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**Integrative taxonomy of macrofungi from the Albertine Rift**

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*To my father*

*To my mother*

*To my wife and my children*

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## Summary

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### **Integrative taxonomy of macrofungi from the Albertine Rift**

The fungi of the Albertine Rift have long remained poorly understood in terms of global species richness and the accuracy of the species concept used.

For these reasons, the study aimed at contributing to the understanding of Albertine Rift mycodiversity at the species level.

A species list was compiled using databases of collections from research missions carried out from colonial times to the present day, available at [www.botanicalcollections.be](http://www.botanicalcollections.be), and data compiled from the FICAC, FICC and FFTA flora volumes, available at [www.FFTA-online.org](http://www.FFTA-online.org).

The results showed 634 species representing 199 genera of basidiomycetes. However, comparison with the temperate mycoflora revealed more than one hundred species taxa with a name already accepted for a European species, supporting the need for revision of many African taxa. In addition, the exact number of large Albertine Rift fungi is limited by the fact that many species remain to be described. The estimated ratio of five flowering plants per macrofungal species indicated that more than 500 large fungal species remain to be described locally. Accordingly, this study contributed to the knowledge of Albertine mycodiversity by revising three little known genera (*Ripartitella*, *Armillaria* and *Laetiporus*) following an integrative approach for a more consolidated (holistic) species concept.

Using an integrative approach, three taxa are proposed as new species, and six taxa are redefined.

In the genus *Ripartitella*, *Ripartitella degreefii* is described as a new species endemic to the African Rift Valley Mountains and the West African islands of São Tomé. *Ripartitella brasiliensis* (Speg.) Singer, reported from Africa in previous studies, is redefined as a non-African but Neotropical endemic species.

The results showed that African *Armillaria* consists of two endemic species that share a common evolutionary history and whose distribution reflects a "highland-lowland" dichotomy. *Armillaria heimii* Pegler, conservatively considered here as s.l., is restricted to the eastern Afromontane region. *A. camerunensis* (Henn.) Courtec., here resolved as s.s., spans the dense lowland Guineo-Congo rainforest.

*Armillaria fuscipes* Petch and *Armillaria mellea* subsp. *mellea* are resolved in this study as not belonging to the African endemic lineage. *Armillaria fuscipes* may represent a lesser known species in the Melleioid or in the South American Australasian major clade. *Armillaria mellea* subsp. *africana*, previously reported from Kenya, is an invalid name. It corresponds to *A. mellea* within the *A. mellea* species complex.

African *Laetiporus*, previously considered to comprise a single species (*Laetiporus discolor*), are here resolved as a monophyletic Afromontane endemic lineage consisting of four species. *Laetiporus discolor* s.s. and s.l. are redefined, while *Laetiporus oboensis* sp. nov. and *L. tenuiculus* sp. nov. are proposed as new species. The status of *Laetiporus* sp. 1 from Ethiopia is still uncertain.

This study opens up new taxonomic perspectives for the genera *Ripartitella*, *Armillaria* and *Laetiporus*. Within *Ripartitella*, further collections from the Gregorian Rift montane systems are needed to confirm whether Pegler's (1977) collections are *R. degreefii* and to establish its distribution in the Great East African Rift.

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## List of acronyms and abbreviations

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|                 |                                                                                 |
|-----------------|---------------------------------------------------------------------------------|
| ARES            | Académie de Recherche et d'Enseignement Supérieur                               |
| BCCM            | Belgium coordinated collections of Microorganisme                               |
| BI              | Basian inference                                                                |
| BPP             | Bayesian Posterior Probabilities                                                |
| BR<br>Herbarium | Herbarium of Meise Botanic Garden                                               |
| CBS             | Centraalbureau Voor Schimmelcultures / Westerdijk Fungal Biodiversity Institute |
| CDB             | Convention sur la Diversité Biologique                                          |
| CTAB            | Bromure de cétyltriméthylammonium                                               |
| DNA             | Deoxyribonucleic acid                                                           |
| DRC             | Democratic Republic of the Congo                                                |
| E Herbarium     | Royal Botanic Garden Edinburgh Herbarium                                        |
| FFTA            | Fungus Flora of Tropical Africa                                                 |
| FICAC           | Flore illustrée des champignons d'Afrique centrale                              |
| FICC            | Flore Iconographique des Champignons du Congo                                   |
| ITS             | nuclear ribosomal Internal Transcribed Spacer                                   |
| IUCN            |                                                                                 |
| JBM             | Jardin Botanique de Meise                                                       |
| K Herbarium     | Kew Herbarium (Royal Botanic Gardens)                                           |
| LSU             | nuclear ribosomal large subunit                                                 |
| ML BS           | Maximum Likelihood Bootstrap                                                    |
| MUCL            | Mycothèque de l'Université Catholique de Louvain                                |

|           |                                                                           |
|-----------|---------------------------------------------------------------------------|
| MycorGL   | Réseau des Mycologues de la région des Grands Lacs                        |
| Obo NP    | Obo National Park                                                         |
| NP        | National Park                                                             |
| PCR       | Polymerase Chain Reaction                                                 |
| PNKB      | Parc National de Kahuzi-Biega                                             |
| PNV       | Parc National des Volcans                                                 |
| PNVi      | Parc National des Virunga                                                 |
| RPB2      | DNA-directed RNA polymerase II subunit                                    |
| Tef       | Translation Elongation Factor                                             |
| UCLouvain | Université Catholique de Louvain                                          |
| UICN      | Union International pour la Conservation de la Nature                     |
| UNESCO    | Organisation des Nations Unies pour l’Education, la Science et la Culture |
| UNIGOM    | Université de Goma                                                        |

## Chapter 1: General Introduction

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## 1.1. Introduction

Interest in fungi is growing due to their potential applications in various fields such as medicine, industry, biotechnology, pest control, mycoremediation, etc. However, over 90% of the fungi remain unknown, which equates to a conservative estimation of about 2 million species yet to be described (Niskanen et al. 2018; Niskanen et al. 2023). On a continental scale, most fungal species have been described in Europe, North America, and Asia. Only 9% of the world's known fungal species have been reported for Africa (Hawksworth & Lücking 2017; Cheek et al. 2020). As far as the large fungi (Basidiomycota, Ascomycota) are concerned, tropical Africa continues to be little surveyed. Based on the ratio of flowering plant species to large fungi (5:1 to 2:1), the total number of African large fungal species would range between 10,000 and 25,000. Of these, only 2,250 species are known, which means that ~75-90% remain to be discovered (Mueller et al. 2007).

Africa's Western Rift, known as the Albertine Rift, is one of the most biodiverse areas in Tropical Africa and is known to be of high conservation importance (Plumptre et al. 2019) and vulnerable to biodiversity erosion, which is rapidly increasing due to human activities and climate change (Klug & Hart 2006; Kenfack 2013; Ponce-Reyes et al. 2017; Ayebare et al. 2018). The region is home to 50% of Africa's birds and 40% of Africa's mammals. It is also home to about 20% of Africa's plants and amphibians, with more being described every year, as well as 14% of Africa's reptiles and 16% of Africa's butterflies (Plumptre et al. 2016; Ponce-Reyes et al. 2017, Ayebare et al. 2018). It also harbors approximately 1000 endemic species (mammals, birds, reptiles, amphibians, fish, butterflies, dragonflies, and plants) that are

restricted to the Albertine Rift (Plumptre et al. 2016; Plumptre et al. 2019). However, some segments of this biodiversity are unevenly recorded, and even are largely unsurveyed. This includes the Mycota.

With more than six thousand plant species, the Albertine Rift is thought to be potentially one of the most species-rich regions for fungi. Estimates based on the Mueller et al. (2007) ratio suggest that the region could host a putative number of larger fungi ranging from 1158 to 2896.

Few mycological studies, taxonomic or ecological, have been completed in the Albertine Rift and, more generally, in the entire Afromontane area. Nevertheless, some scientific works are worth mentioning. These include the comprehensive surveys of the poroid fungi of the Kahuzi-Biega and Ruwenzori mountain ranges in D. R. Congo (Balezi 2013; Balezi & Decock 2009; Decock et al. 2021), as well as Ipulet's (2005) monograph on the polypores of Kibale and Bwindi National Parks in Uganda. Other monographs have been focused on the edible mushrooms of the region, ([www.efta-online.org](http://www.efta-online.org); [www.archives.biodiv.be/mycorgl](http://www.archives.biodiv.be/mycorgl); Härkönen et al. 2003; Degreeef et al. 2016; Rizinde 2016). However, the scientific literature is still insufficient in terms of modern, multiple approaches and geographical coverage. This gap is deepened by the fact that most published macrofungi have been named on the basis of the morphological species concept with reference to European mycofloras. This has led to numerous misidentifications of some African taxa (Rammeloo & Walley 1993; Milenge et al. 2021). A recent study reported more than one hundred taxa with names based on European morphological species (Rizinde et al. 2023b).

Understanding myc biodiversity, as defined by the regional species list, is limited by the definition of a precise species concept and by the

expected extent of undiscovered species. There is a closer interdependence of the “fungal diversity” and the “species concept” (Rojas 1992). However, the accurate circumscription of a 'species' is not always easy. It depends on a number of variables that delimit the species. Several variables have been proposed for a consolidated concept, but researchers seem to agree that the most operational criteria are morphological, biological, ecological, and phylogenetic.

The morphological species concept is related to the morphological divergence that occurred over time. In this point of view, individuals of the same species are congruent in macro- and micro-morphology of quantitative and qualitative characters, especially of the basidiocarp. Furthermore, one should also mention that morphological species concepts are based on type specimens. Applying morphological species concepts requires the definition of or the examination of type specimens. However, in many cases, and this is obviously and desperately the case for the African Mycologists, type specimens are hardly available. In addition, some type specimens are very old and may have been lost or destroyed.

The biological species concept considers reproductive isolation. Accordingly, interbreeding natural groups, reproductively isolated from other groups, are regarded as one biological species. However, applying biological species concept to the Mycota requires in many cases culturing techniques, single spore isolation, and in vitro mating experimentation. This remains challenging for many fungal species that do not or poorly grow, or for which spores germination is hardly achievable.

The ecological species concept refers to species adaptation. In the sense of Van Valen (1976), a species is “a lineage (or closely related

set of lineages) that occupies an adaptive zone that is minimally different from that of any other lineage within its range and that evolves separately from all lineages outside its range”. More operationally, species adaptation and species distribution are modulated by biotic and abiotic environmental conditions that undoubtedly play a role in the speciation event.

The current phylogenetic species concept is based on DNA sequence divergence. It is based on the principle of Genealogical Concordance Phylogenetic Species Recognition (GCPSR) as defined by (Taylor et al. 2000), which suggests the use of more than one gene genealogy.

This study aimed firstly to establish the current “state” of fungal diversity (regional list), and secondly to attempt to contribute to provide consolidated species concept for several groups, as most African taxa defined on the basis of morphological species concept require revision (Rammeloo & Walley 1993; Buyck et al. 2013). The integrative approach was then tested on three little known genera of differential ecological and economic importance in both natural and anthropic ecosystems, including *Ripartitella* Singer, *Armillaria* (Fr.) Staude and *Laetiporus* Murrill. Applying integrative taxonomy to these genera would contribute to the better characterization of these species locally in the Albertine Rift, but also at a continental scale.

*Ripartitella* is a small and rare white decaying fungus whose distribution is restricted to the tropics. In tropical Africa, it is an uncommon genus, known by a single species, *Ripartitella brasiliensis* (Speg.) Singer, reported with a disjunct distribution in the equatorial island west of Sao Tomé (Desjardin & Perry 2017) and in East Africa, Kenya, Tanzania and Uganda (Pegler 1977). However, *R. brasiliensis*

was originally described from the Neotropics and both Desjardin & Perry (2017) and Pegler (1977) noted that the African specimens differed from the Neotropical specimens in lacking hymenial cystidia. *Ripartilla* was not reported from the Albertine rift, but a recent intriguing collection, characterized by the presence of hymenial cystidia, led us to question its identity and the identity of other specimens from Africa. The species is redefined in Africa.

*Laetiporus* is a polypores genera belonging to the brown rot genera. *Laetiporus* species play an important ecological role in forests as tree parasite and wood decomposer, participating in carbon cycling. This role is important for forest resilience. In Africa, but also in the Neotropics, *Laetiporus* is also known as a pathogen of planted trees, used for fuel wood, including *Eucalyptus*, impacting the local economy. It is also an edible fungi, consumed locally.

*Laetiporus* has been well surveyed in the last decade, in many areas worldwide, including the holarctic region, East Asia and the Neotropics but it remains little known in Tropical Africa. It contains 19 phylogenetic species worldwide (Song et al. 2018) with a single taxon known in tropical Africa, *L. discolor* (Klotzsch) Corner (Ryvarden et al. 2022). *Laetiporus discolor* was previously reported in Tropical Africa under the name *L. sulphureus* (Bull.) Murrill (Ryvarden and Johansen 1980), which applied to a species that for a long time, was considered worldwide in distribution. In a global phylogenetic study of *Laetiporus*, Song and Cui also reported a *Laetiporus* sp., originating from South Africa, as an unresolved clade H, so far unidentified.

*Armillaria* also is an important basidiomycete in forest ecosystems, participating in nutrient recycling. It is an important pathogen of trees in natural ecosystems but also has the ability to jump

to anthropic ecosystems causing damage to perennial crops or trees. It is e.g., pathogens on *Eucalyptus*, *Coffea* spp. (coffee), *Theobroma cacao* (cocoa), *Ananas comosus* (pineapple), and *Musa* spp. (banana). In fact, few macrofungal pathogens are known from the region.

*Armillaria* has been reported in the Albertine Rift under names originally coined for temperate, African, or south-east Asian species (e.g., *Armillaria borealis* Marxm. & Korhonen, *A. cepistipes* Valen., *A. heimii* Pegler, or *A. fuscipes* Petch) (Degreef et al. 2016; Rizinde 2016). The taxonomy of African *Armillaria* has never been fully resolved, however, with many confusions (Pegler 1986; Watling 1992; Pérez-Sierra et al. 2004; Coetzee et al. 2005; Mwenje et al. 2006; Ota et al. 2011; Roux and Coetzee 2016; Koch et al. 2017; Coetzee et al. 2018). Their origin also and human mediated inter continental movement were several times questioned. For instance, Watling (1992) suggested that *A. fuscipes*, described from Sri Lanka, was accidentally introduced there from specimens originating in East Africa.

The integrative taxonomy applied here permitted to clarify the taxonomic scheme of *Ripartitella* and *Laetiporus*. Three new taxa, namely *Ripartitella degreefii*, *Laetiporus oboensis* and *L. tenuiculus*, are described in the following chapters. The taxonomic concepts of *Armillaria* species reported to occur in Tropical African, of which especially *A. camerunensis*, *A. heimii*, *A. fuscipes*, and *A. mellea* subsp. *africana* were revised and clarified.

New perspectives for future studies of African fungi in general and the genus revised in this work are given in the general conclusion.

## 1.2. Outline of the thesis

The aim of the thesis is twofold and interdependent:

1. To make an estimate of the potential diversity and list the species present in the region.
2. As diversity depends on the concept of species, the study will provide a consolidated concept of species of three lesser-known genera of the region: *Ripartitella*, *Armillaria* and *Laetiporus*.

With this in mind, the thesis is structured as follows:

### Chapter 1: General introduction

This chapter is devoted to defining the problematic context of the study of African fungi in general and the Albertine Rift fungi in particular. These are generally less well known. It also justifies the importance of a precise definition of the concept of species in order to master mycodiversity and enhance its value in various fields, especially in conservation.

### Chapter 2: Study area

The chapter describes the Albertine Rift, focusing on Virunga NP and Kahuzi-Biega NP, which were the main areas sampled. The geographical location and biodiversity of this region of Africa are presented.

The third chapter lists the species of the Albertine Rift and discusses the accuracy of the species concept used, especially in comparison with the European mycoflora. The results obtained confirm the need for a taxonomic revision of most African taxa.

The revision of the genera *Ripartitella*, *Armillaria* and *Laetiporus* is the subject of chapters four, five and six respectively.

Chapter 7 presents the discussion and general conclusions, as well as the perspectives that have emerged from this research, particularly in terms of taxonomy.

Materials and methods are presented in the individual chapters:

The methods used to compile the species list of the region (Objective 1) are presented in Chapter 3.

The methods used to revise the genera *Ripartitella*, *Armillaria* and *Laetiporus* (Objective 2) are presented in chapters 4, 5 and 6 respectively.

List of publications

The results of the thesis have been the subject of two published articles, one submitted article and one article in progress.

1. Jean-Claude Rizinde Hakizimana, François Muhashy Habiwaremye, Assumpta Mukandera, Héritier Milenge Kamalebo & Jérôme Degreef (2023). First checklist of the African Great Lakes Region basidiomycetes, *Geo-Eco-Trop.*, 46.3: 351-371
2. Jean-Claude Rizinde Hakizimana, Mario Amalfi, Jérôme Degreef, Dennis Desjardin & Cony Decock (2023). *Ripartitella degreefii* (Tricholomataceae), a new species from tropical Africa, *Phytotaxa* 597 (3): 195–207
3. Jean-Claude Rizinde Hakizimana, e, Mario Amalfi, c, Alphonse Balezid, and Cony Decock (2023). *Laetiporus*

(Laetiporaceae, Basidiomycota) in Tropical Africa. *Laetiporus* (Laetiporaceae, Basidiomycota) is represented by a single Afromontane lineage and four species in Tropical Africa, including *Laetiporus discolor*, *Laetiporus oboensis* sp. nov., *Laetiporus tenuiculus* sp. nov., and *Laetiporus* sp. 1., Mycologia. submitted manuscript.

4. Tropical African *Armillaria*: The status of *Armillaria camerunensis* (Henn.) Courtec. *Armillaria heimii* Pegler, *Armillaria fuscipes* Petch, and *Armillaria mellea* (Vahl) P. Kumm. in Tropical Africa. Manuscript in Progress

## Chapter 2. Study site

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## 2.1. Albertine Rift

### 2.1.1. General presentation

The Albertine Rift is the western branch of the Great African Rift and extends over 1380 km long, from the northern tip of Lake Albert to the southern tip of Lake Tanganyika and is approximately 150 km wide (Languy and de Merode 2006). It encompasses natural ecosystems across the international borders of the Democratic Republic of Congo, Uganda, Rwanda, Burundi and Tanzania. The total area of the Albertine region is about 313,000 km<sup>2</sup>, which represents 1% of the African continent (Plumptre et al. 2007; Stabach et al. 2009; Plumptre et al. 2016).

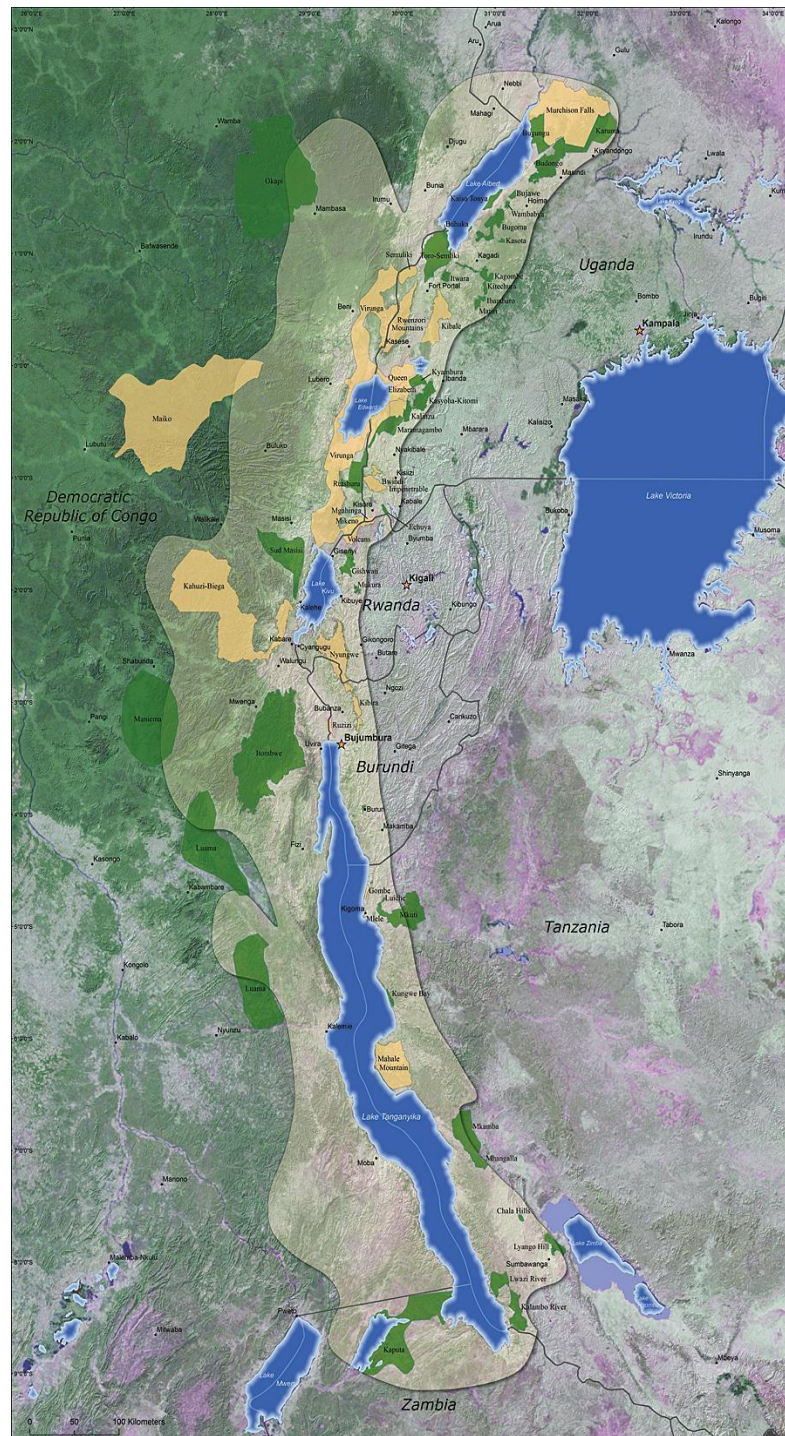


Figure 2.1: Map of the Albertine Rift region and protected areas (Stabach et al. 2009)

The Albertine Rift contains a variety of habitats favorable to high biodiversity and endemism, ranging in altitude from 600m to 5100m.

### 2.1.2. Relief and hydrography

From North to South, the Albertine Rift includes the lakes Albert, Edouard, Kivu and Tanganyika. Lake Edouard is fed by several rivers, including the Rutshuru. It drains into Lake Albert via the Semliki River.

Lake Kivu is drained by the Ruzuzi River into the Tanganyika, and Lake Tanganyika is drained by the Lukuga River into the Congo River.

The Congolese Albertine Rift is crossed by large continuous mountain ranges, the most important of which are the Ruwenzori and Virunga mountain ranges, the Kahuzi-Biega and Itombwe Forest Reserve (RFI) mountains, the Marungu, Mount Kabobo Reserve (RMKA) and the mountain systems in the eastern part of Maiko NP (Fig. 1.2) (Kambale et al. 2022, Mangambu 2013, Plumptre et al. 2007).

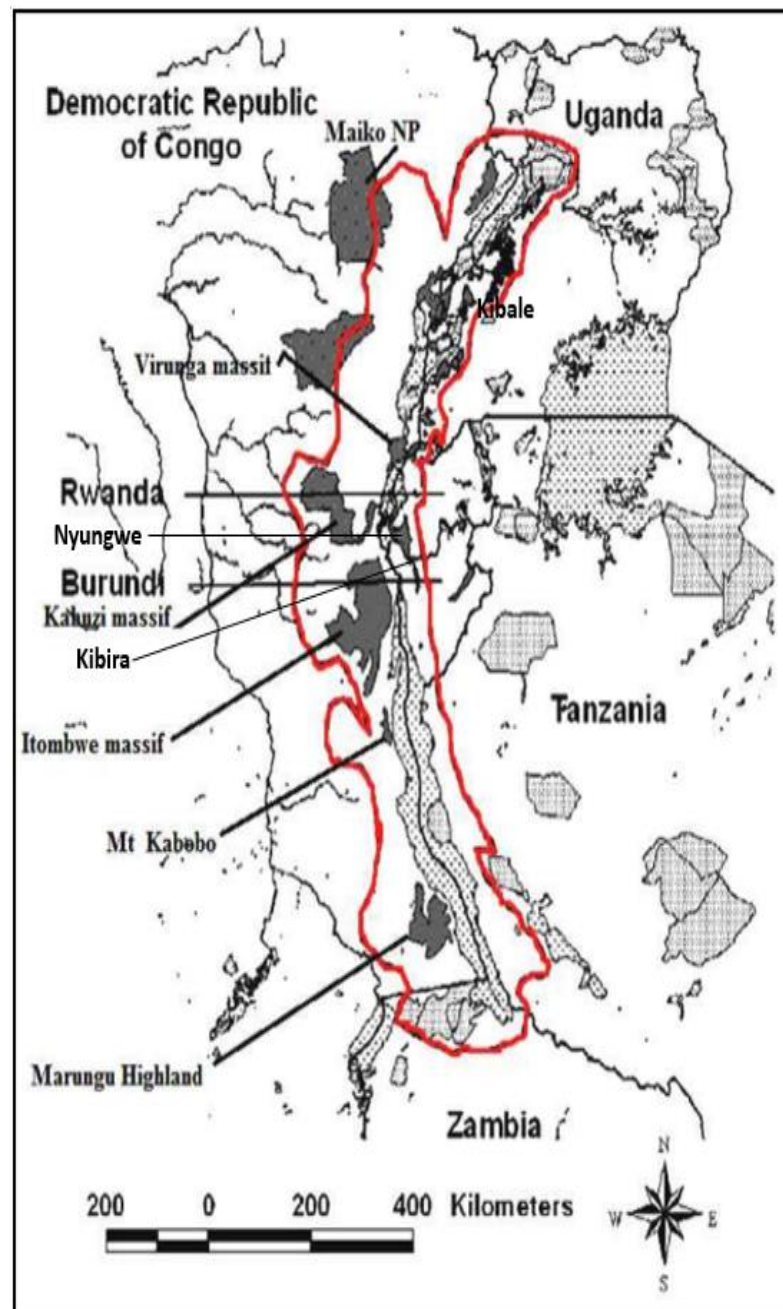


Figure 2.2: Albertine Rift mountain ranges (Plumptre et al. 2007): The main mountain ranges of the DR Congo are: Virunga, Kahuzi-Biega, Itombwe, Marungu and the Mont Kabobo Reserve (RMKA) and part of the Maiko National Park (PNM) mountain ranges.

### 2.1.3. Biodiversity and Conservation

Conservation of the Albertine Rift began in 1925 with the creation of "Parc National Albert", now Virunga NP. It was the first national park in Africa. Other protected areas were established in Uganda, Rwanda, Burundi, and Tanzania in the 1930s, and several were upgraded from reserves or hunting concessions to national parks in the 1950s and 1960s in Uganda and Tanzania, and later in Rwanda and Burundi. Much of the establishment of protected areas was aimed at protecting large mammals such as elephants (*Loxodonta africana*), hippopotamuses (*Hippopotamus amphibius*), mountain gorillas (*Gorilla beringei beringei*), and lions (*Panthera leo*), following observations of declining numbers due to human activities including hunting (Ayebare et al. 2018). Due to the diversity of its ecosystems, the Albertine Rift has a high level of biodiversity. The high biodiversity is a result of diverse habitats which are determined by the elevation range and climate patterns.

It is part of the East Afromontane Biodiversity Hotspot. There are 6658 plant species, 402 mammals, 1061 birds, 171 reptiles and 118 amphibians. There is a high degree of endemism in the subregion (Fig. 1.3). For example, out of a total of 584 plant species recorded in the Ruwenzori, 75 species occur only in this massif, an exceptionally high endemism rate of 13%. In Virunga National Park, 2077 plant species have been recorded, of which 230 are endemic to the Albertine Rift and 10 are threatened (Plumptre et al. 2003; Devers and Vande weghe 2006).

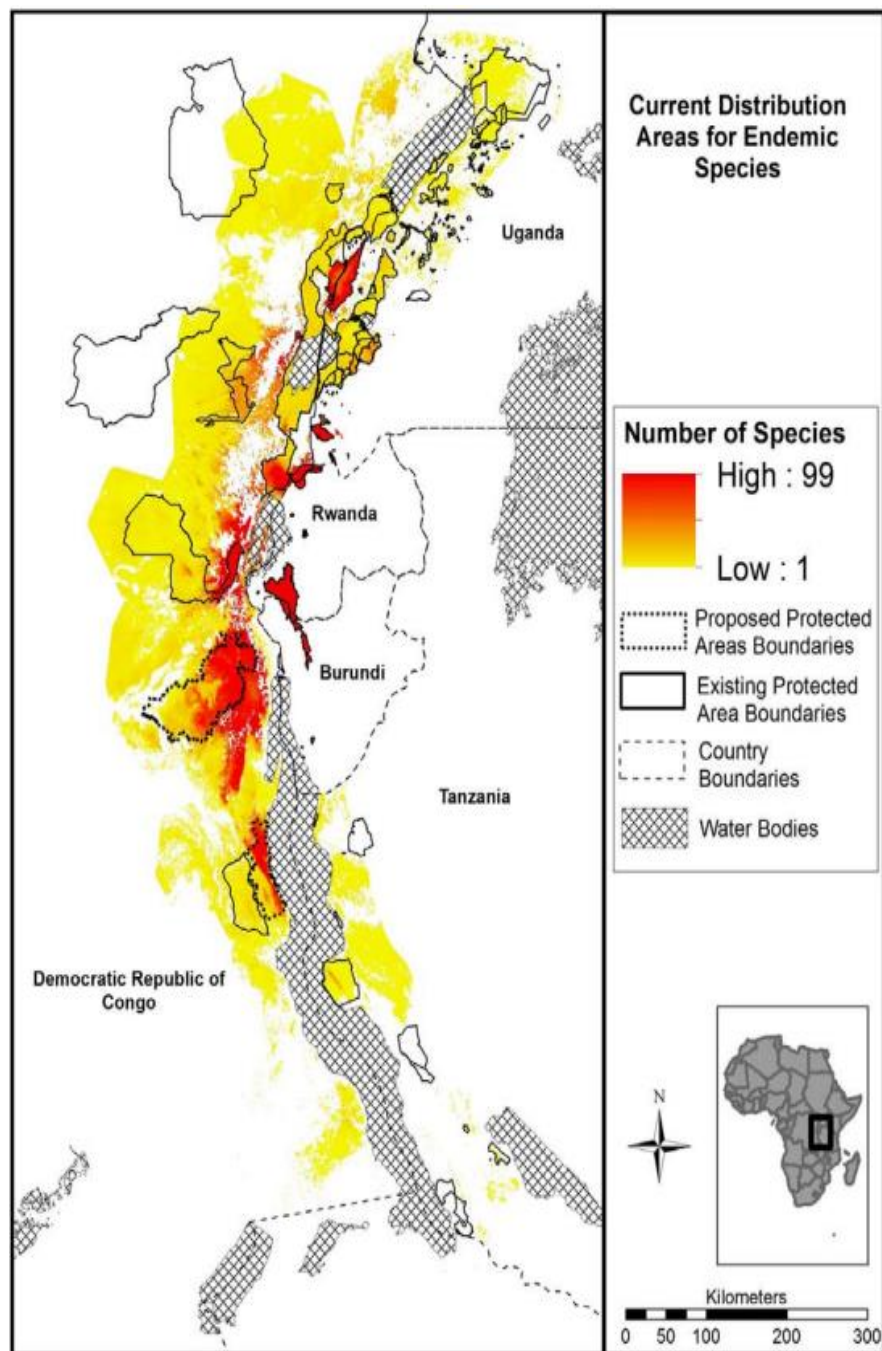


Figure 2.3: Richness of endemic plant species: Fig. 2.3 shows that mountain ecosystems have a high richness (red) of endemic species (Ayebare et al. 2018).

The Albertine Rift is home to more than 50% of Africa's birds, 40% of its mammals, 20% of its plants and amphibians, 14% of its reptiles and 16% of its butterflies.

The Albertine Rift is a very important region for biodiversity conservation and includes many contiguous protected areas across the international borders of DR Congo, Uganda, Rwanda and Burundi. For more efficient conservation, the contiguous protected areas have been grouped into landscapes. According to Plumptre et al. (2016), there are 6 landscapes within the Albertine Rift:

- Murchison-Semliki Landscape

This area is in western Uganda. It stretches from Murchison Falls National Park in the north of the country down the eastern shore of Lake Albert to Semliki Wildlife Reserve.

- The Greater Virunga Landscape

It straddles the borders of south-western Uganda, northern Rwanda, and eastern DR Congo. The Greater Virunga Landscape is sometimes referred to as the Central Albertine Rift. It includes the Rwenzori Mountains NP (Uganda), Bwindi NP (Uganda) Virunga NP (DR Congo), Queen Elizabeth NP (Uganda), Volcanoes NP (Rwanda), and Kibale NP (Uganda).

- Maiko-Itombwe Landscape in Eastern DR Congo

It includes the Maiko and Kahuzi Biega NP, the Tayna, Kisimba-Ikobo and Itombwe Natural Reserves, and some proposed community reserves.

- Congo-Nile Landscape:

It straddles the border between southern Rwanda and northern Burundi. It includes the Nyungwe (Rwanda) and Kibira (Burundi) National Parks, the small remnant forest reserves of Gishwati and Mukura in Rwanda, and Bururi and Rumonge-Vyanda in Burundi.

- Greater Mahale Landscape

The Greater Mahale Landscape in western Tanzania includes the Mahale Mountains NP, the Masito-Ugalla region, the Sitebi Highlands and the Wansisi Hills.

- Marungu-Kabobo Landscape

This landscape includes the Marungu Highlands, Kabobo National Park and Luama Katanga Reserve, Gandja South Reserve, Gandja North Reserve, Elombwe Marsh. The Kabobo-Luama Landscape is located in the south-eastern Democratic Republic of Congo (DRC) on the western shore of Lake Tanganyika.

#### 2.1.4. Threat

Most of the endemic species of the Albertine Rift are found in mountain ranges. The region is affected by high population growth. Human activities such as agriculture and fuelwood harvesting lead to habitat conversion. Habitat conversion has claimed almost 40% of the average species range, and projections suggest that 75% of remaining habitat will be lost by 2080. There are several endangered species in the region. 34 endemic species are currently listed as threatened on the IUCN Red List, but this is an underestimate. Global climate change affects the Albertine Rift. High-altitude ecosystems and the endemic species they support are under immediate threat, with their suitable area predicted to shrink rapidly over the next few decades (Ponce-Reyes et al. 2017; Ayebare et al. 2018).

## 2.2. Virunga National Park

### 2.2.1. Geography

Virunga NP is Africa's oldest park, established in 1925, and one of the most biodiverse areas in the world. Virunga NP is located on the border between the Democratic Republic of Congo and Uganda, and the DR Congo and Rwanda. It lies on the western branch of the East African Rift.

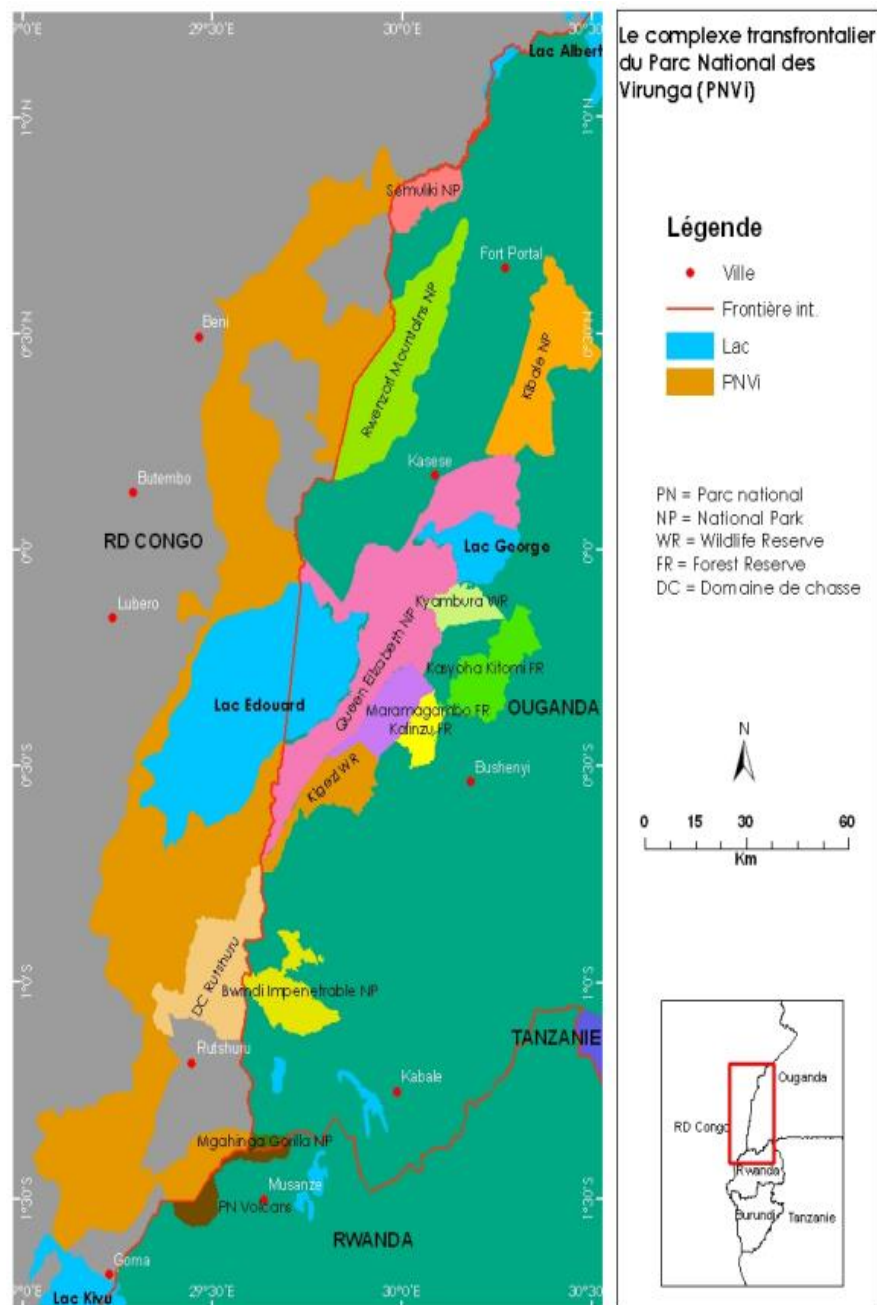


Figure 2.4: Map of Virunga NP in the Central Albertine Rift (Aveling et al. 2014)

Covering an area of 784 368 ha, Virunga NP is bounded to the north by the Puemba River at 00°56'N and to the south by the island of Tshegera in Lake Kivu at 01°39'S. It is almost 300 km long, with an average width of 50 km. Virunga NP has a very rugged topography and therefore a great diversity of ecosystems at altitudes ranging between 750 and 5,000 m (Languy and de Merode 2006; Languy and De Wasseige 2008; Bodson et al. 2008; UNESCO 2018).

### 2.2.2. Physiography

Virunga NP is divided into southern, northern, and central sectors.

The southern sector includes the active Nyamuragira and Nyiragongo volcanoes in the west and the extinct Mikenno, Karisimbi, Visoke and Sabyinyo volcanoes in the east. It extends eastwards into Rwanda's Volcanoes NP and Uganda's Gorilla Game Reserve.

The central sector consists of the alluvial plain of the Rwindi-Rutshuru rivers. This plain, with an average elevation of 983m, is bordered to the west by the Mitumba Mountains range (average elevation 2000m) and to the east by the Ishasha River. This boundary is in fact conventional, and the same type of landscape extends into the neighboring Queen Elizabeth NP. The northern and central sectors are separated by Lake Edward, an immense water reserve covering an area of about 225 000 ha at an altitude of 916 m.

The northern sector consists mainly of the alluvial plain of the Semliki River, which rises at Ishango and drains Lake Edward into Lake Albert. The open savannahs of the south are gradually being replaced by the vast equatorial rainforest of the central Semliki. This plain is squeezed between the western ridge of the Graben and the Congolese face of the Ruwenzori, an ancient and violently uplifted

range whose highest peak (Marguerite Peak, 5119m) dominates the plain (Robyns 1948; Maldague 1978, Habiyaemye and Ruremesha 2020).

### 2.2.3. Climate

The climatic conditions in Virunga NP are very diverse. This is partly due to the rugged terrain. Secondly, the Central African Graben is the region where three atmospheric currents converge and meet, including the Atlantic trade wind, the Indian Ocean trade wind and the Northeast trade wind that blows from the Nile valley.

Data from weather stations in the south (Rumangabo), center (Rwindi) and north (Mutsora) show that the climate is bimodal, with two rainy seasons (September-December and March-May) and two dry seasons (January and July). The wettest months are April and October. The average annual temperature is between 20° and 23° C.

Rainfall and temperatures vary with altitude and relief. The gradients are very steep in places. The plains south of Lake Edouard are warm and receive less than 1,000 mm of rain a year on average, while the saddle between the Karisimbi, Mikenno and Visoke volcanoes at an altitude of 3,000 m receives more than 2,000 mm of rain. The flanks of the Ruwenzori receive large amounts of rain, while the highest peaks above 4,000 m are dry. Rainfall and cloud cover are generally highest on the flanks of the Ruwenzori and volcanoes at around 2,700 m, with local fog effects adding to the rainfall. Above 3,500 m, night frosts are common (Robyns 1948; Languy and de Merode, 2006; Kenfack 2013).

#### 2.2.4. Geology and Soil

Two volcanoes in the southern sector of Virunga NP are still active. These are the Nyamuragira and Nyiragongo volcanoes. The soil derived from the lava and ash is very rich in alterable minerals that can release large quantities of nutrients (Lebrun 1960). The Rwenzori is a block of metamorphosed rock (mainly gneiss) that has been tilted and uplifted in the middle of the Albertine Tectonic Rift, dividing it into two branches: the Semliki branch along the axis of the rift and the Lake George branch further east. The plains to the north and south of Lake Edward are underlain by quaternary alluvium, which produces sandy or sandy-clay soils, but also includes horizons of volcanic dust. The oldest volcanic formations date from the Miocene period (12 million years ago), but some at the foot of active volcanoes are very recent. These volcanic formations produce very permeable soils with low water-holding capacity, which are extremely fertile. The soils of the plains around Lake Edward have also been influenced by the explosive volcanic zone of Queen Elizabeth NP in Uganda, to the east of Virunga NP (Robyns 1948; Maldague 1978).

Geological resources are reported in Virunga NP, especially oil. Its exploitation poses a potential threat to protected species (UNESCO 2018).

### 2.2.5. Biodiversity

Virunga National Park is the richest protected area on the African continent in terms of biological diversity (Table 1.1). It is home to a large number of species that are endemic to the Albertine Rift, i.e. found nowhere else in the world, including species listed in the IUCN Red List of Threatened Species.

Table 2.1: Biodiversity of Virunga NP (Langu & De Wasseige 2008; Plumptre et al. 2016).

| Taxon      | Endemic species | Threatened species | Total Species |
|------------|-----------------|--------------------|---------------|
| Mammals    | 21              | 13                 | 217           |
| Birds      | 25              | 11                 | 706           |
| Reptiles   | 11              | 0                  | 109           |
| Amphibians | 21              | 10                 | 78            |
| Plants     | 230             | 10                 | 2 077         |

### 2.2.6. Vegetation

The Virunga NP is located at the confluence of three biogeographical regions:

- **the Sudano-Zambezian region:**

This zone corresponds to the grassy and shrubby savannahs of the Ruthuru and Semliki sub-districts sensu Robyns (1948). Savannah areas often appear to be richer than predominantly wooded areas. With a species coefficient of 1.81 sensu Lebrun (1960), this region is very species-rich.



Figure 2.5: © Rizinde 2018: Ishango savannah with *Acacia*

- **the Guineo-Congolian region:**

It is a lowland rainforest, represented in the middle Semliki (Languy and De Merode 2006). The region corresponds to the North-East sub-district sensu Robyns (1948).



Figure 2.6: Lowland rainforest with *Celtis philippensis* Blanco (0.448255N, 29.735564E, 1020m) © Rizinde 2016

- **the Afromontane region** with its range of orophilous species found on volcanoes and mountain ranges above 1800 m (Hauman, 1933; Robyns 1948; Lebrun 1957, Delvingt et al. 1990):

In Virunga NP, Afromontane region corresponds to the Volcanoes, lava plain and Rwenzori sub-districts sensu Robyns (1948). The Volcanoes sub-district may have a very high floristic community coefficient sensu Lebrun (1960) with the Ruwenzori sub-district, reflecting a clear similarity in essential climatic conditions. The flora of the lava Plain subdistrict sensu Robyns (1948) is reported to be richer than that of the Ruwenzori. According to Lebrun (1960), floristic similarity depends on ecological analogy. This concept considers the number of common species and the total number of species in the area.

Temperature decreases by 5.2–6.5 °C with each 1000 m increase in altitude on mountains in the Tropics. Vegetation types vary with Altitudinal ranges.

Robyns (1948) and Lebrun (1957) distinguished the following vegetation types associated with substantial altitudinal variation.

- the submontane forest (1150-1750 m);
- the montane forest (1750-2500 m);
- the bamboo (*Sinarundinaria alpina* K. Schum) forest (2300 and 2600 m);
- the *Hagenia-Hypericum* woodland (2600-3100 m);
- the giant heather woodland (2600-3700 m);
- the alpine moorland (> 3600 m);
- the nival range (> 4400 m): only on Karisimbi and Ruwenzori mountains.

The bamboo forest, *Hagenia* and giant heather woodlands correspond to the afro-subalpine stage (Habiyaemye and Ruremesha 2020; Languy and de Merode 2006).



Figure 2.7: *Hagenia-Hypericum* woodland. a: *Hagenia abyssinica*; b: *Hypericum revolutum* S1.488551; E29.405001; 2789 m © Rizinde 2021



Figure 2.8: Giant heather woodland: *Erica kingaensis* S1.48631; E29.44147; 3480m site area: Rukumi/ Mikenno © Bazima Patrick 2021

Bamboo forests are one of the most threatened ecosystems. Projections by Ponce-Reyes et al. (2017) show that by 2070, the predicted loss will increase to 57-100%, with the environmental conditions required by bamboo forests predicted to disappear completely (Fig. 2.9). This will increase the risk of extinction of the critically endangered mountain gorilla (*Gorilla beringei*) and mushroom species whose existence is restricted to bamboo forest (*Engleromyces goetzei* Henn.) (Fig. 2.10).

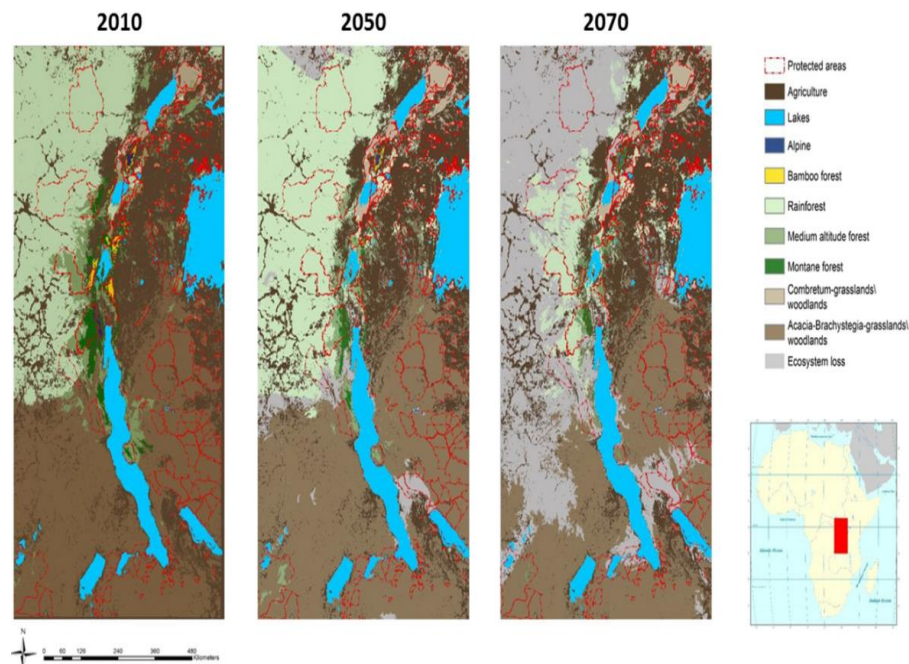


Figure 2.9: Map of current (2010) and future distribution (2050 and 2070) of each of the seven main ecosystems alpine vegetation (dark blue), bamboo forest (yellow) (Ponce-Reyes et al. 2017).



Figure 2.10: Legend: *Engleromyces goetzei* Henn. an Ascomycota fungi which is only found in highland bamboo forest. Lat. -1.491783, Long. E029.403436, Alt. 2755 m. © Rizinde 2021.

The alpine vegetation is found at altitudes above 3 600 m. Alpine ecosystems include Alpine moorland, giant *Senecio* and *Lobelia*,

*Achemillia* and *Helichrysum*. The cold conditions that prevail here limit its vegetation to a few species, in particular *Senecio refractisquamatus* de Wild. *Senecio alticola* (Mildbr) Th. Fries, *Senecio friesiorum*, *Senecio ducisaprutii*, *Lobelia wollastonii*, *Helichrysum erici-rosenii* Rob. E. Fries, *Helichrysum stuhlmannii*, *Alchemilla cryptantha* Steud (Hauman 1933; Robyns 1948).

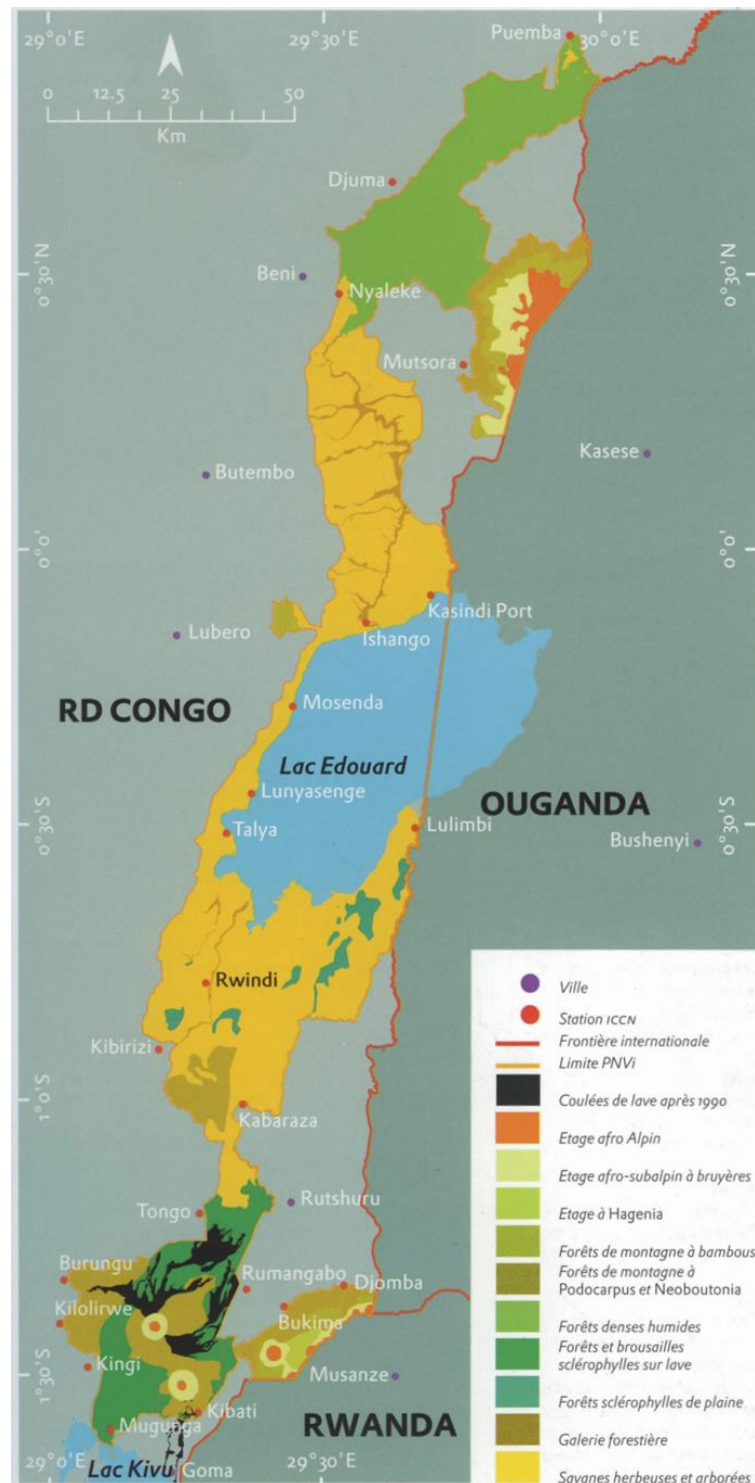


Figure 2.11: Vegetation map of Virunga NP (Languy and de Merode 2006)

### 2.2.7. Threat

Virunga National Park was inscribed on the World Heritage List in 1979. In 1994, between 1.5 and 2 million people fled to the Democratic Republic of Congo from neighboring countries to the east, many of them settling in the Kivu Province. Due to the destructive impact of the refugees on the park's ecology, Virunga National Park was officially declared a World Heritage Site in Danger in 1994.

There is considerable demographic pressure in and around the park. Agricultural encroachment is a major problem in Virunga NP and has resulted in the loss of 9% of the park since 1996. The main direct threats to the landscape include poaching of wildlife for bushmeat and ivory in the case of elephants and hippos; harvesting of timber, fuelwood, bamboo and charcoal; oil exploration; habitat degradation and loss, including loss of habitat connectivity important for maintaining viable populations of landscape species. In particular, the increasing urbanization of local populations has increased the demand for charcoal (Fig. 2.12). For example, 130 tonnes of charcoal are delivered to Goma every day.

The presence of several armed groups in the Virunga National Park makes conservation efforts increasingly difficult (Klug & Hart 2006; Languy et al. 2006; d'Huart et al. 2009; UNESCO 2018).

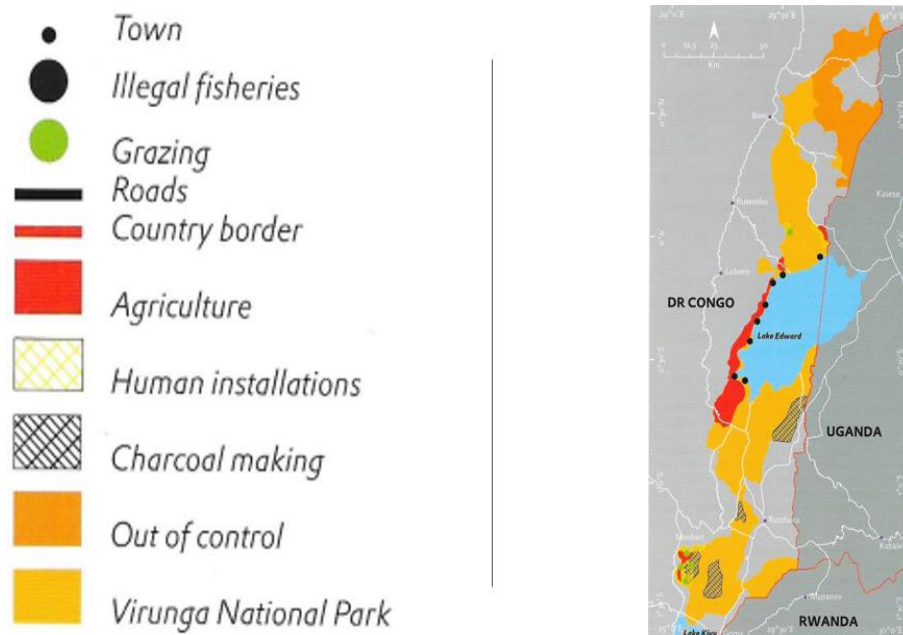


Figure 2.12: Map of the threats to Virunga NP in 2006 (d'Huart et al. 2009)

## 2.3. Kahuzi-Biega National Park

### 2.3.1. Geography and climate

Kahuzi-Biega NP is in the western part of the ridge of the Albertine Rift in the East of the DR Congo. It is located between 27°33' - 28°46' E and 1°36' - 2°37'S, western Kivu Lake.

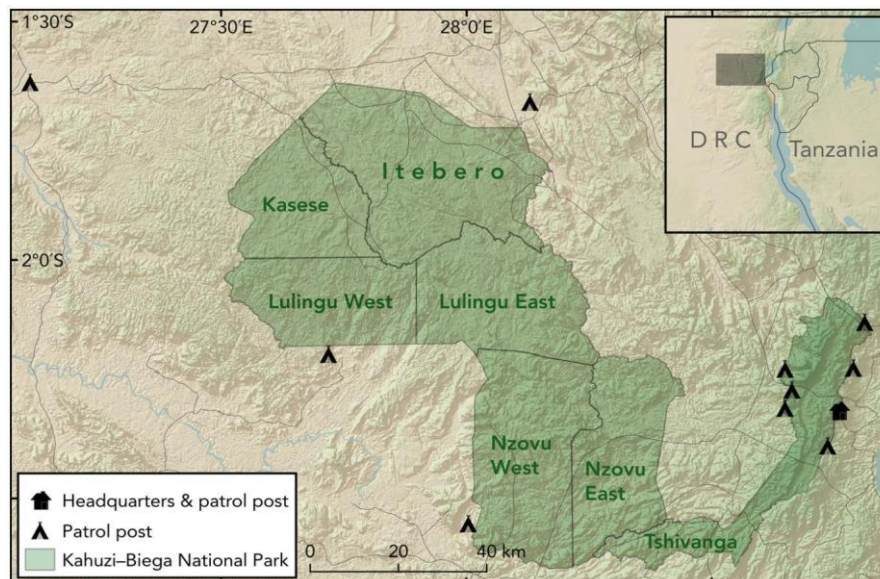


Figure 2.13: Map of Kahuzi-Biega NP (Spira et al. 2019)

This protected area was created in 1937 under the name "Réserve Zoologique et Forestière du Mont Kahuzi". It was converted into a National Park (NP) in 1970. For the efficient protection of lowland gorilla (*Gorilla beringei graueri* Matschie) and its habitat the Kahuzi-Biega NP was extended to 6,000km<sup>2</sup> in 1975.

Kahuzi-Biega NP has a bimodal rainfall regime, with most rainfall occurring in September-December and March-April. Annual rainfall ranges from 1500 to 2000 mm. The average annual temperature is 20°C. However, important climatic differences can be observed with altitude, with fog being a common feature above 2900 m. Frost can sometimes be observed above 3300m, especially in July (Mangambu 2013).

### 2.3.2. Geology and soil

The topography of the Kahuzi-Biega NP is very varied, with altitudes ranging from 650m to 3320m. The Kahuzi-Biega NP is

divided into two main parts: the lowland and the upland. In the lowland part, which begins around Bunyakiri (maximum altitude at Mount Kamami: 1,700 m), the soil is sandy clay. We have clay soils in some places and volcanic rock in others in the highlands, with a variety of mountain ranges.

The upper part of the Kahuzi-Biega National Park contains two extinct volcanoes from the end of the tertiary or quaternary period: Kahuzi and Biega. The soils are sandy and clayey, with an acid pH ranging from 4.8 to 6.2 (Mangambu 2013, Balezi 2013).

#### **2.3.4. Vegetation**

To date, more than 1,178 plant species have been recorded at the high altitude, making it the third richest site in the Albertine Rift after Virunga National Park in the Democratic Republic of Congo and Bwindi Impenetrable Forest in Uganda. Spira et al. (2018) recorded 1088 plant species grouped into 147 families, with the dominant families being Euphorbiaceae, Rubiaceae, Clusiaceae, Acanthaceae, Fabaceae and Apocynaceae. Tree species account for 24%. The surveys recorded 11 endemic species and 4 threatened species.

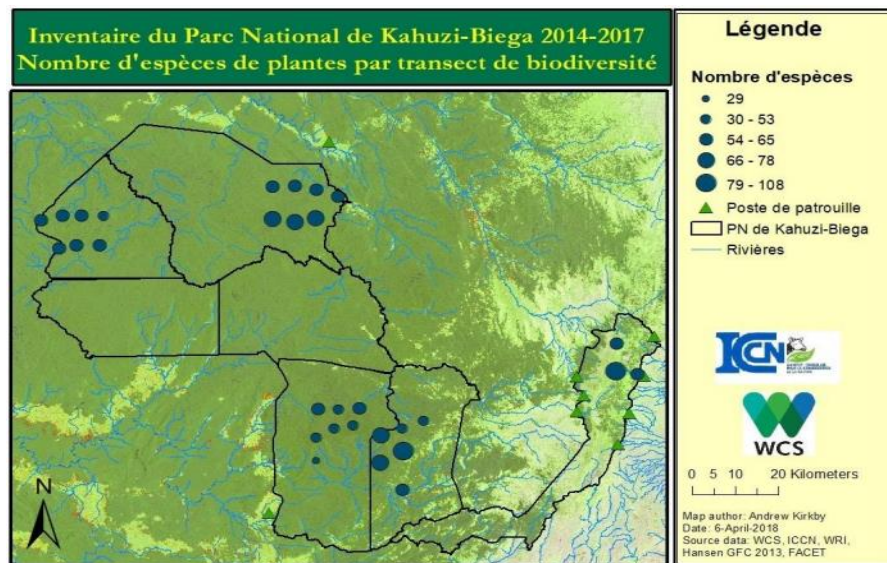


Figure 2.14: Plant species richness in Kahuzi-Biega NP (Spira et al. 2018)

According to elevation, the forests of Kahuzi-Biega NP can be divided into lowland rainforest (678-1250 m), submontane (1250-1700 m), montane (1700-2600 m) and afro-subalpine (2600-3308 m) forests (Mangambu 2013). Imani et al. (2017) classified montane forests into four distinct types: Sub montane (1250 to 1500 m asl), lower montane (1500 to 1800 m asl), middle montane (1800 to 2400 m asl) and upper montane (2400 to 2600 m asl). Bamboo forest and Giant heater woodland occur to 2400-2600 m and 2600-3200 m respectively (Fischer 1993).

### 2.3.5. Threats

Kahuzi-Biega NP is part of the Albertine Afromontane Biodiversity Hotspot which is home to endangered species including Gorillas (*Gorilla beringei graueri*) and elephants. Due to civil unrest and lack of law enforcement, some parts of the Kahuzi-Biega NP, mostly between 1400-1700 m asl, have been significantly degraded by fuelwood

collection, mineral activities and charcoal production (Imani et al. 2017).

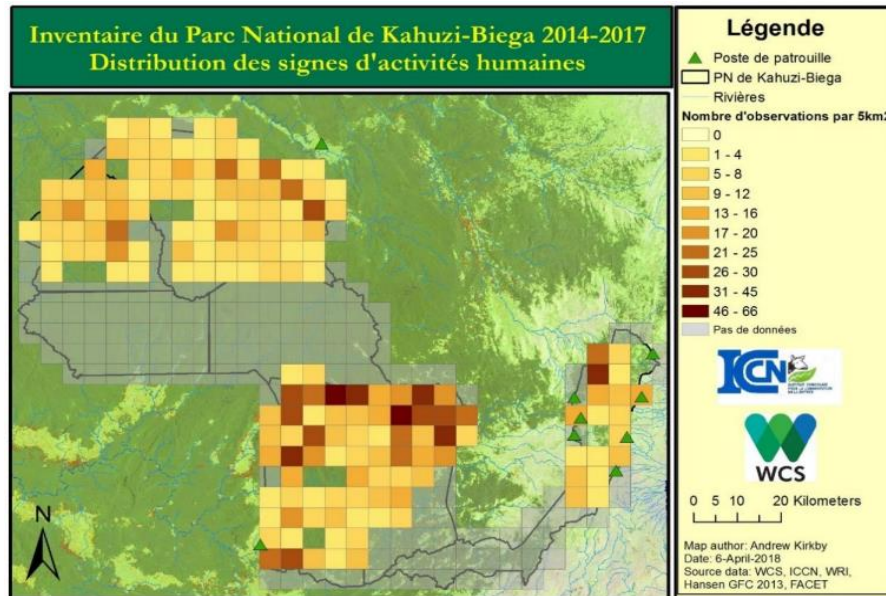


Figure 2.15: Mapping of human activities in Kahuzi-Biega NP (Spira et al. 2018)

Threats from human activities are widespread throughout the Kahuzi-Biega NP (Fig. 2.15). They are associated with agriculture, hunting, charcoal burning, illegal village settlements and mining. Spira et al. (2018) reported an average rate of signs of human activity of 1.51 signs/km (min = 0; max = 8.33) and signs of hunting of 0.46 signs/km (min = 0; max = 4.33).

## Chapter 3: Taxonomic Diversity of large Fungi in Albertine Rift: First checklist of the African Great Lakes Region basidiomycetes

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Adapted from:

Jean-Claude RIZINDE HAKIZIMANA, François MUHASHY HABİYAREMYE, Assumpta MUKANDERA, Héritier MILENGE KAMALEBO & Jérôme DEGREEF, (2023). First checklist of the African Great Lakes Region basidiomycetes. *Geo-Eco-Trop.*, **46.3**: 351-371.

### 3.1. Abstract

A checklist of 634 species of Basidiomycota, of which 115 are edible, was established based on data from missions carried out in the African Great Lakes Region and whose collections are available at the herbarium of the Meise Botanic Garden. About a hundred taxa that have been assigned a name accepted for a European species have been highlighted, demonstrating the need of further taxonomic studies to confirm their identification.

Keywords: checklist, taxonomy, fungi, DR Congo, Burundi, Rwanda

## 3.2. Introduction

“Attempts to estimate and keep biodiversity are hampered by a lack of information on many taxonomic groups, especially the most species-rich groups” (Schmit et al., 2005). Despite the efforts made in the past, a significant gap remains to be filled in our knowledge of species diversity. Only a small number of species have been described by scientists: 14% of those living on the continents and 9% of those living in the oceans (Mora et al., 2011). This gap highlights the fundamental role of taxonomy for biodiversity and biological studies in general (Phukhamsakda et al., 2022). Taxonomic studies are therefore essential as they are the key to studying the ecology of a species, its potential uses, and threats of extinction. According to Cheek et al. (2020), taxonomy is increasingly important for biodiversity conservation because the species that remain unknown are often those most likely to be at risk of extinction.

The gap is the deepest in fungi diversity knowledge where more than 90% of species remain to be discovered (Schmit et al., 2005; Mueller & Schmit, 2007; Blackwell, 2011; Njouonkou, 2011; Hawksworth & Lücking, 2017; Cheek et al., 2020). Out of an estimated total number of 2.2 to 3.8 million species of fungi, only 148,000 species are known, i.e. a proportion of 4 to 7% (Hawksworth & Lücking, 2017; Cheek et al., 2020).

Thanks to the progress made in molecular analysis methods applied to fungi, there has been a tremendous increase in the number of taxa described over the last two decades at rates exceeding 2000 new species per year (Cheek et al., 2020; Phukhamsakda et al., 2022). Nevertheless, at this rate, it will take over 1500 years to describe the remaining fungal species (Mueller & Schmit, 2007).

Large Fungi (part of Ascomycota, and Basidiomycota) are the best studied groups (Blackwell, 2011; Cheek, et al., 2020) with an estimated 16-41% species known (Mueller et al., 2007; Tripathi et al., 2017). However, there are disparities in terms of the number of species described within the different fungal groups. Thus, taxa with species of economic interest have been favored and more than 2,500 species of mushrooms recognized as edible have been described till now (Mossebo, 2002; FAO, 2006; De Kesel et al., 2002; Degreef et al., 2016; Milenge et al., 2021).

Despite their role as a major component of biocenosis, fungi are not often considered in the framework of global biodiversity protection policies, such as the Convention on Biological Diversity (CBD). Moreover, fungi remain foreign to current discussions on major environmental issues while they are also threatened by habitat degradation, land use and climate changes. About 5% of European and Central Asian large fungi are endangered of extinction (Yun Cao et al., 2021), but such data are not yet available for Africa.

What concerns fungal diversity, Africa remains one of the least explored continents (Rammeloo & Walley, 1993; Walley & Rammeloo, 1994) with only 9% of the world's known species (Cheek et al., 2020).

The paucity of literature on African large fungi contrasts with its great diversity (Rammeloo & Walley, 1993; Eyidong et al., 2011; Njouonkou, 2011). Based on ratios of the number of flowering plant species and large fungi (5:1 to 2:1), the total number of African large fungi species would be 10,000 to 25,000. Of these, only 2,250 species are known which means that ~75-90% remains to be discovered (Mueller et al., 2007).

As part of an ongoing study on large fungi in the African Great Lakes Region, a first checklist of basidiomycetes is here proposed. Challenges related to inaccurate methods used for their identification are discussed.

### 3.3. Methods

This checklist is mostly based on data linked with specimens kept at the Herbarium of Meise Botanic Garden and extracted from the BR Herbarium database, partly available online on [www.botanicalcollections.be](http://www.botanicalcollections.be). Additional data from field work carried out in Kivu province (DR Congo), Rwanda and Burundi, from the colonial period up to day, was compiled from volumes of *Flore iconographique des champignons du Congo* (FICC), *Flore illustrée des champignons d’Afrique centrale* (FICAC) and *Fungus Flora of Tropical Africa* (FFTA) all available online on [www.FFTA-online.org](http://www.FFTA-online.org).

### 3.4. Results and discussion

The results obtained show 357 species of basidiomycetes in North- and South-Kivu provinces (DR Congo), 149 in Rwanda and 278 in Burundi (Tab. 3.1).

Table 3.1: Checklist of basidiomycetes of the African Great Lakes region. Specimens named after a European taxon are shown in gray. + indicates that the species is edible. <sup>DRC</sup>: DR Congo; <sup>RW</sup>: Rwanda; <sup>BU</sup>: Burundi

| Scientific name                                                          | Edible | Collector name and country                                       |
|--------------------------------------------------------------------------|--------|------------------------------------------------------------------|
| 1 <i>Abundisporus roseoalbus</i> (Jungh.) Ryvarden                       |        | de Witte G.F. <sup>DRC</sup>                                     |
| 2 <i>Agaricus abruptibulbus</i> Peck                                     |        | Leonetout J.J. <sup>RW</sup>                                     |
| 3 <i>Agaricus agrocyboides</i> Heinem. & Gooss.-Font.                    |        | Goossens-Fontana M. <sup>DRC</sup>                               |
| 4 <i>Agaricus bambusae</i> Beeli                                         |        | Degreef J. <sup>RW</sup> , Goossens-Fontana M. <sup>DRC</sup>    |
| 5 <i>Agaricus benzodorus</i> Heinem. & Gooss.-Font.                      |        | Goossens-Fontana M. <sup>DRC</sup>                               |
| 6 <i>Agaricus bisporus</i> (J.E.Lange) Imbach                            | +      | Goossens-Fontana M. <sup>DRC</sup>                               |
| 7 <i>Agaricus brunneopunctatus</i> Linda J. Chen, Callac & L.A. Parra    |        | Goossens-Fontana M. <sup>DRC</sup>                               |
| 8 <i>Agaricus bukavuensis</i> Heinem. & Gooss.-Font.                     | +      | Goossens-Fontana M. <sup>DRC</sup>                               |
| 9 <i>Agaricus bulbillosus</i> Heinem. & Gooss.-Font.                     |        | Degreef J. <sup>RW</sup> , Goossens-Fontana M. <sup>DRC</sup>    |
| 10 <i>Agaricus campestris</i> L.                                         | +      | Goossens-Fontana M. <sup>DRC</sup> , Rizinde J.C. <sup>DRC</sup> |
| 11 <i>Agaricus carminescens</i> Heinem. & Gooss.-Font.                   |        | Goossens-Fontana M. <sup>DRC</sup>                               |
| 12 <i>Agaricus croceolutescens</i> Heinem. & Gooss.-Font.                | +      | Goossens-Fontana M. <sup>DRC</sup>                               |
| 13 <i>Agaricus fontanae</i> Fraiture                                     |        | Goossens-Fontana M. <sup>DRC</sup>                               |
| 14 <i>Agaricus goossensiae</i> Heinem.                                   | +      | Degreef J. <sup>RW</sup> , Rizinde J.C. <sup>DRC</sup>           |
| 15 <i>Agaricus haematosarcus</i> Heinem. & Gooss.-Font.                  |        | Goossens-Fontana M. <sup>DRC</sup>                               |
| 16 <i>Agaricus heterocystis</i> Heinem. & Gooss.-Font.                   |        | Goossens-Fontana M. <sup>DRC</sup>                               |
| 17 <i>Agaricus iodolens</i> Heinem. & Gooss.-Font.                       |        | Goossens-Fontana M. <sup>DRC</sup>                               |
| 18 <i>Agaricus kivuensis</i> Heinem. & Gooss.-Font.                      | +      | Degreef J. <sup>RW</sup> , Goossens-Fontana M. <sup>DRC</sup>    |
| 19 <i>Agaricus laeticulus</i> Callac, L.A. Parra, Linda J. Chen & Raspé, |        | Goossens-Fontana M. <sup>DRC</sup>                               |
| 20 <i>Agaricus litoralis</i> (Walkef. & Pearson) Pilát                   |        | Degreef J. <sup>RW</sup> , Goossens-Fontana M. <sup>DRC</sup>    |
| 21 <i>Agaricus luteomaculatus</i> (F.H.Møller) F.H.Møller                |        | Goossens-Fontana M. <sup>DRC</sup>                               |
| 22 <i>Agaricus nivescens</i> (F.H.Møller) F.H.Møller                     |        | Goossens-Fontana M. <sup>DRC</sup>                               |
| 23 <i>Agaricus ochrascens</i> Heinem. & Gooss.-Font.                     |        | Goossens-Fontana M. <sup>DRC</sup>                               |
| 24 <i>Agaricus olivellus</i> Heinem. & Gooss.-Font.                      |        | Goossens-Fontana M. <sup>DRC</sup>                               |
| 25 <i>Agaricus panziensis</i> Heinem. & Gooss.-Font.                     |        | Rammeloo J. <sup>BU</sup> , Goossens-Fontana M. <sup>DRC</sup>   |
| 26 <i>Agaricus pseudoniger</i> Heinem. & Gooss.-Font.                    |        | Goossens-Fontana M. <sup>DRC</sup>                               |
| 27 <i>Agaricus roseocingulatus</i> Heinem. & Gooss.-Font.                |        | Goossens-Fontana M. <sup>DRC</sup>                               |
| 28 <i>Agaricus subaeruginosus</i> Berk. & Broome                         |        | Goossens-Fontana M. <sup>DRC</sup>                               |

|                                                                               |                                                                                                                      |
|-------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------|
| 29 <i>Agaricus sylvicola</i> (Vittad.) Peck.                                  | + Degreef J. <sup>RW</sup>                                                                                           |
| 30 <i>Agaricus trisulphuratus</i> Berk.                                       | Rammeloo J. <sup>BU</sup> , Goossens-Fontana M. <sup>DRC</sup> ,<br>Fredericq <sup>DRC</sup> , Becquet <sup>RW</sup> |
| 31 <i>Agaricus volvatulus</i> Heinem. & Gooss.-Font.                          | + Degreef J. <sup>RW</sup> , Goossens-Fontana M. <sup>DRC</sup>                                                      |
| 32 <i>Agaricus xanthosarcus</i> Heinem. & Gooss.-Font.                        | Goossens-Fontana M. <sup>DRC</sup>                                                                                   |
| 33 <i>Agrocybe cameobrunneus</i> Watling                                      | Goossens-Fontana M. <sup>DRC</sup>                                                                                   |
| 34 <i>Agrocybe praecox</i> (Pers.) Fayod                                      | Goossens-Fontana M. <sup>DRC</sup>                                                                                   |
| 35 <i>Agrocybe ochraceobrunnea</i> Watling                                    | Goossens-Fontana M. <sup>DRC</sup>                                                                                   |
| 36 <i>Aleurodiscus botryosus</i> Burt                                         | Lebrun <sup>DRC</sup>                                                                                                |
| 37 <i>Amanita bweyeyensis</i> Fraiture, Raspé & Degreef                       | + Degreef J. <sup>RW, BU</sup>                                                                                       |
| 38 <i>Amanita masasiensis</i> Härk. & Saarim.                                 | + Degreef J. <sup>BU</sup>                                                                                           |
| 39 <i>Amanita miomboensis</i> Pegler & Shah-Smith                             | Nkengurutse J. <sup>BU</sup>                                                                                         |
| 40 <i>Amanita muscaria</i> (L.) Lam.                                          | Leonetout J.J. <sup>RW</sup> , Nkengurutse J. <sup>BU</sup>                                                          |
| 41 <i>Amanita phalloides</i> (Fr.) Link                                       | Nkengurutse J. <sup>BU</sup>                                                                                         |
| 42 <i>Amanita pudica</i> (Beeli) Walley                                       | + Rammeloo J. <sup>BU</sup> , Verbeken A. <sup>BU</sup> , Nkengurutse J. <sup>BU</sup>                               |
| 43 <i>Amanita rubescens</i> Pers.                                             | + Degreef J. <sup>BU</sup>                                                                                           |
| 44 <i>Amanita verna</i> (Bull.) Lam.                                          | Nkengurutse J. <sup>BU</sup>                                                                                         |
| 45 <i>Amauroderma argenteofulvum</i> (Van der Byl)<br>Doidge                  | Rammeloo J. <sup>BU</sup>                                                                                            |
| 46 <i>Amauroderma conicum</i> (Lloyd) Ryvarden                                | Verbeken A. <sup>BU</sup>                                                                                            |
| 47 <i>Amauroderma conjunctum</i> (Lloyd) Torrend                              | Rammeloo J. <sup>BU</sup>                                                                                            |
| 48 <i>Amauroderma fuscoporum</i> Wakef.                                       | Rammeloo J. <sup>BU</sup>                                                                                            |
| 49 <i>Amauroderma grandisporum</i> Gulaid & Ryvarden                          | Rammeloo J. <sup>BU</sup>                                                                                            |
| 50 <i>Amauroderma kwiluense</i> (Beeli) Ryvarden                              | Rammeloo J. <sup>BU</sup>                                                                                            |
| 51 <i>Amauroderma preussii</i> (Henn.) Steyaert                               | Petit E.M.A. <sup>BU</sup> , Rammeloo J. <sup>DRC</sup>                                                              |
| 52 <i>Amauroderma rugosum</i> (Blume & Nees) Torrend                          | Rammeloo J. <sup>BU</sup>                                                                                            |
| 53 <i>Amauroderma sericatum</i> (Lloyd) Wakef.                                | Rammeloo J. <sup>BU</sup> , Verbeken A. <sup>BU</sup>                                                                |
| 54 <i>Amauroderma subrugosum</i> (Bres. & Pat.) Torrend                       | Rammeloo J. <sup>BU</sup>                                                                                            |
| 55 <i>Anthracoystis congensis</i> (Syd. & P. Syd.)<br>McTaggart & R.G. Shivas | Germain R.G.A. <sup>RW</sup>                                                                                         |
| 56 <i>Antrodia albida</i> (Fr.) Donk                                          | Rammeloo J. <sup>BU</sup>                                                                                            |
| 57 <i>Antrodia lenis</i> (P.Karst.) Ryvarden                                  | Rammeloo J. <sup>BU</sup>                                                                                            |
| 58 <i>Antrodiella semisupina</i> (Berk. & M.A.Curtis)<br>Ryvarden             | Rammeloo J. <sup>BU</sup>                                                                                            |
| 59 <i>Armillaria borealis</i> Marxm. & Korhonen                               | + Degreef J. <sup>RW</sup> , Rizinde J.C. <sup>DRC</sup>                                                             |
| 60 <i>Armillaria cepistipes</i> Velen.                                        | + Degreef J. <sup>RW</sup>                                                                                           |
| 61 <i>Armillaria heimii</i> Pegler                                            | + Degreef J. <sup>RW</sup> , Rizinde J.C. <sup>DRC</sup>                                                             |
| 62 <i>Armillaria lutea</i> Gillet                                             | + Degreef J. <sup>RW</sup>                                                                                           |
| 63 <i>Armillaria mellea</i> (Vahl) P.Kumm.                                    | + Fassi B. <sup>DRC</sup> , Hendrickx F.L. <sup>DRC</sup>                                                            |
| 64 <i>Armillaria ostoyae</i> (Romagn.) Herink                                 | + Degreef J. <sup>RW</sup>                                                                                           |

|                                                                         |                                                                        |
|-------------------------------------------------------------------------|------------------------------------------------------------------------|
| 65 <i>Armillaria tabescens</i> (Scop.) Emel                             | + Degreef J. <sup>RW</sup>                                             |
| 66 <i>Aseroe rubra</i> Labill                                           | Demoulin V. <sup>RW</sup>                                              |
| 67 <i>Asterostroma muscicola</i> (Berk. & M.A.Curtis) Massee            | Rammeloo J. <sup>RW</sup>                                              |
| 68 <i>Asterostroma ochroleucum</i> Bres.                                | Rammeloo J. <sup>RW</sup>                                              |
| 69 <i>Athelia rolfsii</i> (Curzi) C.C.Tu & Kimbr.                       | Hendrickx F.L. <sup>DRC</sup>                                          |
| 70 <i>Auricularia auricula-judae</i> (Bull.) Quél.                      | + Hendrickx F.L. <sup>DRC</sup> , Degreef J. <sup>RW</sup>             |
| 71 <i>Auricularia cornea</i> Ehrenb.                                    | + Degreef J. <sup>RW</sup> , Rizinde J.C. <sup>DRC</sup>               |
| 72 <i>Auricularia delicata</i> (Fr.) Henn.                              | + Degreef J. <sup>RW</sup> , Rizinde J.C. <sup>DRC</sup>               |
| 73 <i>Auricularia mesenterica</i> (Dicks.) Pers.                        | + Hendrickx F.L. <sup>DRC</sup>                                        |
| 74 <i>Auricularia nigricans</i> (Sw.) Birkebak, Looney & Sánchez-García | + Hendrickx F.L. <sup>DRC</sup>                                        |
| 75 <i>Auriscalpium dissectum</i> Maas Geest. & Rammeloo                 | Rammeloo J. <sup>DRC</sup>                                             |
| 76 <i>Battarrea phalloides</i> (Dicks.) Pers.                           | Demoulin V. <sup>BU</sup>                                              |
| 77 <i>Bjerkandera adusta</i> (Willd.) P.Karst.                          | Petit E.M.A. <sup>BU</sup> , Rammeloo J. <sup>BU</sup>                 |
| 78 <i>Boletellus velutinus</i> Heinem. & Rammeloo                       | Rammeloo J. <sup>BU</sup>                                              |
| 79 <i>Boletus loosii</i> Heinem.                                        | + Verbeken A. <sup>BU</sup>                                            |
| 80 <i>Bovista aenea</i> Kreisel                                         | Demoulin V. <sup>RW</sup>                                              |
| 81 <i>Bovista aspera</i> Lév.                                           | Lambinon J. <sup>DRC</sup>                                             |
| 82 <i>Bovista fusca</i> Lév.                                            | Demoulin V. <sup>DRC,RW</sup>                                          |
| 83 <i>Bovista plumbea</i> Pers.                                         | Demoulin V. <sup>RW</sup>                                              |
| 84 <i>Bovista pusilla</i> (Batsch) Pers.                                | Demoulin V. <sup>DRC</sup>                                             |
| 85 <i>Calocybe africana</i> Singer                                      | Goossens-Fontana M. <sup>DRC</sup>                                     |
| 86 <i>Calvatia agaricoides</i> Dissing & M.Lange                        | Murhula Cizungu A. <sup>DRC</sup> , Goossens-Fontana M. <sup>DRC</sup> |
| 87 <i>Calvatia cyathiformis</i> (Bosc) Morgan                           | Goossens-Fontana M. <sup>DRC</sup>                                     |
| 88 <i>Calvatia gardneri</i> (Berk.) Lloyd                               | Demoulin V. <sup>BU</sup>                                              |
| 89 <i>Calvatia subtomentosa</i> Dissing & M.Lange                       | Nkengurutse J. <sup>BU</sup>                                           |
| 90 <i>Campanella brunnescens</i> Pegler                                 | Rammeloo J. <sup>BU</sup>                                              |
| 91 <i>Campanella witteana</i> Singer                                    | de Witte G.F. <sup>DRC</sup>                                           |
| 92 <i>Cantharellus alboroseus</i> Heinem.                               | + Rammeloo J. <sup>BU</sup>                                            |
| 93 <i>Cantharellus congolensis</i> Beeli                                | + Verbeken A. <sup>BU</sup>                                            |
| 94 <i>Cantharellus densifolius</i> Heinem.                              | + Verbeken A. <sup>BU</sup> , Rammeloo J. <sup>BU</sup>                |
| 95 <i>Cantharellus lineopunctatus</i> (Beeli) Heinem.                   | + Rammeloo J. <sup>BU</sup>                                            |
| 96 <i>Cantharellus microcibarius</i> Heinem.                            | + Degreef J. <sup>BU</sup>                                             |
| 97 <i>Cantharellus miniatescens</i> Heinem.                             | + Verbeken A. <sup>BU</sup>                                            |
| 98 <i>Cantharellus platyphyllus</i> Heinem                              | + Buyck B. <sup>BU</sup> , Rammeloo J. <sup>BU</sup>                   |
| 99 <i>Cantharellus rubber</i> Heinem.                                   | + Verbeken A. <sup>BU</sup> , Rammeloo J. <sup>BU</sup>                |
| 100 <i>Cantharellus splendens</i> Buyck                                 | + Buyck B. <sup>BU</sup> , Degreef J. <sup>BU</sup>                    |

|                                                                        |                                                                                            |
|------------------------------------------------------------------------|--------------------------------------------------------------------------------------------|
| 101 <i>Cantharellus symoensii</i> Heinem                               | + Verbeke A. <sup>BU</sup> , Rammeloo J. <sup>BU</sup> , Nkengurutse J. <sup>BU</sup>      |
| 102 <i>Cerrena caperata</i> (Berk.) Zmitr.                             | Van der Veken P. <sup>DRC</sup> , de Witte G.F. <sup>DRC</sup>                             |
| 103 <i>Chaetocalathus niduliformis</i> (Murrill) Singer                | Rammeloo J. <sup>BU</sup>                                                                  |
| 104 <i>Chalciporus virescens</i> (Heinem.) Klofac & Krisai             | Rammeloo J. <sup>BU</sup>                                                                  |
| 105 <i>Chlorophyllum abruptibulum</i> (R.Heim) Vellinga                | Goossens-Fontana M. <sup>DRC</sup>                                                         |
| 106 <i>Chlorophyllum globosum</i> (Mossebo) Vellinga                   | Petit E.M.A. <sup>BU</sup>                                                                 |
| 107 <i>Chlorophyllum molybdites</i> (G.Mey.) Massee                    | + Leonetout J.J. <sup>RW</sup> , Hendrickx F.L. <sup>BU</sup>                              |
| 108 <i>Clathrus columnatus</i> Bosc                                    | Vanpuyvelde <sup>RW</sup> , Demoulin V. <sup>RW</sup> , Goossens-Fontana M. <sup>DRC</sup> |
| 109 <i>Clavaria zollingeri</i> Lév.                                    | Hendrickx F.L. <sup>DRC</sup>                                                              |
| 110 <i>Clavulina albiramea</i> (Corner) Buyck & Duhem                  | + Rizinde J.C. <sup>DRC</sup>                                                              |
| 111 <i>Clavulina connata</i> (Berk.) Corner                            | de Witte G.F. <sup>DRC</sup>                                                               |
| 112 <i>Clitocybe cystidiosa</i> Singer                                 | Goossens-Fontana M. <sup>DRC</sup>                                                         |
| 113 <i>Clitocybe nebularis</i> (Batsch) P.Kumm.                        | Rizinde J.C. <sup>DRC</sup>                                                                |
| 114 <i>Clitopilus prunulus</i> (Scop.) P.Kumm.                         | + Degreeef J. <sup>BU</sup>                                                                |
| 115 <i>Clitopilus scyphoides</i> (Fr.) Singer Joss.                    | Rammeloo J. <sup>BU</sup>                                                                  |
| 116 <i>Conocybe anthracophila</i> Hauskn.                              | Goossens-Fontana M. <sup>DRC</sup>                                                         |
| 117 <i>Conocybe bicolor</i> Watling                                    | Goossens-Fontana M. <sup>DRC</sup>                                                         |
| 118 <i>Conocybe cartilaginipes</i> Watling                             | Goossens-Fontana M. <sup>DRC</sup>                                                         |
| 119 <i>Conocybe crispella</i> (Murrill) Singer                         | Rammeloo J. <sup>BU</sup>                                                                  |
| 120 <i>Conocybe fuxlaensis</i> Singer                                  | Rammeloo J. <sup>BU</sup>                                                                  |
| 121 <i>Conocybe merdaria</i> Arnolds & Hauskn.                         | Goossens-Fontana M. <sup>DRC</sup>                                                         |
| 122 <i>Conocybe obscurus</i> Watling                                   | Goossens-Fontana M. <sup>DRC</sup>                                                         |
| 123 <i>Conocybe ochraceodiscus</i> Watling                             | Goossens-Fontana M. <sup>DRC</sup>                                                         |
| 124 <i>Conocybe raphanaceus</i> Watling                                | Goossens-Fontana M. <sup>DRC</sup>                                                         |
| 125 <i>Coprinopsis cinerea</i> (Schaeff.) Redhead, Vilgalys & Moncalvo | Degreeef J. <sup>RW</sup>                                                                  |
| 126 <i>Coprinus comatus</i> (O.F.Müll.) Gray                           | + Goossens-Fontana M. <sup>DRC</sup>                                                       |
| 127 <i>Corditubera kivuensis</i> Demoulin & Dring                      | Rammeloo J. <sup>DRC</sup> , Demoulin <sup>DRC</sup>                                       |
| 128 <i>Coriolopsis byrsina</i> (Mont.) Ryvarden                        | Thoen D. <sup>DRC</sup> , Rammeloo J. <sup>BU</sup>                                        |
| 129 <i>Coriolopsis occidentalis</i> (Klotzsch) Murrill                 | Lewalle J. <sup>BU</sup> , Van Meel L. <sup>DRC</sup> , Hendrickx F.L. <sup>DRC</sup>      |
| 130 <i>Coriolopsis telfairii</i> (Klotzsch) Ryvarden                   | Petit E.M.A. <sup>BU</sup> , Vanderyst H. <sup>DRC</sup>                                   |
| 131 <i>Corticium aureolum</i> Bres.                                    | Hendrickx F.L. <sup>DRC</sup>                                                              |
| 132 <i>Cotylidia aurantiaca</i> (Pers.) A.L.Welden                     | + Degreeef J. <sup>DRC, RW</sup> , Rammeloo J. <sup>BU</sup>                               |
| 133 <i>Cotylidia pannosa</i> (Sowerby) D.A.Reid                        | Lewalle J. <sup>BU</sup>                                                                   |
| 134 <i>Craterellus aureus</i> Berk. & M.A.Curtis                       | Van Onacker J. <sup>BU</sup>                                                               |
| 135 <i>Crepidotus uber</i> (Berk. & M.A.Curtis) Sacc.                  | Goossens-Fontana M. <sup>DRC</sup> , Hendrickx F.L. <sup>DRC</sup>                         |
| 136 <i>Crinipellis calderi</i> Pegler                                  | Rammeloo J. <sup>BU</sup>                                                                  |

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| 137 | <i>Crinipellis pseudostipitaria</i> var. <i>orientalis</i> (Singer) Antonin | Rammeloo J. <sup>RW,BU</sup>                                                                                                |
| 138 | <i>Cyathus africanus</i> H.J. Brodie                                        | Demoulin V. <sup>RW</sup>                                                                                                   |
| 139 | <i>Cyathus limbatus</i> Tul. & C. Tul.                                      | Demoulin V. <sup>DRC</sup>                                                                                                  |
| 140 | <i>Cyathus poeppigii</i> Tul. & C. Tul.                                     | Demoulin V. <sup>RW</sup>                                                                                                   |
| 141 | <i>Cyathus stercoreus</i> (Schwein.) De Toni                                | Goossens-Fontana M. <sup>DRC</sup>                                                                                          |
| 142 | <i>Cyathus striatus</i> (Huds.) Willd.                                      | Hendrickx F.L. <sup>DRC</sup>                                                                                               |
| 143 | <i>Cymatoderma africanum</i> Boidin                                         | Rammeloo J. <sup>RW,BU</sup>                                                                                                |
| 144 | <i>Cymatoderma dendriticum</i> (Pers.) D.A.Reid                             | Degreef J. <sup>RW</sup>                                                                                                    |
| 145 | <i>Cymatoderma elegans</i> Jungh.                                           | Rizinde J.C. <sup>DRC</sup> , de Witte G.F. <sup>DRC</sup> , Rammeloo J. <sup>RW, BU</sup> , Van der Veken P. <sup>RW</sup> |
| 146 | <i>Cyptotrama chrysopepla</i> (Berk. & M.A.Curtis) Singer                   | Thoen D. <sup>DRC</sup>                                                                                                     |
| 147 | <i>Cystidiodontia laminifera</i> (Berk. & M.A.Curtis) Hjortstam             | Rammeloo J. <sup>BU,RW</sup>                                                                                                |
| 148 | <i>Cystoderma cristalliferum</i> Thoen                                      | Goossens-Fontana M. <sup>DRC</sup>                                                                                          |
| 149 | <i>Cystodermella elegans</i> (Beeli) Harmaja                                | + Goossens-Fontana M. <sup>DRC</sup> , Degreef J. <sup>RW, DRC</sup> , Rizinde J.C. <sup>DRC</sup>                          |
| 150 | <i>Dacryopinax spathularia</i> (Schwein.) G.W.Martin                        | + Degreef J. <sup>RW</sup>                                                                                                  |
| 151 | <i>Daedalea ealaensis</i> Beeli                                             | de Witte G.F. <sup>DRC</sup> , Hendrickx F.L. <sup>DRC</sup> , Fassi B. <sup>DRC</sup>                                      |
| 152 | <i>Daedalea flavida</i> Lév.                                                | Verbeken A. <sup>BU</sup>                                                                                                   |
| 153 | <i>Dentocorticium irregulare</i> Ryvariden                                  | Rammeloo J. <sup>RW</sup>                                                                                                   |
| 154 | <i>Earliella scabrosa</i> (Pers.) Gilb. & Ryvariden                         | de Witte G.F. <sup>DRC</sup> , Rammeloo J. <sup>DRC</sup> , Verbeken A. <sup>BU</sup>                                       |
| 155 | <i>Echinochaete brachypora</i> (Mont.) Ryvariden                            | + Degreef J. <sup>DRC</sup> , Rizinde J.C. <sup>DRC</sup> , Rammeloo J. <sup>BU</sup> , Petit E.M.A. <sup>BU</sup>          |
| 156 | <i>Entoloma fibulatum</i> (Romagn.) Noordel. & Co-David.                    | Goossens-Fontana M. <sup>DRC</sup>                                                                                          |
| 157 | <i>Entoloma mammiferum</i> (Romagn.) Noordel. & Co-David.                   | Goossens-Fontana M. <sup>DRC</sup>                                                                                          |
| 158 | <i>Entoloma nidorosiforme</i> (Romagn.) Noordel. & Co-David                 | Goossens-Fontana M. <sup>DRC</sup>                                                                                          |
| 159 | <i>Entoloma tigrinellum</i> (Romagn.) Noordel. & Co-David                   | Goossens-Fontana M. <sup>DRC</sup>                                                                                          |
| 160 | <i>Favolaschia calocera</i> R.Heim                                          | + Rizinde J.C. <sup>DRC</sup>                                                                                               |
| 161 | <i>Favolaschia citrinella</i> Henn.                                         | Dewèvre A. <sup>DRC</sup>                                                                                                   |
| 162 | <i>Favolaschia thwaitesii</i> (Berk. & Broome) Singer                       | + Rammeloo J. <sup>BU</sup> , Rizinde J.C. <sup>DRC</sup>                                                                   |
| 163 | <i>Favolus tenuiculus</i> P.Beauv.                                          | + de Witte G.F. <sup>DRC</sup> , Degreef J. <sup>DRC,RW</sup> , Rizinde J.C. <sup>DRC</sup> , Rammeloo J. <sup>BU</sup>     |
| 164 | <i>Fibrodontia brevidens</i> (Pat.) Hjortstam & Ryvariden                   | Rammeloo J. <sup>RW</sup>                                                                                                   |
| 165 | <i>Flaviporus liebmannii</i> (Fr.) Ginns                                    | Rammeloo J. <sup>BU</sup>                                                                                                   |
| 166 | <i>Flavodon flavus</i> (Klotzsch) Ryvariden                                 | Rammeloo J. <sup>BU</sup>                                                                                                   |
| 167 | <i>Fomitiporia gabonensis</i> Amalfi & Decock                               | Balezi A. <sup>DRC</sup>                                                                                                    |
| 168 | <i>Fomitiporia punctata</i> (P. Karst.) Murrill                             | Balezi A. <sup>DRC</sup>                                                                                                    |
| 169 | <i>Fomitiporia tenuis</i> Decock, Bitew & G. Castillo                       | Balezi A. <sup>DRC</sup>                                                                                                    |

- 170 *Fomitopsis rhodophaea* (Lév.) Imazeki
- 171 *Fomitopsis supina* (Sw.) Murrill
- 172 *Fulvifomes merrillii* (Murrill) Baltazar & Gibertoni
- 173 *Funalia aspera* (Jungh.) Zmitr. & Malysheva
- 174 *Funalia floccosa* (Jungh.) Zmitr. & Malysheva
- 175 *Funalia sanguinaria* (Klotzsch) Zmitr. & Malysheva
- 176 *Fuscoporia callimorpha* (Lév.) Groposo
- 177 *Fuscoporia ferrea* (Pers.) G. Cunn.
- 178 *Fuscoporia senex* (Nees & Mont.) Ghob.-Nejh.
- 179 *Fuscoporia wahlbergii* (Fr.) T. Wagner & M. Fisch.
- 180 *Ganoderma alluaudii* Pat. & Har.
- 181 *Ganoderma amazonense* Weir
- 182 *Ganoderma australe* (Fr.) Pat.
- 183 *Ganoderma chalceum* (Cooke) Steyaert
- 184 *Ganoderma fassii* Steyaert
- 185 *Ganoderma hildebrandii* Henn.
- 186 *Ganoderma hoehnelianum* Bres.
- 187 *Ganoderma lucidum* (Curtis) P.Karst
- 188 *Ganoderma petchii* (Lloyd) Steyaert
- 189 *Ganoderma resinaceum* Boud.
- 190 *Ganoderma sculpturatus* (Lloyd) Ryvarden
- 191 *Ganoderma septatum* Steyaert
- 192 *Ganoderma sublucidum* (Beeli) Steyaert
- 193 *Ganoderma subresinosum* (Murrill) C.J.Humphrey
- 194 *Ganoderma vanmeelii* Steyaert
- 195 *Ganoderma weberianum* (Bres. & Henn. ex Sacc.) Steyaert
- 196 *Ganoderma xylonoides* Steyaert
- 197 *Ganoderma zonatum* Murrill
- 198 *Gastrum lageniforme* Vittad.
- 199 *Gastrum minimum*
- 200 *Gastrum mirabile* Mont.
- 201 *Gastrum rufescens* Pers.
- 202 *Gastrum saccatum* Fr.
- 203 *Gastrum schweinfurthii* Henn.
- Rammeloo J. <sup>RW,BU</sup>
- Rammeloo J. <sup>RW</sup>
- Balezi A. <sup>DRC</sup>
- Rammeloo J. <sup>BU</sup>
- Rammeloo J. <sup>RW</sup>
- Rammeloo J. <sup>RW</sup>, Hendrickx F.L. <sup>DRC</sup>
- Balezi A. <sup>DRC</sup>
- Balezi A. <sup>DRC</sup>
- Balezi A. <sup>DRC</sup>
- Balezi A. <sup>DRC</sup>
- Rammeloo J. <sup>BU</sup>
- Rammeloo J. <sup>DRC</sup>
- de Witte G.F. <sup>DRC</sup>, Rammeloo J. <sup>DRC,BU,RW</sup>, Van der Veken P. <sup>DRC,RW</sup>, Fassi B. <sup>DRC</sup>, Lambinon J. <sup>BU</sup>
- Rammeloo J. <sup>DRC</sup>, de Witte G.F. <sup>DRC</sup>
- Lewalle J. <sup>BU</sup>, de Witte G.F. <sup>DRC</sup>, Rammeloo J. <sup>DRC</sup>, Goossens-Fontana M. <sup>DRC</sup>
- Petit E.M.A. <sup>BU</sup>, Degreef J. <sup>RW</sup>
- de Witte G.F. <sup>DRC</sup>
- de Witte G.F. <sup>DRC</sup>
- de Witte G.F. <sup>DRC</sup>
- de Witte G.F. <sup>DRC</sup>, Rammeloo J. <sup>RW,BU</sup>
- Rammeloo J. <sup>DRC,RW</sup>
- Goossens-Fontana M. <sup>DRC</sup>
- Lebrun J. <sup>DRC</sup>
- de Witte G.F. <sup>DRC</sup>, Rammeloo J. <sup>RW</sup>, Van der Veken P. <sup>RW</sup>, Reekmans R. <sup>BU</sup>
- de Witte G.F. <sup>DRC</sup>
- de Witte G.F. <sup>DRC</sup>
- Lewalle J. <sup>BU</sup>
- Petit E.M.A. <sup>BU</sup>, Hendrickx F.L. <sup>BU</sup>, Reekmans R. <sup>BU</sup>, Rammeloo J. <sup>BU</sup>
- Goossens-Fontana M. <sup>DRC</sup>
- Demoulin V. <sup>DRC</sup>
- Goossens-Fontana M. <sup>DRC</sup>, de Witte G.F. <sup>DRC</sup>, Petit E.M.A. <sup>DRC</sup>
- Goossens-Fontana M. <sup>DRC</sup>
- Goossens-Fontana M. <sup>DRC</sup>
- Reekmans R. <sup>BU</sup>, Demoulin V. <sup>BU</sup>

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| 204 <i>Geastrum schweinitzii</i> (Berk. & Curtis) Zeller                              | Demoulin V. <sup>DRC</sup>                                                                                                                          |
| 205 <i>Geastrum subiculosum</i> Cooke & Massee                                        | Lewalle J. <sup>BU</sup> , Demoulin V. <sup>DRC</sup>                                                                                               |
| 206 <i>Geastrum triplex</i> Jungh.                                                    | Demoulin V. <sup>DRC</sup>                                                                                                                          |
| 207 <i>Geastrum velutinum</i> Morgan                                                  | Goossens-Fontana M. <sup>DRC</sup>                                                                                                                  |
| 208 <i>Gerronema hungo</i> Degreef & Eyi Ndong                                        | + Rizinde J.C. <sup>DRC</sup>                                                                                                                       |
| 209 <i>Gloeoporus dichrous</i> (Fr.) Bres.                                            | Rammeloo J. <sup>RW</sup>                                                                                                                           |
| 210 <i>Gloeoporus theleporoides</i> (Hook.) Cunn.                                     | de Witte G.F. <sup>DRC</sup> , Rammeloo J. <sup>BU</sup>                                                                                            |
| 211 <i>Gloiocephala tezae</i> Antonin                                                 | Rammeloo J. <sup>BU</sup>                                                                                                                           |
| 212 <i>Gomphus brunneus</i> (Heinem.) Comer                                           | Degreef J. <sup>RW</sup>                                                                                                                            |
| 213 <i>Grammothele fuligo</i> (Berk. & Broome) Ryvarden                               | Rammeloo J. <sup>RW</sup>                                                                                                                           |
| 214 <i>Gymnopilus zenkeri</i> (Henn.) Singer                                          | + Rizinde J.C. <sup>DRC</sup>                                                                                                                       |
| 215 <i>Gyrodon miretipis</i> Heinem. & Rammeloo                                       | + Dossin, Lambinon J. <sup>BU</sup>                                                                                                                 |
| 216 <i>Gyrodon xylophilus</i> (Petch) Heinem. & Rammeloo                              | Dossin <sup>BU</sup> , Goossens-Fontana M. <sup>DRC</sup>                                                                                           |
| 217 <i>Gyrodontium sacchari</i> (Spreng.) Hjortstam                                   | Lewalle J. <sup>BU</sup>                                                                                                                            |
| 218 <i>Gyroporus ballouii</i> (Peck) E. Horak                                         | Verbeken A. <sup>BU</sup>                                                                                                                           |
| 219 <i>Gyroporus castaneus</i> var. <i>castaneus</i> (Bull.) Quél.                    | Cocquyt C. <sup>BU</sup>                                                                                                                            |
| 220 <i>Gyroporus heterosporus</i> var. <i>afibulatus</i> Heinem. & Rammeloo           | Rammeloo J. <sup>DRC, BU</sup>                                                                                                                      |
| 221 <i>Gyroporus microsporus</i> var. <i>congolensis</i> (Heinem.) Heinem. & Rammeloo | Dossin <sup>BU</sup> , Rammeloo J. <sup>DRC</sup>                                                                                                   |
| 222 <i>Hapalopilus africanus</i> Ryvarden                                             | Van der Veken P. <sup>RW</sup>                                                                                                                      |
| 223 <i>Helicobasidium brebissonii</i> (Desm.) Donk                                    | Hendrickx F.L. <sup>RW</sup>                                                                                                                        |
| 224 <i>Hexagonia dermatiphora</i> Lloyd                                               | de Witte G.F. <sup>DRC</sup> , Rammeloo J. <sup>RW</sup>                                                                                            |
| 225 <i>Hexagonia glabra</i> (P. Beauv.) Ryvarden                                      | Verbeken A. <sup>BU</sup>                                                                                                                           |
| 226 <i>Hexagonia hirta</i> (P. Beauv.) Fr.                                            | Rammeloo J. <sup>BU</sup>                                                                                                                           |
| 227 <i>Hexagonia hydroides</i> (Sw.) M. Fidalgo                                       | Rammeloo J. <sup>RW</sup>                                                                                                                           |
| 228 <i>Hexagonia pobequini</i> Har.                                                   | Rammeloo J. <sup>RW</sup>                                                                                                                           |
| 229 <i>Hexagonia saclexii</i> Har. & Pat.                                             | Vanderyst H. <sup>DRC</sup>                                                                                                                         |
| 230 <i>Hexagonia tenuis</i> (Hook.) Ryv.                                              | de Witte G.F. <sup>DRC</sup> , Germain R.G.A. <sup>DRC</sup> , Lewalle J. <sup>BU</sup> , Lambinon J. <sup>BU</sup> , Rammeloo J. <sup>RW, BU</sup> |
| 231 <i>Humphreya eminii</i> (Henn.) Ryvarden                                          | Rammeloo J. <sup>BU</sup>                                                                                                                           |
| 232 <i>Hygrocybe conica</i> var. <i>pallidipes</i> Heinem.                            | Goossens-Fontana M. <sup>DRC</sup>                                                                                                                  |
| 233 <i>Hygrocybe cortinata</i> Heinem.                                                | Goossens-Fontana M. <sup>DRC</sup>                                                                                                                  |
| 234 <i>Hygrophoropsis aurantiaca</i> (Wulfen) Maire                                   | Rizinde J.C. <sup>DRC</sup>                                                                                                                         |
| 235 <i>Hygrophoropsis kivuensis</i> Heinem.                                           | Goossens-Fontana M. <sup>DRC</sup>                                                                                                                  |
| 236 <i>Hymenagaricus alphitochrous</i> var. <i>pegleri</i> Heinem.                    | Rammeloo J. <sup>BU</sup>                                                                                                                           |
| 237 <i>Hymenagaricus ardosiaecolor</i> var. <i>rufidulus</i> Heinem.                  | Goossens-Fontana M. <sup>DRC</sup>                                                                                                                  |
| 238 <i>Hymenagaricus kivuensis</i> Heinem.                                            | Goossens-Fontana M. <sup>DRC</sup> , Rammeloo J. <sup>BU</sup>                                                                                      |
| 239 <i>Hymenagaricus laticystis</i> Heinem.                                           | Rammeloo J. <sup>BU</sup>                                                                                                                           |

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| 240 <i>Hymenagaricus nigrovinosus</i> (Pegler) Heinem.                   | Goossens-Fontana M. <sup>DRC</sup>                             |
| 241 <i>Hymenagaricus olivaceus</i> Heinem.                               | Goossens-Fontana M. <sup>DRC</sup>                             |
| 242 <i>Hymenochaete adusta</i> (Lév.) Har. & Pat.                        | de Witte G.F. <sup>DRC</sup>                                   |
| 243 <i>Hymenochaete luteobadia</i> (Fr.) Höhn. & Litsch.                 | Vanderyst H. <sup>DRC</sup>                                    |
| 244 <i>Hymenopellis crassibasidiata</i> (R.H. Petersen)<br>R.H. Petersen | Rammeloo J. <sup>BU</sup>                                      |
| 245 <i>Hyphoderma medioburiense</i> (Burt) Donk                          | Rammeloo J. <sup>RW</sup>                                      |
| 246 <i>Hyphoderma roseocremaeum</i> (Bres.) Donk                         | Rammeloo J. <sup>BU</sup>                                      |
| 247 <i>Hyphodontia alutacea</i> (Fr.) J.Erikss.                          | Rammeloo J. <sup>BU</sup>                                      |
| 248 <i>Hypholoma fasciculare</i> (Huds.) P. Kumm.                        | Rizinde J.C. <sup>DRC</sup> , Rammeloo J. <sup>BU</sup>        |
| 249 <i>Hypholoma subviride</i> (Berk. & M.A. Curtis)<br>Dennis           | + Degreef J. <sup>RW, DRC</sup>                                |
| 250 <i>Inonotus luteoumbinus</i> (Romell) Ryvarden                       | Balezi A. <sup>DRC</sup>                                       |
| 251 <i>Inonotus ochroporus</i>                                           | Balezi A. <sup>DRC</sup>                                       |
| 252 <i>Inonotus pachyphloeus</i>                                         | Balezi A. <sup>DRC</sup>                                       |
| 253 <i>Inonotus pegleri</i>                                              | Balezi A. <sup>DRC</sup>                                       |
| 254 <i>Inonotus rwenzorianus</i> Balezi & Decock                         | Balezi A. <sup>DRC</sup>                                       |
| 255 <i>Intextomyces aureus</i> (Ryvarden) Hjortstam                      | Rammeloo J. <sup>RW</sup>                                      |
| 256 <i>Junghuhnia nitida</i> (Pers.) Ryvarden                            | Rammeloo J. <sup>RW</sup>                                      |
| 257 <i>Kurtia argillacea</i> (Bres.) Karasiński                          | Rammeloo J. <sup>RW, BU</sup>                                  |
| 258 <i>Laccaria lateritia</i> Malençon                                   | Goossens-Fontana M. <sup>DRC</sup> , Rammeloo J. <sup>BU</sup> |
| 259 <i>Lachnocladium schweinfurthianum</i> Henn.                         | de Witte G.F. <sup>DRC</sup>                                   |
| 260 <i>Lactarius baliophaeus</i> var. <i>baliophaeus</i> Pegler          | Verbeken A. <sup>BU</sup>                                      |
| 261 <i>Lactarius barbatus</i> Verbeken                                   | Buyck B. <sup>BU</sup>                                         |
| 262 <i>Lactarius chromospermus</i> Pegler                                | + Verbeken A. <sup>BU</sup>                                    |
| 263 <i>Lactarius kabansus</i> Pegler & Pearce                            | + Verbeken A. <sup>BU</sup> , Rammeloo J. <sup>BU</sup>        |
| 264 <i>Lactarius kivuensis</i> Verbeken                                  | Rammeloo J. <sup>DRC</sup>                                     |
| 265 <i>Lactarius orientalis</i> (Verbeken) Verbeken                      | Verbeken A. <sup>BU</sup>                                      |
| 266 <i>Lactarius pulchrispermus</i> Verbeken                             | Verbeken A. <sup>BU</sup>                                      |
| 267 <i>Lactarius pusilliporus</i> Verbeken                               | Verbeken A. <sup>BU</sup>                                      |
| 268 <i>Lactarius rumongensis</i> Verbeken                                | Verbeken A. <sup>BU</sup>                                      |
| 269 <i>Lactarius saponaceus</i> Verbeken                                 | Verbeken A. <sup>BU</sup>                                      |
| 270 <i>Lactarius subamarus</i> Verbeken                                  | Rammeloo J. <sup>DRC, BU</sup>                                 |
| 271 <i>Lactarius sulcatulus</i> Verbeken                                 | Rammeloo J. <sup>DRC, BU</sup>                                 |
| 272 <i>Lactarius tenellus</i> Verbeken & Walley                          | + Degreef J. <sup>BU</sup>                                     |
| 273 <i>Lactarius undulatus</i> Verbeken                                  | Rammeloo J. <sup>DRC</sup>                                     |
| 274 <i>Lactifluus aurantiifolius</i> (Verbeken) Verbeken                 | Verbeken A. <sup>BU</sup>                                      |
| 275 <i>Lactifluus aureifolius</i> (Verbeken) Verbeken                    | Verbeken A. <sup>BU</sup>                                      |
| 276 <i>Lactifluus brunnescens</i> (Verbeken) Verbeken                    | + Verbeken A. <sup>BU</sup>                                    |

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| 277 <i>Lactifluus cyanovirescens</i> (Verbeken) Verbeken      | Verbeken A. <sup>BU</sup>                                                                                                                                                        |
| 278 <i>Lactifluus edulis</i> (Verbeken & Buyck) Buyck         | + Verbeken A. <sup>BU</sup>                                                                                                                                                      |
| 279 <i>Lactifluus gymnocarpoides</i> (Verbeken) Verbeken      | + Verbeken A. <sup>BU</sup> , Degreef J. <sup>BU</sup>                                                                                                                           |
| 280 <i>Lactifluus gymnocarpus</i> (R.Heim ex Singer) Verbeken | + Rammeloo J. <sup>DRC</sup>                                                                                                                                                     |
| 281 <i>Lactifluus heimii</i> (Verbeken) Verbeken              | + Rammeloo J. <sup>BU</sup> , Verbeken A. <sup>BU</sup>                                                                                                                          |
| 282 <i>Lactifluus indusiatus</i> (Verbeken) Verbeken          | Verbeken A. <sup>BU</sup>                                                                                                                                                        |
| 283 <i>Lactifluus laevigatus</i> (Verbeken) Verbeken          | + Verbeken A. <sup>BU</sup> , Rammeloo J. <sup>BU</sup>                                                                                                                          |
| 284 <i>Lactifluus longipes</i> (Verbeken) Verbeken            | + Rammeloo J. <sup>DRC</sup>                                                                                                                                                     |
| 285 <i>Lactifluus longisporus</i> (Verbeken) Verbeken         | + Verbeken A. <sup>BU</sup>                                                                                                                                                      |
| 286 <i>Lactifluus luteopus</i> (Verbeken) Verbeken            | + Verbeken A. <sup>BU</sup> , Degreef J. <sup>BU</sup> , Rammeloo J. <sup>BU</sup>                                                                                               |
| 287 <i>Lactifluus pumilus</i> (Verbeken) Verbeken             | + Verbeken A. <sup>BU</sup>                                                                                                                                                      |
| 288 <i>Lactifluus roseolus</i> (Verbeken) Verbeken            | Verbeken A. <sup>BU</sup>                                                                                                                                                        |
| 289 <i>Lactifluus ruvubuensis</i> (Verbeken) Verbeken         | Nkengurutse J. <sup>BU</sup> , Verbeken A. <sup>BU</sup>                                                                                                                         |
| 290 <i>Lactifluus sesemotani</i> (Beeli) Buyck                | Nkengurutse J. <sup>BU</sup> , Verbeken A. <sup>BU</sup>                                                                                                                         |
| 291 <i>Lactifluus urens</i> (Verbeken) Verbeken               | Dossin <sup>BU</sup> , Verbeken A. <sup>BU</sup> , Rammeloo J. <sup>BU</sup>                                                                                                     |
| 292 <i>Lactifluus velutissimus</i> (Verbeken) Verbeken        | + Rammeloo J. <sup>BU</sup> , Verbeken A. <sup>BU</sup>                                                                                                                          |
| 293 <i>Laeticorticium odontoides</i> Ryvarden                 | Rammeloo J. <sup>BU</sup>                                                                                                                                                        |
| 294 <i>Laetiporus discolor</i> (Klotzsch) Corner              | + Rizinde J.C. <sup>DRC</sup>                                                                                                                                                    |
| 295 <i>Langermannia fenzlii</i> (Reichardt) Kreisel           | Goossens-Fontana M. <sup>DRC</sup> , Demaire <sup>RW</sup>                                                                                                                       |
| 296 <i>Langermannia wahlbergii</i> (Fr.) Dring                | Demoulin V. <sup>RW</sup>                                                                                                                                                        |
| 297 <i>Laxitextum bicolor</i> (Pers.) Lentz                   | de Witte G.F. <sup>DRC</sup> , Demoulin V. <sup>DRC</sup>                                                                                                                        |
| 298 <i>Leccinum foetidum</i> Heinem.                          | Nkengurutse J. <sup>BU</sup>                                                                                                                                                     |
| 299 <i>Lentaria surculus</i> (Berk.) Corner                   | Bequaert J. <sup>DRC</sup> , de Witte G.F. <sup>DRC</sup> , Lewalle J. <sup>BU</sup>                                                                                             |
| 300 <i>Lentinus arcularius</i> (Batsch) Zmitr.                | Rammeloo J. <sup>BU</sup> , Hendrickx F.L. <sup>DRC</sup>                                                                                                                        |
| 301 <i>Lentinus brunneofloccosus</i> Pegler                   | + Rizinde J.C. <sup>DRC</sup>                                                                                                                                                    |
| 302 <i>Lentinus cladopus</i> Lév.                             | + Rammeloo J. <sup>DRC</sup> , Degreef J. <sup>RW</sup> , Verbeken A. <sup>BU</sup>                                                                                              |
| 303 <i>Lentinus connatus</i> Berk.                            | de Witte G.F. <sup>DRC</sup>                                                                                                                                                     |
| 304 <i>Lentinus crinitus</i> (L.) Fr.                         | Petit E.M.A. <sup>BU</sup> , Goossens-Fontana M. <sup>DRC</sup> ,<br>Rammeloo J. <sup>DRC, RW</sup>                                                                              |
| 305 <i>Lentinus panziensis</i> Singer                         | Goossens-Fontana M. <sup>DRC</sup>                                                                                                                                               |
| 306 <i>Lentinus retinervis</i> Pegler                         | + Degreef J. <sup>BU</sup>                                                                                                                                                       |
| 307 <i>Lentinus sajor-caju</i> (Fr.) Fr.                      | + Verbeken A. <sup>BU</sup> , de Witte G.F. <sup>DRC</sup> , Bequaert J. <sup>DRC</sup> ,<br>Degreef J. <sup>RW</sup> , Rammeloo J. <sup>DRC</sup> , Rizinde J.C. <sup>DRC</sup> |
| 308 <i>Lentinus similis</i> Berk. & Broome                    | Rammeloo J. <sup>BU</sup>                                                                                                                                                        |
| 309 <i>Lentinus squarrosulus</i> Mont.                        | + Rammeloo J. <sup>BU</sup> , Rizinde J.C. <sup>DRC</sup>                                                                                                                        |
| 310 <i>Lentinus stipiteus</i> Klotzsch                        | de Witte G.F. <sup>DRC</sup> , Rammeloo J. <sup>DRC</sup>                                                                                                                        |
| 311 <i>Lentinus velutinus</i> Fr.                             | + Rammeloo J. <sup>DRC</sup> , Vanderyst H. <sup>DRC</sup> , Bequaert J. <sup>DRC</sup> ,<br>Murhula Cizungu A. <sup>BU</sup> , de Witte G.F. <sup>DRC</sup>                     |
| 312 <i>Lentinus villosus</i> Klotzsch                         | Rammeloo J. <sup>BU</sup> , Murhula Cizungu A. <sup>DRC</sup> ,<br>Reekmans R. <sup>BU</sup>                                                                                     |

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| 313 <i>Lepizites repandus</i> (Mont.) Fr.                  | G.F. <sup>DRC</sup>                                             | Hendrickx F.L. <sup>DRC</sup> , Vanderyst H. <sup>DRC</sup> , de Witte |
| 314 <i>Lepizites vespaceus</i> (Pers.) Ryvarden            | Rammeloo J. <sup>BU</sup>                                       |                                                                        |
| 315 <i>Lepiota coactilia</i> Beeli                         | Goossens-Fontana M. <sup>DRC</sup>                              |                                                                        |
| 316 <i>Lepiota montagnei</i> var. <i>congolensis</i> Beeli | Goossens-Fontana M. <sup>DRC</sup>                              |                                                                        |
| 317 <i>Lepiota purpureoimbricata</i> Beeli                 | Goossens-Fontana M. <sup>DRC</sup>                              |                                                                        |
| 318 <i>Lepista sordida</i> (Fr.) Singer                    | + Degreef J. <sup>RW</sup> , Rizinde J.C. <sup>DRC</sup>        |                                                                        |
| 319 <i>Leucoagaricus bisporus</i> Heinem.                  | Dewèvre A. <sup>DRC</sup>                                       |                                                                        |
| 320 <i>Leucoagaricus bulbillosus</i> Heinem.               | Goossens-Fontana M. <sup>DRC</sup>                              |                                                                        |
| 321 <i>Leucoagaricus carminescens</i> Heinem.              | Goossens-Fontana M. <sup>DRC</sup>                              |                                                                        |
| 322 <i>Leucoagaricus ferruginosus</i> Heinem.              | Goossens-Fontana M. <sup>DRC</sup>                              |                                                                        |
| 323 <i>Leucoagaricus griseus</i> Heinem.                   | Goossens-Fontana M. <sup>DRC</sup>                              |                                                                        |
| 324 <i>Leucoagaricus leucothites</i> (Vittad.) Wasser      | Goossens-Fontana M. <sup>DRC</sup>                              |                                                                        |
| 325 <i>Leucoagaricus malvaceus</i> Heinem.                 | Goossens-Fontana M. <sup>DRC</sup>                              |                                                                        |
| 326 <i>Leucoagaricus pepinus</i> Heinem.                   | Goossens-Fontana M. <sup>DRC</sup>                              |                                                                        |
| 327 <i>Leucoagaricus roseolus</i> (Beeli) Heinem.          | Goossens-Fontana M. <sup>DRC</sup>                              |                                                                        |
| 328 <i>Leucoagaricus squamosus</i> Heinem.                 | Goossens-Fontana M. <sup>DRC</sup>                              |                                                                        |
| 329 <i>Leucoagaricus striatulus</i> Heinem.                | Goossens-Fontana M. <sup>DRC</sup>                              |                                                                        |
| 330 <i>Leucoagaricus testaceus</i> Heinem.                 | Goossens-Fontana M. <sup>DRC</sup>                              |                                                                        |
| 331 <i>Leucocoprinus birnbaumii</i> (Corda) Singer         | Goossens-Fontana M. <sup>DRC</sup>                              |                                                                        |
| 332 <i>Leucocoprinus discoideus</i> (Beeli) Heinem.        | Goossens-Fontana M. <sup>DRC</sup>                              |                                                                        |
| 333 <i>Leucocoprinus elaeidis</i> (Beeli) Heinem.          | Goossens-Fontana M. <sup>DRC</sup>                              |                                                                        |
| 334 <i>Leucocoprinus flavus</i> (Beeli) Heinem.            | Goossens-Fontana M. <sup>DRC</sup>                              |                                                                        |
| 335 <i>Leucocoprinus medioflavus</i> (Boud.) Bon           | Goossens-Fontana M. <sup>DRC</sup>                              |                                                                        |
| 336 <i>Leucocoprinus noctiphilus</i> (Ellis) Heinem.       | Goossens-Fontana M. <sup>DRC</sup>                              |                                                                        |
| 337 <i>Leucocoprinus pepinosporus</i> Heinem.              | Goossens-Fontana M. <sup>DRC</sup>                              |                                                                        |
| 338 <i>Leucocoprinus violaceus</i> Heinem.                 | Goossens-Fontana M. <sup>DRC</sup>                              |                                                                        |
| 339 <i>Lignosus dimiticus</i> Ryvarden                     | Verbeke A. <sup>BU</sup>                                        |                                                                        |
| 340 <i>Lignosus sacer</i> (Fr.) Ryvarden                   | Verbeke A. <sup>BU</sup> , Lewalle J. <sup>BU</sup>             |                                                                        |
| 341 <i>Lopharia cinerascens</i> (Schwein.) G.Cunn.         | Rammeloo J. <sup>RW, BU</sup>                                   |                                                                        |
| 342 <i>Lycogalopsis solmsii</i> E. Fisch.                  | Demoulin V. <sup>DRC</sup>                                      |                                                                        |
| 343 <i>Lycoperdon abyssinicum</i> (Mont.) Dring            | Demoulin V. <sup>DRC</sup>                                      |                                                                        |
| 344 <i>Lycoperdon bicolor</i> Welw. & Curr.                | Goossens-Fontana M. <sup>DRC</sup> , Demoulin V. <sup>DRC</sup> |                                                                        |
| 345 <i>Lycoperdon endotephrum</i> Pat.                     | Demoulin V. <sup>DRC</sup>                                      |                                                                        |
| 346 <i>Lycoperdon perlatum</i> Pers.                       | Demoulin V. <sup>RW</sup>                                       |                                                                        |
| 347 <i>Lycoperdon pratense</i> Pers.                       | Demoulin V. <sup>RW</sup>                                       |                                                                        |
| 348 <i>Lysurus corallocephalus</i> Welw. & Curr.           | Demoulin V. <sup>DRC</sup>                                      |                                                                        |
| 349 <i>Lysurus gardneri</i> Berk.                          | Gille P. <sup>DRC</sup>                                         |                                                                        |
| 350 <i>Macrocybe lobavensis</i> (R. Heim) Pegler & Lodge   | + Rizinde J.C. <sup>DRC</sup>                                   |                                                                        |

- 351 *Macrolepiota africana* (R.Heim) Heinem.
- 352 *Macrolepiota dolichaula* (Berk. & Broome) Pegler & R.W.Rayner
- 353 *Macrolepiota gracilentata* var. *congolensis* (Beeli) Heinem.
- 354 *Macrolepiota odorata* Heinem.
- 355 *Macrolepiota zeyheri* Heinem.
- 356 *Marasmiellus inoderma* (Berk.) Singer
- 357 *Marasmiellus purpureoalbus* (Petch) Singer
- 358 *Marasmius africanus* (Pat.) Sacc.
- 359 *Marasmius albertianus* Singer
- 360 *Marasmius allium* Eichelb.
- 361 *Marasmius arborescens* (Henn.) Beeli
- 362 *Marasmius atrorubens* Berk.
- 363 *Marasmius bekolacongoli* Beeli
- 364 *Marasmius bingaensis* Singer
- 365 *Marasmius brunneolus* (Beeli) Singer
- 366 *Marasmius bururiensis* Antonin
- 367 *Marasmius confertus* var. *tenuicystidiatus* Antonin
- 368 *Marasmius conicopapillatus* Henn.
- 369 *Marasmius crinisequi* F.Muell.
- 370 *Marasmius episemus* Singer
- 371 *Marasmius grandisetulosus* Singer
- 372 *Marasmius haediniformis* Singer
- 373 *Marasmius haematocephalus* (Mont.) Fr.
- 374 *Marasmius kigwenensis* Antonin
- 375 *Marasmius megistus* Singer
- 376 *Marasmius muramwyanensis* Antonin
- 377 *Marasmius rotalis* var. *latisporus* Antonin
- 378 *Marasmius striipileus* Antonin
- 379 *Marasmius witteanus* Singer
- 380 *Microporellus violaceocinerascens* (Petch) A. David & Rajchenb.
- 381 *Microporus affinis* (Blume & T.Nees) Kuntze
- 382 *Microporus atrovillosus* Ryvarden
- 383 *Microporus vernicipes* (Berk.) Kuntze
- 384 *Microporus xanthopus* (Fr.) Kuntze
- + Goossens-Fontana M.<sup>DRC</sup>, Degreef J.<sup>RW, BU</sup>, Rizinde J.C.<sup>DRC</sup>, de Witte G.F.<sup>DRC</sup>
- + Degreef J.<sup>BU</sup>, Mukandera A.<sup>RW</sup>
- de Witte G.F.<sup>DRC</sup>, Hendrickx F.L.<sup>BU</sup>, Reekmans R.<sup>BU</sup>
- Goossens-Fontana M.<sup>DRC</sup>
- Goossens-Fontana M.<sup>DRC</sup>, Hendrickx F.L.<sup>DRC</sup>
- + Degreef J.<sup>RW</sup>
- Hendrickx F.L.<sup>DRC</sup>, Lebrun J.<sup>DRC</sup>
- Bequaert J.<sup>DRC</sup>
- de Witte G.F.<sup>DRC</sup>
- Degreef J.<sup>DRC</sup>
- + Degreef J.<sup>RW</sup>, Rizinde J.C.<sup>DRC</sup>, Rammeloo J.<sup>BU</sup>
- Rammeloo J.<sup>BU</sup>
- + Degreef J.<sup>RW</sup>, Rizinde J.C.<sup>DRC</sup>, Verbeken A.<sup>BU</sup>, Rammeloo J.<sup>BU</sup>, de Witte G.F.<sup>DRC</sup>
- Rammeloo J.<sup>BU</sup>, de Witte G.F.<sup>DRC</sup>
- + Rizinde J.C.<sup>DRC</sup>
- Rammeloo J.<sup>BU</sup>
- Rammeloo J.<sup>BU</sup>
- Rammeloo J.<sup>BU</sup>, Petit E.M.A.<sup>BU</sup>, Lewalle J.<sup>BU</sup>
- Goossens-Fontana M.<sup>DRC</sup>
- Goossens-Fontana M.<sup>DRC</sup>
- de Witte G.F.<sup>DRC</sup>
- Hendrickx F.L.<sup>DRC</sup>
- Rammeloo J.<sup>BU</sup>
- Rammeloo J.<sup>BU</sup>
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- Rammeloo J.<sup>BU</sup>
- Rammeloo J.<sup>BU</sup>
- de Witte G.F.<sup>DRC</sup>
- de Witte G.F.<sup>DRC</sup>
- Lewalle J.<sup>DRC</sup>, de Witte G.F.<sup>DRC</sup>, Lebrun J.<sup>DRC</sup>, Van der Veken P.<sup>RW, DRC</sup>, Hendrickx F.L.<sup>DRC</sup>, Bequaert J.<sup>DRC</sup>, Rammeloo J.<sup>DRC</sup>
- Rammeloo J.<sup>DRC</sup>, Van der Veken P.<sup>DRC</sup>
- Lambinon J.<sup>RW</sup>, Rammeloo J.<sup>DRC, RW</sup>, Hendrickx F.L.<sup>RW</sup>, Lebrun J.<sup>DRC</sup>, Van der Veken P.<sup>RW</sup>
- Petit E.M.A.<sup>BU</sup>, Verbeken A.<sup>BU</sup>, de Witte G.F.<sup>DRC</sup>, Rammeloo J.<sup>BU, DRC</sup>, Vanderyst H.<sup>DRC</sup>, Lambinon J.<sup>BU</sup>

- 385 *Micropsalliota campestris* (Heinem. & Gooss.-Font.) Heinem.
- 386 *Micropsalliota heterocystis* Heinem.
- 387 *Micropsalliota pholiotinoides* Heinem.
- 388 *Mutinus bambusinus* (Zoll.) E. Fisch.
- 389 *Mutinus elegans* (Mont.) E. Fisch.
- 390 *Mutinus simplex* Lloyd
- 391 *Mutinus zenkeri* (Henn.) E. Fisch.
- 392 *Mycena chlorinosma* Singer
- 393 *Mycena oreadeoides* Singer
- 394 *Mycena pura* (Pers.) P.Kumm.
- 395 *Mycena sabali* (Murrill) Murrill
- 396 *Mycosyrinx microspora* Cant.
- 397 *Neonothopanus hygrophanus* (Mont.) De Kesel & Degreef
- 398 *Nidula niveotomentosa* (Henn.) Lloyd
- 399 *Nigrofomes melanoporus* (Mont.) Murrill
- 400 *Nigroporus vinosus* (Berk.) Murrill
- 401 *Oxyporus latemarginata* (E.J.Durieu & Mont.) Donk
- 402 *Pachykytospora papyracea* (Schwein.) Ryvarden
- 403 *Panaeolus antillarum* (Fr.) Dennis
- 404 *Panaeolus cyanescens* (Berk. & Broome) Sacc.
- 405 *Panaeolus foenicisii* (Pers.) J.Schröt.
- 406 *Panaeolus goossensiae* Beeli
- 407 *Panaeolus semiovatus* (Sow.) S.Lundell & Nannf.
- 408 *Paxillus brunneotomentosus* Heinem. & Rammeloo
- 409 *Paxillus piperatus* Heinem. & Rammeloo
- 410 *Perenniporia contraria* (Berk. & M.A.Curtis) Ryvarden
- 411 *Perenniporia dendrohyphidia* Ryvarden
- 412 *Perenniporia inflexibilis* (Berk.) Ryvarden
- 413 *Perenniporia latissima* (Bres.) Ryvarden
- 414 *Perenniporia martia* (Berk.) Ryvarden
- 415 *Perenniporia medulla-panis* (Jacq.) Donk
- 416 *Perenniporia ochroleuca* (Berk.) Ryvarden
- 417 *Perenniporia vicina* (Lloyd) Decock & Ryvarden
- 418 *Phaeoclavulina flaccida* (Fr.) Giachini
- 419 *Phallus indusiatus* Vent.
- Goossens-Fontana M. <sup>DRC</sup>
- Rammeloo J. <sup>DRC</sup>
- Goossens-Fontana M. <sup>DRC</sup>, Rammeloo J. <sup>BU</sup>
- Demoulin V. <sup>DRC</sup>
- Degreef J. <sup>BU</sup>
- Goossens-Fontana M. <sup>DRC</sup>
- Demoulin V. <sup>DRC</sup>
- Goossens-Fontana M. <sup>DRC</sup>
- Goossens-Fontana M. <sup>DRC</sup>
- Degreef J. <sup>RW</sup>
- Goossens-Fontana M. <sup>DRC</sup>
- Seret F. <sup>BU</sup>
- de Witte G.F. <sup>DRC</sup>
- Demoulin V. <sup>DRC,RW</sup>
- Hendrickx F.L. <sup>RW</sup>
- Verbeken A. <sup>BU</sup>
- Thoen D. <sup>DRC</sup>
- Rammeloo J. <sup>BU</sup>
- Becquet A. <sup>RW</sup>, Goossens-Fontana M. <sup>DRC</sup>, Hendrickx F.L. <sup>DRC</sup>
- Goossens-Fontana M. <sup>DRC</sup>
- Goossens-Fontana M. <sup>DRC</sup>
- Goossens-Fontana M. <sup>DRC</sup>, Rammeloo J. <sup>BU</sup>
- Becquet A. <sup>RW</sup>
- Degreef J. <sup>RW, DRC</sup>, Rammeloo J. <sup>BU</sup>
- Rammeloo J. <sup>BU</sup>
- Rammeloo J. <sup>RW</sup>
- Rammeloo J. <sup>BU</sup>
- Rammeloo J. <sup>DRC</sup>
- de Witte G.F. <sup>DRC</sup>
- Rammeloo J. <sup>DRC</sup>
- Rammeloo J. <sup>RW,BU</sup>
- Petit E.M.A. <sup>BU</sup>
- de Witte G.F. <sup>DRC</sup>
- de Witte G.F. <sup>DRC</sup>, Goossens-Fontana M. <sup>DRC</sup>
- Bequaert J. <sup>DRC</sup>, Rammeloo J. <sup>BU</sup>, Rizinde J.C. <sup>DRC</sup>, Demoulin V. <sup>DRC</sup>

- 420 *Phallus rubicundus* (Bosc) Fr.
- 421 *Phanerochaete salmonicolor* (Berk. & Broome) Jülich
- 422 *Phanerochaete tuberculascens* Hjortstam
- 423 *Phellinus adamantinus* (Berk.) Ryvarden
- 424 *Phellinus allardii* (Bres.) S. Ahmad
- 425 *Phellinus badius* (Berk. Ex Cooke) G.Cunn.
- 426 *Phellinus contiguus* (Pers.) Pat.
- 427 *Phellinus cupreus* (Berk.) Ryvarden
- 428 *Phellinus discipes* (Berk.) Ryvarden
- 429 *Phellinus fastuosus* (Lév.) Ryvarden
- 430 *Phellinus fastuosus* (Lév.) S. Ahmad
- 431 *Phellinus ferrugineovelutinus* (Henn.) Ryvarden
- 432 *Phellinus gabonensis* Decock & Yombiy.
- 433 *Phellinus gilvus* (Schwein.) Pat.
- 434 *Phellinus glaucescens* (Petch) Ryvarden
- 435 *Phellinus grenadensis* (Murrill) Ryvarden
- 436 *Phellinus macrosporus* Gibertoni & Ryvarden
- 437 *Phellinus melanodermus* (Pat.) M.Fidalgo
- 438 *Phellinus newtoniae* Niemelä & Mrema
- 439 *Phellinus noxius* (Corner) G.Cunn.
- 440 *Phellinus pachyphloeus* (Pat.) Pat.
- 441 *Phellinus purpureogilvus* (Petch) Ryvarden
- 442 *Phellinus rimosus* (Berk.) Pilát
- 443 *Phellinus senex* (Nees & Mont.) Imazeki
- 444 *Phellinus setulosus* (Lloyd) Imazeki
- 445 *Phellinus torulosus* (Pers.) Bourdot & Galzin
- 446 *Phlebiopsis crassa* (Lév.) Floudas & Hibbett
- 447 *Phlebopus colossus* (R.Heim) Singer
- 448 *Phlebopus silvaticus* Heinem.
- 449 *Phlebopus sudanicus* (Har. & Pat.) Heinem.
- 450 *Pholiota spumosa* (Fr.) Singer
- 451 *Phragmidium mucronatum* (Pers.) Schltdl.
- 452 *Phylloporia afrospathulata* Yombiy. & Decock
- 453 *Phylloporia minutispora* Ipuleit & Ryvarden
- 454 *Phylloporia pectinata* (Klotzsch) Ryvarden
- Demoulin V. <sup>RW</sup>
- Hendrickx F.L. <sup>DRC</sup>
- Rammeloo J. <sup>BU</sup>
- Balezi A. <sup>DRC</sup>
- Balezi A. <sup>DRC</sup>
- Rammeloo J. <sup>RW</sup>
- Rammeloo J. <sup>BU</sup>
- Van der Veken P. <sup>RW</sup>
- Rammeloo J. <sup>BU</sup>, Balezi <sup>DRC</sup>
- de Witte G.F. <sup>DRC</sup>, Lewalle J. <sup>BU</sup>, Rammeloo J. <sup>RW</sup>, Van der Veken P. <sup>RW</sup>
- Balezi A. <sup>DRC</sup>
- Rammeloo J. <sup>RW</sup>, Balezi <sup>DRC</sup>
- Balezi A. <sup>DRC</sup>
- Lewalle J., de Witte G.F. <sup>DRC</sup>, Lebrun J. <sup>DRC</sup>, Petit E.M.A. <sup>BU</sup>, Louis J. <sup>DRC</sup>, Van der Veken P. <sup>RW</sup>, Hendrickx F.L. <sup>RW,DRC</sup>, Reekmans R. <sup>BU</sup>, Van Meel L. <sup>BU</sup>, Rammeloo J. <sup>RW,BU</sup>, Balezi <sup>DRC</sup>
- Balezi A. <sup>DRC</sup>
- Balezi A. <sup>DRC</sup>, Rammeloo J. <sup>DRC</sup>
- Balezi A. <sup>DRC</sup>
- Rammeloo J. <sup>DRC</sup>, Balezi <sup>DRC</sup>
- Balezi A. <sup>DRC</sup>
- de Witte G.F. <sup>DRC</sup>, Balezi <sup>DRC</sup>
- De Witte G.F. <sup>DRC</sup>
- Balezi A. <sup>DRC</sup>
- Rammeloo J. <sup>RW</sup>
- Rammeloo J. <sup>RW</sup>, Van der Veken P. <sup>RW,DRC</sup>, Lambinon J. <sup>BU,RW</sup>, de Witte G.F. <sup>DRC</sup>, Fassi B. <sup>DRC</sup>
- Van der Veken P. <sup>RW</sup>, Balezi <sup>DRC</sup>
- Rammeloo J. <sup>RW,BU</sup>
- Rammeloo J. <sup>RW</sup>
- Rammeloo J. <sup>BU</sup>
- Rammeloo J. <sup>DRC</sup>
- Van der Veken P. <sup>RW</sup>
- Degreef J. <sup>RW</sup>, Mukandera A. <sup>RW</sup>
- Hendrickx F.L. <sup>DRC</sup>
- Balezi A. <sup>DRC</sup>
- Balezi A. <sup>DRC</sup>
- Balezi A. <sup>DRC</sup>

- 455 *Phylloporia resupinata* Douanla-Meli & Ryvarden
- 456 *Phylloporia spathulata* (Hook.) Ryvarden
- 457 *Phylloporus ampliporus* Heinem. & Rammeloo
- 458 *Phylloporus carmineus* Heinem.
- 459 *Phylloporus gomphidioides* Heinem. & Rammeloo
- 460 *Phylloporus nigrescens* Heinem. & Rammeloo
- 461 *Phylloporus purpureus* var. *ambiguus* Heinem.
- 462 *Phylloporus rhodophaeus* Heinem. & Rammeloo
- 463 *Phylloporus tubipes* Heinem.
- 464 *Phyllostopsis salmonea* (Kalchbr. & MacOwan) D.A.Reid
- 465 *Physalacria macrocystidiata* Rammeloo
- 466 *Pisolithus arhizus* (Scop.) Rauschert
- 467 *Pleurotus cystidiosus* O.K.Mill.
- 468 *Pleurotus djamor* (Rumph. ex Fr.) Boedijn
- 469 *Pleurotus flabellatus* Sacc.
- 470 *Pleurotus tuber-regium* (Fr.) Singer
- 471 *Pluteus albobipitatus* (Dennis) Singer
- 472 *Pluteus glaucotinctus* E.Horak
- 473 *Pluteus phaeoleucus* E.Horak
- 474 *Pluteus pulverulentus* Murrill
- 475 *Podoscypha bolleana* (Mont.) Boidin
- 476 *Podoscypha involuta* (Klotzsch) Imazeki
- 477 *Podoscypha nitidula* (Berk.) Pat.
- 478 *Podoscypha parvula* (Lloyd) D.A.Reid
- 479 *Podoscypha petalodes* subsp. *rosulata* D.A.Reid
- 480 *Podoscypha thozetii* (Berk.) Boidin
- 481 *Polyporus badius* (Pers.) Schwein.
- 482 *Polyporus dictyopus* Mont.
- 483 *Polyporus fasciculatus* (Pat.) Lloyd
- 484 *Polyporus leprieurii* Mont.
- 485 *Polyporus squamosus* Huds.
- 486 *Polyporus tricholoma* Mont.
- 487 *Polyporus tuberaster* (Jacq. ex Pers.) Fr.
- 488 *Polyporus virgatus* Berk. & M.A.Curtis
- Balezi A. <sup>DRC</sup>
- Rammeloo J. <sup>BU</sup>
- Rammeloo J. <sup>DRC</sup>, Van der Veken P. <sup>DRC</sup>
- Rammeloo J. <sup>DRC</sup>
- Rammeloo J. <sup>BU</sup>
- Rammeloo J. <sup>DRC</sup>
- Rammeloo J. <sup>BU</sup>
- Thoen D. <sup>DRC</sup>
- Cocquyt C. <sup>BU</sup>
- Rammeloo J. <sup>BU</sup>
- Rammeloo J. <sup>RW</sup>
- Murhula Cizungu A. <sup>DRC</sup>, Nkengurutse J. <sup>BU</sup>, Petit E.M.A. <sup>BU</sup>, Demaire <sup>RW</sup>, Van Puyvelde L. <sup>RW</sup>, Goossens-Fontana M. <sup>DRC</sup>
- + Degreef J. <sup>RW</sup>
- + Degreef J. <sup>RW</sup>, Rizinde J.C. <sup>DRC</sup>
- + Hendrickx F.L. <sup>DRC</sup>, Degreef J. <sup>RW</sup>, Rizinde J.C. <sup>DRC</sup>
- + Rizinde J.C. <sup>DRC</sup>
- Goossens-Fontana M. <sup>DRC</sup>
- Goossens-Fontana M. <sup>DRC</sup>
- Goossens-Fontana M. <sup>DRC</sup>
- Goossens-Fontana M. <sup>DRC</sup>
- de Witte G.F. <sup>DRC</sup>
- de Witte G.F. <sup>DRC</sup>, Hendrickx F.L. <sup>DRC</sup>, Van der Veken P. <sup>DRC</sup>, Rammeloo J. <sup>BU</sup>, Goossens-Fontana M. <sup>DRC</sup>
- Rammeloo J. <sup>BU</sup>, Petit E.M.A. <sup>BU</sup>
- de Witte G.F. <sup>DRC</sup>, Hendrickx F.L. <sup>DRC</sup>, Rammeloo J. <sup>BU</sup>, Petit E.M.A. <sup>BU</sup>
- Goossens-Fontana M. <sup>DRC</sup>
- Petit E.M.A. <sup>BU</sup>, Rammeloo J. <sup>BU</sup>
- Rammeloo J. <sup>BU</sup>
- Rammeloo J. <sup>BU</sup>
- Rammeloo J. <sup>DRC, BU</sup>
- de Witte G.F. <sup>DRC</sup>
- Degreef J. <sup>RW</sup>
- Verbeken A. <sup>BU</sup>
- Degreef J. <sup>RW</sup>
- Rizinde J.C. <sup>DRC</sup>, Rammeloo J. <sup>RW</sup>

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| 489 | <i>Porostereum spadiceum</i> (Pers.) Hjortstam & Ryvarden         | Rammeloo J. <sup>RW</sup> , de Witte G.F. <sup>DRC</sup>                                                            |
| 490 | <i>Porphyrellus niger</i> Heinem. & Gooss.-Font.                  | Goossens-Fontana M. <sup>DRC</sup> , Verbeken A. <sup>BU</sup>                                                      |
| 491 | <i>Postia africana</i> (Ryvarden) V.Papp                          | Rammeloo J. <sup>BU</sup>                                                                                           |
| 492 | <i>Psathyrella atroumbonata</i> Pegler                            | + Degreef J. <sup>RW</sup> , Mukandera A. <sup>RW</sup>                                                             |
| 493 | <i>Psathyrella tuberculata</i> (Pat.) A.H.Sm.                     | + Degreef J. <sup>RW</sup>                                                                                          |
| 494 | <i>Psilocybe semilanceata</i> Singer                              | Goossens-Fontana M. <sup>DRC</sup>                                                                                  |
| 495 | <i>Pterygellus funalis</i> (Henn.) D.A.Reid                       | Rammeloo J. <sup>BU</sup>                                                                                           |
| 496 | <i>Pulveroboletus carminiporus</i> Heinem.                        | Rammeloo J. <sup>DRC</sup>                                                                                          |
| 497 | <i>Pulveroboletus cavipes</i> Heinem.                             | Rammeloo J. <sup>DRC</sup>                                                                                          |
| 498 | <i>Ranadivia stereoides</i> (Fr.) Zmitr.                          | Rammeloo J. <sup>DRC</sup>                                                                                          |
| 499 | <i>Rectipilus natalensis</i> (W.B.Cooke) Agerer                   | Rammeloo J. <sup>BU</sup>                                                                                           |
| 500 | <i>Rickenella fibula</i> (Bull.) Raithehl.                        | Rammeloo J. <sup>BU</sup>                                                                                           |
| 501 | <i>Rigidoporus biokoensis</i> (Bres. ex Lloyd) Ryvarden           | de Witte G.F. <sup>DRC</sup>                                                                                        |
| 502 | <i>Rigidoporus lineatus</i> (Pers.) Ryvarden                      | Lebrun J. <sup>DRC</sup>                                                                                            |
| 503 | <i>Rigidoporus microporus</i> (Sw.) Overeem                       | de Witte G.F. <sup>DRC</sup> , Rammeloo J. <sup>DRC</sup> , Lebrun J. <sup>RW</sup> , Hendrickx F.L. <sup>DRC</sup> |
| 504 | <i>Rigidoporus vinctus</i> (Berk.) Ryvarden                       | Rammeloo J. <sup>RW, BU</sup>                                                                                       |
| 505 | <i>Ripartitella degreefii</i> Rizinde, Desjardin, Amalfi & Decock | Rizinde J.C. <sup>DRC</sup>                                                                                         |
| 506 | <i>Royoporus spatulatus</i> (Jungh.) A.B.De                       | de Witte G.F. <sup>DRC</sup> , Rammeloo J. <sup>BU, DRC, RW</sup> , Degreef J. <sup>RW</sup>                        |
| 507 | <i>Rubinoboletus ballouii</i> (Peck) Heinem. & Rammeloo           | Rammeloo J. <sup>BU</sup> , Lambinon J. <sup>BU</sup> , Dossin <sup>BU</sup>                                        |
| 508 | <i>Rubinoboletus griseus</i> Heinem. & Rammeloo                   | Cocquyt C. <sup>BU</sup>                                                                                            |
| 509 | <i>Rubinoboletus luteopurpureus</i> (Beeli) Heinem. & Rammeloo    | Nkengurutse J. <sup>BU</sup> , Rammeloo J. <sup>DRC</sup> , Verbeken A. <sup>BU</sup>                               |
| 510 | <i>Rubinoboletus phlebopoides</i> Heinem. & Rammeloo              | Rammeloo J. <sup>BU</sup>                                                                                           |
| 511 | <i>Russula afrodelica</i> Buyck                                   | Dossin <sup>BU</sup>                                                                                                |
| 512 | <i>Russula afronigricans</i> Buyck                                | Degreef J. <sup>BU</sup>                                                                                            |
| 513 | <i>Russula albobloccosa</i> Buyck                                 | Verbeken A. <sup>BU</sup> , Rammeloo J. <sup>BU</sup>                                                               |
| 514 | <i>Russula annulata</i> var. <i>tshopoensis</i> Buyck             | Verbeken A. <sup>BU</sup>                                                                                           |
| 515 | <i>Russula areolata</i> Buyck                                     | Rammeloo J. <sup>BU</sup>                                                                                           |
| 516 | <i>Russula brunneofloccosa</i> Buyck                              | Verbeken A. <sup>BU</sup>                                                                                           |
| 517 | <i>Russula brunneorigida</i> Buyck                                | Rammeloo J. <sup>BU</sup>                                                                                           |
| 518 | <i>Russula bururiensis</i> Buyck                                  | Rammeloo J. <sup>BU</sup>                                                                                           |
| 519 | <i>Russula cellulata</i> Buyck                                    | + Verbeken A. <sup>BU</sup> , Degreef J. <sup>BU</sup>                                                              |
| 520 | <i>Russula ciliata</i> Buyck                                      | + Verbeken A. <sup>BU</sup> , Dossin <sup>BU</sup> , Degreef J. <sup>BU</sup>                                       |
| 521 | <i>Russula compressa</i> Buyck                                    | + Rammeloo J. <sup>BU</sup>                                                                                         |
| 522 | <i>Russula congoana</i> Pat.                                      | + Degreef J. <sup>BU</sup> , Dossin <sup>BU</sup>                                                                   |
| 523 | <i>Russula cyanoxantha</i> (Schaeff.) Fr.                         | + Verbeken A. <sup>BU</sup>                                                                                         |

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| 524 <i>Russula diffusa</i> Buyck                               | Rammeloo J. <sup>DRC</sup>                                                                                                                                                                                                                   |
| 525 <i>Russula flavobrunnea</i> var. <i>flavobrunnea</i> Buyck | + Rammeloo J. <sup>BU</sup>                                                                                                                                                                                                                  |
| 526 <i>Russula hiemisilvae</i> Buyck                           | + Degreef J. <sup>BU</sup>                                                                                                                                                                                                                   |
| 527 <i>Russula kivuensis</i> Buyck                             | Rammeloo J. <sup>DRC</sup>                                                                                                                                                                                                                   |
| 528 <i>Russula madagassensis</i> R.Heim                        | Nkengurutse J. <sup>BU</sup>                                                                                                                                                                                                                 |
| 529 <i>Russula meleagris</i> Buyck                             | + Rammeloo J. <sup>DRC</sup>                                                                                                                                                                                                                 |
| 530 <i>Russula murinacea</i> R.Heim                            | Verbeken A. <sup>BU</sup>                                                                                                                                                                                                                    |
| 531 <i>Russula oleifera</i> var. <i>oleifera</i> Buyck         | Rammeloo J. <sup>BU</sup>                                                                                                                                                                                                                    |
| 532 <i>Russula parvulospora</i> Buyck                          | Rammeloo J. <sup>BU</sup>                                                                                                                                                                                                                    |
| 533 <i>Russula patouillardii</i> Singer                        | Verbeken A. <sup>BU</sup> , Degreef J. <sup>BU</sup>                                                                                                                                                                                         |
| 534 <i>Russula pectinata</i> Fr.                               | Verbeken A. <sup>BU</sup>                                                                                                                                                                                                                    |
| 535 <i>Russula pellucida</i> (Gooss.-Font. & R.Heim) Buyck     | Rammeloo J. <sup>DRC</sup>                                                                                                                                                                                                                   |
| 536 <i>Russula phaeocephala</i> Buyck                          | + Rammeloo J. <sup>BU</sup>                                                                                                                                                                                                                  |
| 537 <i>Russula pseudocarmesina</i> Buyck                       | Nkengurutse J. <sup>BU</sup>                                                                                                                                                                                                                 |
| 538 <i>Russula roseoviolacea</i> Buyck                         | + Degreef J. <sup>BU</sup> , Rammeloo J. <sup>DRC</sup>                                                                                                                                                                                      |
| 539 <i>Russula sejuncta</i> Buyck                              | + Rammeloo J. <sup>BU</sup> , Dossin <sup>BU</sup>                                                                                                                                                                                           |
| 540 <i>Russula striatoviridis</i> Buyck                        | + Verbeken A. <sup>BU</sup>                                                                                                                                                                                                                  |
| 541 <i>Russula subfistulosa</i> Buyck                          | Dossin <sup>BU</sup> , Rammeloo J. <sup>BU</sup>                                                                                                                                                                                             |
| 542 <i>Russula testacea</i> Buyck                              | Dossin <sup>BU</sup> , Rammeloo J. <sup>BU</sup> , Degreef J. <sup>BU</sup>                                                                                                                                                                  |
| 543 <i>Russula testaceoaurantiaca</i> Beeli                    | Rammeloo J. <sup>DRC</sup>                                                                                                                                                                                                                   |
| 544 <i>Russula velutina</i> (Bres.) Buyck                      | Verbeken A. <sup>BU</sup>                                                                                                                                                                                                                    |
| 545 <i>Russula viscidula</i> Buyck                             | Verbeken A. <sup>BU</sup>                                                                                                                                                                                                                    |
| 546 <i>Russula yaeneroensis</i> Buyck                          | Rammeloo J. <sup>DRC</sup>                                                                                                                                                                                                                   |
| 547 <i>Schizophyllum commune</i> Fr.                           | + Degreef J. <sup>DRC</sup> , Rizinde J.C. <sup>DRC</sup> , Rammeloo J. <sup>DRC, BU</sup> , Petit E.M.A. <sup>BU</sup> , de Witte G.F. <sup>DRC</sup> , Hendrickx F.L. <sup>DRC</sup> , Lewalle J. <sup>BU</sup> , Lebrun J. <sup>DRC</sup> |
| 548 <i>Scleroderma aurantium</i> (L.) Pers.                    | Hendrickx F.L. <sup>DRC</sup>                                                                                                                                                                                                                |
| 549 <i>Scleroderma cepa</i> Pers.                              | Demoulin V. <sup>DRC, RW, BU</sup>                                                                                                                                                                                                           |
| 550 <i>Scleroderma citrinum</i> Pers.                          | Lambinon J. <sup>BU</sup> , Demaire <sup>RW</sup> , Demoulin <sup>DRC</sup>                                                                                                                                                                  |
| 551 <i>Scleroderma dictyosporum</i> Pat.                       | Demoulin V. <sup>DRC</sup>                                                                                                                                                                                                                   |
| 552 <i>Scleroderma leptopodium</i> Pat. & Har.                 | Demoulin V. <sup>DRC</sup>                                                                                                                                                                                                                   |
| 553 <i>Scytinostroma duriusculum</i> (Berk. & Broome) Donk     | Rammeloo J. <sup>RW</sup>                                                                                                                                                                                                                    |
| 554 <i>Septobasidium bogoriense</i> Pat.                       | Hendrickx F.L. <sup>DRC</sup>                                                                                                                                                                                                                |
| 555 <i>Sericeomyces violaceus</i> Heinem.                      | Goossens-Fontana M. <sup>DRC</sup>                                                                                                                                                                                                           |
| 556 <i>Sericeomyces viscidulus</i> Heinem.                     | Goossens-Fontana M. <sup>DRC</sup>                                                                                                                                                                                                           |
| 557 <i>Serpula similis</i> (Berk. & Broome) Ginns              | Rammeloo J. <sup>DRC</sup>                                                                                                                                                                                                                   |
| 558 <i>Setogyroporus verus</i> Heinem. & Rammeloo              | Cocquyt C. <sup>BU</sup> , Rammeloo J. <sup>BU</sup>                                                                                                                                                                                         |
| 559 <i>Setulipes afibulatus</i> Antonin                        | Rammeloo J. <sup>BU</sup>                                                                                                                                                                                                                    |

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| 560 <i>Setulipes curvistipitatus</i> Antonin                    | Rammeloo J. <sup>BU</sup>                                                                                                                                                                                                                                                                |
| 561 <i>Setulipes rhizomorphicola</i> Antonin                    | Rammeloo J. <sup>BU</sup>                                                                                                                                                                                                                                                                |
| 562 <i>Skeletocutis nivea</i> (Jungh.) Jean Keller              | Rammeloo J. <sup>RW,BU</sup>                                                                                                                                                                                                                                                             |
| 563 <i>Sphacelotheca ischaemi</i> (Fuckel) G.P.Clinton          | Bequaert J. <sup>DRC</sup>                                                                                                                                                                                                                                                               |
| 564 <i>Steccherinum ethiopicum</i> Maas Geest.                  | Rammeloo J. <sup>RW</sup>                                                                                                                                                                                                                                                                |
| 565 <i>Steccherinum ochraceum</i> (Pers.) Gray                  | Rammeloo J. <sup>RW</sup>                                                                                                                                                                                                                                                                |
| 566 <i>Steccherinum scalare</i> Maas Geest. & Lanq.             | Rammeloo J. <sup>DRC</sup>                                                                                                                                                                                                                                                               |
| 567 <i>Stereopsis hiscens</i> (Berk. & Ravenel) D.A.Reid        | Rammeloo J. <sup>BU</sup>                                                                                                                                                                                                                                                                |
| 568 <i>Stereum hirsutum</i> (Willd.) Pers.                      | Rammeloo J. <sup>DRC, RW, BU</sup> , Verbeken A. <sup>BU</sup> , Lebrun J. <sup>DRC</sup> , Hendrickx F.L. <sup>DRC</sup> , de Witte G.F. <sup>DRC</sup> , Van der Veken P. <sup>DRC</sup> , de Witte G.F. <sup>DRC</sup> , Van der Veken P. <sup>RW</sup> , Vanderyst H. <sup>DRC</sup> |
| 569 <i>Stereum lobatum</i> (Kunze ex Fr.) Fr.                   | Rammeloo J. <sup>BU</sup>                                                                                                                                                                                                                                                                |
| 570 <i>Stereum ochraceoflavum</i> (Schwein.) Sacc.              | Rammeloo J. <sup>RW, BU</sup> , Hendrickx F.L. <sup>DRC</sup> , Lebrun J. <sup>DRC</sup> , de Witte G.F. <sup>DRC</sup> , Goossens-Fontana M. <sup>DRC</sup> , Lewalle J. <sup>BU</sup>                                                                                                  |
| 571 <i>Stereum ostrea</i> (Blume & T.Nees) Fr.                  | Petit E.M.A. <sup>BU</sup>                                                                                                                                                                                                                                                               |
| 572 <i>Stereum reflexulum</i> Lloyd                             | Degreef J. <sup>RW</sup>                                                                                                                                                                                                                                                                 |
| 573 <i>Stropharia aeruginosa</i> (Curtis) Quél.                 | + Leonetout J.J. <sup>RW</sup> , Rammeloo J. <sup>BU</sup> , Mukandera A. <sup>RW</sup>                                                                                                                                                                                                  |
| 574 <i>Suillus granulatus</i> (L.) Roussel                      | + Leonetout J.J. <sup>RW</sup> , Gaie <sup>BU</sup>                                                                                                                                                                                                                                      |
| 575 <i>Suillus luteus</i> (L.) Roussel                          | Rammeloo J. <sup>RW</sup>                                                                                                                                                                                                                                                                |
| 576 <i>Terana coerulea</i> (Lam.) Kuntze                        | + de Witte G.F. <sup>DRC</sup>                                                                                                                                                                                                                                                           |
| 577 <i>Termitomyces clypeatus</i> R.Heim                        | + Rizinde J.C. <sup>DRC</sup>                                                                                                                                                                                                                                                            |
| 578 <i>Termitomyces lesteui</i> (Pat.) R. Heim                  | + Degreef J. <sup>BU</sup>                                                                                                                                                                                                                                                               |
| 579 <i>Termitomyces mammiformis</i> R.Heim                      | + Goossens-Fontana M. <sup>DRC</sup> , Verbeken A. <sup>BU</sup> , de Witte G.F. <sup>DRC</sup> , Rizinde J.C. <sup>DRC</sup> , Mukandera A. <sup>RW</sup>                                                                                                                               |
| 580 <i>Termitomyces microcarpus</i> (Berk. & Broome) R.Heim     | + Goossens-Fontana M. <sup>DRC</sup> , Degreef J. <sup>RW, BU</sup> , Rizinde J.C. <sup>DRC</sup> , Cocquyt C. <sup>BU</sup> , Mukandera A. <sup>RW</sup>                                                                                                                                |
| 581 <i>Termitomyces robustus</i> (Beeli) R.Heim                 | + Mukandera A. <sup>RW</sup>                                                                                                                                                                                                                                                             |
| 582 <i>Termitomyces schimperi</i> (Pat.) R.Heim                 | + Mukandera A. <sup>RW</sup>                                                                                                                                                                                                                                                             |
| 583 <i>Termitomyces striatus</i> (Beeli) R.Heim                 | Rammeloo J. <sup>BU</sup>                                                                                                                                                                                                                                                                |
| 584 <i>Theleporus calcicolor</i> (Sacc. & P.Syd.) Ryvarden      | Lambinon J. <sup>BU</sup> , Troupin O. <sup>BU, RW</sup>                                                                                                                                                                                                                                 |
| 585 <i>Tilletia ayresii</i> Berk.                               | Rammeloo J. <sup>BU</sup>                                                                                                                                                                                                                                                                |
| 586 <i>Tinctoporellus epimiltimus</i> (Berk. & Broome) Ryvarden | Petit E.M.A. <sup>BU</sup>                                                                                                                                                                                                                                                               |
| 587 <i>Trametes cervina</i> (Schwein.) Bres.                    | Petit E.M.A. <sup>BU</sup> , Rammeloo J. <sup>RW</sup> , Thoen D. <sup>DRC</sup> , Hendrickx F.L. <sup>DRC</sup>                                                                                                                                                                         |
| 588 <i>Trametes cingulata</i> Berk.                             | Rammeloo J. <sup>BU</sup> , Hendrickx F.L. <sup>DRC</sup>                                                                                                                                                                                                                                |
| 589 <i>Trametes cinnabarina</i> (Jacq.) Fr. (Jacq.) P.Karst.    | de Witte G.F. <sup>DRC</sup> , Hendrickx F.L. <sup>DRC</sup> , Rammeloo J. <sup>DRC, RW, BU</sup> , Lewalle J. <sup>BU</sup> , Lebrun J. <sup>DRC</sup> , Germain R.G.A. <sup>DRC</sup> , Petit E.M.A. <sup>BU</sup>                                                                     |
| 590 <i>Trametes coccinea</i> (Fr.) Hai J. Li & S.H. He          |                                                                                                                                                                                                                                                                                          |

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| 591 <i>Trametes cotonea</i> (Pat. & Har.) Ryvarden                         | Goossens-Fontana M. <sup>DRC</sup> , Van der Veken P. <sup>DRC, RW</sup>                                                                                                                                                                          |
| 592 <i>Trametes elegans</i> (Spreng.) Fr.                                  | de Witte G.F. <sup>DRC</sup> , Rammeloo J. <sup>RW, BU</sup> , Reekmans R. <sup>BU</sup>                                                                                                                                                          |
| 593 <i>Trametes hirsuta</i> (Wulfen) Pilát                                 | Van der Veken P. <sup>RW</sup> , Rammeloo J. <sup>BU, DRC, RW</sup> , de Witte G.F. <sup>DRC</sup> , Lebrun J. <sup>DRC</sup> , Petit E.M.A. <sup>BU</sup> , Hendrickx F.L. <sup>DRC</sup> , Murhula Cizungu A. <sup>DRC</sup>                    |
| 594 <i>Trametes leonina</i> (Klotzsch) Pat.                                | Rammeloo J. <sup>DRC, RW, BU</sup>                                                                                                                                                                                                                |
| 595 <i>Trametes meyenii</i> (Klotzsch) Lloyd                               | Rammeloo J. <sup>RW, BU</sup>                                                                                                                                                                                                                     |
| 596 <i>Trametes mimetes</i> (Wakef.) Ryvarden                              | Rammeloo J. <sup>RW, BU</sup> , Hendrickx F.L. <sup>DRC</sup> , Lambinon J. <sup>BU</sup>                                                                                                                                                         |
| 597 <i>Trametes occidentalis</i> (Klotzsch) Fr.                            | Petit E.M.A. <sup>BU</sup>                                                                                                                                                                                                                        |
| 598 <i>Trametes palisotii</i> (Fr.) Imazeki                                | de Witte G.F. <sup>DRC</sup> , Hendrickx F.L. <sup>DRC</sup>                                                                                                                                                                                      |
| 598 <i>Trametes polyzona</i> (Pers.) Justo                                 | de Witte G.F. <sup>DRC</sup> , Becquet A. <sup>BU</sup>                                                                                                                                                                                           |
| 599 <i>Trametes strumosa</i> (Fr.) Zmitr., Wasser & Ezhov                  | de Witte G.F. <sup>DRC</sup> , Lebrun J. <sup>DRC</sup> , Rammeloo J. <sup>DRC, BU, RW</sup> , Hendrickx F.L. <sup>DRC</sup> , Verbeken A. <sup>BU</sup> , Van der Veken P. <sup>RW</sup>                                                         |
| 600 <i>Trametes versicolor</i> (L.) Lloyd                                  | Rammeloo J. <sup>RW, BU</sup> , de Witte G.F. <sup>DRC</sup>                                                                                                                                                                                      |
| 601 <i>Tranzschelia pruni-spinosae</i> (Pers.) Dietel                      | Lebrun J. <sup>DRC</sup> , de Witte G.F. <sup>DRC</sup> , Rammeloo J. <sup>BU, RW, DRC</sup> , A., Lewalle J. <sup>BU</sup> , Petit E.M.A. <sup>BU</sup> , Lambinon J. <sup>RW</sup> , Reekmans R. <sup>BU</sup> , Van der Veken P. <sup>RW</sup> |
| 602 <i>Tricholomopsis aurea</i> (Beeli) Desjardin & B.A.Perry              | Hendrickx F.L. <sup>DRC</sup>                                                                                                                                                                                                                     |
| 603 <i>Trogia infundibuliformis</i> Berk. & Broome                         | + Rammeloo J. <sup>BU</sup> , Degreef J. <sup>DRC, RW</sup> , Mukandera A. <sup>RW</sup> , Rizinde J.C. <sup>DRC</sup>                                                                                                                            |
| 604 <i>Tropicoporus linteus</i> (Berk. & M.A. Curtis) L.W. Zhou & Y.C. Dai | + Rizinde J.C. <sup>DRC</sup> , Goossens-Fontana M. <sup>DRC</sup> , Rammeloo J. <sup>DRC</sup>                                                                                                                                                   |
| 605 <i>Tubosaeta alveolata</i> Heinem.                                     | Balezi A. <sup>DRC</sup>                                                                                                                                                                                                                          |
| 606 <i>Tubosaeta brunneosetosa</i> (Singer) E.Horak                        | Rammeloo J. <sup>DRC</sup>                                                                                                                                                                                                                        |
| 607 <i>Tubosaeta heterosetosa</i> Heinem.                                  | + Rammeloo J. <sup>BU</sup>                                                                                                                                                                                                                       |
| 608 <i>Tulostoma carneum</i> Pat.                                          | Rammeloo J. <sup>BU</sup> , Lambinon J. <sup>BU</sup> , Verbeken A. <sup>BU</sup>                                                                                                                                                                 |
| 609 <i>Tulostoma exasperatum</i> Mont.                                     | Reekmans R. <sup>BU</sup>                                                                                                                                                                                                                         |
| 610 <i>Tylopilus striatulus</i> Heinem.                                    | Lambinon J. <sup>BU</sup> , Lewalle J. <sup>BU</sup> , Demoulin V. <sup>RW</sup>                                                                                                                                                                  |
| 611 <i>Tylopilus violaceus</i> (Beeli) Heinem.                             | Rammeloo J. <sup>DRC</sup>                                                                                                                                                                                                                        |
| 612 <i>Tyromyces atrostrigosus</i> (Cooke) G.Cunn.                         | Rammeloo J. <sup>DRC</sup>                                                                                                                                                                                                                        |
| 613 <i>Tyromyces setiger</i> (Cooke) Teng                                  | Rammeloo J. <sup>BU</sup>                                                                                                                                                                                                                         |
| 614 <i>Ustilago catherinae</i> Zambett.                                    | Rammeloo J. <sup>BU</sup>                                                                                                                                                                                                                         |
| 615 <i>Ustilago ischaemi</i> Fuckel                                        | Bequaert J. <sup>DRC</sup>                                                                                                                                                                                                                        |
| 616 <i>Ustilago kamerunensis</i> Syd. & P.Syd.                             | Stuhlmann F. <sup>RW</sup>                                                                                                                                                                                                                        |
| 617 <i>Veloporphyrellus africanus</i> Watling                              | Hendrickx F.L. <sup>DRC, RW</sup>                                                                                                                                                                                                                 |
| 618 <i>Volvariella congolensis</i> N.C.Pathak                              | + Rammeloo J. <sup>BU</sup>                                                                                                                                                                                                                       |
| 619 <i>Volvariella gloiocephala</i> (DC.) Boekhout & Enderle               | Goossens-Fontana M. <sup>DRC</sup>                                                                                                                                                                                                                |
| 620 <i>Volvariella goossensiae</i> (Beeli) Shaffer                         | Goossens-Fontana M. <sup>DRC</sup>                                                                                                                                                                                                                |

|                                                                                 |                                    |
|---------------------------------------------------------------------------------|------------------------------------|
| 621 <i>Volvariella insignis</i> Heinem.                                         | Goossens-Fontana M. <sup>DRC</sup> |
| 622 <i>Volvariella mammosa</i> N.C.Pathak                                       | Goossens-Fontana M. <sup>DRC</sup> |
| 623 <i>Volvariella surrecta</i> (Knapp) Singer                                  | Goossens-Fontana M. <sup>DRC</sup> |
| 624 <i>Volvariella villosovolva</i> (Lloyd) Singer                              | Goossens-Fontana M. <sup>DRC</sup> |
| 625 <i>Volvariella volvacea</i> (Bull.) Sing.                                   | + Rizinde J.C. <sup>DRC</sup>      |
| 626 <i>Wrightoporia pouzarii</i> A.David & Rajchenb.                            | Rammeloo J. <sup>BU</sup>          |
| 627 <i>Xerocomus becquetii</i> Heinem.                                          | Becquet A. <sup>RW</sup>           |
| 628 <i>Xerocomus pseudotristic</i> Heinem. & Gooss.-Font.                       | Rammeloo J. <sup>DRC</sup>         |
| 629 <i>Xerocomus schmitzii</i> Heinem.                                          | Rammeloo J. <sup>DRC,BU</sup>      |
| 630 <i>Xerocomus spinulosus</i> Heinem. & Gooss.-Font.                          | + Rammeloo J. <sup>DRC</sup>       |
| 631 <i>Xylobolus princeps</i> (Jungh.) Boidin                                   | Rammeloo J. <sup>BU</sup>          |
| 632 <i>Xylobolus subpileatus</i> (Berk. & M.A.Curtis) Boidin                    | Van der Veken P. <sup>RW</sup>     |
| 633 <i>Xylodon flaviporus</i> (Berk. & M.A. Curtis ex Cooke) Riebesehl & Langer | Rammeloo J. <sup>BU</sup>          |
| 634 <i>Xylodon rimosissimus</i> (Peck) Hjortstam & Ryvarde                      | Rammeloo J. <sup>RW</sup>          |

Considering the ratio 5:1 (five plant species per macrofungus species) to 2:1 (two plant species per macrofungus species) (Mueller et al., 2007), the Albertine Rift botanical diversity which encompasses 5793 plant species (Plumptre et al., 2007) host a putative number of larger fungi ranging from 1158 to 2896. At a lesser scale, the Virunga National Park in DR Congo which harbors 2077 plant species (Plumptre et al., 2007) would host 415 to 1038 macrofungi species and the Nyungwe forests in Rwanda, which vegetation is composed of 1105 plant species, would host 220-550 macrofungi species (Plumptre et al., 2007).

With only 634 species of larger fungi here reported for the whole region, encompassing a range of ecosystems (montane forest, bamboo forest, rain forest, miombo, savannah, agricultural fields), the basidiomycete diversity in the African Great Lakes region is without any doubt insufficiently known.

Species list in Table 2. 1 highlights that 102 taxa collected in the African Great Lakes Region have been assigned in the BR database a name accepted for a European species. Although the identification of some species is not in doubt (e.g. *Schizophyllum commune* known to be cosmopolitan), many specimens identified as European taxa (e.g. *Amanita rubescens* or *Lepista sordida*) would deserve to be re-studied using modern microscopy techniques and molecular tools to confirm their identification. Studies on African *Armillaria* are namely ongoing to clarify the confused systematics of this group and reject the presence of European taxa in the African Great Lakes Region (Figure 2.1).



Figure 3.1: A. *Amanita rubescens* in open forests of Burundi. B. *Lepista sordida* in bamboo forests of Rwanda. C. The cosmopolitan *Schizophyllum commune* in the Virunga NP (DRC) . D. A presumably new *Armillaria* species to be described from Kahuzi-Biega NP (DRC).

The analysis of Table 3.1 also reveals that 115 fungal species present in the African Great Lakes Region are known to be edible. Edible fungi are very important in the region as both a source of food and income. Traditional mycological knowledge varies according to communities and is passed on through generations. In southern and eastern Burundi, mushrooms are mainly gathered in open forests areas and are mainly ectomycorrhizal taxa associated with Caesalpiniaceae (Buyck, 1994). In montane forests of DR Congo and Rwanda saprotrophic species are the most abundant but the most popular edible ones are termitophilic species (mainly *Termitomyces microcarpus* and *Termitomyces robustus*) which are commonly sold on the markets and along the roads (Degreef et al., 2016).

### 3.5. Conclusion

For decades, morphological features have been used as the basis for identification of most species in tropical Africa ((Rammeloo & Walley, 1993; Njouonkou, 2011; Eyi Ndong et al., 2011; Buyck et al., 2013 ; Rizinde, 2016). The use of macroscopical characters for identification is delicate because of their dependency with environment and with the maturity of the specimen. In some cases, microscopical studies are not possible on herbarium material because sporophores are immature or badly conserved.

In the past, the lack of local documentation has forced most mycologists to identify African fungi and name the species based on European floras. Some African specimens very close to European species have been consequently erroneously identified. The availability of new identification tools (molecular techniques, Scanning Electron Microscopy) and the improvement of the optical microscopy equipment

plus the availability of softwares for measuring and analysing of the data should make it possible to solve these recurring taxonomic problems which are repeated from generation to generation of mycologists since the beginning of the 20th century.

## Chapter 4. *Ripartitella degreefii* (Tricholomataceae), a new species from tropical Africa

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Adapted from:

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## 4.1. Abstract

A new species of *Ripartitella*, *R. degreefii*, is proposed based on phylogenetic, morphological, and ecological evidence from specimens collected in medium elevation (1000 to 2100 masl) forests of the Albertine Rift, in the Democratic Republic of Congo and São Tomé (Africa). The species is described and compared to phylogenetically related or morphologically similar species.

Keywords: Agaricales, Basidiomycota, wood-inhabiting fungus

## 4.2. Introduction

*Ripartitella* Singer (1947: 85) (Tricholomataceae, Basidiomycota) is a small, pantropical genus, originally typified by *R. squamosidisca* (Murrill) Singer (1947: 85), nowadays a synonym of *R. brasiliensis* (Speg.) Singer (1951: 452) (Ovrebo 1988). *Ripartitella brasiliensis* was originally described from Brazil (Apiaí, São Paulo State) as *Pleurotus brasiliensis* Speg. (1889: 398), whereas *R. squamosidisca* was described as *Marasmius squamosidisca* Murrill (1940: 151) from Southeastern Florida, USA. Subsequently, several species were added, viz., *R. alba* Halling & Franco-Mol. (1996: 669), *R. brunnea* Ming Zhang, T.H. Li & T.Z. Wei (2019: 256), *R. ponderosa* (A.H. Sm. & Singer) Franco-Mol. (1993: 675), *R. rickenii* (Bohus) Singer (1986: 510), and *R. sipariana* (Dennis) Dennis (1970: 58).

However, DNA-based phylogenetic studies showed that *R. ponderosa* belonged to *Cercopemyces* T.J. Baroni, Kropp & V.S. Evenson (2014: 786), whereas *R. sipariana* has been transferred into *Cystodermella* Harmaja (2002: 43) (Capelari & Asai 2009, Zhang et al. 2019). *Ripartitella rickenii* was also transferred to *Cercopemyces* (Dima & Nagy 2015), without much comment, however. Therefore, currently, only three species are accepted in *Ripartitella*, viz., *R. brasiliensis*, *R. alba*, and *R. brunnea*.

*Ripartitella* is a wood-inhabiting genus characterized by the combination of small to medium-sized basidiomata with a collybioid habit; a central to slightly eccentric stipe, variably attached lamellae; hyaline, inamyloid, and rugulose basidiospores, and lageniform pleurocystidia the apex of which is often covered with crystals (Singer 1947, Wartchow et al. 2007; Battistin et al. 2016, Zhang et al. 2019).

*Ripartitella* was originally placed in the Agaricaceae Chevall. (1826: 121), Tribe Cystodermatae Fayod, together with *Cystoderma* Fayod (1889: 350) (Singer 1947, 1986). However, DNA-based phylogenetic analyses revealed that *Ripartitella* is phylogenetically closely related to *Cercopemyces* and *Cystodermella* (Harmaja 2002, Saar et al. 2009, Baroni et al. 2014).

As far as tropical Africa is concerned, *R. brasiliensis* is the sole species currently reported for the continent (Pegler 1977, Desjardin & Perry 2017). Pegler (1977) reported the species from Eastern Africa (Kenya, Tanzania, and Uganda), whereas Desjardin & Perry (2017) reported it from a medium elevation forest of the western insular São Tomé. It is noteworthy that Pegler (1977) described the African specimens without cystidia. Based on the known distribution, *R. brasiliensis* in tropical Africa (sensu Pegler 1977, Desjardin & Perry 2017) is likely an Afromontane species.

As part of an ongoing survey of agarics (Basidiomycota) in tropical Africa (Degreef & De Kesel, 2017—[www.efta-online.org](http://www.efta-online.org)), a collection of a *Ripartitella* species was found in the Kahuzi-Biega mountain range in eastern Democratic Republic of the Congo. Its phylogenetic affinities were inferred using the combined nuclear ribosomal ITS (ITS1–5.8S–ITS2) and LSU sequences. It was shown that it clustered with the specimen of *R. brasiliensis sensu* Desjardin and Perry (2017) from São Tomé, forming a well-supported terminal clade, distinct from the neotropical *R. brasiliensis* clade and any other, named or unnamed, species clade known to date.

Subsequent morphological examinations showed that our specimens from the Congo and São Tomé differed from *R. brasiliensis* by the scarcity of pleurocystidia and hyphae as cutus. Consequently,

*Ripartitella degreefii* sp. nov. is proposed, illustrated and described. Similarities and differences with the other species of *Ripartitella* are discussed.

### 4.3. Materials and methods

#### 4.3.1. Site description

The specimens examined are from the Kahuzi-Biega mountain range, in the eastern Democratic Republic of the Congo (DRC) (2.331733°S, 28.74848°E, elev. 2139 m. a.s.l, average precipitation 1900 mm/y, average temperature 20°C) and São Tomé (0.27595°N, 6.608767°E, elev. 1100 m a.s.l, average precipitation 1382 mm/y, average temperature 24.7°C). The specimens were collected in old growth forest at São Tomé (Desjardin & Perry 2017) and from a secondary forest in the Kahuzi-Biega mountain range, where the vegetation is dominated by the tree species *Maesa lanceolata* Forssk. (Myrsinaceae), *Alangium chinense* (Lour.) Harms (Cornaceae) *Tabernaemontana johnstonii* (Stapf) Pichon (Apocynaceae), and *Polyscias fulva* (Hiern) Harms (Araliaceae).

#### 4.3.2. Morphological examination

Colour codes are according to Kornerup & Wanscher (1981) and were estimated in both fresh and dry specimens. Handmade sections of dry specimens were examined in lactic acid, Cotton blue, Congo Red, and in Melzer's reagent to show any amyloid or dextrinoid staining reaction. All the microscopic measurements were done in Melzer's reagent. In presenting the size range of the microscopic structures, 5 % of the measurements at each end of the range are given in parentheses when

relevant. In the text, the following abbreviations are used: Mean = arithmetic mean, Q = ratio of length/width of basidiospores. The dried specimens are deposited at the BR (Meise Botanic Garden, Belgium) and at the H.D. Thiers Herbarium (San Francisco State University (herbarium acronyms according to Thiers, continuously updated (<http://sciweb.nybg.org/science2/IndexHerbariorum.asp>)).

#### 4.3.3. Scanning Electron Microscopy

A few gills were placed in a fold of a filter paper (medium filtration rate; particle retention  $>5\ \mu\text{m}$ ) which was placed in a sample holder (stainless steel tube with meshed top and bottom) for critical point drying. The holder was submerged respectively for 30 min in 12 % ammonia,  $2 \times 20$  min in 70 % ethanol,  $4 \times 15$  min in dimethoxymethane and then 15 min in acetone, after which the sample was dried in a critical point dryer (Leica EP CDP 300). The dried sample was mounted on a 12.7 mm  $\varnothing$  aluminium specimen (Agar Scientific Ltd) stub with a double-sided carbon sticker (Agar Scientific Carbon Tabs). The stub was placed in a High Resolution Fine Sputter Coater for FE-SEM (JFC-2300HR Coating Unit, JEOL) and coated with a layer of approximately 10 nm Pt/Pd (using Argon gas, under 0.05 mbar pressure). The scanning electron microscopy was carried out in Meise Botanic Garden with a JEOL JSM-7100FLV Field Emission SEM with a tension of 2 kV and working distance of 6 mm.

#### 4.3.4. DNA extraction, amplification, and sequencing

Genomic DNA was extracted from fresh tissues of specimens using a CTAB 3 % solution isolation procedure adapted from Doyle & Doyle

(1990). PCR amplification of the ITS region (nuclear ribosomal internal transcribed spacer) and LSU (large subunit ribosomal DNA) was performed using the primer pairs ITS1/ITS4, and LR0R/LR5, respectively (White et al. 1990). PCR products were purified by adding 1 U of Exonuclease I and 0.5 U FastAP Alkaline Phosphatase (Thermo Scientific, St. Leon-Rot, Germany) and incubating at 37 °C for 1 h, followed by inactivation at 80 °C for 15 min.

Sequencing was performed by Macrogen Inc. (Korea and The Netherlands) using the same primer combinations as for PCR. The sequences were assembled in Geneious Pro v. 6.0.6 (Biomatters).

#### 4.3.5. Phylogenetic analysis

Materials and sequences used in this study are listed in Table 1. Initial BLAST searches (<http://blast.ncbi.nlm.nih.gov>) of both LSU and ITS-5.8S sequences were performed to estimate similarity with *Ripartitella* / other Agaricales sequences already present in the GenBank database (Table 1). Following the results of the BLAST search, sixteen sequences of *Ripartitella*, three of *Cercopemyces*, twelve of *Cystodermella*, 21 of *Cystoderma* and six *Ripartites* sequences were included in the dataset, including the newly generated sequences from our own specimens of *Ripartitella* from DRC and São Tomé (Table 3.1).

A combined dataset (including nuclear ribosomal partial LSU and ITS-5.8S) comprising sequences from 59 collections including the outgroup was constructed and used for further phylogenetic analyses. *Lepiota cristata* (Bolton) P. Kumm. (1871: 137), strain HKAS 61649, was used as the outgroup for the combined ITS-LSU dataset, following Capelari & Asai (2009).

Nucleotide sequences were automatically aligned using the MUSCLE algorithm (Edgar 2004) with default settings. The alignment was further optimized and manually adjusted as necessary by direct examination with the software Se-Al v. 2.0a11 (University of Oxford).

Potential ambiguously aligned segments, especially in ITS-5.8S alignment, were detected by Gblocks v0.91b (Castresana 2000; <http://molevol.cmima.csic.es/castresana/Gblocks.html>) with the following parameter settings: minimum number of sequences for a conserved position = 30 (minimum possible); minimum number of sequences for a flank position = 30 (minimum possible); maximum number of contiguous non-conserved positions = 4 bp, minimum block size = 4 bp, and gaps allowed within selected blocks in half of the sequences.

To detect the possible bias from substitution saturation and evaluate the phylogenetic signal, we tested each partition by using Xia's test (Xia et al. 2003, Xia & Lemey 2009), as implemented in DAMBE (Xia & Xie 2001). Because the Iss.c is based on simulation results, there is a problem with more than 32 species. To circumvent this problem, DAMBE was used to randomly sample subsets of 4, 8, 16 and 32 OTUs multiple times and to perform the test for each subset to see if substitution saturation exists for these subsets of sequences. In order to confirm the results of the Xia's method we also plotted the raw number of transversions and transitions against Tamura-Nei genetic distances with the aid of the DAMBE package, with an asymptotic relationship indicating the presence of saturation.

Models of evolution for BI were estimated using the Akaike information criterion (AIC) as implemented in Modeltest 3.7 (Posada & Crandall 1998).

Phylogenetic analyses were performed separately for each individual and concatenated loci using Bayesian Inference (BI) as implemented in MrBayes v3. 2 (Ronquist et al. 2011) and Maximum Likelihood (ML) as implemented in RAxML 7.2.7 (Stamatakis et al. 2008).

The best-fit models for each partition were implemented as partition specific models within partitioned mixed-model analyses of the combined dataset. All parameters were unlinked across partitions. Bayesian analyses were implemented with two independent runs, each with four simultaneous independent chains for six million generations, starting from random trees, and keeping one tree every 1000th generation. All trees sampled after convergence (average standard deviation of split frequencies < 0.01 and confirmed using Tracer v1.4 [Rambaut & Drummond 2007]) were used to reconstruct a 50 % majority-rule consensus tree (BC) and to calculate Bayesian Posterior Probabilities (BPP). BPP of each node was estimated based on the frequency at which the node was resolved among the sampled trees with the consensus option of 50 % majority-rule (Simmons et al. 2004). A probability of 0.95 was considered significant. Maximum Likelihood (ML) searches conducted with RAxML involved 1000 replicates under the GTRGAMMAI model, with all model parameters estimated by the program. In addition, 1000 bootstrap (ML BS) replicates were run with the same GTRGAMMAI model. We provided an additional alignment partition file to force RAxML software to search for a separate evolution model for each dataset. Clades with Maximum Likelihood bootstrap values of 75 % or greater were considered supported by the data.

To detect topological conflicts among data partitions, the nodes between the majority-rule consensus trees obtained in the ML analysis

from the individual data sets were compared with the software `compat.py` (available at [www.lutzonilab.net/downloads](http://www.lutzonilab.net/downloads)). Paired trees were examined for conflicts only involving nodes with ML BS > 75 % (Mason-Gamer & Kellogg 1996, Lutzoni et al. 2004, Reeb et al. 2004). A conflict was assumed to be significant if two different relationships for the same set of taxa (one being monophyletic and the other not) were observed in rival trees.

Table 4.1: List of collections used for DNA analyses, with origin, GenBank accession numbers and references

| Name of the speices                             | Specimen Voucher                       | Country        | GenBank accession no. |           | Reference                                        |
|-------------------------------------------------|----------------------------------------|----------------|-----------------------|-----------|--------------------------------------------------|
|                                                 |                                        |                | ITS                   | LSU       |                                                  |
| <i>Cercopemyces crocodilinus</i> holotype       | UTC 258260                             | USA            | JX409899              | NG_071239 | Kropp B and Baroni T 2012, unpublished           |
| <i>Cercopemyces ponderosus</i> holotype         | NR_119888                              | USA, Tennessee | NR_119888             | -         | Matheny PB and Wolfenbarger AD 2014, unpublished |
| <i>Cercopemyces rickenii</i>                    | G0771                                  | Hungary        | -                     | MK277686  | Varga et al. 2019                                |
| <i>Cystoderma amianthinum</i>                   | AFTOL-ID 1553                          | Sweden         | DQ192177              | DQ154108  | Matheny PB and Hibbett DS 2005, unpublished      |
| <i>Cystoderma andinum</i> isotype               | C57998                                 | Ecuador        | NR_119475             | AM946425  | Saar et al. 2009                                 |
| <i>Cystoderma arcticum</i>                      | KA16-1045                              | Kyrgyzstan     | MK351684              | -         | Cho S 2018, unpublished                          |
| <i>Cystoderma carcharias</i> var. <i>fallax</i> | I. Kytovuori 92-1309                   | Finland        | AM946485              | AM946430  | Saar et al. 2009                                 |
| <i>Cystoderma carcharias</i> var. <i>fallax</i> | H (as holotype <i>C. intermedium</i> ) | Finland        | AM946488              | -         | Saar et al. 2009                                 |

|                                                   |                            |             |           |          |                                                      |
|---------------------------------------------------|----------------------------|-------------|-----------|----------|------------------------------------------------------|
| <i>Cystoderma castellanum</i> holotype            | LOU-F19663                 | Spain       | LN878148  | -        | Saar 2016                                            |
| <i>Cystoderma chocoanum</i>                       | NY-EFM629                  | Colombia    | -         | U85302   | Johnson 1999                                         |
| <i>Cystoderma clastotrichum</i>                   | PDD 83705                  | New Zealand | AM946490  | AM946434 | Saar et al. 2009                                     |
| <i>Cystoderma granosum</i>                        | ZRL 20181937               | -           | MW242931  | MW242943 | Li J 2020, unpublished                               |
| <i>Cystoderma japonicum</i> holotype              | Hongo 6221/BR5020079022647 | Japan       | NR_119476 | AM946435 | Saar et al. 2009                                     |
| <i>Cystoderma jasonis</i>                         | RAS200                     | USA         | MG773835  | -        | Matheny PB, Hobbs AM and Swenie RA 2017, unpublished |
| <i>Cystoderma jasonis</i>                         | GLM 45917                  | Germany     | -         | AY207196 | Walther et al. 2005                                  |
| <i>Cystoderma jasonis</i> var. <i>jasonis</i>     | TAA 182013                 | Estonia     | AM946492  | AM946436 | Saar et al. 2009                                     |
| <i>Cystoderma jasonis</i> var. <i>lilacipes</i>   | TAA 147362                 | Finland     | AM946495  | AM946437 | Saar et al. 2009                                     |
| <i>Cystoderma jasonis</i> var. <i>niveum</i>      | R. Saarenoksa 52585 (H)    | Finland     | AM946497  | AM946438 | Saar et al. 2009                                     |
| <i>Cystoderma jasonis</i> var. <i>saarenoksae</i> | TAA 147361                 | Finland     | AM946499  | AM946440 | Saar et al. 2009                                     |

|                                                               |                               |             |          |          |                                          |
|---------------------------------------------------------------|-------------------------------|-------------|----------|----------|------------------------------------------|
| <i>Cystoderma liliaceum</i><br>holotype                       | ZRL 20161878                  | China       | MW242922 | MW242948 | Li J 2020, unpublished                   |
| <i>Cystoderma muscicola</i>                                   | MEL 2362094                   | Australia   | KP311425 | KP311368 | Bonito G and May TW<br>2014, unpublished |
| <i>Cystoderma</i><br><i>subvinaceum</i>                       | WU19742                       | Austria     | AM946501 | AM946441 | Saar et al. 2009                         |
| <i>Cystoderma superbum</i>                                    | BR22288-75                    | Belgium     | AM946504 | AM946442 | Saar et al. 2009                         |
| <i>Cystoderma tuomikoskii</i><br>holotype                     | H                             | Finland     | AM946505 | AM946444 | Saar et al. 2009                         |
| <i>Cystodermella</i><br><i>adnatifolia</i>                    | TAA 175640                    | Estonia     | AM946510 | AM946421 | Saar et al. 2009                         |
| <i>Cystodermella</i><br><i>cinnabarina</i>                    | TAA 147423                    | Estonia     | AM946512 | AM946429 | Saar et al. 2009                         |
| <i>Cystodermella</i><br><i>cinnabarina</i> f. <i>nogalesi</i> | BR5020002523012               | Spain       | LN878147 | -        | Saar 2016                                |
| <i>Cystodermella</i><br><i>crystallifera</i> holotype         | BR5020031802836               | Africa, RDC | LN878146 | -        | Saar 2016                                |
| <i>Cystodermella granulosa</i>                                | TAA 147491                    | Estonia     | AM946518 | AM946431 | Saar et al. 2009                         |
| <i>Cystodermella granulosa</i><br>var. <i>ambrosii</i>        | T. Ulvinen 23 Aug 1974<br>(H) | Finland     | AM946516 | AM946422 | Saar et al. 2009                         |

|                                             |                                   |                |           |           |                                           |
|---------------------------------------------|-----------------------------------|----------------|-----------|-----------|-------------------------------------------|
| <i>Cystodermella lactea</i> holotype        | LUG9395                           | Switzerland    | LN878144  | -         | Saar 2016                                 |
| <i>Cystodermella myriadocystis</i> holotype | BR5020018682581                   | Belgium        | LN878145  | -         | Saar 2016                                 |
| <i>Cystodermella papallactae</i> isotype    | C58002                            | Ecuador        | NR_119478 | AM94643   | Saar et al. 2009                          |
| <i>Cystodermella</i> sp                     | PDD 94849                         | New Zealand    | KF727402  | KF727340  | Johnston PR, and Park D 2013, unpublished |
| <i>Cystodermella</i> sp                     | Smith-2018 iNaturalist # 17339256 | USA, Wisconsin | MK573917  | -         | Russell SD 2019, unpublished              |
| <i>Cystodermella terryi</i>                 | 2016-295                          | China          | KY820054  | -         | Zhang et al 2019                          |
| <i>Lepiota cristata</i>                     | HKAS 61649                        | China          | JN944090  | JN940284  | Ge ZW 2011, unpublished                   |
| <i>Ripartitella alba</i> isotype            | NY 80066                          | Costa Rica     | NR_119479 | NG_060064 | Saar et al. 2009                          |
| <i>Ripartitella alba</i>                    | R.E. Halling 7182 (NY)            | Costa Rica     | AM946525  | AM946464  | Saar et al. 2009                          |
| <i>Ripartitella brasiliensis</i>            | A.E. Franco-Molano 499 (NY)       | Colombia       | AM946524  | AM946465  | Saar et al. 2009                          |
| <i>Ripartitella brasiliensis</i>            | NY-EFM744                         | Colombia       | -         | U85300    | Johnson and Vilgalys 1998                 |

|                                               |                                 |                         |                   |                   |                                           |
|-----------------------------------------------|---------------------------------|-------------------------|-------------------|-------------------|-------------------------------------------|
| <i>Ripartitella brasiliensis</i>              | FLAS-F-61262                    | USA, Florida            | MH211841          | -                 | Kaminsky et al 2018, unpublished          |
| <i>Ripartitella brunnea</i>                   | GDGM 70592                      | China                   | MH660405          | MH660408          | Zhang et al 2019                          |
| <i>Ripartitella brunnea</i>                   | GDGM 70834                      | China                   | MH660406          | MH660409          | Zhang et al 2019                          |
| <i>Ripartitella brunnea</i>                   | HMAS 279808                     | China                   | MH660407          | MH660410          | Zhang et al 2019                          |
| <b><i>Ripartitella degreefii</i> sp. nov.</b> | <b>SFSU DED 8323</b>            | <b>Africa, São Tomé</b> | <b>MF100952</b>   | -                 | <b>Desjardin &amp; Perry 2017</b>         |
| <b><i>Ripartitella degreefii</i> sp. nov.</b> | <b>RHJ305 / BR5020189043549</b> | <b>Africa, RDC</b>      | <b>this study</b> | <b>this study</b> | <b>this study</b>                         |
| <i>Ripartitella</i> sp                        | 4-841                           | Japan, Yakushima Island | AB509988          | -                 | Sato et al 2009, unpublished              |
| <i>Ripartitella</i> sp                        | 4-201                           | Japan, Yakushima Island | AB509611          | -                 | Sato et al 2009, unpublished              |
| <i>Ripartitella</i> sp                        | BZ-1689                         | Belize                  | JX462554          | JX462553          | Kropp and Baroni., unpublished            |
| <i>Ripartitella</i> sp                        | FLAS-F-61822                    | USA, Florida            | MH281887          | -                 | Kaminsky et al 2018, unpublished          |
| <i>Ripartitella</i> sp                        | PDD 71285                       | New Zealand             | KF727403          | KF727348          | Johnston PR, and Park D 2013, unpublished |

|                                    |                          |             |          |          |                                                 |
|------------------------------------|--------------------------|-------------|----------|----------|-------------------------------------------------|
| <i>Ripartitella sp</i>             | FUNNZ 2017/1339          | New Zealand | MF461603 | -        | Matheny PB, Swenie RA and Cooper J, unpublished |
| <i>Ripartites albidoincarnatus</i> | 16177                    | Italy       | JF908756 | -        | Garbelotto MM et al 2013, unpublished           |
| <i>Ripartites metrodii</i>         | 5981                     | Italy       | JF908748 | -        | Garbelotto MM et al 2013, unpublished           |
| <i>Ripartites odoratus</i>         | ma010                    | Italy       | MN595290 | -        | Rita et al. 2020                                |
| <i>Ripartites sp</i>               | JAC 13105                | Australia   | KP191949 | KP191768 | Lebel T and Cooper J 2014, unpublished          |
| <i>Ripartites sp</i>               | Mushroom Observer 248705 | USA         | MK559718 | MF765759 | Clements TA 2019, unpublished                   |
| <i>Ripartites tricholoma</i>       | CBS 484.50               | France      | MH856715 | MH868234 | Vu et al. 2019                                  |

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## 4.4. Results

### 4.4.1. Phylogenetic analysis

The test of substitution saturation showed that the observed index of substitution saturation (Iss) for the ITS and LSU partitions (considered individually) was significantly lower than the corresponding critical index substitution saturation (Iss.c), indicating that there was little saturation in our sequences (P indicating that there was little saturation in our sequences ( $P < 0.001$ ) (Table 3.2).

By comparing the tree topologies obtained for the individual datasets, no significant conflict involving significantly supported nodes was found using the 75 % ML BP criterion; the datasets were therefore combined.

Once excluding the 16 ambiguously aligned characters, the combined data set comprised 59 sequences including the outgroup and 1940 positions (840 position the ITS-5.8S partition and 1100 the nucLSU partition).

The general time reversible model (GTR+I+G), using the proportion of invariant sites and distribution of rates at variable sites modeled on a discrete gamma distribution with four rate classes, was estimated as the best-fit likelihood model of evolution for the [28S + ITS] full dataset, for BI and ML, using the Akaike information criterion (AIC) as implemented in Modeltest 3.7 (Posada and Crandall 1998). The two Bayesian runs (6,000,000 generations) converged to stable likelihood values after 1,000,000 generations; the first 25 % of the tree were discarded as burnin. The remaining stationary trees from each analysis were used to compute a 50 % majority rule consensus tree (BC) and to

calculate posterior probabilities. In the ML searches, the alignment had 772 distinct patterns with a proportion of gaps and undetermined characters of 37.10 %.

Table 4.2: Summary of data sets used for phylogenetic inferences

| Properties                      | Datasets Datasets |           |
|---------------------------------|-------------------|-----------|
|                                 | ITS               | LSU       |
| Alignment size                  | 840               | 1100      |
| Excluded characters             | 16                | -         |
| Model selected                  | GTR+I+G           | GTR+I+G   |
| -Likelihood score               | 5875.1128         | 3211.9116 |
| Base frequencies                |                   |           |
| Freq. A =                       | 0.2715            | 0.2753    |
| Freq. C=                        | 0.1830            | 0.1940    |
| Freq. G                         | 0.1929            | 0.2760    |
| Freq. T                         | 0.3526            | 0.2547    |
| Proportion of invariable sites  | 0.2877            | 0.6059    |
| Gamma shape                     | 1.0176            | 0.5928    |
| Test of substitution saturation |                   |           |
| Iss                             | 0.453             | 0.445     |
| Iss.cSym                        | 0.692             | 0.754     |
| P (Sym)                         | <0.0001           | <0.0001   |
| Iss.cAsym                       | 0.364             | 0.454     |
| P (Asym)                        | <0.0001           | <0.0001   |

Note: Iss: index of substitution saturation. Iss.cSym: critical value for symmetrical tree topology. Iss.cAsym: critical value for extremely asymmetrical tree topology. P: probability that Iss is significantly different from the critical value (Iss.cSym or Iss.cAsym).

The topologies of the consensus tree obtained from the Bayesian Inference (BI) and the most likelihood tree were nearly identical. The 50 % majority-rule consensus tree from BI of the combined dataset is presented in Figure 1. The phylogenetic analyses recovered the specimens from the eastern African and São Tomé Mountain range as a single, independent lineage that is sister to the *R. brunnea* clade, and distant from all other species clades shown to date (Fig. 4.1.).

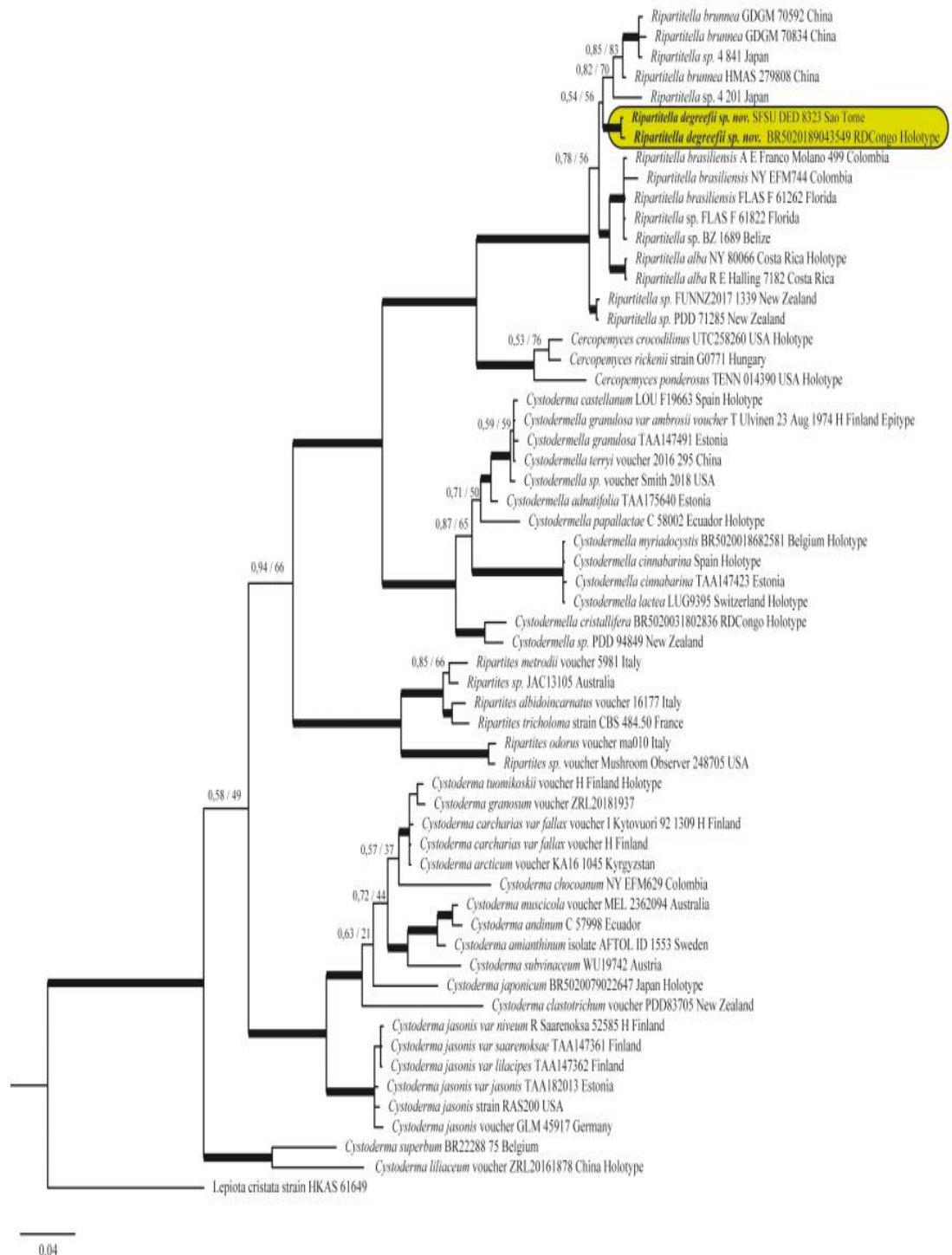


Figure 4.1: The 50 % majority-rule consensus tree from Bayesian Inference of the combined dataset. Thickened branches in bold

represent ML BS support greater than 75 % and BPP greater than 0.95; thickened branches in black denote branches supported by either ML BS or BPP; for selected nodes ML BS support value and BPP are respectively indicated to the left and right of slashes; the new taxa are highlighted in the shaded box.

#### 4.4.2. Taxonomy

***Ripartitella degreefii*** Rizinde, Desjardin, Amalfi, & Decock, *sp. nov.*  
Figs. 2 & 3

[Mycobank: MB842786]

Diagnosis:—The species is similar to *R. brasiliensis* in the basidioma habit, but differs in the paucity of pleurocystidia, a pileipellis as a cutis, and its habitat in mountain areas of tropical Africa.

Description:—*Basidiomata* cespitose, small to medium-sized (Fig. 2A, B). *Pileus* 25–70 mm diam., convex to plano-convex, becoming applanate and depressed, with (or without) a small obtuse umbo; surface dull, dry, pure white to off-white, disc with (or without) tiny, brownish orange (ferruginous 7C6–7) scales when young, wearing off with age. *Margin* decurved to sometimes uplifted in age, centrally pure white to cream (4A3) with white appendiculate veil remnants. *Context* 1–2 mm thick, soft, white. *Lamellae* shallowly adnexed to adnate, crowded to very crowded, unequal, (24 (L+1) / cm), with 2–4 series of lamellulae, narrow (2–3 mm deep), with smooth edge, pale yellowish white (4A2). *Stipe* central to slightly eccentric, terete, subclavate to bulbous, 15–70 (–100) mm long, 3–10 mm broad, solid, annulate, concolorous with pileus, squarrose, with superficial, scattered white velar remnants toward base, glabrous above the annulus. *Annulus* evanescent, single, membranous, felted, often incomplete, attached to

the upper quarter of the stipe. *Odor* fungoid, *taste* not tested. *Spore print* white.

*Hyphal system* monomitic, composed of generative hyphae with clamp connections in all tissues. *Pileipellis* a cutis, made up of repent, subparallel, radially oriented, cylindric hyphae, 3.5–7  $\mu\text{m}$  diam, smooth, thin-walled. *Pileus squamules* composed of subcatenulate, rarely encrusted hyphae, 5–10  $\mu\text{m}$  diam. *Pileitrama* made up of interwoven hyaline, smooth, thin- to slightly thick-walled, hyphae, 2.5–7  $\mu\text{m}$  diam. *Lamellar trama* similar to pileitrama. *Stipitipellis* a layer of  $\pm$ parallel, longitudinally oriented hyphae, with scattered clusters of subcatenulate elements similar to those of pileipellis (Fig. 3.3C), individual cells 3.5–7  $\mu\text{m}$  diam, smooth, thin-walled.



Figure 4.2: Basidiomes of *Ripartitella degreefii* (A=RHJ 305, holotype; B=DED 8323). Scale bar = 10 mm. Photos by J.C. Rizinde (RHJ 305) and D. Desjardin (DED 8323).

Basidiospores hyaline (Fig. 3G, H), broadly ellipsoid to subglobose, thin-walled, verrucose, inamyloid, acyanophilous, (3.5–) 4–5 × 3–3.8 µm (n = 30, mean = 4.3 × 3.4 µm, Q = 1.13–1.5). Basidia with a basal clamp, clavate, with 4 sterigmata (Fig. 3F), not siderophilous, 14–24 × 6–8 µm. Pleurocystidia absent or present (Fig. 3.3D), then scarce, difficult to observe, with a basal clamp, lageniform, thin- to thick-walled, apically smooth or slightly, finely or coarsely incrustated (Fig. 3E), 32–40 × 5.0–7.5 µm, the apical digitate part 2–2.5 µm diam (mean = 36 × 6.5 µm, 2.3 µm in the apical section). Cheilocystidia not observed.

Distribution:—AFRICA. Known from the Eastern Democratic Republic of the Congo and São Tomé.

Ecology (substrate, host, habitat):—On fallen trunks of angiosperms, including, in DRC, *Xymalos monospora* (Harv.) Baill. (Monimiaceae, locally named “Cinyalubombo”), mountain forests, at 1100 and 2139 m a.s.l.

Etymology:—The species name is a tribute to Jérôme Degreef, scientific director at Meise Botanic Garden for his devotion to African mycology and his efforts for promoting the training of students from tropical Africa.

Material examined:—AFRICA. Democratic Republic of the Congo, South Kivu: Kahuzi Biega mountain range, Kahuzi Biega National Park, 2.331733°S, 28.74848°W, 2139 m a.s.l., on fallen trunk of *Xymalos monospora* (Harv.) Baill. (Monimiaceae), November 2018, J.C. Rizinde leg., RHJ 305 (BR #5020189043549, **Holotype**), culture exholotype MUCL 57374; SÃO TOMÉ: Macambrara radio antenna area; 0.27595°N, 6.608767°E, 1100 m elev., 25 April 2008, D. E. Desjardin leg. DED 8323; SÃO TOMÉ; Macambrara radio antenna

area; 0.27595°N, 6.608767°E; 1100 m elev., April 2006, D. E. Desjardin leg., DED 7937 (but material lost in transit to the USA).

Notes:—*Ripartitella degreefii* is phylogenetically distant from all other *Ripartitella* known to date (Fig. 3.1). Morphologically, *R. degreefii* is similar in many respects to *R. brasiliensis* (Capelari & Asai 2009, Desjardin & Perry 2017), but differs in having a pileipellis as a cutis (Fig. 3.3C) as opposed to a trichoderm (Capelari & Asai 2009), scarce (Fig. 3.3D–E) in contrast to abundant pleurocystidia (Capelari & Asai 2009), and a distribution in Afromontane forests in contrast to lowland neotropics. *Ripartitella brasiliensis* also has dense, brown to reddish brown squamules, covering the whole cap when young (Capelari & Asai 2009, Battistin et al. 2016). Squamules are variably present in young specimens of *R. degreefii* (Fig. 4.2), but soon wear off with age.

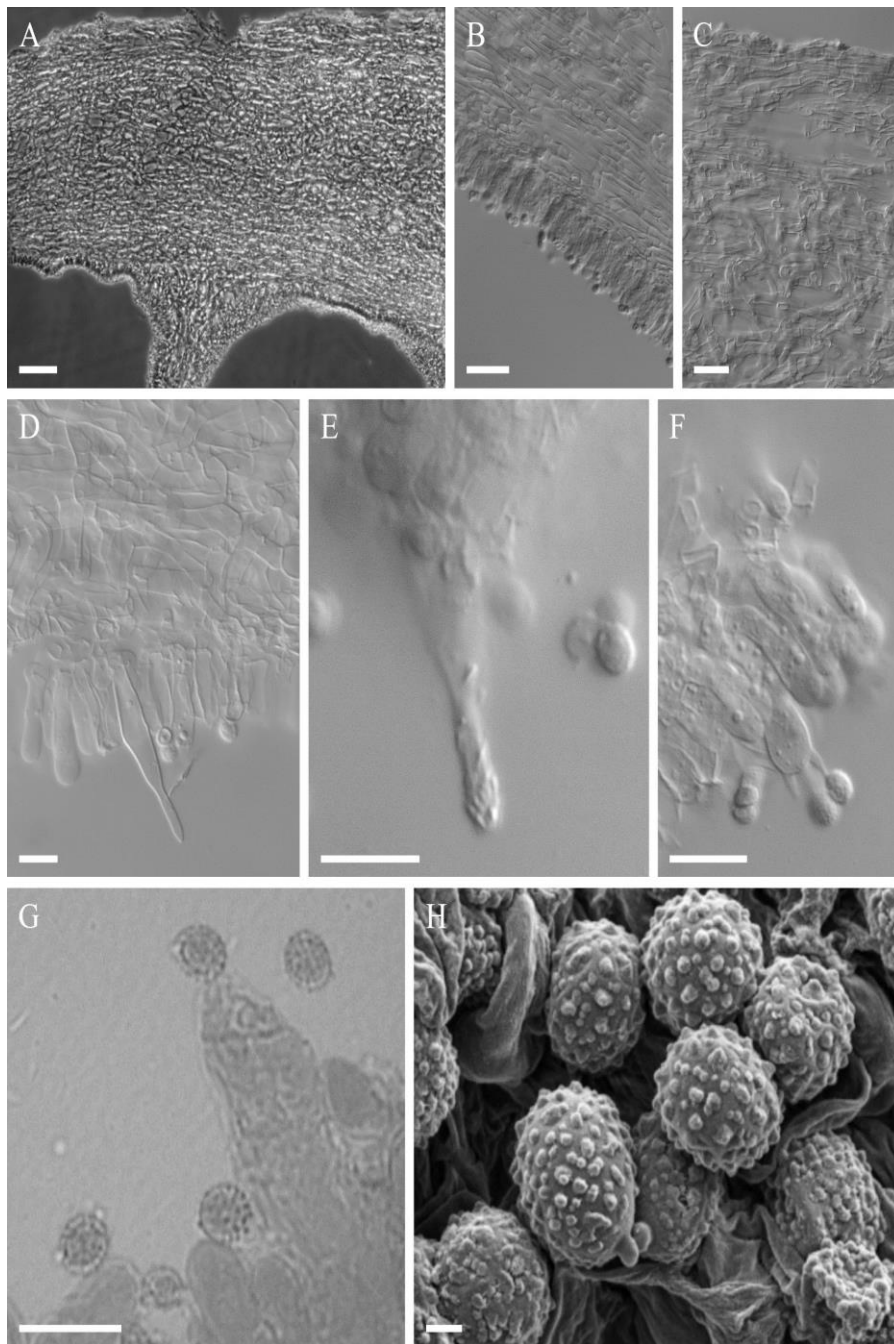


Figure 4.3: A. section of pileus; B. transversal section of lamellae; C. Pileipellis; D, E. Cystidia; F. Basidia; G = basidiospores from RHJ 305, optical microscopy; H = verrucose basidiospores from RHJ 305, SEM. Photos by C. Decock (A–F) and Mario Amalfi (G–H). Scale bars A= 100  $\mu$ m; B, C = 20  $\mu$ m; D–G= 10  $\mu$ m.

*Ripartitella degreefii* is known so far from two collections originating from two spots of medium elevation forests, in the continental and insular Afromontane range, in the Albertine rift (DRC) and São Tomé. It is the first *Ripartitella* described from Tropical Africa. Pegler (1977) reported *R. brasiliensis* from Eastern Africa, in Kenya, Tanzania and Uganda. He described the eastern African collections as lacking cystidia (Pegler 1977). Pleurocystidia were observed in *R. degreefii*, in both specimens available. However, they are scarce and difficult to see. Desjardin and Perry (2017) reported *R. degreefii* under *R. brasiliensis* from São Tomé, stating that it matched “nicely the description of African material provided by Pegler (1977)”. A closer examination of the São Tomé specimen revealed the presence of scarce pleurocystidia. The identity of the specimens cited by Pegler (1977) remains to be ascertained but they could represent *R. degreefii*.

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## Chapter 5: The African *Armillaria*

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**Manuscript in progress**

**Tropical African *Armillaria*: The status of *Armillaria camerunensis* (Henn.) Courtec. *Armillaria heimii* Pegler, *Armillaria fuscipes* Petch, and *Armillaria mellea* (Vahl) P. Kumm. in Tropical Africa**

## 5.1. Abstract

### **Background:**

*Armillaria* has been reported to cause damage to African cash crops such as coffee, tea, cocoa, cassava, pineapple, and woody plants including *Eucalyptus*. Because of their economic importance as plant pathogens and their ecological importance as wood-decaying fungi, the understanding of their taxonomy is of interest from many perspectives including biology, ecology and pest control. However, the African *Armillaria* taxonomy remains controversial. Phylogenetic inference analyses were performed using four loci (ITS, LSU, (Tef1- $\alpha$ ), RPB2) and complemented by morphological and ecological data. The dataset used includes a set of *Armillaria* collections from different African biogeographic regions, together with collections from the Albertine Rift, a sequence of an historical, authentic specimen *A. camerunensis* (courtesy of Mario Amalfi, Meise Botanic Garden) and two cultures from Sri Lanka, the type locality of *A. fuscipes*.

### **Results:**

African *Armillaria* clustered into three major clades: an African endemic major clade, a South American-Australasian major clade, and the Melleioid major clade. The African endemic major clade includes two internal clades whose distribution reflects a low vs highland dichotomy. Several isolates from the Rwandan and Kenyan highlands form a new clade within the Australasian major clade.

### **Conclusion:**

The major African clade consists of two clades. The first clade corresponds to *A. heimii* s.l. This name therefore replaces *A. fuscipes*,

which was erroneously used for African *Armillaria*. *Armillaria fuscipes* does not belong to the African lineage. It may correspond to a lesser-known species of a Southeast Asian - Australasian or of the melleioid lineage. The second clade corresponds to *A. camerunensis* and contains a sequence derived from an authentic sequence. In a biogeographical scheme, *A. camerunensis* is a lowland rainforest species, whereas *A. heimii* is an afromontane species. *Armillaria mellea* subsp. *africana* is an invalid name (unpublished). A third clade present in Tropical Africa belongs to an Australasian lineage and remains uncertain. Further studies could also provide more data on whether the subclades within *A. heimii* s.l. represent independent species and define *A. heimii* s.s.

## 5.2. Introduction

*Armillaria* (Fr.) Staude (Basidiomycota, Agaricales and Physalacriaceae) is best known for its role as a forest pathogen. *Armillaria* root rot is responsible for tree mortality in natural forests and agricultural plantations. The damage not only results in plant death, but also in reduced plant vigor and yield. Worldwide, more than 500 woody hosts have been reported to be attacked by *Armillaria* species (Roux and Coetzee 2016). The impact is compounded by their ability to survive as parasites and saprotrophs. They can survive as saprotrophs for 4-5 years (Dadant 1963) to many decades, depending on stem size and environmental conditions (Legrand 2018; Jayawardena et al. 2020).

*Armillaria* is a widespread and very diverse genus. It comprises 50-60 species grouped into 4 major (super) clades: Holarctic (North America, Europe, and East Asia), South American-Australasian, African, and the transcontinental melleioid super-clade. This diversity is unevenly distributed. Species diversity peaks in the Northern Hemisphere (Holarctic), particularly in East Asia, which accounts for almost 50% of known *Armillaria* taxa. The Southern hemisphere is less diverse, with 12 species for the South American-Australasian regions and 2 or 3 species reported to form an African lineage (Coetzee et al. 2011; Koch et al. 2017; Klopfenstein et al. 2017; Coetzee et al. 2018).

In Tropical areas, African *Armillaria* remains comparatively understudied. Some studies have been carried out on African taxa, but many basic taxonomic questions remain unanswered. Nevertheless, *Armillaria* has also been recognised as a threat to cash crops such as coffee, tea, cacao (Dadant 1963; Roux and Coetzee 2016), penja pepper (Tigang et al. 2020), cassava (Mwenje et al. 1998) and woody

production trees such as *Eucalyptus*, *Pinus*, *Acacia*, *Tectona* etc. (Coetzee et al. 2000; Gezahgne et al. 2004).

African *Armillaria* were previously considered to be tropical variants of the globally distributed European *Armillaria* taxa. Accordingly, Hennings (1895) reported *A. mellea* var *camerunensis* Henn. from Cameroon. Beeli (1927) later recorded *A. elegans* Beeli, *A. pelliculosa* Beeli and *A. pelliculata* Beeli from the DR Congo. However, *A. elegans* Beeli and *A. pelliculata* Beeli are currently, respectively, accepted into *Cystoderma* Fayod (Thoen 1969) and *Lactifluus* (Pers.) Roussel (Verbeken et al. 2011). *Armillaria mellea* var *camerunensis* Henn. is now accepted as *A. camerunensis* (Henn.) Courtec. (Courtecuisse 1995). There are no further records of *A. pelliculosa* Beeli in the literature.

The controversial history of African species classification dates back to Heim (1937; 1963; 1967), who reported *Clitocybe* (*Armillariella*) *elegans* Heim as the probable cause of the death of *Albizia lebbbeck* (L.) Benth and *Albizia stipulata* (DC.) Boivin, two tree species associated with coffee in Madagascar.

Because of the obvious similarity to *A. mellea* (Vahl.) P. Kumm., Pegler (1977) transferred *Clitocybe elegans* Heim to *Armillaria* and renamed it *A. heimii* Pegler, the binomial *A. elegans* being preoccupied (Beeli 1927).

Another species, *A. fuscipes* Petch, has been reported from tropical Africa as a pathogen of several exotic trees (Coetzee et al. 2000; Gezahgne et al. 2004). The type specimen of *A. fuscipes* originates from Sri Lanka (Petch 1909). In the annotated description of *C. elegans* (Heim, 1937), *A. fuscipes* was listed together with *A. mellea* as the causal agent of damage to *Albizzia lophantha* in tea plantations in Sri

Lanka. This suggests that Heim (1937; 1963) found *C. elegans* (*A. heimii*) to be distinct from both *A. mellea* and *A. fuscipes*.

Later, based on the morphological congruence of both types, *A. heimii* and *A. fuscipes* were proposed as conspecific, with *A. fuscipes* having nomenclatural priority (Pegler 1986; Watling 1992).

However, the synonymy has been questioned by several mycologists. Using molecular methods, Coetzee et al. (2000) suggested that *Armillaria* from South African pine plantations and La Réunion formed an *A. fuscipes* clade, distinct from an *A. heimii* clade comprising collections from Cameroon, Zimbabwe, and Zambia. Based on ITS and IGS phylogenetic analyses, Pèrez-Sierra et al. (2004) reached the same conclusions. However, sexual compatibility tests showed that isolates from both groups were interfertile. Based on these constations, the two phylogenetic clades were proposed to represent two different populations of the same species, named *A. heimii*.

In contrast, Coetzee et al (2005) showed that the African collections represent at least 2 independent species. They were grouped into 2 clades named A and B. Clade A is divided into 3 subgroups (A1, A2 and A3). It is recognised as representing *A. fuscipes*. Clade B was thought to represent an as yet unnamed species. However, in some studies, clade B is also referred to as *A. camerunensis* (Tigang et al. 2020; Koch et al. 2017).

*Armillaria fuscipes* would differ from *A. camerunensis* by the presence of striated spores, according to Courtecuisse (1995). However, mycologists seem to agree that all *Armillaria* have smooth spores under the light microscope. Faint ornamentation can be seen under the electron microscope (Bennell et al. 1985).

Ota et al. (2011) raised doubts and showed that the status of tropical African *A. fuscipes* remains unresolved. According to Ota et al. (2011), the macro- and micromorphological characters of southern Japanese *Armillaria* specimens were consistent with the type of *A. fuscipes*, and were quite different from those of the African *A. fuscipes* (Ota et al. 2011). The phylogenetic studies showed no relationship between the African and Japanese *Armillaria*. Based on both findings, it was suggested that *A. fuscipes* in tropical Africa is a separate species from tropical Asian *A. fuscipes* sensu Ota et al. (2011).

The enigma of African *Armillaria* could therefore be solved by molecular methods. The main problem encountered in previous phylogenetic studies was the lack of type sequences for *A. fuscipes*, *A. heimii*, and *A. camerunensis*. We could not solve this issue so far.

To address this problem, this study included a sequence of an authentic collection of *A. camerunensis* and DNA data from two living strains originating from Sri Lanka, the type locality of *A. fuscipes*.

In addition, previous literature shows that collections studied have often been from South Africa, Zimbabwe, La Réunion, Malawi and Cameroon. In the Great East African Rift, Ethiopia, Kenya and Tanzania have sometimes been included. Less well studied are the mountain ecosystems of the Albertine Rift. This region is known to be a hotspot for fungal biodiversity (Rizinde 2016).

This current study included *Armillaria* collections originating on one side from mountainous ecosystems of the Albertine rift (Eastern DR Congo and Rwanda) and on the other side from the lowland rainforests of Gabon and Cameroon, and from São Tomé.

The results obtained show that two strains of *Armillaria* cf. *fuscipes* from Sri Lanka belong to two distant lineages, the melleioid and the South American-Australasian major clades, but it is not known which of these two species, if any, represents *A. fuscipes*. None of the African *Armillaria* collections examined here are related to either of these species.

Conversely, our African collection is shown to form an endemic African lineage divided into two clades. These two clades would correspond to a "lowland" vs. "highland" dichotomy. The phylogenetic diversity within the highland clade remains difficult to interpret in a taxonomic scheme.

A third lineage, formed by several collections from Western Rwanda and Kenya, is shown to be sister to *Armillaria hinnulea*, which is a species originally described from Tasmania, Australasia. The origin of this species, whether it is native from or introduced to Africa, remains uncertain. In this paper, the *A. heimii* is redefined based on ecological data. The status of *A. camerunensis* is fixed and *A. mellea* subsp. *africana* will be discussed.

## 5.3. Materials and methods

### 5.3.1. Data collection

Samples were collected in Virunga NP and Kahuzi-Biega NP (Fig 5.1.) in the Albertine rift, and from Gabon and Cameroon in the low land guineo Congo rainforest. Dried samples were obtained using a pulsed hot air dryer. Fungal cultures were obtained from spore prints.

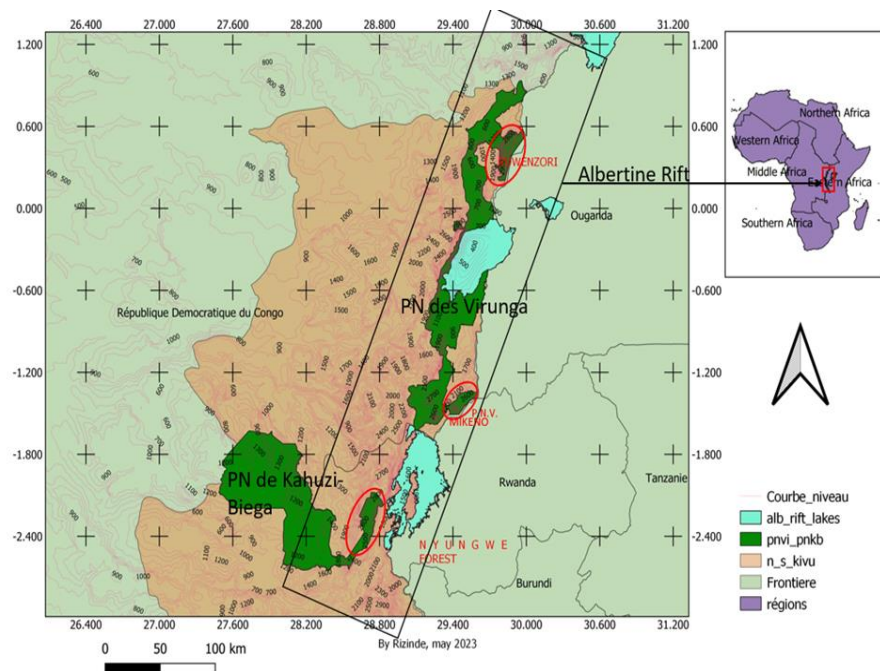


Figure 5.1: Sites sampled: Ruwenzori, Virunga (Mikeno), and Kahuzi-Biega mountain ranges in the Albertine Rift

### 5.3.2. Morphological examination

Color was determined according to Kornerup & Wanscher (1978). Macroscopic examinations were carried out using the standardized description sheets proposed by Eyi Ndong et al. (2011). The description included anatomical elements visible with the naked eye or with a magnifying glass, in particular the pileus, margin, stipe, annulus, veil

remnant and hymenium (consisting of lamellae). Microscopic observations were made using an Olympus microscope BX 50 equipped with phase contrast. The basidia, basidiospores and cystidia, stipitipellis, pileitrama, lamellar trama, pileipellis hyphae and annulus hyphae were observed.

### 5.3.3. Isolates used in the study

African *Armillaria* collections used in this study originated from both lowland rainforests and mountain forests in Albertine Rift (Fig. 4. 1.) along with additional areas of Cameroon, Gabon, and Sao Tomé deposited at MUCL and JBM. The specimens and/or culture are stored at the Meise Botanical garden and MUCL. Two historical living strains of *A. fuscipes* obtained from specimens collected from Sri Lanka received from the CBS were used to infer their identity and phylogenetic affinities. An ITS sequence from an historical specimen of *A. camerunensis* (Zenker 2165) was obtained by courtesy of Mario Amalfi, Meise Botanical Garden. Collections and related ecological data are listed in table 5.1.

Table 5.1: African *Armillaria* collections and related ecological data

| Name                  | Coll n°    | Substrat                        | Alt (m) | Origine | Country  | Réf        |
|-----------------------|------------|---------------------------------|---------|---------|----------|------------|
| <i>Armillaria</i> sp. | RHJ 117    | <i>Entandrophragma excelsum</i> | 1735    | PNVi    | DR Congo | This study |
| <i>Armillaria</i> sp. | RHJ 166    | <i>Leptaulus</i> sp.            | 1008    | PNVi    | DR Congo | This study |
| <i>Armillaria</i> sp. | RHJ 228    | <i>Celtis Philippensis</i>      | 966     | PNVi    | DR Congo | This study |
| <i>Armillaria</i> sp. | MUCL 56899 | <i>Celtis Philippensis</i>      | 966     | PNVi    | DR Congo | This study |
| <i>Armillaria</i> sp. | RHJ 233    | <i>Pancovia harmsiana</i>       | 989     | PNVi    | DR Congo | This study |
| <i>Armillaria</i> sp. | RHJ 237    | <i>Alstonia bonei</i>           | 1626    | PNVi    | DR Congo | This study |
| <i>Armillaria</i> sp. | MUCL 57358 |                                 | 2134    | PNKB    | DR Congo | This study |
| <i>Armillaria</i> sp. | MUCL 57370 | <i>Polyscias fulva</i>          | 2128    | PNKB    | DR Congo | This study |
| <i>Armillaria</i> sp. | MUCL 57389 | <i>Dombea torrida</i>           | 2139    | PNKB    | DR Congo | This study |
| <i>Armillaria</i> sp. | MUCL 57390 |                                 | 2138    | PNKB    | DR Congo | This study |
| <i>Armillaria</i> sp. | MUCL 57008 |                                 | ND      | PNKB    | DR Congo | This study |
| <i>Armillaria</i> sp. | RHJ 539    | <i>Maesa lanceolata</i>         | 2106    | PNKB    | DR Congo | This study |
| <i>Armillaria</i> sp. | JD 1369    | <i>Arundinaria alpina</i>       | 2592    | PNV     | Rwanda   | This study |
| <i>Armillaria</i> sp. | JD 1386    |                                 | 2535    | PNV     | Rwanda   | This study |
| <i>Armillaria</i> sp. | JD 1370    | <i>Arundinaria alpina</i>       | 2592    | PNV     | Rwanda   | This study |
| <i>Armillaria</i> sp. | JD 1368    |                                 | 2592    | PNV     | Rwanda   | This study |
| <i>Armillaria</i> sp. | JD 1403    |                                 | 2780    | PNV     | Rwanda   | This study |
| <i>Armillaria</i> sp. | JD 1388    |                                 | 2757    | PNV     | Rwanda   | This study |
| <i>Armillaria</i> sp. | JD 1372    |                                 | 2560    | PNV     | Rwanda   | This study |
| <i>Armillaria</i> sp. | JD531      |                                 |         | Dja     | Cameroon | This study |
| <i>Armillaria</i> sp. | JD1308     |                                 | 2049    | Bweyeye | Rwanda   | This study |
| <i>Armillaria</i> sp. | JD806      |                                 |         | Obo NP  | Sao tomé | This study |
| <i>Armillaria</i> sp. | MUCL 55467 |                                 | 2008    | Nyungwe | Rwanda   | This study |
| <i>Armillaria</i> sp. | JD 589     |                                 |         |         | Gabon    | This study |

|                        |             |                                  |           |               |              |                          |
|------------------------|-------------|----------------------------------|-----------|---------------|--------------|--------------------------|
| <i>Armillaria</i> sp.  | JD 1191     |                                  | 2278      | Nyungwe       | Rwanda       | This study               |
| <i>Armillaria</i> sp.  | ADK 5230    |                                  | 445       | Yangambi      | RD Congo     | This study               |
| <i>Armillaria</i> sp.  | ADK 5953    |                                  | 420       | Yangambi      | RD Congo     | This study               |
| <i>Armillaria</i> sp.  | MUCL 51422  |                                  | 400 m     | Ipasa Makokou | Gabon        | This study               |
| <i>Armillaria</i> sp.  | MUCL 53184  | <i>Ananas comosus</i>            |           |               | Cameroon     | This study               |
| <i>A. camerunensis</i> | Zenker 2165 |                                  |           | Bipinde       | Cameroon     | This study               |
| <i>A. fuscipes</i>     | CMW 3164    | <i>Pelargonium asperum</i>       | >2000     | Saint-Denis   | La Reunion   | Coetzee et al. 2005      |
| <i>A. fuscipes</i>     | CMW 4953    | <i>Pelargonium asperum</i>       |           |               | La Reunion   | Coetzee et al. 2005      |
| <i>A. fuscipes</i>     | CMW 2717    | <i>Pinus elliottii</i>           | 1500-2000 | Sabie         | South Africa | Coetzee et al. 2005      |
| <i>A. fuscipes</i>     | CMW 4871    | <i>Widdringtonia whytei</i>      |           |               | Malawi       | Coetzee et al. 2005      |
| <i>A. fuscipes</i>     | CMW 4873    |                                  |           |               | Malawi       | Coetzee et al. 2005      |
| <i>A. fuscipes</i>     | CMW 2740    | <i>Pinus patula</i>              |           | Entabeni      | South Africa | Coetzee et al. 2005      |
| <i>A. fuscipes</i>     | CMW 10165   | <i>Prunus persica</i>            |           | Chimanimani   | Zimbabwe     | Mwenje et al. 2003       |
| <i>A. fuscipes</i>     | CMW 4950    | <i>Pinus strobes</i>             |           |               | Tanzania     | Coetzee et al. 2005      |
| <i>A. fuscipes</i>     | CMW 4949    | <i>Pinus elliottii</i>           | 1500-2000 |               | Tanzania     | Coetzee et al. 2005      |
| <i>A. fuscipes</i>     | CMW 4874    | <i>Araucaria cunninghamii</i>    |           | Stapleford    | Zimbabwe     | Coetzee et al. 2005      |
| <i>A. fuscipes</i>     | CMW 5846    | <i>Pinus patula</i>              | 1890      |               | Ethiopia     | Gezahgne et al. 2004     |
| <i>A. fuscipes</i>     | CMW 5844    | <i>Pinus patula</i>              | 1890      |               | Ethiopia     | Gezahgne et al. 2004     |
| <i>A. fuscipes</i>     | CMW 7187    | <i>Camellia sinensis</i>         |           |               | Kenya        | Coetzee et al. 2005      |
| <i>A. fuscipes</i>     | CMW 7184    | <i>Cypressus</i> sp.             |           |               | Kenya        | Coetzee et al. 2005      |
| <i>Armillaria</i> sp.  | CMW 9954    |                                  |           | Pondo         | Zimbabwe     | Maphosa 2006             |
| <i>Armillaria</i> sp.  | CMW 4455    | <i>Camellia sinensis</i>         |           | Eastern       | Zimbabwe     | Coetzee et al. 2005      |
| <i>Armillaria</i> sp.  | CMW15584    | <i>Camellia sinensis</i>         |           |               | Kenya        | Pildain et al. 2009      |
| <i>Armillaria</i> sp.  | CMW 15585   | <i>Camellia sinensis</i>         |           |               | Kenya        | Pildain et al. 2009      |
| <i>Armillaria</i> sp.  | CMW 4456    | <i>Brachystegia utilis</i>       |           | Stapleford    | Zimbabwe     | Mwenje et al. 2003       |
| <i>Armillaria</i> sp.  | TH 9926     | <i>Gilbertiodendron dewevrei</i> |           | Dja           | Cameroon     | Koch et al. 2017         |
| <i>Armillaria</i> sp.  | TH DJA 91   | <i>Uapaca</i> sp.                |           | Dja           | Cameroon     | Koch et al. 2017         |
| <i>A. heimii</i>       | 173         | <i>Manihot usitatissimum</i>     |           |               | Congo        | Pérez-Sierra et al. 2004 |
| <i>A. heimii</i>       | 167         | <i>Camellia sinensis</i>         |           |               | Uganda       | Pérez-Sierra et al. 2004 |

|                  |           |                               |           |        |            |                            |
|------------------|-----------|-------------------------------|-----------|--------|------------|----------------------------|
| <i>A. heimii</i> | 5H1       | <i>Camellia sinensis</i>      |           |        | Kenya      | Pérez-Sierra et al. 2004   |
| <i>A. heimii</i> | 168       | <i>Araucaria cunninghamii</i> |           |        | Zimbabwe   | Pérez-Sierra et al. 2004   |
| <i>A. heimii</i> | 166       | <i>Pelargonium</i> sp.        |           |        | La Reunion | Pérez-Sierra et al. 2004   |
| <i>A. heimii</i> | 11MA2     | <i>Camellia sinensis</i>      | 1800-2000 |        | Kenya      | Pérez-Sierra et al. 2004   |
| <i>A. heimii</i> | 14C1      | <i>Camellia sinensis</i>      | 1800-2000 |        | Kenya      | Pérez-Sierra et al. 2004   |
| <i>A. heimii</i> | 170       | <i>Vitex keniensis</i>        | >2000     | Ragati | Kenya      | Pérez-Sierra et al. 2004   |
| <i>A. heimii</i> | K59       | <i>Vitex keniensis</i>        | >2000     | Ragati | Kenya      | Abomo-Ndongo et al. 1997   |
| <i>A. heimii</i> | 174       | <i>Vitex keniensis</i>        |           |        | Kenya      | Pérez-Sierra et al. 2004   |
| <i>A. heimii</i> | PH87.24   |                               |           |        | La Reunion | Stefani et al. Unpublished |
| <i>A. heimii</i> | 1BU1      | <i>Camellia sinensis</i>      | 1800-2000 |        | Kenya      | Pérez-Sierra et al. 2004   |
| <i>A. mellea</i> | HKAS86600 |                               |           |        | Kenya      | Guo et al. 2016            |
| <i>A. mellea</i> | HKAS86598 |                               |           |        | Kenya      | Guo et al. 2016            |
| <i>A. mellea</i> | HKAS86599 |                               |           | Muguga | Kenya      | Guo et al. 2016            |

For the phylogenetic analysis, additional GenBank sequences from 8 sub-Saharan countries treated as *A. fuscipes*, *A. heimii*, *A. camerunensis* and *Armillaria* sp. were added to the data matrix (Table 5.2).

Non-African GenBank sequences known to represent the Holarctic super clade, the South America-Australasian super clade and melleioid super clade are listed in the table (annex 1). GenBank sequences of *Gyanagaster* and *Oudemansiella mucida* chosen as outgroups were included in the data matrix as recommended for a fair phylogenetic analysis.

Table 5.2: List of collections used for DNA analyses, with origin, GenBank accession numbers and references. MC: Major Clade; I: African major clade; II: South American-Australasian major clade; III: Melleioid major clade; IV: Holarctic major clade; V: *Desarmillaria*; VI: Non Armillarioid

| Name                   | Coll n°     | Origin          | Réf                      | ITS      | LSU      | (Tef1- $\alpha$ ) | RPB2     | MC |
|------------------------|-------------|-----------------|--------------------------|----------|----------|-------------------|----------|----|
| <i>A. affinis</i>      | JMCR.126    | Central America | Moncalvo et al./Genbank  |          | AF261356 |                   |          | II |
| <i>A. altimontana</i>  | D82         | North America   | Brazee et al. 2012       |          |          | JN944611          |          | IV |
| <i>A. altimontana</i>  | Mac4        | North America   | Brazee et al. 2012       |          |          | JN944608          |          | IV |
| <i>A. aotearoa</i>     | NZFS 2425   | New Zealand     | Hood & Ramsfield 2016    | KR063261 |          |                   |          | II |
| <i>A. borealis</i>     | HKAS86616   | Finland         | Guo et al. 2016          | KT822291 |          | KT822427          |          | IV |
| <i>A. borealis</i>     | CMW 31072   | China           | Koch et al. 2017         |          | KM205304 | KM205251          |          | IV |
| <i>A. borealis</i>     | PA87-82     | Russia          | Koch et al. 2017         |          | FJ618728 | FJ618642          | FJ618773 | IV |
| <i>A. calvescens</i>   | III MD52A1  | Canada          | Stefani et al./ Genbank  |          | FJ618758 | FJ618671          | FJ618801 | IV |
| <i>A. calvescens</i>   | Ac154       | USA             | Brazee, et al. 2012      | KM594877 | JF895899 | JF895834          |          | IV |
| <i>A. calvescens</i>   | ST18        | Canada          | Klopfenstein et al. 2017 |          |          | JF313129          |          | IV |
| <i>A. calvescens s</i> | III MD543A2 | Canada          | Stefani et al./ Genbank  |          | FJ618759 | FJ618672          | FJ618802 | IV |
| <i>A. camerunensis</i> | Zenker 2165 | Cameroun        | This study               | Pending  |          |                   |          | I  |
| <i>A. cepistipes</i>   | CMW6909     | USA             | Maphosa et al. 2006      |          | DQ338563 | DQ435630          |          | IV |
| <i>A. cepistipes</i>   | HKAS 86583  | China           | Guo et al. 2016          | KT822290 |          | KT822417          |          | IV |
| <i>A. cepistipes</i>   | HKAS 86584  | China           | Guo et al. 2016          | KT822278 |          | KT822419          |          | IV |
| <i>A. cepistipes</i>   | PB71.1      | France          | Koch et al. 2017         |          | FJ618727 | FJ618641          | FJ618772 | IV |
| <i>A. fumosa</i>       | CMW4955     | Australia       | Koch al. 2017            | AF329918 | DQ338552 | DQ435646          |          | II |
| <i>A. fumosa</i>       | CMW4960     | Australia       | Koch al. 2017            | AF329916 |          | DQ435645          |          | II |
| <i>A. fuscipes</i>     | CMW 3164    | La Reunion      | Coetzee et al. 2005      | AY882975 |          |                   |          | I  |
| <i>A. fuscipes</i>     | CMW 4953    | La Reunion      | Coetzee et al. 2005      | AY882974 |          |                   |          | I  |
| <i>A. fuscipes</i>     | CMW 2717    | South Africa    | Coetzee et al. 2005      | AY882971 |          |                   |          | I  |
| <i>A. fuscipes</i>     | CMW 4871    | Malawi          | Coetzee et al. 2005      | AY882976 |          |                   |          | I  |

|                    |           |                        |                          |          |          |          |          |  |    |
|--------------------|-----------|------------------------|--------------------------|----------|----------|----------|----------|--|----|
| <i>A. fuscipes</i> | CMW 4873  | Malawi                 | Coetzee et al. 2005      | AY882977 |          |          |          |  | I  |
| <i>A. fuscipes</i> | CMW 2740  | Entabeni/ South Africa | Coetzee et al. 2005      | AY882970 |          |          |          |  | I  |
| <i>A. fuscipes</i> | CMW 10165 | Zimbabwe               | Coetzee et al. 2005      | AY882966 |          |          |          |  | I  |
| <i>A. fuscipes</i> | CMW 4950  | Tanzania               | Coetzee et al. 2005      | AY882979 |          |          |          |  | I  |
| <i>A. fuscipes</i> | CMW 4949  | Tanzania               | Coetzee et al. 2005      | AY882978 |          |          |          |  | I  |
| <i>A. fuscipes</i> | CMW 4874  | Zimbabwe               | Coetzee et al. 2005      | AY882967 |          |          |          |  | I  |
| <i>A. fuscipes</i> | CMW 5846  | Ethiopia               | Gezahgne et al. 2004     | AY882968 |          |          |          |  | I  |
| <i>A. fuscipes</i> | CMW 5844  | Ethiopia               | Gezahgne et al 2004      | AY882969 |          |          |          |  | I  |
| <i>A. fuscipes</i> | CMW 7187  | Kenya                  | Coetzee et al. 2005      | AY882972 |          |          |          |  | I  |
| <i>A. fuscipes</i> | CMW 7184  | Kenya                  | Coetzee et al. 2005      | AY882973 |          |          |          |  | I  |
| <i>A. gallica</i>  | HKAS86569 | China                  | Guo et al. 2016          | KT822277 |          | KT822414 |          |  | IV |
| <i>A. gallica</i>  | PE80.37   | France                 | Stefani et al./ Genbank  |          | FJ618725 | FJ618639 | FJ618770 |  | IV |
| <i>A. gallica</i>  | Aga33     | Canada                 | Koch et al. 2017         |          | JF895909 | JF895845 | JF895877 |  | IV |
| <i>A. gallica</i>  | ST23      | USA                    | Ross-Davis et al 2011    | AY213571 | JF895913 | JF895849 | JF895880 |  | IV |
| <i>A. gemina</i>   | JB-38A    | Canada                 | Koch et al. 2017         | FJ664586 | FJ618757 | FJ618670 | FJ618800 |  | IV |
| <i>A. gemina</i>   | M3-3      | USA                    | Koch et al. 2017         |          | JF895916 | JF895854 | JF895885 |  | IV |
| <i>A. heimii</i>   | 173       | Congo                  | Pérez-Sierra et al. 2004 | AY333917 |          |          |          |  | I  |
| <i>A. heimii</i>   | 167       | Uganda                 | Pérez-Sierra et al. 2004 | AY333914 |          |          |          |  | I  |
| <i>A. heimii</i>   | 5H1       | Kenya                  | Pérez-Sierra et al. 2004 | AY333920 |          |          |          |  | I  |
| <i>A. heimii</i>   | 168       | Zimbabwe               | Pérez-Sierra et al. 2004 | AY333915 |          |          |          |  | I  |
| <i>A. heimii</i>   | 166       | La Reunion             | Pérez-Sierra et al. 2004 | AY333913 |          |          |          |  | I  |
| <i>A. heimii</i>   | 11MA2     | Kenya                  | Pérez-Sierra et al. 2004 | AY333921 |          |          |          |  | I  |
| <i>A. heimii</i>   | 14C1      | Kenya                  | Pérez-Sierra et al. 2004 | AY333922 |          |          |          |  | I  |
| <i>A. heimii</i>   | 170       | Kenya                  | Pérez-Sierra et al. 2004 | AY333916 |          |          |          |  | I  |
| <i>A. heimii</i>   | K59       | Kenya                  | Stefani et al./ Genbank  | FJ664588 | FJ618730 | FJ618644 | FJ618775 |  | I  |
| <i>A. heimii</i>   | 174       | Kenya                  | Pérez-Sierra et al. 2004 | AY333918 |          |          |          |  | I  |

|                         |            |                  |                            |          |          |          |          |     |
|-------------------------|------------|------------------|----------------------------|----------|----------|----------|----------|-----|
| <i>A. heimii</i>        | PH87.24    | La Reunion       | Stefani et al./ Genbank    |          | FJ618737 | FJ618651 | FJ618782 | I   |
| <i>A. heimii</i>        | 1BU1       | Kenya            | Pérez-Sierra et al. 2004   | AY333919 |          |          |          | I   |
| <i>A. hinnulea</i>      | Lot2       | Australia        | Koch et al. 2017           |          | FJ618749 | FJ618663 | FJ618793 | II  |
| <i>A. hinnulea</i>      | CMW4980    | Australia        | Koch et al. 2017           |          | DQ338555 | DQ435648 |          | II  |
| <i>A. hinnulea</i>      | DAR 37770  | Australia        | Smith-White et al. 2000    | AF394918 |          |          |          | II  |
| <i>A. hinnulea</i>      | RP7088     | Patagonian Andes | Pildain et al. 2009        | FJ711636 |          |          |          | II  |
| <i>A. limonea</i>       | Plim84.66  | New Zealand      | Koch al. 2017              |          | FJ618740 | FJ618654 | FJ618785 | II  |
| <i>A. limonea</i>       | CMW4680    | New Zealand      | Koch al. 2017              | AF329930 | AF445073 |          |          | II  |
| <i>A. luteobubalina</i> | CMW 5446   | Argentina        | Koch al. 2017              |          | DQ338562 | DQ435650 |          | II  |
| <i>A. luteobubalina</i> | V M5.2     | Australia        | Koch al. 2017              |          | FJ618753 | FJ618666 | FJ618797 | II  |
| <i>A. mellea</i>        | HKAS86600  | Kenya            | Guo et al. 2016            | KT822247 |          | KT822355 |          | III |
| <i>A. mellea</i>        | HKAS86598  | Kenya            | Guo et al. 2016            | KT822248 |          | KT822348 |          | III |
| <i>A. mellea</i>        | HKAS86599  | Kenya            | Guo et al. 2016            | KT822250 |          | KT822350 |          | III |
| <i>A. mellea</i>        | HKAS86588  | Japan            | Guo et al. 2016            | KT822246 |          | KT822352 |          | III |
| <i>A. mellea</i>        | DF1        | China            | Huang,et al. 2014/ genbank | KF032530 | KJ643353 | KJ643388 |          | III |
| <i>A. mellea</i>        | HKAS 86590 | China            | Guo et al. 2016            | KT822251 |          | KT822354 |          | III |
| <i>A. mellea</i>        | HKAS86592  | China            | Guo et al. 2016            | KT822253 |          | KT822344 |          | III |
| <i>A. mellea</i>        | HKAS86597  | China            | Guo et al. 2016            | KT822255 |          | KT822351 |          | III |
| <i>A. mellea</i>        | PBM 2470   |                  | Koch et al. 2017           |          |          | AY881023 | AY780938 | III |
| <i>A. mellea</i>        | VI49.5     | USA              | Koch et al. 2017           |          | FJ618762 | FJ618675 | FJ618806 | III |
| <i>A. mellea</i>        | PVI85.43   | USA              | Koch et al. 2017           |          | FJ618734 | FJ618648 | FJ618779 | III |
| <i>A. mellea</i>        | D1         | France           | Tsykun et al, Genbank      | JN657464 |          | JN657491 |          | III |
| <i>A. mellea</i>        | H7000666   | Denmark          | Liang et al, Genbank       | MG931762 | MG931536 | MH002746 |          | III |
| <i>A. mexicana</i>      | MEX88      | Mexico           | Elias-Roman et al. 2017    | KR061311 | KR061307 | KR061315 |          | III |
| <i>A. mexicana</i>      | MEX85      | Mexico           | Elias-Roman et al. 2017    | KR061308 | KR061305 | KR061313 |          | III |
| <i>A. nabsnona</i>      | IX SP83-61 | Canada           | Stefani et al./ Genbank    |          | FJ618743 | FJ618657 | FJ618787 | IV  |

|                           |            |             |                          |          |          |          |          |    |
|---------------------------|------------|-------------|--------------------------|----------|----------|----------|----------|----|
| <i>A. nabsnona</i>        | HKAS 85523 | China       | Guo et al. 2016          | KT822333 |          | KT822411 |          | IV |
| <i>A. nabsnona</i>        | HKAS 85499 | China       | Guo et al. 2016          | KT822265 |          | KT822410 |          | IV |
| <i>A. nabsnona</i>        | IX SP84-15 | Canada      | Stefani et al./ Genbank  |          | FJ618746 | FJ618660 | FJ618790 | IV |
| <i>A. nabsnona</i>        | CMW 6905   | USA         | Maphosa et al. 2006      |          | DQ338542 | DQ435631 |          | IV |
| <i>A. novae-zelandiae</i> | CMW3951    | Malaysia    | Pildain et al. 2009      | AF448419 | DQ338553 |          |          | II |
| <i>A. novae-zelandiae</i> | CMW 5448   | Australia   | Maphosa et al 2006       | AF448417 | DQ338554 | DQ435653 |          | II |
| <i>A. novae-zelandiae</i> | CMW4722    | New Zealand | Maphosa et al 2006       | AF329926 | DQ338551 | DQ435652 |          | II |
| <i>A. ostoyae</i>         | JB13       | Canada      | Stefani et al./ Genbank  |          | FJ618723 | FJ618637 | FJ618768 | IV |
| <i>A. ostoyae</i>         | V91-02     | Canada      | Stefani et al./ Genbank  | HQ891860 | FJ618754 | FJ618667 | FJ618798 | IV |
| <i>A. ostoyae</i>         | HKAS86581  | China       | Guo et al. 2016          | KT822292 |          | KT822429 |          | IV |
| <i>A. pallidula</i>       | CMW4971    | Australia   | Koch al. 2017            |          |          | DQ435647 |          | II |
| <i>A. pallidula</i>       | 3626       | Australia   | Koch al. 2017            | FJ664607 | FJ618752 | FJ618665 | FJ618796 | II |
| <i>A. puiggarii</i>       | MCA3111    | Guyana      | Koch et al. 2017         | KU170954 | KU170944 | KU289104 |          | II |
| <i>A. puiggarii</i>       | TH 9751    | Guyana      | Koch et al. 2017         | KU170953 | KU170943 | KU289113 |          | II |
| <i>A. puiggarii</i>       | PPg85-63   | Mexico      | Koch et al. 2017         |          | FJ618722 | FJ618636 | FJ618767 | II |
| <i>A. sinapina</i>        | V SP82-23  | Canada      | Klopfenstein et al. 2017 |          | FJ618741 | FJ618655 | FJ618794 | IV |
| <i>A. sinapina</i>        | P2-7       | USA         | Koch et al. 2017         |          | JF895914 | JF895850 | JF895882 | IV |
| <i>A. sinapina</i>        | V48.5      | Canada      | Koch et al. 2017         |          | FJ618763 | FJ618676 | FJ618807 | IV |
| <i>A. sinapina</i>        | HKAS 86566 | China       | Guo et al. 2016          | KT822323 |          | KT822422 |          | IV |
| <i>A. solidipes</i>       | W1-9       | USA         | Brazee et al. 2012       |          | JF895919 | JF895853 | JF895886 | IV |
| <i>A. solidipes</i>       | MS2-11     | USA         | Klopfenstein et al. 2017 |          | JF895918 | JF895852 | JF895887 | IV |
| <i>A. sparrei</i>         | PSpa86.5   | Argentina   | Stefani et al./ Genbank  |          | FJ618750 |          |          | II |
| <i>A. gallica</i>         | PE71.2     | France      | Stefani et al./ Genbank  |          | FJ618724 | FJ618638 | FJ618769 | IV |
| <i>Armillaria</i> sp.     | RHJ 117    | DR Congo    | This study               | Pending  |          |          |          | I  |
| <i>Armillaria</i> sp.     | RHJ 166    | DR Congo    | This study               | Pending  |          |          |          | I  |
| <i>Armillaria</i> sp.     | RHJ 228    | DR Congo    | This study               | Pending  |          |          |          | I  |
| <i>Armillaria</i> sp.     | MUCL 56899 | DR Congo    | This study               | Pending  |          |          |          | I  |

|                       |             |           |            |         |         |         |         |  |     |
|-----------------------|-------------|-----------|------------|---------|---------|---------|---------|--|-----|
| <i>Armillaria</i> sp. | RHJ 233     | DR Congo  | This study | Pending |         |         |         |  | I   |
| <i>Armillaria</i> sp. | RHJ 237     | DR Congo  | This study | Pending |         |         |         |  | I   |
| <i>Armillaria</i> sp. | MUCL 57358  | DR Congo  | This study | Pending | Pending | Pending | Pending |  | I   |
| <i>Armillaria</i> sp. | MUCL 57370  | DR Congo  | This study | Pending | Pending | Pending | Pending |  | I   |
| <i>Armillaria</i> sp. | MUCL 57389  | DR Congo  | This study | Pending | Pending | Pending | Pending |  | I   |
| <i>Armillaria</i> sp. | MUCL 57390  | DR Congo  | This study | Pending | Pending | Pending | Pending |  | I   |
| <i>Armillaria</i> sp. | MUCL 57008  | DR Congo  | This study | Pending | Pending | Pending | Pending |  | I   |
| <i>Armillaria</i> sp. | RHJ 539     | DR Congo  | This study | Pending |         |         |         |  | I   |
| <i>Armillaria</i> sp. | JD 1369     | Rwanda    | This study | Pending |         |         |         |  | II  |
| <i>Armillaria</i> sp. | JD 1386     | Rwanda    | This study | Pending |         |         |         |  | II  |
| <i>Armillaria</i> sp. | JD 1370     | Rwanda    | This study | Pending |         |         |         |  | II  |
| <i>Armillaria</i> sp. | JD 1368     | Rwanda    | This study | Pending |         |         |         |  | II  |
| <i>Armillaria</i> sp. | JD 1403     | Rwanda    | This study | Pending |         |         |         |  | II  |
| <i>Armillaria</i> sp. | JD 1388     | Rwanda    | This study | Pending |         |         |         |  | II  |
| <i>Armillaria</i> sp. | JD 1372     | Rwanda    | This study | Pending |         |         |         |  | II  |
| <i>Armillaria</i> sp. | JD531       | Cameroon  | This study | Pending |         |         |         |  | I   |
| <i>Armillaria</i> sp. | JD1308      | Rwanda    | This study | Pending |         |         |         |  | I   |
| <i>Armillaria</i> sp. | JD806       | Sao tomé  | This study | Pending |         |         |         |  | I   |
| <i>Armillaria</i> sp. | MUCL 55467  | Rwanda    | This study | Pending | Pending | Pending | Pending |  | II  |
| <i>Armillaria</i> sp. | JD 589      | Gabon     | This study | Pending |         |         |         |  | I   |
| <i>Armillaria</i> sp. | JD 1191     | Rwanda    | This study | Pending |         |         |         |  | I   |
| <i>Armillaria</i> sp. | ADK 5230    | RD Congo  | This study | Pending |         |         |         |  | I   |
| <i>Armillaria</i> sp. | ADK 5953    | RD Congo  | This study | Pending |         |         |         |  | I   |
| <i>Armillaria</i> sp. | MUCL 51422  | Gabon     | This study | Pending | Pending | Pending | Pending |  | I   |
| <i>Armillaria</i> sp. | MUCL 53184  | Cameroon  | This study | Pending | Pending | Pending | Pending |  | I   |
| <i>Armillaria</i> sp. | MUCL R58324 | Sri Lanka | This study | Pending | Pending | Pending | Pending |  | II  |
| <i>Armillaria</i> sp. | CBS 110.29  | Sri Lanka | This study | Pending | Pending | Pending | Pending |  | III |

|                       |                |                |                         |          |          |          |          |     |
|-----------------------|----------------|----------------|-------------------------|----------|----------|----------|----------|-----|
| <i>Armillaria</i> sp. | MUCL 38985     | Belgique       | This study              | Pending  | Pending  | Pending  | Pending  | III |
| <i>Armillaria</i> sp. | CMW 9954       | Zimbabwe       | Maphosa 2006            |          | EU380246 | DQ435620 |          | I   |
| <i>Armillaria</i> sp. | CMW 4455       | Zimbabwe       | Coetzee et al. 2005     | AY882985 |          |          |          | I   |
| <i>Armillaria</i> sp. | CMW15584       | Kenya          | Pildain et al. 2009     | AF513024 | FJ711634 |          |          | I   |
| <i>Armillaria</i> sp. | CMW 15585      | Kenya          | Pildain et al. 2010     | AF513022 | FJ711633 |          |          | I   |
| <i>Armillaria</i> sp. | CMW 4456       | Zimbabwe       | Coetzee et al. 2005     | AY882984 |          |          |          | I   |
| <i>Armillaria</i> sp. | TH 9926        | Cameroon       | Koch et al. 2017        | KU170951 | KU254222 | KU289111 |          | I   |
| <i>Armillaria</i> sp. | TH DJA 91      | Cameroon       | Koch et al. 2017        | KU170952 | KU170942 | KU289112 | KY359141 | I   |
| <i>Armillaria</i> sp. | 00-13          | Japan          | Ota et al. 2011         | AB558998 |          | AB558990 |          | II  |
| <i>Armillaria</i> sp. | 00-14          | Japan          | Ota et al. 2012         | AB558999 |          | AB558991 |          | II  |
| <i>Armillaria</i> sp. | CMW4994        | New Zealand    | Maphosa et al. 2006     | AF329932 | FJ875697 | DQ435643 |          | II  |
| <i>Armillaria</i> sp. | PIII87.9       | Kenya          | Stefani et al./ Genbank |          | FJ618733 | FJ618647 | FJ618778 | II  |
| <i>Armillaria</i> sp. | PIII87.42      | Kenya          | Stefani et al./ Genbank |          | FJ618738 | FJ618652 | FJ618783 | II  |
| <i>Armillaria</i> sp. | PIII87.5       | Kenya          | Stefani et al./ Genbank |          | FJ618756 | FJ618669 | FJ618799 | II  |
| <i>Armillaria</i> sp. | CMW 10581      | Bhutan         | Coetzee et al. 2011     | AY554329 | DQ338548 | FJ875699 |          | IV  |
| <i>D. caespitosa</i>  | MEX21WF        | Mexico         | Antonin et al. 2021     |          | MT163178 | MT232066 | MN990677 | V   |
| <i>D. caespitosa</i>  | OHIO_2018PB-1A | USA            | Antonin et al. 2021     | MT007923 | MT238204 | MT232065 | MN990681 | V   |
| <i>D. caespitosa</i>  | AT-MU-S2       | USA            | Antonin et al. 2021     | AY213588 | AY509189 | JF313113 | MN990680 | V   |
| <i>D. caespitosa</i>  | OOI-210        | USA            | Antonin et al. 2022     | AY213590 | AY509191 | JF313111 | MN990679 | V   |
| <i>D. ectypa</i>      | HKAS86565      | France         | Guo et al. 2016         | KT822340 |          | KT822438 |          | V   |
| <i>D. ectypa</i>      | MY84-94-1      | France         | Koch et al. 2017        |          | FJ618729 | FJ618643 | FJ618774 | V   |
| <i>D. ectypa</i>      | CMW15693       | France         | Koch et al. 2017        |          | DQ338547 | FJ875698 |          | V   |
| <i>D. tabescens</i>   | RAK07          | USA            | Koch et al. 2017        |          | KY358225 | KY366987 | KY359140 | V   |
| <i>D. tabescens</i>   | HKAS 86605     | Slovenia       | Guo et al. 2016         | KT822337 |          | KT822439 |          | V   |
| <i>D. tabescens</i>   | MENDELU 519    | Czech Republic | Antonin et al. 2021     | DQ784799 | MT163173 | MT221655 | MN990672 | V   |
| <i>D. tabescens</i>   | HKAS86603      | China          | Guo et al. 2016         | KT822240 |          | KT822441 |          | V   |

|                                 |          |         |                         |          |          |          |          |    |
|---------------------------------|----------|---------|-------------------------|----------|----------|----------|----------|----|
| <i>D. tabescens</i>             | PT89.84  | Italy   | Stefani et al./ Genbank |          | FJ618761 | FJ618674 | FJ618805 | V  |
| <i>D. tabescens</i>             | PT84-12  | France  | Stefani et al./ Genbank |          | FJ618744 | FJ618658 | FJ618788 | V  |
| <i>Guyanagaster lucianii</i>    | RAK88    | Guyana  | Koch et al. 2017        |          |          |          |          | VI |
| <i>Guyanagaster lucianii</i>    | RAK89    | Guyana  | Koch et al. 2017        |          |          |          | KY359143 | VI |
| <i>Guyanagaster necrorhizus</i> | RAK31    | Guyana  | Koch et al. 2017        | KU170948 | KU254225 | KU289108 | KY359145 | VI |
| <i>Guyanagaster necrorhizus</i> | MCA3950  | Guyana  | Koch et al. 2017        |          |          |          |          | VI |
| <i>Oudemansiella cubensis</i>   | MCA 5434 | Guyana  | Koch et al. 2017        | KU170955 |          | KU289105 |          | VI |
| <i>Pholiota</i> sp.             | JD1312   | Rwanda  | This study              |          |          |          |          | VI |
| <i>Strobilurus esculentus</i>   | Yang5027 | Germany | Koch et al. 2017        |          |          | KF530581 | KT201660 | VI |

### 5.3.4. DNA extraction and amplification

DNA extraction, amplification and sequencing of the 5' end of the nuclear ribosomal LSU rDNA gene, (region including the domains D1–D3), the ITS-5.8S regions, partial *tef1- $\alpha$*  gene, and the region between domains 6 and 7 of the second largest subunit of the *rpb2* gene were as described in Frøslev et al. (2005), Matheny (2005), and Amalfi and Decock (2013). Materials and sequences used in this study are listed in table 5.2. Successful PCR reactions resulted in a single band observed on a 0.8% agarose gel.

Table 5.3: Primers used in this study

|   | Region                          | Primer pair | Primer sequence (5'-3')    | Reference                |
|---|---------------------------------|-------------|----------------------------|--------------------------|
|   | /Gen                            |             |                            |                          |
| 1 | ITS                             | ITS1        | TCC GTA GGT GAA CCT GCG G  | Pérez-Sierra et al. 2004 |
|   |                                 | ITS4        | TCC TCC GCT TAT TGA TAT GC |                          |
| 2 | LSU                             | LR0R        | ACC CGC TGA ACT TAA GC     | Brazee et al. 2011       |
|   |                                 | LR5         | TCC TGA GGG AAA CTT CG     |                          |
| 3 | <i>Tef1-<math>\alpha</math></i> | EF983F      | GCYCCYGGHCAYCGTGAYTTYAT    | Matheny et al. 2007      |
|   |                                 | EF2218R     | ATGACACCRACRGCRACRGTYTG    |                          |
| 4 | RPB2                            | RPB2-6F     | TGG GKG WTG GTY TGYC CTGC  | Brazee et al. 2011       |
|   |                                 | RPB2-7.1R   | CCC ATW GCY TGC TTM CCC AT |                          |

All the sequencing reactions were performed by MacroGen Inc. (Korea and The Netherlands), with primers LROR, LR3, LR3R, LR5 for the LSU region; ITS1, ITS4 for the ITS-5.8S region, 2212R, 1577F, 983F, 1567R for *tef1- $\alpha$*  gene (Rehner and Buckley 2005; Matheny et al. 2007); and bRPB2-6F and bRPB2-7.1R for *rpb2* gene (Matheny 2005). Sequences were assembled and edited with Sequencher™ 4.8 software (Gene Codes Corporation, Ann Arbor, MI, U.S.A.). Based on

BLAST results (BLAST searches done on 14/06/2022), a combined dataset (nuclear ribosomal LSU rRNA gene and ITS regions (including 5.8S) and of partial *tef1- $\alpha$*  and *rpb2* genes) comprising sequences from 146 collections (including the outgroup) was constructed and used for further phylogenetics analyses.

### 5.3.5. Phylogenetic analysis

Nucleotide sequences were automatically aligned using the MUSCLE algorithm with default settings in MEGA (Molecular Evolutionary Genetics Analysis). The alignment was further optimized and manually adjusted as necessary by direct examination with the software PhyDE (phylogenetic Data Editor).

The phylogenetic relationships were inferred by the Maximum Likelihood hypothesis using the RaxmlGUI 2.0 graphical user interface (Edler et al. 2021) with default option (GTR, GAMMA distribution). 100-bootstrap replicates were taken to test the robustness of the branches. Bootstrap values are noted on the branches.

The analysis involved 167 collections of worldwide origin. Final trees were designed using FigTree v1.4.4.

## 5.4. Results

Our phylogenetic analysis (Fig.5.2 and Fig. 5.4) confirmed that the African *Armillaria* specimens are grouped into the well-supported Armillarioid lineage sensu Koch et al. (2017). The Armillarioid clade consists of the genera *Armillaria* (annulate) and *Desarmillaria* (exannulate) (Koch et al. 2021). The phylogenetic analysis showed that

*Desarmillaria* is sister to the *Armillaria* clade (Fig. 5.2) (Klofestein et al. 2017; Koch et al. 2017).

The *Armillaria* lineage is further subdivided into several major (super) clades (Fig. 5.2) referred to as Holarctic, South American-Austral-Asian, tropical African, and melleioid (Coetzee et al. 2011; Koch et al. 2017; Coetzee et al. 2018), reflecting their biogeographical origin sensu Cox (2001).

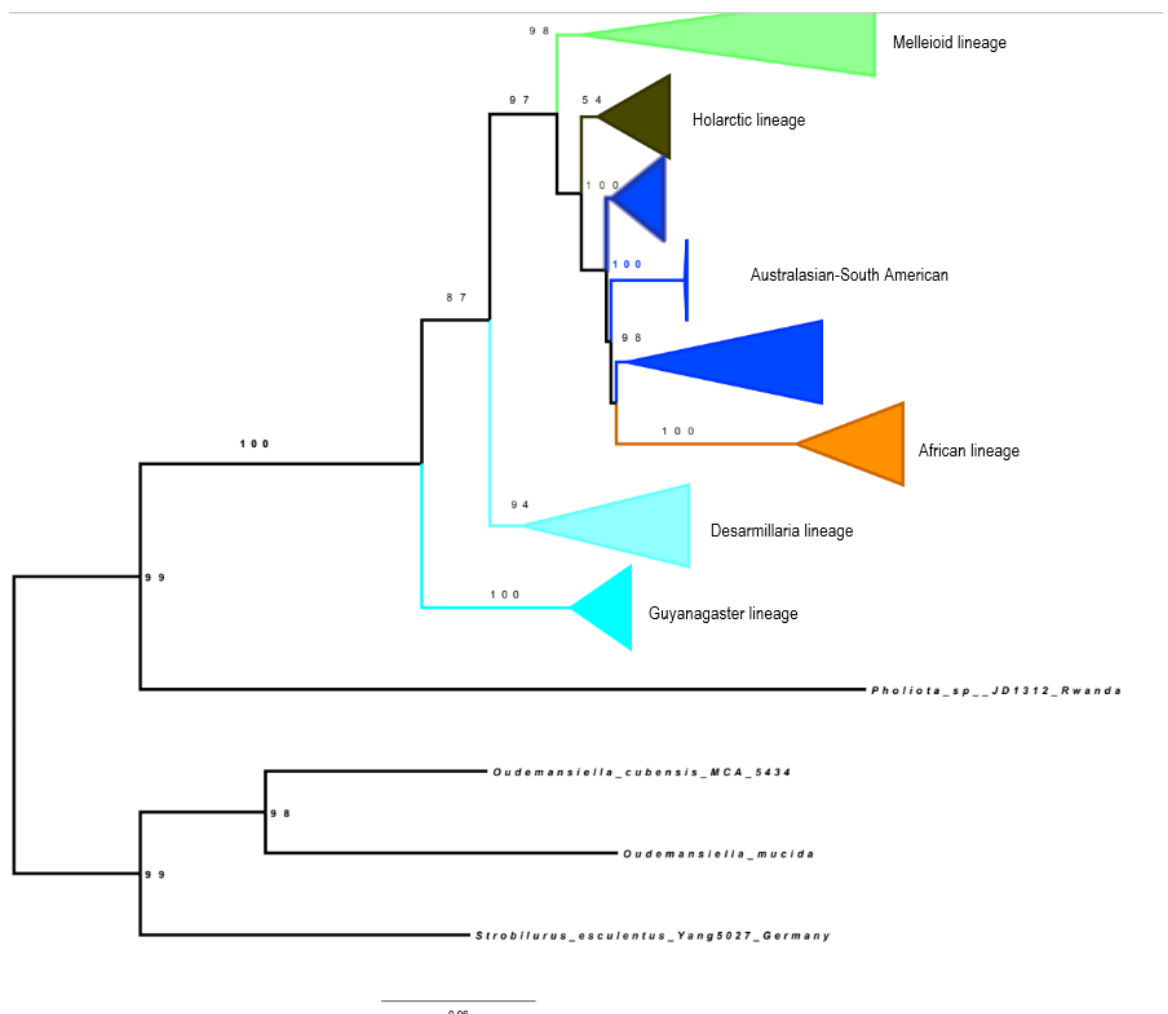


Figure 5.2: Synthetic phylogram generated from the analysis of four gene regions (28S, Tef1- $\alpha$ , RPB2, and ITS). light green: Melleioid major clade; dark green: Holarctic major clade; Blue: Australasian - South American clades; Orange: African major clade; light blue: *Desarmillaria* clade; turquoise: *Guyanagaster* clade.

The African *Armillaria* clustered within three of these major clades within the *Armillaria* lineage: the tropical African major clade, one of the South American-Austral-Asian major clade sensu Coetzee et al. (2011) and Koch et al. (2017), and the melleioid major clade (Fig.5.3).

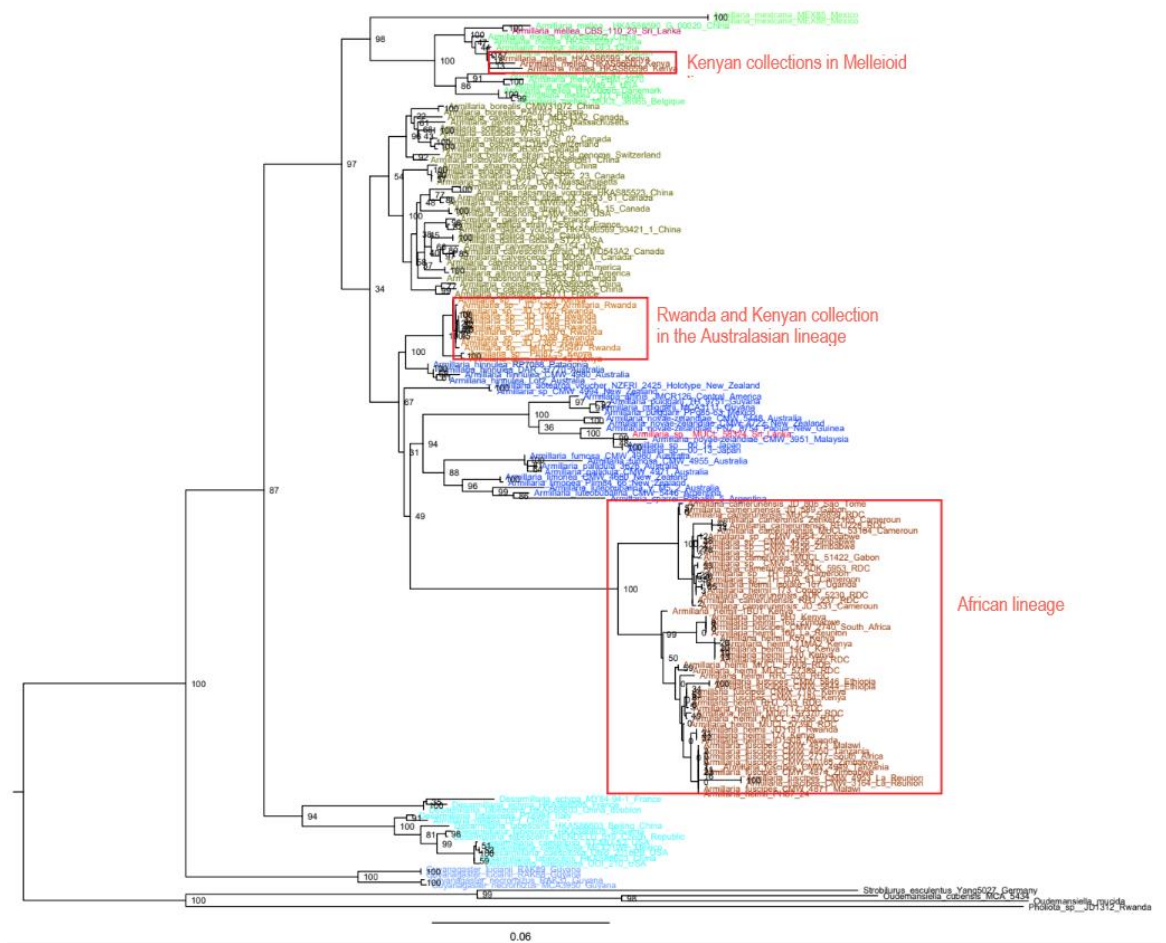


Figure 5.3: Maximum likelihood tree showing that the African collections have clustered into three major clades (African collection in red).

The tropical Africa endemic lineage is further subdivided into two main clades, in accordance with Coetzee et al. (2005) as shown below (Fig. 5.4.).



Figure 5.4: Maximum likelihood tree of African major clade

Two *Armillaria* from Sri Lanka represented by two cultures (MUCL 58324 / CBS-109-29; MUCL 58325 / CBS-110-29) were shown to belong to 2 distant major lineages, a Southeast Asian - Australian lineage (CBS-109-29 / MUCL 58324), and the melleioid super lineage (CBS-110-29 / MUCL 58325), respectively (Fig 5.5.).

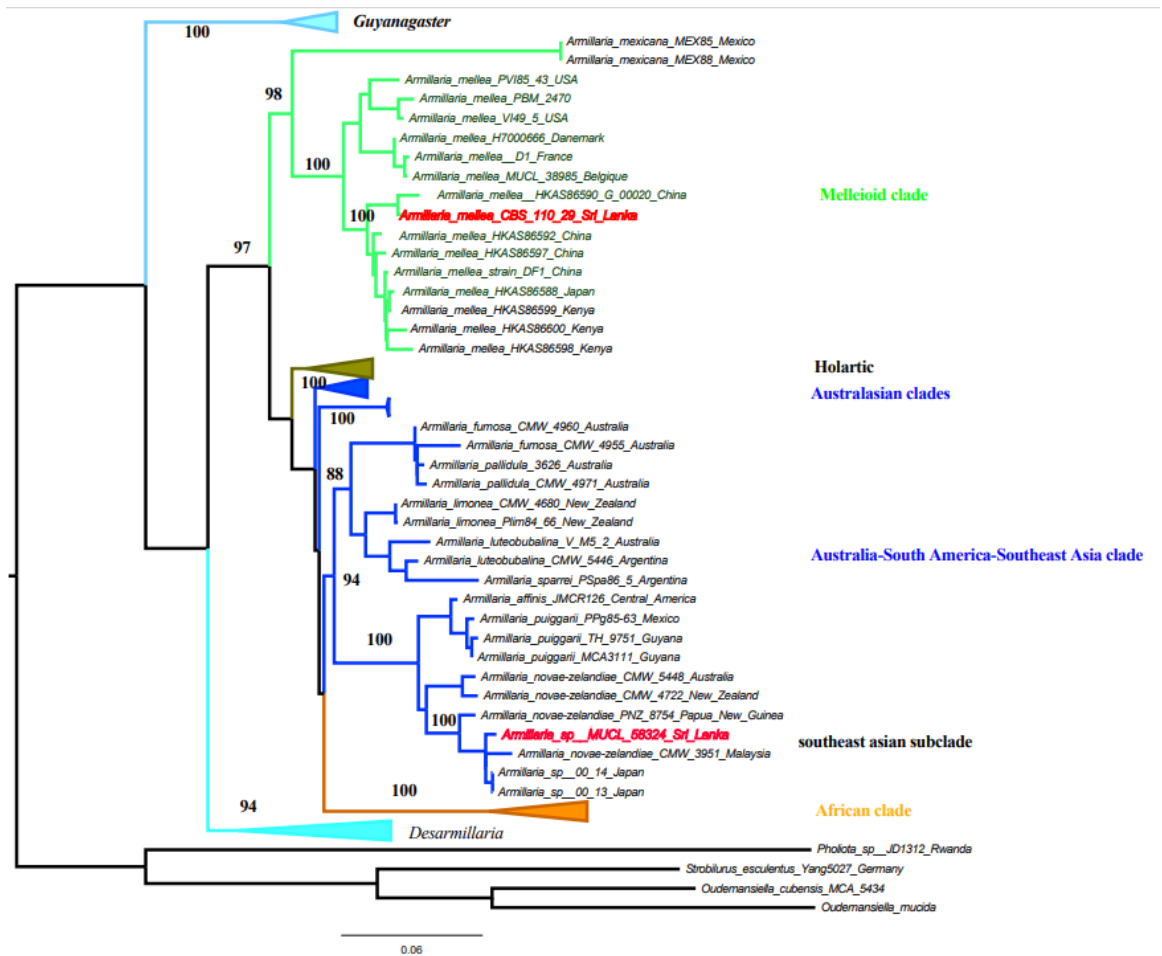


Figure 5.5: Maximum likelihood tree showing the position of two isolates from Sri Lanka (highlighted in red): CBS-110-29 / MUCL 58325 within Melleioid lineage and CBS-109-29 / MUCL 58324 within South American-Australasian lineage.

The specimens from lowland tropical rainforests collected at the foothills of the Ruwenzori (< 1000 masl) and Yangambi (500 masl) in DR Congo clustered with other collections from the Guinea-Congolian rainforest in Cameroon and Gabon (<500 masl).

## 5.5. Discussion

This study aimed to clarify the taxonomy of *A. heimii*, *A. fuscipes*, and *A. camerunensis*, as well as potential undescribed species in tropical Africa, with emphasis on those that span over the Albertine Rift, using a phylogenetic approach based on ITS, LSU, Tef1- $\alpha$ , and RPB2 and additional ecological and distributional data.

*Armillaria* collections from the Albertine Rift region (eastern DR Congo, Rwanda), Cameroon, Gabon, and São Tomé were sequenced, including an authentic collection of *A. camerunensis*. They were compared with sequences of specimens identified in previous studies and/or in GenBank as *A. camerunensis*, *A. fuscipes*, *A. heimii*, and *Armillaria* sp. (Table 5. 2).

The tropical African major clade is divided into two well-supported clades (Fig 5.4), as shown by Coetzee et al. (2005), who named these clades A and B. Clade A of Coetzee et al. (2000) included collections from South Africa, La Réunion, and Ethiopia. Coetzee et al. (2005) and Perez-Sierra et al. (2004) later on added collections from Kenya, Malawi, Zimbabwe, and Tanzania. Coetzee et al. (2000) and Gezahgne et al. (2004) initially considered clade A to represent *A. fuscipes*, distinct from *A. heimii*, a name attributed to clade B. Perrez-Sierra et al. (2004) argued that clade A and clade B represented two populations within the same species, named *A. heimii*. Coetzee et al. (2005), Pegler (1986) and Watling (1992) however considered *A. heimii* to be a synonym of *A. fuscipes*.

### ***Armillaria fuscipes* or *Armillaria heimii* in East Africa?**

*Armillaria fuscipes* has been regarded as the correct name for East African *Armillaria* collections corresponding to clade A (Coetzee et al. 2005; Coetzee et al. 2018; Koch et al. 2017). However, the very identity of *A. fuscipes* remains uncertain, as well as its relation to *A. heimii*, and its occurrence in Tropical Africa.

The type of *A. heimii* originated from Madagascar, Ambre mountain in 1935 (Heim 1937). *Armillaria fuscipes* was first described from Sri Lanka in a montane environment in the Central Province (Uda Pessellawa [currently Walapane Divisional Secretariat of Nuwara Eliya District, Central Province]) on a stump of *Acacia decurrens* Willd. (Mimosaceae) (Petch 1909). Petch later on (1944) provided more accurate data on the circumstance related to the discovery of the type specimen, which was collected at “Peradeniya (1560 ft.), where it was developed in a plant pot under a bell glass on an *Acacia* stump from an up-country district [Uda Pessellawa]”. *Acacia decurrens* is an exotic tree in Sri Lanka, originating from Central Australia, and extensively planted in tea plantations at high elevations (fide Pegler 1986).

The identity of *A. fuscipes* was much debated. Petch himself (1944) revised his concept of *A. fuscipes*. Based on a specimen identified as *A. mellea* and found on a stump in “the jungle” at Nuwara Eliya (now Nuwara Eliya District, Central Province) he (Petch 1944) came to the conclusion that *A. fuscipes* was the same as *A. mellea*.

Pegler (1986) noted that “it is extremely likely that *A. fuscipes* was introduced to the island with the expansion of the tea industry” but did not speculate on an hypothetical original distribution of *A. fuscipes*, notwithstanding that later authors (e.g., Kile and Watling 1988; Watling

1992) noted that Pegler (1986) had suggested that *A. fuscipes* was introduced into Sri Lanka from Africa.

Pegler (1986) reported that both macro- and micromorphological features of *A. fuscipes* were congruent to those of *A. heimii*, based on specimens from Tanzania and Uganda he studied earlier (Pegler 1977). Therefore, the two names were considered synonyms, with *A. fuscipes* taking nomenclatural priority (Pegler 1986; Watling 1992; Coetzee et al. 2005). Previously, Chandra and Watling (1981), however, examined the type of *A. fuscipes*, and hesitated in reducing both Pegler and Heim's names to synonymy. They also rejected the synonymy of *A. fuscipes* with *A. mellea* (Chandra and Watling 1981).

Ota et al. (2011) also revised the type specimen of *A. fuscipes*, which they compared with collections from southern Japan and concluded that they were morphologically closely related. They also showed that their taxon from subtropical Japan belongs, from a phylogeographic perspective, to an Australasian lineage (Ota et al. 2011). This taxon forms a clade together with some collections from Southeast Asia, including Indonesia, Malaysia, and Papua New Guinea, although with some genetic variations (Ota et al. 2011). It forms a sister clade to *A. novae-zelandiae*. This Southeast Asian clade is distant from the *A. fuscipes* clade *sensu* African authors (Coetzee et al 2000; Ota et al. 2011), which belongs to the African major clade. Ota et al. (2011) then suggested that *A. fuscipes* from Africa could be distinct from *A. fuscipes* s.s., as described by Petch (1909), and that their taxon from subtropical Japan remains undetermined, although morphologically affine to *A. fuscipes*.

Two historical *Armillaria* collections from Sri Lanka, represented by two cultures (CBS 109.29 / MUCL 58324 and CBS 110.29 / MUCL 58325), were incorporated into our dataset. Phylogenetic inference showed that they belong to two distinct major clades within *Armillaria*, neither of which is related to the African major clade (Fig. 5.4; Fig. 5.5). The isolates CBS 109.29 / MUCL 58324 clustered within an southeast Asian / Australasian lineage together with Japanese collections (#0013 and 0014, Fig. 5.5) from the Amami-Oshima region of southern Japan (Ota et al. 2011). MUCL 58324 / CBS 109.29 is the phylogenetic closest relative of the *Armillaria* species shown by Ota et al. (2011) to be morphologically related to *A. fuscipes*. MUCL 58324 / CBS 109.29 was isolated from a specimen growing on *Albizia lophanta*.

The strain CBS 110.29 / MUCL 58325, on the other hand, clustered within the melleioid major clade (Fig. 5.5). It is closely related to *A. cf. mellea* from southwestern subtropical China (Fig. 5.5). The ITS sequence of CBS 110.29 / MUCL 58325 is 100 % identical to the ITS sequence KT822251 of *Armillaria cf. mellea* from Yunnan, China; they may be considered as conspecific. CBS 110.29 / MUCL 58325 is also related to KT822253 from Guizhou, China. CBS 110.29 / MUCL 58325 was isolated from a specimen growing on *Camellia sinensis*.

Consequently, (at least) two distinct *Armillaria* species with two very distant biogeographical backgrounds coexist in Sri Lanka. However, it is not yet known which of these two strains, if any, might represent *A. fuscipes* s.s. A sequence of the type specimen has yet to be obtained, and the very circumscription of *A. fuscipes* cannot be determined.

Considering the hypothesis of Pegler (1986) that *A. fuscipes* was an exotic species introduced in Sri Lanka with the development of the tea industry, it could have been introduced with the tea or with exotic trees planted for windbreak and shadowing. Tea was mostly imported into Sri Lanka from Assam in Northern India, but shadowing trees are mostly Australian native Fabales including *Acacia decurrens* or *Albizia lophantha*, extensively planted in tea plantations around the 1870s, likely imported through seeds.

If introduced with Australian native trees such as *A. decurrens*, from its original distribution range, *A. fuscipes* should belong to an Australasian lineage. This is the case of the Sri Lanka strain CBS 109.29 / MUCL 58324, isolated in 1929 (or slightly before) from *A. lophantha*, and which belongs to a Southeast Asian - Australasian lineage. Nevertheless, within this lineage, CBS 109.29 / MUCL 58324 is more closely related to other Southeast Asian collections than to Australian collections (Fig. 5.5). This strain forms a well-supported clade with collections originating from southern Japan (Ota et al. 2011), Malaysia, and Papua New Guinea. These phylogenetic affinities indicate that CBS 109.29 / MUCL 58324 is closely related to, and perhaps conspecific with the *Armillaria* sp. shown by Ota et al. (2011) from southern Japan. It could also represent *A. fuscipes* s.s. Under this hypothesis, *A. fuscipes* should be considered to be native from Southeast Asia, including Sri Lanka.

The strain CBS 110.29 / MUCL 58325 clustered within the melleioid major clade (Fig. 5.5.) forming a well-supported clade with *A. cf. mellea* HKAS86590 and HKAS86597, both from southwestern China in Yunnan and Guizhou (Guo et al. 2016). The ITS sequence of CBS 110.29 / MUCL 58325 is 100% identical to the ITS sequence of

*A. cf. mellea* HKAS86590 from Yunnan. They may be conspecific. This species may well have been introduced into Sri Lanka from Northwestern India with tea. Tea was mostly introduced into Sri Lanka from Assam, in northeastern India (Wijetunga and Sung 2015).

DNA sequences of the type specimen of *A. fuscipes*, but also of other species described from Northern India (Chandra and Watling 1981) and further exploration of *Armillaria* in Sri Lanka, Northern India and, more generally, Southeast Asia, are needed to confirm these hypotheses.

Nonetheless, and importantly for our purposes, none of these two species identified in Sri Lanka is related to *A. fuscipes sensu* Auctores in Africa, nor are they related to the African lineage. Although CBS 109.29 / MUCL 58324 belongs to an Australasian lineage, it is also not closely related to the African collections nesting within this major lineage (Fig. 5.5 and Fig. 5.7).

If one excludes *A. fuscipes* in Tropical Africa, the next available name for the clade A would therefore be *Armillaria heimii*. The species was first described as *Clitocybe elegans*, from the "Ambre" mountain region of Madagascar (Heim 1937). Clade A is, for the time being, conservatively accepted as *A. heimii* s.l.

The phylogenetic analysis also shows that the *A. heimii* s.l. clade A is genetically diversified, with internal subclades (Fig. 5.4). Our results confirmed previous studies (Coetzee et al. 2000; Coetzee et al. 2005; Maphosa et al. 2006; Coetzee et al. 2018; Koch et al. 2021). In line with Coetzee et al. (2005), taxonomic status of subclades remain unclear. Further studies are necessary to specify which of the subclades would represent, if any, *A. heimii sensu stricto*. This would necessitate recollection in the type locality in Madagascar. It could be

hypothesized, for the time being, that specimens from the Mascarene Islands of La Réunion may represent the *A. heimii* s.s. However, specimens from La Réunion are dispersed into both subclades.

### ***Armillaria camerunensis***

It has been shown in the previous paragraphs that the African clade A (Fig. 4.4.) would represent *A. heimii sensu lato*. However, the identity of clade B also remains controversial.

In addition to the type collection from Madagascar, Heim (1963) reported collections of *Clitocybe elegans* from Cameroon and the Ivory Coast. Coetzee et al (2000) therefore considered their clade B, including the Cameroon specimens, *A. heimii*. However, Perez-Sierra et al. (2004) interpreted the same data differently, and concluded that clade B and clade A represent two populations within *A. heimii*. Coetzee et al. (2005) and Koch et al. (2017) later suggested that clade B represents an unknown species, which Koch et al. (2017), conservatively, related to *A. camerunensis* (collections TH 9926 and TH DJA 91).

*Armillaria camerunensis* is based on *Armillaria mellea* var. *camerunensis*, which was described on the basis of two collections by the Swedish botanist P. Dusén: Cameroon, Bomana region, 670 masl, P. Dusén n°1a, 19 July 1892 and N'dian, P. Dusén 39a (Hennings 1895/1897<sup>1</sup>). The specimen P. Dusén n°1a is the original type (Hennings 1895/1897; Watling 1992). The Dusén 39a specimen is mentioned only in some additional comments. However, specimen P.

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<sup>1</sup> It is unclear to us if the publication dates from 1895 or 1897. Index fungorum reports a publication in 1895, but the periodical mentions 1897.

Dusén no. 1a was not found by Hein (1988) in B, and was probably lost in the fire at the Berlin herbarium during the Second World War (fide Watling 1992). It is likely the case also of the specimen P. Dusén 39a although this should be ascertained. Later on, Hennings labeled under *A. camerunensis* (handwritten note, fide Watling 1992) a specimen from Cameroon, referenced "Zenker 2165" (Bipinde, south Cameroon, 1900s). A duplicate of this collection is housed at E and was studied by Watling (1992).

Var. *camerunensis* was first raised to the species rank by Singer (1986) as *Armillariella camerunensis* (Henn.) Singer. However, *Armillariella* (P. Karst.) P. Karst. (1881) is a synonym of *Armillaria* (Fr.) Staude (Watling et al. 1982). It is Courtecuisse (1995) that proposed the nowadays accepted recombination in *Armillaria* as *Armillaria camerunensis* (Henn.) Courtecuisse, on the basis of a collection "Coll. Y. Ankei All, Ngoli village, Kindu Maniema, DRC, 5th sept. 1990".

In the present study, an ITS sequence was obtained from the historical, authentic specimen "Zenker 2165" (E!). This specimen nested within our clade B (Fig. 5.4.), together with collections from the Ruwenzori foothills, Cameroon, Gabon and Sao Tomé. Clade B is therefore equated with *A. camerunensis*.

"Zenker 2165", which is an authentic specimen, could be designated as the neotype of *A. mellea* var. *camerunensis*. However, it would be preferable to select a recent collection for which a living strain and a set of sequences exist.



Figure 5.6: *Armillaria camerunensis*. a: Collection RHJ 237 (0.348477 N, 29.773154 E, 1626 masl); b1 and b2: Collection RHJ 228 (0.443474 N, 29.727159 E, 966 masl). Scale bar: 2.2 cm

Two collections from Kenya, CMW 15584 and CMW 15585, collected from tea plantations (*Camellia sinensis*) and published by Mwenje et al. (2006) and Pildain et al. (2009) are uncertain. Pildain et al. (2009) reported ITS sequences, but the GenBank accession number given corresponds to an IGS sequence. These IGS sequences are related to other sequences from specimens clustered within an Australasian lineage, next to *A. hinnulea* (Mwenje et al. 2006). In contrast, their LSU sequences (Pildain et al. 2009) were 100% identical to the 28S sequences of two specimens from Zimbabwe, CMW 4456 and CMW 10115, both clustering within the African major clade.

The fact that the IGS and LSU sequences from these collections belong to very distant lineages suggests that there are errors in the sequences deposited in GenBank.

The following description of *A. camerunensis* is based on an updated description adapted from Hennings (1895), Courtecuisse (1995), Koch et al (2017), and some of our collections:

#### Description

*Basidiomata* cespitose, small to medium-sized (Fig. 2A, B). *Pileus* 10–60 mm diam., convex to plano-convex, becoming applanate and depressed, with (or without) a small obtuse umbo; surface dull, dry, dark brown, (6F8) becoming lighter brown (5C5-5C4) to almost cream at the margin (5A2-5A3). *Margin* decurved to sometimes uplifted in age, centrally dark brown (6F8). *Context* ~5 mm thick, thinning evenly to ~0.5 mm at margin off-white.

Lamellae adnexed, thick, crowded, not forking, cream (4A2-5A2), becoming light brown with age; edges entire, brown (5C5), unequal, (16 (L+I) / cm), with 2–4 series of lamellulae, lamellulae typically 3 per lamellae (one long in-between two short), occasionally 2 to 4, rarely up to 8, corresponding to marginal striations above.

Stipe central to slightly eccentric, terete, subclavate to bulbous, 10–65 (–73) mm long, 3–6 mm broad, dark gray-brown (8F3), becoming lighter towards the apex (5C4-5C5) longitudinally striate, upper third covered with erect fibrillose off-white tufts.

Annulus well-developed, persistent, occurring 5–10 mm below stipe apex, protruding 2–3 mm from stipe, 1–5 mm thick, membranous, off-white, upper side densely tomentose, lower side covered with brown tufts, margin irregularly enrolled. Stipe context off-white, becoming darker towards base, solid.

*Odor* fungoid, *taste* not tested. *Spore print* white

*Hyphal system* monomitic, composed of generative hyphae with clamp connections in all tissues.

*Pileipellis* consisting of a *subpellis* of hyphae 6–18 µm wide, thin-walled, branching, septate, hyaline, which blend into aggregations of brown to hyaline, verrucose, ellipsoid to clavate cells of the *suprapellis*, 20–100 × 8–35 µm, intermixed with filamentous units. *Stipitipellis hyphae* 5–22 µm wide, hyaline, septate. *Pileus squamules* composed of subcatenulate, rarely encrusted hyphae, 5–10 µm diam. *Pileitrama* made up of interwoven hyaline, smooth, thin- to slightly thick-walled, hyphae, 2.5–7 µm diam. *Lamellar trama* similar to pileitrama.

*Basidia* 28–35 × 7.5–10 µm (mean = 31.7 ± 2.4 × 8.5 ± 0.6 µm; n = 30), clavate, with four sterigmata, sclerified, clamp connection absent at the base. *Basidiospores* inamyloid, thick walled, 6–9.0 (9.3) × (4.5) 5.2–6.4 (7) µm (mean = 7.7 × 6.0, Q<sub>r</sub> = 1.1–1.6, Q<sub>m</sub> = 1.3). *Cheilocystidia* resembling basidioles, abundant, 18–31 × 5–7 µm, mostly clavate, some lageniform, hyaline. *Pleurocystidia* not observed

### ***Armillaria mellea* and *Armillaria mellea* subsp. *africana***

The name *Armillaria mellea* subsp. *africana*, attributed to Kenyan collections K6 (CMW 15586) and K7 (CMW 15587), has been proposed as an African subspecies of temperate *A. mellea* (Kile et al. 1994; Mohammed and Guillaumin 1993; Chillali et al. 1997). However, *A. mellea* subsp. *africana* has never been officially proposed and is not listed in Index Fungorum (<https://www.indexfungorum.org/Names/Names.asp>). The name is not to be considered.

Several of the Kenyan *Armillaria* sequences added to our dataset clustered into the African major clades. The Kenyan group I

named *A. fuscipes* (Mwenje et al. 2006) and the isolate K59 (this study) belong to *A. heimii* sensu lato.

Other Kenyan collections HKAS 86600, HKAS 86598 (Guo et al. 2016) clustered in the melleioid major clade together with *A. mellea* subsp. *nipponica* (Japan, HKAS86588), CBS 110.29 (present study) from Sri Lanka, and several collections from southwestern China. This topology is similar to that of Mwenje et al. (2006) and Guo et al. (2016). Kenyan isolates K6 and K7, corresponding to Kenyan Group II sensu Mwenje et al. (2006), on which the name *A. mellea* subsp. *africana* was cited (Mohammed and Guillaumin 1993), are proposed to be conspecific with Kenyan isolates HKAS 86600, HKAS 86598 in our phylogeny and in Guo et al. (2016). The strain *A. mellea* subsp. *nipponica* (Japan, HKAS86588), the southern chinese isolates (HKAS 86592) and the Kenyan isolates (HKAS 86600, HKAS 86598) are homothallic (Guo et al. 2016).

The close phylogenetic affinities of several Kenyan isolates of the melleioid major clade with strains from southwest China (DF1) and Japan (HKAS86588 strain) and their homothallism support the hypothesis of human introduction from East Asia, as suggested previously (Ota et al., 2000; Guo et al., 2016; Coetzee et al., 2018; Koch et al., 2021). Ota et al (2000) suggested that a migration of this species from Japan or another Asian country was associated with the introduction of exotic plants such as tea.

The *Armillaria mellea* cluster shows considerable intraspecific variation. Differences are observed in their sexual systems, with homothallic forms occurring in Africa, China and Japan.

***Armillaria* sp. (South American-Australasian super clade)**

The third African clade is made by several specimens originating from mountain forests of Western Rwanda and from Kenya. The collection Kenya PIII87.9 belongs to the same clade, whereas two other Kenyan collections (PIII87.42 and PIII87.5) nested in a basal position. These specimens clustered within an Australasian clade, sister to the *A. hinnulea* clade that is known only from Australia and Tasmania (Smith-White et al. 2002; Koch et al. 2017). Mwenje et al. (2006) previously identified this clade as Kenyan III (CMW15584; CMW15585) based on Kenyan collections. The clade is found at higher altitudes (> 2000 masl). It constitutes an independent clade and may represent an undescribed species.



As for *A. mellea*, the most likely hypothesis is one or more introduction events in Africa with exotic plants from Australia.

### **Morphology (morphological species concept) and Biology (Biological species concept)**

Macro- and micromorphological analysis carried out in this study did not reveal any critical distinguishing criteria between *A. heimii* and *A. camerunensis* collections. The comparison of basidiospores size ranges prove to be inoperant in distinguishing the two species (Fig. 5.8).

Previous studies have shown that morphological characters are less useful for species identification due to the low interspecific variation within African *Armillaria* (Chillali et al. 1997).

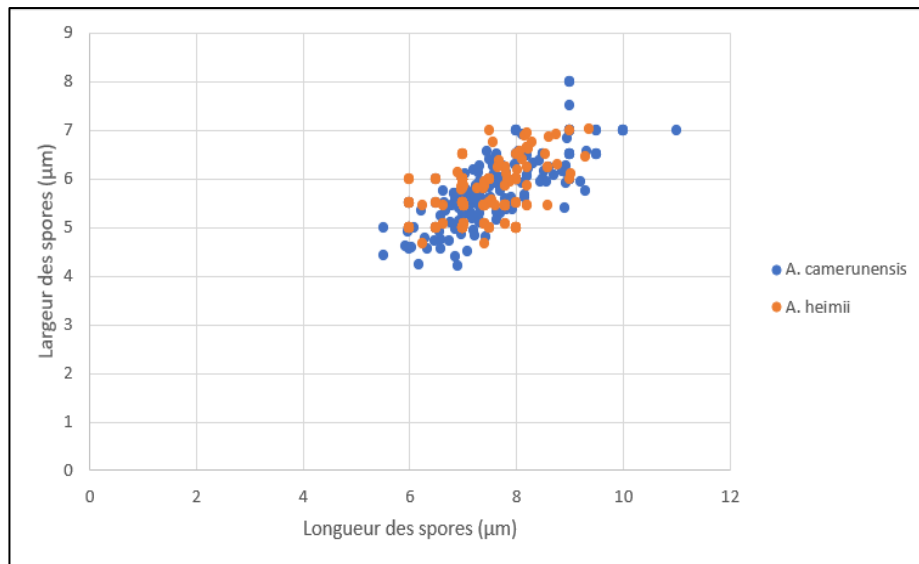


Figure 5.8: Graphical comparison of spore size in specimens identified as *A. camerunensis* (blue dots) and *A. heimii* (orange dots)

The use of morphological criteria to define *A. heimii* and *A. camerunensis* has led to confusion. Heim (1963) reported *Clitocybe*

*elegans* (*A. heimii*) in the lowland rainforest of Cameroon on the basis of morphology. We suggest that this was *A. camerunensis*. Courtecuisse (1995) suggested that striate spores in *A. camerunensis* could be a distinguishing feature. We have re-examined the authentic specimen (Zenker 2165) and found no striate spores (Fig 5.9.).

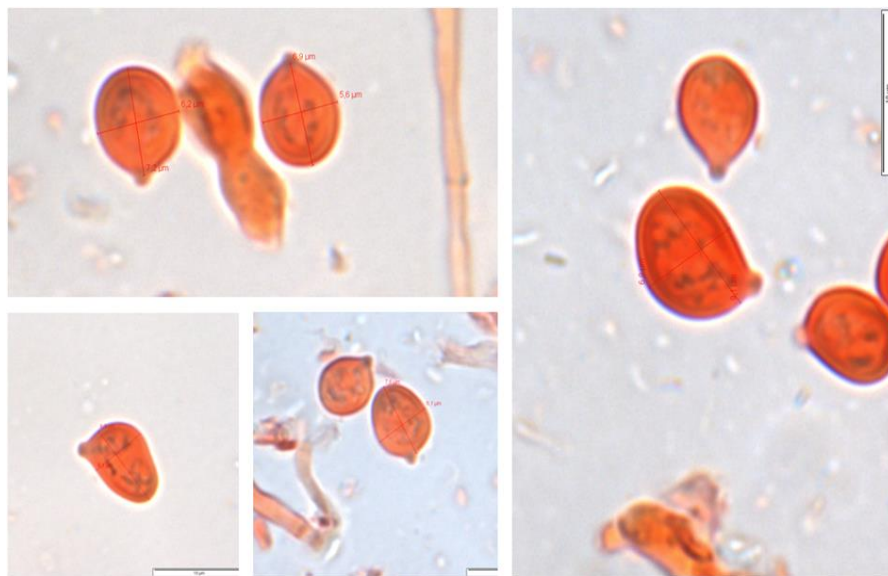


Figure 5.9: *Armillaria camerunensis* basidiospores extract on specimen “Zenker 2165” © Mario Amalfi

According to the sexual status assigned to some isolates in previous studies and included in our phylogeny, *A. heimii* s.l. would include both heterothallic (unifactorial) and homothallic individuals (Table 5.4). Some isolates (e.g. CMW 4456; 167 and 173) that were also reported as homothallic in previous studies (Abomo-Ndong et al. 1997) were nested within the *A. camerunensis* clade, although the latter was assumed to be heterothallic based on previous literature (Augustian et al. 1994; Perez-Sierra et al. 2004).

Table 5.4: Sexual system in heimii and camerunensis clades

| <i>Name</i>            | <b>N°</b> | <b>Other n°</b> | <b>Origin</b>           | <b>SS</b>     | <b>Ref</b>               |
|------------------------|-----------|-----------------|-------------------------|---------------|--------------------------|
| <i>A. camerunensis</i> | CMW 4456  | Z1              | Zimbabwe                | Homothallic   | Coetzee et al. 2005      |
| <i>A. camerunensis</i> | 173       | PHo 99 6        | Congo                   | Homothallic   | Pérez-Sierra et al. 2004 |
| <i>A. camerunensis</i> | 167       | PHo 87 45       | Uganda                  | Homothallic   | Pérez-Sierra et al. 2004 |
| <i>A. heimii</i>       | CMW 3164  | LR3             | Saint-Denis/ La Reunion | Homothallic   | Coetzee et al. 2005      |
| <i>A. heimii</i>       | CMW 4953  | LR2             | La Reunion              | Homothallic   | Coetzee et al. 2005      |
| <i>A. heimii</i>       | CMW 4871  | M1              | Malawi                  | Homothallic   | Coetzee et al. 2005      |
| <i>A. heimii</i>       | CMW 4873  | M3              | Malawi                  | Homothallic   | Coetzee et al. 2005      |
| <i>A. heimii</i>       | CMW 4950  | T2              | Tanzania                | Homothallic   | Coetzee et al. 2005      |
| <i>A. heimii</i>       | CMW 4949  | T1              | Tanzania                | Homothallic   | Coetzee et al. 2005      |
| <i>A. heimii</i>       | CMW 4874  | Z2              | Zimbabwe                | Homothallic   | Coetzee et al. 2005      |
| <i>A. heimii</i>       | 168       | PHo 87 36       | Zimbabwe                | Homothallic   | Pérez-Sierra et al. 2004 |
| <i>A. heimii</i>       | 166       | PHo 87 24       | Reunion                 | Homothallic   | Pérez-Sierra et al. 2004 |
| <i>A. heimii</i>       | 170       | K59             | Kenya                   | Heterothallic | Pérez-Sierra et al. 2004 |
| <i>A. heimii</i>       | 174       |                 | Kenya                   | Heterothallic | Pérez-Sierra et al. 2004 |
| <i>A. mellea</i>       | HKAS86600 |                 | Kenya                   | Homothallic   | Guo et al. 2016          |
| <i>A. mellea</i>       | HKAS86598 |                 | Africa                  | Homothallic   | Guo et al. 2016          |
| <i>A. mellea</i>       | HKAS86599 |                 | Kenya                   | Homothallic   | Guo et al. 2016          |

Sexual compatibility tests have been widely used to delimit temperate *Armillaria* species. However, these tests were found to be less efficient in defining African *Armillaria* species, as isolates with different sexual systems were found to nest within the same clade. In addition, isolates from different clades (clades heimii and camerunensis) were reported to be compatible (Perez-Sierra et al. 2004; Coetzee et al. 2005). Therefore, from a biological species concept, *A. camerunensis* and *A. heimii* were reported to represent distinct populations within a single species (Perez-Sierra et al. 2004; Coetzee et al. 2005). Somatic incompatibility tests showed similar results. The

ability to interbreed could therefore be attributed to a retained ancestral trait.

Biological testing has some limitations in tropical Africa, such as lack of test strains, haploid isolates and degeneracy of cultures. In addition, homothallic strains cannot be used for sexual compatibility testing due to the lack of a haploid stage (Coetzee et al. 2005). However, at the species level, only the sexual compatibility test is recommended to highlight reproductive isolation. Sexual compatibility requires the production of a fertile basidiome and is only possible between heterothallic species. Furthermore, the results of mating interactions are sometimes ambiguous.

It is for these reasons that DNA-based methods have been the preferred method for the taxonomy of *Armillaria* (Jayawardena et al. 2020). For the future, we suggest more in-depth studies of sexuality within *A. camerunensis* s.s. and *A. heimii* s.l.

## 5.6. Conclusion

Our results confirm previous results (Coetzee et al. 2005; Mwenje et al. 2006; Coetzee et al. 2011; Koch et al. 2017; Coetzee et al. 2018; Koch et al. 2021) and showed the African *Armillaria* to be distributed over several clades. The majority of the specimens from natural environments formed a native African major lineage. Several collections, mostly originating from anthropogenic habitats, clustered into the melleioid and an Australasian lineage, suggesting human-mediated introductions respectively from eastern Asia and from Australia. This study has established that *A. fuscipes* is not native to Africa, and does not occur in Africa.

The main indigenous African lineage is subdivided into two clades A and B. Geographically, these two clades illustrate the dichotomy between West (B) and East Africa (A) or, in a more relevant biogeographical scheme, a distinction between the lowland Guinean-Congolian rainforest, home to *A. camerunensis* (clade B) and the eastern highlands, home to *A. heimii* s.l. (clade A).

*Armillaria camerunensis*, as accepted here, is found westwards from the equatorial island of Sao Tomé to the foothills of the Rwenzori in Congo DRC eastward, mostly in the Guinea-Congolian region of central Africa. The species may also occur in dense forest areas in West Africa; Heim (1963) indeed reported a collection of *Clitocybe elegans* from the Ivory Coast, that may well represent *A. camerunensis*. This should be ascertained once additional collections and sequences become available. Several collections from Zimbabwe are more problematic in terms of habitat, but few data are available concerning these collections.

*Armillaria heimii* s.l. (clade A) comprises collections from East Africa, both continental and insular. It includes the Albertine Rift in the DRC and Rwanda, and specimens from the Gregorian Rift including Ethiopia, Kenya, Tanzania, South Africa, Zimbabwe, the Mascarene islands of Reunion, and Madagascar. All our *Armillaria* specimens from the montane forests of the Albertine Rift recorded in eastern Democratic Republic of Congo and western Rwanda (alt > 1800 m) have been grouped in clade A, *A. heimii* s.l.

Both species occur sympatrically in the submontane forest range sensu Lebrun (1957) (transitional forest between Guineo-Congolian and montane forests) covering the Rwenzori foothills, which extends between 1150 and 1750 masl. This is exemplified by *A. heimii* (RHJ

166, and 233) and *A. camerunensis* (RHJ 228), both recorded at neighbouring sites ~1000 masl and ~1700 masl (RHJ 237: *A. camerunensis* and RHJ 117: *A. heimii*). Locally, this may represent the lower limit of *A. heimii* and the upper limit of *A. camerunensis*. This clade is rather genetically homogeneous, except for three collections from Gabon and São Tomé.

## Chapter 6: Revision of African *Laetiporus*

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Adapted from

**Jean-Claude Rizinde Hakizimana, Mario Amalfi, Alphonse Balezi, and Cony Decock. (2023). *Laetiporus* (Laetiporaceae, Basidiomycota) is represented by a single Afromontane lineage and four species in Tropical Africa, including *Laetiporus discolor*, *Laetiporus oboensis* sp. nov., *Laetiporus tenuiculus* sp. nov., and *Laetiporus* sp. 1.**

Submitted Manuscript, Mycologia

## 6.1. Abstract

The tropical African *Laetiporus* species are revised, based on morphological, ecological, distribution, and phylogenetic data. *Laetiporus discolor*, originally described from insular Mauritius, is accepted for the species spanning over the African eastern mountain range. *Laetiporus oboensis* and *Laetiporus tenuiculus* are described as new from the African equatorial insular São Tomé, based on phylogenetic, morphological, and distribution data. *Laetiporus oboensis* is characterized by compound basidiomes, with densely imbricated pilei in pale orange tint, a lobed margin, 3–4 pores / mm, and basidiospores averaging  $4.8 \times 3.7 \mu\text{m}$ . *Laetiporus tenuiculus* has mostly solitary, small, thin basidiomes, with pale flesh to pale orange pileus, an incised margin, 4–5 pores / mm, and basidiospores averaging  $5.4 \times 4.2 \mu\text{m}$ . A fourth species, known from two isolates from Ethiopian highlands, but for which voucher specimens were not available for description, is uncertain. These four species form an African endemic lineage, whose distribution is afro-mountainous.

Keywords – Afromontane ranges, Mycology, Phylogeny, Tropical Africa.

## 6.2. Introduction

*Laetiporus* Murrill (1904) (Laetiporaceae, Basidiomycota, Han et al. 2016, Justo et al. 2017) is typified by *L. sulphureus* (Murrill 1904; Singer 1944). The genus remained little studied for about a century, however, and almost exclusively based on the presumed widely distributed *L. sulphureus* (e.g, Bourdot and Galzin 1928; Overholts 1953; Gilbertson and Ryvarden 1986; Ryvarden and Gilbertson 1993; Ryvarden and Johansen 1980). Nonetheless, Overeem (1925) proposed a detailed monograph of the southeast Asian *Laetiporus miniatus* (Jungh.) van Overeem. Imazeki and Hongo (1968) also considered the name *L. versisporus* for specimens from Japan, whereas Corner (1984) accepted *L. discolor*, and declined it into three varieties in South-East Asia.

Nevertheless, it was not until the end of the twentieth century that the species concept of *L. sulphureus* was questioned, both in Europe and North America (Banik et al. 1998; Banik and Burdsall 1999; Rogers 1999; Burdsall and Banik 2001). Using both genetic and sexual compatibility data, complemented by morphological and ecological features, six species were documented in North America, including three by then undescribed taxa, and one variety (Banik et al. 1998; Banik and Burdsall 1999; Burdsall and Banik 2001). Subsequently, the genus has been continuously surveyed in Europe, Eastern Asia, and Meso-America, considering morphological, ecological, and DNA-based phylogenetic evidences (Tomšovský & Jankovský 2008; Ota et al. 2009; Banik et al. 2010; Banik et al. 2012; Song et al. 2014; Pires et al. 2016; Song and Cui 2017; Song et al. 2018; Kout et al. 2019; Campi et al. 2022; Paez et al. 2022).

Song and Cui (2017) proposed the first comprehensive multilocus phylogeny of *Laetiporus*, showing clade support for at least seventeen phylogenetic species, of which 11 were named and six unnamed, and 4 well-supported lineages (I-IV). Song et al. (2018) showed later on statistical support for nineteen species-level clades. They described the clade P of lineage III (Song and Cui 2017) as *L. medogensis* and added *L. xinjiangensis*. Kout et al. (2019) described the clade L of group II (Song and Cui 2017) as *Laetiporus lobatus*, a Neotropical species. Santos et al. (in Crous et al. 2023) also added *L. pratigiensis* from montane Atlantic forest in Brazil. Campi et al. (2022) have also added *Laetiporus dilatohyphus*, a species distinguished from all other *Laetiporus* by a resupinate basidiome and a monomitic hyphal system. Liu et al. (2023) accepted this species as *Wolfiporiella dilatohypha* (Ryvarden & Gilb.) B.K. Cui & Shun Liu.

Sixteen *Laetiporus* species are then currently named and several phylogenetic species remain yet unnamed in the Linnean scheme. *Laetiporus sulphureus* in North America and Eurasia (*L. sulphureus* s.l.), *L. gilbertsonii* in Meso- and South America, and *L. versisporus* in East Asia were shown to represent species complexes, with a higher than expected phylogenetic and, ahead, taxonomic diversity (Song and Cui 2017; Song et al. 2018; Campi et al. 2022).

In Tropical Africa, *Laetiporus* remains little known. Ryvarden and Johansen (1980) first reported only *L. sulphureus*, whereas Ryvarden et al. (2022) reported *L. baudonii*, *L. discolor*, and *L. persicinus*. However, *L. baudonii* was shown to be affine to *Piptoporellus* B.K. Cui, M.L. Han & Y.C. Dai (*Fomitopsidaceae*, Han et al. 2016), forming an independent lineage (Tibhuwa et al. 2020); hence, the recombination *Piptoporellus baudonii* (Pat.) Tibuhwa, Ryvarden & S. Tibell was

proposed. Nonetheless, Tibhuwa et al. (2020) overlooked the fact that *L. baudonii* is also the type species of *Pseudophaeolus* Ryvarden (Ryvarden in Ofosu-Asiedu 1975). Hence, *Pseudophaeolus* (1975) has priority over *Piptoporellus* (2016) and the correct name for this species is *Pseudophaeolus baudonii*. On the other hand, the African specimens of *L. persicinus* (a species originally described from south-eastern USA, Berkeley and Curtis 1872) were shown to represent a distinct species in its own genus, *Kusaghiporia usambarensis* (Hussein et al. 2018). This species is affine to the Neotropical *K. talpae* (Cooke) Campi et al. (Campi et al. 2022). *Kusaghiporia* belongs to the Laetiporaceae (Hussein et al. 2018).

Therefore, *L. discolor* is the sole Tropical African *Laetiporus* to date. Its identity remains questionable, however. The species was described originally from the Mascarene island of Mauritius, east of Madagascar. Ryvarden (1976) noted that the type represents a pale, sterile specimen of *L. sulphureus*. Ota et al. (2009) also stated that the type is sterile, and published a brief description of what is left of it. Corner (1984) considered the species in south-eastern Asia, which he declined into four southeast Asian varieties. However, he (Corner 1984) did not describe *L. discolor* s.s. (var. *discolor*). Banik et al. (2010), Song and Cui (2017), and Song et al. (2018) showed a clade (clade H, Banik et al. 2010, Song and Cui 2017), which voucher specimens originated from South Africa, but that was left unnamed.

As part of an ongoing survey of polypores (Basidiomycota) in sub-Saharan Africa (Decock 2001, 2007, 2011; Decock and Mossebo 2001, 2002; Decock and Ryvarden 2002; 2015, Decock and Masuka 2003; Decock et al. 2011; Decock and Bitew 2012; Decock et al. 2021, 2022; Ryvarden et al. 2022; Kouagou Yayoro et al. 2023), the type specimen

of *L. discolor* was revised, together with original collections of *Laetiporus* from both insular and continental Tropical Africa. Their affinities were inferred also using phylogenetic inferences based on multilocus DNA sequence data, including the nuclear ribosomal ITS (ITS1–5.8S–ITS2), the 5' end of the 28S, translation elongation factor 1- $\alpha$  (*tef1- $\alpha$* ), and DNA-directed RNA polymerase II subunit 1 (*rpb2*).

As a result of these studies, *L. discolor* is redescribed, and considered as an Eastern African species. Three additional species clades are shown, of which two are interpreted representing undescribed taxa. They are proposed and described as *Laetiporus oboensis* and *L. tenuiculus*. The third clade, *Laetiporus* sp. 1, is left unnamed due to lack of voucher specimens. Their phylogenetic affinities and distributions are discussed.

### 6.3. Material and methods

**Material and collection localities.**— African specimens originate from the Mount Elgon range, Kenya; the Virunga, Kahuzi-Biega and Ruwenzori Mountain ranges, eastern Democratic Republic of Congo; Kibale National Park, western Uganda; and Ôbo de São Tomé National Park, São Tomé. The specimens are preserved at BR and MUCL (acronyms according to Thiers (Thiers 2016, continuously updated, <http://sciweb.nybg.org/science2/IndexHerbariorum.asp>).

**Description.**—Colours are described according to Kornerup and Wanscher (1981). Sections were carefully dissected under a stereomicroscope and examined in Melzer's reagent and lactic acid Cotton blue to show staining reaction. All the microscopic measurements were done in Melzer's reagent. In presenting the size range of several microscopic elements, 5% of the measurements at each

end of the range are given in parentheses when relevant. In the text, the following abbreviations are used: av. = arithmetic mean, R = the ratio of length/width of basidiospores, and av<sub>R</sub> = arithmetic mean of the ratio R.

***Molecular study and phylogenetic analysis.***—DNA extraction, amplification and sequencing of the 5' end of the nuclear ribosomal LSU rDNA gene, (region including the domains D1–D3), the ITS-5.8S regions, partial *tef1-α* gene, and the region between domains 6 and 7 of the second largest subunit of the *rpb2* gene were as described in Frøslev et al. (2005), Matheny (2005), and Amalfi and Decock (2013). Materials and sequences used in this study are listed in table 6.1. Successful PCR reactions resulted in a single band observed on a 0.8% agarose gel. PCR products were purified by adding 1 U of Exonuclease I and 0.5 U FastAP Alkaline Phosphatase (Thermo Scientific, St. Leon-Rot, Germany) and incubating at 37 °C for 1 h, followed by inactivation at 80 °C for 15 min. All the sequencing reactions were performed by MacroGen Inc. (Korea and The Netherlands), with primers LROR, LR3, LR3R, LR5 for the LSU region; ITS1, ITS4 for the ITS-5.8S region, 2212R, 1577F, 983F, 1567R for *tef1-α* gene (Rehner and Buckley 2005; Matheny et al. 2007); and bRPB2-6F and bRPB2-7.1R for *rpb2* gene (Matheny 2005). Sequences were assembled and edited with Sequencher™ 4.8 software (Gene Codes Corporation, Ann Arbor, MI, U.S.A.). Based on BLAST results (BLAST searches done on 14/06/2022), a combined dataset (nuclear ribosomal LSU rRNA gene and ITS regions (including 5.8S) and of partial *tef1-α* and *rpb2* genes) comprising sequences from 146 collections (including the outgroup) was constructed and used for further phylogenetics analyses. *Wolfiporiella dilatohypha* (Ryvarden & Gilb.) was chosen as outgroup following the results in Song and Cui (2017).

Table 6.1: List of species, collections, and sequences used in the phylogenetic analyses

| Genus / Species names                                                 |                 | GenBank accession number |                   |                   |                   |  |
|-----------------------------------------------------------------------|-----------------|--------------------------|-------------------|-------------------|-------------------|--|
| Voucher specimens / cultures reference                                |                 |                          |                   |                   |                   |  |
|                                                                       | Locality        | nLSU                     | ITS               | <i>tefl-a</i>     | rpb2              |  |
| <i>Laetiporus ailaoshanensis</i> B.K. Cui & J. Song 2014              |                 |                          |                   |                   |                   |  |
| HKAS 52508 (T)                                                        | Southwest China | NG_059499                | NR_154610         | -                 | -                 |  |
| HKAS 53092 (PT)                                                       | Southwest China | KF951318                 | KF951288          | -                 | -                 |  |
| Dai 13256                                                             | Southwest China | KF951317                 | KF951289          | KT894786          | KT894786          |  |
| Dai 15629                                                             | Southwest China | KY886740                 | KY886714          | KY886781          | KY886795          |  |
| Yuan 3302                                                             | Southwest China | KF951316                 | KF951286          | -                 | KT894787          |  |
| <i>Laetiporus caribensis</i> Banik & D.L. Lindner 2012                |                 |                          |                   |                   |                   |  |
| CFMR PR-6583 (T)                                                      | Puerto Rico     | -                        | NR_119999         | -                 | -                 |  |
| PR6521                                                                | Guadeloupe      | -                        | JN684771          | -                 | -                 |  |
| PR914                                                                 | Puerto Rico     | -                        | JN684762          | -                 | -                 |  |
| <b>MUCL 46022<sup>s,h</sup></b>                                       | <b>Cuba</b>     | <b>This study</b>        | <b>This study</b> | <b>This study</b> | <b>This study</b> |  |
| <i>Laetiporus cincinnatus</i> (Morgan) Burds., Banik & T.J. Volk 1998 |                 |                          |                   |                   |                   |  |
| JV 0709/168-J                                                         | USA             | KF951305                 | KF951290          | KX354606          | KT894789          |  |
| CFMR: DA-37                                                           | USA             | EU402521                 | KU668950          | AB472661          | -                 |  |
| Dai 12811                                                             | USA             | KF951304                 | KF951291          | KX354605          | KT894788          |  |
| <i>Laetiporus conifericola</i> Burds. & Banik 2001                    |                 |                          |                   |                   |                   |  |
| JV 0709/81-J                                                          | USA             | KF951327                 | KF951292          | -                 | KX354683          |  |
| CA 8-2                                                                | USA             | EU402523                 | AB472631          | AB472663          | -                 |  |
| Jam 1-12                                                              | USA             | EU402524                 | AB472632          | AB472664          | -                 |  |
| <i>Laetiporus cremeiporus</i> Y. Ota & T. Hatt. 2010                  |                 |                          |                   |                   |                   |  |
| Cui 10586                                                             | China           | KF951297                 | KF951277          | KX354602          | KX354648          |  |
| Cui 10586b (clone)                                                    | China           | KF951297                 | KJ480734          | KX354602          | KX354648          |  |
| Cui 10988                                                             | China           | KF951299                 | KF951278          | -                 | -                 |  |
| Cui 10988b (clone)                                                    | China           | KF951299                 | KJ480739          | -                 | -                 |  |
| Cui 10991                                                             | China           | KF951298                 | KF951279          | KX354641          | KX354679          |  |

|                                                                  |            |            |            |            |            |
|------------------------------------------------------------------|------------|------------|------------|------------|------------|
| Dai 10045                                                        | China      | KF951300   | KF951280   | -          | -          |
| Dai 10107                                                        | China      | KF951301   | KF951281   | KX354604   | KX354650   |
| <i>Laetiporus discolor</i> (Klotzsch) Comer 1984                 |            |            |            |            |            |
| CD_KE16_199                                                      | Kenya      | This study | This study | This study | This study |
| CD_CO08_25                                                       | RDC        | This study | This study | This study | This study |
| CD_CO08_29                                                       | RDC        | This study | This study | This study | This study |
| CD_CO_22_442                                                     | RDC        | This study | This study | This study | This study |
| MUCL 49955 <sup>c,h</sup>                                        | RDC        | This study | This study | This study | This study |
| MUCL 49988 <sup>c,h</sup>                                        | RDC        | This study | This study | This study | This study |
| MUCL 55532 <sup>c,h</sup>                                        | Kenya      | This study | This study | This study | This study |
| MUCL 55534 <sup>c,h</sup>                                        | Kenya      | This study | This study | This study | This study |
| MUCL 55532 <sup>c,h</sup>                                        | Kenya      | This study | This study | This study | This study |
| MUCL 56026 <sup>c,h</sup>                                        | Kenya      | This study | This study | This study | This study |
| MUCL 56066 <sup>c,h</sup>                                        | Kenya      | This study | This study | This study | This study |
| MUCL 57392 <sup>c,h</sup>                                        | Kenya      | This study | This study | This study | This study |
| MUCL 57744 <sup>h</sup>                                          | Kenya      | This study | This study | This study | This study |
| RHJ273                                                           | RDC        | This study | This study | This study | This study |
| <i>Laetiporus gilbertsonii</i> Burds. 2001                       |            |            |            |            |            |
| JV 1109/31                                                       | USA        | KF951306   | KF951293   | KX354630   | KX354671   |
| CA-13-1                                                          | USA        | EU402527   | AB472637   | AB472666   | -          |
| <i>Laetiporus gilbertsonii</i> var. <i>pallidus</i> Burds. 2001  |            |            |            |            |            |
| FP150268                                                         | Jamaica    | EU402529   | EU402552   | -          | -          |
| TJV2000-101                                                      | USA        | EU402528   | EU402553   | AB472668   | -          |
| <i>Laetiporus huroniensis</i> Burds. & Banik 2001                |            |            |            |            |            |
| MI14 (T)                                                         | USA        | EU402539   | EU402573   | AB472672   | -          |
| HMC-1-3                                                          | USA        | KX065985   | AB472641   | AB472670   | -          |
| <i>Laetiporus lobatus</i> J. Vlasák, J. Kout & D.L. Lindner 2019 |            |            |            |            |            |
| CFMR Núñez 207 (T)                                               | Costa Rica | -          | JN684764   | -          | -          |
| JV1704_52_1 (PT)                                                 | Costa Rica | -          | MK098490   | -          | -          |
| JV1704_52_2 (PT)                                                 | Costa Rica | -          | MK098491   | -          | -          |

*Laetiporus medogensis* J. Song & B.K. Cui 2018

|                |       |          |          |          |          |
|----------------|-------|----------|----------|----------|----------|
| Cui 12240 (T)  | China | KX354501 | KX354473 | KX354627 | KX354668 |
| Cui 12390 (PT) | China | KX354502 | KX354474 | KX354628 | KX354669 |
| Cui 12219 (PT) | China | KX354500 | KX354472 | KX354626 | KX354667 |

*Laetiporus montanus* Černý ex Tomšovský & Jankovský 2009

|                     |                |          |          |          |          |
|---------------------|----------------|----------|----------|----------|----------|
| Cui 10011           | China          | KF951315 | KF951274 | KX354617 | KT894790 |
| Cui 10015           | China          | KF951311 | KF951273 | KX354618 | KT894791 |
| Cui 10015b (Clone)  | China          | KF951311 | KJ480732 | KX354618 | KT894791 |
| Cui 1710            | China          | KF951314 | KF951275 | -        | -        |
| Dai 15888           | China          | KX354494 | KX354466 | KX354619 | KX354662 |
| VS4269              | Russia         | KF951314 | MK098498 | -        | -        |
| Dai 11203           | China          | KF951313 | KF951276 | -        | KT894793 |
| JV 0407/27          | Czech Republic | KF951294 | KF951312 | -        | KT894792 |
| JV 0407/27d (Clone) | Czech Republic | KF951294 | KJ480747 | -        | KT894792 |

*Laetiporus oboensis* Decock, Rizinde & Amalfi, sp. nov.

|                                         |          |            |            |            |            |
|-----------------------------------------|----------|------------|------------|------------|------------|
| MUCL 53519 (T) clone 1 <sup>c, h</sup>  | Sao Tome | This study | This study | This study | This study |
| MUCL 53519 (T) clone 2 <sup>c, h</sup>  | Sao Tome | This study | This study | This study | This study |
| MUCL 53520 (PT) clone 1 <sup>c, h</sup> | Sao Tome | This study | This study | This study | This study |
| MUCL 53520 (PT) clone 2 <sup>c, h</sup> | Sao Tome | This study | This study | This study | This study |
| MUCL 53020 (PT) clone 1 <sup>c, h</sup> | Sao Tome | This study | This study | This study | This study |
| MUCL 53020 (PT) clone 2 <sup>c, h</sup> | Sao Tome | This study | This study | This study | This study |
| MUCL 53109 (PT) <sup>c, h</sup>         | Sao Tome | This study | This study | This study | This study |

*Laetiporus pratigiensis* C.D. Santos, J.L. Bezerra, J.P.A.F. Oliveira, P.A.S. Marbach & G. Marques 2023

|              |           |   |            |   |   |
|--------------|-----------|---|------------|---|---|
| HURB9802 (T) | Brazil    | - | MF618367   | - | - |
| Robledo1122  | Argentina | - | JN684765   | - | - |
| MA-AR08-33   | Argentina | - | This study | - | - |

*Laetiporus* sp.

|                            |          |            |            |            |            |
|----------------------------|----------|------------|------------|------------|------------|
| MUCL 55812 <sup>c, h</sup> | Ecuador  | This study | This study | This study | This study |
| CD PU21 03 <sup>c, h</sup> | Peru     | This study | This study | This study | This study |
| MUCL 44796 <sup>c, h</sup> | Ethiopia | This study | This study | This study | This study |

|                            |                |            |            |            |            |
|----------------------------|----------------|------------|------------|------------|------------|
| MUCL 44797 <sup>c, h</sup> | Ethiopia       | This study | This study | This study | This study |
| UOS-CZ                     | Czech Republic | -          | EU840554   | -          | -          |
| JV1708_3                   | Czech Republic | -          | MK098497   | -          | -          |
| JV1610_7                   | Czech Republic | -          | MK098496   | -          | -          |
| 6674                       | Uruguay        | -          | EU840672   | -          | -          |
| Dai 15825                  | China          | KX354493   | KX354465   | KX354616   | KX354661   |
| KOA-1                      | Hawaii         | EU402542   | EU402546   | -          | -          |
| EUC-1                      | Hawaii         | EU402541   | EU402545   | -          | -          |
| Dai 15902                  | China          | KX354491   | KX354463   | KX354614   | KX354659   |
| Dai 15905                  | China          | KX354490   | KX354462   | KX354613   | KX354658   |
| Dai 15953                  | China          | KX354488   | KX354460   | KX354611   | KX354656   |
| Dai 15828                  | China          | KX354523   | KX354461   | KX354612   | KX354657   |
| Dai 15898a                 | China          | -          | KX354464   | KX354615   | KX354660   |
| Dai 15838                  | China          | KY886737   | KY886711   | KY886780   | KY886794   |
| Dai 15893                  | China          | KY886736   | KY886710   | KY886779   | KY886793   |
| RVS3                       | Lithuania      | -          | EU840591   | -          | -          |
| RVS4                       | Lithuania      | -          | EU840592   | -          | -          |
| RVS5                       | Lithuania      | -          | EU840593   | -          | -          |
| RVS7                       | Lithuania      | -          | EU840595   | -          | -          |
| 11208A                     | South Korea    | -          | EU840623   | -          | -          |
| L13-706696                 | Czech Republic | -          | EU840565   | -          | -          |

*Laetiporus sulphureus* (Bull.) Murrill 1920

|                            |              |            |            |            |            |
|----------------------------|--------------|------------|------------|------------|------------|
| MUCL 56531 <sup>c, h</sup> | France       | This study | This study | This study | This study |
| MAS-2                      | USA          | EU402531   | EU402568   | -          | -          |
| TJV99-150                  | USA          | EU402530   | EU402567   | -          | -          |
| NJ-2                       | USA          | -          | EU402562   | -          | -          |
| 02089                      | -            | -          | AY835668   | -          | -          |
| A1                         | Poland       | -          | HM245764   | -          | -          |
| STE_U_7916                 | South Africa | -          | KU255084   | -          | -          |
| RGM_2720                   | Chile        | -          | MK934586   | -          | -          |

|              |                |          |          |          |          |
|--------------|----------------|----------|----------|----------|----------|
| Cui 12371    | China          | KX354505 | KX354478 | KX354632 | KX354673 |
| Z.R.L. CA04  | Canada         | KX354506 | KX354479 | KX354633 | KX354674 |
| Z.R.L. CA08  | Canada         | KX354507 | KX354480 | KX354634 | KX354675 |
| CT-1         | USA            | EU402532 | EU402565 | AB472659 | -        |
| He 2087      | USA            | KY886756 | KY886730 | KY886789 | KY886803 |
| DA-41        | USA            | EU402533 | EU402566 | AB472660 | -        |
| AFTOL-ID 769 | USA            | AY684162 | DQ221108 | -        | DQ408118 |
| GR-12        | USA            | EU402534 | EU402561 | AB472658 | -        |
| MUCL 8890    | Belgium        | -        | AB472605 | AB472644 | -        |
| MUCL 34165   | Germany        | -        | AB472608 | AB472645 | -        |
| MUCL 39390   | Belgium        | -        | AB472609 | AB472646 | -        |
| Dai 12154    | China          | KF951302 | KF951295 | KX354610 | KR610841 |
| JV 1106/15   | Czech Republic | KF951303 | KF951296 | KX354609 | KX354654 |

*Laetiporus sulphureus* var. *miniatus* (P. Karst.) Imazeki 1943

|           |             |   |          |          |   |
|-----------|-------------|---|----------|----------|---|
| WD723     | Japan       | - | AB308166 | AB308243 | - |
| WD3       | Japan       | - | AB308164 | AB308242 | - |
| NAAS04758 | South Korea | - | KP004986 | -        | - |

*Laetiporus sulphureus* var. *sulphureus* (Bull.) Murrill 1920

|            |                |          |          |          |          |
|------------|----------------|----------|----------|----------|----------|
| L48        | Japan          | -        | AB308142 | AB308227 | -        |
| WD820      | Japan          | -        | AB308135 | AB308219 | -        |
| JV 1106/15 | Czech Republic | KF951303 | KF951296 | KX354609 | KX354654 |

*Laetiporus tenuiculus* Decock, Rizinde & Amalfi, sp. nov.

|                                        |          |            |            |            |            |
|----------------------------------------|----------|------------|------------|------------|------------|
| MUCL 53539 (T) clone 1 <sup>s, h</sup> | Sao Tome | This study | This study | This study | This study |
| MUCL 53539 (T) clone 2 <sup>s, h</sup> | Sao Tome | This study | This study | This study | This study |
| MUCL 53539 (T) clone 3 <sup>s, h</sup> | Sao Tome | This study | This study | This study | This study |
| MUCL 53539 (T) clone 4 <sup>s, h</sup> | Sao Tome | This study | This study | This study | This study |
| MUCL 53539 (T) clone 5 <sup>s, h</sup> | Sao Tome | This study | This study | This study | This study |

*Laetiporus versisporus* (Lloyd) Imazeki 1943

|          |       |          |          |          |          |
|----------|-------|----------|----------|----------|----------|
| Cui 5488 | China | KF951321 | KF951268 | -        | -        |
| Cui 7882 | China | KF951323 | KF951269 | KX354642 | KT894783 |

|                                                                              |       |          |          |          |          |
|------------------------------------------------------------------------------|-------|----------|----------|----------|----------|
| Cui 9154                                                                     | China | KF951322 | KF951270 | KX354645 | KT894784 |
| Dai 10992                                                                    | China | KF951325 | KF951272 | KX354646 | KX354681 |
| Dai 10992b                                                                   | China | KF951325 | KJ480745 | KX354646 | KX354681 |
| Dai 13052                                                                    | China | KF951324 | KF951271 | KX354647 | KX354682 |
| Dai 13052b                                                                   | China | KF951324 | KJ480736 | KX354647 | KX354682 |
| Dai 13108                                                                    | China | KY886745 | KY886719 | KY886784 | KY886798 |
| Dai 13160                                                                    | China | KF951320 | KF951266 | KX354643 | KT894785 |
| Dai 7268                                                                     | China | KF951326 | KF951267 | -        | -        |
| Yuan 2103                                                                    | China | KY886744 | KY886718 | -        | -        |
| Yuan 6319                                                                    | China | KX354503 | KX354475 | KX354629 | KX354670 |
| <i>Wolfiporiella cartilaginea</i> (Ryvarden) B.K. Cui & Shun Liu 2022        |       |          |          |          |          |
| M. Nunez 13122                                                               | Japan | -        | GU256260 | -        | -        |
| Dai 3764                                                                     | China | -        | GU256260 | -        | -        |
| O 913120                                                                     | Japan | -        | KX354455 | -        | -        |
| <i>Wolfiporiella dilatohypha</i> (Ryvarden & Gilb.) B.K. Cui & Shun Liu 2022 |       |          |          |          |          |
| CS-63-59-13-A-R                                                              | USA   | KC585234 | KC585400 | -        | -        |
| FP72162                                                                      | USA   | EU402517 | EU402556 | -        | -        |

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T, PT = type, paratype; ND\*: available at MUCL

<sup>c</sup> = culture available; <sup>h</sup> = voucher herbarium specimen corresponding to the culture available at the MUCL herbarium;

Nucleotide sequences were automatically aligned with the MUSCLE algorithm (Edgar 2004) with default settings, then manually adjusted as necessary with PhyDE® v0.9971 (Müller et al. 2010). Potentially ambiguously aligned segments were also detected using the Gblocks v0.91b program (Castresana 2000) with the following parameter settings: minimum number of sequences for a conserved position = 77 (minimum possible); minimum number of sequences for a flank position = 77 (minimum possible); maximum number of contiguous non-conserved positions = 8 bp, minimum block size = 10 bp and gaps allowed within selected blocks in half of the sequences. The assignment of codon positions was confirmed by translating nucleotide sequences into predicted amino acid sequences using MacClade 4.0 (Maddison and Maddison 2005) and then compared with several annotated *Laetiporus* sequences available on GenBank. Phylogenetic analyses were performed separately for each individual and concatenated loci using Bayesian inference (BI) as implemented in MrBayes v3.2.6 (Ronquist et al. 2011) and Maximum likelihood (ML) as implemented in RAxML 7.0.4 (Stamatakis 2006; Stamatakis et al. 2008). Models of evolution for BI were estimated using the Akaike information criterion (AIC) as implemented in Modeltest 3.7 (Posada and Crandall 1998). the dataset was subdivided into 7 partitions: (ITS) (nucLSU) (*rpb2* codons 1) (*rpb2* codons 2) (*rpb2* codon 3) (*tef1- $\alpha$*  codons 1) (*tef1- $\alpha$*  codon 2) (*tef1- $\alpha$*  codon 3) (*tef1- $\alpha$*  introns, *rpb2* intron). The best-fit models for each partition were implemented as partition-specific models within partitioned mixed-model analyses of the combined dataset and all parameters were unlinked across partitions. The combined dataset Bayesian analyses were implemented with two independent runs, each with four simultaneous independent chains for 50 million generations, starting from random trees, and keeping one tree

every 1000th generation. All trees sampled after convergence (ave. standard deviation of split frequencies  $< 0.01$ ) and confirmed using Tracer v1.4 (Rambaut and Drummond 2007) were used to reconstruct a 50% majority-rule consensus tree (BC) and to calculate Bayesian posterior probabilities (PP). PP of each node was estimated based on the frequency at which the node was resolved among the sampled trees with the consensus option of 50% majority-rule (Simmons et al. 2004). A probability of 0.95 was considered significant. Maximum likelihood (ML) searches were conducted with RAxML involving 1000 replicates under the GTRGAMMAI model, with all model parameters estimated by the program. In addition, 1000 bootstrap (ML BS) replicates were run with the same GTRGAMMAI model. In order to force RaxML software to search for a separate evolution model for each dataset, we provided an additional alignment partition file to the software. Clades with Maximum likelihood bootstrap values of 75% or greater were considered supported by the data. Before combining the data partitions, topological incongruence between the datasets was assessed using 1000 replicates of ML BS under the same models described above, on each locus separately. Paired trees were examined for conflicts only involving nodes with ML BS  $> 75\%$  (Mason-Gamer and Kellogg 1996; Lutzoni et al. 2004; Reeb et al. 2004) compared with the software `compat.py` (Kauff and Lutzoni 2002) available at [www.lutzonilab.net/downloads](http://www.lutzonilab.net/downloads). A conflict was assumed to be significant if two different relationships for the same set of taxa (one being monophyletic and the other non-monophyletic) were observed in rival trees.

## 6.4. Results

**Phylogenetic analysis.**—The *Laetiporus* combined dataset comprised 146 sequences and 3492 positions including gaps (ITS: 630 characters; LSU: 984 characters; *tef 1- $\alpha$* : 1133 characters, of which 953 in the exon partition and 180 in the combined introns partition; *rpb2*: 772 characters, of which 693 in the exon partition and 79 in the combined introns partition).

The models selected were SYM+I+G for ITS partition, GTR+I+G for LSU, F81+I for *tef 1- $\alpha$*  1st codon position, F81 for *tef 1- $\alpha$*  2nd codon position, GTR+G for *tef 1- $\alpha$*  3rd codon position, GTR+I for *rpb2* 1st codon position, F81 for *rpb2* 2nd codon position, GTR+G for *rpb2* 3rd codon position and HKY+G for the combined introns partition. No conflict involving significantly supported nodes was found between the tree topologies obtained for the individual datasets, using the 75% ML BS criterion; the datasets were therefore combined.

The two Bayesian runs converged to stable likelihood values after 31200000 generations. 18800 stationary trees from each analysis were used to compute a 50% majority rule consensus tree and to calculate posterior probabilities (PP). In the ML searches, the alignment had 965 distinct patterns with a proportion of gaps and undetermined characters of 50.07%. The consensus of the most parsimonious trees, the consensus tree of the BI and the Maximum Likelihood tree were nearly congruent. The ML tree ( $-\ln L = -9332.081375$ ) is presented in Fig. 5.1.



The consensus tree of the BI and the most likelihood tree of ML were congruent as far as the terminal clades or supported lineages are concerned. The overall topologies of the trees were highly congruent, whatever the phylogenetic methodology and in accordance with previous published trees (Song and Cui 2017, Song et al. 2018, Campi et al. 2022, Liu et al. 2023).

All African *Laetiporus* specimens belong to a single, well supported, monophyletic lineage, divided into two sublineages, and four terminal clades, or phylogenetic species (I-IV, Fig. 5.1). The phylogenetic analyses recovered the specimens from São Tomé as two closely related terminal clades and the specimens from the east African mountain range as two other closely related terminal clades (I, II, Fig. 5.1).

Subsequent morphological examinations of the various collections pertaining to each of these subclades showed combinations of morphological features unique to and characteristic of each, thereby defining four morphospecies. The critical morphological features are the pileus and pore surface colour, as well as the pores and basidiospores sizes, and distribution.

## 6.5. Taxonomic conclusions

The current phylogenetic analyses showed that a set of Tropical African *Laetiporus* specimens and/or cultures formed a single well-supported African lineage (Fig. 5.1). This lineage is subdivided into two sublineages, with a dichotomy Western insular vs. Eastern Africa, and four terminal species clades I–IV (Fig. 5.1). Each of these terminal clades also showed differential morphological characters, hence defining concordantly morphological and phylogenetic species. However, uncertainties remain as to which of these species clades would correspond to *L. discolor* s.s., if any.

*Laetiporus discolor* (as *Polyporus discolor*) was little considered after its original description (Klotzsch 1833). Ryvar den (1976) noted that the type represents “a pale specimen of *Laetiporus sulphureus*” and is sterile. He also noted that *Polyporus miniatus* Jungh. represents the same species. Overeem (1925), in his monographic study of the southeast Asian *L. miniatus* (*P. miniatus*) did not mention *L. discolor*. However, Corner (1984) reported the species from Southeast Asia, through three varieties (Corner 1984), and reduced *L. miniatus* to a var. of *L. discolor*. However, he did not provide any modern description of *L. discolor* s.s. [var. *discolor*] (Corner 1984). Ota et al. (2009) revised the type specimen of *L. discolor* and of its Southeast Asian varieties. They provided a very little detailed description of the type of *L. discolor*. They confirmed the observations of Ryvar den (1976) when they noted “the type is [constituted of] sterile, pale, small, and thin [pieces of basidiome] (Ota et al. 2009). More recently, Ryvar den et al. (2022) accepted *L. discolor* as an independent species in Tropical Africa that they described with a pileus ranging from white to reddish

(e.g., Fig. 49 in Ryvarden et al. 2022), with 3–4 pores / mm and basidiospores  $5\text{--}8 \times 4\text{--}5 \mu\text{m}$ .

Three historical specimens of *L. discolor* from Mauritius are preserved at K, of which two are annotated as type, whereas the third specimen bears the same data as the type and is very likely a part of it. Only small fragments remain of the type, most of which are glued to carboards. Although Ryvarden (1976) and Ota et al. (2009) declared the type to be sterile, close examination led to the observation of a reasonable number of non-collapsed, measurable basidiospores. They are broadly ellipsoid to obovoid, or lacrymoid, thin-walled, hyaline,  $5.0\text{--}6.0 \times 3.5\text{--}4.8 \mu\text{m}$ , averaging  $5.6 \times 4.2 \mu\text{m}$ . The hyphal system is typical of *Laetiporus*, as originally described by Corner (1953), with both thin- and thick-walled generative hyphae in the hymenophoral trama and binding hyphae (sensu Corner 1953) in the context. The pores are small, 5–6 / mm, as noted by Klotzsch (1833).

The morphological studies of our African specimens and comparison with *L. discolor* led us to conclude that the East African phylogenetic species clade IV (Fig. 5.1) is morphologically the closest to *L. discolor*. These specimens share with *L. discolor* the pileus color and the pores and basidiospores of a comparable size range, although slightly larger in the type specimen. The specimens from São Tomé (clade I and II, Fig. 1) represent two distinct morphospecies, characterized by orange-tinged pilei and larger pores (3–4 and 4 (–5) / mm), and are probably endemic in insular western equatorial Africa, characteristics by which they differ from *L. discolor*. The specimens from the second Eastern African clade (*Laetiporus* sp. 1, clade III, Fig. 1) differ in having a bright yellow pileus when fresh (field notes by C.

Decock). However, the voucher specimens were lost during loan, making it impossible to describe the microscopic elements.

Consequently, the species represented by clade IV, from East Africa, is here, conservatively, accepted as representing *L. discolor*. However, it cannot be ruled out that *L. discolor* represents a species distinct from the mainland species and that would be endemic to Mauritius or the Mascarene Islands. The level of fungal endemism is unknown in the Mascarene Archipelago. Nevertheless, it might be as high as it is in the neighbouring island of Madagascar (Rivas-Ferreiro et al. 2023). This is also the case for the two species from São Tomé, both of which so far endemic to the Atlantic insular São Tomé.

## TAXONOMY

***Laetiporus discolor*** (Klotzsch) Corner

FIGS. 6.2–6.4

Mycobank MB#107516

Basionym: *Polyporus discolor* Klotzsch, Linnaea 8: 483. 1833.

Mycobank MB#198263

*Typification*: MAURITIUS. Telfair, No. 99878 (holotype K).

Type description:

*Basidiome* with imbricate, sessile, flabelliform, irregularly lobed, longitudinally rugose pileus [*imbricato-multiplex*, *sessilis*, *pilei flabelliformibus...pileus irregulares lobatis, ...rugulosus*], 7–15 cm in radius (remaining pieces are up to 4 × 1.5 cm), with whitish lobes [*lobatis albidis*]; in the remaining pieces, pileus surface is smooth or

faintly longitudinally wrinkled, dull, pale cork-coloured (5B3, greyish orange) to light brown (6D[5–6], sunburn, cinnamon), locally slightly reddish brown (7D5), darker brown near the base (6F6); *context* up to 4 mm thick, chalky, pale creamy, orange white to pale corky (5[A–B]2–3); *tube layer* up to 1.5 mm deep; *pore surface* dark olive [*pori fusco-olivacei*], in the type, grayish brown (5C(3–4)) to light brown (6[D–E]5); pores (very) small, subrounded to angular [*pori fusco-olivacei, minutissimis, subrotundis, subindex laceratis*], 5 (–6) / mm, 100–200 µm diam, ave = 168 µm; *dissepiments* thin, slightly lacerated.

*Hyphal system* monomitic in the hymenophoral trama, with thin- to thick-walled generative hyphae, dimitic in the contextual trama, with skeleto-binding hyphae; *contextual skeleto-binding hyphae* with a core hyphae and lateral branches, parallel to the pileus surface, more compacted and intricate toward the tubes, the core hyphae slightly thick-walled, the lumen largely open, 7–12 µm diam (ave 9.8 µm), the lateral branches often emerging at right angle, radiating, short to medium, 5–8 µm at the emerging point down to 3.0–4 µm diam (ave = 3.7 µm) in the main part, straight to sinuous, or (abruptly) bended, unbranched or once forked, the overall branching progressively more developed and more densely intricate toward the tube layer; *hymenophoral generative hyphae* with a subparallel orientation, hyaline, thin to faintly thick-walled, simple septate, 4.0–5.5 µm diam (ave 4.8 µm); *hymenophoral thick-walled hyphae* hyaline, thick-walled but with an open lumen, the wall sometimes sinuous, septate, occasionally once branched, 3.5–4.8 µm diam (ave = 4.0 µm).

*Hymenium. Basidia* not seen; *basidiospores* broadly ellipsoid to obovoid, or lacrymoid, thin-walled, hyaline, 5.0–6.0 × 3.5–4.8 µm (ave = 5.6 × 4.2 µm).

***Laetiporus discolor*** sensu auctores:

*Basidiomes* annual, sessile to laterally substipitate, merismatoid, compound, commonly with imbricated pilei, with up to 15 pilei superposed, or solitary, substipitate when emerging from surfacing roots, fleshy fragile when fresh, crumbly when dry; individual pileus flabelliform, applanate, projecting 5–10 cm, up to 12 cm wide and 0.5–1.5 cm thick at the base down to 3–4 mm at the rounder margin; pileal surface variable in colour when fresh from white all over to whitish, pinkish-buff near the margin then irregularly clay-buff (5C4, golden blonde) darkening to brownish yellow to light brown toward the base (5[C–D]7–8, golden brown) 5[A–B]3, upon drying, grayish brown (5[C–D]5) near the margin to dark grayish brown (5F[3–4]) toward the base, glabrous, azonate to slightly radially wrinkled; margin irregular, lobed, rounded, white when fresh; pore surface whitish when fresh, becoming ivory to whitish grey on drying; pores round to angular, 4–5 (–6) per mm, 150–250 µm diam., ave = 203 µm diam., with some larger pores up to 375 µm; *dissepiments* thin, entire, smooth to slightly fibrillose, with numerous hyphal ends; *context* white when fresh, becoming whitish to pale grayish cream when dry, up to 8.5 mm thick; *tubes* white to grayish when fresh, drying pale corky, fragile, crumbly when dry, up to 3 mm deep.



Figure 6.2: Basidiomata of *Laetiporus discolor* in situ. A. Specimen UG-08-15. A. Cluster of pilei (scale bar = 3.5 cm); B. Pore surface (scale bar = 1.5 cm)

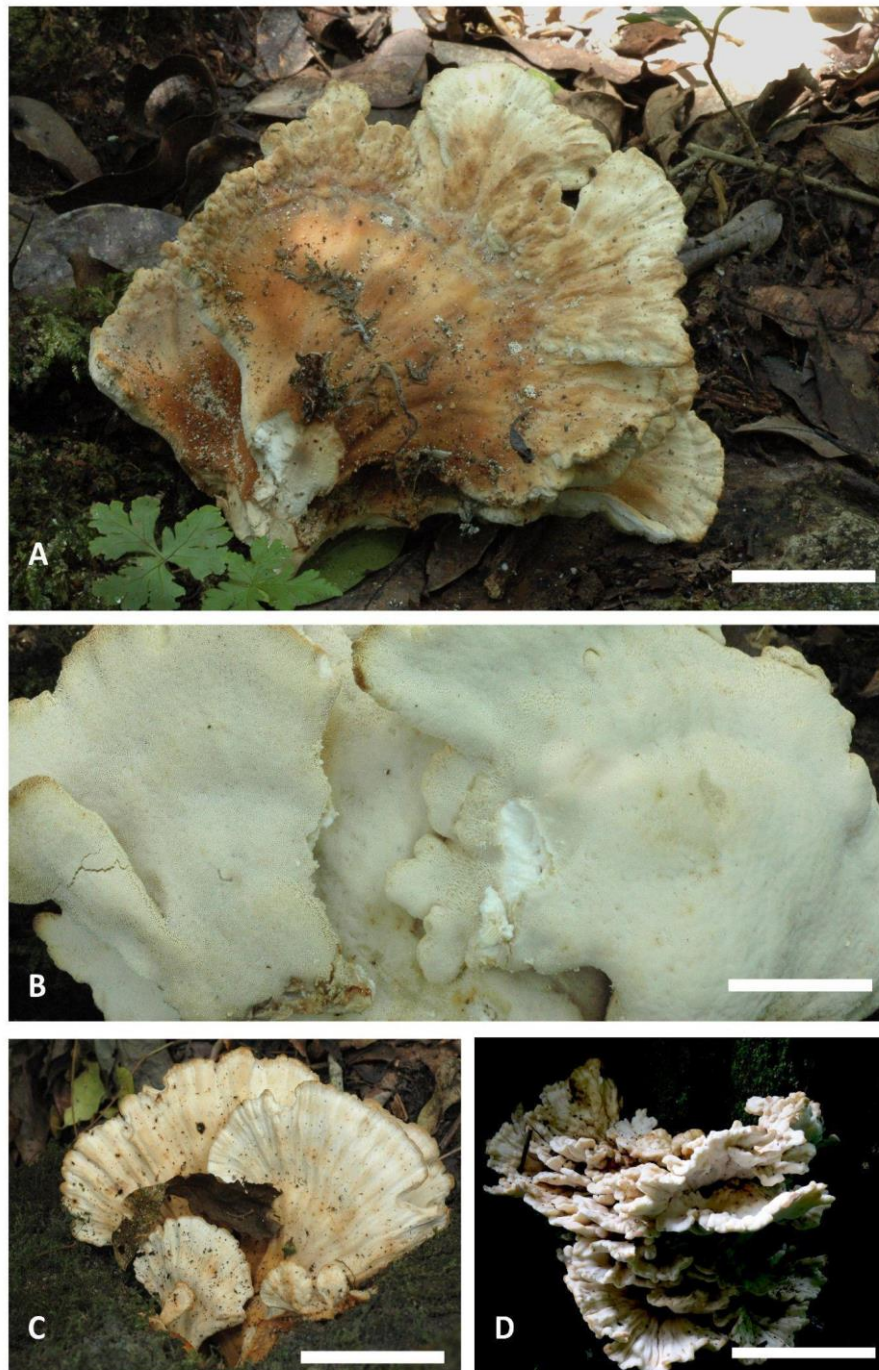


Figure 6.3: Basidiomata of *Laetiporus discolor* in situ. Specimen UG-08-45. A. pileus surface (scale bar = 2.5 cm); B. Pore surface (scale bar = 2.5 cm); C. pale coloured pileus (scale bar = 5 cm); D. specimen RHJ-442, white coloured pileus (scale bar = 5 cm).

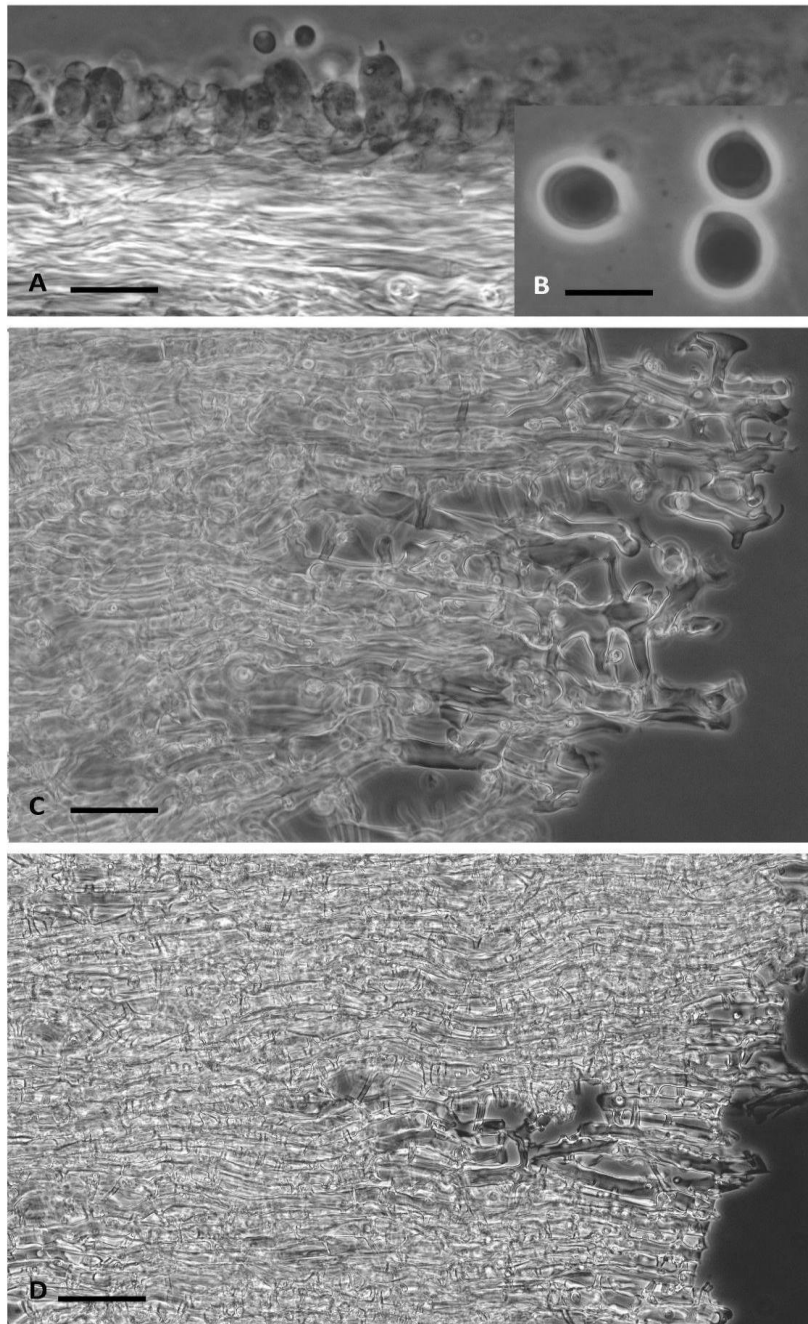


Figure 6.4: *Laetiporus discolor*, micromorphology, UG-08-. A. longitudinal section of the hymenohoral trama (scale bar = 15  $\mu\text{m}$ ); B. Basidiospores (scale bar = 5  $\mu\text{m}$ ); C. Section through the upper part of the context (scale bar = 20  $\mu\text{m}$ ); D. Section through the context

*Hyphal system* monomitic in the hymenophoral trama, with thin- to thick-walled generative hyphae, dimitic in the contextual trama, with skeleto-binding hyphae; *contextual skeleto-binding hyphae* with a core hyphae and lateral branches, arranged parallel to the pileus surface, more intricate toward the tubes, the core hyphae slightly thick-walled, the lumen largely open, 7–12  $\mu\text{m}$  diam (ave = 9.7  $\mu\text{m}$ ), the lateral branches often emerging at right angle, radiating, short to medium, 6–8  $\mu\text{m}$  at the emerging point down to 3.5–4 (–4.5)  $\mu\text{m}$  diam (ave = 3.7  $\mu\text{m}$ ) in the main part, straight to sinuous, or (abruptly) bended, unbranched or once forked, the overall branching progressively more developed and more densely intricate toward the tube layer; *hymenophoral generative hyphae* with a subparallel orientation, hyaline, thin- to faintly thick-walled, simple septate, 3.5–5.0  $\mu\text{m}$  diam (ave 4.2  $\mu\text{m}$ ); *hymenophoral thick-walled hyphae* hyaline, thick-walled but with an open lumen, the wall sometimes sinuous, septate, occasionally once branched, 3.5–4.5  $\mu\text{m}$  diam (ave 4.3  $\mu\text{m}$ ).

*Hymenium: basidia* clavate, bearing four sterigmata, simple-septate at the basal septum; *basidioles* clavate, smaller than basidia, 11–13  $\times$  4.5–6  $\mu\text{m}$ ; *basidiospores* broadly ellipsoid to obovoid, or lacrymoid, hyaline, thin- to faintly thick-walled, smooth, IKI-, CB-, (4.5–) 4.5–5.6 (– 6.0)  $\times$  (3.3–) 3.5–4.3 (–4.7)  $\mu\text{m}$ , ave = 5.0  $\times$  3.8  $\mu\text{m}$ , Q = 1.15–1.56, ave<sub>Q</sub> = 1.31.

*Physiology (type of rot)*: a brown rot;

*Ecology (substrate, host, habitat)*: living or dead trunks of undetermined angiosperms, also on *Eucalyptus* sp. (Myrtaceae), in medium elevation montane forests;

*Distribution:* both branches of the eastern African Rift, the Albertine and Eastern (Gregorian) branches; confirmed from the Democratic Republic of Congo, Kenya, Mauritius, South Africa, Tanzania, and Uganda; likely widespread in the eastern mountain ranges.

*Phylogenetic affinities:* the closest known relatives of *L. discolor* are *Laetiporus* sp. 1, *L. oboensis*, and *L. tenuiculus* (Fig. 5.1).

*Other specimens examined:* DEMOCRATIC REPUBLIC OF THE CONGO. Nord-Kivu, Virunga National Park, Ruwenzori mountain range, on the way from Mutsora to the first (Kyandolire, N 0.347836, E 29.776995, 1700 masl) and second ICCN-WWF chalet (Kalonge), N 00°19'60, E 29°48', elev. ~2100 m, at the base and surfacing roots of living tree, unidentified angiosperm, C. Decock, 03–05 Feb. 2008, CO-08-29, MUCL; *ibid.*, at the base and surfacing roots of living tree, unidentified angiosperm, C. Decock, 03–05 Feb. 2008, CO-08-25, MUCL 49988; *Ibid.* Mikenno mountain range, S 1.414895, E 29.373774, 1864 masl, dead trunk of *Eucalyptus* sp., Mar. 2022, J.C. Rizinde, RHJ 442, MUCL; Sud-Kivu, Kahuzi-Biega National Park, S 2.300954, E 28.760219, 2160 masl, base of living trunk, *Eucalyptus* sp., C. Decock and J.C. Rizinde, Apr. 2018, RHJ 273; KENYA. Kakamega National Park area, N 0°17', E 34°51', elev. ~1500 m, Feb. 2015, C. Decock, KE-15-23, MUCL; *ibid.*, garden, base of a living trunk, unidentified angiosperm, Feb. 2015, C. Decock, KE-15-22, MUCL 55532; *ibid.*, Feb. 2015, C. Decock, KE-15-32, MUCL 55533; *ibid.*, KE-15-33, MUCL 55534; KENYA. Mount Elgon National Park, N 1°084, E 34°35', elev. ~2000 m, Apr. 2016, C. Decock, KE-16-102, MUCL 56026; *ibid.*, KE-16-199, MUCL 56066; UGANDA. Kabarole district, Kibale National Park, 0°30', E 30°24', elev. ~1500 m, medium altitude

evergreen forest (*Parinari* dominant forest), living trunk, ~80–100 cm diam, unidentified angiosperm, C. Decock, 28 Jan. 2008, UG-08-15, MUCL 49955; *ibid.* large dead trunk, ~ 80–100 cm diam, unidentified angiosperm, 29 Jan. 2008, UG-08-45, MUCL 49970.

**Comments.**—*Laetiporus discolor*, as accepted here, is characterized by solitary to more commonly compound, merismatoid basidiome, with pilei in a range of colour from white to pallid ochraceous, becoming brown from the base when fresh. A specimen with a white pileus was collected growing from a living *Eucalyptus* in dense plantation, and the lack of light may explain the white colour.

The specimens from the second Eastern African clade (*Laetiporus* sp. 1,) differ morphologically in having bright yellow pilei when fresh (field notes by C. Decock). However, the reference specimens (MUCL 44796 & 44797: Ethiopia, Oromia Region, Shewa Province, Menagesha state forest, elev. ~2300 masl, *Eucalyptus* mixed with *Juniperus procera*, on a living trunk of *Eucalyptus* sp., 24 Jul. 2003, C. Decock & A. Bitew, ET-03-59) and between Ginchi and Addis Ababa, elev. ~2200 masl, *Eucalyptus* mixed with *Juniperus procera*, on living trunk of *Eucalyptus* sp., 25 Jul. 2003, C. Decock & A. Bitew, ET-03-76) are no longer available. *Laetiporus oboensis* and *L. tenuiculus* are characterized by pale orange-tinged pilei and a probable endemism in insular western equatorial Africa, features by which they differ from *L. discolor*.

Out of tropical Africa, *L. discolor* var. *brunnescens* (Corner 1984) is morphologically the most comparable taxa. It shares with *L. discolor* a set of characters, of which the imbricate pileus with an “upper surface white, alutaceous, to pallid ochraceous, becoming brown from the base

when fresh” (Corner 1984; Ota et al. 2009) and basidiospores of a comparable size range, although narrower in var. *brunnescens* (viz.  $4.7\text{--}5.5 \times 3.7\text{--}4.6 \mu\text{m}$ , ave  $5.2 \times 4.2 \mu\text{m}$  vs  $4.5\text{--}5.0 \times 3\text{--}3.7 \mu\text{m}$  [fide Corner 1984] or  $4.2\text{--}6.0 \times 3.0\text{--}4.2$ , ave  $5.1 \times 3.6 \mu\text{m}$  [fide Ota et al. 2009]). *Laetiporus discolor* var. *brunnescens* differs also in having smaller pores, 120–200 (Corner 1984) or 4–7 / mm (Ota et al. 2009). *Laetiporus discolor* var. *miniatus* and var. *pallidus* differ in having pale orange to reddish-tinged pilei when fresh.

From a biogeographical perspective, *L. discolor* as accepted here is an eastern Afro-montane taxa, widely distributed in both branches of the East African rift, Albertine and Gregorian, in addition to the Mascarene. The species inhabits, in the continent, medium elevation forests, up to 2000 masl. In the Albertine rift, it is known from the Democratic Republic of the Congo, both in North and South Kivu, from the Rwenzori, Virunga, and Kahuzi Biega mountain ranges, at elevation ranging 800–2000 masl. It is also known from Western Uganda in Kibale National Park, at an elevation of ~1500 masl. In east Africa, it has been observed from Mount Elgon National Park in Kenya, Tanzania (Genbank # KM593880), and South Africa.

*Laetiporus oboensis* Decock, Rizinde & Amalfi, sp. nov.

FIG. 6.5

Mycobank MB849822

Characterized by a combination of compound basidiomes, densely imbricated, superposed pileus, yellowish orange pileus surface, lobed, rounded margin, mainly 3–4 pores / mm, broadly ellipsoid to obovoid basidiospores mainly  $4.4\text{--}5.0 \times 3.5\text{--}4.0 \mu\text{m}$ , ave =  $4.8 \times 3.7 \mu\text{m}$ , occurring at medium elevation at Obô de São Tomé National Park.

*Typification:* SÃO TOMÉ. Obô de São Tomé National Park, ~ N  $00^{\circ}16.95'$  – E  $006^{\circ}35.48'$ , elev. ~ 800-1000 masl, on a dead fallen trunk, 12 Apr. 2011, Cony Decock, ST-11-06 (**holotype**, BR, **isotype**, MUCL 53519), ex-holotype living strain MUCL 53519).

*Etymology:* “*oboensis*”, from the type locality, Obô de São Tomé National Park.

*Basidiomes* annual, sessile, merismatoid, compounds, with multiple (up to 10) imbricate pilei, the all basidiomes up to 35 cm from side to side, projecting up to 10 cm from the base to the margin, up 14 cm thick at the base, cheesy fragile when fresh, crumbly when dry, odour or taste unrecorded when fresh; individual *pileus* imbricated, individually shortly flabelliform, applanate, glabrous, azonate to faintly zonate, radially wrinkled, 6–13 cm wide, projecting up to 12 cm, 5–8 mm thick, mainly pale yellowish white 4[A2–3] to orange white, pale orange 5A[2–3], slightly darker at the base when fresh, fading to pale orange, greyish orange 5[A–B][3–4], with some fleshy hue (6B3) upon drying, locally brownish orange (6C6) toward the base; *margin* thick, rounded, lobed; *pore surface* pale yellow to pale orange when fresh,

becoming pale greyish orange 5B[4–6] on drying; *pores* round to angular, 3–4 per mm, 125–270  $\mu\text{m}$  diam, ave = 200  $\mu\text{m}$ , with some larger pores up to 375  $\mu\text{m}$ ; *dissepiments* thin, entire, slightly fibrillose, with numerous hyphal ends; *context* white when fresh, watery, becoming pale greyish cream when dry, up to 8 mm thick; *tubes* slightly darker than the context when fresh, pale greyish yellow, drying darker, greyish, cork-coloured, soft, watery when fresh, drying crumbly, up to 2 mm long.

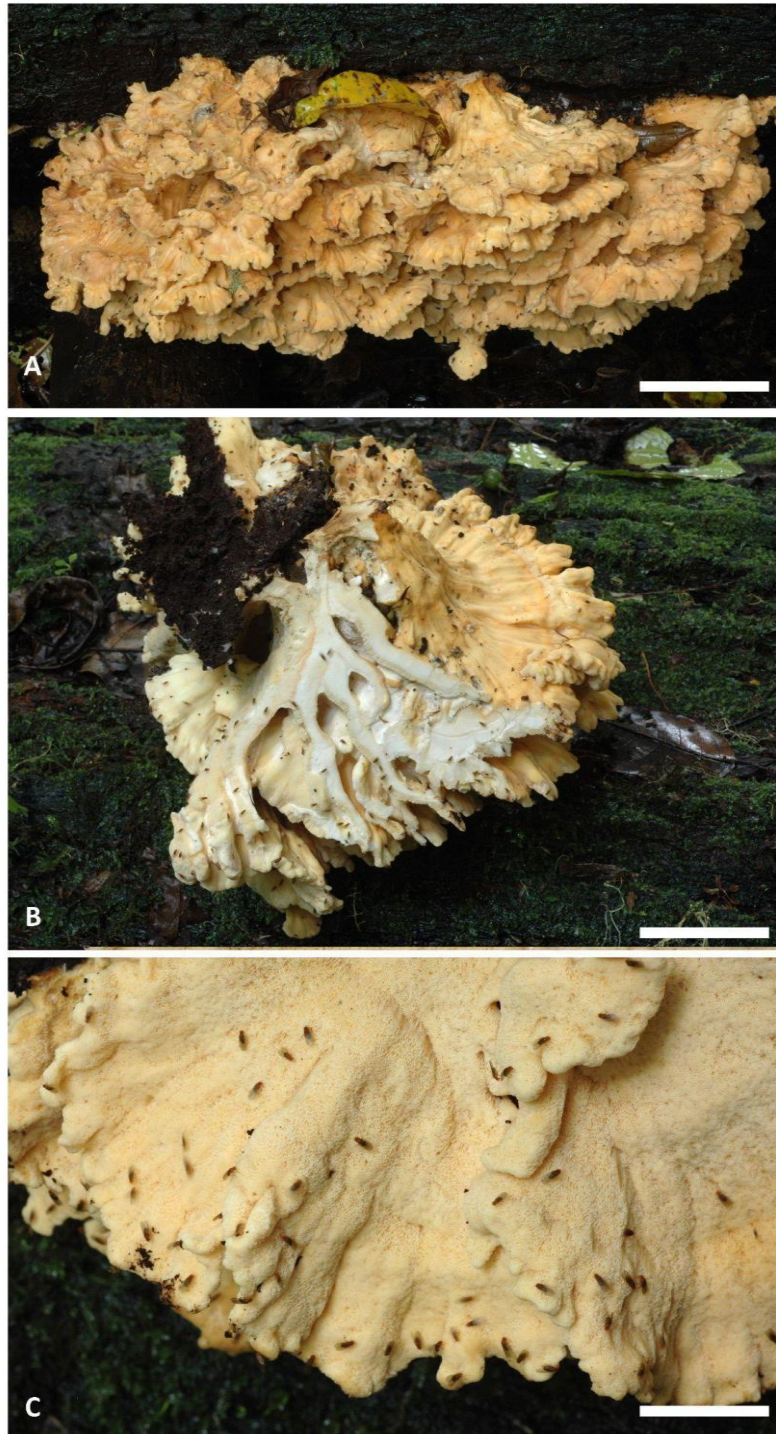


Figure 6.5: Basidiomata of *Laetiporus oboensis* in situ. Holotype ST-11-06. A. Basidiomata in situ (scale bar = 7 cm); B. Transversal section (scale bar = 5 cm); C. Pore surface (scale bar = 3cm)

*Hyphal system* monomitic in the hymenophoral trama, with thin- to thick-walled generative hyphae, dimitic in the contextual trama, with skeleto-binding hyphae; *contextual skeleto-binding hyphae* with a core hyphae and lateral branches, parallel to the pileus surface, more compacted and intricate toward the tubes, the core hyphae slightly thick-walled, the lumen largely open, 7–12  $\mu\text{m}$  diam (ave = 8.9  $\mu\text{m}$ ), the lateral branches often emerging at right angle, radiating, straight to sinuous, or (abruptly) bended, unbranched or once forked, short to medium, 6–8  $\mu\text{m}$  at the emerging point down to (3–) 3.5–4 (–4.5)  $\mu\text{m}$  diam (ave = 3.7  $\mu\text{m}$ ) in the main part, the overall branching progressively more developed and more densely intricate toward the tube layer; *hymenophoral generative hyphae* with a subparallel orientation, hyaline, thin- to faintly thick-walled, simple septate, 3.5–5.0  $\mu\text{m}$  diam (ave = 4.2  $\mu\text{m}$ ); *hymenophoral thick-walled hyphae* hyaline, thick-walled but with an open lumen, the wall sometimes sinuous, septate, occasionally once branched, 3.5–5.0  $\mu\text{m}$  diam (ave 4.3  $\mu\text{m}$ ).

*Hymenium: basidia* mostly collapsed, clavate, bearing four sterigmata, simple-septate at the basal septum; *basidioles* clavate, smaller than basidia,  $12 \times 5 \mu\text{m}$ ; *basidiospores* broadly ellipsoid to obovoid, or lacrymoid, hyaline, thin-to faintly thick-walled, smooth, IKI-, CB-, (4.0–) 4.4–5.0 (–5.3)  $\times$  (3.3–) 3.5–4.0 (–4.2)  $\mu\text{m}$ , ave =  $4.8 \times 3.7 \mu\text{m}$ , some rare basidiospores larger,  $6.0\text{--}7.0 \times 4.5\text{--}5.0 \mu\text{m}$   $Q = 1.1\text{--}1.4$ , ave<sub>Q</sub> = 1.27.

*Physiology (type of rot):* a brown rot;

*Ecology (substrate, host, habitat):* dead fallen trunks, unidentified angiosperms, medium elevation montane forest;

*Distribution:* known so far only from elevation ~ 800–1000 masl, at Obô de São Tomé, São Tomé.

*Phylogenetic affinities:* the closest known relatives of *L. oboensis* (Fig. 5.1) are *L. tenuiculus*, *L. discolor*, and *Laetiporus* sp. 1.

*Additional specimens examined:* São Tomé, Obô de São Tomé National Park, ~ N 00°16.95' – E 006°35.48', elev. ~1000 masl, on dead fallen trunk, 12 Apr. 2011, Cony Decock, ST-11-07 (BR, MUCL 53520; living strain ex ST-11-07, MUCL 53520).

*Laetiporus tenuiculus* Decock, Rizinde & Amalfi, sp. nov.

FIG. 6.6

Mycobank MB849823

The species is characterized by a combination of small (projecting up to 10 cm), pale orange, flabelliform basidiomes, solitary or in group of two or three from a common base, with a dentate to incised margin, mostly 4 pores / mm, basidiospores ellipsoid to obovoid,  $5\text{--}6 \times 3.8\text{--}5.0$   $\mu\text{m}$  (av.  $5.4 \times 4.2$   $\mu\text{m}$ ), and occurring from medium elevation ( $\sim 1300$  masl) at Obô de São Tomé National Park.

*Typification:* SÃO TOMÉ. Obô de São Tomé National Park,  $\sim$  N  $00^{\circ}16.95'$  – E  $006^{\circ}35.48'$ , elev.  $\sim 1500$  masl, on dead fallen trunk, April 2011, Cony Decock, ST-11-53, (**holotype**, BR, **isotype**, MUCL 53539) (living strain ex holotype MUCL 53539).

*Etymology:* from the small basidiome.

*Basidiomes* annual, laterally substipitate, solitary or with two or four pilei emerging simultaneously from a common base but not umbricate, soft, fragile and easily broken when fresh, crumbly when dry, odor or taste unknown when fresh; *pileus* flabelliform, with a short stipe-like base, up to 10 mm long, to dimidiate, applanate, projecting up to 70 mm, 55 mm wide, 5–6 mm thick at the base down to 1.5–2 mm thick at the margin, pale orange when fresh, becoming pale yellow, creamy (4[A3–A5]) with some greyish hue upon drying, glabrous, azonate to faintly zonate, faintly radially wrinkled; *margin* slightly to deeply incised; *pore surface* white when fresh, greyish yellow, brownish orange ([4–5]B4) on drying; *pores* small, 4 (–5) per mm, 125–250  $\mu\text{m}$  diam., ave = 193; *dissepiments* thin, entire, slightly lacerated to

lanose with bundles of hyphal ends; *context* white to whitish cream when fresh, unchanged on drying, up to 4 mm thick; *tubes* darker than the context, contrasting, grayish orange, cork-coloured, crumbly, up to 1.5 mm deep.

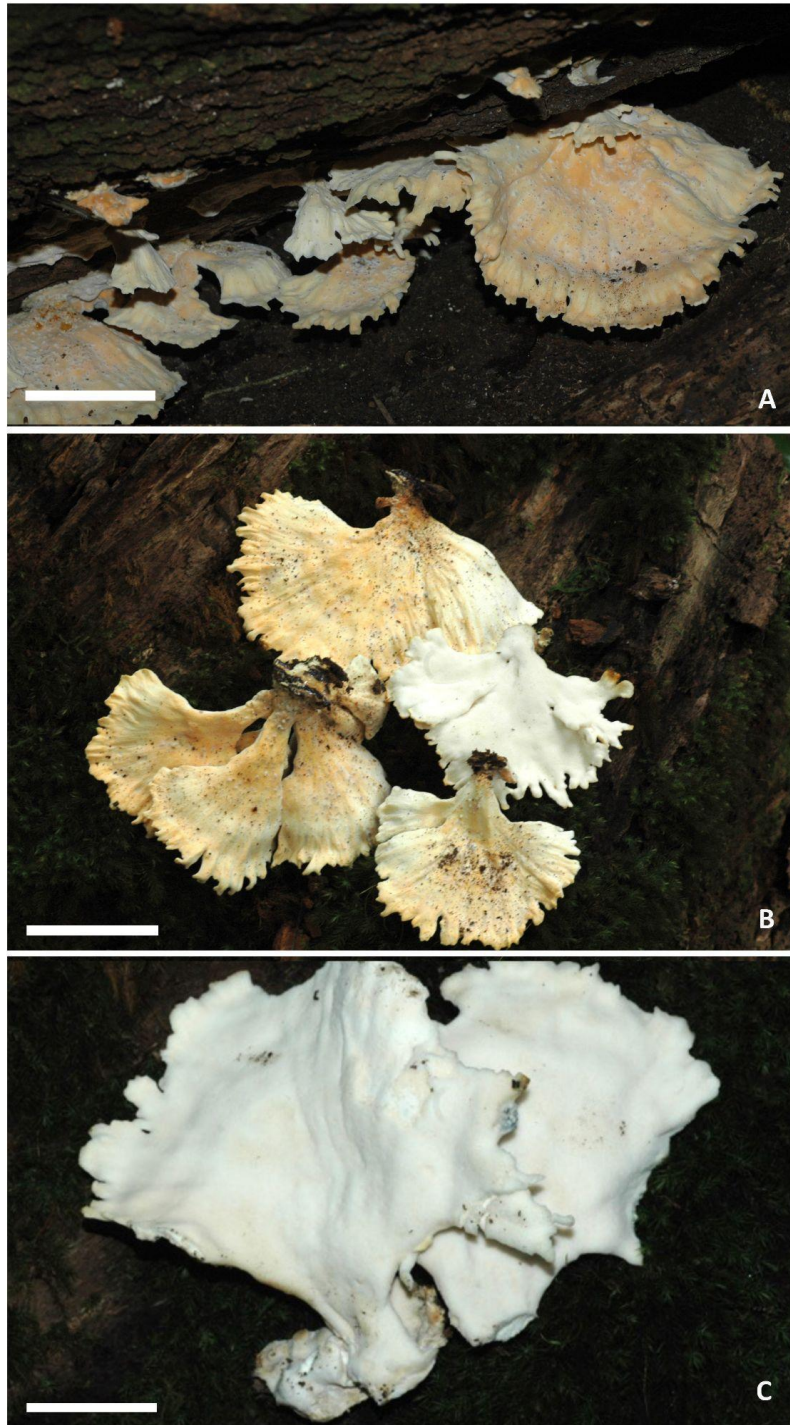


Figure 6.6: Basidiomata of *Laetiporus tenuiculus* in situ. Holotype ST-11-53. A. Basidiomata in situ (scale bar = 25 mm); B. Basidiomata in situ (scale bar = 30 mm); C. Pore surface (scale bar = 15 mm)

*Hyphal system* monomitic in the hymenophoral trama, with thin- to thick-walled generative hyphae, dimitic in the contextual trama, with skeleto-binding hyphae; *contextual skeleto-binding hyphae* with a core hyphae and lateral branches, arranged subparallel to the pileus surface, more compacted and intricate toward the tubes, the core hyphae slightly thick-walled, the lumen largely open, 5–12  $\mu\text{m}$  diam (ave = 8.6  $\mu\text{m}$ ), with a progressive reduction of the diam. from the pileus surface toward the hymenophoral trama, with lateral branches often emerging at right angle, radiating, straight to sinuous, or (abruptly) bended, unbranched or once forked, short to medium, 5.5–8  $\mu\text{m}$  (6.2  $\mu\text{m}$ ) at the emerging point down to 3.0–4.0  $\mu\text{m}$  diam (ave = 3.7  $\mu\text{m}$ ) in the main part, the overall branching progressively more developed and more densely intricate toward the tube layer; *hymenophoral generative hyphae* with a subparallel orientation, hyaline, thin- to faintly thick-walled, simple septate, 3.0–4.0  $\mu\text{m}$  diam (ave = 3.6  $\mu\text{m}$ ); *hymenophoral thick-walled generative hyphae* hyaline, thick-walled but with a widely open lumen, the wall sometimes sinuous, septate, occasionally once branched, 3.5–5.0  $\mu\text{m}$  diam (ave 4.3  $\mu\text{m}$ ).

*Hymenium: basidia* clavate, with a basal simple-septum, 20–25  $\times$  8–9  $\mu\text{m}$ , bearing four sterigmata; *basidioles* clavate, slightly smaller than basidia; *basidiospores* ellipsoid to obovoid, hyaline, thin-walled, smooth, IKI-, CB-, 5–6  $\times$  (3.5–) 3.8–5.0  $\mu\text{m}$  (ave = 5.4  $\times$  4.2  $\mu\text{m}$ ), Q = 1.1–1.4 (–1.5).

*Physiology (type of rot)*: brown rot;

*Ecology (substrate, host, habitat)*: dead fallen trunks, unidentified angiosperm, montane forest;

*Distribution:* known so far only from ~ 1500 masl, at Mt Obô de São Tomé, São Tomé.

*Phylogenetic affinities:* the closest known relatives of *L. tenuiculus* are *L. oboensis*, *L. discolor*, and *Laetiporus* sp. (Fig. 5.1). Outside Africa, the closest relatives are several East Asian taxa of the *L. versisporus* complex.

Comments.—*Laetiporus oboensis* and *L. tenuiculus* are phylogenetically closely related and, in a biogeographical perspective, are sympatric and, likely, endemic at Obô de São Tomé, São Tomé. *Laetiporus tenuiculus* differs from *L. oboensis* in having smaller, thinner, flesh-coloured to pale fleshy orange basidiomes, an incised margin, a white pore surface, on average smaller pores (4–5 / mm vs 3–4 / mm) and, on average, larger basidiospores (mostly 5–6 × 3.8–5.0, av. = 5.4 × 4.2 µm vs 4.4–5.0 × 3.5–4.0 µm, av. = 4.8 × 3.7 µm). These two species may also have a differential autecology. The single specimen of *L. tenuiculus* was collected at a higher altitude than the two collections of *L. oboensis*, but this should be ascertained when more material is available.

*Laetiporus oboensis* and *L. tenuiculus* differ also in a 15 bp indel in the ITS1. This indel is present in three haplotypes of *L. tenuiculus* whereas it is absent in six haplotypes of the two specimens of *L. oboensis*.

*Laetiporus oboensis* and *L. tenuiculus* differ from *L. discolor* in having pale orange-tinged pileus vs whitish to greyish or greyish brown in the latter. Furthermore, *L. discolor* is an east African taxa, widely distributed in both branches of the great African rift. *Laetiporus* sp. 1 differs from *L. oboensis* and *L. tenuiculus* in having a yellowish pileus.

Out of tropical Africa, *L. discolor* var. *miniatus* and *L. discolor* var. *diffluens* (Corner 1984, Ota et al. 2009) are comparable to *L. oboensis* and *L. tenuiculus*. *Laetiporus discolor* var. *miniatus* is based on *L. miniatus* (Jungh.) Overeem (basionym *Polyporellus miniatus* P. Karst. 1879), originally described from high elevation in Java, Indonesia (Junghun 1838). The species has been dealt with in detail by Overeem (1925), who cited several collections originating from medium to medium to high elevation vegetation (800–3000 m) in Java (Indonesia). Corner (1984) based his description of *L. discolor* var. *miniatus* on a specimen also collected from high elevation in Papua New Guinea (2000 m) and a second from Solomon Island (300 m). Ota et al. (2009) examined the type that they described as reddish. Its phylogenetic affinities are unknown. *Laetiporus miniatus* was also reported from Japan under *L. sulphureus* var. *miniatus* (P. Karst.) Imazeki. However, *L. sulphureus* var. *miniatus* in Japan was based on specimens originating from the Northern temperate area, and has been redescribed as *L. cremeiporus* (Ota et al. 2009). *Laetiporus cremeiporus* belongs to the phylogenetic group I of Song and Cui (2017).

*Laetiporus miniatus* shares with *L. oboensis* imbricate, pale orange-tinted pileus and basidiospores of a comparable size range (viz.  $4.5\text{--}5.0 \times 3\text{--}3.7 \mu\text{m}$ , Corner 1984). However, Overeem (1925) reported basidiospores longer than those reported by Corner,  $5\text{--}6.5 \times 3\text{--}4 \mu\text{m}$ . *Laetiporus miniatus* differs in having a “bright orange-pink to pale orange cinnamon context (Corner 1994). *Laetiporus tenuiculus* differs in having smaller, thinner basidiome. *Laetiporus miniatus* var. *diffluens* differs from both species *L. oboensis* and *L. tenuis* in having their hyphae diffluent in potasse solution.

### Key to the species of *Laetiporus* found in Tropical Africa

1. Basidiomes whitish, greyish to brownish orange; East African rift down to South Africa and insular Mauritius

*L. discolor*

Known at medium elevation (~800–~2000 masl), both branches of the African rift, montane forests.

- 1'. Basidiomes in yellow to orange tint

2. Basidiomes with yellow pileus

*Laetiporus* sp1.

Known from Ethiopia, *hitherto* only known on *Eucalyptus*.

- 2'. Basidiomes with orange-tinged pilei

3. Basidiomes with imbricated pilei, > 10 cm; margin slightly lobed

*L. oboensis*

Known from São Tomé, medium elevation forest.

- 3'. Basidiomes mostly solitary, up to 10 cm long, thin; margin incised *L. tenuiculus*

Known from São Tomé, at medium elevation forest.

## 6.6. Discussion

Tropical African *Laetiporus* were shown hereinabove to be distributed into four species clades, corresponding to as many morphotypes. These species are phylogenetically closely related, monophyletic, and form a single African lineage. The unicity of this lineage suggests local dispersion / speciation events from a common ancestor. Geographic isolation is suggested to represent a key determinant in local speciation and lineage divergence, with a dichotomy western vs. eastern Africa. The African *Laetiporus* are related to the east Asian *L. versisporus* s.l. (Fig. 5.1) that is spanning over Southern China, South Korea, and Japan.

In a biogeographic perspective, the African *Laetiporus* has a distribution restricted to the Afromontane archipelago. The genus is here considered absent from the Central African lowland rainforest, or the Guineo-Congolian Regional Centre of Endemism, and from the open forest / woody savannah of the Zambezian Regional Centre of Endemism (as defined by White 1986). In other tropical areas, in Southeast Asia and in the Neotropics, *Laetiporus* also seems to be restricted to mountainous areas (Overeem 1925; Corner 1984; Campi et al. 2022; Santos et al. in Crous et al. 2023; CD, pers. obs.).

Physiologically, *Laetiporus* belongs to the brown rot polypores (Laetiporaceae, Polyporales). Brown rot polypores are little diversified in Tropical Africa (Decock et al. 2022; Ryvarden et al. 2022; Kouagou Yayoro et al. 2023) and are mainly found in mountainous forest ecosystems. In that sense, the distribution of *Laetiporus* species over the Tropical Afromontane archipelago is congruent to that of other brown rot genera of polypores. Species of the other brown rot genera of

the *Antrodia* / *Fomitopsis* clade (Han et al. 2016), including *Fomitopsis*, *Niveoporofomes*, *Rhodofomes*, *Rhodofomitopsis*, *Antrodia* s.l., or the *Cyanosporus* complex, are mostly known from medium to high elevation forests of the Afromontane ranges (Ryvarden et al. 2022). *Niveoporofomes*, e.g., is represented by two species in Tropical Africa, including *N. oboensis* Decock, Amalfi & Ryvarden that is sympatric with *L. oboensis* and *L. tenuiculus* at Obô de São Tomé (Decock et al. 2022; Ryvarden et al. 2022), and *N. wriddingtoniae* (Masuka & Ryvarden) Decock & Ryvarden, from montane of Malawi (Decock et al. 2022).

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**Conflict of interest** The authors declare that they have no conflict of interest.

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## Chapter 7. Discussion, general conclusion, and perspectives

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## 7.1. Discussion and General conclusion

The fungi of the African Albertine Rift are still incompletely known at two levels. Firstly, in terms of accurate species concepts, and secondly, in terms of global mycodiversity, which is a direct consequence of the first. Detailed taxonomic studies and accurate species definitions are therefore key issues for knowledge of fungal diversity and downstream conservation processes. These two gaps are interdependent, as we cannot pretend to apprehend fungal biodiversity without accurately defining its basic taxonomic units.

This justifies the fact that the first step in this study was to list the globally reported macrofungal diversity of the region (Table 2.1). We mainly use data from field missions available at [www.botanicalcollections.be](http://www.botanicalcollections.be) and in several floras. 634 species of large fungi are reported in our results for the region. Considering a ratio of 5:1 (five plant species per macrofungal species) to 2:1 (two plant species per macrofungal species) (Mueller et al., 2007), this region, which hosts ~6000 plant species (Plumptre et al. 2016), would host a putative fungal diversity of 1158 to 2896 species. According to Mueller et al. (2007), the ratio 5:1 (five plant species per macrofungal species) is the most credible for estimating tropical macrofungal diversity. With only 634 species of larger fungi reported here for the whole region, which harbor a high diversity of ecosystems, the fungal diversity of the Albertine Rift is undoubtedly largely incompletely known and more than 500 macrofungal species, at minima, would remain to be discovered.

The study also challenged previously used species concepts. Most of the species reported were identified by European mycologists using

the morphological species concept and species described from European or American specimens (Rammeloo and Walley 1993). As a result, more than one hundred species names already recognised for European taxa were highlighted as doubtful. Most of these were the result of misidentification and required revision. We have attempted to apply more accurate species definitions to several genera as models, based on multiple approaches, often referred to as a 'holistic' species concept.

This study contributed to the revision of three little-known genera, *Ripartitella*, *Armillaria*, and *Laetiporus*, by integrating multiple points of view, using a combination of morphological, ecological and DNA-based phylogenetic criteria. *Ripartitella* and *Laetiporus* had not been reported from the Albertine Rift in previous studies, and Albertine Rift *Armillaria* have never been the subject of an in-depth taxonomic study, as shown by the mentions of several species names (e.g., *Armillaria borealis* Marxm. & Korhonen, *A. cepistipes* Valen., *A. heimii* Pegler, or *A. fuscipes* Petch).

The morphological species concept has been the basis for fungal classification in the past. However, the morphological species concept has been reported to have some limitations. It does not allow an efficient delimitation of species in all cases, resulting in so-called “cryptic species”. This was the case of the *Armillaria mellea* species complex and the temperate *Laetiporus sulphureus*. In addition, quantitative and qualitative morphological variables can be influenced by environmental variables and the age of the specimen. Finally, the mycologist's experience could influence the interpretation of fine quantitative and qualitative morphological variables.

The morphological species concept sometimes also requires comparison with type specimens. However, and this is obviously and desperately the case for the African Mycologists, in many cases, type specimens are hardly available. In addition, some type specimens are very aged. For instance, the type of *Laetiporus discolor*, first described as *Polyporus discolor*, dates back from 1904. It is preserved at Kew Garden (UK), and without a research stay at the MUCL, the type would not have been available for this study. The types of *A. mellea* (*Agaricus melleus*), *A. camerunensis*, *A. fuscipes*, *A. heimii* (*Clytocybe elegans*) were described in 1790, 1895, 1909, and 1937, respectively.

An additional challenge is that morphological and genetic changes are sometimes asymmetrically linked. Small changes in the genome can lead to huge changes in morphology, and large genomic changes can lead to small morphological changes (Mishler 1985).

For a more objective species diagnosis, the morphological species concept has been challenged and complemented by ecological and DNA-based phylogenetic data.

Based on distinctive morphological characters, one species within the genus *Ripartitella* and two species of *Laetiporus* were described as new in this study.

African *Ripartitella* have previously been reported under *Ripartitella brasiliensis* by Pegler (1977) and Desjardin and Perry (2017), both of which noted the absence of cystidia. In the third chapter, congruent morphological, ecological and phylogenetic data were used to demonstrate that *Ripartitella degreefii* represents an African species, independent and distinct from *R. brasiliensis*. In combination with phylogenetic data, the ecological species concept was essential to define the endemism of this species. Accordingly, *R. brasiliensis*,

erroneously reported in Africa in previous studies (Pegler 1977; Desjardin and Perry 2017), is resolved here as endemic to the Neotropics. In Africa, the sole species known *hitherto* is *R. degreefi*, which is recorded from several localities of the Afromontane ranges. *Ripartitella* is a tropical genus with four named species that are biogeographically well characterized: *Ripartitella degreefi* spanning over the African paleotropics, *R. brunnea* in Southeast Asian paleotropics, *R. brasiliensis* and *R. alba* in the Neotropics. One should also mention the unnamed *Ripartitella* sp. from the Southern Pacific (New Zealand).

For the African *Laetiporus*, the classical monograph on East African polypores (Ryvarden and Johansen 1980) reported only *L. sulphureus* in tropical Africa, a species well-known in the temperate northern hemisphere. Later on, *L. discolor*, originally described from Mauritius, was found to represent the sole African *Laetiporus*.

In the present work, four distinct genotypes, morphotypes and ecotypes were concordant in delimiting four species, two of which being described as new, *Laetiporus oboensis* and *L. tenuiculus*. They differ in pileus size and color, and hymenial pores size. In micromorphology, they differ in basidiospores size.

At a continental scale, tropical African *Laetiporus* are restricted to the afromontane area, with an east-west dichotomy. Geographically, *L. discolor* and *Laetiporus* sp.1 are native and hypothetically restricted to the East African montane range down and the Mascarene. This study reports for the first time *L. discolor* in the Albertine Rift. In the Gregorian Rift, it was reported by Chepkirui et al. (2017) under *Laetiporus* sp. from the Kakamega forest in western Kenya, that stands at 1500 masl. We also support that the unnamed clade H (*sensu* Song

and Cui 2017) (EU840662/RV4A; EU840663/RV5A) from South Africa corresponds to *L. discolor*. *Laetiporus* sp.1 is represented by two collections from Ethiopia and remains undescribed, due to lack of voucher specimens. *Laetiporus oboensis* and *L. tenuiculus* are conservatively considered endemic to the Sao Tomé montane range, where they occur sympatrically, although their autecology should be better characterized. Their potential distribution in the western Africa montane ranges remains to be ascertained.

This study also confirms that each African *Armillaria* is geographically confined, with no or few overlap in the marginal areas of distribution. The African endemic major lineage consists of two species, resolved as *A. heimii* s.l. and *A. camerunensis*. Their distribution reflects a dichotomy high vs. lowland. In the biogeographical scheme, *A. camerunensis* would span mainly to the Guineo-Congolian region sensu White (1986). Conversely, *A. heimii* s.l. is spanning over the Afromontane range sensu White (1986). Nevertheless, the two species may occur sympatrically in the Ruwenzori foothills (Virunga NP) where there exists a transitional submontane forest (1150-1750 m asl) (Lebrun 1960). *Armillaria heimii* and *A. camerunensis* may be considered morphological cryptic species, morphologically similar. However, ecological and phylogenetic species concepts are retained here as the main distinguishing criteria.

Current fungi taxonomies tend to regard the phylogenetic species concept, based on DNA divergence and the Genealogical concordance, as the most powerful (Taylor et al. 2000). It has the value of clarifying ambiguous morphologically cryptic species and allopatric biological groups. However, in some cases, without ecological data, the phylogenetic species concept may be less conclusive. In this study, the

divergent distribution (highland vs lowland) of the two African *Armillaria* clades was of great importance in delineating *A. heimii* and *A. camerunensis*. This has not been noted in previous studies.

Previous phylogenetic studies (Coetzee et al. 2000; Pérez-Sierra et al. 2004; Coetzee et al. 2005) also failed to clarify the status of *Armillaria fuscipes*, because biogeographic issues were not sufficiently integrated. It is intriguing that *A. fuscipes*, which type is from Sri Lanka (Petch 1909), had been considered as an African endemic species for a long time (Pegler 1986; Watling 1992). Previous studies also supported that *A. fuscipes* is the correct name in stand of *A. heimii*. But their conclusions were limited by lacking the type sequence of *A. fuscipes*. This study questioned African *A. fuscipes* concept by integrating collection from Sri Lanka, the type locality of *A. fuscipes* Petch (1909). Phylogenetic data showed that at least two *Armillaria* species are present in Sri Lanka, with two distinct evolutionary backgrounds. They belong to the Australasian and the Melleioid major clade, respectively. This confirms that it was not introduced into Sri Lanka from Africa nor did it originate from Africa.

Our results, furthermore, would confirm that *A. fuscipes* is not present at all in Africa. This assumption marks a turning point to previous literature which had erroneously considered *A. fuscipes* as an African endemic species introduced to Sri Lanka on tea or on trees associated with tea plantations.

Integrative approach also confirmed that *A. borealis*, *A. ostoyea*, *A. cepistipes*, *A. lutea* and *A. tabescens* reported from the Albertine rift in previous publications are based on misidentifications. These taxa belong to the Holarctic major clade, a lineage that has no representative native from Tropical Africa. This clade, nonetheless, is represented in

Tropical Africa by a species of the *A. mellea* complex, as a result of human mediated introductions of species through agriculture or forestry.

## 7.2. Perspectives

This study has provided many perspectives on fungal diversity in Africa. Globally, the study supports that, a large fraction of the 199 genera reported in Albertine Rift need revision. Additionally, at least 500 large fungi species remain to be discovered.

Within the genus *Ripartitella*, Pegler (1977) reported *R. brasiliensis* from Kenya, Tanzania and Uganda. Further studies should confirm that these reports also represent *R. degreefii*, whose distribution and related ecology remain to be more ascertained. Further collections from the mountain ranges of the Great East African Rift (especially from Ethiopia, Tanzania, Kenya) and from the West African mountain ranges (Mount Cameroon, Bioko, etc.) are needed to confirm the distribution and ecology of the species. Future studies could also evaluate the bioactives compounds and other potential uses of the new species "*Ripartitella degreefii*". Out of Africa, *Ripartitella* sp. from New Zealand remains uncertain.

In the genus *Armillaria*, the status of *A. fuscipes* s.s. remains to be ascertained. DNA sequences from the type would greatly help to ascertain the species concept of *A. fuscipes*, and its origin. Further collections are also needed to confirm its range and ecology. Collection in natural ecosystems could provide more information to support the hypothesis of a native or, conversely, a human introduced species in Sri Lanka, in the context of the development of the tea industry, whose origins should be searched for in northern India. Several species of

*Armillaria* have been described from northern India (Chandra and Watling 1981); type studies and recollections in its native range in northern India may allow a name to be found for these species. A comprehensive phylogeny combining the sequences from the North Indian collections (Chandra and Watling 1981) with the sequences from the Sri Lankan isolates of the Melleiod clade should allow the status of the latter and its hypothetical introduction into Sri Lanka through the development of the tea industry to be established.

Phylogenetic data revealed subclades within *A. heimii* s.l. However, it is still uncertain which of these subclades would represent *A. heimii* s.s., if any. Recollection of the species in Madagascar, in the vicinity of the type locality, and addition of sequences could bring clues to better circumscribe *A. heimii* s.s. Epitypification would fix the circumscription of *A. heimii*.

We also recommend an in-depth revision of the sexual systems within the African *Armillaria* to check whether or not they are consistent with the phylogenetic structure, which is especially pertinent in the *A. heimii* s.l. clade. It could be searched for correspondences between subclades and the mating system, or in phylogenetic terms, if the mating system represents subclade apomorphy (e.g., subclade 1 and homothally vs subclade 2 and heterothallic), within the *A. heimii* s.l. clade. The mating system could represent a species marker, or a population marker.

The mating system within *A. camerunensis* also should be ascertained. It has been reported to be homothallic and heterothallic (Table 5.4). A new study is needed to definitively confirm whether *A. camerunensis* is strictly heterothallic bipolar or if both homothallic and heterothallic monofactorial coexist.

*Armillaria* is a root rot pathogen of forest trees and of several perennial crops. Studies on African species should be continued from a plant pathology perspective.

*Armillaria* is one of the edible wild mushrooms of the Albertine Rift region. It is sometimes seen in local markets in villages around Virunga NP. However, little is known about its nutritional value and bioactive compounds such as secondary metabolites.

This study also opens new research perspectives for the genus *Laetiporus* on the continent. From a taxonomic point of view, the unresolved clade from the Ethiopian collections (*Laetiporus* sp.1) requires further study once sufficient material becomes available.

*Laetiporus discolor* is an edible species found in eastern DRC. It is consumed by local people around Kahuzi-Biega NP and Virunga NP. Working on Kenyan collections, Chepkirui et al. (2017) showed *L. discolor* has a potential medicinal use. We have no data on the local use of *L. oboensis* and *L. tenuiculus*. This work suggests further studies from nutritional and medicinal perspectives, as it is the case for the European *L. sulphureus* (Hassan et al. 2021; Adamska 2023). Further studies could also provide more data to consider the cultivation of African species.

*Laetiporus* has been reported as a pathogen of several woody species in Africa, particularly on imported *Eucalyptus*. *Eucalyptus* is an important fuelwood in the region. More data is needed from the pathological, and ahead, economic perspectives.

The approaches used in this thesis could be applied to revise many of the African taxa whose identity remain uncertain or debated. For instance, an ongoing study of the African *Echinochaete* (Rizinde et

al. in progress) showed that the polypore species *E. brachypora*, which is currently reported as a pantropical taxon, is absent from Tropical Africa. *Echinochaete brachypora* s.s. is restricted to the Neotropics. In tropical Africa, it is replaced by at least two taxa, whose distribution “lowland” vs “highland” is similar to that of *Armillaria heimii* and *A. camerunensis*.

This is the case for more African species. In addition, future studies could consolidate biological approaches based on reproductive isolation. However, matting tests are difficult for fungi lacking meiospores, or because of homothallism of some fungal taxa (*Armillaria*) and difficulties in spore germination on artificial media (*Laetiporus*, *Termitomyces*).

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