 1 – 2 mm in diameter, pubescent to sparsely pubescent. Bracts 1 to 3 at base and one towards the lower 10% of pedicel, upper bract 1 – 3.5 mm long, 1.5 – 5 mm wide, broadly ovate, adpressed, semi clasping the pedicel, pubescent outside, glabrous inside. Sepals 2, 1 – 7.5 mm long, 2 – 6.5 mm wide, broadly ovate, basely fused, pubescent outside, glabrous inside, dull tan. Petals 4, 10 – 38 mm long, 4 – 10 mm wide, length:width ratio 2.5 – 7, narrowly ovate, fused at base, pubescent outside, glabrous and verrucose inside, cream to brownish outside, cream to pinkish inside. Stamens numerous (exact number unknown), 0.5 – 0.8 mm long, 0.1 – 0.3 mm wide, anthers linear, connective truncate. Female inflorescences borne on thickenings of the trunk, mainly at the base of the trunk, towards up to 3.8 m, composed of 2 to 3 flowers. Flower pedicel 20 – 50 mm long, 1.5 – 2.5 mm in diameter, pubescent to sparsely pubescent. Bracts 1 to 3 at base and one towards the lower 10% of pedicel, upper bract 1 – 3.5 mm long, 1.5 – 5 mm wide, broadly ovate, adpressed, semi clasping the pedicel, pubescent outside, glabrous inside. Sepals 2, 3 – 5 mm long, 4 – 5 mm wide, broadly ovate, basely fused, pubescent outside, glabrous inside, dull tan. Petals 4, 15 – 35 mm long, 7 – 12 mm wide, length:width ratio 2.2 – 5, narrowly ovate, fused at base, pubescent outside, glabrous and verrucose inside, cream to brownish outside, cream to pinkish inside. Carpels 25 – 120, 1.5 – 2.5 mm long, 0.5 – 1 mm wide, velutinous, free; stigma ca. 0.6 mm long, 0.8 – 1.3 mm wide, truncate pyramidal. Fruiting pedicel 45 – 90 mm long, ca. 3 mm in diameter, glabrous. Monocarps, 5 – 9, 29 – 45 mm long, 18 – 30 mm wide, length:width ratio 1.4 – 1.9, ellipsoid to cylindrical, smooth, glabrous, clear orangish yellow, sessile to shortly stipitate; stipe up to 5 mm long, ca. 2 mm wide, glabrous. Seeds 8 – 14 per monocarp, biseriate, 10 – 22 mm long, 5 – 14 mm wide, ellipsoid to oblong.

**Distribution.** Cameroon, Equatorial Guinea, Gabon.

**Notes.** This species resembles *Up. bakeriana*, *Up. citrata* and *Up. submontana* in having large obovate leaves (from 28 to 62 cm long), with rounded to cordate bases. *Up. korupensis* differs from *Up. bakeriana* and *Up. citrata* in having longer flower pedicel (6 – 70 mm vs. less than 8 mm), and differs from *Up. bakeriana* in having fused and

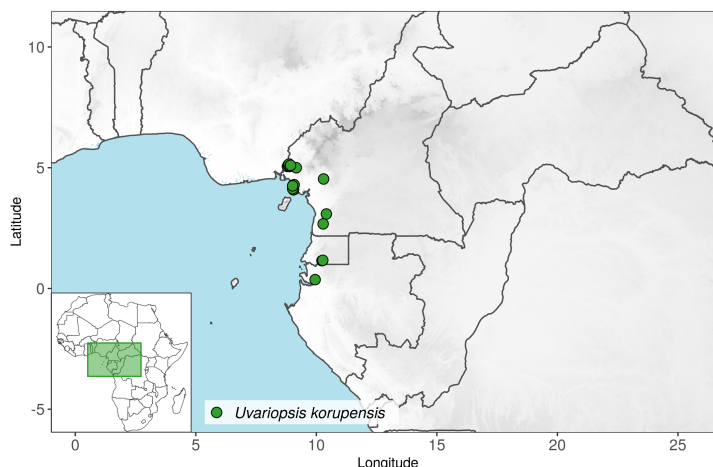


Figure 40: Distribution of *Uvariopsis korupensis*

cream petals (vs. free and pinkish red). It is harder to differentiate *Up. korupensis* and *Up. submontana*. *Up. korupensis* has generally larger leaves than *Up. submontana* (28 – 62 cm vs. 16 – 38 cm). The female flowers of *Up. korupensis* have smaller sepals (3 – 5 mm long vs. 6 – 8 mm long in *Up. submontana*), and generally longer petals (15 – 35 mm long, vs. 15 – 17 mm long), which results in petals more than 3 times longer than the sepals (vs. petals less than 3 times longer than the sepals in *Up. submontana*). Petals of *Up. korupensis* are cream to brownish outside and cream to pinkish inside whereas petals of *Up. submontana* are pinkish to dark red inside and outside.

**Specimens examined.** CAMEROON – Littoral • D. Kenfack 1620 (MO), Nkam, Yingui. Ekem River bank; 4°32'N, 10°18'E; alt. 500 m; 05 Mar. 2002 – South Region • G.A. Zenker 3971 (BM, G, G, K), Bipinde; 3°05'N, 10°25'E; 1911 • G.P. Tchouto Mbatchou BIFAX 25 (WAG), Campo Ma'an area, Bifa, in the National Park; 2°40'28"N, 10°16'54"E; alt. 60 m; 13 Oct. 2001 – South-West Region • A.H. Gentry 62456 (MO), Banyong, Batanga area, between Awong and Banyu, ca 15 km W of Manyemen. TRANSECT 3; 5°00'N, 9°10'E; alt. 420 m; 03 May. 1988 • D.W. Thomas 3182 (L, MO, P); Ndian, Cameroon. South-West, forest in the Korup National Park; 5°03'N, 8°48'E; alt. 50 m; 28 Feb. 1984 • D.W. Thomas 631 (K); Ndian, Korup National Park, transect R; 5°06'N, 8°55'50"E; Jul. 1979 • G.P. Tchouto Mbatchou 675 (K, SCA, YA), Bomana forest. Transect OA, Plot OA0X; 4°15'N, 9°01'E; alt. 200 m; 05 Oct. 1993 • J. Nning 284 (K, MO, SCA, YA); Fako, Bakingili, along a hill slope to drink gari Camp above the 6th plot; 4°05'N, 9°03'E; alt. 480 m; 16 Feb. 1997 • M.R. Cheek 5486 (K, SCA, YA), Low altitude forest above oil palm plantation. Reached after c. 40 minutes walk N then E from Njonji. Hunters path to 'Lake Njonji'; 4°08'N, 9°01'E; alt. 300 m; 19 Nov. 1993 • M.R. Cheek 8258 (K, YA); Ndian, Korup National Park, Ekundu Kundu, Transect 9, c. 7.5 km; 5°07'N, 8°50'E; alt. 170 m; 28 Apr. 1996 • M.R. Cheek 8815 (K, YA); Ndian, Korup National Park, path from village of Ekundu Kundu to top of Mt Juahan; 5°09'N, 8°52'E; alt. 550 m; 09 Jan. 1998 • R.E. Gereau 5192 (MO, P, WAG), Ndian Division; NW of Mundemba and W of Fabe Village, less than 1 km NE of confluence of Six Cup Garri Creek with Ndian (Mana) River; 5°03'N, 8°53'E; alt. 90 m; 05 Mar. 1993 • T.L.P. Couvreur 1039 (MPU, WAG, YA), Mount Cameroon National Park, Bakinguili trail, above Bakinguili village; 4°05'47.97"N, 9°03'24.72"E; alt. 563 m; 02 Apr. 2016 • T.L.P. Couvreur 1052 (MPU, WAG, YA), Mount Cameroon National Park, on the Bomona trail, behind Bomona village, 10 km NW from Idenau; 4°17'48.99"N, 9°04'43.07"E; alt. 688 m; 03 Apr. 2016. EQUATORIAL GUINEA – Rio Muni, Littoral • C.M. Wilks 1784 (LBV, WAG), Monts de Cristal. 11 km ENE d'Okuamkos; 1°09'N, 10°14'E; 10 Aug. 1988 – Unknown major area • C.M. Wilks 1818 (LBV, P, P, WAG), Monts de Cristal. 15 km d'Okuamkos; 1°10'N, 10°16'E; 23 Aug. 1988. GABON – Estuaire • A.M. Louis 1863 (BR, K, LBV, MO, WAG), Andem, Kougouleu-Kango ± 10 km, 2 km N; 0°22'N, 9°57'E; 09 Oct. 1985.

*Uvariopsis lovettiana* Couvreur & Q.Luke, Blumea 55(1): 70 (2010)

**TYPE.** TANZANIA – Morogoro • T.L.P. Couvreur 97 b (holotype: WAG; isotypes: DSM, MO); Kilo-mbero District, E Udzungwa National Park. In forest S of Mwanihana hill. c. 2 km S of last camping site on Mwanihana trail; 7°48'35.4"S, 36°49'26.4"E; alt. 1400 m; 30 Nov. 2006.

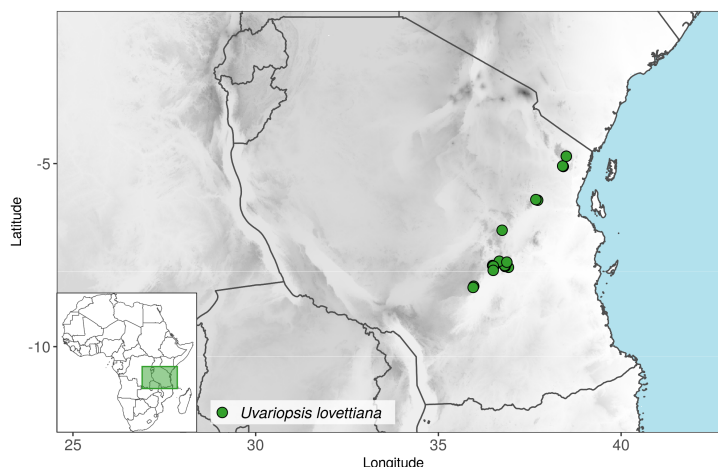
**Description.** Tree 3 – 30 m tall, D.B.H 3.5 – 50 cm; young branches sparsely pubescent to glabrous, old branches glabrous. Leaves distichous, simple, pinnately veined, margins entire and flat. Petiole 4 – 9 mm long, 1.2 – 1.5 mm wide, sparsely pubescent to glabrous. Leaf lamina 150 – 280 mm long, 45 – 72 mm wide, length:width ratio 2.5 – 4, elliptic, coriaceous, base acute to decurrent, apex acute to acuminate, acumen 5 – 25 mm long, above glabrous when young and old, below sparsely pubescent to glabrous when young, glabrous when old; mid rib sunken above, raised below, above glabrous, below glabrous; secondary veins 9 – 16 pairs, weakly brochidodromous, impressed above, raised below; tertiary veins reticulate. Flowers actinomorphic, unisexual, male and female flowers similar, on same individuals (plant monoecious). Male and female inflorescences axillary, composed of 1 flower. Peduncle inconspicuous. Flower pedicel 14 – 50 mm long, 0.7 – 3 mm in diameter, sparsely pubescent. Bracts 1 to 2 at base, upper bract 0.5 – 3 mm long, 0.5 – 3 mm wide, broadly ovate, puberulent outside, glabrous inside. Sepals 2, 1 – 4 mm long, 2 – 5 mm wide, depressed to broadly ovate, basely fused, pubescent to glabrous outside, glabrous inside, green. Petals 4, 6 – 15 mm long, 5 – 8 mm wide, length:width ratio 1.4 – 1.7, ovate, free, sparsely pubescent to glabrous outside, glabrous inside, light green outside, white inside. Male flowers: stamens ca. 160, 1.1 – 2 mm long, 0.3 – 0.5 mm wide, anthers linear, connective truncate. Female flowers: stamens 1 – 5, ca. 1 mm long, minute, fertile. Carpels 32 – 100, 2 – 3.5 mm long, 1 – 3 mm wide, densely pubescent, free; stigma ca 0.5 mm long, 0.2 – 1 mm wide. Fruiting pedicel 14 – 42 mm long, 1 – 2.5 mm in diameter, glabrous to sparsely pubescent. Monocarps, 2 – 7, 13.5 – 37 mm long, 4.5 – 17 mm wide, length:width ratio 1.1 – 3, cylindrical, smooth to lumpy, strongly constricted between the seeds, apex rounded to slightly acuminate, sparsely pubescent to glabrous, glossy yellow to red, stipitate; stipe 2.5 – 14 mm long, 1.5 – 3 mm wide, sparsely pubescent to glabrous. Seeds 2 – 6 per monocarp, uniseriate, 13.5 – 15 mm long, ca. 10 mm wide, ellipsoid, testa smooth, papery, peeling off.

**Distribution.** Tanzania.

**Notes.** *Up. lovettiana* resemble *Up. congensis* in having elliptic leaves with acute to decurrent base and attenuate to acuminate apex, and cylindrical monocarps strongly constricted between the seeds. However, *Up. lovettiana* has generally larger leaves than *Up. congensis* (15 – 28 cm long vs. 7 – 17.7 cm long), longer flower pedicels (14 – 50 mm long vs. 3 – 11 mm long), and larger petals (6 – 15 mm long and 5 – 8 mm wide vs. 2.5 – 8 mm long and 1.5 – 5 mm wide).

**Specimens examined.** TANZANIA – Iringa

• Bracebridge, C.E 102 (MO); Kilolo District, Kilombero Nature Reserve, Udekwa Village; 7°48'06"S, 36°30'21"E; alt. 1415 m; 22 Oct. 2009 • C. Frimodt-Møller TZ 95 (DSM, K), Luhega Forest Reserve, Iringa District, T7; 8°21'S, 35°58'E; alt. 1600 m; 20 Jan. 1997 • D.W. Thomas 3921 (K, MO); Iringa Rural District, Mwanihana Forest Reserve, above Sanje village. Forest on steep slope with small streams and swamps, and patches of elfin forest on ridge top; 7°50'S, 36°55'E; alt. 1400 m; 10 Oct. 1984 • L. Festo 2014 (MO); Kilolo District, Udzungwa Mountains National park, Udzungwa forest, c. 10 km from Msolwa village at source of Msolwa stream; 7°42'11"S,

Figure 41: Distribution of *Uvariopsis lovettiana*

36°52'23"E; alt. 1350 m; 24 Oct. 2005 • M.A. Mwangoka 8670 (MO); Kilolo District, Uzungwa Scarp Forest Reserve, Idegenda area, E part of Idegenda village; 8°23'S, 35°57'E; alt. 1650 m; 04 Dec. 2012 • W.A. Rodgers 2252 (DSM, K); Iringa Rural District, Udekwa village, forest blowk to East. West of Kilombero F.R; 7°55'S, 36°30'E; alt. 1676 m; Oct. 1982 • W.R.Q. Luke 10369 (K, MO); Kilolo District, Ndundulu Forest reserve, Camp 589 - Camp 590; 7°47'S, 36°29'E; alt. 1440 m; 06 Sep. 2004 • W.R.Q. Luke 6722 (MO); Iringa Rural District, Udzungwa Mountain NP Mt Luhombero Pt 129-131; 7°47'S, 36°32'E; alt. 1440 m; 27 Sep. 2000 • W.R.Q. Luke 7730 (EA, K, NHT), Pt 211; 7°47'S, 36°49'E; alt. 1080 m; 23 Sep. 2001 • W.R.Q. Luke 9195 (EA, K), Pt 370-371; 7°40'S, 36°40'E; alt. 1780 m; 16 Oct. 2002 – Morogoro • A.R. Marshall 1116 (K), Gologolo - PSP10. Uddzungwa Nationa Park. Udzungwa Mountains; 7°41'31.93"S, 36°52'21.02"E; alt. 1772 m; 07 Aug. 2007 • A.R. Marshall 2010 (K); Kilombero District, Ndundulu - Kipunji Plot 1. Kilombero Nature Reserve. udzungwa Mountains; 7°48'17.84"S, 36°30'09.69"E; alt. 1425 m; 30 Jul. 2010 • A.R. Marshall 2114 (K), Udzungwa Forest, Kipunji; 7°48'14.03"S, 36°30'10.01"E; 28 May. 2011 • M.A. Mwangoka 3973 (MO); Mvomero District, Kanga Forest Reserve, Kwamndolwa area; 6°00'S, 37°43'E; 29 Jun. 2005 • M.A. Mwangoka 7178 (MO); Kilosa District, Lumuma Ward, Lunezi Village, Mianzini forest between Lunenzi and Manyomis subvillage; 6°49'18"S, 36°44'36"E; alt. 1530 m; 15 Dec. 2010 • Y.S. Abeid 2625 (MO); Mvomero District, Kanga Forest Resrve, Work Unit 1, North East Transect, 500m from centre point; 5°59'S, 37°40'E; alt. 900 m; 21 Feb. 2006 – Tanga • A.L. Borhidi 82177 (DSM); Lushoto District, SE corner of Mazumbai University Forest Reserve with 'Lundgren's plot'; 4°48'S, 38°30'E; alt. 1400 m; 24 Feb. 1982 • B.J. Harris 6257 (DSM), West Usambara Mountains, Mwazumbai; 4°48'S, 38°30'E; alt. 1450 m; 06 Apr. 1972 • C.J. Kayombo 1406 (MO); Korogwe District, T3. Ambangulu Tea Estate, Forest Reserve 5 km W of Ambangulu Tea Factory above Estate road to Makunga; 5°04'48"S, 38°25'05"E; alt. 1300 m; 03 Nov. 1998 • L.-P.M.J. Dagallier 64 (DSM, MPU, WAG); Korogwe District, East Usambaras, Ambangulu, top of the mountain above the tea plantations; 5°04'08.97"S, 38°24'30.45"E; alt. 1316 m; 20 Nov. 2019 • L.-P.M.J. Dagallier 66; Korogwe District, East Usambaras, Ambangulu, top of the mountain above the tea plantations; 5°03'57.64"S, 38°23'59.43"E; alt. 1208 m; 20 Nov. 2019.

*Uvariopsis noldeae* Exell & Mendonça, Bol. Soc. Brot. sér. 2, 25: 101 (1951)

**TYPE.** ANGOLA – Malanje • I. von Nolde 576 (holotype: BM), Quela; 9°16'06.09"S, 17°04'12.72"E; alt. 1200 m; Dec. 1938.

**Description.** Tree height and D.B.H. unknown, D.B.H. Young branches sparsely pubescent to glabrous, old branches glabrous. Leaves distichous, simple, pinnately veined, margins entire and flat. Petiole 1 – 2.5 mm long, ca. 1.5 mm wide, sparsely pubescent to glabrous. Leaf lamina 110 – 204 mm long, 40 – 60 mm wide, length:width ratio ca. 3.4, elliptic to obovate, coriaceous, base rounded, apex acuminate, acumen ca. 21 mm long, above glabrous when young and old, below glabrate to glabrous when young,

glabrous when old; mid rib sunken above, raised below, above glabrous, below glabrous; secondary veins 11 – 12 pairs, weakly brochidodromous, impressed above, raised below; tertiary veins reticulate. Flowers actinomorphic, unisexual, male and female flowers dimorphic, on same individuals (plant monoecious). Male inflorescences borne on trunk, composed of 1 flower. Peduncle inconspicuous. Flower pedicel 2 – 4 mm long, ca. 0.5 mm in diameter, pubescent. Bracts 1 to 2 at base, upper bract 0.5 – 1 mm long, 0.5 – 1 mm wide, broadly ovate, pubescent outside, glabrous inside. Sepals 2, 1 – 2 mm long, ca. 2 mm wide, broadly ovate, pubescent outside, glabrous inside. Petals 4, 6.5 – 10 mm long, 2 – 3.5 mm wide, length:width ratio 2.8 – 3.2, ovate, free, pubescent outside, glabrous inside, brownish red outside, cream inside. Stamens numerous (exact number unknown), 0.3 – 0.6 mm long, 0.1 – 0.4 mm wide, anthers linear, connective truncate. Female inflorescences borne on trunk, composed of 1 flower. Flower pedicel 70 – 83 mm long, ca. 1 mm in diameter, sparsely pubescent. Bracts 1 to 2 at base, upper bract ca. 1.5 mm long, ca. 1.5 mm wide, broadly ovate, pubescent outside, glabrous inside. Sepals 2, 3 – 4 mm long, ca. 4 mm wide, broadly ovate, pubescent outside, glabrous inside, color unknown. Petals 4, 14 – 16 mm long, 5 – 8 mm wide, length:width ratio 1.8 – 3.2, ovate, free, pubescent outside, glabrous inside, brownish red outside, cream inside. Carpels 40 – 45, ca. 2 mm long, ca. 1 mm wide, velutinous, free, ovules ca. 20 per ovary, biseriate; stigma flat. Fruits unknown.

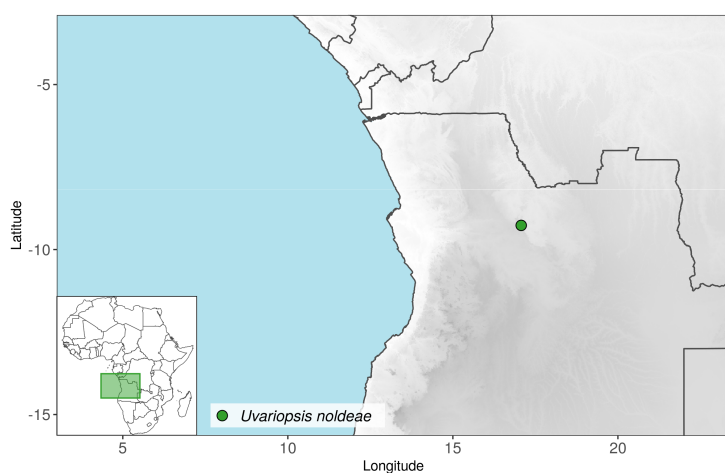


Figure 42: Distribution of *Uvariopsis noldeae*

glabrous below (vs. tomentose to glabrous below). *Up. noldeae* has very dimorphic flowers with pedicels of male flowers 2 – 4 mm long (vs. 9 – 30 mm long in *Up. solheidii*) and pedicels of female flowers 70 – 83 mm long (vs. 30 – 198 mm long in *Up. solheidii*).

**Distribution.** Known from only one locality in Angola: Quela in Malange region.

**Notes.** *Up. noldeae* closely resembles *Up. solheidii* in having similar leaves and flowers. However, *Up. noldeae* differs from *Up. solheidii* in having young branches and petioles sparsely pubescent to glabrous (vs. tomentose to shortly tomentose) and leaf mid rib

***Uvariopsis oligocarpa* Dagallier, sp. nov.**

**TYPE.** GHANA – Western Region • M.C. Merello 1380 (holotype: MO (MO3055200); isotype: WAG (WAG.1570507)), Bia National Forest and Production Reserve. Secondary logging roads west from MIM Timber Company Camp; 6°24'15"N, 3°02'30"W; alt. 140 m; 04 Mar. 1996.

**Diagnosis.** Can be distinguished from all the other *Uvariopsis* species by the combination of the following characters: plant with glabrous branches and elliptic leaves less than 150 mm, unisexual flowers, female flowers with less than 21 carpels, fruits composed of 1 – 3 monocarps reaching maturity, monocarps pubescent to sparsely pubescent and not constricted between the seeds.

**Description.** Tree 2 – 3 m tall, D.B.H unknown; young branches glabrous, old branches glabrous. Leaves distichous, simple, pinnately veined, margins entire and flat. Petiole 4 – 6 mm long, 1.7 – 2.5 mm wide, glabrous. Leaf lamina 90 – 149 mm long, 32 – 53 mm wide, length:width ratio 2.2 – 4, elliptic, papyraceous to coriaceous, base acute to decurrent, apex acuminate, acumen 10 – 21 mm long, above glabrous when young and old, below glabrous when young and old; mid rib slightly sunken above, raised below, above glabrous, below glabrous; secondary veins 5 – 11 pairs, brochidodromous to weakly brochidodromous, impressed above, raised below; tertiary veins reticulate. Flowers actinomorphic, unisexual, male and female flowers similar, on same individuals (plant monoecious). Male and female inflorescences axillary or sometimes borne on branches, composed of 1 flower. Peduncle inconspicuous. Flower pedicel 2 – 7 (20) mm long, 1 – 1.5 mm in diameter, pubescent. Bracts 1 to 3 at base, upper bract 0.5 – 3 mm long, 0.5 – 2 mm wide, broadly ovate, pubescent outside, glabrous inside. Sepals 2, 0.7 – 2.5 mm long, 2 – 3 mm wide, depressed ovate, free to basely fused, pubescent outside, glabrous inside, color unknown. Petals 4, 4 – 6.5 (10) mm long, 2.5 – 6 (10) mm wide, length:width ratio 1 – 1.4, broadly ovate, free, pubescent outside, glabrous inside, yellowish cream to yellow outside. Male flowers: stamens more than 300, 0.5 – 1.6 mm long, 0.1 – 0.3 mm wide, anthers linear, connective truncate. Carpels ca. 20, ca. 1 mm long, ca. 0.5 mm wide, free, stunted, sterile (seen on only one male flower). Female flowers: carpels 13 – 20, 1 – 2 mm long, 0.5 – 1.1 mm wide, velutinous, free; stigma ca. 0.1 mm long, ca. 0.5 mm wide, coiled, glabrous. Fruiting pedicel 4 – 10 mm long, 1 – 3 mm in diameter, glabrous. Monocarps, 1 – 3, 25 – 60 mm long, 11 – 35 mm wide, length:width ratio 1.7 – 2.7, cylindrical, smooth, pubescent to sparsely pubescent, green ripening yellow to orange, sessile to very shortly stipitate; stipe 0 – 1 mm long, 2 – 3 mm wide, pubescent. Seeds 8 – 13 per monocarp, biseriate, 8.5 – 14 mm long, 7 – 8 mm wide, ellipsoid to semicircular, in an orange pulp.

**Distribution.** Ghana, Ivory Coast, Liberia, Sierra Leone.



**Etymology.** The specific epithet refers to the low number of monocarps reaching maturity in this species.

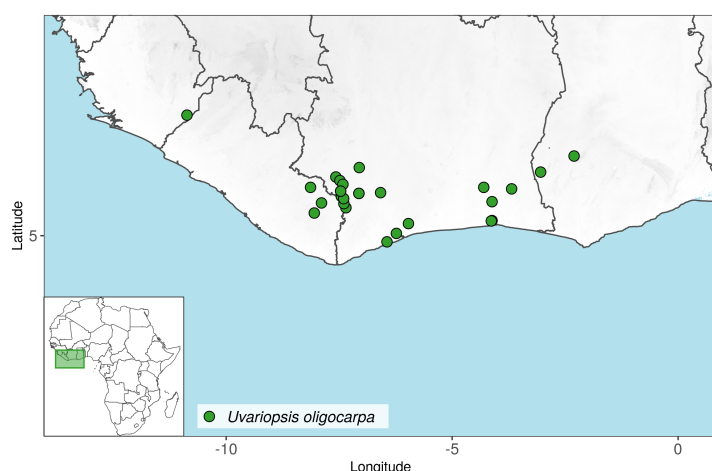


Figure 43: Distribution of *Uvariopsis oligocarpa*

reaching maturity on the ripe fruit (vs. up to 15 mature monocarps in *Up. congensis*). The monocarps of *Up. oligocarpa* are pubescent to sparsely pubescent (vs. glabrate to glabrous in *Up. congensis* and tomentose in *Up. zenkeri*), not constricted between the seeds (vs. strongly to slightly constricted between the seeds in *Up. congensis* and *Up. zenkeri*), yellow to orange when ripe and brown to dark brown when dry (vs. green to red when ripe and black when dry in *Up. congensis*), and sessile to very shortly stipitate with stipes shorter than 1 mm (vs. sessile to stipitate with stipes between 0 and 7 mm in *Up. congensis*).

**Notes.** Similar to *Up. bisexualis*, *Up. congensis* and *Up. zenkeri* when sterile, having elliptic leaves generally less than 15 cm long with decurrent base, but differs clearly when fertile. *Up. oligocarpa* has unisexual flowers (vs. bisexual flowers in *Up. bisexualis*). *Up. oligocarpa* has less carpels (13 to 20 vs. 20 to 40 in *Up. congensis*), which results in generally 1 to 3 monocarps

**Specimens examined.** GHANA – Brong-Ahafo Region • J.B. Hall 44553 (K), Desiri F.R; 6°45'30.2"N, 2°18'06.66"W; 20 Jun. 1973. IVORY COAST – Abidjan • F.M. van der Laan 640 (U, WAG), Centre Orstom Adiopodoumé, 17km Dabou rd. from Abidjan, Jardin Botanique; 29 Jun. 1983 • J.J. Bos 10345 (WAG), Centre Orstom Adiopodoumé, 17km Dabou road from Abidjan, Jardin Botanique; 5°20'N, 4°07'W; 16 Jun. 1978 – Adzopé • L. Aké Assi 12872 (G), Forêt de la Besso; 6°02'N, 3°41'W; 01 Apr. 1975 – Agboville • A.J.B. Chevalier 16721 (P), Bouroukrou, chemin de fer km 92; 6°04'N, 4°18'W; 20 Jan. 1907 • L. Bernardi 8623 (G, K, P), in regione Yapo-Nord, 60-70 km ad septentrionem Abidjan; 5°45'N, 4°07'W; 14 Mar. 1962 – Guiglo • A. Bakayoko 140 (G, P, WAG), Zagné; 6°13'N, 7°29'W; 23 May. 2002 • A.J.B. Chevalier 19308 (P), Keeta, Bassin du moyen Cavally. Pays des Oubi: village de Ke'eta et environs; 5°59'N, 7°28'W; 09 Jul. 1907 • A.J.B. Chevalier 19347 (P), Keeta, Bassin du moyen Cavally. Pays des Oubi: village de Ke'eta et environs; 5°59'N, 7°28'W; 09 Jul. 1907 • L. Aké Assi 12088 (K), Forêt près de Ziriglo; 5°37'N, 7°21'W; 04 Jun. 1973 • L. Aké Assi 13218 (G), entre Taï et Grabo: Troya; 5°42'28.06"N, 7°23'42.49"W; 10 Jan. 1976 • L. Bernardi 8403 (G, K, P), De oppido Tienkulà, ad orientem per 5-9 km in silva alta; 6°08'N, 7°25'W; 02 Mar. 1962 • N. Stäuble 848 (G, MO), Taï; 5°52'N, 7°27'W; Feb. 1982 • N. Stäuble 849 (G, MO), Taï; 5°52'N, 7°27'W; 27 Dec. 1981 • P.R.J. Bamps 2600 (P), Zro; 6°17'45.96"N, 7°34'22.69"W; Apr. 1970 – San-Pédro • C.C.H. Jongkind 4737 (WAG), Forêt Classée Monogaga, just south of Sassandra - San Pedro road; 4°51'48"N, 6°26'30"W; 25 Mar. 2000 – Sassandra • C. Geerling 2328 (WAG), Dakpadou-Sago; 5°16'N, 5°58'W; 29 Mar. 1968 • J. de Koning 2657 (BR, MO, WAG), near Fuyt plantation; 5°03'N, 6°14'W; 11 Nov. 1973 – Soubré • A.J.B. Chevalier 19061 (P), Guideko, Bassin de la moyenne Sassandra entre Guidéko et la Zozro; 5°57'N, 6°35'W; 10 Jun. 1907 • A.J.B. Chevalier 19222 (P), entre le moyen Sassandra et le moyen Cavally; 5°55'59.75"N, 7°03'46.35"W; 06 Jul. 1907 • A.J.B. Chevalier 19253 bis (P), entre moy. Sassandra et moy. Cavally; 5°55'59.75"N, 7°03'46.35"W; 06 Jul. 1907 • A.J.B. Chevalier 19282 (P), entre le moyen Sassandra et le moyen Cavally; 5°55'59.75"N, 7°03'46.35"W; 04 Jul. 1907 • M. Scoupe 222 (G), Taï National Park, P.N. de Taï, zone du Centre, secteur Soubré, groupe de transect VH, RL6; 5°43'21.19"N, 7°53'25.45"W; alt. 220 m; 28 Jan. 2010 • P.R.J. Bamps 2507 (P), Guézou - Buyo; 6°30'12.96"N, 7°03'18.22"W; Feb. 1970 – Unknown major area • A. de Rouw 334

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(WAG), Pauleoula; 5°49'N, 7°24'W; 08 Dec. 1986. LIBERIA – Grand Gedeh • J.J.F.E. de Wilde 3656 (K, MA, MO, P, U, WAG), Eastern Province, Putu District. Near Kanweake, a village c. 70 km S. of Chiehn (Zwedru village); 5°30'N, 8°03'W; 26 Mar. 1962 • J.T. Baldwin jr 7091 (K), Zwedru; 6°04'N, 8°08'W; 09 Aug. 1947. SIERRA LEONE – Eastern Province • B. Saradugu 57 (K, SL, WAG), Gola National Park, central block; 7°39'42.7"N, 10°52'02.6"W; alt. 285 m; 31 Oct. 2013.

*Uvariopsis pedunculosa* (Diels) Robyns & Ghesq., Ann. Soc. Sci. Bruxelles, Ser. B liii. 321 (1933)

*Tetrastemma pedunculosum* Diels, Bot. Jahrb. Syst. 53(3-5): 441 (1915)

*Uvariopsis vanderystii* Robyns & Ghesq., Ann. Soc. Sci. Bruxelles, Ser. B liii. 64 (1933)

**TYPE.** CAMEROON – South Region • G.A. Zenker 3868 (holotype: B; isotypes: BM, BR, G, K, L, MO, P), Bipinde, Urwaldgebiet; 3°05'N, 10°25'E; 1909.

**Description.** Shrub to tree 2 – 8 m tall, D.B.H 1.5 – 5 cm; young branches pubescent to glabrous, old branches glabrous. Leaves distichous, simple, pinnately veined, margins entire and flat. Petiole 2 – 5 mm long, 1.8 – 3 mm wide, glabrous. Leaf lamina 172 – 290 mm long, 57 – 108 mm wide, length:width ratio 2.3 – 3.9, elliptic to obovate, coriaceous, base acute, apex acuminate, acumen 3 – 23 mm long, above glabrous when young and old, below glabrous when young and old; mid rib sunken above, raised below, above glabrous, below glabrous; secondary veins 8 – 15 pairs, brochidodromous to weakly brochidodromous, impressed above, raised below; tertiary veins reticulate. Flowers actinomorphic, unisexual, male and female flowers dimorphic, on same individuals (plant monoecious). Male inflorescences borne on trunk, composed of 1 flower. Peduncle inconspicuous. Flower pedicel 14 – 320 mm long, 0.9 – 3 mm in diameter, sparsely pubescent to glabrous. Bracts 1 at base and 1 towards the middle or lower half of the pedicel, upper bract ca. 2 mm long, ca. 2 mm wide, broadly ovate, adpressed, semi clasping the pedicel. Sepals 2, 2 – 7 mm long, 6 – 7.5 mm wide, very broadly ovate, basely fused, enclosing the petals in bud, sparsely pubescent outside, glabrous inside, dark purplish red. Petals 4, 9 – 12 mm long, 5 – 7 mm wide, length:width ratio 1.3 – 2.2, broadly elliptic to elliptic, fused at base over 20 – 40 % of their length, pubescent outside, glabrous inside, cream outside, orangish to reddish brown inside. Stamens 650 – 900, 0.5 – 1 mm long, 0.1 – 0.3 mm wide, anthers linear, connective truncate or absent. Female inflorescences borne on trunk, composed of 1 flower. Flower pedicel 80 – 325 mm long, 1 – 3 mm in diameter, sparsely pubescent. Bracts 1 at base and 1 towards the middle or lower half of the pedicel, upper bract ca. 2 mm long, ca. 2 mm wide, broadly ovate, adpressed, semi clasping the pedicel. Sepals 2, 6 – 18 mm long, 9 – 12 mm wide, very broadly ovate, basely fused, enclosing the petals in bud, sparsely pubescent outside, glabrous inside, dark purplish red. Petals 4, 8 – 14 mm long, 6 – 10 mm wide, length:width ratio 1.3 – 2.2, broadly elliptic to elliptic, fused at base over 20 – 40 % of their length, pubescent outside, glabrous inside, cream outside, orangish to reddish brown inside. Carpels 50 – 140, 2 – 4 mm long, 1 – 1.5 mm wide, pubescent, free; stigma 0.2 – 0.5 mm long, 0.2 – 0.5

mm wide, globose. Fruiting pedicel 129 – 197 mm long, 2 – 2.2 mm in diameter, pubescent to glabrous. Monocarps, 4 – 9, 10 – 17 mm long, 7 – 11 mm wide, length:width ratio 1.3 – 1.6 (measures taken from unripe fruits), cylindrical, very verrucose, pubescent, blackish brown, sessile.

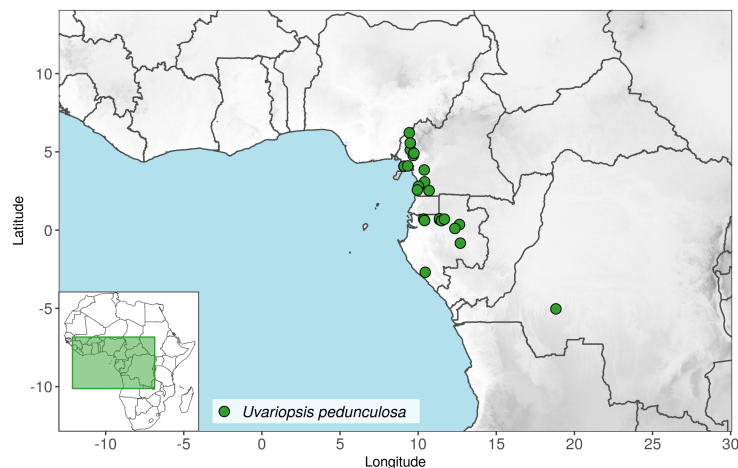


Figure 44: Distribution of *Uvariopsis pedunculosa*

**Distribution.** Cameroon, Democratic Republic of the Congo, Gabon.

**Notes.** *Up. pedunculosa* resembles *Up. dioica*, *Up. guineensis* and *Up. solheidii* in having elliptic to obovate leaves, with acute base and acuminate apex. It has female flower pedicels 80 – 325 mm long, which is longer than in all *Uvariopsis* species, except in *Up. congolana* (200 – 400 mm

long) and *Up. solheidii* (up to 198 mm long). It differs from *Up. congolana* in having 4 petals (vs. 3 petals) and verrucose monocarps (vs. longitudinally ridged monocarps). It differs from *Up. solheidii* in having broadly elliptic to elliptic petals, fused at base over 20 – 40% of their length (vs. ovate to narrowly ovate and free petals).

**Specimens examined.** CAMEROON – Littoral • T.L.P. Couvreur 1173 (K, MPU, P, WAG, YA), Mapubi, 30 km before Edea on Yaoundé-Edea road. On forestry road, 5 km direction to Sanaga river; 3°50'44.56"N, 10°23'21.98"E; alt. 219 m; 28 Feb. 2018 – South Region • G.P. Tchouto Mbatchou ELEX 15 (WAG), Campo Ma'an area, Mont d' Elephant, Bidou area towards Hevecam, path to the summit; 2°47'52"N, 10°01'12"E; alt. 180 m; 16 Oct. 2001 • G.P. Tchouto Mbatchou ONOX 182 (WAG), Campo Ma'an area, Onoyong, between plots ONO1 and 10; 2°31'39"N, 10°41'49"E; alt. 360 m; 18 Mar. 2001 • G.P. Tchouto Mbatchou ONOX 274 (WAG), Campo Ma'an area, Onoyong, between plots ONO1 and 10; 2°31'39"N, 10°41'49"E; alt. 360 m; 18 Mar. 2001 • G.P. Tchouto Mbatchou 3242 (KRIBI, SCA, WAG, WAG), Campo-Ma'an area, Massif des Mamelles, along the path to Mamelles highlands; 2°33'57"N, 9°56'58"E; alt. 280 m; 23 Apr. 2001 – South-West Region • D.W. Thomas 2756 (K, MO), on the southern slope of Mount Cameroon, above Batoke; 4°05'N, 9°06'E; alt. 500 m; 29 Dec. 1983 • D.W. Thomas 7364 (P), Takamanda Forest Reserve; 6°13'N, 9°26'E; alt. 500 m; 30 Apr. 1987 • G.K. Gottsberger 170307/ 11 (ULM, WAG), c. 2 km from Banyang Mbo Research Station; 5°08'N, 9°30'E; 17 Mar. 2007 • G.W.J. Mildbraed 10745 (B, K), Likomba - Pflanzung, 15-35km NE von Victoria; 4°06'N, 9°20'E; alt. 50 m; 03 Dec. 1928 • J.F. Villiers 1427 (P), Massif Ntali, crête sommitale, 30km SE Mamfé; 5°33'53.69"N, 9°29'26.07"E; alt. 1100 m; 14 Jun. 1982 • R.G. Letouzey 13849 (MO, P), Crête de Nta Ali, entre cotes 1009 et 1202; 30km SE Mamfe (feuille IGN 1/200.000 Mamfe); 5°33'39.99"N, 9°30'09.81"E; alt. 1266 m; 19 Jun. 1975 • T.L.P. Couvreur 1063 (MPU, WAG, YA), on forest trail, north of Ngomboku village; 4°54'48.49"N, 9°43'28.73"E; alt. 793 m; 06 Apr. 2016 • T.L.P. Couvreur 1066 (MPU, WAG, YA), on forest trail, north of Ngomboku village; 4°54'38.74"N, 9°43'48.18"E; alt. 815 m; 06 Apr. 2016 • T.L.P. Couvreur 517 (MPU, YA); Fako, on trail trough palm oil plantation, 3 km before lava flow and Seme Beach hotel when coming from Limbe; 4°04'28.6"N, 9°05'06.64"E; alt. 479 m; 18 Oct. 2013 – Unknown major area • W.G. Gosline 244 (K, MO, P, WAG, YA), Kupe-Muanenguba Division, Ajang saprophyte plot; 4°46'N, 9°41'E; alt. 950 m; 01 Dec. 1999. DEMOCRATIC REPUBLIC OF THE CONGO – Bandundu • H.J.R. Vanderyst 9973 (BR); Kikwit, Kikwit; 5°02'S, 18°49'E; 1921. GABON – Estuaire • T.L.P. Couvreur 602 (MPU, YA), Crystal Mountains, on trail behind the dam at Tchimbélé; 0°37'02.43"N, 10°24'41.26"E; alt. 617 m; 16 Nov. 2013 • T.L.P. Couvreur 607 (MPU, YA), Crystal Mountains, on trail behind tunnel leading under dam; 0°36'47.64"N, 10°24'10.96"E; alt. 492 m; 16 Nov. 2013 – Nyanga • J.L.C.H. van Valkenburg 2940

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(BR, LBV, WAG, WAG), Moukalaba Doudou, national park, south of the road to Kachimba; 2°41'36"S, 10°27'06"E; alt. 500 m; 22 Feb. 2004 – Ogooué-Ivindo • E. Bidault 2300 (BR, BRLU, LBV, MO, MO, P, WAG), concession forestière Rougier-Ivindo; 0°06'23.9"N, 12°21'06.3"E; alt. 380 m; 29 Oct. 2015 • M.S.M. Sosef 2241 (BR, K, LBV, MO, WAG), c. 30 km down the Ivindo River from the IRET Research Station, SW of Makokou; 0°21'30"N, 12°38'42"E; alt. 350 m; 07 Nov. 2005 – Ogooué-Lolo • G.M.P.C. Le Testu 8525 (P), region de Lastoursville, Lastoursville; 0°50'N, 12°42'E; 18 Nov. 1930 – Woleu-Ntem • J.M. Reitsma 2554 (LBV, MO, WAG), Inventory Oveng; primary rain forest, ca 25 km WSW of Mintsic; 0°44'N, 11°22'E; 08 Nov. 1986 • J.M. Reitsma 891 (LBV, MO, WAG, WAG), chantier Rougier-Océan, Oveng; 0°40'N, 11°22'E; alt. 760 m; 08 May. 1985 • T.L.P. Couvreur 594 (MPU, YA), 40 km from Sam, on raod main road to Medouneu; 0°42'14.82"N, 10°20'53.39"E; alt. 589 m; 14 Nov. 2013 • T.L.P. Couvreur 878 (LBV, WAG, YA), on road from Mitzic to Lalara (N2), just after the bridge over the Lara, c.500 m in forest; 0°36'15.66"N, 11°29'12"E; alt. 574 m; 15 Nov. 2015 • T.L.P. Couvreur 885 (LBV, WAG, YA), c.15 km south of Mitzic (N2), in Foreex logging consession, 5 km after the bridge after the main base camp (Saint Germain, c.25 km from road N2), on abandoned logging road left to the main road; 0°41'51.34"N, 11°40'50.29"E; alt. 531 m; 16 Nov. 2015.

*Uvariopsis sessiliflora* (Mildbr. & Diels) Robyns & Ghesq., Ann. Soc. Sci. Bruxelles, Ser. B liii. 322 (1933)

*Tetrastemma sessiliflorum* Mildbr. & Diels, Bot. Jahrb. Syst. 53(3-5): 440 (1915)

**TYPE.** CAMEROON – East Region • G.W.J. Mildbraed 5239 (holotype: B); Haut-Nyong, Lomié; 3°09'N, 13°38'E; 1911.

**Description.** Tree height and D.B.H. unknown, D.B.H. Young branches glabrous, old branches glabrous. Petiole 3 – 5 mm long, ca. 2 mm wide, glabrous. Leaf lamina 120 – 180 mm long, 50 – 60 mm wide, length:width ratio ca 2.5, elliptic to obovate, coriaceous, base acute, apex acuminate, above glabrous when young and old, below pubescent when young, glabrous when old; mid rib sunken above, raised below, abovebelowsecondary veins 8 – 12 pairs, brochidodromous, impressed above, raised below; tertiary veins reticulate. Flowers actinomorphic, unisexual (?), male and female flowers on same individuals (plant monoecious) (?). male inflorescences unknown peduncle inconspicuous. Female inflorescences borne on small thickenings of the trunk, composed of 1 flower. Flower pedicel sessile, 0 – 2 mm long, ca. 2 mm in diameter. Bracts seem absent. Sepals 2, ca. 2 mm long, ca. 1 mm wide, ovate, pubescent outside, glabrous inside. Petals 4, 10 – 16 mm long, 6 – 8 mm wide, length:width ratio 1.6 – 2, ovate, free, sparsely pubescent outside, glabrous inside, color unknown. Carpels number unknown, 1.5 – 2.5 mm long, ca. 1 mm wide, pubescent, free; stigma unknown. Monocarps, 1 seen, ca. 19 mm long, ca. 15 mm wide, length:width ratio ca. 1.3, cylindrical, smooth, glabrous, sessile. Seeds ca. 2 per monocarp, biseriate, ca. 8 mm long, ca. 6 mm wide, ellipsoid.

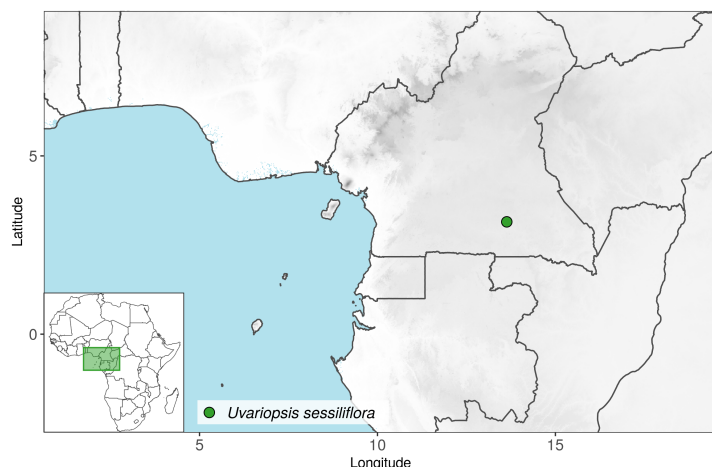


Figure 45: Distribution of *Uvariopsis sessiliflora*

(Mildbraed 5239). Further collection of *Up. sessiliflora* is needed in order to have better knowledge of its morphology and to confirm this species still exists.

**Distribution.** Known from only one locality in the East Region in Cameroon.

**Notes.** This species has sessile flowers borne on the trunk that differentiate it all the other *Uvarioidendron* except *Up. citrata*. It differs from *Up. citrata* in having smaller leaves (12 – 18 cm vs. 31.2 – 50 cm in *Up. citrata*). This species is a poorly known species and the single collection dates back 1911

***Uvariopsis solheidii*** (De Wild.) Robyns & Ghesq., Ann. Soc. Sci. Bruxelles, Ser. B liii. 321 (1933)

*Tetrastemma solheidii* De Wild., Ann. Mus. Congo Belge, Bot. sér. 5, 3(1): 85 (1909)

*Uvariopsis batesii* Robyns & Ghesq., Ann. Soc. Sci. Bruxelles, Ser. B liii. 320 (1933)

*Uvariopsis letestui* Pellegr. **syn. nov.**, Bull. Soc. Bot. France 95: 139 (1948)

**TYPE.** DEMOCRATIC REPUBLIC OF THE CONGO – Orientale • A.F. Solheid 96 (holotype: BR); Banalia, Env. de Yambuya; 1°16'N, 24°33'E; 1906.

**Description.** Shrub to tree 1.5 – 8 m tall, D.B.H 2 – 6 cm; young branches tomentose to shortly tomentose, old branches glabrous. Leaves distichous, simple, pinnately veined, margins entire and flat. Petiole 2 – 5 mm long, 1.5 – 3 mm wide, tomentose to glabrous. Leaf lamina 131 – 260 (285) mm long, 40 – 93 mm wide, length:width ratio 2.1 – 3.9, elliptic to obovate, coriaceous, base acute to rounded to subcordate, apex attenuate to narrowly acuminate, acumen 4 – 20 mm long, above glabrous when young and old, below glabrous when young and old; mid rib sunken above, raised below, above glabrous, below tomentose to glabrous; secondary veins 7 – 13 pairs, brochidodromous to weakly brochidodromous, impressed above, raised below; tertiary veins reticulate. Flowers actinomorphic, unisexual, male and female flowers dimorphic, on same individuals (plant monoecious, but individuals with only pistillate flowers were also reported; e.g. Le Testu 8458). male inflorescences borne on small thickenings of the trunk, mainly between the base towards 50 cm, up to ca. 2.50 m, above the female inflorescence, composed of 1 to 2 flowers. Peduncle inconspicuous. Flower pedicel 9 – 30 mm long, 0.5 – 1 mm in diameter, pubescent to sparsely pubescent. Bracts 1 to 2 at base and none to 1 towards the lower half

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of the pedicel, upper bract 1 – 2 mm long, 1.5 – 3 mm wide, broadly ovate, adpressed, semi clasping the pedicel, pubescent outside, glabrous inside. Sepals 2, 1.5 – 2 mm long, 1.5 – 2 mm wide, broadly ovate, free, pubescent outside, glabrous inside, brown to red. Petals 4, 5 – 10 mm long, 2.5 – 3.5 mm wide, length:width ratio 2 – 3.2, ovate to narrowly ovate, free, straight to curving outward at anthesis, pubescent to sparsely pubescent outside, glabrous inside, brown to light red outside, dull pink to dark purplish red inside. Stamens ca. 300, 0.2 – 0.5 mm long, 0.2 – 0.3 mm wide, anthers linear, connective truncate. Female inflorescences borne on small thickenings of the trunk, mainly between the base towards ca. 50 cm, up to ca. 2.50 m, below the male inflorescence, composed of 1 to 2 flowers. Flower pedicel 30 – 198 mm long, 1 – 1.5 mm in diameter, pubescent to glabrous. Bracts 1 to 2 at base and none to 1 towards the lower 30% of the pedicel, upper bract 1 – 2 mm long, 1.5 – 3 mm wide, broadly ovate, adpressed, semi clasping the pedicel, pubescent outside, glabrous inside. Sepals 2, 1.5 – 4 mm long, 2 – 5 mm wide, broadly ovate, free, pubescent outside, glabrous inside, brown to red. Petals 4, 7.5 – 17 mm long, 3.5 – 7 mm wide, length:width ratio 1.3 – 3.6, ovate to narrowly ovate, free, straight to curving outward at anthesis, pubescent outside, glabrous inside, brown to light red outside, dull pink to dark purplish red inside. Carpels 30 – 65, 1 – 3.5 mm long, 1 – 1.5 mm wide, velutinous, free; stigma globose. Fruiting pedicel 30 – 176 mm long, 1 – 2 mm in diameter, pubescent to glabrous. Monocarps, 1 – 5, 21 – 70 mm long, 12 – 30 mm wide, length:width ratio 1.8 – 3 (measures taken from both dried fruits and their associated specimen label, note that monocarps seem to sink when drying), cylindrical, with longitudinal and transversal ridges, sparsely pubescent to glabrous, bright red, subsessile; stipe 0 – 4 mm long, 4 – 5 mm wide, pubescent to glabrous. Seeds 2 – 10 per monocarp, uniseriate to biseriate, 11 – 18 mm long, 10 – 12 mm wide, ellipsoid.

**Distribution.** Cameroon, Central African Republic, Democratic Republic of the Congo, Gabon, Republic of the Congo.

**Notes.** *Up. solheidii* resembles *Up. dioica*, *Up. guineensis*, and *Up. pedunculosa* in having elliptic to obovate leaves, with acute to rounded base and attenuate to acuminate apex.

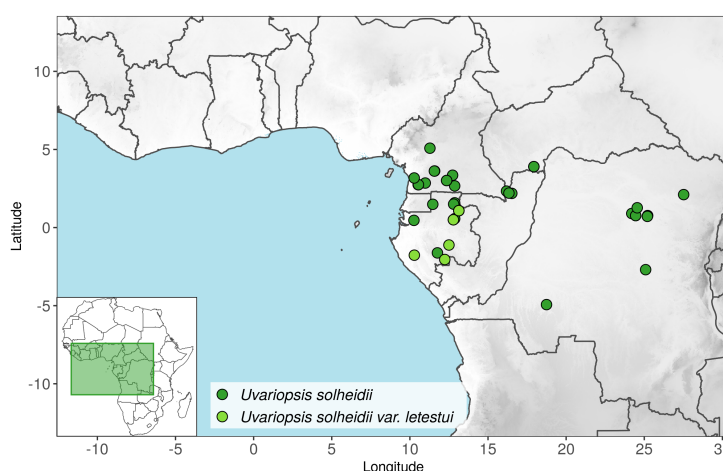


Figure 46: Distribution of *Uvariopsis solheidii*

Leaf base of *Up. solheidii* can also be subcordate, and differs from these species in having young branches and petioles tomentose to shortly tomentose (vs. pubescent to glabrous) and in having cylindrical monocarps with longitudinal and trans-



## CHAPTER 4

versal ridges (vs. smooth in *Up. dioica*, with a single longitudinal ridge in *Up. guineensis* and verrucose in *Up. pedunculosa*).

**Specimens examined.** CAMEROON – Central Region • B.-A. Nkongmeneck 273 (P), Mt Ngoro à 58km de Lint. Feuille IGN 1/200.000 LINTE; 5°04'53.52"N, 11°16'56.76"E; 17 Apr. 1982 • J.-M. Onana 2848 (K, SCA, WAG, YA), Mefou Proposed National Park, Ndanan 1, River N Didoumou; 3°37'N, 11°34'E; alt. 720 m; 26 Mar. 2004 • M.R. Cheek 11606 (K, SCA, WAG, YA), Mefou National Park Ndanan 1. Trail to Oncoba flag. (l after bridge); 3°37'13"N, 11°35'04"E; alt. 710 m; 10 Mar. 2004 – East Region • J.N. Asonganyi 310 (P), between Somalomo and Milon, 69km SE Akonolinga, Map IGN 1/200.000 Akonolinga; 3°21'N, 12°44'E; 18 Jun. 1981 – South Region • A. Koufani 154 (P), Ngongonjie hill, near Akonetye; 2°40'N, 12°52'E; alt. 650 m; 30 Aug. 1978 • G.L. Bates 1367 (BM), Bitey; 3°00'41.45"N, 12°21'04.18"E; 1919 • G.L. Bates s.n (BM), Bitey, Yaunde, Cameroons; 3°00'41.45"N, 12°21'04.18"E; 1919 • G.P. Tchouto Mbatchou EGONX 191 (WAG), Campo Ma'an area, Akom II, Efulan and Egongo hills; 2°44'46"N, 10°32'53"E; alt. 840 m; 06 Dec. 2000 • G.P. Tchouto Mbatchou 2843 (KRIBI, WAG), Efulan, Ongongo and Nkolomekok hills in Akom II area; 2°44'43"N, 10°31'48"E; alt. 1000 m; 25 Apr. 2000 • G.P. Tchouto Mbatchou 3089 (KRIBI, SCA, WAG, WAG, YA), Efulan; 2°44'45"N, 10°32'52"E; alt. 960 m; 04 Dec. 2000 • J.F. Villiers 893 (P), colline de Nkoltsia, 23km NW de Bipindi; 3°10'30"N, 10°16'30"E; 27 Apr. 1974 • J.J.F.E. de Wilde 8373 B (WAG), East face of Zingui hill, 21 km on the road from Ebolowa to Kribi (counted from the crossing at Ebolowa); 2°51'N, 10°59'E; alt. 760 m; 21 Jul. 1975. CENTRAL AFRICAN REPUBLIC – Lobaye • Équipe C. Tisserant 2422 (BM, P, WAG); Mbaïki, Station de Boukoko; 3°54'N, 17°56'E; 26 Apr. 1952 • Équipe C. Tisserant 804 (K, P, WAG); Mbaïki, Forêt Soms bois; 3°54'N, 17°56'E; 23 Mar. 1948 – Sangha-Mbaéré • J.M. Fay 8384 (K, MO, P, WAG), Ndakan Gorilla Study Area; 2°20'N, 16°11'E; alt. 380 m; 26 May. 1988. DEMOCRATIC REPUBLIC OF THE CONGO – Bandundu • J.L.P. Louis 15474 (BM, K, P); 4°55'54"S, 18°44'42"E; alt. 470 m; 05 Dec. 1939 – Maniema • R.E. Gereau 7613 (MO), Secteur Bangengele; parc National proposé de la Lomani, ca. 330m à l'Est du camp T7 Lomami et 1.3km à l'Est de la rivière Lomami sur la piste au camp Kaka Barkata; 2°41'42"S, 25°05'18"E; alt. 450 m; 28 Apr. 2015 – Orientale • J. Bokdam 3674 (KIS, WAG, WAG); Banalia, 22km along road from Kisangani to Bengamisa; 0°43'N, 25°12'E; 16 Nov. 1972 • J. Bokdam 4153 B (WAG); Banalia, 23km along road from Kisangani to Bengamisa; 0°46'N, 25°13'E; 31 May. 1973 • J.-B. Ndjango 549 (EPU, K, K, YBI); Haut-Uele, Asonga Hill, c. 75 km South of Isiro. Outskirts of the Ituri forest. Temporary camp; 2°06'35"N, 27°31'17"E; alt. 960 m; 24 Jul. 2011 • J.L.P. Louis 13439 (K); Isangi, Bassao (île), Un peu en aval de Loléko; 0°54'N, 24°12'E; 27 Jan. 1939 • J.L.P. Louis 14540 (BM, K, MO, P); Isangi, Yangambi; 0°46'N, 24°27'E; alt. 470 m; 09 Sep. 1939 • J.L.P. Louis 8357 (BR, MO, P); Isangi, Yangambi; 0°46'N, 24°27'E; alt. 470 m; 08 Mar. 1938. GABON – Estuaire • M.E. Leal 268 (LBV, WAG), Monts de Cristal, Mbe National Parc, south of Mont Mbilan; 0°27'40"N, 10°15'30"E; alt. 550 m; 12 Feb. 2005 – Ngounié • M.E. Leal 1906 (LBV, MO, WAG), Bouvala hills. Col between the two summits; 1°37'15"S, 11°45'45"E; alt. 995 m; 06 Oct. 2007 – Ogooué-Ivindo • A.H. Gentry 33052 (MO, P), Makokou. Transect 1; 0°34'N, 12°52'E; alt. 480 m; 01 Jul. 1981 • J. Florence 1158 (P), Station d'Ipasa, 10km S de Makokou; 0°30'N, 12°47'E; alt. 500 m; 04 May. 1978 • N. Hallé 3474 (K, P, P, U), Bélinga. Route de Mvadi; 1°05'N, 13°08'E; alt. 800 m; 12 Dec. 1964 – Woleu-Ntem • MINKÉbé Series W 289 (WAG), crest to the south of Mount Minkébé; 1°35'N, 12°52'E; 10 May. 1990 • MINKÉbé Series R 67 (WAG), Minkébé area, 10 x 10 m inventory plot R, placed 2-12 m south at 1380-1390 m on transect A; 1°30'N, 12°48'E; Apr. 1990 • T.L.P. Couvreur 856 (LBV, WAG, YA), Oyem, on road to Mbolonzok (off main road to Mongono and Equatorial Guinea); 1°29'21.34"N, 11°27'58.98"E; alt. 675 m; 13 Nov. 2015 – Unknown major area • N. Hallé 2975 (U). REPUBLIC OF THE CONGO – Sangha • S.T. Ndolo Ebika 294 (E, IEC, WAG), Nouablé-Ndoki National Park, Goulougo Study Site, 37.53 km E-SE de Bomassa; 2°11'21.34"N, 16°31'24.35"E; alt. 383 m; 18 Jan. 2008 • S.T. Ndolo Ebika 659 (E, IEC, WAG), Périphérie du Nouable Ndoki National Park; 19 Km E de Bomassa; 2°12'23.29"N, 16°20'19.93"E; alt. 381 m; 06 Jun. 2011.

***Uvariopsis solheidii* var. *letestui* (Pellegr.) Dagallier, **comb. nov.****

*Uvariopsis letestui* Pellegr., Bull. Soc. Bot. France 95: 139 (1948)

**TYPE.** GABON – Ogooué-Lolo • G.M.P.C. Le Testu 8458 (sheets here designated, holotype: P (P00362609); isotypes: BM (BM000554079, BM000554080), P (P00362607)), region de Lastoursville, Koulamotou; 1°07'S, 12°30'E; 20 Oct. 1930.

## TAXONOMIC REVISION OF UVARIODENDRON AND UVARIOPSIS

**Description.** Shrub to tree 2.5 – 5 m tall, D.B.H ca. 3 cm; young branches tomentose to shortly tomentose, old branches glabrous. Leaves distichous, simple, pinnately veined, margins entire and flat. Petiole 2 – 3 mm long, 1.5 – 2.5 mm wide, tomentose to glabrous. Leaf lamina 190 – 260 mm long, 55 – 90 mm wide, length:width ratio 2.1 – 3.9, elliptic to obovate, coriaceous, base rounded to subcordate, apex attenuate to acuminate, acumen 6 – 20 mm long, above glabrous when young and old, below glabrous when young and old; mid rib sunken above, raised below, above glabrous, below sparsely pubescent to glabrous; secondary veins 7 – 13 pairs, brochidodromous to weakly brochidodromous, impressed above, raised below; tertiary veins reticulate. Flowers actinomorphic, unisexual, male and female flowers dimorphic, on same individuals (plant monoecious, but individuals with only pistillate flowers were also reported; e.g. Le Testu 8458). male inflorescences borne on small thickenings of the trunk between 5 cm towards 20 cm, composed of 1 to 2 flowers. Peduncle inconspicuous. Flower pedicel 9 – 23 mm long, ca. 1 mm in diameter, sparsely pubescent. Bracts 1 minute at base and 1 towards the lower half of the pedicel, upper bract ca. 2 mm long, ca. 3 mm wide, broadly ovate, adpressed, semi clasping the pedicel, pubescent outside, glabrous inside. Sepals 2, ca. 1.5 mm long, ca. 1.5 mm wide, broadly ovate, free, pubescent outside, glabrous inside, brown to red. Petals 4, 5 – 7 mm long, ca. 3 mm wide, length:width ratio ca. 2, ovate, free, straight at anthesis, sparsely pubescent outside, glabrous inside, reddish orange outside, dull pink to dark purplish red inside. Stamens ca. 300, ca. 0.5 mm long, ca. 0.3 mm wide, anthers linear, connective truncate. Female inflorescences borne on small thickenings of the trunk, between the base towards ca. 50 cm, composed of 1 to 2 flowers. Flower pedicel 30 – 110 mm long, 1 – 1.5 mm in diameter, sparsely pubescent. Bracts 1 to 2 at base, upper bract ca. 2 mm long, 2 – 3 mm wide, broadly ovate, adpressed, semi clasping the pedicel, pubescent outside, glabrous inside. Sepals 2, 1.5 – 3 mm long, 3 – 5 mm wide, broadly ovate, free, pubescent outside, glabrous inside, brown to red. Petals 4, 7.5 – 10 mm long, 4.5 – 7 mm wide, length:width ratio 1.3 – 1.8, ovate, free, straight at anthesis, pubescent outside, glabrous inside, reddish orange outside, dull pink to dark purplish red inside. Carpels 30 – 65, 1 – 3 mm long, 1 – 1.5 mm wide, velutinous, free; stigma globose. Fruiting pedicel 30 – 110 mm long, 1 – 1.5 mm in diameter, sparsely pubescent. Monocarps, 1, 30 – 62 mm long, 17 – 20 mm wide, length:width ratio 1.8 – 3 (measures taken from both dried fruits and their associated specimen label, note that monocarps seem to sink when drying), cylindrical, with 4 – 6 longitudinal ridges and several transversal ridges or wrinkles, glabrous, bright red, sessile; stipe 0 – 4 mm long, ca. 5 mm wide, sparsely pubescent to glabrous. Seeds 2 – 4 per monocarp, uniseriate, 11 – 18 mm long, 10 – 12 mm wide, ellipsoid.

**Distribution.** Gabon.



**Notes.** *Up. solheidii* var. *letestui* differs from the type variety in having slightly different flowers. The male flowers of *Up. solheidii* var. *letestui* have ovate petals 5 – 7 mm long, with a length:width ratio of ca. 2 (vs. ovate to narrowly ovate petals, 7 – 10 mm long with a length:width ratio of ca. 3). The female flowers of *Up. solheidii* var. *letestui* have generally smaller flower pedicels (30 – 110 mm long vs. 63 – 198 mm long), and ovate petals 7.5 – 10 mm long, with a length:width ratio between 1.3 and 1.8 (vs. ovate to narrowly ovate petals, 9 – 17 mm long with a length:width ratio between 1.8 and 3.6). Both male and female flowers of *Up. solheidii* var. *letestui* have straight petals at anthesis (vs. curved outward at anthesis in the type variety).

**Specimens examined.** GABON – Ngounié • T.O.B.E.B. Stévert 3993 (BR, LBV, MO, WAG), Birougou National Park, Massif du Chaillu, 40 km SE of Mbigou, 5.5 km E of Moukimbi village. MBG transect T59; 2°02'39"S, 12°14'01"E; alt. 780 m; 16 Feb. 2011 – Ogooué-Ivindo • J. Florence 1578 (P), Station d'Ipassa, 10 Km S de Makokou; 0°30'N, 12°47'E; alt. 500 m; 22 Jan. 1979 • N. Hallé 2975 (K, P, P), Bélinga; 1°05'N, 13°08'E; alt. 950 m; 03 Nov. 1964 • N. Hallé 3006 (P), Bélinga; 1°05'N, 13°08'E; 04 Nov. 1964 • N. Hallé 3029 (P), Bélinga; 1°05'N, 13°08'E; 05 Nov. 1964 • N. Hallé 3060 (P), Bélinga; 1°05'N, 13°08'E; 06 Nov. 1964 – Ogooué-Maritime • T.L.P. Couvreur 550 (MPU, YA), along road between Mandji and Rabi. About km 19 from Mandji; 1°46'05.4"S, 10°17'01.5"E; alt. 282 m; 08 Nov. 2013.

*Uvariopsis submontana* Kenfack, Gosline & Gereau, Novon 13(4): 444 (2003)

**TYPE.** CAMEROON – South-West Region • D. Kenfack 1334 (holotype: YA; isotypes: K, MO, SCA), Rumpi Hills; 4°57'N, 9°02'E; alt. 800 m; 06 Feb. 2000.

**Description.** Tree 4.5 – 25 m tall, D.B.H 5 – 30 cm; young branches sparsely pubescent to glabrous, old branches glabrous. Leaves distichous, simple, pinnately veined, margins entire and flat. Petiole 3 – 8 mm long, 2.5 – 4 mm wide, sparsely pubescent to glabrous. Leaf lamina 160 – 380 mm long, 50 – 110 mm wide, length:width ratio 2.7 – 4.3, obovate, coriaceous, base rounded to subcordate, apex attenuate to acuminate, acumen 8 – 30 mm long, above glabrous when young and old, below glabrous when young and old; mid rib sunken above, raised below, above glabrous, below glabrous; secondary veins 9 – 25 pairs, brochidodromous to weakly brochidodromous, impressed above, raised below; tertiary veins reticulate. Flowers actinomorphic, unisexual, male and female flowers slightly dimorphic, on same individuals (plant monoecious). Male inflorescences borne in dense clumps on thickenings at base of the trunk, sparser above 2 m., above the clumps of female inflorescences, mainly between the base and the lower 5 m of the trunk, composed of 6 to 50 flowers. Peduncle inconspicuous. Flower pedicel 25 – 50 mm long, ca. 1 mm in diameter, pubescent to sparsely pubescent. Bracts 2 to 4 at base, upper bract 1 – 1.6 mm long, 1 – 1.6 mm wide, broadly ovate, pubescent outside, glabrous inside. Sepals 2, 5 – 11 mm long, 6 – 12 mm wide, broadly ovate, pubescent to sparsely pubescent outside, glabrous inside, dark red. Petals 4, 8 – 19 mm long, 4 – 8 mm wide, length:width ratio 1.8 – 4.7, ovate to narrowly ovate, free to fused at base over 30% of their length, pubescent outside, glabrous inside, pinkish to dark red outside. Stamens more than 100, 0.4 – 0.7 mm long, 0.3 – 0.4 mm wide, anthers linear, connective trun-

## TAXONOMIC REVISION OF UVARIODENDRON AND UVARIOPSIS

cate. Female inflorescences borne in dense clumps on thickenings at base of the trunk, below the clumps of male inflorescences, composed of 6 to 50 flowers. Flower pedicel 24 – 60 mm long, ca. 1 mm in diameter, pubescent to sparsely pubescent. Bracts 2 to 4 at base, upper bract 1 – 1.6 mm long, 1 – 1.6 mm wide, broadly ovate, pubescent outside, glabrous inside. Sepals 2, 6 – 8 mm long, 6 – 9 mm wide, broadly ovate, pubescent to sparsely pubescent outside, glabrous inside, dark red. Petals 4, 15 – 17 mm long, 5 – 9 mm wide, length:width ratio 1.8 – 4.7, ovate to narrowly ovate, free to fused over 30% of their length, pubescent outside, glabrous inside, pinkish to dark red outside. Carpels 50 – 100, 1.5 – 3.5 mm long, 0.8 – 1.5 mm wide, pubescent, free; stigma ca. 0.5 mm long, ca. 0.2 mm wide, globular, glabrous. Fruiting pedicel 25 – 90 mm long, 3 – 7 mm in diameter, glabrous. Monocarps, 9 – 25, 17 – 80 mm long, 13 – 55 mm wide, length:width ratio, ovoid to cylindrical, constricted between seeds in dried specimens, sparsely pubescent to glabrous, pale green ripening dark yellow, sessile. Seeds 6 – 12 per monocarp, biseriate, 18 – 25 mm long, 8 – 13 mm wide, ellipsoid.

**Distribution.** Only known from the South-West and Littoral Regions in Cameroon.

**Notes.** This species resembles *Up. bakeriana*, *Up. citrata* and *Up. korupensis* in having large obovate leaves (up to 38 cm long), with rounded to cordate bases. It differs from *Up. bakeriana* and *Up. citrata* in having

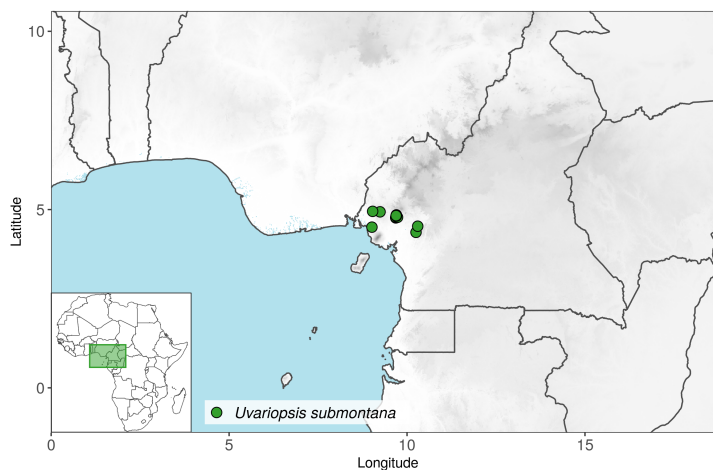


Figure 47: Distribution of *Uvariopsis submontana*

longer flower pedicel (24 – 60 mm vs. 0 – 8 mm). It is very similar to *Up. korupensis*, but has generally smaller leaves (16 – 38 cm vs. 28 – 62 cm in *Up. korupensis*). The female flowers of *Up. submontana* have longer sepals (6 – 8 mm long vs. 3 – 5 mm long) and smaller petals (15 – 17 mm long vs. 15 – 35 mm long) than *Up. korupensis*, which results in petals less than 3 times longer than the sepals (vs. petals more than 3 times longer than the sepals). Petals of *Up. submontana* are pinkish to dark red inside and outside whereas petals of *Up. korupensis* are cream to brownish outside and cream to pinkish inside.

**Specimens examined.** CAMEROON – Littoral • D. Kenfack 1602 (MO), Nkam, Yingui, Bataba. PE80; 4°32'N, 10°18'E; alt. 780 m; 20 Feb. 2002 • T.L.P. Couvreur 627 (MPU, YA), Ebo Wildlife Reserve, Djuma permanent camp. On east trail; 4°21'39.35"N, 10°15'07.7"E; alt. 957 m; 15 Feb. 2013 – South-West Region • J.F. Villiers 2490 (P), 6km WNW Bomana, 34 km NW Limbé; 4°30'24.99"N, 9°00'50.26"E; 15 Dec. 1984 • M.R. Cheek 7034 (K, WAG, YA), Mount Kupe. Kupe village. Esense river near farm of Philip Taza; 4°46'N, 9°41'E; alt. 1000 m; 19 Jan. 1995 • M.R. Cheek 7131 (K, WAG), Kupe village. Hunters path from Kupe village to the mountain top, running to S and parallel with Esense river (now dry). Towards village largely coffee farms with shade trees. Grid ref. from Magellan reading where path enters forest;

## CHAPTER 4

4°47'N, 9°41'E; alt. 840 m; 24 Jan. 1995 • P. Lane 490 (K, SCA, WAG, YA), Mount Kupe. Ndum. Forest trail 2 km S from Etube-Tape village; 4°51'N, 9°42'E; alt. 1100 m; 01 Feb. 1995 • S. Cable 1221 (K, MO, SCA, WAG, YA), Mt Kupe, Nyasoso, Shrike trail; 4°49'00.12"N, 9°42'E; alt. 1100 m; 08 Feb. 1995 • S. Cable 2736 (K, MO, P, SCA, WAG, YA), Kupe-Muanenguba Division. Path on to ridge between Daniel's saprophyte site and Kupe rock; 4°47'N, 9°44'E; alt. 1000 m; 30 May. 1996 • T.L.P. Couvreur 1059 (MPU, WAG, YA), Nyasoso village, on max's trail to Mt Kupe; 4°49'47.02"N, 9°41'34.79"E; alt. 1024 m; 05 Apr. 2016 • T.L.P. Couvreur 965 (MPU, WAG, YA), Rumpi mountains, forest trail, ca. 5 km after Dikome Balue village, ca. 40 km north of Kumba; 4°56'10.37"N, 9°14'30.34"E; alt. 1418 m; 10 Jan. 2016.

*Uvariopsis zenkeri* Engl., Notizbl. Königl. Bot. Gart. Berlin 2: 298 (1899)

**TYPE.** CAMEROON – South Region • G.A. Zenker 1117 (holotype: B; isotypes: BM, G, K, L, M, WU, Z), Bipinde, Urwaldgebiet; 3°05'N, 10°25'E; 1896.

**Description.** Shrub to tree 2 – 5 m tall, D.B.H 1.5 – 2 cm; young branches densely pubescent to pubescent, old branches glabrous. Leaves distichous, simple, pinnately veined, margins entire and flat. Petiole 2 – 5.5 mm long, 1 – 1.5 mm wide, pubescent to glabrous. Leaf lamina 110 – 158 mm long, 36 – 58 mm wide, length:width ratio 2.1 – 3.4, elliptic to obovate, papyraceous to coriaceous, base acute to decurrent, apex acuminate, acumen 10 – 24 mm long, above glabrous when young and old, below puberulent to glabrous when young, glabrous when old; mid rib sunken above, raised below, above glabrous, below pubescent to glabrous; secondary veins 6 – 13 pairs, brochidromous, impressed above, raised below; tertiary veins reticulate. Flowers actinomorphic, unisexual, male and female flowers similar, on same individuals (plant monoecious). Male and female inflorescences borne on trunk, old branches or old axillary, composed of 1, (sub)sessile flower. Peduncle inconspicuous. Flower pedicel 0 – 7 mm long, 1 – 1.5 mm in diameter, pubescent. Bracts 1 to 2 (5 in bud) at base, upper bract 1 – 4 mm long, 2 – 5 mm wide, ovate, pubescent outside, glabrous inside. Sepals 2, 3 – 7 mm long, 4.5 – 7 mm wide, broadly ovate, basely fused, pubescent outside, glabrous inside, brown. Petals 4, 6 – 13 mm long, 4 – 7 mm wide, length:width ratio 1.5 – 2.2, ovate to triangular, fused at base over ca. 50 % of their length, pubescent outside, glabrous inside, brown outside. Male flowers: stamens 100 to 150, ca. 0.5 mm long, ca. 0.3 mm wide, anthers linear, connective truncate or absent. Female flowers: carpels 13 – 22, 1.5 – 3 mm long, 1 – 1.5 mm wide, velutinous, free; stigma 0.1 – 0.5 mm long, ca. 1 mm wide, coiled, glabrous. Fruiting pedicel 2 – 10 mm long, ca. 2.5 mm in diameter, pubescent. Monocarps, 1 – 3, ca. 37 mm long, ca. 17 mm wide, length:width ratio ca. 2.2, cylindrical, slightly veined and constricted between the seed when dried, tomentose, brown, subsessile; stipe ca. 1 mm long, ca. 2 mm wide, tomentose. Seeds 10 – 12 per monocarp, biseriata, ca. 13 mm long, ca. 7 mm wide, ellipsoid.

**Distribution.** Cameroon.

**Notes.** This species resembles *Up. bisexualis*, *Up. congensis* and *Up. oligocarpa* in having elliptic leaves generally less than 16 cm long with decurrent base. It differs from these species in having densely pubescent to pubescent young branches (vs. pubescent to glabrous). It also differs from *Up. bisexualis* with its unisexual flowers

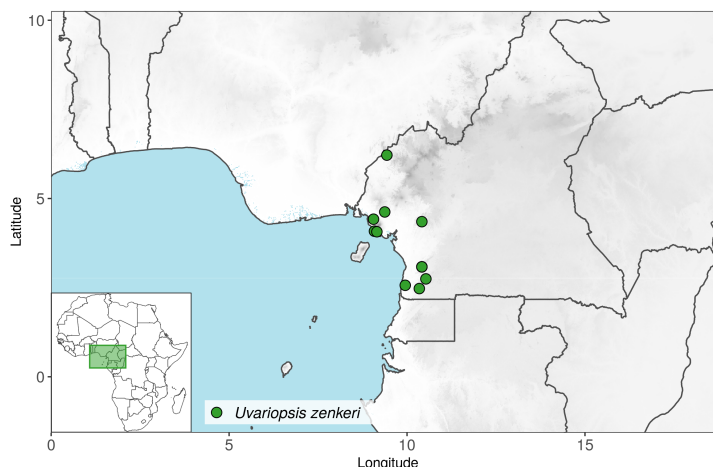


Figure 48: Distribution of *Uvariopsis zenkeri*

(vs. bisexual flowers). *Up. zenkeri* has less carpels (13 to 22 vs. 20 to 40 in *Up. congensis*), which results in generally 1 to 3 monocarps reaching maturity on the ripe fruit (vs. up to 15 mature monocarps in *Up. congensis*). The monocarps of *Up. zenkeri* are tomentose (vs. glabrate to glabrous in *Up. congensis* and pubescent to sparsely pubescent in *Up. oligocarpa*), slightly constricted between the seeds (vs. not constricted between the seeds in *Up. oligocarpa*).

**Specimens examined.** CAMEROON – South Region • G.A. Zenker 3045 (B, BM, G, K, L, M, MA, WAG), Bipindi; 3°05'N, 10°25'E; 1904 • G.A. Zenker 3228 (G, L, M), Bipinde, Urwaldgebiet; 3°05'N, 10°25'E; 1904 • G.A. Zenker 515 (B, G, G, M, MA, MO, WAG), Bipindi; 3°05'N, 10°25'E; Mar. 1914 • G.P. Tchouto Mbatchou 2846 (KRIBI, WAG, WAG), Efulan, Ongongo and Nkolomekok hills in Akom II area; 2°44'43"N, 10°31'48"E; alt. 1000 m; 25 Apr. 2000 • G.P. Tchouto Mbatchou 3252 (KRIBI, SCA, WAG, WAG), Campo-Ma'an area, Massif des Mamelles, Mamelles highlands; 2°33'57"N, 9°56'58"E; alt. 280 m; 23 Apr. 2001 • T.L.P. Couvreur 707 (MPU, WAG, YA), Campo Ma'an National Park, 11 km on trail from Ebinanemeyong village, on road, 7 km from Nyabessan to Campo town; 2°28'24.59"N, 10°20'41.79"E; 14 Feb. 2015 – South-West Region • D.W. Thomas 3455 (B, K, LBV, MO, WAG), forested lower slope of Mount Cameroon, above Batoke; 4°05'N, 9°05'E; alt. 300 m; 24 Apr. 1984 • D.W. Thomas 7372 (MO, P, WAG), Takamanda Forest Reserve; 6°13'N, 9°26'E; alt. 500 m; 30 Apr. 1987 • S.N. Ekema 944 (K, SCA); Ndian, Dikome, Mokoko Forest Reserve; 4°25'11.64"N, 9°03'29.16"E; alt. 120 m; 05 May. 1994 • T.L.P. Couvreur 1027 (MPU, WAG, YA), on trail leading to top of Mt Etinde, after Ekonjo village; 4°04'02.29"N, 9°09'11.15"E; alt. 756 m; 01 Apr. 2016 • T.L.P. Couvreur 978 (WAG, YA), on top of hill, near Small Ekombe village, 3 km after Kumba on road to Ekondo Titi town; 4°37'21.52"N, 9°22'26.62"E; alt. 589 m; 13 Jan. 2016 – Unknown major area • J. Osborne 200 (K, WAG), Littoral Province, Ebo Forest proposed National Park. Ebo Forest Research Station-Bekob drinking stream trail; 4°21'N, 10°25'E; 27 Oct. 2006.

*Uvariopsis* sp. nov. 1 'Uganda' Dagallier, sp. nov.

**Description.** Tree ca. 3 m tall, D.B.H unknown; young branches glabrous, old branches glabrous. Leaves distichous, simple, pinnately veined, margins entire and flat. Petiole ca. 6 mm long, ca. 1.7 mm wide, glabrous. Leaf lamina ca. 160 mm long, ca. 60 mm wide, length:width ratio ca. 2.6, elliptic, coriaceous, base acute to decurrent, apex attenuate, above glabrous when young and old, below glabrous when young and old; mid rib sunken above, raised below, above glabrous, below glabrous; secondary veins ca. 12 pairs, brochidodromous to weakly brochidodromous, impressed above, raised below; tertiary veins reticulate. Flowers unknown. Fruits unknown.

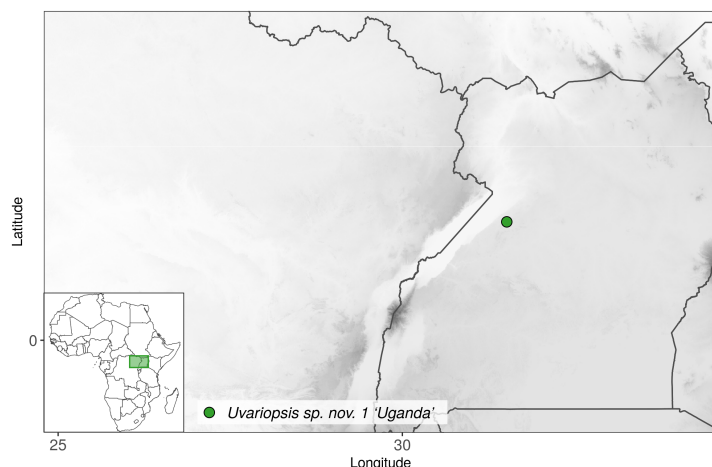


Figure 49: Distribution of *Uvariopsis sp. nov. 1 'Uganda'* *Up. congensis* and *Up. lovettiana*. Further collection of this species is needed to provide a more complete description (particularly for the flowers and fruits).

**Specimens examined.** UGANDA – Western Province • ATBP (Africa Tropical Biodiversity Programme) 666 (MO); Masindi District, Budongo Forest Reserve, Nyakafunjo Nature Reserve; 1°43'N, 31°31'E; alt. 1051 m; 26 Jun. 1998.

***Uvariopsis sp. nov. 2 'Tanzania'* Dagallier, sp. nov.**

**Description.** Shrub to tree 4 – 6 m tall, D.B.H unknown; young branches glabrous, old branches glabrous. Leaves distichous, simple, pinnately veined, margins entire and flat. Petiole ca. 2 mm long, ca. 2 mm wide, glabrous. Leaf lamina 150 – 180 mm long, ca. 60 mm wide, length:width ratio ca. 3, elliptic to obovate, coriaceous, base rounded, apex attenuate, above glabrous when young and old, below glabrous when young and old; mid rib sunken above, raised below, above glabrous, below glabrous; secondary veins ca. 13 pairs, brochidodromous to weakly brochidodromous, impressed above, raised below; tertiary veins reticulate. Flowers not seen (label says 5 petals). Fruiting pedicel ca. 51 mm long, ca. 1 mm in diameter, pubescent. Monocarps, 1 – 2, ca. 30 mm long, ca. 15 mm wide, length:width ratio ca. 2, cylindrical to obpyriform, smooth, slightly constricted between the seeds, pubescent, subsessile; stipe 0 – 1 mm long, ca. 1 mm wide, pubescent.

**Distribution.** Only known from the Kigoma region in eastern Tanzania.

**Distribution.** Known from only one locality in Uganda: the Budongo Forest Reserve.

**Notes.** This species resemble *Up. congensis* in having elliptic leaves with acute to decurrent base and attenuate apex, but it differs in having longer petioles (ca. 6 mm vs. 2 – 5 mm). Molecular analysis retrieves this species as sister species of the clade formed by

**Notes.** This species is very similar to *Up. lovettiana* having similar elliptic leaf shape, but differs by the leaf base being rounded (vs. acute to decurrent in *Up. lovettiana*) and in having pubescent monocarps slightly constricted between the seeds (vs. sparsely pubescent to glabrous monocarps, strongly constricted between the seeds). The monocarps are also sessile (stipe 0 – 1 mm long, vs. stipitate, stipe 2.5 – 14 mm long in *Up. lovettiana*). Confirming the status of new species with molecular analysis is however essential in order to make sure these specimens are not a morphological variation of *Up. lovettiana*.

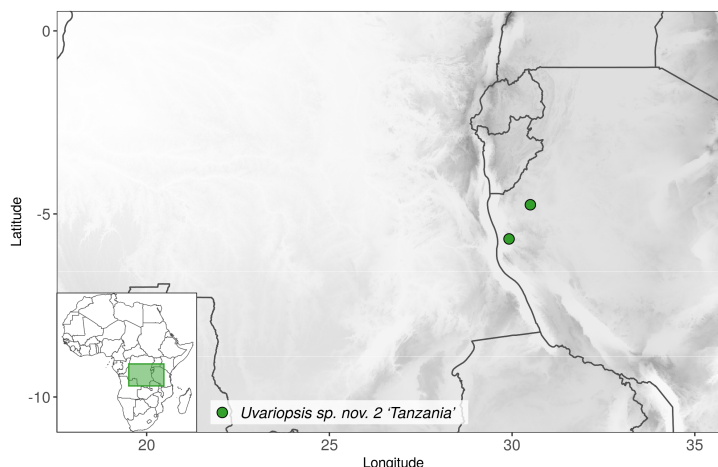


Figure 50: Distribution of *Uvariopsis sp. nov. 2 'Tanzania'*

**Specimens examined.** TANZANIA – Kigoma • G.S. Bidgood 2783 (DSM, K, P, WAG); Kigoma Rural District, T4. Kigoma Distr.: Kasye Forest; 5°41'S, 29°55'E; alt. 900 m; 18 Mar. 1994 • Kyoto University Expedition 1039 (EA); Kigoma Rural District; 4°45'S, 30°30'E; 24 Dec. 1963.

***Uvariopsis sp. nov. 3 'Congo'* Dagallier, sp. nov.**

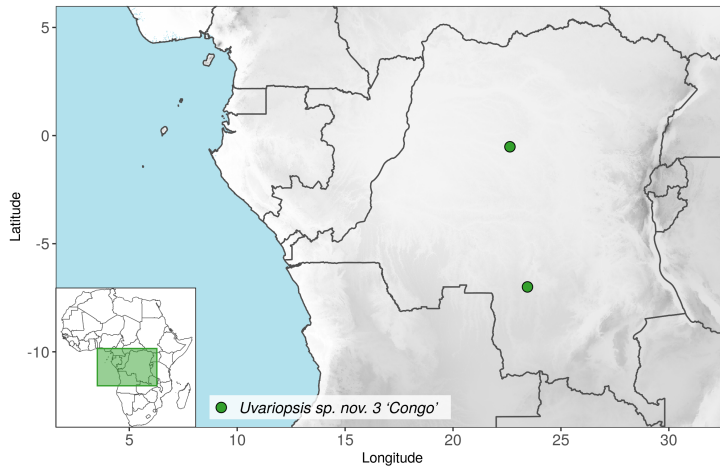
**Description.** Tree ca. 3.5 m tall, D.B.H unknown; young branches glabrous, old branches glabrous. Leaves distichous, simple, pinnately veined, margins entire and flat. Petiole ca. 2 mm long, ca. 2 mm wide, glabrous. Leaf lamina ca. 160 mm long, ca. 58 mm wide, length:width ratio ca. 2.8, elliptic, coriaceous, base rounded, apex attenuate, above glabrous when young and old, below glabrous when young and old; mid rib sunken above, raised below, above glabrous, below glabrous; secondary veins ca. 9 pairs, brochidodromous, impressed above, raised below; tertiary veins reticulate. Flowers only flower bud seen. Inflorescences axillary, composed of 1 flower. Peduncle inconspicuous. Flower pedicel 20 – 65 mm long, ca. 1 mm in diameter, glabrate to glabrous. Bracts 1 in the lower half of the pedicel, upper bract ca. 1 mm long, ca. 1 mm wide, broadly ovate, sparsely pubescent outside, glabrous inside. Sepals 2, ca. 2 mm long, ca. 3 mm wide. Petals 4, ca. 7 mm long, ca. 4 mm wide, length:width ratio red outside. Fruits unknown.

**Distribution.** Only known from the Kasai-Oriental and Equateur regions in the Democratic Republic of the Congo.

**Notes.** This species resembles *Up. solheidii* and *Up. noldeae* in having elliptic leaves with rounded leaf base. It differs from *Up. solheidii* in having young branches and petioles completely glabrous (vs. tomentose in *Up. solheidii*). It differs from *Up. noldeae* in having flowers borne on young branches

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and axillary (vs. borne on trunk in *Up. noldeae*, but see the discussion in Chapter 3 about the unreliability of the flower position to discriminate the species), and in having flower pedicels 20 – 65 mm long (vs. 70 – 83 mm long in *Up. noldeae*).



**Specimens examined.** DEMOCRATIC REPUBLIC OF THE CONGO – Equateur • C.M. Evrard 6276 (K); Ikela, Yalifake; 0°31'06"N, 22°38'12"E; 06 May. 1959 – Kasai-Oriental • L. Liben 3854 (K); Mwene Ditu, Mwene Ditu, Mwene-Ditu; 7°00'S, 23°27'E; 24 Oct. 1957.

Figure 51: Distribution of *Uvariopsis sp. nov. 3 'Congo'*



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# Chapter 5 | Macroevolution of Monodoreae supports the role of Miocene extinction and speciation linked to mountain uplift and climate change in African tropical rain forests\*

**Abstract.** Tropical Africa underwent several climatic and geological changes during the Cenozoic. This affected the evolutionary history of the TRF, leading them to be distributed in 2 major distinct blocks in East and Central-West Africa. Several mechanisms were invoked to explain this pattern. In particular, African TRF are supposed to have extended from East to West in a ‘pan-African’ rain forest during favorable climates, and to contract in isolated blocks during drier climate periods. This dynamic of expansion-contraction linked to climate oscillation, called the ‘fragmentation-refugia’ mechanism, was invoked to explain the synchronously diverging vicariant species observed in molecular phylogenies of TRF clades. During the Miocene, climate cooling and mountain uplift led to the aridification of tropical Africa and open habitats expanded at the expense of TRF clades, that likely experienced extinction. However, in plants, these mechanisms invoked to explain the current TRF patterns, were previously inferred using few data at the taxonomic and molecular marker sampling levels. Here, we tested these mechanisms focusing on the Monodoreae, an Annonaceae tribe composed of 92 species restricted to African TRF. We reconstructed a near complete phylogenetic tree, based on 32 nuclear genes, and dated with relaxed clock and fossil calibration in a Bayesian framework. We inferred the biogeographic history and the diversification dynamic of the clade. We found that the Monodoreae originated in East African TRF ca. 25 Ma, and expanded toward Central-Africa during the early to middle Miocene, supporting the existence of a pan-African rain forest until ca. 13.5 Ma. We found no evidence for discrete and synchronous vicariance events in the TRF during the middle Miocene, but we inferred range contractions possibly due to aridification in Africa. However, our results also suggest that the TRF blocks were more connected than previously thought during the middle Miocene. We found that the Monodoreae likely experienced a sudden extinction during the late Miocene, supporting the drastic reduction of the TRF linked to aridification. Just after the sudden extinction, we inferred high speciation rates, suggesting that both the fragmentation and the following re-connection of the TRF in the early Pliocene stimulated diversification. Such a high diversification was likely associated with the increasing African paleo-elevation during the late Miocene and Pliocene, supporting the idea that the uplift of East Africa was a factor that promoted diversification.

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\* Manuscript in preparation

## 1. Introduction

Tropical rain forests (TRF) are one of the more biodiverse ecosystems on Earth. Covering just 7% of land, they contain over half of the world's biodiversity (Wilson, 1988; Eiserhardt *et al.*, 2017). After the Amazon basin, the Guineo-Congolian region of Africa contains the second largest continuous extent of TRF in the world (Malhi *et al.*, 2013). The African TRF is divided in two major forested blocks: West-Central and East TRF (Figure 52; Olson *et al.*, 2001; Couvreur *et al.*, 2008; Droissart *et al.*, 2018; Brée *et al.*, 2020). The West-Central block is divided into two smaller blocks separated by the Dahomey gap located in Benin. The current distribution of TRF across the continent is thought to be the result of various climatic and tectonic events that have shaped the distribution and evolution African TRF biodiversity (Morley, 2000; Couvreur *et al.*, 2021). A recent review identified six major geo-climatic periods affecting tropical Africa biodiversity evolution (Couvreur *et al.*, 2021). In particular, the Miocene (ca. 23–5.3 million years ago, Ma) is considered crucial in terms of diversification of the African flora (Plana, 2004; Couvreur *et al.*, 2021). For example, the temperature increased during the middle Miocene Climatic Optimum (MMCO, ca. 17 – 14.7 Ma) and the TRF expanded all across tropical Africa due to warmer and moister climate (Morley, 2000, 2011). Then, from the middle Miocene Climatic Transition (MMCT, ca. 15 – 13 Ma), the global temperatures and  $p\text{CO}_2$  dropped (Zachos *et al.*, 2008; Westerhold *et al.*, 2020). These climate changes, as well as the uplift of East Africa, led to the aridification of Africa throughout the Miocene (Sepulchre *et al.*, 2006; Herbert *et al.*, 2016) favoring the expansion of open, grass-dominated habitats (Retallack *et al.*, 1990; Morley, 2000; Jacobs, 2004; Senut *et al.*, 2009). From 10 Ma, paleovegetation records show increasing percentage of C4 plants until the present (Ségalen *et al.*, 2007; Uno *et al.*, 2016; Polissar *et al.*, 2019) and increases in diversification rates of herbaceous plants like Poaceae and Asteraceae (Kergoat *et al.*, 2018; Palazzesi *et al.*, 2021), indicating increasing dominance of grasslands across Africa. While open grassland expanded, TRF contracted across its distribution (Plana, 2004). This contraction is suggested to have led to vicariance events within TRF clades before the MMCT, as was detected in several dated phylogenetic studies (Couvreur *et al.*, 2008; Dimitrov *et al.*, 2012; Menegon *et al.*, 2014; Brée *et al.*, 2020). Also, as drier habitats expanded, some forest-adapted clades experienced habitat shifts towards drier habitats during the Miocene (Davis *et al.*, 2002; Bouchenak-Khelladi *et al.*, 2010; Armstrong *et al.*, 2014; Veranso-Libalah *et al.*, 2018; Tosso *et al.*, 2018). In the early Pliocene (ca. 5.3 – 3.6 Ma), the climate became warmer and moister (Haywood *et al.*, 2013) and the TRF re-expanded while savannas contracted (Morley, 2000; Plana, 2004), suggesting reconnection of West-Central and East TRF blocks (Fer *et al.*, 2017; Joordens *et al.*, 2019).

This climatic changes and rain forest dynamics gave rise to one of the major hypotheses explaining the distribution of TRF plants clades in Africa: the fragmentation-refugia mechanism (Couvreur *et al.*, 2008, 2021; Pokorny *et al.*, 2015). This mechanism links multi-million year climatic fluctuations and continental wide expansion-contraction of TRF dynamics to numerous vicariant speciation events in TRF-restricted clades (Moritz *et al.*, 2000; Plana, 2004; Loader *et al.*, 2007; Couvreur *et al.*, 2008, 2021). This suggests the existence of a ‘pan-African forest’ extending continuously from Western to Eastern Africa during favorable climatic times, and fragmenting into isolated Western-Central and Eastern blocks during drier climate periods (Morley, 2000, 2011; Plana, 2004; Couvreur *et al.*, 2021). The fragmentation-refugia mechanism was suggested to explain the present-day distribution patterns of some African TRF clades with species restricted to East or West-Central Africa in plants (Davis *et al.*, 2002; Couvreur *et al.*, 2008; Brée *et al.*, 2020), butterflies (Aduse-Poku *et al.*, 2021), birds (Fjeldså *et al.*, 2007; Fjeldså & Bowie, 2008; Voelker *et al.*, 2010; Huntley & Voelker, 2016; Fuchs *et al.*, 2017), chameleons (Tolley *et al.*, 2013), frogs (Bell *et al.*, 2017; Leaché *et al.*, 2019), and mammals (Demos *et al.*, 2014; Bryja *et al.*, 2017; Nicolas *et al.*, 2020). To date, this biogeographic mechanism was inferred based on few data (Couvreur *et al.*, 2008) at the taxonomic and molecular marker sampling level, especially in plants. In particular, the number of vicariant events used to infer this mechanism was generally low (Davis *et al.*, 2002; Couvreur *et al.*, 2008; Brée *et al.*, 2020).

Another major hypothesis explaining African TRF diversity is the impact of extinction (Morley & Richards, 1993; Couvreur, 2015). Under the environmental changes, the contraction of the forests did not only trigger speciation via allopatric speciation, but also likely triggered extinction across TRF clades (Morley & Richards, 1993; Plana, 2004; Aduse-Poku *et al.*, 2021). Major extinction events in TRF clades were suggested to occur at the Eocene-Oligocene boundary ca. 33.9 Ma (Pan *et al.*, 2006; Faye *et al.*, 2016; Currano *et al.*, 2021), in the first half of the Miocene (23 – 13.8 Ma; Morley, 2000; Couvreur, 2015), in the late Miocene around 11.6 Ma and 7.2 Ma (Morley, 2011) and in the late Pliocene ca. 3.6 – 2.58 Ma (Morley, 2000; Couvreur, 2015). However, signal of past extinction in African TRF plants has rarely been tested with a comprehensive dated phylogeny (e.g. Brée *et al.*, 2020).

The opposite view to these hypotheses is that speciation and extinction remained relatively constant through time in African TRF. Indeed, African TRF have lower extant species richness compared to TRF from the Americas and from South-East Asia (Parmentier *et al.*, 2007; Couvreur, 2015). One of the hypotheses invoked to explain such a pattern is that diversification was rather constant in African TRF, whereas American and South-East Asian TRF experienced bursts of speciation (Gentry, 1982; Couvreur, 2015). This hypothesis has been supported by global-scale molecular studies of TRF clades

showing no diversification shifts in the African lineages (Erkens *et al.*, 2012; Kissling *et al.*, 2012; Baker & Couvreur, 2013).

The bursts of speciation in the American TRF are in part attributed to the Andean uplift (Hoorn *et al.*, 2010; Lagomarsino *et al.*, 2016; Boschman & Condamine, 2022). Indeed, mountain uplift is generally linked to increased diversification, through various mechanisms such as the creation of new habitats or population isolation (Dimitrov *et al.*, 2012; Antonelli *et al.*, 2018; Muellner-Riehl, 2019; Rahbek *et al.*, 2019; Couvreur *et al.*, 2021). These topographic uplifts also have indirect effects via the modification of climate (Sepulchre *et al.*, 2006). In Africa, mountains harbor high levels of species diversity and endemism (Fjeldså & Lovett, 1997; Burgess *et al.*, 2007). East Africa, which has the highest topographical complexity compared to the rest of Africa, has been inferred to be rich in both neo- and paleo-endemics (Chapter 2). Several geological uplifts occurred during the Cenozoic (Guillocheau *et al.*, 2018; Couvreur *et al.*, 2021), and the uplift of East Africa was documented to occur during the late Miocene

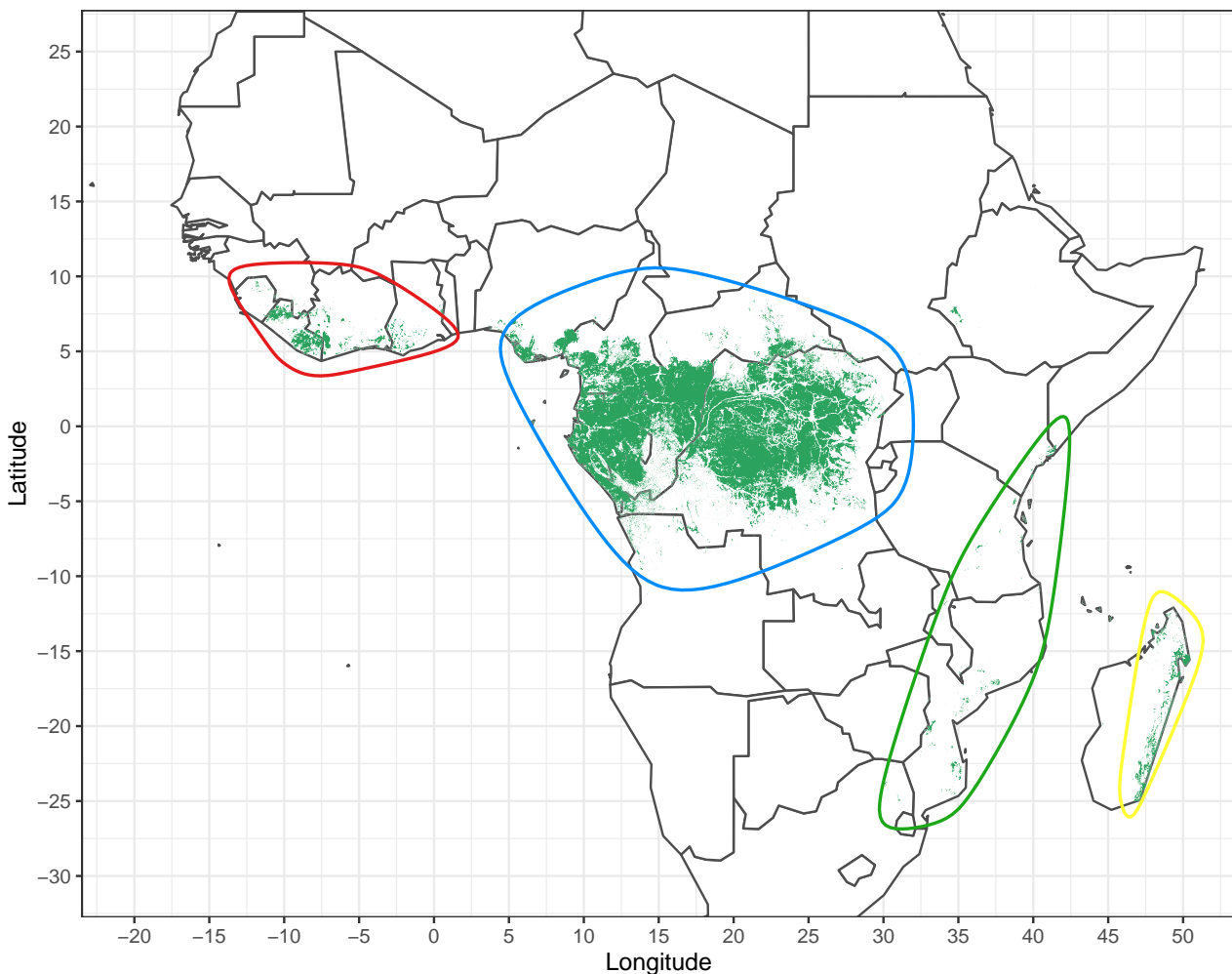


Figure 52: Map of the tropical rain forest of Africa (after Mayaux *et al.*, 2004), Western block (red), Central block (blue), Eastern block (green) and Madagascar (yellow).

(Griffiths, 1993; Sepulchre *et al.*, 2006; Macgregor, 2015; Couvreur *et al.*, 2021). However, the impact of mountain uplift on TRF clade diversification has never been tested.

The Monodoreae tribe is an African TRF restricted clade of the plant family Annonaceae. The tribe contains to date 11 genera and 92 species (see Chapter 3) restricted to Africa, with one genus also occurring in Madagascar. Species present high levels of endemism across the discrete TRF blocks, occurring either in West-Central or East Africa, with a single species occurring across both blocks (Chapter 3; Couvreur *et al.*, 2008). To date, there is little knowledge about the mode of dispersal across the tribe. However, fruit morphology provides some indication about dispersal. Species of this tribe have large fruits (generally larger than 3 cm), most of them cauliflorous (i.e. growing on the trunk), lack the typical stipe at the base of each individual monocarp composing the fruit in Annonaceae (van Setten & Koek-Noorman, 1992) and are generally dull-colored, varying from brown, green, or orange. This fruit morphology suggests dispersal syndromes targeting mainly ruminant mammals (Gautier-Hion *et al.*, 1985). Indeed, some studies have shown that species of Monodoreae were included in the diet of TRF understory mammals such as gorillas, chimpanzees and forest elephants (Gautier-Hion *et al.*, 1985; Tutin & Fernandez, 1993; White *et al.*, 1993; Remis *et al.*, 2001; Rogers *et al.*, 2004). Cauliflorous fruits in particular limit plant dispersal because they target understory dispersers, which are relatively sedentary and habitat specific (Onstein *et al.*, 2018). Monodoreae are thus unlikely to disperse over long distances i.e. distance such as hundreds or thousands of kilometers, and especially not across different habitats. Thus Monodoreae species are mainly TRF restricted with limited opportunities for long distance dispersal, and thus is a good model to test hypotheses about TRF evolution across Africa, in particular the fragmentation-refugia mechanism (Couvreur *et al.*, 2008). After inferring a near complete species-level dated phylogenomic tree of Monodoreae, we tested:

- If the ancestral range of the tribe extended across Africa, supporting the existence of a pan-African rain forest as suggested under the fragmentation-refugia mechanism;
- If multiple discrete and synchronous speciation events occurred between major forest blocks and if they coincided with increased climatic aridity in Africa leading to TRF fragmentation;
- If diversification was constant, or if it experienced major increases or decreases of diversification, or sudden extinctions;
- If diversification was associated with changes in paleotemperature, proportion of C4 plants or elevation linked to mountain uplifts.



## 2. Material & Methods

### 2.1. Taxon sampling and species distribution

Species delimitation within Monodoreae was previously investigated and validated using a densely sampled phylogenetic tree and morphology (Chapter 3 and 4). This led to several new species to be described, and the placement of two genera into the new tribe Ophrypetaleae. Here, we sampled 88 of the 92 known species of Monodoreae (95.6% of the total species richness). One specimen per species was sampled, except in two specific cases: for species with known varieties or subspecies described, one specimen per variety or subspecies was sampled. Most of the species are geographically restricted to one of the following regions: East Africa, West Africa, Central Africa or West and Central Africa. For the species distributed in more than one region, we included one specimen per region when possible. Our dataset also comprised outgroups within the Annonaceae from different closely related tribes, such as the Ophrypetaleae (see Chapter 3) and Uvarieae tribes, from more distantly related tribes (Malmeoideae, Annonoideae). We also included one specimen of *Anaxagorea* which is the most early diverging Annonaceae genus (Couvreur *et al.*, 2019), and one specimen of Eupomatiaceae (*Eupomatia*), which is the sister family of Annonaceae (Sauquet *et al.*, 2003). DNA extractions and library preparations were done following the protocol described in (Chapter 3; Couvreur *et al.*, 2019). DNA was sequenced on an Illumina HiSeq 2500 with paired reads of 150 pb.

### 2.2. Molecular dataset

For each specimen in our dataset, we retrieved cleaned reads from previous analyses (Chapter 3). These reads were then assembled into “supercontigs” (i.e. reconstructed genes with multiple exons and introns) using HybPiper (Johnson *et al.*, 2016). The reads were aligned to the reference (i.e. the sequences of the 469 nuclear genes targeted) using Burrow Wheeler Alignment (Li & Durbin, 2009) and sorted according to the targeted gene. Reads were then assembled into contigs using SPAdes (Bankevich *et al.*, 2012). Contigs were then aligned to the reference and intron sequences were then generated partially (or completely in case of short introns). Finally, the contigs and the introns were assembled into supercontigs (later also called “genes” or “loci”).

The sequences of each gene were then aligned using MAFFT version (Katoch *et al.*, 2002). Poorly aligned regions were cleaned using Gblocks 0.91b (Talavera & Castresana, 2007), and the alignments were filled with gaps so that all the sequences in the alignment have the same length and so that every species is included in the alignment. We filtered the dataset to retain only the genes for which the exons

sequences mapped at least at 75% of the reference gene and that were retrieved in 75% of the species (75/75 dataset).

HybPiper also includes a tool that flags some of the retrieved genes as potential paralogs in case were different contigs targeted the same reference gene with similar coverage depth (i.e. meaning that variants of the same gene may occur). We executed an exploratory maximum-likelihood phylogenetic reconstruction of these putative paralogs using RAxML 8.2.9 (Stamatakis, 2014), and examined the reconstructed phylogeny to check whether the variants of the genes formed two clear clusters of species. If so, the alignment for this gene was discarded from the dataset.

Using a Bayesian inference (BI) to simultaneously infer phylogenetic relationships and divergence times allows incorporating explicitly topological and age uncertainties. However, the use of BI with hundreds of genes is computationally impossible to achieve in a reasonable time. We thus applied a “gene shopping” approach to select a subset of the most clock-like genes to ease convergence and reduce the computational time (Smith *et al.*, 2018). We first reconstructed a maximum likelihood phylogenetic tree with RAxML for each gene. Each gene tree was then rooted with the outgroup *Eupomatia* using phyx (Brown *et al.*, 2017) and we calculated the root-to-tip variance of the trees using SortaDate (<https://github.com/FePhyFoFum/SortaDate>). We then selected a subset composed of the 32 most clock-like genes, that is the 32 genes with the lowest root-to-tip variance. This gene selection strategy has already been used to infer dated phylogenetic trees in Annonaceae (Brée *et al.*, 2020; Helmstetter *et al.*, 2020). Note that we tried with a higher number of genes but BEAST could not run. For each of these 32 genes, we inferred the best fitting substitution model using ModelTest-NG based on the Bayesian Information Criterion (Darriba *et al.*, 2020).

### 2.3. Phylogenetic reconstruction and molecular dating

We simultaneously reconstructed and dated the phylogenetic tree of Monodoreae using BEAST 2.6.4 (Bouckaert *et al.*, 2019). The alignment of the 32 selected genes (see above) was first converted from fasta to nexus format using PGDSpider (Lischer & Excoffier, 2012) and was assigned a molecular partition in BEAUTi (Bouckaert *et al.*, 2019). Substitution models were defined for each gene following the best model retrieved by ModelTest-NG (see Table SI.9) with no estimation of the substitution rate.

To calibrate the molecular clock, we relied on primary fossil calibrations to provide age priors at specific nodes. First, the fossil *Endressinia brasiliensis* is a leafy shoot dated from the Aptian-Albian boundary (113.4 – 112.6 million years ago, Ma), which confers a maximum age for the crown node of Magnoliineae (i.e. including Annonaceae and Eupomatiaceae) as shown by its phylogenetic placement (Massoni *et al.*, 2015b). Second, the fossil *Futabanthus asamigawaensis* is a flower dated from the early

Coniacian (ca. 89 Ma) and provides a minimum age for the crown node of Annonaceae (Pirie & Doyle, 2012). We thus constrained the root of the tree (i.e. Annonaceae + Eupomatiaceae) with a hard upper bound at 112.6 Ma and we set a wide uniform prior from 89 to 112.6 Ma on the crown Annonaceae.

We set the tree prior as the Yule (pure birth) model, and the clock model as the uncorrelated log-normal (UCLD) model (Drummond *et al.*, 2006) with estimation of the clock rate. We ran 4 Markov chain Monte Carlo (MCMC) in parallel, running for 500 million generations each, sampling every 50,000 generations. To test for the sensitivity of the results to the tree prior, we also ran 2 additional analyses with a Birth-Death (BD) tree prior, running for 1 billion generations each, sampling every 50,000 generations. Finally, as the Bayesian phylogenetic inference can take a very long time to run, we also ran 2 additional analyses, running for 500 million generations each, sampling every 50,000 generation, with the Yule prior and the optimized relaxed clock (ORC) model (Douglas *et al.*, 2021) with estimation of the clock rate. The ORC model is similar to the UCLD model, but relies on operators that explore more efficiently the parameter space during the MCMC (Douglas *et al.*, 2021), thus reducing convergence time for the MCMC run. We evaluated the convergence of the MCMC with the Effective Sampling Size (ESS) using Tracer 1.7 (Rambaut *et al.*, 2018). We then used TreeAnnotator to draw the Maximum Clade Credibility (MCC) tree, and to compute the mean node ages, the 95% highest posterior density (HPD) of node ages, and the posterior probability (PP) for each node, after discarding the burn-in. We then pruned the dated MCC tree to keep only the Monodoreae tribe and perform the downstream analyses.

## 2.4. Biogeographic history

To reconstruct the ancestral ranges of the Monodoreae and to identify vicariant events, we relied on the Dispersion-Extinction-Cladogenesis (DEC) model (Ree & Smith, 2008) as implemented in the *BioGeoBEARS* R package (Matzke, 2014). We did not run the DEC+J model (Matzke, 2014), firstly because founder events (or colonization of new ranges via jump dispersal without intermediate widespread dispersion) are very unlikely in Monodoreae due to their low dispersal abilities (see Introduction), and also because DEC+J model inflates the contribution of time-independent cladogenetic events to the likelihood of the model (Ree & Sanmartín, 2018).

First, we assigned each Monodoreae species to a geographical area, corresponding to a TRF region (Figure 52) in which the species are currently distributed (West Africa, Central Africa, East Africa or Madagascar). Most of the species were assigned to a single region (endemic range), but some of them were assigned to a widespread range (e.g. West-Central Africa). We restricted the allowed ranges to West (W), Centre (C), East (E), Madagascar (M), West-Centre (WC), Centre-East (CE), East-Madagascar

(EM) and West-Centre-East (WCE), and constrained the maximum number of areas per ancestral range to three. We also defined an “area adjacency” matrix in which Madagascar is only adjacent to East-Africa, and defined the dispersal probabilities between areas to one, except for the dispersal probability from and to Madagascar that were set to zero, and the dispersal from East to Madagascar that was set to 0.1.

The marginal probabilities of each range were then plotted on the ancestral nodes, and considered the most likely ancestral range as the one having the highest marginal probability. We then considered several biogeographic events to occur at the ancestral nodes. A branch starting at an ancestral node with an endemic range (W, C, E or M) leading to at least one daughter node with a widespread range (WC, CE, EM or WCE) was considered as a range expansion (similar to “dispersal” in BioGeoBEARS, Matzke, 2014). A branch starting at an ancestral node with widespread range (WC, CE, EM or WCE) leading to one daughter node with an endemic range (W, C, E or M) was considered as a range contraction (“sympatry subset” in BioGeoBEARS). Finally, an ancestral node with widespread range (WC, CE, EM or WCE) leading to two daughter nodes with a different endemic range each (W, C, E or M) was considered as a vicariance event (“vicariance narrow” in BioGeoBEARS). The branches (for range expansion or range contraction events) and nodes (for vicariance events) at which each of these events occurred were then plotted.

## 2.5. Diversification analyses

### 2.5.1. Testing for branch-specific and clade-specific diversification rates

To test for diversification rate shifts across the reconstructed tree, we used three different methods designed to estimate the branch-specific or clade-specific speciation and extinction rates. The net diversification rate is defined as speciation minus extinction (later referred as “diversification rate”). The use of several different models allows to cross-check the estimations. Nonetheless, it is worth mentioning that each method differs at several points in the way speciation and extinction rates are estimated.

First, we used the cladogenetic diversification rate shift (ClaDS) model to estimate branch-specific diversification rates. This model is a birth-death model where speciation rates are inherited at a speciation event, but with a shift drawn from a probability distribution parameterized with the parental rates (Maliet *et al.*, 2019). The extinction rate also varies across branches, but the turnover (that is speciation divided by extinction) is constant across the branches. The model is then computed using data augmentation in a MCMC with 3 chains. To assess convergence, the Gelman statistics are then computed every 200 iterations and the chains stop when these statistics drop below 1.05. We used the ClaDS model as implemented in the PANDA Julia package (Maliet & Morlon, 2021).

Second, we used RevBayes to model the estimation of branch-specific diversification (speciation and extinction) rates (BSDR; Höhna *et al.*, 2019). The BSDR model is a birth-death model that breaks time into small intervals and for which speciation and extinction rates can change at each time interval. The new speciation and extinction rates at a new interval are drawn from a lognormal distribution. To ease the computation, the lognormal distribution is approximated using discrete rate categories. We set up the model following the RevBayes tutorial (available at: [https://revbayes.github.io/tutorials/divrate/branch\\_specific.html](https://revbayes.github.io/tutorials/divrate/branch_specific.html)). The parameters were then estimated using two reverse-jumping Markov Chain Monte Carlo (rjMCMC) of 4'000 iterations each, sampling every 200 iterations. We performed several analyses with different sets of priors to check the consistency of the results between the different prior specifications. We set the discrete rate categories prior to 6 or 10, and the initial value of the number of expected rate shift to 1, 4 or 10. The convergence of the rjMCMC was checked with ESS above 200 using Tracer 1.7 (Rambaut *et al.*, 2018).

Third, we used the Bayesian analysis of macroevolutionary mixtures (BAMM) to estimate the variation of speciation and extinction rates through time, but also to detect significant clade-specific shifts in these rates (Rabosky, 2014). BAMM uses reversible-jump Markov Chain Monte Carlo (rjMCMC) to explore the space of parameters and the number of rate shifts. We set prior values using the *BAMMtools* R package (Rabosky *et al.*, 2014), with an expected number of rate shifts equal to 1. We ran four rjMCMC for 10'000'000 generations, sampling every 10'000 generations. We then calculated the ESS of the log-likelihood and the number of shifts using the *coda* R package (Plummer *et al.*, 2020) after discarding 10% of burn-in in order to assess the convergence of the chains (ESS > 200).

Each of these three models account for the sampling fraction in the calculation of the parameters. For ClaDS and BAMM, we set the sampling fraction to be clade specific, with every genus fully sampled (i.e. a sampling fraction of 1) except for *Uvariopsis* and *Lukeya* having a sampling fraction of 0.85 and 0.5, respectively. For the BSDR model, we set the sampling fraction for the whole phylogeny at ca. 0.956.

### 2.5.2. Testing for sudden extinction events

To test whether the evolutionary history of the Monodoreae was impacted by one or several sudden extinction events, we used the compound Poisson process on Mass-Extinction Times model (CoMET; May *et al.*, 2016) as implemented in the *TESS* R package (Höhna *et al.*, 2016). This model estimates the tree-wide speciation and extinction rates, and the probability of several tree-wide events to occur: shifts in speciation rate, shifts in extinction rates, or sudden extinction events, i.e. when several lineages go extinct with a prior probability. The speciation and extinction rates are constant between two events.

The events are estimated under the independent compound Poisson process. Parameters are estimated using a reverse jump MCMC (rjMCMC) over various episodic birth-death models. Model confidence is assessed by computing the Bayes factors (BF) between each model (May *et al.*, 2016). For our CoMET analysis, we set the priors on the number of extinction event and number of expected change to 2. Note that the prior on the number of events does not impact the results as the models are compared using BF (Höhna *et al.*, 2015). We executed 10 different CoMET analyses with prior values on the survival probability to an extinction event ranging every 5% from 5% to 50%. The rjMCMC was run until the ESS for each parameter reaches at least 500. We considered the support for a rate shift or for a ME event as substantially significant for  $2\ln\text{BF}>2$ , as strongly significant for  $2\ln\text{BF}>6$  and as decisive for  $2\ln\text{BF}>10$  (Kass & Raftery, 1995; Höhna *et al.*, 2015).

### 2.5.3. Testing the impact of the paleoenvironment

To test if the diversification of the Monodoreae was associated with changes in past environmental variables (temperature, elevation variation of the African continent, and proportion of C4 plants in the African paleoflora), we fitted several birth-death models that estimate the speciation and extinction rates along a continuous time in a maximum-likelihood framework. We set the models allowing the speciation and extinction rates to vary exponentially with time (time-dependent models) or exponentially with environmental variables (environment-dependent models) (Condamine *et al.*, 2013). We also fitted models with constant or null speciation and extinction rates. The best fitting model was then evaluated using the corrected Akaike Information Criterion (AICc). The complete list of models fitted is given in Table 4.

The environment-dependent models use environmental data spanning the time interval covered by the phylogenetic tree. Missing values were interpolated using the spline interpolation implemented in the *sm.spline* function from the *pspline* R package (Ripley, 2017). Past temperature at global scales was inferred from the widely used oxygen isotope data recovered from benthic foraminifer shells (Zachos *et al.*, 2008; Westerhold *et al.*, 2020). Past elevation change across the African continent was newly computed using the data from Scotese & Wright (2018). First, the geo-referenced occurrences of the Monodoreae species was extracted from the RAINBIO database (Dauby *et al.*, 2016), and the convex hull containing all the point coordinates was computed using the *chull* function from the *grDevices* R package. After conversion to *SpatialPolygonsDataFrame* object with the *sp* R package (Pebesma *et al.*, 2021), the intersection of the envelope with the African coastline was computed using *gIntersection* function in the *rgeos* R package (Bivand *et al.*, 2020). Within this intersected envelope, we computed the geo-coordinates of every unique point with latitude and longitude values at 1 degree precision (e.g. points with coordinates 10°N 10°E, 10°N 11°E, 10°N 12°E, etc.), and extracted the elevation value for

each of these points every 5 Myr (million years) from the present to 30 Ma, using the reconstruct function in the *chronosphere* R package (Kocsis & Raja, 2021). We then computed the mean elevation for each time (red line in Figure 58).

Finally, the proportion of C4 plants in the African paleoflora is taken from the reconstructions made by Pollisar *et al.* (2019) based on the composition of  $^{13}\text{C}$  isotope in plant waxes). To represent the proportion of C4 plants in tropical Africa, we selected the data from the sites 959 (Guinean Gulf), 241 and 235 (East Africa). Given the oldest C4 value at 23.38 Ma is very low compared to the values from 15 to 20 Ma (1.66 vs. 10.69 – 13.05), we replaced it by the lowest value found between 15 and 20 Ma (that is 10.69) in order to avoid distortion of the interpolation toward negative values. Moreover, as 23.38 Ma is younger than the length of our tree (25 Ma), we artificially duplicated the 10.69 a C4 value at 25.1 Ma (Figure SI.26).

## 3. Results

### 3.1. Gene recovery

We recovered all the 369 exons, at least partially, targeted by the Annonaceae bait kit (Couvreur *et al.*, 2019). After filtering and removal of the paralogous loci, the 75/75 dataset contained 318 supercontigs. The 32 supercontigs most clock-like used for the phylogenetic reconstruction and dating had a length comprised between 509 and 4,796 bp. Their best substitution models are listed in the Table SI.9

### 3.2. Phylogeny

Among the six independent MCMC with a Yule tree prior, only one fully converged to a likelihood of -399,351.6164 after discarding 14% of burn-in (ESS for all the parameters above 200 after discarding the burn-in). The other chains were converging toward a slightly higher likelihood value, but the ESS values for several loci, for the prior and for the Yule model was below 150. One of the MCMC with the BD prior also converged to a likelihood of -399,207.1297, after discarding 32% of burn-in. However, it required twice as many iterations as the MCMC with Yule prior to converge and was not reached sufficiently early for achieving the subsequent analyses in a realistic time frame, so we relied on the MCMC with Yule prior. Note that age differences between the Yule and BD priors are small, ranging between 1 and 2 million years.

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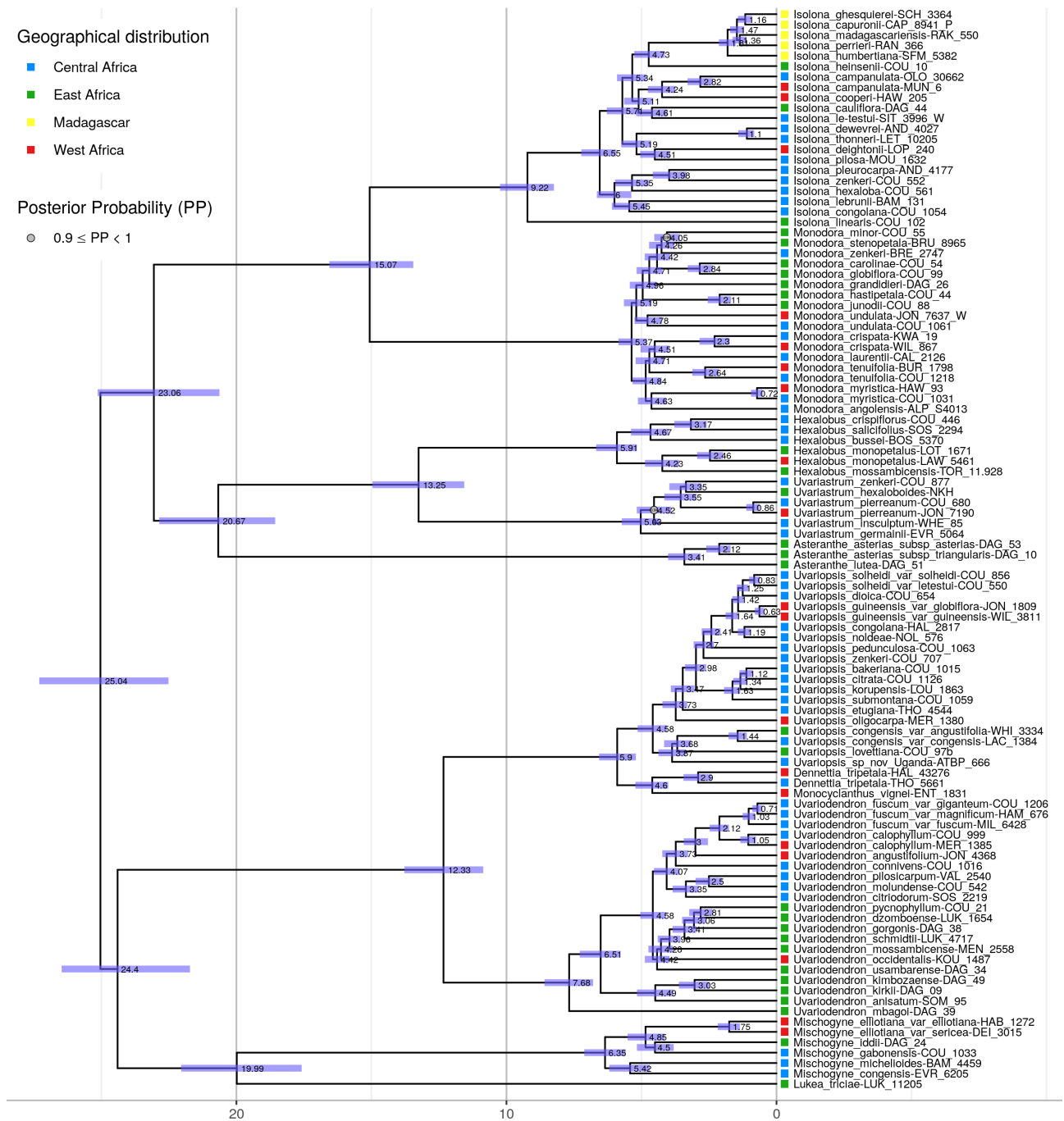


Figure 53: Phylogenetic tree of the Monodoreae specimens, as pruned from the Maximum Credibility Clade tree estimated from 8,601 posterior tree inferred on 32 nuclear loci with uncorrelated molecular clock and fossil calibration in BEAST. The value at the node indicates the mean age from the posterior probability density, and the blue bar indicates the 95% highest posterior density interval of the age. All nodes received a posterior probability of 1 except for those indicated by a grey circle. The colour square at the tip indicates the geographic origin of the specimen. Colours follow Figure 52.



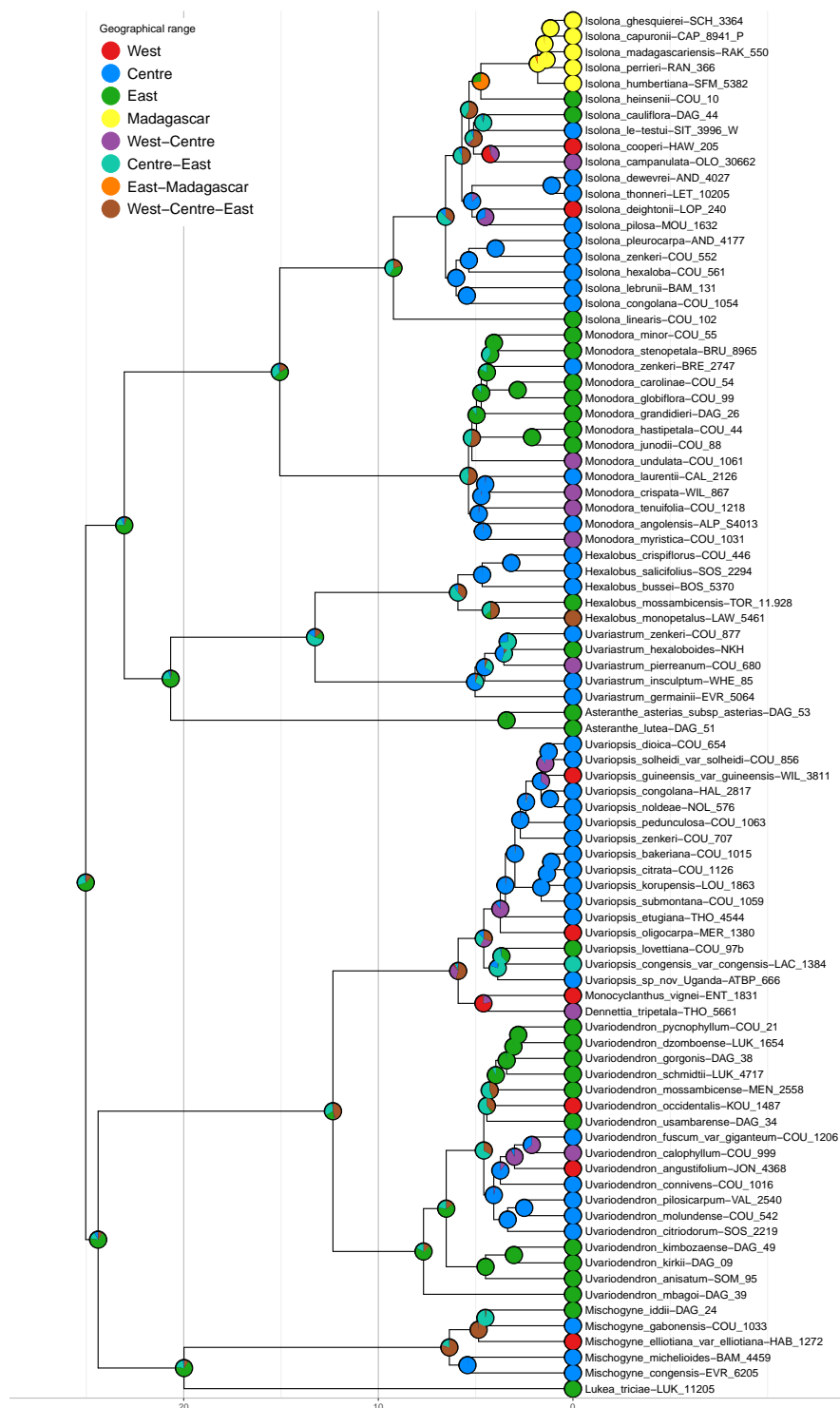


Figure 54: Phylogenetic tree of the Monodoreae species, as pruned from the Maximum Credibility Clade tree estimated from 8,601 posterior tree inferred on 32 nuclear loci with uncorrelated molecular clock and fossil calibration in BEAST, with present day (next to names) and ancestral ranges (pies at the internal nodes) reconstructed using the dispersal-extinction-cladogenesis (DEC) analysis implemented in BioGeoBEARS. The relative proportions of the colours slices in the pies are proportional to the likelihood of each state.

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After discarding the burn-in (14%), the MCC tree was estimated from 8,601 posterior trees. All the nodes in the MCC tree show strong support with all the nodes having a posterior probability (PP) of 1, except for two nodes having a PP > 0.9 (Figure 53). All the genera were retrieved monophyletic. The relationship between the species follow the previous results we obtained with the gene trees approach and the concatenation approach with 315 loci, except for some nodes (mainly in *Isolona* and *Monodora*) for which gene trees conflict was inferred (see Chapter 3). Reticulate processes of evolution might occur at these nodes (see Discussion in Chapter 3), and the selection of only 32 loci for the molecular dating might increase the bias towards one or the other topology.

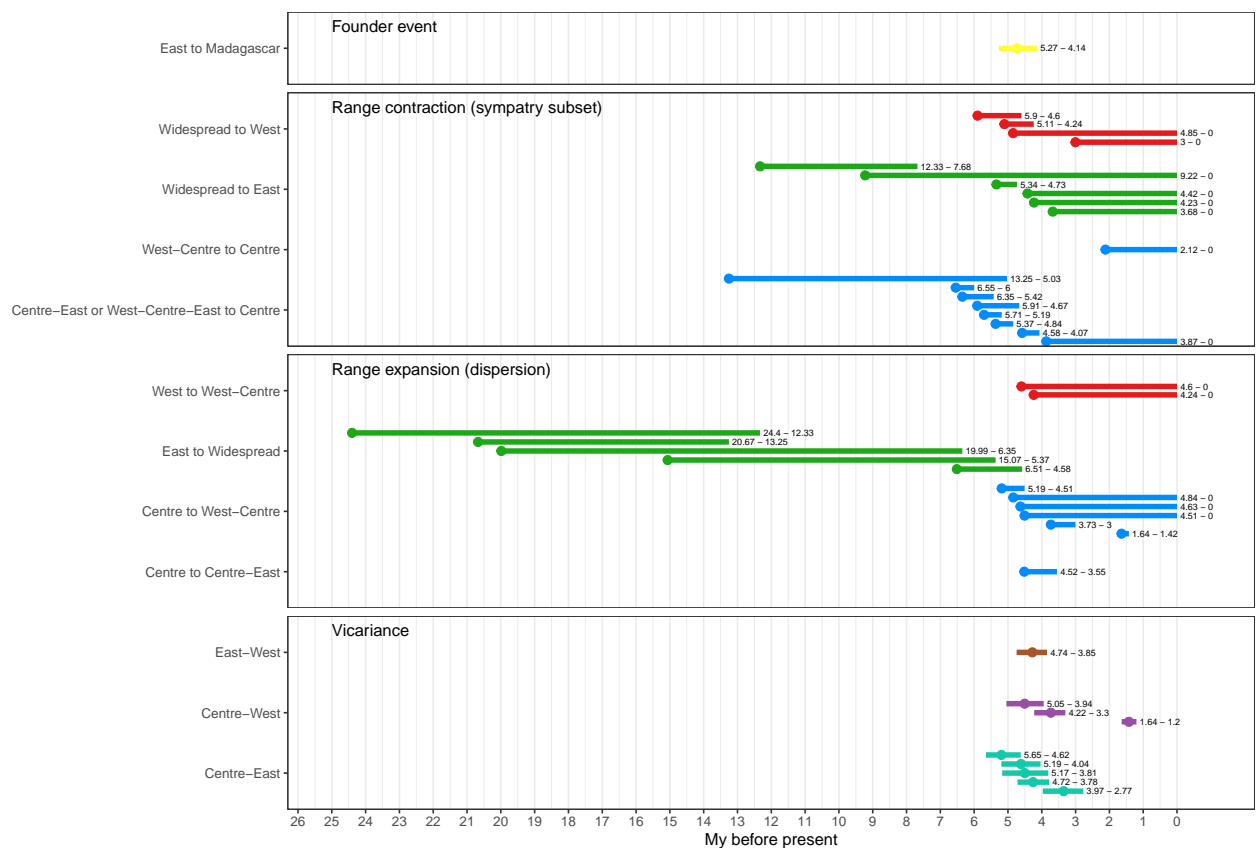


Figure 55: Chronological time frame of the biogeographical events as interpreted from the DEC model. The founder event and vicariance events occurred at nodes of the tree in Figure 54: the dot and horizontal bar represent the mean age and 95% highest posterior density interval of the age of the node, respectively. Range contraction (RC) and range expansion (RE) events occurred along branches connecting two nodes: the dot represents the mean age of the widespread (RC) or endemic (RE) ancestral node, and the horizontal bar extends toward the mean age of the endemic (RC) or widespread (RE) daughter node. Colours follow the dispersal–extinction–cladogenesis ranges (see Figure 54) and have different meaning depending on the event: for founder event, it is the colour of the range after the founder event; range contraction, it is the colour of the endemic range after range contraction; range expansion, it is the colour of the endemic range before range expansion; vicariance, it is the colour of the widespread range before the vicariance event. The labels on the y-axis indicates the direction of the event (e.g. range expansion from East to Widespread). ‘Widespread’ includes all the widespread ranges (West-Centre, Centre-East or West-Centre-East). See Material & Methods for the details on the events.

The mean age of the divergence between the *Eupomatia* (outgroup) and the Annonaceae (i.e. the crown node of Magnoliineae) is estimated in the Early Cretaceous at 110.68 Ma (95% HPD: 105.53 – 112.60 Ma). The crown node of Annonaceae is estimated in the Late Cretaceous at 89.87 Ma (95% HPD: 89.00 – 92.55 Ma) (Figure SI.10). Although the distribution probabilities of the calibration points set on these nodes were broad uniforms, the age estimates for the crown node of Monodoreae and the crown node of Annonaceae have respectively converged to the lower and upper bounds of the prior distribution. This indicates that the data contain enough information to overcome the lack of precise information of such wide priors. The age of the Monodoreae tribe is estimated in the late Oligocene at 25.07 Ma (95% HPD: 22.52 – 27.30 Ma) (Figure 53).

### 3.3. Biogeographical events

The DEC analysis estimated the rate of ‘dispersal’ (range expansion) to 0.039 events/lineage/Myr and the rate of ‘extinction’ (range contraction) to 0.008. East Africa was identified as the most likely geographic origin of the Monodoreae (Figure 54), as well as for most of the ancestral nodes until ca. 15 Ma. The ancestral range of *Hexalobus*, *Isolona*, *Mischogyne*, *Monodora*, and *Uvariopsis* was likely widespread (Centre-East or West-Centre-East), whereas the ancestral range of *Asteranthe*, *Lukea* and *Uvariadendron*, and was likely East Africa, while the ancestral range of *Uvariastrum* was likely Central Africa. Between the origin and ca. 13.5 Ma, the range of the Monodoreae expanded, and from ca. 13.5 Ma to ca. 6.5 Ma the range of some taxa contracted while the range of some other taxa possibly expanded (Figure 55). From the late Miocene (ca. 6.5 Ma) the Monodoreae underwent several synchronous range expansion events, range contraction events and vicariance events. Within the Monodoreae, the only clade in Madagascar is the genus *Isolona*. The divergence between the East African *Isolona heinsenii* and Malagasy *Isolona* is dated between 5.27 and 4.14 Ma, and led to a small radiation with five known Malagasy species (Figure 54). The DEC model retrieved this divergence as a vicariance event (Figure 54). However, as Madagascar was already separated from the continent, it seems unlikely that the ancestor (node 153, Figure SI.10) was distributed in both East Africa and Madagascar. We thus interpret this event as a founder event (Figure 55).

### 3.4. Diversification analyses

#### 3.4.1. Branch-specific and clade-specific diversification rates

The three methods found a variation in the speciation and extinction rates across the phylogenetic tree. ClADS indicated low diversification rates in the species-poor (5 species or less) genera *Asteranthe*, *Hexalobus*, *Lukea*, *Mischogyne* and *Uvariastrum*, and relatively high speciation rate in the species-rich

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genus *Uvariopsis* (Figure 56). RevBayes estimated higher speciation rates around the crown of the genera *Isolona*, *Monodora*, *Uvariodendron* and *Uvariopsis* (Figure SI.12a). The variation of the speciation rate estimated by BAMM was very low, from 0.17 event/lineage/Myr around the root of the phylogeny to 0.2 event/lineage/Myr in the genus *Uvariopsis* (Figure SI.13a). These three methods estimated very low extinction rates (less than 0.03 event/lineage/Myr; Figure SI.11, Figure SI.12b, Figure SI.13b). The three methods have also in common higher diversification rate in the genus *Uvariopsis*. Although the rates were detected to vary in the above models, BAMM did not detect any significant diversification rate shifts across the phylogeny (Figure SI.14, Figure SI.15).

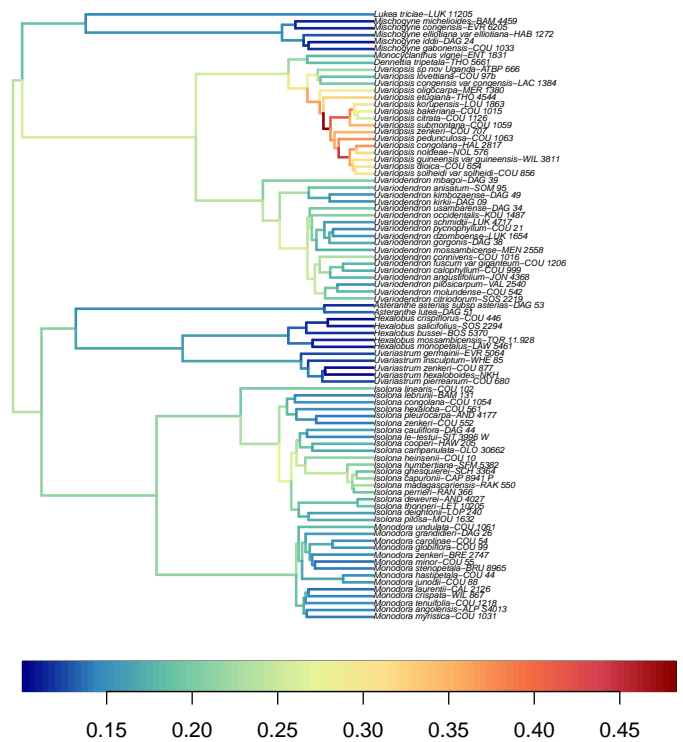


Figure 56: Species-specific speciation rates through time of Monodoreae estimated using ClADS.

### 3.4.2. Tree-wide diversification rates

Even when using different priors on the survival probability of a sudden extinction event, the different CoMET analyses return similar results (Figure SI.16 – Figure SI.25). CoMET found the speciation rate to vary through time: speciation is rather constant around ca. 0.2 event/lineage/Myr until ca. 7 Ma, then rises around 3.5 event/lineage/Myr between 6.5 and 4 Ma, and finally drops (Figure 57), which corresponds to the detected shifts (see below). The extinction rate is found rather low and constant (Figure SI.16 – Figure SI.25) over time. CoMET detected speciation rate shifts with substantial ( $2\ln\text{BF} > 2$ ) to strong ( $2\ln\text{BF} > 6$ ) support showing a shift towards a higher speciation rate between 6.5 and 7 Ma with substantial support, followed by a shift towards lower speciation rate between 2.5 and 4.25 Ma with substantial support, and a shift towards lower speciation rate around 1 Ma with strong support (Figure 57). CoMET also identified several extinction events with substantial support in the late Miocene (between 10 and 6.5 Ma), with a strong support between 6 and 6.25 Ma when the survival probability was less than 10% (Figure 57).

### 3.4.3. Paleoenvironmental birth-death models

The environmental birth-death model with the lowest AICc score is the BDPercC4 model (4 parameters), which is a model with speciation and extinction rates varying exponentially with the proportion of C4 plants through time (Table 4). However, the estimated parameters for this model are unrealistic as the diversification rate retrieved is negative (i.e. extinction rate higher than speciation rate) at the beginning of the clade's history, which is biologically implausible. The second best model is the BElev model (2 parameters), which is a model with speciation rate varying with mean elevation in tropical Africa through time and no extinction (Table 4, Figure 58). Note that the difference of AICc between BElev and the BElevDConst (speciation varying with elevation through time and constant extinction) is low, but these two models are actually very similar as the constant extinction rate estimated for the BElevDConst is 0.006 events/lineage/Myr (Table 4).

Table 4. Results of the birth-death models applied to the Monodoreae with RPANDA. When the rates are not constant, they vary exponentially with time or with the environmental variables (temperature = Temp, or elevation = Elev, or percentage of C4 plants = PercC4). logL, log-likelihood;  $\lambda_0$ , speciation rate;  $\alpha$ , rate of variation of the speciation according to the paleo-environmental variable;  $\mu_0$ , extinction rate;  $\beta$ , rate of variation of the extinction according to the paleo-environmental variable.

Model	Speciation varies with:	Extinction varies with:	logL	AICc	$\lambda_0$	$\alpha$	$\mu_0$	$\beta$	$\Delta AICc$
BDPercC4	C4 proportion	C4 proportion	-224.08	456.63	1.6829	-0.0439	-2.1736	-0.0656	-12.66
<b>BElev</b>	<b>elevation</b>	<b>no extinction</b>	<b>-232.57</b>	<b>469.29</b>	<b>0.0017</b>	<b>0.0066</b>	<b>NA</b>	<b>NA</b>	<b>0</b>
BElevDConst	elevation	constant	-232.63	471.55	0.0029	0.0059	-0.0005	NA	2.26
BTemp	temperature	no extinction	-234.17	472.48	0.1255	0.0829	NA	NA	3.19
BConst	constant	no extinction	-235.75	473.55	0.1797	NA	NA	NA	4.26
BPercC4	C4 proportion	no extinction	-234.83	473.81	0.2396	-0.0072	NA	NA	4.52
BConstDPercC4	constant	C4 proportion	-234.06	474.41	0.1963	NA	0.3638	-0.0958	5.12
BTempDConst	temperature	constant	-234.17	474.62	0.1254	0.083	0	NA	5.33
BTime	time	no extinction	-235.67	475.49	0.1865	-0.0072	NA	NA	6.2
BDConst	constant	constant	-235.75	475.63	0.1796	NA	0	NA	6.34
BPercC4DConst	C4 proportion	constant	-234.83	475.96	0.2396	-0.0072	0	NA	6.67
BDTemp	temperature	temperature	-234.17	476.82	0.1255	0.0829	0	0.0156	7.53
BTimeDConst	time	constant	-235.67	477.63	0.1864	-0.0071	0	NA	8.34
BConstDTime	constant	time	-235.75	477.78	0.1797	NA	0	-0.0499	8.49
BConstDElev	constant	elevation	-235.75	477.79	0.1797	NA	0.0809	-0.0781	8.5
BConstDTemp	constant	temperature	-235.75	477.79	0.1796	NA	0	-0.0016	8.5
BDTime	time	time	-235.67	479.83	0.1865	-0.0072	0	0.0259	10.54
BDElev	elevation	elevation	-236.44	481.36	0.2674	-0.0005	0	0.0022	12.07

## 4. Discussion

### 4.1. Origin and biogeographic history of the Monodoreae

Monodoreae likely originated in what are now the East African rain forests in the late Oligocene (ca. 25 Ma) (Figure 54), which contrasts with other TRF groups likely originating in Central Africa (Brée *et al.*, 2020; Aduse-Poku *et al.*, 2021). At that time, TRF were likely to occur in East Africa, such as in northern Ethiopia (Jacobs *et al.*, 2005, 2010; Pan, 2010), and in northern Kenya as mosaics of TRF and semi-deciduous forests (Vincens *et al.*, 2006).

The Monodoreae then expanded toward Central Africa during the early to middle Miocene (ca. 24 – 13.5 Ma) (Figure 54, Figure 55), suggesting a connection between the East African TRF and the Central-African TRF as a pan-African rain forest. This coincides with the warmer climate of the MMCO (ca. 17–14.7 Ma) during which the TRF was suggested to occur from coast to coast (Morley, 2000, 2011). It is during the early Miocene (ca. 20 – 21 Ma) that the genera *Asteranthe* and *Lukea* originated (Figure 54). These genera are species poor (two species each) and are endemic to East African coastal and mountains forests (Verdcourt, 1971; Vollesen, 1980; Cheek *et al.*, 2021). Such long-term persistence of clades originating in the Oligocene-Miocene has also been documented in plants and animals (Tolley *et al.*, 2011; Dimitrov *et al.*, 2012; Loader *et al.*, 2014), and is associated with climate stability of the region in the East African mountains region (Lovett *et al.*, 2005). The divergence between *Asteranthe* and the clade *Hexalobus* – *Uvariastrum* was interpreted as a vicariance event ca. 16.8 Ma by Couvreur *et al.* (2008). Here, with a full taxon sampling of these genera, we rather estimate a range expansion from the East to East-Centre ca. 20.7 Ma with a long-term persistence of the genus *Asteranthe* in the East.

Just after the MMCO, during the MMCT (ca. 15 – 13 Ma), the global temperatures and  $p\text{CO}_2$  dropped (Westerhold *et al.*, 2020). The MMCT is known to have affected tropical African ecosystems leading to the expansion of open grasslands and contraction of TRF (Jacobs, 2004; Plana, 2004; Couvreur *et al.*, 2021). Previous molecular studies detected vicariance events in TRF restricted clades before the MMCT, supporting the contraction of the TRF during the MMCT (Couvreur *et al.*, 2008; Dimitrov *et al.*, 2012; Menegon *et al.*, 2014; Brée *et al.*, 2020). However, in Monodoreae, we didn't find evidence of vicariance before 6 Ma (Figure 55). Rather, we find evidence of range contraction from ca. 13.5 to ca. 6.5 Ma (Figure 55), leading to the origins of *Uvariadendron* in East Africa, *Uvariastrum* in Central Africa and corresponding to the divergence between the East African species *Isolona linearis* and the rest of *Isolona* (Figure 54). Even if these clades evolved in isolation, and would support for a contraction of the TRF at that time, their sister clades are inferred as widespread (i.e. as spanning both East

and Central Africa, Figure 54). Moreover, possible range expansions also continued between ca. 13.5 and ca. 6.5 Ma (Figure 55). This suggests that the East and Central African TRF were actually more connected than previously thought after the MMCT. Gallery forests might have occurred maintaining a connection between the forest patches. Also, as the Monodoreae experienced sudden extinction in the late Miocene (see below), we miss the ancestral ranges of the extinct (and unknown) species, which may overshadow the signal inferred by DEC between two nodes separated by a long branch.

From the late Miocene and during the Pliocene (6.5 – 2 Ma), the biogeographic history of the Monodoreae is more complex. Most of the extant Monodoreae species diverged during this time interval (Figure 54), and we found various simultaneous range expansions, contractions and vicariance events (Figure 55). This suggests that if TRF fragmentation events occurred, it was not strong enough to affect the whole tribe. Instead, the TRF blocks were likely connected during the early Pliocene, as previously suggested based on paleo-vegetation record (Morley, 2000), either as a continuous forest block (Fer *et al.*, 2017) or via forested corridors between East and Centre-West Africa (Joordens *et al.*, 2019). Thus, the late Miocene and Pliocene divergences in the Monodoreae might be explained by species-specific or region-specific mechanisms.

During the late Miocene, tropical Africa was likely dominated by open habitats (Jacobs, 2004; Bonnefille, 2010). In Monodoreae, *Hexalobus monopetalus* and *H. mossambicensis* are more dry-adapted than the other *Hexalobus* species distributed in Central Africa (Botermans *et al.*, 2011), and *H. monopetalus* has the typical savanna distribution all around the Guineo-Congolian region (Botermans *et al.*, 2011) like other savanna species (Lehmann *et al.*, 2011; Gonçalves *et al.*, 2021). This indicates that a habitat shift from forested habitat to a drier habitat occurred during the late Miocene (ca. 6.68 – 5.17 Ma) in *Hexalobus*. This single habitat shift to adapt to drier condition in Monodoreae contrasts with other plant groups for which several shifts in habitat has been documented during the late Miocene, such as in the African Melastomataceae (Veranso-Libalah *et al.*, 2018), Cucurbitaceae (Holstein & Renner, 2011), Fabaceae (Bouchenak-Khelladi *et al.*, 2010; Tosso *et al.*, 2018), and Sapotaceae (Armstrong *et al.*, 2014). This supports previous results showing that geographical speciation is stronger than ecological speciation in *Isolona* and *Monodora* (Couvreur *et al.*, 2011b).

Several Monodoreae species span both West and Centre TRF blocks (Figure 54). The Dahomey Gap (DG) mediates the connection between the West African and the Central African blocks. The DG was suggested to be dominated by open vegetation during most of the late Quaternary, from ca. 1.05 Ma (Demenou *et al.*, 2018), and became forested during the mid-Holocene (ca. 8000 – 4000 years before present), before being dominated again by open vegetation until the present due to climatic variations (Salzmann & Hoelzmann, 2005). These vegetation changes show signatures in the intraspecific genetic

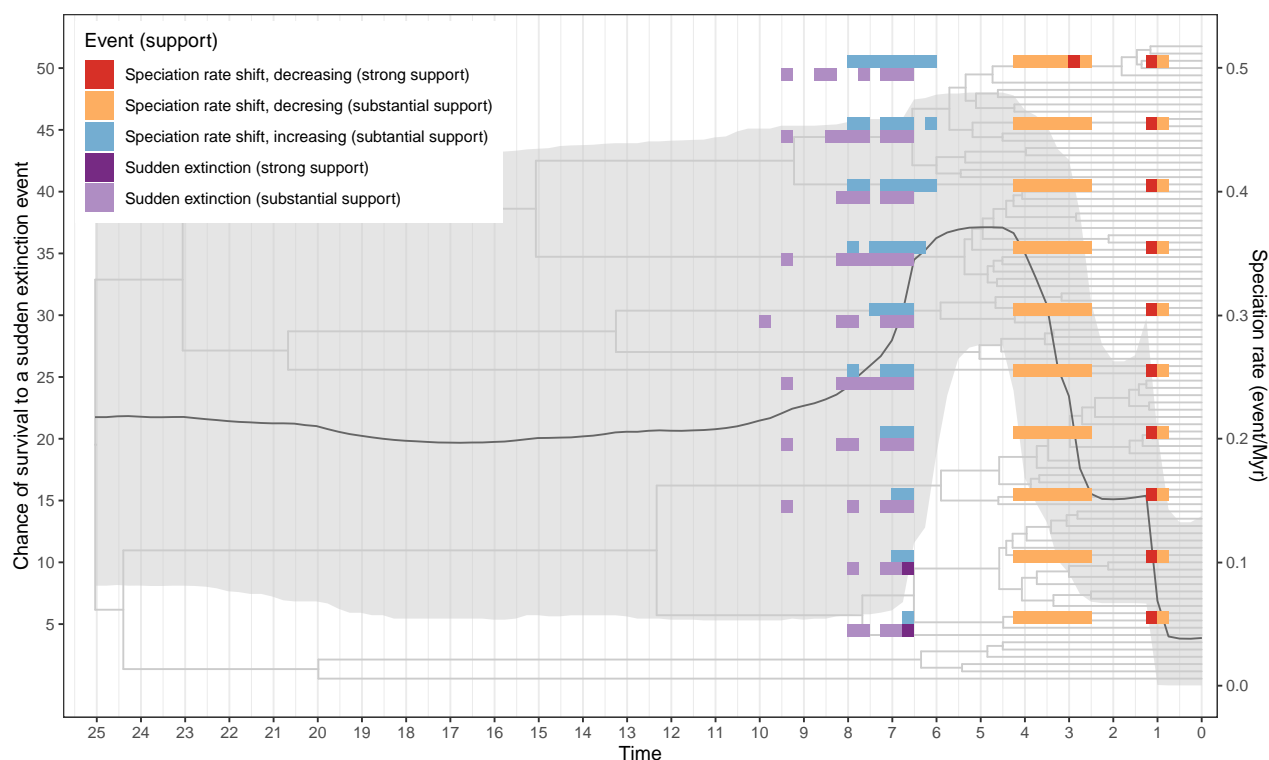


Figure 57: Summary of speciation rate shifts and sudden extinction (ME) events at each time slice in the CoMET analysis, with the priors on the chance of survival to a sudden events (ME) ranging from 5% to 50% (Figure SI.16 – Figure SI.25). Strong support indicates  $2\ln\text{BF} > 6$  in, substantial support indicates  $2\ln\text{BF} > 2$ . Black line represents the speciation rate and grey shading its 95% credibility interval, both averaged from all the CoMET analyses (Figure SI.16 – Figure SI.25).

structure of forest trees species (Duminil *et al.*, 2015; Demenou *et al.*, 2018, 2020; Lompo *et al.*, 2018). We found intraspecific divergence between the Western population and the Central population of *Monodora myristica*, *Uvariastrum pierreanum*, and *Uvariadendron calophyllum* to occur during the late Quaternary (i.e. after 1.05 Ma) (Figure 53), but found no interspecific vicariance event between West and Centre species during this period (Figure 54), suggesting the DG acted as a barrier for genetic differentiation, but was not strong enough to differentiate the Western and Central populations into different species. We also found both inter- and intraspecific vicariance and range expansion events between the West and Central TRF blocks between 6.57 and 1.20 Ma (Figure 53, Figure 54, Figure 55). This suggests that the DG acted as a biogeographic barrier before its known aridification at 1.05 Ma. In particular, the climatic variations in the Pliocene and the early Pleistocene (mainly glacial and interglacial cycles, (mainly glacial and interglacial cycles; Couvreur *et al.*, 2021) triggered strong isolation of some populations, leading to West and Central African vicariant species (e.g. leading to *Isolona deightonii*, *Uvariopsis guineensis*, or *Uvariopsis oligocarpa*), but also seem to allow the re-connection of the populations of some species both distributed in West and Central Africa (e.g. *Monodora undulata*, *Dennettia tripetala*). A similar pattern with both inter- and intraspecific divergence between West and Centre



forest blocks has been observed during the Pliocene and Pleistocene in the bird genera *Bleda* and *Criniger* (Huntley & Voelker, 2016; Huntley *et al.*, 2018).

Madagascar broke apart from Africa in the Early Cretaceous (more than 100 Ma; Kocsis & Scotese, 2021) and the shortest distance today separating the African coast to Madagascar is ca. 400 km (Rabinowitz & Woods, 2006). Similar recent splits between Malagasy clades and continental relatives have been inferred in animals and plants (Renner, 2004; Rabinowitz & Woods, 2006; Yoder & Nowak, 2006; Tolley *et al.*, 2013), including other Annonaceae (Thomas *et al.*, 2015; Chen *et al.*, 2019), and have generally been explained by long-distance dispersal (LDD). Small vertebrates and invertebrates are hypothesized to have drifted on vegetation rafts from continental African rivers with the help of eastwards oceanic currents (Rabinowitz & Woods, 2006; Ali & Huber, 2010). LDD from the continent to Madagascar is likely in wind-dispersed plant species, and is also documented in bird-dispersed plants species (Renner, 2004; Yao *et al.*, 2016). The genus *Isolona* is the only Monodoreae taxon that reached Madagascar. It happened during the early Pliocene between 5.27 and 4.14 Ma followed by a small radiation of five species (Figure 54, Figure 55). The fruits of *Isolona* are large syncarps supposedly eaten by large to medium-bodied primates (Couvreur, 2009), and terrestrial long distance dispersal is considered unlikely in this genus (Couvreur *et al.*, 2008). To explain the presence of *Isolona* in Madagascar, we speculate that some propagules (fruits, seeds, or seedlings) of *Isolona* derived from mainland rivers to the ocean and reached Madagascar by drifting via eastward oceanic current. This kind of dispersal by drifting to Madagascar has already been suggested in the Annonaceae genus *Uvaria*, for which the African species are also unlikely to disperse across the ocean (Zhou *et al.*, 2012). It is also possible that the propagules reached Madagascar via intermediate islands such as the Comoros archipelago. However, land bridges across the Mozambique Channel and crossing when sea level is low seem unlikely because the bathymetry in the channel is deep, and even a drop of 200 m would only reduce the distance between the continent and Madagascar to 360 km (Rabinowitz & Woods, 2006). The resistance of Annonaceae growth to salinity has been tested in *Cananga odorata* and *Annona muricata*, which show no survival of *Cananga* seedling and a survival of ca. one third of *Annona* seedlings (De Sedas *et al.*, 2019). Although the resistance of *Isolona* and the survival of seeds in salted water remain unknown, it is possible that some propagules survived during the crossing.

## 4.2. Diversification of the Monodoreae

As indicated above, the late Miocene of tropical Africa was marked by the expansion of open grasslands (Jacobs, 2004; Uno *et al.*, 2016). The CoMET analysis detects a possible sudden extinction event in Monodoreae between 10 and 6.5 Ma (Figure 57, Figure SI.16 – Figure SI.25). Similarly, Brée *et al.*

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(2020) found substantial support in favor of a sudden extinction between 8 and 6.5 Ma in the Piptostigmatae, another TRF African Annonaceae tribe, although they do not consider it significant (see Figure 4 in Brée *et al.*, 2020). This supports growing evidence that the open grasslands in the late Miocene occurred at the expense of the TRF, which might have experienced drastic and sudden extinction due to the reduction of areas having the suitable warm and wet climate (Morley, 2000, 2011). This pattern has also been retrieved in the butterfly genus *Bicyclus* for which the forest clade underwent a drop in diversification rate from ca. 15 Ma (Aduse-Poku *et al.*, 2021). Interestingly, the sudden extinction is synchronous with a potential speciation shift leading to higher speciation rate between 6.5

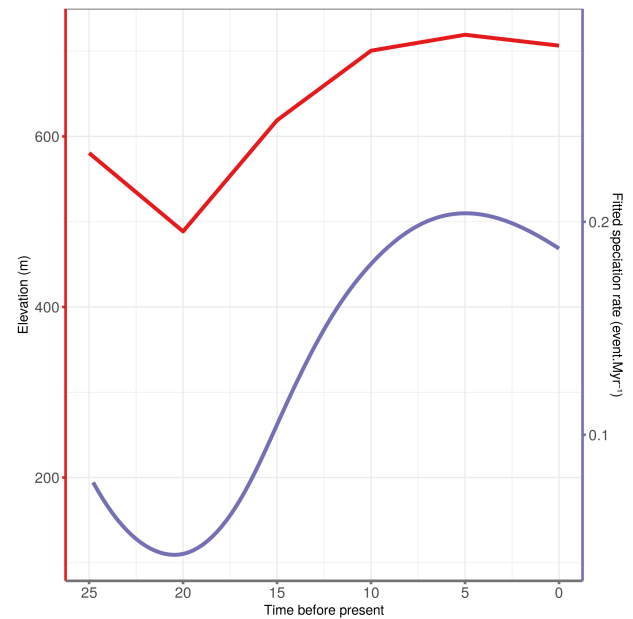


Figure 58: Clade-independent speciation rate through time of Monodoreae, as estimated in RPANDA with the speciation rate varying exponentially with the mean elevation of tropical Africa through time (BElev model, Table 4).

and 4.25 Ma (Figure 57, Figure SI.16 – Figure SI.25), suggesting that climatic and geological events in the late Miocene did not only trigger extinction but also stimulated the differentiation of the populations, via the fragmentation of the forests. This period of higher diversification rate (Figure 57) also overlaps with the early Pliocene (ca. 5.3 – 3.6 Ma), a period of re-expansion of the TRF due to warmer and moister climate (Morley, 2000; Plana, 2004). Early Pliocene diversification has been retrieved in other TRF clades (Plana, 2004; Brée *et al.*, 2020; Aduse-Poku *et al.*, 2021) and can be attributed to the expansion of TRF likely providing opportunities to speciate in sympatry via the colonization of new localities such as mountains (e.g. Cameroon volcanic line, East Arc Mountains). Moreover, the best fitting environment-dependent diversification model estimates that speciation varied with elevation through time (Table 4), and also retrieves a higher speciation rate around 5 Ma (Figure 58). Geological activities such as the uplift of East Africa are well documented during this period (Griffiths, 1993; Sepulchre *et al.*, 2006; Macgregor, 2015; Couvreur *et al.*, 2021). Our results suggest that the uplift of East Africa would have contributed to promote speciation in Monodoreae, supporting a model where the topographic heterogeneity and climatic gradients in mountains enhance the opportunities of isolating populations (Hughes & Eastwood, 2006; Schwery *et al.*, 2014). However, Monodoreae species that diverged in this period are not all restricted to East Africa, some are also restricted to Central Africa or West Africa (Figure 54). East African uplift itself participated to aridification via changes in atmospheric circulation (Sepulchre *et al.*, 2006). Thus, the impact of East African uplift on the diversi-

fication was likely not only directly linked to the emergence of new mountain environments, but was also probably indirect, via the aridification.

### 4.3. *Uvariopsis*, an outlier in the diversification of Monodoreae?

Previous studies have found that the Annonaceae, and in particular the Annonoideae subfamily (to which belongs the Monodoreae), showed no significant diversification shifts (Couvreur *et al.*, 2011a; Erkens *et al.*, 2012; Massoni *et al.*, 2015a), which is in line with the BAMM inference that did not detect significant diversification rate shifts in the phylogeny (Figure SI.14, Figure SI.15). However, although no significant rate shift was detected, we found the diversification rates in the Monodoreae tribe are not homogeneous across the genera (Figure 56, Figure SI.12, Figure SI.13). In particular, all analyses found higher diversification rates in the genus *Uvariopsis* than in other genera. With 21 species (18 described and 3 undescribed, see Chapter 4), *Uvariopsis* is the most species-rich genus of the tribe. Using the methods of moments (Magallon & Sanderson, 2001), that is using species richness and origin, *Uvariopsis* has been found as one of the fastest diversifying Annonaceae genera under a no extinction hypothesis (Couvreur *et al.*, 2011a). Indeed, all extant species diverged between ca. 4.5 and 1 Ma, whereas most of the species in the other rich genera (*Isolona* (20 species), *Monodora* (14 species), *Uvariodendron* (18 species)) diverged between 10 and 4 Ma (Figure 53). *Uvariopsis* has several features that differentiates it from the other Monodoreae: all but one species are monoecious, i.e. have separated male (staminate) and female (pistillate) flowers on the same individual (except *U. bisexualis*, not included in this study) and they all present a reduction of the perianth parts (2 sepals and 3 or 4 petals) when compared to the typical Annonaceae flower (3 sepals and 6 petals) (Chapter 3). Such association between monoecy and reduction of perianth parts has been suggested to be an optimization of resources allocation to sex (Jong *et al.*, 2008). Monoecy could be evolutionary advantageous in order to avoid self-pollination (Pang *et al.*, 2013), but the flowers of most Annonaceae species generally avoid self-pollination with temporal variation of the stamens and carpels maturation (Pang & Saunders, 2014). Another evolutionary advantage of monoecy is likely conferred by the flexibility in resource allocation to male and female functions (Bertin, 1993). However, recent analyses found unisexual flowers associated with lower diversification rates than in bisexual flowers and androdioecous flowers at the population level (Xue *et al.*, 2020). Three species of *Uvariopsis* are pollinated by Diptera (Gottsberger *et al.*, 2011; Mertens *et al.*, 2018), which is quite uncommon in Annonaceae (Saunders, 2012). Shifts in pollination syndromes have been suggested to be responsible for shifts in diversification (Valente *et al.*, 2012; Breitkopf *et al.*, 2015; Lagomarsino *et al.*, 2016; Serrano-Serrano *et al.*, 2017). One would be tempted to relate the peculiarities of *Uvariopsis* (monoecy and Diptera pollination) to its higher diversification rates relatively to the other Monodoreae genera. However given these characters

appeared only once in Monodoreae, testing for their influence on diversification rates (e.g. with SSE models; Maddison *et al.*, 2007) could provide spurious inferences (Maddison & FitzJohn, 2015).

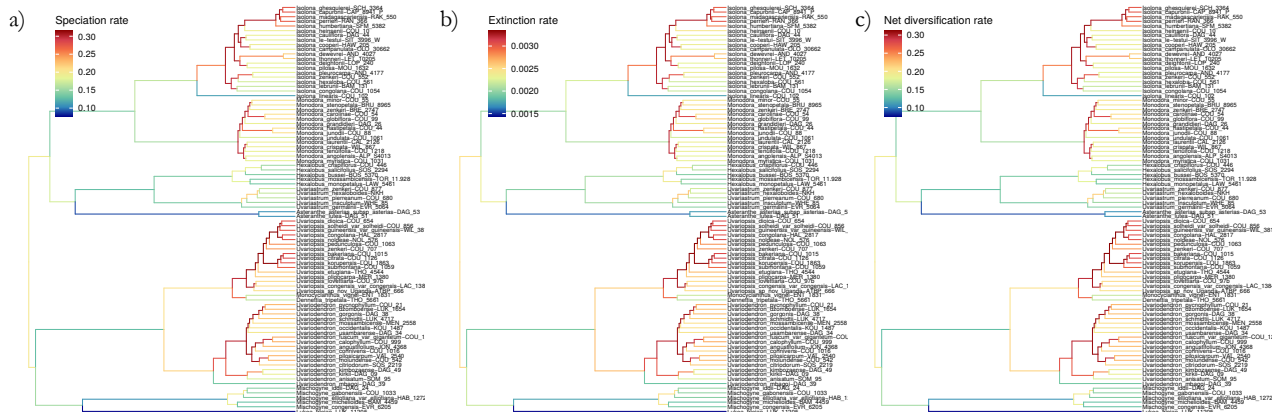
#### 4.4. Conclusion

Our study brings new insights into the evolution of TRF in Africa during the Cenozoic. Focusing on Monodoreae, we found that this clade originated in East African TRF during the late Oligocene (ca. 25 Ma), and expanded toward Central-Africa during the early to middle Miocene, supporting the existence of a pan-African rain forest until ca. 13.5 Ma. There is no evidence for clear discrete and synchronous vicariance events between forest blocks during the middle Miocene, but instead range contractions that led to speciation and supporting the hypothesis of TRF fragmentation due to aridification in Africa. However, we also inferred clades spanning several forest blocks during the middle Miocene, suggesting that the TRF blocks were more connected than previously thought. The Monodoreae likely experienced a sudden extinction during the late Miocene, supporting the drastic reduction of the TRF linked to aridification. This is immediately followed by high speciation rates, suggesting that both the fragmentation and the following re-connection of the TRF in the early Pliocene stimulated diversification. Such a high diversification was likely associated with the increasing African paleo-elevation during the late Miocene and Pliocene, supporting the idea that the uplift of East Africa was a factor that promoted diversification.

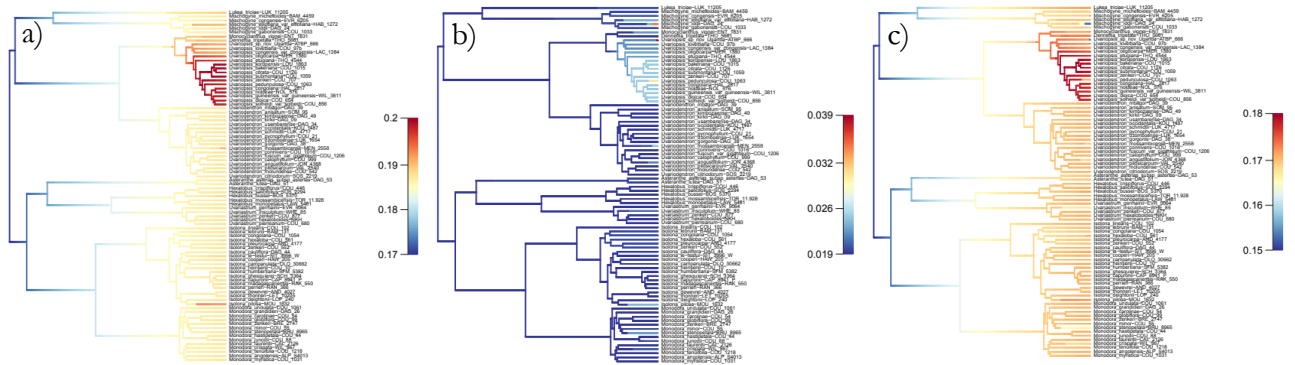


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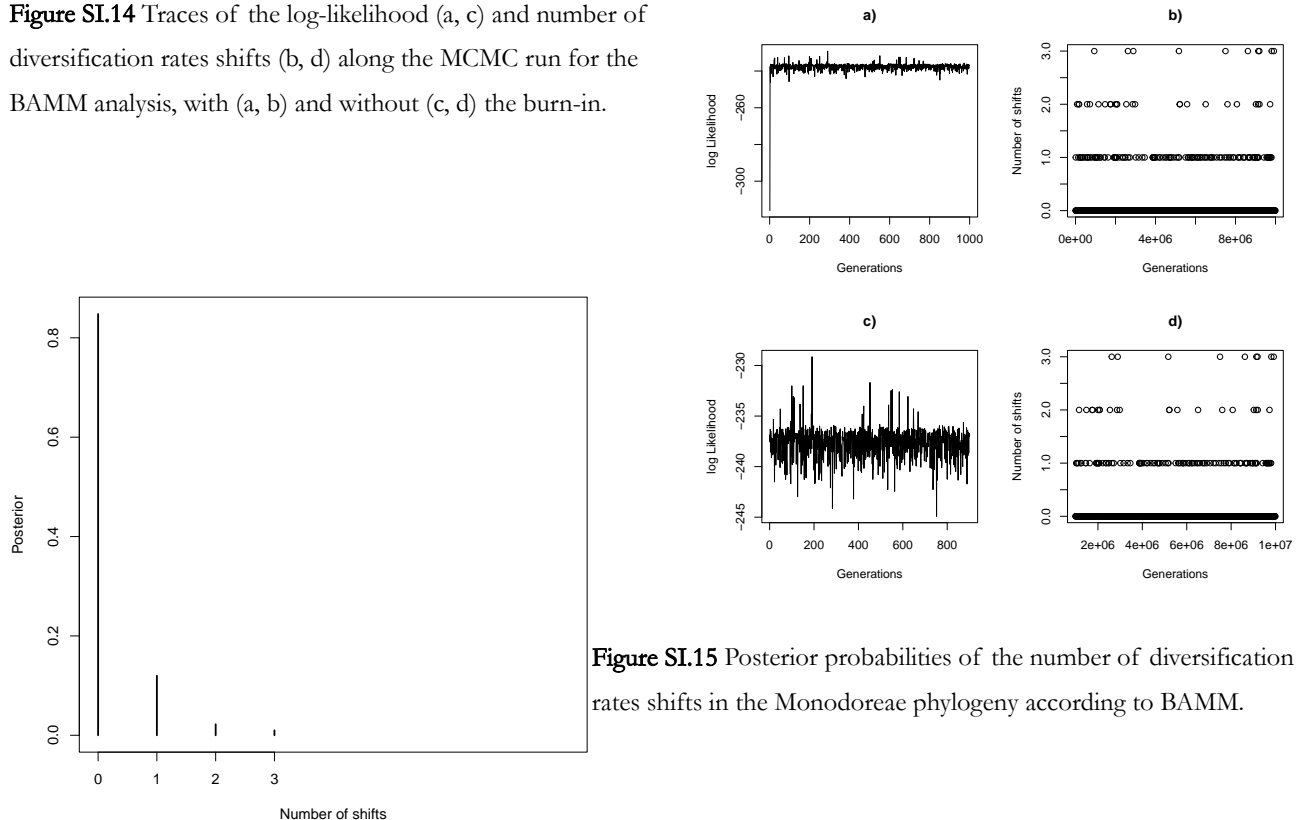
**Figure SI.12** Branch-specific speciation rates (a), extinction rates (b) and diversification rates (c) through time of Monodoreae estimated in the BSDR model in RevBayes.



**Figure SI.13** Clade-specific speciation (a), extinction (b) and diversification (c) rates through time of Monodoreae estimated using BAMM.

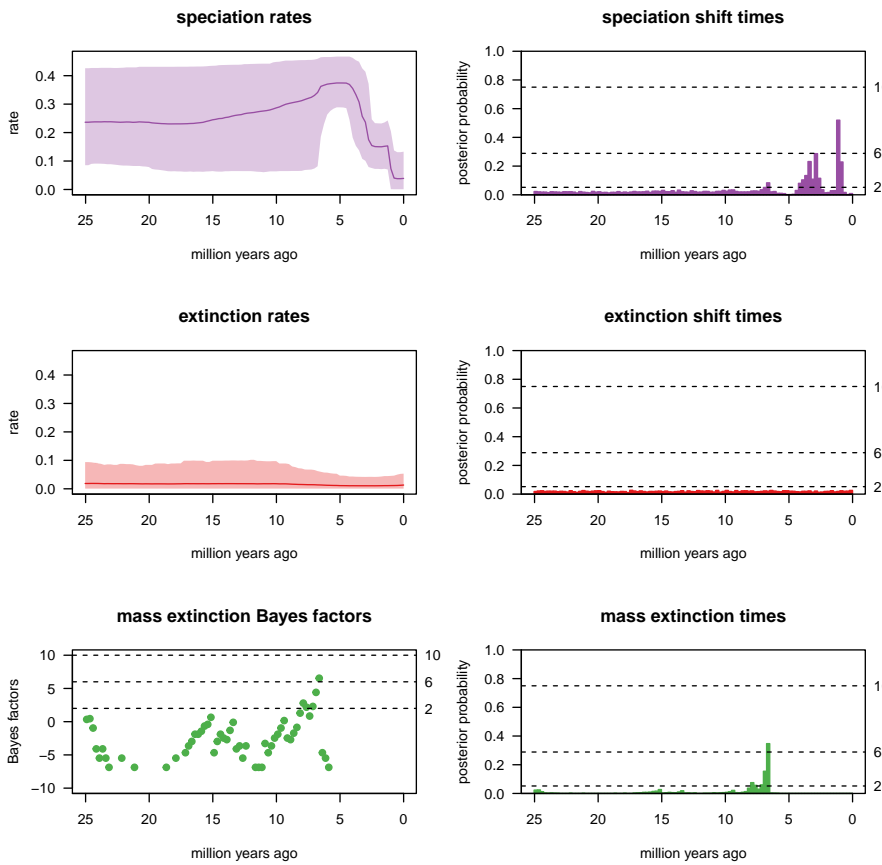


**Figure SI.14** Traces of the log-likelihood (a, c) and number of diversification rates shifts (b, d) along the MCMC run for the BAMM analysis, with (a, b) and without (c, d) the burn-in.



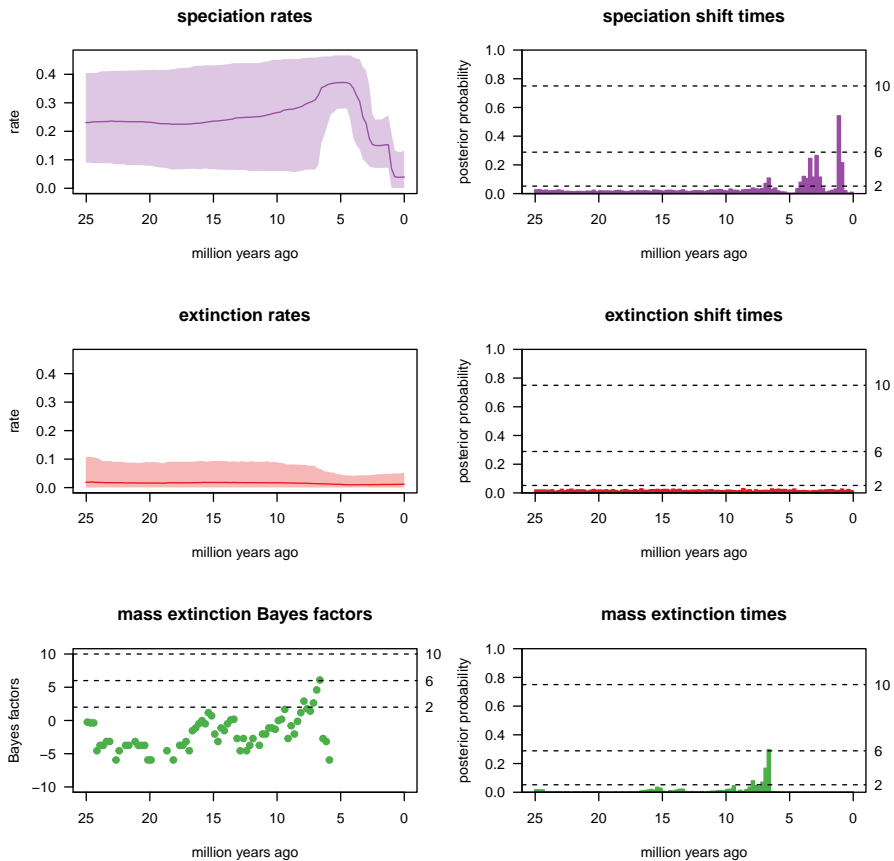
**Figure SI.15** Posterior probabilities of the number of diversification rates shifts in the Monodoreae phylogeny according to BAMM.

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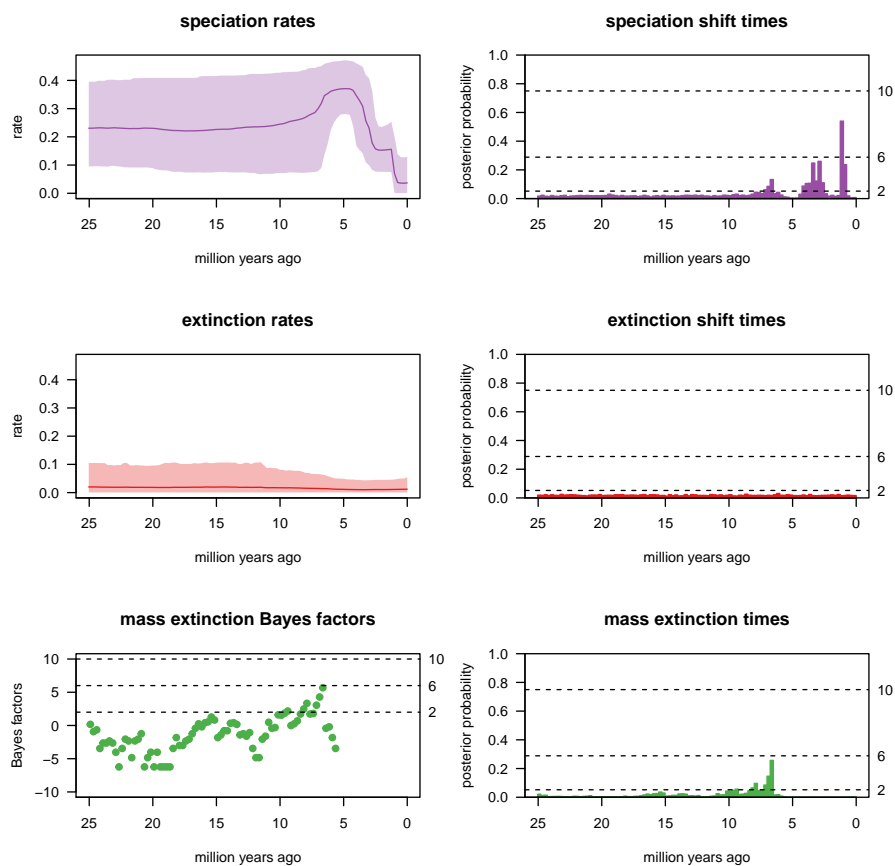
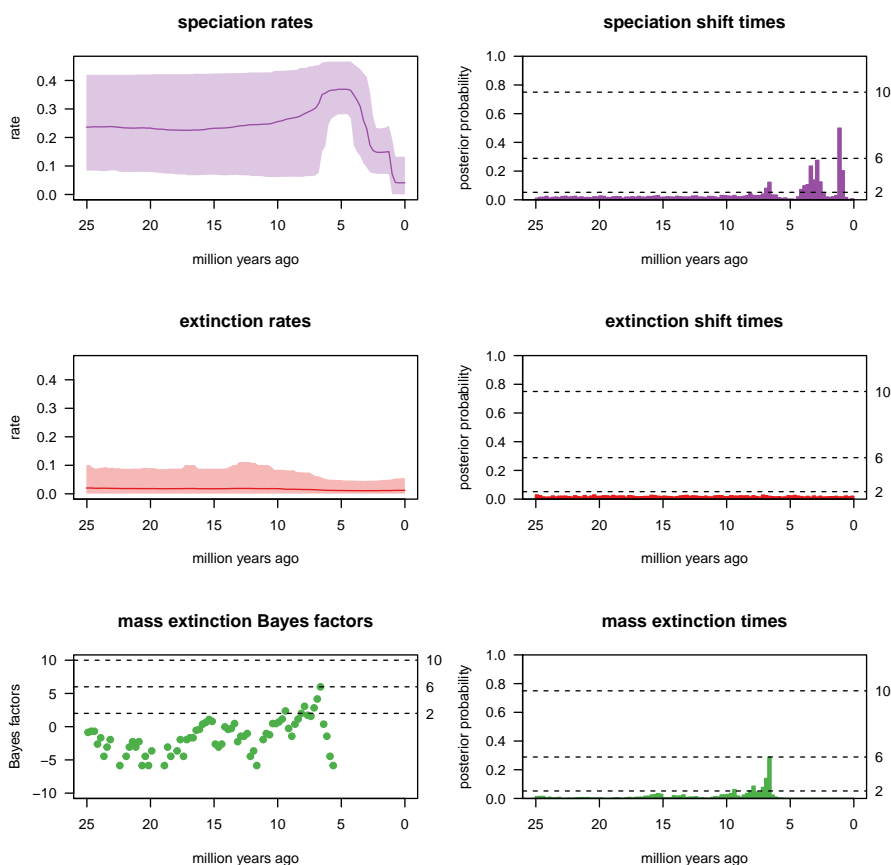
**Figure SI.16** Results of the CoMET analysis, with 5% as prior on the chance of survival to a mass extinction event (ME). Estimated speciation (A) and extinction (C) rates of the Monodoreae through time. Posterior probabilities (left axis) of the models with shifts in speciation rate (B), in extinction rate (D) and of a ME event (F) at each time slice (the 25 Myr of the phylogeny is divided in 100 slices of 0.25 Myr each), against a model with no rate shift or no ME, with their corresponding  $2 \ln$  Bayes Factor (right axis). Values of the Bayes Factor (BF) of the models with a ME event at each time slice against a mode with no ME (E).

**Figure SI.17** Results of the CoMET analysis, with 10% as prior on the chance of survival to a mass extinction event (ME). Estimated speciation (A) and extinction (C) rates of the Monodoreae through time. Posterior probabilities (left axis) of the models with shifts in speciation rate (B), in extinction rate (D) and of a ME event (F) at each time slice (the 25 Myr of the phylogeny is divided in 100 slices of 0.25 Myr each), against a model with no rate shift or no ME, with their corresponding  $2 \ln$  Bayes Factor (right axis). Values of the Bayes Factor (BF) of the models with a ME event at each time slice against a mode with no ME (E).



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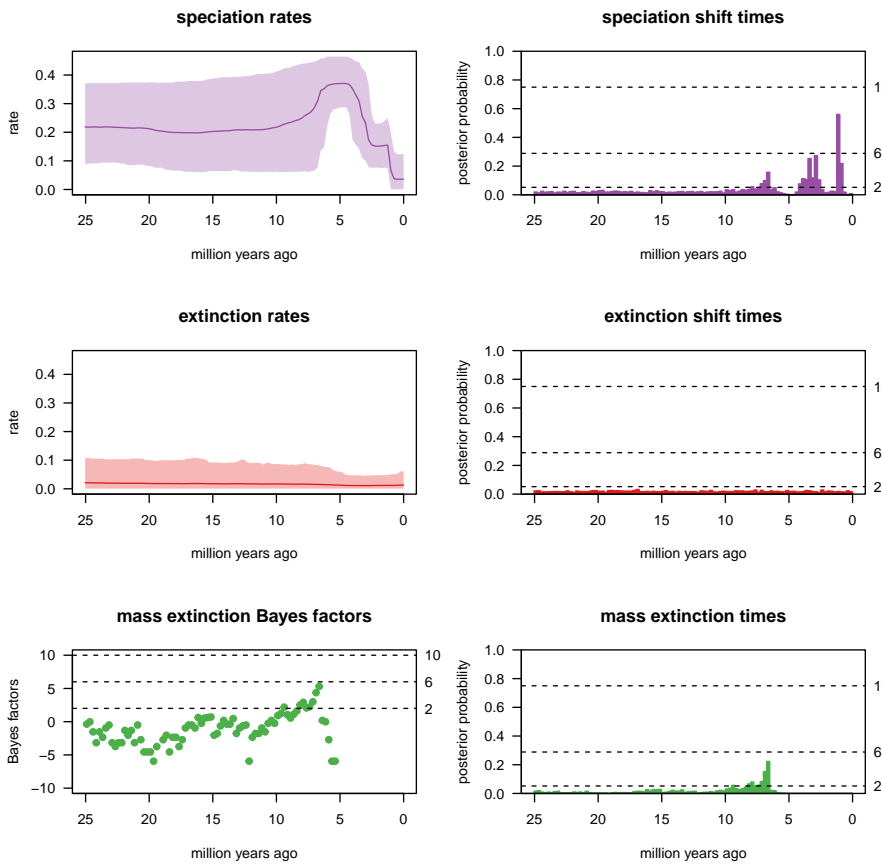
**Figure SI.18** Results of the CoMET analysis, with 15% as prior on the chance of survival to a mass extinction event (ME). Estimated speciation (A) and extinction (C) rates of the Monodoreae through time. Posterior probabilities (left axis) of the models with shifts in speciation rate (B), in extinction rate (D) and of a ME event (F) at each time slice (the 25 Myr of the phylogeny is divided in 100 slices of 0.25 Myr each), against a model with no rate shift or no ME, with their corresponding  $2 \ln$  Bayes Factor (right axis). Values of the Bayes Factor (BF) of the models with a ME event at each time slice against a mode with no ME (E).



**Figure SI.19** Results of the CoMET analysis, with 20% as prior on the chance of survival to a mass extinction event (ME). Estimated speciation (A) and extinction (C) rates of the Monodoreae through time. Posterior probabilities (left axis) of the models with shifts in speciation rate (B), in extinction rate (D) and of a ME event (F) at each time slice (the 25 Myr of the phylogeny is divided in 100 slices of 0.25 Myr each), against a model with no rate shift or no ME, with their corresponding  $2 \ln$  Bayes Factor (right axis). Values of the Bayes Factor (BF) of the models with a ME event at each time slice against a mode with no ME (E).

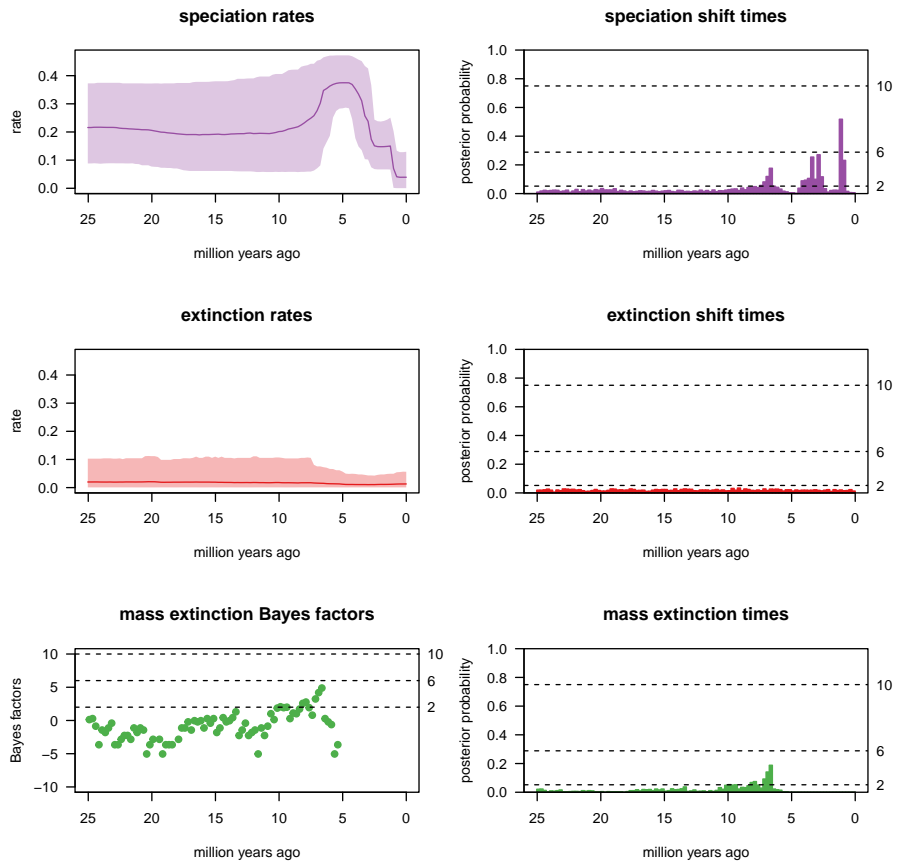


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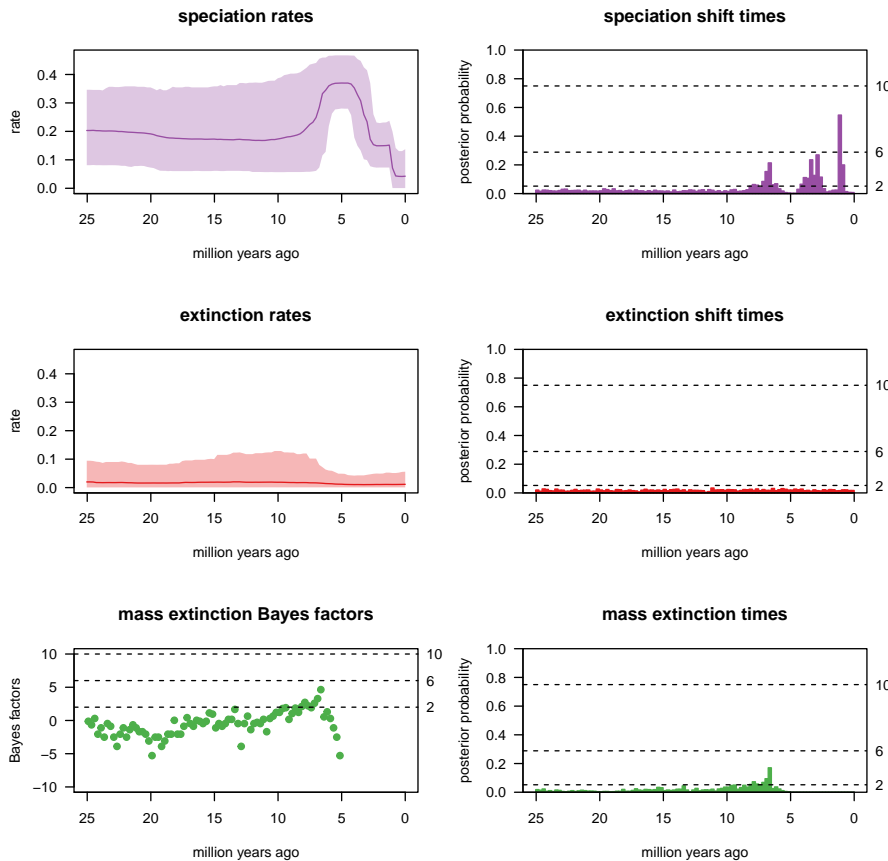
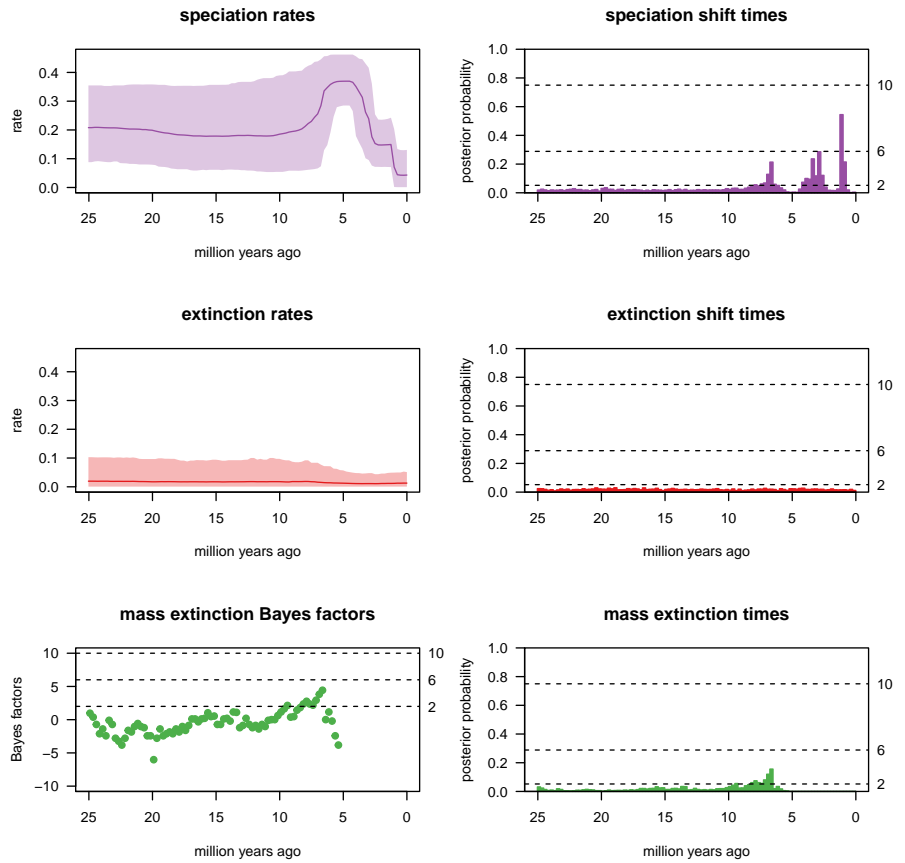
**Figure SI.20** Results of the CoMET analysis, with 25% as prior on the chance of survival to a mass extinction event (ME). Estimated speciation (A) and extinction (C) rates of the Monodoreae through time. Posterior probabilities (left axis) of the models with shifts in speciation rate (B), in extinction rate (D) and of a ME event (F) at each time slice (the 25 Myr of the phylogeny is divided in 100 slices of 0.25 Myr each), against a model with no rate shift or no ME, with their corresponding  $2 \ln$  Bayes Factor (right axis). Values of the Bayes Factor (BF) of the models with a ME event at each time slice against a mode with no ME (E).

**Figure SI.21** Results of the CoMET analysis, with 30% as prior on the chance of survival to a mass extinction event (ME). Estimated speciation (A) and extinction (C) rates of the Monodoreae through time. Posterior probabilities (left axis) of the models with shifts in speciation rate (B), in extinction rate (D) and of a ME event (F) at each time slice (the 25 Myr of the phylogeny is divided in 100 slices of 0.25 Myr each), against a model with no rate shift or no ME, with their corresponding  $2 \ln$  Bayes Factor (right axis). Values of the Bayes Factor (BF) of the models with a ME event at each time slice against a mode with no ME (E).



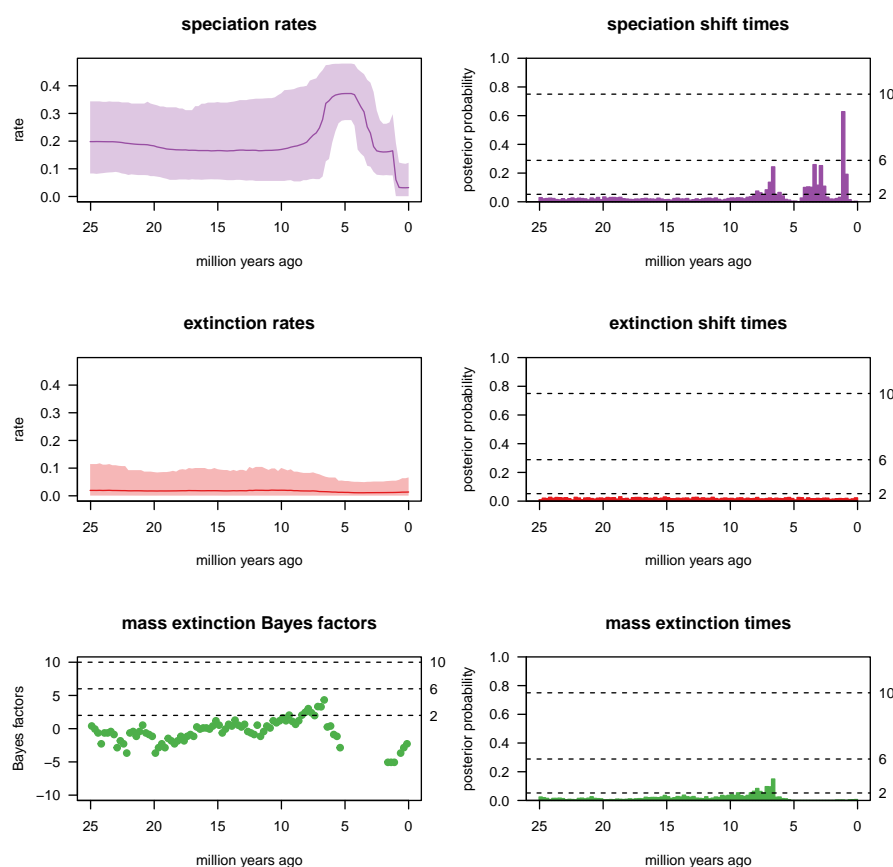
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**Figure SI.22** Results of the CoMET analysis, with 35% as prior on the chance of survival to a mass extinction event (ME). Estimated speciation (A) and extinction (C) rates of the Monodoreae through time. Posterior probabilities (left axis) of the models with shifts in speciation rate (B), in extinction rate (D) and of a ME event (F) at each time slice (the 25 Myr of the phylogeny is divided in 100 slices of 0.25 Myr each), against a model with no rate shift or no ME, with their corresponding  $2 \ln$  Bayes Factor (right axis). Values of the Bayes Factor (BF) of the models with a ME event at each time slice against a mode with no ME (E).



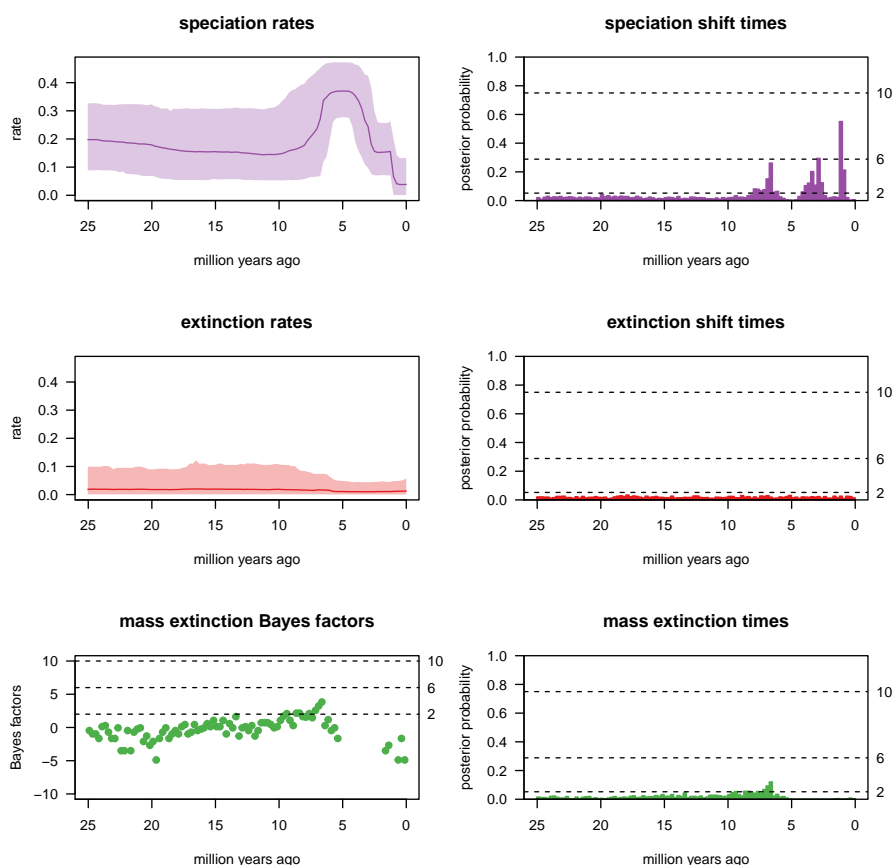
**Figure SI.23** Results of the CoMET analysis, with 40% as prior on the chance of survival to a mass extinction event (ME). Estimated speciation (A) and extinction (C) rates of the Monodoreae through time. Posterior probabilities (left axis) of the models with shifts in speciation rate (B), in extinction rate (D) and of a ME event (F) at each time slice (the 25 Myr of the phylogeny is divided in 100 slices of 0.25 Myr each), against a model with no rate shift or no ME, with their corresponding  $2 \ln$  Bayes Factor (right axis). Values of the Bayes Factor (BF) of the models with a ME event at each time slice against a mode with no ME (E).

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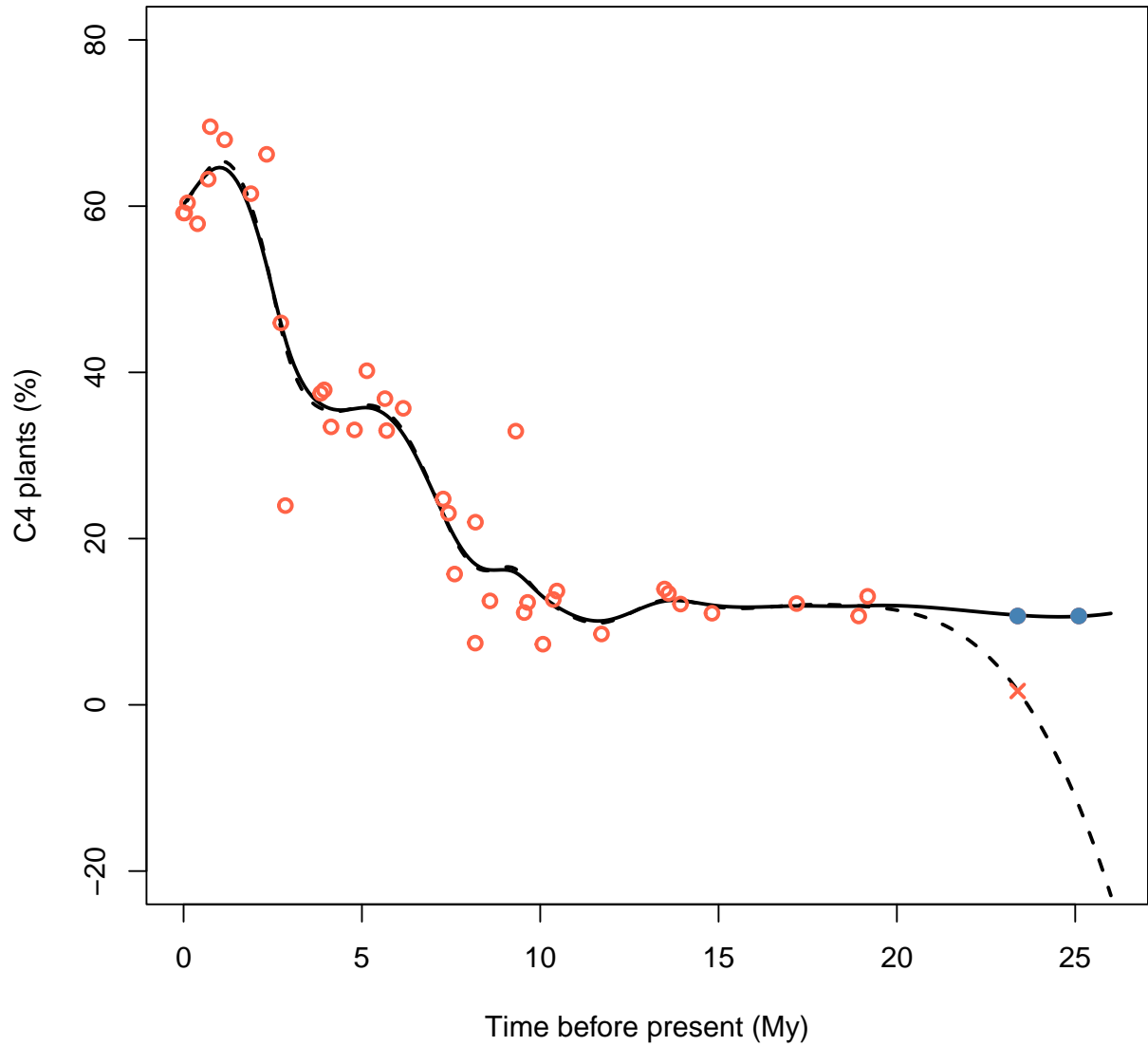
**Figure SI.24** Results of the CoMET analysis, with 45% as prior on the chance of survival to a mass extinction event (ME). Estimated speciation (A) and extinction (C) rates of the Monodoreae through time. Posterior probabilities (left axis) of the models with shifts in speciation rate (B), in extinction rate (D) and of a ME event (F) at each time slice (the 25 Myr of the phylogeny is divided in 100 slices of 0.25 Myr each), against a model with no rate shift or no ME, with their corresponding  $2 \ln$  Bayes Factor (right axis). Values of the Bayes Factor (BF) of the models with a ME event at each time slice against a mode with no ME (E).

**Figure SI.25** Results of the CoMET analysis, with 50% as prior on the chance of survival to a mass extinction event (ME). Estimated speciation (A) and extinction (C) rates of the Monodoreae through time. Posterior probabilities (left axis) of the models with shifts in speciation rate (B), in extinction rate (D) and of a ME event (F) at each time slice (the 25 Myr of the phylogeny is divided in 100 slices of 0.25 Myr each), against a model with no rate shift or no ME, with their corresponding  $2 \ln$  Bayes Factor (right axis). Values of the Bayes Factor (BF) of the models with a ME event at each time slice against a mode with no ME (E).



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**Figure SI.26** Estimated proportion of C4 versus non-C4 plants in tropical Africa from the last 25 Myr using spline interpolation (solid line) from the punctual estimations in the sites 959, 241 and 235 in Polissar *et al.* 2019 (red circles), with an outlier removed (red cross). Blue dots are artificial values that replace the outlier in order to avoid distortion towards negative values of the spline interpolation (dotted line) and that allow the estimation to span the temporal frame (0 – 25 Myr) of the Monodoreae phylogeny (see Material & Methods for the details).



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**Table SI.9** List of the 32 most clock-like supercontigs used in this study, with their length and best substitution model according to Bayesian Information Criterion as inferred by ModelTest-NG.

Supercontig name	Length (bp)	Best substitution model
DN1535_963_Q9FZH7_supercontig	3342	GTR+G
DN26939_9475_Q8RYD9_supercontig	1278	HKY+I+G
DN26970_9544_nomatch_supercontig	1090	HKY+G
DN30699_16825_Q9FHK0_supercontig	776	HKY+G
DN32048_21361_Q9MA20_supercontig	2945	HKY+I+G
DN32549_23539_Q8W4Q3_supercontig	3251	GTR+G
DN34416_34725_Q9SKE1_supercontig	819	GTR+G
DN34518_35383_Q9LX10_supercontig	2647	HKY+I+G
DN34827_37789_O48696_supercontig	727	K80+G
DN36158_49870_Q8GYM8_supercontig	738	GTR+I+G
DN37740_71419_Q8RWR3_supercontig	2388	GTR+I+G
DN6177_4563_Q8W4G4_supercontig	4796	GTR+I+G
DN68704_26115_O81153_supercontig	723	HKY+G
DN70244_112355_Q94AD8_supercontig	1718	HKY+G
DN70624_112688_O82484_supercontig	724	GTR+G
DN7142_1430_Q8H0U4_supercontig	1151	SYM+I+G
DN72390_32089_Q9SMY9_supercontig	776	HKY+G
DN74895_124004_Q8S8M1_supercontig	854	HKY+I+G
DN76306_128605_Q9FKR5_supercontig	726	K80+G
DN77328_49269_Q84WS4_supercontig	730	HKY+G
DN77447_50189_Q94A41_supercontig	820	HKY+G
DN78202_54956_O48849_supercontig	1413	GTR+I+G
DN78983_138427_Q9LJH5_supercontig	956	HKY+I+G
DN79594_140275_P92996_supercontig	2051	GTR+G
DN79971_143901_Q9LJA3_supercontig	822	HKY+G
DN80031_144930_Q9LFT1_supercontig	509	K80+G
DN80103_66247_Q9LXY0_supercontig	695	K80+G
DN80477_146516_Q9SU83_supercontig	803	GTR+G
DN80493_145662_O82392_supercontig	734	K80+G
DN81422_153845_Q9FKA8_supercontig	782	K80+G
DN81890_78861_Q84LG4_supercontig	743	K80+G
DN82030_157571_Q9SHL0_supercontig	669	HKY+G

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**Table SI.10** List of the internal nodes in the MCC tree (Figure 53 and Figure SI.10), with their support, mean age, median age, and lower and upper bound of the 0.95 highest posterior density (HPD) of the age, in million years ago.

Node number	Node support	Mean Age	Median Age	Age 0.95 HPD lower bound	Age 0.95 HPD upper bound
119	1.00	105.53	112.60	110.07	110.68
120	1.00	89.00	92.55	90.21	89.87
121	1.00	58.40	67.80	63.16	63.17
122	1.00	47.04	55.35	51.22	51.23
123	1.00	45.22	53.25	49.21	49.23
124	1.00	37.99	45.00	41.56	41.60
125	1.00	32.02	37.94	35.05	35.11
126	1.00	22.52	27.30	25.04	25.07
127	1.00	20.63	25.14	23.06	23.07
128	1.00	13.45	16.56	15.07	15.06
129	1.00	4.80	5.85	5.37	5.37
130	1.00	4.26	5.33	4.84	4.85
131	1.00	4.07	5.13	4.63	4.64
132	1.00	0.51	0.95	0.72	0.71
133	1.00	4.16	5.22	4.71	4.72
134	1.00	2.15	3.12	2.64	2.64
135	1.00	3.98	5.03	4.51	4.52
136	1.00	1.74	2.85	2.30	2.28
137	1.00	4.62	5.65	5.19	5.20
138	1.00	4.44	5.43	4.96	4.96
139	1.00	1.68	2.55	2.11	2.10
140	1.00	4.22	5.18	4.71	4.71
141	1.00	3.94	4.88	4.42	4.42
142	1.00	3.78	4.72	4.26	4.26
143	0.96	3.58	4.52	4.05	4.05
144	1.00	2.36	3.29	2.84	2.84
145	1.00	4.24	5.26	4.78	4.79
146	1.00	8.24	10.24	9.22	9.20
147	1.00	5.94	7.23	6.55	6.54
148	1.00	5.16	6.29	5.71	5.70
149	1.00	4.65	5.75	5.19	5.18
150	1.00	3.94	5.05	4.51	4.51

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Node number	Node support	Mean Age	Median Age	Age 0.95 HPD lower bound	Age 0.95 HPD upper bound
151	1.00	0.82	1.42	1.10	1.09
152	1.00	4.82	5.91	5.34	5.33
153	1.00	4.14	5.27	4.73	4.72
154	1.00	1.51	2.13	1.81	1.80
155	1.00	1.20	1.72	1.47	1.46
156	1.00	1.11	1.62	1.36	1.35
157	1.00	0.92	1.43	1.16	1.15
158	1.00	4.58	5.64	5.11	5.10
159	1.00	3.75	4.77	4.24	4.23
160	1.00	2.37	3.30	2.82	2.82
161	1.00	4.04	5.19	4.61	4.61
162	1.00	5.38	6.65	6.00	5.99
163	1.00	4.73	5.98	5.35	5.34
164	1.00	3.34	4.58	3.98	3.96
165	1.00	4.80	6.10	5.45	5.45
166	1.00	18.56	22.86	20.67	20.67
167	1.00	11.56	14.96	13.25	13.22
168	1.00	4.32	5.73	5.03	5.00
169	0.94	3.89	5.16	4.52	4.50
170	1.00	2.97	4.16	3.55	3.54
171	1.00	0.63	1.12	0.86	0.86
172	1.00	2.77	3.97	3.35	3.34
173	1.00	5.17	6.68	5.91	5.90
174	1.00	3.61	4.87	4.23	4.23
175	1.00	1.98	2.94	2.46	2.46
176	1.00	4.00	5.39	4.67	4.65
177	1.00	2.59	3.78	3.17	3.15
178	1.00	2.81	4.02	3.41	3.41
179	1.00	1.70	2.60	2.12	2.11
180	1.00	21.72	26.47	24.40	24.43
181	1.00	10.86	13.78	12.33	12.32
182	1.00	6.79	8.59	7.68	7.67
183	1.00	5.78	7.29	6.51	6.50
184	1.00	4.10	5.04	4.58	4.58

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Node number	Node support	Mean Age	Median Age	Age 0.95 HPD lower bound	Age 0.95 HPD upper bound
185	1.00	3.60	4.54	4.07	4.06
186	1.00	2.88	3.85	3.35	3.35
187	1.00	2.01	3.00	2.50	2.50
188	1.00	3.27	4.23	3.73	3.72
189	1.00	2.54	3.44	3.00	3.00
190	1.00	1.76	2.48	2.12	2.11
191	1.00	0.76	1.34	1.05	1.04
192	1.00	0.81	1.25	1.03	1.03
193	1.00	0.53	0.89	0.71	0.70
194	1.00	3.97	4.88	4.42	4.42
195	1.00	3.85	4.74	4.28	4.28
196	1.00	3.55	4.40	3.96	3.96
197	1.00	2.97	3.85	3.41	3.41
198	1.00	2.63	3.50	3.06	3.06
199	1.00	2.37	3.23	2.81	2.81
200	1.00	3.82	5.17	4.49	4.47
201	1.00	2.49	3.62	3.03	3.02
202	1.00	5.21	6.57	5.90	5.90
203	1.00	4.06	5.15	4.58	4.59
204	1.00	3.30	4.22	3.73	3.73
205	1.00	3.04	3.91	3.47	3.46
206	1.00	2.61	3.39	2.98	2.97
207	1.00	2.32	3.07	2.70	2.70
208	1.00	2.07	2.77	2.41	2.41
209	1.00	1.41	1.88	1.64	1.64
210	1.00	1.20	1.64	1.42	1.42
211	1.00	1.04	1.47	1.25	1.25
212	1.00	0.62	1.02	0.83	0.82
213	1.00	0.46	0.80	0.63	0.63
214	1.00	0.97	1.43	1.19	1.19
215	1.00	1.34	1.94	1.63	1.62
216	1.00	1.07	1.60	1.34	1.33
217	1.00	0.88	1.37	1.12	1.11
218	1.00	3.36	4.37	3.87	3.87



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Node number	Node support	Mean Age	Median Age	Age 0.95 HPD lower bound	Age 0.95 HPD upper bound
219	1.00	3.16	4.16	3.68	3.67
220	1.00	1.10	1.78	1.44	1.43
221	1.00	4.01	5.23	4.60	4.59
222	1.00	2.41	3.45	2.90	2.89
223	1.00	17.58	22.04	19.99	19.99
224	1.00	5.59	7.12	6.35	6.34
225	1.00	4.14	5.51	4.85	4.85
226	1.00	3.81	5.17	4.50	4.50
227	1.00	1.35	2.18	1.75	1.74
228	1.00	4.70	6.19	5.42	5.41
229	1.00	31.09	36.89	34.05	34.12
230	1.00	21.49	26.69	24.15	24.11
231	1.00	20.47	25.56	22.89	22.88
232	1.00	6.71	9.08	7.85	7.83
233	1.00	5.05	7.17	6.09	6.08
234	1.00	7.74	11.09	9.34	9.31
235	1.00	31.59	38.42	35.00	35.01

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# Chapter 6 | Conclusion and perspectives

## 1. The story in a nutshell

This thesis explored the diversification of the tropical African flora, using different spatial and temporal scales. At the continental scale, and focusing on angiosperms, we inferred that the East African montane region was acting as both cradles and museums of generic diversity, whereas lowland rain forests of the Guineo-Congolian region were acting as museum of diversity (Chapter 2). Focusing on the tropical rain forests (TRF), we inferred the geographic origin of the Annonaceae tribe Monodoreae to have originated in East Africa during the late Oligocene (Chapter 5). From there the tribe expanded toward Central Africa supporting the existence of a pan-Africa rain forest during the early to middle Miocene. Then during the middle Miocene, the TRF likely fragmented but we suggest they remained more connected than previously suggested. During the aridification of tropical Africa in the late Miocene, the Monodoreae experienced sudden extinction followed by high diversification rates, due to the fragmentation and the following re-connection of the TRF in the early Pliocene. Interestingly, we also found that the African montane uplift in the Late Miocene and early Pliocene (mainly in East Africa) stimulated the Monodoreae diversification. The topography of East Africa seems to have played a great role in shaping the current patterns of diversity in the tropical African flora. The focus on the Monodoreae was made possible thanks to the clarification of the systematics of the tribe (Chapter 3), in combination to the taxonomic revision of the genera *Uvariadendron* and *Uvariopsis* (Chapter 4). In particular, we created the new tribe Ophrypetaleae, re-erected the monotypic genus *Dennettia*, and described one new *Uvariopsis* species and three new *Uvariadendron* species, which adds to three new species I already described in a side paper during my thesis (Dagallier *et al.*, 2021).

## 2. Perspectives

This thesis brings another brick in the wall of biodiversity knowledge in tropical Africa. Although we used the most up to date data and methods for the given purposes, further accuracy may emerge with the integration of more data. For example, present day data about species' geographical occurrences, such as RAINBIO, are the result of hundreds of years of botanical exploration (Dauby *et al.*, 2016). Using this data in Chapter 2, we completed the picture about the distribution of old and young lineages that Fjeldså & Lovett (1997) had already begun to depict with a far smaller plant distribution data set. Yet, for some regions of tropical Africa, plants are under-collected or data is not accessible, like in Angola, Nigeria or the Republic of the Congo (Sosef *et al.*, 2017). Thus, more botanical sampling or

databasing efforts in these countries will bring valuable insights into the African biodiversity patterns. In this same Chapter 2, we inferred the patterns of phylogenetic diversity and phylogenetic endemism (in particular neo- and paleo-endemism) using the best time-calibrated angiosperm phylogenetic tree we could expect for this purpose (Janssens *et al.*, 2020). It included ca. 75% of the genera for which we had a geographical distribution. I expect that a phylogenetic tree including all the genera would refine the retrieved patterns of phylogenetic diversity and endemism. Several other studies reconstructed angiosperm mega-phylogenies integrating more and more species (e.g. Hinchliff & Smith, 2014; Zanne *et al.*, 2014; Hinchliff *et al.*, 2015; Smith & Brown, 2018; Li *et al.*, 2019). Reconstructing the complete phylogenetic tree of all the angiosperms is a challenge undertaken by the ‘Plant and Fungi Tree of Life’ (PAFTOL) project (Baker *et al.*, 2021). Such a project is a robust input in the understanding of the evolutionary relationships between the plant taxa, especially since it is led in a phylogenomic framework, i.e. relying on nuclear genomic data thanks to high throughput sequencing (Dodsworth *et al.*, 2019; Johnson *et al.*, 2019). Phylogenomics contributes to a better understanding of the evolution of biodiversity, but also brings new challenges, such as the development of new algorithms that can handle such amount of data in the reconstruction of phylogenetic hypotheses (e.g. Minh *et al.*, 2013; Douglas *et al.*, 2021). In Chapter 3, we also have seen that incorporating hundreds of genes in phylogenetic reconstruction led to the detection of gene trees conflict in regions where reticulate evolution happened. This necessitates to explicitly model processes of evolution at the population levels (Zhang *et al.*, 2018; Bouckaert *et al.*, 2019).

In the Chapter 5, we used different models for inferring the time-calibrated phylogenetic tree, the biogeographic history and the diversification dynamic of the Monodoreae. As stated in the Introduction, “all models are wrong, but some are useful” (Box, 1979). We thus integrated as much of our prior knowledge in the models. For example, the molecular dating was calibrated using two fossils (*Endressinia* to the crown node of Magnoliineae, and *Futabanthus* attributed to the crown node of Annonaceae). Unfortunately, to date there are no fossil attributed to nodes within the Monodoreae in the paleobotanical records. The hypothetical future discovery of such fossil may refine the time calibration of the Monodoreae tree of life. Concerning the biogeographical history, we used the Dispersion-Extinction-Cladogenesis (DEC) model in a maximum likelihood (ML) framework to reconstruct the ancestral range of the Monodoreae. This could have also been achieved in a Bayesian inference (BI) framework thus allowing to estimate uncertainty in biogeographic scenarios (e.g. Landis *et al.*, 2018; Lator *et al.*, 2019), or with models accounting for range-dependent diversification rates such as the GeoSSE-like models (Goldberg *et al.*, 2011; Caetano *et al.*, 2018). These biogeographic models (DEC, GeoSSE) consider the geographic range of the species as discrete units (in our case: West, Centre, East

regions and Madagascar). But a species' geographic range is a polygon in two dimensions, and modeling the species' biogeographic history using continuous geographic range is possible with the *rasc* model (Quintero *et al.*, 2015; Maestri *et al.*, 2019). The use of these alternative models could improve or corroborate the inferences we retrieved with the DEC model.

In the Chapter 3, we have seen that the Monodoreae tribe is morphologically very diverse, particularly when looking at the flowers, with species being unisexual (most of *Uvariopsis*), syncarpous (*Isolona*, *Monodora*) or having fused petals (*Asteranthe*, *Hexalobus*, *Isolona*, *Monodora*, *Uvariastrum*, some *Uvariopsis*). Further investigation of the evolutionary history of this clade could be done in reconstructing the ancestral state of these morphological characters (Sauquet *et al.*, 2017), or in testing for their influence of the diversification of the clade with state dependent diversification models (SSE models, Maddison *et al.*, 2007). However, as these characters evolved only once in the clade (except the fusion of petals), detecting a potential impact on the diversification rate remains statistically unreliable (Maddison & FitzJohn, 2015).

### 3. Conclusion

To conclude, this thesis presents 'a' story about the diversification of the tropical African flora, with a focus on the TRF restricted clade Monodoreae. Using the most comprehensive data to date and cutting edge methods in the fields of phylogenomics, biogeography and macroevolution, we inferred the past to understand the present. This contribution for a better understanding of the African flora, might serve as a basis for further enhancement of our knowledge about biodiversity as a whole, and help -on its scale- to mitigate the biodiversity crisis the planet is undergoing.

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# Résumé en français

Cette thèse étudie la diversification de la flore tropicale africaine, avec différentes approches spatiales et temporelles. La distribution actuelle des espèces à travers le continent est le résultat de divers changements environnementaux, et ici nous étudions comment ces changements ont affecté la flore à l'aide de la distribution géographique des espèces, de phylogénies moléculaires, et de plusieurs modèles biogéographiques et de diversification. La thèse peut être divisée en 2 grandes parties d'échelles spatiales et taxonomiques différentes.

La première partie est à grande échelle géographique et taxonomique, et se concentre sur l'ensemble de la flore du continent. Dans le chapitre 2, nous avons décrit les patrons d'endémisme végétal en Afrique tropicale, et identifié des « berceaux » et des « musées » de diversité des angiospermes au niveau générique (c'est à dire des régions avec significativement plus de taxons ayant divergé récemment ou de taxons ayant divergé anciennement, respectivement). Nous montrons que les zones montagneuses de l'Afrique de l'Est sont à la fois des berceaux et des musées de diversité, soulignant le rôle important joué par les montagnes dans la diversification de la flore. En revanche, la région forestière guinéo-congolaise de basse altitude est caractérisée par des taxons anciens et à large répartition géographique.

La deuxième partie de la thèse réduit les échelles géographique et taxonomique. Elle se concentre sur les forêts tropicales humides (FTH) africaines, et sur leur évolution, en passant par l'étude des Monodoreae (Annonaceae), une tribu de 92 espèces de plantes inféodées aux FTH. Pour ce faire, la systématique et la taxonomie des Monodoreae doivent être bien résolues, en particulier pour les deux genres *Uvariadendron* et *Uvariopsis* qui manquent d'une révision récente. Ainsi, le chapitre 3 est consacré à la systématique des Monodoreae, pour laquelle nous reconstruisons un arbre phylogénétique robuste en utilisant plus de 300 gènes nucléaires. Nos résultats soutiennent plusieurs changements systématiques, tels que l'érection de la tribu Ophrypetaleae, la réintégration du genre monotypique *Dennettia* Baker f., et plusieurs descriptions d'espèces et synonymies dans les genres *Uvariadendron* et *Uvariopsis*. En outre, le chapitre 4 est consacré à la révision taxonomique des genres *Uvariadendron* et *Uvariopsis*. A partir de l'examen de plus de 800 spécimens d'herbier, nous fournissons une description pour chaque espèce, dont plusieurs espèces nouvellement décrites. Nous discutons également de leur morphologie, de leur biologie de la pollinisation, de la dispersion des graines, de leurs usages locaux, et nous fournissons des cartes de leurs distributions géographiques. Enfin, le chapitre 5 étudie la biogéographie et la diversification des FTH africaines, en se concentrant sur les Monodoreae. Nous reconstruisons une phylogénie moléculaire de la tribu dans un cadre bayésien, datée par calibration fossile, et appliquons plusieurs modèles de biogéographie et de diversification pour tester l'impact des changements environ-

nementaux passés sur l'évolution de la tribu. Nous avons estimé que les Monodoreae sont originaires des FTH d'Afrique de l'Est il y a environ 25 millions d'années (Ma), et qu'elles se sont étendues vers l'Afrique centrale du début au milieu du Miocène. Nous n'avons trouvé aucun indice de vicariance dans les FTH au cours du milieu du Miocène, et nos résultats suggèrent que les blocs de FTH étaient plus connectés que suggéré auparavant durant le milieu du Miocène. Nous avons aussi trouvé que les Monodoreae ont probablement subi une extinction soudaine au cours de la fin du Miocène, ce qui soutient l'hypothèse d'une réduction drastique des FTH liée à l'aridification de l'Afrique. Nos résultats suggèrent également que la fragmentation et la reconnexion des FTH ont stimulé la diversification, probablement associée à l'augmentation de l'altitude de l'Afrique à la fin du Miocène et au Pliocène.

## Résumé en français (version longue)

### 1. Introduction générale

#### 1.1. Contexte

La biodiversité, ou « diversité biologique », est le concept qui représente l'ensemble des organismes vivants, des gènes aux écosystèmes, et englobe leur variabilité et leur complexité (McNeely *et al.*, 1990). La biodiversité, subit une crise critique due au changement climatique et aux activités humaines, conduisant à ce consensus scientifique que la biodiversité est confrontée à sa sixième extinction de masse (Barnosky *et al.*, 2011; Pimm *et al.*, 2014). Gérer cette crise pour éviter l'effondrement de la biodiversité et de l'humanité est probablement l'un des plus importants défis que les humains auront à relever (Ceballos & Ehrlich, 2018).

##### 1.1.1. Le présent et l'avenir

Pour relever ce défi, les sciences de la biodiversité ne cessent de repousser les limites de nos connaissances. Les études qui décrivent la biodiversité actuelle sont primordiales pour établir l'état des connaissances en matière de biodiversité. Des espèces inconnues de la science<sup>2</sup> sont continuellement découvertes et décrites (e.g. Dagallier *et al.* 2021, Sharkey *et al.* 2021, Zhurbenko *et al.* 2021), et les estimations des espèces non décrites sont d'environ 15 % pour les plantes à fleurs (Joppa *et al.*, 2011) et vont de 21 à 86 % pour l'ensemble de la biodiversité terrestre (Mora *et al.*, 2011; Costello *et al.*, 2012). Au-delà de la description des espèces, l'évaluation de leur degré de menace d'extinction est une mesure

2 Par "inconnues de la science", j'entends inconnues de la science dirigée par les institutions occidentales (Trisos *et al.*, 2021). En effet, certaines espèces (sinon beaucoup) sont connues des communautés locales (c'est-à-dire faire partie de la science locale) (e.g. Whaanga *et al.*, 2013), mais ne sont pas décrites selon les standards internationaux (Turland *et al.*, 2018), et ne sont donc pas reconnues comme "connues" par la communauté scientifique occidentale, bien qu'elles soient clairement "connues" localement.

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importante pour mettre en œuvre des politiques de conservation adéquates (Margules & Pressey, 2000). A ce jour, 28% des espèces décrites et évaluées sont menacées d'extinction (IUCN, 2020). Similairement, certaines régions du monde, principalement dans les régions tropicales, sont considérées comme des « points chauds de la biodiversité » (« biodiversity hotspots ») car elles abritent une grande quantité de biodiversité menacée et irremplaçable (Myers *et al.*, 2000; Sechrest *et al.*, 2002).

Les études prédictives, qui permettent de comprendre comment la biodiversité pourrait répondre aux changements climatiques à l'avenir, sont également d'une grande importance pour anticiper et se préparer aux changements planétaires (e.g. Bellard *et al.* 2012, Réjou-Méchain *et al.* 2021, Saatchi *et al.* 2021). Il a été suggéré que pour préserver le potentiel de la biodiversité à s'adapter à l'avenir (pour préserver le "potentiel évolutif"), nous ne devrions pas seulement considérer les espèces comme de simples unités de biodiversité, mais nous devrions également nous concentrer sur leur histoire évolutive et préserver les régions avec des espèces qui représentent une grande portion de l'histoire évolutive de la Terre (c'est-à-dire avec une diversité phylogénétique élevée) (Sechrest *et al.*, 2002; Mace *et al.*, 2003; Forest *et al.*, 2007).

### 1.1.2. Le passé

Se concentrer sur les histoires évolutives signifie regarder dans le passé. Dans un contexte plus large, nous pouvons dire que nos capacités à comprendre le présent et à prévoir l'avenir reposent sur notre connaissance du passé. En effet, la biodiversité actuelle est le résultat de millions d'années d'histoire évolutive, qui ont conduit à la variabilité et à la complexité de formes et de fonctionnements que nous observons aujourd'hui. En outre, cette évolution a également conduit à une répartition inégale de la biodiversité sur la planète, une caractéristique qui a depuis longtemps interrogé les biogéographes (von Humboldt & Bonpland, 1805; de Candolle, 1820; Prichard, 1836; Sclater, 1858; Wallace, 1876). La répartition de la biodiversité forme différentes régions biogéographiques, c'est-à-dire des régions où la composition des espèces est relativement homogène, également appelées biorégions ou écorégions (Olson *et al.*, 2001; Kreft & Jetz, 2010). Certaines régions du monde, comme les tropiques, abritent un plus grand nombre d'espèces que dans d'autres parties du monde (Stevens, 1989; Barthlott *et al.*, 1996; Gaston, 2000; Mutke & Barthlott, 2005). De manière similaire, certaines régions, comme les montagnes ou les îles, abritent un grand nombre d'espèces dont la répartition géographique est restreinte et qu'on ne trouve nulle part ailleurs (les espèces endémiques) (Burgess *et al.*, 1998; Lamoreux *et al.*, 2006; Kier *et al.*, 2009; López-Pujol *et al.*, 2011; Rosauer & Jetz, 2015).

Les patrons de diversité actuels sont le résultat de facteurs biotiques et abiotiques qui ont eu un impact sur l'histoire évolutive des espèces (Benton, 2009; Ezard *et al.*, 2011; Smith *et al.*, 2014; Couvreur *et al.*,

2021). Les facteurs biotiques qui influencent la spéciation ou l'extinction des taxons sont liés à l'interaction entre les espèces (e.g. compétition, mutualisme) ou aux caractéristiques intrinsèques des espèces (e.g. capacités de dispersion pour coloniser de nouvelles régions isolées, acquisition de caractères conduisant à un isolement reproductif) (Van Valen, 1973). Les facteurs abiotiques qui influencent la spéciation ou l'extinction des taxons sont liés aux processus physiques qui se produisent sur Terre, tels que les mouvements géologiques et les changements climatiques à travers le temps (Benton, 2009).

Si l'on tient compte de l'échelle temporelle, certaines régions peuvent être identifiées comme des « berceaux » de diversité, en tant que lieux jouant un rôle important dans l'évolution des espèces, abritant principalement des espèces qui ont divergé récemment, tandis que d'autres régions sont identifiées comme des « musées » de diversité, en tant que lieux de survie des espèces, abritant principalement des espèces qui ont divergé anciennement et ont persisté au fil du temps (López-Pujol *et al.*, 2011; Rangel *et al.*, 2018). Par exemple, les régions montagneuses ont été suggérées être à la fois des « berceaux » et des « musées » de diversité (López-Pujol *et al.*, 2011). Elles agissent comme des « berceaux » de diversité en ayant des habitats fragmentés qui favorisent la divergence par l'isolement de petites populations (Hughes & Eastwood, 2006; Wen *et al.*, 2014; Schwery *et al.*, 2014; Merckx *et al.*, 2015), et comme des « musées » de diversité, car leur topographie complexe favorise des habitats relativement stables qui permettent la persistance des espèces sur de longues périodes de temps (Peterson *et al.*, 1997; Fjeldså & Lovett, 1997; Hewitt, 2000; Tzedakis *et al.*, 2002; Loarie *et al.*, 2009; López-Pujol *et al.*, 2011; Tolley *et al.*, 2011).

### 1.1.3. Afrique tropicale

L'Afrique tropicale est une mosaïque de plusieurs biorégions différentes, composées principalement de zones forestières (forêts tropicales humides de plaine, de montagne) autour de l'équateur, entourées de zones non forestières comme des prairies ouvertes, des savanes ou des zones arbustives (White, 1983; Olson *et al.*, 2001; Mayaux *et al.*, 2004; Linder *et al.*, 2005; Sayre *et al.*, 2013; Droissart *et al.*, 2018). Une grande richesse en espèces et des centres d'endémisme se trouvent au Cameroun, au Gabon, à l'est de la République Démocratique du Congo (RDC) et à l'est de la Tanzanie (Linder, 2001; Küper *et al.*, 2004; Sosef *et al.*, 2017). Elle abrite certains des points chauds de biodiversité mondiale, dans les zones côtières de l'Afrique de l'Ouest et de l'Afrique centrale autour du golfe de Guinée, dans les zones côtières de l'Afrique de l'Est et autour des Grands Lacs (Myers *et al.*, 2000; Küper *et al.*, 2004), et un tiers de sa flore a été évaluée comme étant potentiellement menacée d'extinction (Stévant *et al.*, 2019). Géologiquement, l'Afrique tropicale est hétérogène, avec une grande variabilité topographique en Afrique de l'Est, et une Afrique de l'Ouest et du Centre relativement peu élevée en altitude, bien que présentant quelques régions montagnardes comme la lignée volcanique du Cameroun (Guillocheau *et*

*al.*, 2018). La deuxième plus grande étendue de forêt tropicale humide (FTH) du monde se trouve dans la région guinéo-congolaise (Malhi *et al.*, 2013). En Afrique, les FTH sont divisées en deux grands blocs forestiers d'affinités floristiques similaires: les FTH du Centre-Ouest et les FTH de l'Est (Couvreur *et al.*, 2008; Droissart *et al.*, 2018; Brée *et al.*, 2020).

#### 1.1.4. Forêts tropicales humides et Annonaceae

Les FTH sont des formations dominées par des arbres à feuilles persistantes, avec une canopée fermée et généralement haute, sous laquelle poussent de nombreuses strates d'arbres, d'arbustes et d'herbes de sous-bois, mais aussi des lianes et des épiphytes (Whitmore, 1998; Corlett & Primack, 2011; Eiserhardt *et al.*, 2017). Elles se développent sous des climats chauds et humides avec un minimum de 2000 mm de précipitations annuelles et 24°C de température moyenne annuelle, et avec généralement une saison sèche nulle ou très courte (moins de quatre mois avec moins de 100 mm de précipitations) (Morley, 2000; Hill & Hill, 2001). Les FTH abritent une grande diversité d'espèces d'arbres appartenant à diverses familles emblématiques, telles que les Arecaceae (palmiers), les Apocynaceae, les Malvaceae, les Melastomataceae, les Moraceae, ou les Rubiaceae, pour n'en citer que quelques-unes (Turner, 2001).

Les Annonaceae sont l'une de ces familles tropicales emblématiques (Chatrou *et al.*, 2012a). Cette famille est principalement connue pour certaines de ses espèces produisant des fruits comestibles (corossol, cœur de bœuf, chérimole ; plusieurs espèces d'*Annona* L.), et pour l'huile essentielle d'ylang-ylang (*Cananga odorata* (Lam.) Hook.f. & Thomson), largement utilisée en aromathérapie et comme fragrance rendue célèbre par plusieurs parfumeries de luxe (Couic-Marinier & Laurain-Mattar, 2019). Certaines autres Annonaceae présentent également des propriétés pharmacologiques (Takahashi *et al.*, 2006) et sont utilisées par les communautés locales pour la médecine, l'alimentation et l'artisanat (Focho *et al.*, 2010; Bele *et al.*, 2011). Les Annonaceae sont composées d'environ 2400 espèces et d'environ 108 genres d'arbres, d'arbustes et de lianes, et sont principalement inféodées au FTH (Chatrou *et al.*, 2012b; Guo *et al.*, 2017), ce qui en fait un bon modèle pour étudier l'histoire évolutive des FTH (Couvreur *et al.*, 2008; Chatrou *et al.*, 2012a; Brée *et al.*, 2020). Plusieurs analyses moléculaires antérieures ont permis de déduire les relations au sein de la famille, ce qui a aidé à clarifier la systématique avec plusieurs sous-familles et tribus (Richardson *et al.*, 2004; Pirie *et al.*, 2006; Couvreur *et al.*, 2011a, 2019; Chatrou *et al.*, 2012b; Guo *et al.*, 2017). Au sein de la sous-famille des Annonoideae, la tribu des Monodoreae est composée de 11 genres et 92 espèces d'Afrique et de Madagascar (Guo *et al.*, 2017, Chapitre 2). Les espèces de Monodoreae sont principalement inféodées aux FTH, avec des capacités de dispersion sur de longues distances assez limitées (voir Chapitre 5), et les deux genres *Isolona* et *Monodora* ont surtout subi de la spéciation géographique (Couvreur *et al.*, 2011b). Les Monodoreae peuvent donc être considérées comme un bon proxy pour comprendre l'évolution et la diversification des FTH en Afrique

(Couvreur *et al.*, 2008). Mais les proxy sont discutables. En particulier, faire des extrapolations à l'ensemble de la flore à partir d'études sur des clades uniques, ou à des processus à l'échelle du continent à partir de processus à l'échelle locale, pourrait être un raccourci dans notre compréhension de l'évolution de la biodiversité. En effet, dans les FTH africaines, il a été démontré qu'au niveau populationnel, au lieu d'avoir une réponse commune, les espèces ont des réponses variées et spécifiques aux changements environnementaux (Helmstetter *et al.*, 2020a).

## 1.2. Les outils

### 1.2.1. Les spécimens d'herbier comme unité de base

L'exploration botanique du monde au cours des siècles passés a collecté des millions de spécimens de plantes séchées aujourd'hui archivés dans des herbiers (James *et al.*, 2018). Les spécimens d'herbier sont très précieux car ils fournissent des données importantes sur la morphologie de chaque plante, l'histoire de sa collecte, sa géographie, son habitat et son écologie, ainsi que ses noms vernaculaires et ses utilisations. Ils constituent le matériel de base pour la rédaction des monographies taxonomiques, qui sont la référence en matière de documentation de la biodiversité (Grace *et al.*, 2021). Plusieurs institutions ont entrepris de numériser les spécimens d'herbiers et les données qui leur sont associées, ce qui constitue une avancée dans les sciences de la biodiversité car cela facilite grandement l'accès à ces (Le Bras *et al.*, 2017; Soltis, 2017). Les agrégateurs de données, tels que le Global Biodiversity Information Facility (GBIF), facilitent également l'accessibilité des données en les centralisant, même si ces bases de données doivent être utilisées avec une extrême prudence (Maldonado *et al.*, 2015). En plus de ces vastes sources de données, les bases de données complètes géoréférencées et vérifiées sur le plan taxonomique apportent des ensembles de données géographiques de haute qualité prêtes à être utilisées. Pour l'Afrique tropicale, c'est le cas de la base de données RAINBIO (Dauby *et al.*, 2016). Cette base de données contient plus de 600'000 géoréférencements vérifiés représentant plus de 25'000 espèces de plantes, et a servi de base à l'amélioration de nos connaissances sur la biodiversité végétale d'Afrique tropicale (Sosef *et al.*, 2017; Veranso-Libalah *et al.*, 2018; Droissart *et al.*, 2018; Cosiaux *et al.*, 2018; Demenou *et al.*, 2018; Pironon *et al.*, 2019; Stévant *et al.*, 2019). Dans le chapitre 2, nous avons utilisé cet ensemble de données pour déduire les patrons de diversité générique et d'endémisme des angiospermes à travers l'Afrique, et les avons combinés à une « mégaphylogénie » (voir ci-dessous) pour déduire les patrons de diversité phylogénétique et identifier les berceaux et les musées de la diversité végétale (chapitre 2).

### 1.2.2. Phylogénies moléculaires

Les spécimens d'herbier sont également source d'un autre type de données précieuses : l'ADN des plantes. Bien que l'ADN contenu dans des plantes séchées être dégradé (Staats *et al.*, 2011), des extractions de qualité à partir des spécimens d'herbier peuvent être réalisées grâce à des protocoles d'extraction d'ADN optimisés (Taylor & Swann, 1994; Särkinen *et al.*, 2012), et à des technologies de séquençage de courts fragments d'ADN (Metzker, 2010). L'utilisation de l'ADN dans les sciences de la biodiversité a trouvé des adeptes pour l'identification des taxons, le fameux DNA-barcoding (Moritz & Cicero, 2004; Vijayan & Tsou, 2010), et aussi pour reconstruire l'histoire évolutive des espèces, via des modèles d'évolution moléculaire (Fitch & Margoliash, 1967). L'idée de base de la phylogénétique moléculaire est que le degré de divergence évolutive entre deux espèces est proportionnel aux différences entre les séquences moléculaires. À partir de là, le domaine de la phylogénétique s'est développé, et de nombreuses méthodes et outils ont été mis au point pour déduire l'histoire de l'évolution des espèces (e.g. Sanderson, 2002; Posada, 2008; Smith & O'Meara, 2012; Stamatakis, 2014; Nguyen *et al.*, 2015; Bouckaert *et al.*, 2019; Bromham, 2019). Initialement, les reconstructions phylogénétiques se concentraient sur quelques taxons et utilisaient un petit nombre de gènes. L'augmentation de la disponibilité des données de séquences -mais aussi l'augmentation des performances de calcul- a permis la reconstruction de « méga-phylogénies », c'est-à-dire d'arbres phylogénétiques contenant des milliers d'espèces (Chase *et al.*, 1993; Hilu *et al.*, 2003), et un nombre croissant de gènes (Hinchliff & Smith, 2014; Zanne *et al.*, 2014; Magallón *et al.*, 2015; Smith & Brown, 2018; Janssens *et al.*, 2020).

### 1.2.3. Phylogénomique

Les progrès des technologies de séquençage (Mardis, 2008, 2013, 2017; Shendure & Ji, 2008; Metzker, 2010; Rohland & Reich, 2012; Hu *et al.*, 2021) ont permis de séquencer de plus en plus de gènes, voire des génomes complets (Ng & Kirkness, 2010). Cela a déclenché de grandes avancées dans les études phylogénétiques avec l'essor de la phylogénomique, c'est-à-dire la phylogénétique avec des données de séquence à l'échelle du génome (Eisen & Fraser, 2003; Scornavacca *et al.*, 2020). Grâce à la disponibilité croissante de données de séquençage à grande échelle pour un large éventail d'organismes non-modèles (Ekblom & Galindo, 2011), les approches phylogénomiques améliorent nos connaissances sur l'évolution de l'arbre (ou des arbres) de la vie, en éclairant nos connaissances et en posant de nouvelles questions tant biologiques que méthodologiques (e.g. (Delsuc *et al.*, 2005; Pease *et al.*, 2018; Allio *et al.*, 2020; Smith *et al.*, 2020; Redmond & McLysaght, 2021; Valencia-Montoya *et al.*, 2021; Pavón-Vázquez *et al.*, 2021). Chez les plantes, plusieurs outils phylogénomiques spécifiques à certaines familles de plantes, tels que des kits d'amorces pour le séquençage ciblé, ont été développés pour répondre à des questions spécifiques à ces familles (Barrett *et al.*, 2016; Heyduk *et al.*, 2016; Reginato *et al.*, 2016; Pease

*et al.*, 2016; Morales-Briones *et al.*, 2018; Helmstetter *et al.*, 2020b; Koenen *et al.*, 2020; Stull *et al.*, 2020; Meleshko *et al.*, 2021). Dans le chapitre 3, nous avons utilisé un tel kit développé spécifiquement pour la famille des Annonaceae (Couvreur *et al.*, 2019), pour reconstruire un arbre phylogénétique robuste de la tribu des Monodoreae basé sur plus de 300 gènes nucléaires, afin de tester les limites entre les genres et les espèces. Un kit d’amorces pouvant cibler tous les angiospermes a également été conçu pour permettre un séquençage ciblé dans n’importe quel clade de plantes à fleurs (Johnson *et al.*, 2019), et il a été montré que la combinaison de kits « universels » et de kits spécifiques aux familles constitue une bonne stratégie pour limiter les biais dans les reconstructions phylogénétiques (Shah *et al.*, 2021; Yardeni *et al.*, 2021).

#### 1.2.4. Datation moléculaire

Un arbre phylogénétique représente les relations évolutives entre les espèces. Cependant, afin de représenter l’histoire évolutive du clade en question, l’arbre phylogénétique doit être ancré dans le temps. Ceci est fait avec la datation moléculaire et utilise la calibration des fossiles. L’idée de base de la datation moléculaire est que le temps de divergence entre deux espèces peut être mesuré par les différences entre deux séquences moléculaires (ADN, protéine), comme une « horloge moléculaire » (Zuckerkandl & Pauling, 1965). Cependant, les taux d’évolution des molécules ne sont pas constants dans le temps, entre les taxons ou entre les gènes, c’est pourquoi des modèles d’horloges moléculaires « relâchées » ont été développées pour prendre en compte cette hétérogénéité de taux (Sanderson *et al.*, 2004; Drummond *et al.*, 2006; Rutschmann, 2006). Les horloges moléculaires sont ensuite généralement calibrées par des fossiles datés géologiquement pour obtenir un arbre phylogénétique daté sur une échelle de temps de plusieurs millions d’années (Ho & Phillips, 2009; Sauquet, 2013).

#### 1.2.5. Modèles de diversification

Un arbre phylogénétique daté est un phylogramme, c’est-à-dire un graphique reliant les espèces avec leurs relations et leur rythme de divergence à partir de leur nœud ancestral. À partir de ce graphe, il est possible de déduire la dynamique de diversification du clade représenté. La diversification est l’équilibre entre la spéciation (divergence d’une nouvelle espèce) et l’extinction (disparition d’une espèce). Une multitude de modèles ont été développés pour déduire la dynamique de diversification à partir d’un arbre phylogénétique (Morlon, 2014), tels que pour modéliser les variations de taux de diversification entre les espèces (Rabosky, 2014; Höhna *et al.*, 2019; Maliet *et al.*, 2019), pour modéliser les variations de taux dans le temps (Morlon *et al.*, 2011), avec des variables environnementales (Condamine *et al.*, 2013), avec des états morphologiques ou géographiques spécifiques aux espèces (modèles SSE, Maddison *et al.* 2007, FitzJohn 2010, 2012, Goldberg *et al.* 2011, Goldberg and Igić 2012, Beaulieu and



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O'Meara 2016, Caetano *et al.* 2018, Nakov *et al.* 2019), ou pour modéliser des changements soudains dans les taux de diversification, affectant toutes les espèces de l'arbre (Stadler, 2011; May *et al.*, 2016). Une approche communément utilisée dans la modélisation de la diversification consiste à ajuster un ensemble de modèles différents sur l'arbre daté estimé, et à déduire à quel modèle les données observées s'ajustent le mieux, afin d'avoir une idée du processus modélisé sous lequel les données ont probablement été générées (e.g. Condamine *et al.* 2013).

Récemment, il a été suggéré qu'une infinité de dynamiques de diversification peuvent être modélisées à partir d'arbres phylogénétiques de taxons étendus, en raison de la non-identifiabilité des paramètres dans les modèles (Louca & Pennell, 2020). Cela a conduit à une interprétation telle que nous devrions abandonner ce type de modélisation (Pagel, 2020). Cependant, Helmstetter *et al.* (2021) ont suggéré que le problème de non-identifiabilité pourrait ne s'appliquer qu'aux modèles espèces-indépendants et temps-dépendant, pour lesquels les valeurs exactes des taux de spéciation et d'extinction ne peuvent pas être estimées, mais qu'il pourrait ne pas s'appliquer aux modèles clades-spécifiques ou caractères-spécifiques, concluant que nous devrions continuer à explorer l'utilisation de ces modèles, tout en étant conscients de leurs limites (Helmstetter *et al.*, 2021). De plus, dans la mesure où l'on se base sur des hypothèses, on s'intéresse davantage à l'adéquation relative de différents scénarios qu'aux valeurs exactes des paramètres (Morlon *et al.*, 2020; Helmstetter *et al.*, 2021).

### 1.2.6. « Tous les modèles sont faux, mais certains sont utiles »

De la reconstruction phylogénétique aux modèles de diversification, plusieurs outils présentés ci-dessus reposent sur la modélisation mathématique. Il est important de garder à l'esprit que « tous les modèles sont faux, mais certains modèles sont utiles » (Box, 1979). La première partie de cet aphorisme, « tous les modèles sont faux », indique qu'étant donné la complexité des systèmes biologiques, il est impossible de modéliser précisément le « vrai » processus. La seconde partie, « certains modèles sont utiles », indique qu'en dépit de cette complexité, certains modèles peuvent répondre aux préoccupations concernant le processus biologique en question, en étant aussi proches que possible du « vrai » processus. Le défi consiste donc à informer autant que possible le modèle de nos connaissances préalables du processus, afin de construire des modèles réalistes et plausibles. Par exemple, le développement des modèles d'horloge relâchée pour la datation phylogénétique mentionnés ci-dessus (Drummond *et al.*, 2006), ont été conçus à partir des modèles d'horloge constante (Zuckerkandl & Pauling, 1965), intégrant la connaissance préalable que les taux d'évolution moléculaire n'étaient pas constants entre les clades (Britten, 1986; Hasegawa & Kishino, 1989). De manière similaire, dans le cadre des modèles de diversification exposés ci-dessus, les modèles ajustés simplifient probablement trop la réalité, et certains modèles non considérés pourraient être plus proches du « vrai » processus que les

modèles considérés (Louca & Pennell, 2020). Cependant, nos croyances préalables sur la dynamique de la diversification réduisent la gamme des modèles ajustés (par exemple, les modèles avec des taux de spéciation ou d'extinction négatifs sont écartés car ils sont biologiquement impossibles, même s'ils pourraient mieux expliquer les données), et comme nous construisons les modèles sur la base d'hypothèses préalables, nous évaluons l'ajustement relatif (et non l'ajustement absolu) des différents modèles, ce qui, en fin de compte, nous informe sur l'hypothèse la plus probable (Morlon *et al.*, 2020).

Les différents modèles utilisés et ajustés tout au long de cette thèse ne modélisent peut-être pas exactement les « vrais » processus biologiques en question, mais ils reflètent la « vérité » autant que possible en incorporant le meilleur de nos connaissances préalables.

### 1.3. Plan de la thèse

Dans cette thèse, j'ai exploré le passé afin de comprendre le présent, en utilisant différentes échelles spatiales et temporelles. Je ne prétends pas présenter « l'histoire » de la flore tropicale africaine, mais plutôt « une » histoire de sa diversification. La thèse peut être divisée en deux grandes parties. La première partie est à grande échelle géographique et taxonomique, se concentrant sur l'ensemble de la flore à travers le continent. Nous avons décrit les modèles d'endémisme végétal en Afrique tropicale, et identifié les régions qui agissent comme des « berceaux » et des « musées » de la diversité des angiospermes au niveau générique (chapitre 2). La deuxième partie réduit les échelles géographiques et taxonomiques, et se concentre sur les FTH africaines, riches en espèces, et leur évolution, éclairée par l'étude de la tribu des Monodoreae. Pour ce faire, la systématique et la taxonomie des Monodoreae doivent être bien résolues, en particulier pour les deux genres *Uvari dendron* et *Uvariopsis* qui manquent d'une révision taxonomique récente. Ainsi, le chapitre 3 est consacré à la systématique des Monodoreae, pour laquelle nous avons reconstruit un arbre phylogénétique robuste en utilisant des données de séquençage ciblées et exploré les relations entre les espèces et les genres. De plus, le chapitre 4 est consacré à la révision taxonomique des genres *Uvari dendron* et *Uvariopsis* susmentionnés, avec la description détaillée de toutes leurs espèces, y compris plusieurs espèces nouvellement décrites. Enfin, le chapitre 5 étudie la biogéographie et la diversification des FTH africaines, en se concentrant sur les Monodoreae. Nous avons reconstruit une phylogénie moléculaire des Monodoreae, calibrée dans le temps, et appliqué plusieurs modèles de biogéographie et de diversification pour tester l'impact des changements environnementaux passés sur l'évolution de la tribu.

## 2. Berceaux et musées de diversité générique des plantes en Afrique tropicale<sup>#</sup>

Déterminer où les espèces se diversifient (berceaux) et persistent (musées) au cours de l'évolution est fondamental pour comprendre la distribution de la biodiversité et pour établir des priorités de conservation. Dans ce chapitre, nous identifions les berceaux et les musées de diversité générique des angiospermes en Afrique tropicale, l'une des régions les plus riches en biodiversité de la planète.

Les régions contenant des concentrations non aléatoires de taxons endémiques jeunes (néo-endémiques) et anciens (paléo-endémiques) ont été identifiées à l'aide des données de distribution de 1719 genres, combinées à un méga-arbre phylogénétique daté. Nous avons ensuite comparé les régions identifiées avec la couverture actuelle des aires protégées (AP) africaines.

Au niveau générique, la diversité phylogénétique et l'endémisme sont principalement concentrés dans la région biogéographiquement complexe de l'Afrique de l'Est. Nous montrons que les zones montagneuses sont des centres de néo- et de paléo-endémisme. En revanche, la région de FTH de la plaine guinéo-congolaise est caractérisée par des lignées anciennes à large distribution géographique. Nous avons constaté que le chevauchement entre les centres d'endémisme phylogénétique et les AP est élevé (> 85%).

Nous montrons le rôle vital joué par les montagnes qui agissent simultanément comme berceaux et musées de la biodiversité végétale en Afrique tropicale. En revanche, les FTH de plaine agissent principalement comme des musées de diversité générique. Notre étude montre que combiner des bases de données de distribution à grande échelle, vérifiées sur le plan taxonomique, et des méga-phylogénies permet de mieux comprendre l'évolution de la biodiversité végétale tropicale.

## 3. Systématique de la tribu des Monodoreae, avec un focus sur les genres *Uvari dendron* et *Uvariopsis*\*

Les Monodoreae (Annonaceae, Annonoideae) sont une tribu composée de 11 genres et 92 espèces principalement restreintes aux forêts tropicales humides d'Afrique. Elles ont des fleurs morphologiquement variables, mais peuvent être caractérisées par un port d'arbre ou d'arbuste, un indument de poils simples, et des monocarpes sessiles ou brièvement stipités. Tous les genres sont taxonomiquement bien circonscrits, à l'exception des genres *Uvari dendron* et *Uvariopsis*, riches en espèces, qui n'ont pas fait l'objet d'une révision taxonomique récente. La tribu des Monodoreae est phylogénétiquement bien soutenue par des travaux antérieurs qui ont déduit les relations phylogénétiques de la famille des Anno-

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\* Manuscrit en préparation

naceae, ou qui se sont concentrés sur des genres de Monodoreae particuliers. Cependant, les relations phylogénétiques des Monodoreae avec relativement peu de données en ce qui concerne l'échantillonnage taxonomique et le nombre de marqueurs moléculaires utilisés. Ici, nous avons généré un arbre phylogénomique robuste des Monodoreae, incluant 95% des espèces, avec plusieurs spécimens par espèce, basé sur plus de 300 gènes nucléaires. Nous avons utilisé deux approches, l'approche par concaténation et l'approche par arbres de gènes, pour déduire l'arbre phylogénétique des Monodoreae et tester les limites entre les genres et les espèces. Étant donné que les genres *Uvari dendron* et *Uvariopsis* n'ont jamais été complètement évalués phylogénétiquement, nous nous sommes concentrés sur ces deux genres. Tous les genres ont été retrouvés monophylétiques, sauf le genre *Uvariopsis* pour lequel l'espèce *Uvariopsis tripetala* (Baker f.) Schatz a été exclue. Nous avons donc réintégré le genre monotypique *Dennettia* et son unique espèce *Dennettia tripetala* Baker f. Les genres *Ophrypetalum* et *Sanrafaelia* ont été exclus de la tribu Monodoreae, et nous avons érigé une nouvelle tribu, Ophrypetaleae, pour accueillir ces deux genres frères. Au sein des genres *Isolona*, *Monodora*, *Uvariastrum*, *Uvari dendron* et *Uvariopsis*, on retrouve des nœuds faiblement soutenus et des conflits phylogénétiques entre les deux approches, ce qui suggère que des processus d'évolution au niveau de la population pourraient se produire dans ces taxons. Nos résultats soutiennent également, au niveau moléculaire, la description de plusieurs nouvelles espèces d'*Uvari dendron* et d'*Uvariopsis*, ainsi que plusieurs noms synonymes.

#### 4. Révision taxonomique des genres *Uvari dendron* and *Uvariopsis* d'Afrique tropicale\*

Les genres *Uvari dendron* et *Uvariopsis* (tribu Monodoreae, Annonaceae) sont deux genres des forêts tropicales humides d'Afrique, comprenant chacun 18 espèces décrites. Morphologiquement, *Uvari dendron* représente la fleur typique des Annonaceae, étant hermaphrodite avec trois sépales et deux verticilles de trois pétales, alors que *Uvariopsis* présente deux sépales et quatre pétales (sauf *Up. congolana* qui a trois pétales) et des fleurs unisexuées (sauf *Up. bisexualis*). Quatre nouvelles espèces d'*Uvari dendron* sont décrites : *Ud. citriodorum* Dagallier **nom. nov.**, *Ud. kimbozaense* Dagallier **sp. nov.**, *Ud. mossambicense* Dagallier **sp. nov.** et *Ud. pilosicarpum* Dagallier **sp. nov.** Les noms *Ud. giganteum* et *Ud. magnificum* sont réduits en synonymie avec *Ud. fuscum* en tant que deux nouvelles variétés *Ud. fuscum* var. *giganteum* **comb. nov.** et *Ud. fuscum* var. *magnificum* **comb. nov.** Chez *Uvariopsis*, une nouvelle espèce est entièrement décrite, *Up. oligocarpa* Dagallier & Couvreur **sp. nov.** et trois espèces potentiellement nouvelles sont décrites de façon préliminaire. Le nom *Up. globiflora* est réduit en synonymie avec *Up. guineensis* et regroupé comme la variété *U. guineensis* var. *globiflora* **comb. nov.** et le nom *Up. letestui* est réduit en synonymie avec *Up. solheidii* comme la nouvelle variété *Up. solheidii* var.

\* Manuscrit en préparation

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*letestui* **comb. nov.** La nouvelle variété *Up. congensis* var. *angustifolia* **var. nov.** est également décrite. Cette révision taxonomique fournit une taxonomie à jour d'*Uvariodendron* et d'*Uvariopsis* ainsi qu'une discussion sur leur morphologie, leur biologie de la pollinisation, leur dispersion des graines et leurs usages. Enfin, toutes les espèces sont cartographiées.

### **5. La macro-évolution des Monodoreae confirme le rôle de l'extinction et de la spéciation liées au soulèvement des montagnes et aux changements climatiques du Miocène dans les forêts tropicales africaines\***

L'Afrique tropicale a subi plusieurs changements climatiques et géologiques au cours du Cénozoïque. Ces changements ont affecté l'histoire de l'évolution des FTH, les amenant à se répartir en deux grands blocs distincts : un bloc en Afrique de l'Est et un bloc au Centre-Ouest. Plusieurs mécanismes ont été invoqués pour expliquer ce patron de distribution. En particulier, les FTH africaines sont supposées s'être étendues d'Est en Ouest dans une forêt tropicale « pan-africaine » pendant les climats favorables, et s'être contractées dans des blocs isolés pendant les périodes de climat plus sec. Cette dynamique d'expansion-contraction liée à l'oscillation climatique, appelée le mécanisme de « fragmentation-refuge », a été invoquée pour expliquer des espèces vicariantes et divergentes de manière synchrone dans les phylogénies moléculaires des clades de FTH. Au cours du Miocène, le refroidissement du climat et le soulèvement des montagnes ont entraîné l'aridification de l'Afrique tropicale et l'expansion des habitats ouverts au détriment des clades de FTH, qui ont probablement subi de l'extinction. Cependant, chez les plantes, ces mécanismes invoqués pour expliquer les patrons actuels de distribution des FTH, ont été déduits en se basant sur relativement peu de données en termes d'échantillonnage taxonomique et de marqueurs moléculaires. Ici, nous avons testé ces mécanismes en nous concentrant sur les Monodoreae, une tribu d'Annonaceae composée de 92 espèces restreintes au FTH africaines. Nous avons reconstruit un arbre phylogénétique presque complet, basé sur 32 gènes nucléaires, et daté avec une horloge moléculaire variable et une calibration par fossiles, dans un cadre bayésien. Nous avons reconstruit l'histoire biogéographique et la dynamique de diversification du clade. Nous avons trouvé que les Monodoreae sont originaires des FTH d'Afrique de l'Est il y a 25 Ma (million d'années), et se sont étendus vers l'Afrique centrale pendant le début et le milieu du Miocène, soutenant l'existence d'une forêt tropicale « pan-africaine » jusqu'il y a environ 13,5 Ma. Nous n'avons trouvé aucune preuve d'événements de vicariance synchrones dans les FTH au cours du milieu du Miocène, mais nous avons estimés des contractions de leur aire de répartition, probablement à cause de l'aridification en Afrique à cette période. Cependant, nos résultats suggèrent également que les blocs de FTH étaient plus

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\* Manuscrit en preparation

connectés qu'on ne le pensait auparavant durant le milieu du Miocène. Nous avons trouvé que les Monodoreae ont probablement subi une extinction soudaine au cours de la fin du Miocène, ce qui soutient l'hypothèse d'une réduction drastique des FTH liée à l'aridification de l'Afrique. Juste après cette extinction soudaine, nous avons trouvé des taux de spéciation élevés, ce qui suggère que la fragmentation et la reconnexion des FTH au début du Pliocène ont stimulé la diversification. Une telle diversification était probablement associée à l'augmentation de la paléo-altitude de l'Afrique à la fin du Miocène et au Pliocène, soutenant l'idée que le soulèvement de l'Afrique de l'Est est un facteur qui a favorisé la diversification.

## 6. Conclusion et perspectives

### 6.1. L'histoire en bref

Cette thèse a exploré la diversification de la flore tropicale africaine, en utilisant différentes échelles spatiales et temporelles. À l'échelle continentale, et en nous concentrant sur les angiospermes, nous avons trouvé que la région montagneuses d'Afrique de l'Est étaient à la fois des berceaux et des musées de diversité générique, tandis que les forêts tropicales humides (FTH) de basse altitude de la région guinéo-congolaise étaient des musées de diversité (chapitre 2). En nous focalisant sur les FTH, nous avons déduit que l'origine géographique des Monodoreae, une tribu d'Annonaceae, est apparue en Afrique de l'Est à la fin de l'Oligocène (chapitre 5). De là, la tribu s'est étendue vers l'Afrique centrale, soutenant l'existence d'une forêt pluviale panafricaine entre le début et le milieu du Miocène. Puis, au cours du milieu du Miocène, les FTH se sont probablement fragmentées mais nous suggérons qu'elles sont resté plus connectées que ce qui avait été suggéré précédemment. Au cours de l'aridification de l'Afrique tropicale à la fin du Miocène, les Monodoreae ont connu une extinction soudaine suivie de taux de diversification élevés, en raison de la fragmentation et de la reconnexion des TRF au début du Pliocène. Il est intéressant de noter que le soulèvement des montagnes africaines à la fin du Miocène et au début du Pliocène (principalement en Afrique de l'Est) a stimulé la diversification des Monodoreae. La topographie de l'Afrique de l'Est semble avoir joué un rôle important dans le façonnement des patrons actuels de diversité de la flore tropicale africaine. Le focus sur les Monodoreae a été rendue possible grâce à la clarification de la systématique de la tribu (chapitre 3), en combinaison avec la révision taxonomique des genres *Uvari dendron* et *Uvariopsis* (chapitre 4). En particulier, nous avons érigé la nouvelle tribu des Ophrypetaleae, réinvestit le genre monotypique *Dennettia*, et décrit une nouvelle espèce d'*Uvariopsis* et trois nouvelles espèces d'*Uvari dendron*, qui s'ajoutent aux trois nouvelles espèces que j'avais déjà décrites dans un article parallèle pendant ma thèse (Dagallier *et al.*, 2021).

## 6.2. Perspectives

Cette thèse apporte une nouvelle brique dans le mur de la connaissance de la biodiversité en Afrique tropicale. Bien que nous ayons utilisé les données et les méthodes les plus récentes pour les objectifs fixés, l'intégration d'un plus grand nombre de données pourrait apporter une plus grande précision. Par exemple, les données actuelles sur les occurrences géographiques des espèces, comme RAINBIO, sont le résultat de centaines d'années d'exploration botanique (Dauby *et al.*, 2016). En utilisant ces données dans le chapitre 2, nous avons complété l'image sur la distribution des anciennes et jeunes lignées que Fjeldså & Lovett (1997) avaient déjà commencé à décrire avec beaucoup moins de données sur la distribution des plantes. Cependant, dans certaines régions d'Afrique tropicale, les plantes sont sous-collectées ou les données ne sont pas accessibles, comme en Angola, au Nigeria ou en République du Congo (Sosef *et al.*, 2017). Ainsi, davantage d'efforts d'échantillonnage botanique ou de bases de données dans ces pays apporteront des informations précieuses sur les patrons de la biodiversité africaine. Dans ce même chapitre 2, nous avons obtenus les patrons de diversité phylogénétique et d'endémisme phylogénétique (en particulier de néo- et de paléo-endémisme) en utilisant le meilleur arbre phylogénétique des angiospermes calibré dans le temps que nous pouvions espérer à cette fin (Janssens *et al.*, 2020). Il comprenait environ 75 % des genres pour lesquels nous disposions d'une répartition géographique. Je m'attends à ce qu'un arbre phylogénétique incluant tous les genres affine les patrons estimés de diversité phylogénétique et d'endémisme. Plusieurs autres études ont reconstruit des méga-phylogénies d'angiospermes intégrant de plus en plus d'espèces (e.g. Hinchliff & Smith, 2014; Zanne *et al.*, 2014; Hinchliff *et al.*, 2015; Smith & Brown, 2018; Li *et al.*, 2019). La reconstruction de l'arbre phylogénétique complet de tous les angiospermes est un défi entrepris par le projet « Plant and Fungi Tree of Life » (PAFTOL) (Baker *et al.*, 2021). Un tel projet constitue une contribution robuste dans la compréhension des relations évolutives entre les taxons végétaux, d'autant plus qu'il est mené dans un cadre phylogénomique, c'est-à-dire en s'appuyant sur des données de génomique nucléaire grâce au séquençage à haut débit (Dodsworth *et al.*, 2019; Johnson *et al.*, 2019). La phylogénomique contribue à une meilleure compréhension de l'évolution de la biodiversité, mais apporte également de nouveaux défis, tels que le développement de nouveaux algorithmes capables de gérer une telle quantité de données dans la reconstruction d'hypothèses phylogénétiques (e.g. Minh *et al.*, 2013; Douglas *et al.*, 2021). Dans le chapitre 3, nous avons également vu que l'incorporation de centaines de gènes dans la reconstruction phylogénétique a conduit à la détection de conflits d'arbres de gènes dans les régions où une évolution réticulée s'est probablement produite. Cela nécessite de modéliser explicitement les processus d'évolution au niveau des populations (Zhang *et al.*, 2018; Bouckaert *et al.*, 2019).

Dans le chapitre 5, nous avons utilisé différents modèles pour déduire l'arbre phylogénétique daté, l'histoire biogéographique et la dynamique de diversification des Monodoreae. Comme indiqué dans l'introduction, « tous les modèles sont faux, mais certains sont utiles » (Box, 1979). Nous avons donc intégré le maximum de nos connaissances préalables dans les modèles. Par exemple, la datation moléculaire a été calibrée à l'aide de deux fossiles (*Endressinia* au nœud couronne des Magnoliineae, et *Futabanthus* attribué au nœud couronne des Annonaceae). Malheureusement, à ce jour, il n'existe aucun fossile attribué aux nœuds au sein Monodoreae dans les relevés paléobotaniques. L'hypothétique découverte future d'un tel fossile pourrait affiner le calibrage temporel de l'arbre de vie des Monodoreae. En ce qui concerne l'histoire biogéographique, nous avons utilisé le modèle Dispersion-Extinction-Cladogenesis (DEC) dans un cadre de maximum de vraisemblance (ML) pour reconstruire l'aire de répartition ancestrale des Monodoreae. Cela aurait également pu être réalisé dans un cadre d'inférence bayésienne (IB), permettant ainsi d'estimer l'incertitude des scénarios biogéographiques (e.g. Landis *et al.*, 2018; Lavor *et al.*, 2019), ou avec des modèles tenant compte des taux de diversification dépendant de l'aire de répartition, comme les modèles de type GeoSSE (Goldberg *et al.*, 2011; Caetano *et al.*, 2018). Ces modèles biogéographiques (DEC, GeoSSE) considèrent l'aire de répartition géographique de l'espèce comme des unités discrètes (dans notre cas : régions Ouest, Centre, Est et Madagascar). Mais l'aire de répartition géographique d'une espèce est un polygone en deux dimensions, et la modélisation de l'histoire biogéographique de l'espèce en utilisant une aire de répartition géographique continue est possible avec le modèle *rase* (Quintero *et al.*, 2015; Maestri *et al.*, 2019). L'utilisation de ces modèles alternatifs pourrait améliorer ou corroborer les inférences que nous avons réalisées avec le modèle DEC.

Dans le chapitre 3, nous avons vu que la tribu des Monodoreae est morphologiquement très diversifiée, notamment en ce qui concerne les fleurs, avec des espèces unisexuées (la plupart des *Uvariopsis*), syncarpées (*Isolona*, *Monodora*) ou ayant des pétales fusionnés (*Asteranthe*, *Hexalobus*, *Isolona*, *Monodora*, *Uvariastrum*, certains *Uvariopsis*). Une étude plus approfondie de l'histoire évolutive de ce clade pourrait être réalisée en reconstruisant l'état ancestral de ces caractères morphologiques (Sauquet *et al.*, 2017), ou en testant leur influence sur la diversification du clade avec des modèles de diversification état-dépendant (modèles SSE, Maddison *et al.*, 2007). Cependant, comme ces caractères n'ont évolué qu'une seule fois dans le clade (sauf la fusion des pétales), la détection d'un impact potentiel sur le taux de diversification reste statistiquement peu fiable (Maddison & FitzJohn, 2015).

### 6.3. Conclusion

En conclusion, cette thèse présente « une » histoire de la diversification de la flore d'Afrique tropicale, en mettant l'accent sur le clade Monodoreae inféodé aux FTH. En utilisant les données les plus



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complètes à ce jour et des méthodes de pointe dans les domaines de la phylogénomique, de la biogéographie et de la macroévolution, nous avons examiné le passé pour comprendre le présent. Cette contribution à une meilleure compréhension de la flore africaine, pourrait servir de base à l'amélioration de nos connaissances sur la biodiversité dans son ensemble, et aider -à son échelle- à atténuer la crise de la biodiversité que subit la planète.

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