



# A comprehensive multigene phylogeny of *Phylloporia* (*Hymenochaetaceae*, *Basidiomycota*), with an emphasis on tropical African species

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**Abstract:** *Phylloporia* (*Hymenochaetaceae*) is becoming a very large and complex genus and the species definition is becoming a challenge, as for many other groups of *Hymenochaetaceae*. *Phylloporia* comprises 79 species up to date. However, this number is probably still largely underestimated. A comprehensive, multigene phylogeny of *Phylloporia* (*Hymenochaetaceae*, *Basidiomycota*), inferred from the large subunit nuclear ribosomal region (LSU), portions of the translation elongation factor 1- $\alpha$  (*TEF-1 $\alpha$* ), and second largest subunit of RNA polymerase II (*RPB2*) genes is presented and discussed. The multigene phylogeny reveals several undescribed paleotropical or neotropical phylogenetic species. On this basis, complemented by both morphological and ecological data, six new species from tropical Africa are described: *P. afropectinata*, *P. cinnamomea*, *P. memecylii*, *P. miomboensis*, *P. pseudoweberiana*, and *P. warneckeicola*. A new combination, *P. microspora* (basionym *Inonotus microsporus*), is also proposed. A synthesis of the taxonomic and ecological knowledge of *Phylloporia* in tropical Africa is presented, with an identification key for the African species known to date. Although the multigene phylogenetic inferences do not resolve the backbone structure within *Phylloporia*, it reveals two main lineages, a basal A and a core B lineage. The basal lineage contains six species whereas the core lineage comprises most of the described species and a number of unnamed taxa. The multigene phylogenetic inferences also resolved several well-supported, multiple species lineages within the core lineage. These lineages are predominantly biogeographically structured with a dichotomy Neotropics vs Paleotropics. They are discussed in relation to the morpho-ecological types.

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## INTRODUCTION

*Hymenochaetaceae* (*Hymenochaetales*, *Basidiomycota*) represent a very diverse family, and its taxonomic, phylogenetic, biogeographic, and ecological knowledges are continuously improving (e.g., Zhou *et al.* 2016a, 2018, Corfixen & Parmasto 2017, Ji *et al.* 2017a, Korotkin *et al.* 2018, Chen *et al.* 2019, Zhu *et al.* 2019, Salvador-Montoya *et al.* 2022, Wu *et al.* 2022). Several genera have been well studied, at a local or worldwide scale, including e.g., *Fomitiporia* (Chen & Cui 2017, Morera *et al.* 2017, Alves *et al.* 2020a, b), *Fulviformes* (Zhou 2015a, Ji *et al.* 2017b, Salvador-Montoya *et al.* 2018b, Olou *et al.* 2019, Zheng *et al.* 2021), *Fomitiporella* (Zhou 2014, Ji *et al.* 2018, Pildain *et al.* 2018, Salvador-Montoya *et al.* 2020), *Phellinus* (Brazee 2015, Campos-Santana *et al.* 2016, Cloete *et al.* 2016, Zhou *et al.* 2016c, Zhu *et al.* 2018), *Phylloporia* (e.g., Zhou 2015b,

Ferreira Lopes *et al.* 2016, Chen *et al.* 2017, Wu *et al.* 2019, 2020a, Chamorro-Martínez *et al.* 2022, Zhou *et al.* 2022, Olou *et al.* 2023), or the pair *Sanghuangporus* / *Tropicoporus*, previously known as the *Inonotus linteus* complex (e.g., Ghobad-Nejhad 2015, Tomšovský 2015, Coelho *et al.* 2016, Zhou *et al.* 2016b, Salvador-Montoya *et al.* 2018a, Zhu *et al.* 2019, Wu *et al.* 2020b, Shen *et al.* 2021).

Nevertheless, although the knowledge about *Hymenochaetaceae* has improved greatly, the geographical coverage remains significantly uneven, with large gaps. For instance, the vast equatorial forests of Southeast Asia have received little attention since Corner (1991). Similarly, tropical Africa, and more specifically areas such as the plant-rich Guineo-Congolian centre of endemism, or the forests of the Congo basin, remain also largely under surveyed (Cheek *et al.* 2020).

*Phylloporia* is typified by *P. parasitica* (Murrill 1904), a species originally described from South America



(Colombia), growing on an unidentified species of *Bignonia* (*Bignoniaceae*). Its basidiomes are unique within the *Hymenochaetaceae*, emerging from the abaxial sides of living leaves, with an intrafolial vegetative phase. *Phylloporia parasitica* is known only from a handful of specimens. This dearth of records may result from the peculiar substrate, making it difficult to observe, but also from the very narrow ecological requirements for growth and reproduction. Hence, the species can be catalogued as rare.

*Phylloporia* remained monospecific for seven decades, until Ryvarden (1972) broadened its concept, including species with distinctly pileate basidiomes. The first monographic revision of the genus, including phylogenetic data, dates to Wagner & Ryvarden (2002), who proposed a comprehensive review and eventually accepted 12 species. Since then, numerous studies, based on phylogenetic, morphological, and ecological data, revealed a much higher than expected taxonomic diversity, and the number of described species to date has risen to 79 (e.g., Yombiyeni & Decock 2017, Wu *et al.* 2019, 2020a, Chamorro-Martínez *et al.* 2022, Zhou *et al.* 2022, Castro Hernández *et al.* 2023, Olou *et al.* 2023).

Seventy-nine species might represent a low figure, however. Olou *et al.* (2021), using model-based methods for species delimitation and relying on the variability of LSU sequences data, estimated the number of putative species ranging from 82 to 100. A handful of undescribed species were also shown by previous phylogenetic inferences (Decock *et al.* 2015, Yombiyeni & Decock 2017, Jerusalem *et al.* 2019) and remain to date unnamed in the Linnaean system. Furthermore, Yombiyeni & Decock (2017) also pointed out that several species currently known as circumtropical have variable autecological parameters such as, and significantly, multiple botanical hosts. Given that most, if not all, *Phylloporia* species might be habitat, substrate, and host specific (e.g., Valenzuela *et al.* 2011, Decock *et al.* 2013, Yombiyeni & Decock 2017, Bittencourt *et al.* 2018, Jerusalem *et al.* 2019, Wu *et al.* 2020a, 2021, 2022, Zhou *et al.* 2022), these circumtropical “multiple hosts” species may each represent a collective species, harbouring a taxonomic diversity that is arguably as diverse as that of their hosts. It includes the tropical species *P. chrysites*, *P. fruticum*, *P. parasitica*, *P. pectinata*, *P. spathulata*, or still *P. weberiana* (Wagner & Ryvarden 2002). This is also the case for the pantemperate species *P. ribis*, reported from North America and Eurasia. *Phylloporia ribis* was declined into as many multiple forms as their known host plants (e.g., *f. arbuti*, *f. euonymi*, *f. loniceriae*, *f. rosae*, etc., Bourdot & Galzin 1928, Bondartsev 1971, Wagner & Ryvarden 2002), each representing a potential host-specific species. Speciation in *Phylloporia* may have been driven by substrate and host specialisation, with multiple host jumps. The number of potential species should therefore still rise significantly.

*Phylloporia* species are very variable regarding several traits of their life cycles, morphologies, mitism (i.e., the differentiation of the hyphal system), and substrate relationships (e.g., Yombiyeni *et al.* 2015, Wu *et al.* 2019, 2022). Their nutritional strategy (biotrophic interaction with the host plant) is not fully understood, if at all (e.g., Decock *et al.* 2015, Wu *et al.* 2019, 2022, Chamorro-Martínez *et al.* 2022). Based on the combination of life history, basidiome habit, hyphal system, and substrate relationships, Yombiyeni

*et al.* (2015) proposed to sort *Phylloporia* species into several morphotypes, each assigned to a specific ecology, thereby defining morpho-ecological types; these include e.g., the *P. parasitica*, *P. pectinata*, *P. ribis*, or *P. spathulata* morpho-ecological types (MET). These METs could represent hypotheses of structuring within *Phylloporia*, but this has not been tested by DNA-based approaches. Indeed, although knowledge of the taxonomic diversity of *Phylloporia* has improved considerably (see above), its phylogenetic structure remains largely unresolved.

So far, most phylogenetic analyses have relied on nuclear LSU sequence data that was shown to be appropriate for species delimitation (e.g., Decock *et al.* 2015, Ferreira Lopes *et al.* 2016, Wu *et al.* 2019, 2020a, 2022, Olou *et al.* 2021, 2023). However, the LSU-based phylogenetic inferences provide no resolution in deeper nodes. Olou *et al.* (2021, 2023) proposed a “multigene” phylogenetic analysis, including data either from LSU and ITS (2021) or LSU, ITS, and partial *TEF-1α* (2023). However, the number of ITS and partial *TEF-1α* in these two analyses is low to very low comparatively to the LSU sequences. Olou *et al.* (2023) used 38 sequences of ITS and 20 sequences of partial *TEF-1α*, scattered in the data set, and 127 LSU sequences. De facto, the phylogenetic signal of the LSU predominates in the tree reconstruction whereas the phylogenetic signal of *TEF-1α* is very restricted or even insignificant. The resulting phylogenetic structure does not differ from that retrieved based on LSU alone, with no support of the internal nodes. Furthermore, the ITS sequences of *Phylloporia* proved to be difficult to align (Decock *et al.* 2015, Wei *et al.* 2024) and species present various indels of variable length. For instance, Decock *et al.* (2015) showed presence of two indels of 85 and 13 bp long in the ITS1 and ITS2 of *P. flabelliformis* and *P. gabonensis*, compared to, e.g., the sequence of *P. parasitica*, and this is not at all discussed by Olou *et al.* (2021, 2023).

Wu *et al.* (2019), using the most comprehensive LSU dataset available by then, showed four lineages within *Phylloporia*, designated as “neutral term groups (A–D)”. However, none of these “neutral term groups” were statistically supported, regardless of the phylogenetic hypothesis tested (parsimony or probabilistic). The species within these “neutral term groups” are also heterogeneous when it concerns the basidiome habit, the hyphal system, the substrate preference, the host plants (when known), and the geographic distribution. Olou *et al.* (2021) recognized only two well-supported lineages within *Phylloporia* but without any further discussion.

Continuing the ongoing taxonomic and phylogenetic studies of *Phylloporia* in tropical Africa and worldwide (Valenzuela *et al.* 2011, Decock *et al.* 2013, 2015, 2024, Yombiyeni *et al.* 2015, Yombiyeni & Decock 2017, Jerusalem *et al.* 2019), we provide in this study comprehensive multilocus phylogenetic analyses (LSU, partial *TEF-1α*, and *RPB2* genes) of the genus, which were performed on the most complete datasets to date, including specimens and species from diverse areas of the Paleo- and Neotropics and Northern pantemperate area.

Numerous unnamed terminal clades emerged, of which 12 are based on tropical African specimens, and correspond to as many phylogenetic species. Seven of these African phylogenetic species showed also a unique combination

of morphological (although sometimes subtle) character and ecological features, including substrate affinities and, for some taxa, host specificity, that allow distinguishing concomitantly seven morpho- and ecological species. On this basis, and according to the consolidated species concept (Quaedvlieg *et al.* 2014), six species are described as new and illustrated, *Phylloporia afropectinata*, *P. cinnamomea*, *P. memecylii*, *P. miomboensis*, *P. pseudoweberiana*, and *P. warneckeicola*. The new combination *Phylloporia microspora* is also proposed. A dichotomous key to the described species currently reported from tropical Africa is provided.

The objective of this study was also to investigate the relevance of the morpho-ecological types (Yombiyeni *et al.* 2015) as structuring elements within *Phylloporia*, using this multilocus molecular phylogenetic analysis, which is discussed.

## MATERIALS AND METHODS

### Collection localities

The specimens examined were collected in several locations of tropical Africa, corresponding to distinct ecosystems (White 1983, Kindt *et al.* 2014, Marshall *et al.* 2021). Four locations are situated within the range of the Guineo-Congolian phytogeographic region, administratively in Gabon, Southern Cameroon, and Western Kenya, including the Rabi forest monitoring plot (~ S 01°55'28.5", E09°52'48", elev. ~ 30–60 masl), that belongs to the network of the Centre for Tropical Forest Science – Forest Global Earth Observatory (CTFS-ForestGEO, Anderson-Teixera *et al.* 2014) in Gabon; the Northern/North-eastern area of the Ipassa-Makokou Biosphere Reserve, next to the Ipassa-Makokou Research Station (~ N 00°31'18", E12°45'24", elev. ~ 540 masl), in the Ivindo National Park (Vande Weghe 2006) in Gabon; The Southern area of the Dja Biosphere Reserve (Sonké & Couvreur 2014) in Cameroon (~ N 03°01'31", E12°59'59", elev. ~ 675 masl); and the Kakamega Forest (Wagner *et al.* 2008) in Western Kenya (~ N00°17'30", E34°51'22", elev. ~ 1500 masl). The Rabi Forest monitoring plot belongs to the Lower Guinean rainforests whereas the Dja Reserve, and the Northern/North-eastern area of the Ipassa-Makokou Reserve are to some extent influenced by Congolian rainforests. The Kakamega Forest is an isolated remnant of the Guineo-Congolian rainforests, constituted with a mix of Guineo-Congolian species at their easternmost limits of distribution (White 1983, Wagner *et al.* 2008, Kindt *et al.* 2014).

Two other locations are situated inside the Zambezian phytogeographic region and belong to the seasonally dry Zambezian open forests (White 1983, Mapaire 1994), in Zimbabwe. They are the Victoria Falls National Park (~ S17°55'14", E25°50'55", elev. ~ 890 masl) and an area in the vicinity of the Kariba Lake (~ S17°08'23", E27°50'30", elev. ~ 480 masl), perhaps corresponding to the Miombo open woodlands (White 1983).

Finally, a last spot is located inside the Afromontane phytogeographic region, in the medium elevation Afromontane Forest in the Mount Elgon National Park, in Kenya (~ N01°2'42.30", E34°47'18.18", elev. ~ 2130 masl).

### Identification and description of specimens

The type specimens of the new species are deposited at BR, MUCL, NMK/EA (Herbarium acronyms are noted according to Thiers, continuously updated). Colours are described according to Kornerup & Wanscher (1981). Sections of the basidiomes were incubated for one hour at 40 °C in a NaOH 3 % solution, then carefully dissected under a stereomicroscope and examined in NaOH 3 % solution at room temperature (Decock *et al.* 2010, 2013). To study the staining reaction of the hyphae and basidiospores, sections of the basidiomes were examined in Melzer's reagent, lactic acid Cotton blue, and KOH 4 %. All microscopic measurements were done in Melzer's reagent. In presenting the size range of microscopic elements, 5 % of the measurements at each end of the range are given in parentheses when relevant. The following abbreviations are used: av. = arithmetic mean, R = the ratio of length/width of basidiospores, and ave<sub>R</sub> = arithmetic mean of the ratio R. As a rule, whenever possible, 30 microscopic elements of the basidiomes (pores / hyphae / basidiospores) were measured from each specimen.

### Molecular study and phylogenetic analysis

DNA extraction, amplification and sequencing of the 5' end of the nuclear ribosomal LSU rDNA gene, partial *TEF-1α* 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 & Decock (2013). Successful PCR amplifications resulted in a single band observed on a 0.8 % agarose gel. The 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 LR0R, LR3, LR3R, LR5 for the LSU region; 2212R, 1577F, 983F, 1567R for the *TEF-1α* gene (Rehner & Buckley 2005, Matheny *et al.* 2007); and bRPB2-6F and bRPB2-7.1R for the *RPB2* gene (Matheny 2005). Sequences were assembled and edited with Sequencher™ v. 4.8 software (Gene Codes Corporation, Ann Arbor, MI, USA).

Based on BLAST results (BLAST searches done on 21/12/2023), a combined dataset (including nuclear ribosomal partial LSU and partial *TEF-1α* and *RPB2* genes) comprising sequences from 296 collections (including the outgroup) was constructed and used for further phylogenetics analyses.

Materials and sequences used in this study are listed in Table 1. Nucleotide sequences were automatically aligned with the MUSCLE algorithm (Edgar 2004) with default settings, then manually adjusted as necessary with PhyDE® v. 0.9971 (Müller *et al.* 2010). Potentially ambiguously aligned segments were also detected using the Gblocks v. 0.91b program (Castresana 2000) with the following parameter settings: minimum number of sequences for a conserved position = 154 (minimum possible); minimum number of sequences for a flank position = 154 (minimum possible); maximum number of contiguous non-conserved positions = 4 bp, minimum block size = 4 bp and gaps allowed within



Table 1. GenBank accession numbers of sequences used in this study.

(Genera) / Species	Country	Collection reference	Substrate / host	GenBank Accession No.			References
				LSU	RPB2	TEF-1 $\alpha$	
<b><i>Flaviporellus</i></b>							
<i>F. splitgerberi</i>	French Guiana	JV 1908/6	Hardwoods of many kinds	MZ437386	—	—	Wu <i>et al.</i> (2022)
<b><i>Fomitiporella</i></b>							
<i>F. caryophylli</i>	Indonesia	MUCL 43120 / FRI-359-C	<i>Shorea robusta</i> (Dipterocarpaceae), trunk	PP851445	PP853863	—	This study
<i>F. resupinata</i>	Cameroon	DMC 476 (IT)	<i>Entandrophragma cylindricum</i> (Meliaceae), dead wood	JF712935	—	—	Douanla-Meli <i>et al.</i> (2007)
<b><i>Fulvifomes</i></b>							
<i>F. cf. rimosus</i>	Zimbabwe	MUCL 38440	Fabaceae, living trunk	PP853446	PP853864	PP853674	This study
	Zimbabwe	MUCL 38446	Fabaceae, living trunk	PP853447	PP853865	PP853675	This study
<b><i>Phylloporia</i></b>							
<i>P. afropectinata</i> sp. nov.	Kenya	KE 16 107	<i>Turraea</i> cf. <i>holstii</i> (Meliaceae), living trunk	KY349147	PP853866	PP853676	Yombiyeni & Decock (2017), this study
	Kenya	MUCL 58359	<i>Turraea</i> cf. <i>holstii</i> (Meliaceae), living trunk	KY349148	PP853867	PP853677	Yombiyeni & Decock (2017), this study
	Kenya	KE 16 148	<i>Turraea</i> cf. <i>holstii</i> (Meliaceae), living trunk	PP851450	PP853868	PP853678	This study
	Kenya	KE 17 212	<i>Turraea</i> cf. <i>holstii</i> (Meliaceae), living trunk	PP851451	PP853869	PP853679	This study
	Kenya	KE 17 214	<i>Turraea</i> cf. <i>holstii</i> (Meliaceae), living trunk	PP851452	PP853870	PP853680	This study
	Kenya	KE 17 215	<i>Turraea</i> cf. <i>holstii</i> (Meliaceae), living trunk	PP851453	PP853871	PP853681	This study
	Kenya	KE 17 216	<i>Turraea</i> cf. <i>holstii</i> (Meliaceae), living trunk	PP851454	PP853872	PP853682	This study
	Kenya	KE 17 218	<i>Turraea</i> cf. <i>holstii</i> (Meliaceae), living trunk	PP851455	PP853873	PP853683	This study
<i>P. afrospathulata</i>	Gabon	MUCL 53983	Ground, probably associated with roots	KJ743249	PP853874	PP853684	Yombiyeni <i>et al.</i> (2015), this study
	Gabon	MUCL 54511 (HT)	Ground, probably associated with roots	KJ743248	PP853875	PP853685	Yombiyeni <i>et al.</i> (2015), this study
<i>P. alyxiae</i>	Taiwan	Chen 1182 (HT)	<i>Alyxia insularis</i> (Apocynaceae), living branches	LC514407	—	—	Wu <i>et al.</i> (2020)
	Taiwan	GC 1604-28	<i>Alyxia insularis</i> (Apocynaceae), living branches	LC514408	—	—	Wu <i>et al.</i> (2020)
<i>P. atlantica</i>	Brazil	URM 91182 (HT)	<i>Eschweilera</i> cf. <i>ovata</i> (Lecythidaceae), living trunk	NG_068815	—	—	Wu <i>et al.</i> (2019)
<i>P. beninensis</i>	Benin	MA-RB22-22 / F23-111	<i>Trichilia emetica</i> (Meliaceae), base of living trunk	PP851458	—	PP853686	This study
	Benin	MA-RB22-29 / F23-113	<i>Trichilia emetica</i> (Meliaceae), base of living trunk	PP851459	—	PP853687	This study
	Benin	OAB0107	Unidentified angiosperm, dead stump	MW244097	—	—	Olou <i>et al.</i> (2021)
	Benin	OAB0511 (HT)	Unidentified angiosperm, dead stump	MW244096	—	—	Olou <i>et al.</i> (2021)
<i>P. boldo</i>	Chile	MR 12573	<i>Peumus boldus</i> (Monimiaceae), living stems	MK193759	—	PP853688	Rajchenberg <i>et al.</i> (2019), this study
	Chile	BAFC 52947	<i>Peumus boldus</i> (Monimiaceae), living stems	MK193756	—	PP853689	Rajchenberg <i>et al.</i> (2019), this study
	Chile	BAFC 52945 (HT)	<i>Peumus boldus</i> (Monimiaceae), living stems	MK193758	—	PP853690	Rajchenberg <i>et al.</i> (2019), this study



Table 1. (Continued).

(Genera) / Species	Country	Collection reference	Substrate / host	GenBank Accession No.			References
				LSU	RPB2	TEF-1 $\alpha$	
<i>P. chrysites</i>	Chile	BAFC 52946	<i>Peumus boldus</i> (Monimiaceae), living stems	MK193757	—	—	Rajchenberg <i>et al.</i> (2019), this study
	Mexico	MUCL 52763	Unidentified angiosperm	HM635665	PP853876	—	Valenzuela <i>et al.</i> (2011), this study
	Mexico	MUCL 52764	Unidentified angiosperm	HM635666	PP853877	—	Valenzuela <i>et al.</i> (2011), this study
	Mexico	MUCL 52862	<i>Neopringlea</i> sp. (Salicaceae)	HM635667	PP853878	PP853691	Valenzuela <i>et al.</i> (2011), this study
	Mexico	RV 856	Unidentified angiosperm	PP851466	—	—	This study
<i>P. cinnamomea</i> sp. nov.	Cameroon	LR 50722 (HT)	Unidentified angiosperm, unknown plant organs	PP851467	PP853879	PP853692	This study
	Gabon	YOM 5	Unidentified angiosperm, living small stems	KJ743283	PP853880	PP853693	Yombiyeni <i>et al.</i> (2015), this study
<i>P. clausenae</i>	China	Cui 8463	<i>Clausena</i> sp. (Rutaceae), living tree	MH165868	MH161216	MH167424	Zhou (2015b) and unpublished GenBank sequences
<i>P. crataegi</i>	China	Dai 18133	<i>Crataegus</i> sp. (Rosaceae), living roots	MH165865	MH161224	MH167431	Zhou & Dai (2012) and unpublished GenBank sequences
<i>P. crystallina</i>	Ecuador	JV2106-102 (HT)	Unidentified angiosperm, freshly dead stump	ON006467	—	—	Zhou <i>et al.</i> (2022)
<i>P. cystidiolophora</i>	China	Dai 13945	Unidentified angiosperm, living tree	MG738798	MH161226	—	Wu <i>et al.</i> (2019) and unpublished GenBank sequences
	China	Dai 13953 (HT)	Unidentified angiosperm, living tree	NG_068812	MH161227	MH167438	Wu <i>et al.</i> (2019) and unpublished GenBank sequences
<i>P. dependens</i>	China	BJFC 013379 (HT)	Unidentified angiosperm, rotten stump	NG_064385	—	—	Liu <i>et al.</i> (2015)
	China	Cui 13763	Unidentified angiosperm, rotten stump	KX242353	—	—	Chen <i>et al.</i> (2017)
<i>P. elegans</i>	China	Dai 13167	Unidentified angiosperm, rotten stump	KP698746	—	—	Liu <i>et al.</i> (2015)
<i>P. ephedrae</i>	Brazil	FLOR 51178 (HT)	Unidentified angiosperm, living roots	KJ631408	—	—	Ferreira Lopes <i>et al.</i> (2016)
	Turkmenistan	TAA 72-2	<i>Ephedra</i> sp. (Ephedraceae), on base of living stems	AF411826	—	—	Wagner & Ryvarden (2002)
<i>P. flabelliformis</i>	Gabon	MUCL 55568	<i>Dichostemma</i> sp. (Euphorbiaceae), living trunk	KU198351	PP853881	PP853694	Decock <i>et al.</i> (2015), this study
	Gabon	MUCL 55569 (HT)	<i>Dichostemma</i> sp. (Euphorbiaceae), living trunk	KU198349	PP853882	PP853695	Decock <i>et al.</i> (2015), this study
<i>P. flacourtiae</i>	Gabon	MUCL 55570	<i>Dichostemma</i> sp. (Euphorbiaceae), living trunk	KU198350	PP853883	—	Decock <i>et al.</i> (2015), this study
	China	Yuan 6204 (PT)	<i>Flacourtia</i> sp. (Salicaceae), living branches	KJ787802	—	—	Zhou (2015b)
<i>P. fontanesiae</i>	China	Yuan 6360 (PT)	<i>Flacourtia</i> sp. (Salicaceae), living branches	KJ787801	—	—	Zhou (2015b)
	China	Li 194	<i>Fontanesia</i> sp. (Oleaceae), living trunk	JF712924	—	—	Zhou & Dai (2012)
	China	Li 199 (HT)	<i>Fontanesia</i> sp. (Oleaceae), living trunk	JF712925	—	—	Zhou & Dai (2012)
<i>P. cf. fruticum</i>	Mexico	MX11	Unidentified angiosperm, living trees and bushes	HM635669	PP853884	PP853696	Valenzuela <i>et al.</i> (2011), this study
<i>P. fulva</i>	Gabon	MUCL 54472 (IT)	Unidentified angiosperm, living small-stemmed tree	KJ743247	PP853885	PP853697	Yombiyeni <i>et al.</i> (2015), this study
<i>P. gabonensis</i>	Gabon	MUCL 55572 (HT)	<i>Dichostemma glaucescens</i> (Euphorbiaceae), living trunk	KU198353	PP853886	PP853698	Decock <i>et al.</i> (2015), this study
<i>P. gutta</i>	China	Cui 6945	<i>Abelia</i> sp. (Caprifoliaceae), dead stump	—	MH161214	MH167422	Unpublished GenBank sequences



Table 1. (Continued).

(Genera) / Species	Country	Collection reference	Substrate / host	GenBank Accession No.			References
				LSU	RPB2	TEF-1 $\alpha$	
<i>P. hainaniana</i>	China	Dai 16070	<i>Abelia</i> sp. ( <i>Caprifoliaceae</i> ), dead stump	MH165863	MH161215	MH167423	Zhou & Dai (2012) and unpublished GenBank sequences
	China	Dai 9460 (HT)	Unidentified angiosperm, living tree	JF712928	—	—	Cui <i>et al.</i> (2010)
	China	Dai 16142	Unidentified angiosperm, living tree	MH165866	—	MH167437	Unpublished GenBank sequences
<i>P. inonotoides</i>	Gabon	GA17-01	<i>Crotonogyne gabonensis</i> ( <i>Euphorbiaceae</i> ), living trunk	PP851475	PP853887	—	This study
	Gabon	MJ-GA19-034	<i>Crotonogyne gabonensis</i> ( <i>Euphorbiaceae</i> ), living trunk	PP851476	—	—	This study
	Gabon	MJ-GA19-108	<i>Crotonogyne gabonensis</i> ( <i>Euphorbiaceae</i> ), living trunk	PP851477	—	PP853699	This study
<i>P. lespedezae</i>	Gabon	MUCL 54468 (HT)	<i>Crotonogyne gabonensis</i> ( <i>Euphorbiaceae</i> ), living trunk	KJ743250	PP853888	PP853700	Yombiyeni <i>et al.</i> (2015), this study
	Gabon	MUCL 54469	<i>Crotonogyne gabonensis</i> ( <i>Euphorbiaceae</i> ), living trunk	KJ743251	PP853889	PP853701	Yombiyeni <i>et al.</i> (2015), this study
	Gabon	MUCL 54470	<i>Crotonogyne gabonensis</i> ( <i>Euphorbiaceae</i> ), living trunk	KJ743252	PP853890	PP853702	Yombiyeni <i>et al.</i> (2015), this study
	China	Dai 17065	<i>Lespedeza bicolor</i> ( <i>Fabaceae</i> ), base of living trunk	KY242602	MH161211	MH167419	Ren & Wu (2017) and unpublished GenBank sequences
	China	Dai 17067 (HT)	<i>Lespedeza bicolor</i> ( <i>Fabaceae</i> ), base of living trunk	KY242603	MH161212	MH167420	Ren & Wu (2017) and unpublished GenBank sequences
<i>P. littoralis</i>	China	Dai 17069	<i>Lespedeza bicolor</i> ( <i>Fabaceae</i> ), base of living trunk	KY242601	—	—	Ren & Wu (2017) and unpublished GenBank sequences
	Gabon	MUCL 56144 (IT)	<i>Nichallea</i> sp. ( <i>Rubiaceae</i> ), living stems	KY349140	PP853891	PP853703	Yombiyeni & Decock (2017), this study
	Gabon	MUCL 56145	<i>Nichallea</i> sp. ( <i>Rubiaceae</i> ), living stems	KY349141	PP853892	—	Yombiyeni & Decock (2017), this study
<i>P. loniceræ</i>	Japan	Dai 17898	<i>Loniceræ japonica</i> ( <i>Caprifoliaceae</i> ), living stems	MG738800	MH161208	MH167416	Qin <i>et al.</i> (2018) and unpublished GenBank sequences
	Japan	IFP 019172 (HT)	<i>Loniceræ japonica</i> ( <i>Caprifoliaceae</i> ), living stems	MG647808	—	—	Qin <i>et al.</i> (2018) and unpublished GenBank sequences
<i>P. manglietiae</i>	China	Cui 5497	<i>Manglietia hainanensis</i> ( <i>Magnoliaceae</i> ), living trunk	MH165872	—	MH167435	Unpublished GenBank sequences
	China	Cui 13709 (HT)	<i>Manglietia hainanensis</i> ( <i>Magnoliaceae</i> ), living trunk	KX242358	MH161223	MH167430	Chen <i>et al.</i> (2017) and unpublished GenBank sequences
<i>P. memecylii</i> sp. nov.	Gabon	CD-GA12-812 (HT)	<i>Memecylon viride</i> ( <i>Melastomataceae</i> ), living trunk	KJ743281	PP853893	PP853704	Yombiyeni <i>et al.</i> (2015), this study
	Gabon	MJ-GA19-091	<i>Memecylon viride</i> ( <i>Melastomataceae</i> ), living trunk	PP851484	PP853894	PP853705	This study
	Gabon	MJ-GA19-093	<i>Memecylon viride</i> ( <i>Melastomataceae</i> ), living trunk	PP851485	PP853895	PP853706	This study
<i>P. microspora</i> comb. nov.	Zimbabwe	LR 26485 (HT)	<i>Colophospermum mopane</i> ( <i>Fabaceae</i> ), dying standing trunk	PP851486	—	PP853707	This study

Table 1. (Continued).

(Genera) / Species	Country	Collection reference	Substrate / host	GenBank Accession No.			References
				LSU	RPB2	TEF-1 $\alpha$	
<i>P. minima</i>	Australia	MUCL 43132 (PT)	<i>Vitis</i> sp. ( <i>Vitaceae</i> ), living stems	PP851487	PP853896	PP853708	Wu <i>et al.</i> (2022), This study
<i>P. minuta</i>	Brazil	FURB 55085	<i>Dolioscarpus schottianus</i> ( <i>Dileniaceae</i> ), living young stems	MG264040	—	—	Bittencourt <i>et al.</i> (2018)
	Brazil	FURB 55088 (HT)	<i>Dolioscarpus schottianus</i> ( <i>Dileniaceae</i> ), living young stems	NG_064479	—	—	Bittencourt <i>et al.</i> (2018)
<i>P. minutipora</i>	China	Dai 16172	Unidentified angiosperm, living tree	MH165873	—	MH167436	Unpublished GenBank sequences
<i>P. minutispora</i>	DRC	MUCL 52865	Unidentified angiosperm, living roots	HM635671	PP853897	PP853709	Valenzuela <i>et al.</i> (2011), this study
<i>P. miomboensis</i> sp. nov.	Zimbabwe	LR 25885 (HT)	Unidentified angiosperm, small-stemmed living trunk	PP851489	PP853898	PP853710	This study
<i>P. montana</i>	Brazil	BDNA2388	Unidentified angiosperm	MG738810	—	—	Wu <i>et al.</i> (2019)
	Brazil	BDNA2472	Unidentified angiosperm	MG738812	—	—	Wu <i>et al.</i> (2019)
<i>P. mori</i>	Taiwan	Wu 1105-2 (HT)	<i>Morus</i> sp. ( <i>Moraceae</i> ), living trunk	LC514412	—	—	Wu <i>et al.</i> (2020)
<i>P. moricola</i>	China	Wu 1807-1 (HT)	<i>Morus</i> sp. ( <i>Moraceae</i> ), living trunk	LC589617	—	—	Wu <i>et al.</i> (2021)
<i>P. murrayae</i>	Taiwan	Wu 1404-4 (HT)	<i>Murraya paniculata</i> ( <i>Rutaceae</i> ), living trunk	LC514409	—	—	Wu <i>et al.</i> (2020)
<i>P. mutabilis</i>	Benin	OAB0643 (HT)	On soil under angiosperm of dry dense forest	OR096136	—	OR161068	Olou <i>et al.</i> (2023)
	Benin	OAB0666	On soil under angiosperm of dry dense forest	OR096137	—	OR359376	Olou <i>et al.</i> (2023)
<i>P. nandinae</i>	China	Dai 10588 (HT)	<i>Nandina domestica</i> ( <i>Berberidaceae</i> ), living stems	JF712930	—	—	Zhou & Dai (2012)
	China	Dai 10625	<i>Nandina domestica</i> ( <i>Berberidaceae</i> ), living stems	JF712931	MH161228	MH167439	Zhou & Dai (2012) and unpublished GenBank sequences
<i>P. nouraguensis</i>	French Guiana	MUCL 53816 (HT)	<i>Myrcia</i> cf. <i>guyanensis</i> ( <i>Myrtaceae</i> ), living twigs	KC136222	PP853899	PP853711	Decock <i>et al.</i> (2013), this study
	French Guiana	MUCL 5381	<i>Myrcia</i> cf. <i>guyanensis</i> ( <i>Myrtaceae</i> ), living twigs	KC136223	PP853900	PP853712	Decock <i>et al.</i> (2013), this study
	French Guiana	MUCL 53818	<i>Myrcia</i> cf. <i>guyanensis</i> ( <i>Myrtaceae</i> ), living twigs	KC136224	PP853901	PP853713	Decock <i>et al.</i> (2013), this study
<i>P. oblongospora</i>	China	Zhou 179 (HT)	Unidentified angiosperm, living branches	JF712932	—	—	Cui <i>et al.</i> (2010)
<i>P. oreophila</i>	China	Cui 2219	Unidentified angiosperm, living roots	JF712933	—	—	Zhou & Dai (2012)
	China	Cui 9503 (HT)	Unidentified angiosperm, living roots	JF712934	—	—	Zhou & Dai (2012)
<i>P. osmanthi</i>	China	Yuan 5655 (HT)	<i>Osmanthus</i> sp. ( <i>Oleaceae</i> ), base of living stems	KF729938	—	—	Zhou (2015a)
<i>P. pectinata</i>	India	MUCL 58123 / CBS 445.76	<i>Murraya</i> sp.	PP851493	—	PP853714	This study
	Australia	R. Coveny 113	<i>Rhodamnia rubescens</i> ( <i>Myrtaceae</i> ), living trunk	AF411823	MH161213	MH167421	Wagner & Ryvarden (2002) and unpublished GenBank sequences
<i>P. pendula</i>	China	Cui 13691 (HT)	Unidentified angiosperm, living trunk	KX242357	MH161218	MH167426	Chen <i>et al.</i> (2017) and unpublished GenBank sequences
	China	Cui 13876	Unidentified angiosperm, living trunk	KX901670	MH161219	MH167427	Chen <i>et al.</i> (2017) and unpublished GenBank sequences
<i>P. perangusta</i>	China	Dai 18139 (HT)	Unidentified angiosperm, living trunk	NG_068813	MH161204	MH167413	Wu <i>et al.</i> (2019) and unpublished GenBank sequences



Table 1. (Continued).

(Genera) / Species	Country	Collection reference	Substrate / host	GenBank Accession No.			References
				LSU	RPB2	TEF-1 $\alpha$	
<i>P. peristrophidis</i>	Pakistan	Ahmad 27088 (HT)	<i>Peristrophe bicalyculata</i> (Acanthaceae), living stems	AF411824	—	—	Wu <i>et al.</i> (2022)
<i>P. pseudopectinata</i>	China	Cui 13746	Unidentified angiosperm, living trunk	KX 242355	MH161221	MH167428	Chen <i>et al.</i> (2017) and unpublished GenBank sequences
	China	Cui 13749 (HT)	Unidentified angiosperm, living trunk	KX242356	MH161222	MH167429	Chen <i>et al.</i> (2017) and unpublished GenBank sequences
<b><i>P. pseudoweberiana</i> sp. nov.</b>	Kenya	KE15-02 (HT)	<i>Rawsonia lucida</i> (Achariaceae), living trunk	KU358722	PP853902	PP853715	Decock <i>et al.</i> (2015), this study
	Kenya	KE15-19	<i>Rawsonia lucida</i> (Achariaceae), living trunk	KU358723	PP853903	PP853716	Decock <i>et al.</i> (2015), this study
<i>P. radiata</i>	China	LWZ 20141122-5	Living liana	KU904470	—	MH167434	Zhou (2016) and unpublished GenBank sequences
	China	LWZ 20141122-6 (HT)	Living liana	KU904471	—	MH167433	Zhou (2016) and unpublished GenBank sequences
<i>P. rattanicola</i>	China	Dai 18232	Dead <i>Rattan</i> sp. (Areaceae)	MG738806	MH161205	MH167414	Wu <i>et al.</i> (2019) and unpublished GenBank sequences
	China	Dai 18235 (HT)	Dead <i>Rattan</i> sp. (Areaceae)	MG738808	MH161207	MH167415	Wu <i>et al.</i> (2019) and unpublished GenBank sequences
<i>P. ribis</i> (f. on <i>Ribes rubrum</i> )	France	CL—F09-041	<i>Ribes rubrum</i> (Grossulariaceae), base of living trunk	MN239483	PP853904	PP853717	Jerusalem <i>et al.</i> (2019), this study
	Belgium	MA02—F19-158	<i>Ribes rubrum</i> (Grossulariaceae), base of living trunk	PP851497	PP853905	PP853718	This study
	France	MJ-HL21-028	<i>Ribes rubrum</i> (Grossulariaceae), base of living trunk	PP851498	PP853906	—	This study
	France	MJ-HL21-029	<i>Ribes rubrum</i> (Grossulariaceae), base of living trunk	PP851499	PP853907	PP853719	This study
	USA	MUCL 58155 / FP-94142-T	<i>Ribes alpinum</i> (Grossulariaceae), base of living trunk	PP851500	PP853908	PP853720	This study
<i>P. ribis</i> (f. on <i>Cornus mas</i> )	France	LY 7658	<i>Cornus mas</i> (Cornaceae), base of living trunk	PP851501	PP853909	PP853721	This study
<i>P. ribis</i> (f. on <i>Crataegus monogyna</i> )	France	Duchemin 15311	<i>Crataegus monogyna</i> (Rosaceae), base of living trunk	PP851502	PP853910	PP853722	This study
<i>P. ribis</i> (f. on <i>Euonymus europaeus</i> )	France	CD-AV-SN	<i>Euonymus europaeus</i> (Celastraceae), base of living trunk	MN251251	PP853911	PP853723	Jerusalem <i>et al.</i> (2019), this study
	France	CD-HL-03	<i>Euonymus europaeus</i> (Celastraceae), base of living trunk	PP851504	—	—	This study
	France	CD-HL-04	<i>Euonymus europaeus</i> (Celastraceae), base of living trunk	PP851505	—	—	This study
	France	GC-AUDE-01	<i>Euonymus europaeus</i> (Celastraceae), base of living trunk	PP851506	PP853912	PP853724	This study
	France	GC-AUDE-02	<i>Euonymus europaeus</i> (Celastraceae), base of living trunk	PP851507	PP853913	PP853725	This study



Table 1. (Continued).

(Genera) / Species	Country	Collection reference	Substrate / host	GenBank Accession No.			References
				LSU	RPB2	TEF-1 $\alpha$	
<i>P. ribis</i> (f. on <i>Jasminum fruticans</i> )	Czech Republic	LZ 2360	Unidentified angiosperm, base of living trunk	PP851508	PP853914	PP853726	This study
	Italy	MC1 F19-172a	<i>Euonymus europaeus</i> (Celastraceae), base of living trunk	PP851509	PP853915	PP853727	This study
	Italy	MC2 F19-173a	<i>Euonymus europaeus</i> (Celastraceae), base of living trunk	PP851510	PP853916	PP853728	This study
	France	MJ-HL21-001	<i>Euonymus europaeus</i> (Celastraceae), base of living trunk	PP851511	PP853917	PP853729	This study
	France	MJ-HL21-002	<i>Euonymus europaeus</i> (Celastraceae), base of living trunk	PP851512	PP853918	PP853730	This study
	France	MJ-HL21-003	<i>Euonymus europaeus</i> (Celastraceae), base of living trunk	PP851513	PP853919	PP853731	This study
	France	MUCL 35089	<i>Euonymus europaeus</i> (Celastraceae), base of living trunk	—	—	PP853732	This study
	France	LY 256	<i>Jasminum fruticans</i> (Oleaceae), living stems	PP851514	PP853920	PP853733	This study
	France	LY 1198	<i>Jasminum fruticans</i> (Oleaceae), living stems	PP851515	—	—	This study
	France	MJ-HL21-023	<i>Jasminum fruticans</i> (Oleaceae), living stems	PP851516	PP853921	PP853734	This study
	France	MJ-HL21-024	<i>Jasminum fruticans</i> (Oleaceae), living stems	PP851517	PP853922	PP853735	This study
	France	MJ-HL21-025	<i>Jasminum fruticans</i> (Oleaceae), living stems	PP851518	PP853923	PP853736	This study
	France	MJ-HL21-026	<i>Jasminum fruticans</i> (Oleaceae), living stems	PP851519	PP853924	PP853737	This study
<i>P. ribis</i> (f. on <i>Prunus spinosa</i> )	France	MJ-HL21-027	<i>Jasminum fruticans</i> (Oleaceae), living stems	PP851520	PP853925	—	This study
	France	CD-AV-SN2	<i>Prunus spinosa</i> (Rosaceae), base of living trunk	MN240847	PP853926	PP853738	Jerusalem <i>et al.</i> (2019), this study
<i>P. ribis</i> (f. on <i>Rosa</i> sp.)	France	MJ-HL21-017-CL1	<i>Rosa canina</i> (Rosaceae), base of dead branches	PP851522	—	—	This study
	France	MJ-HL21-017-CL2	<i>Rosa canina</i> (Rosaceae), base of dead branches	PP851523	—	—	This study
	France	MJ-HL21-018-CL1	<i>Rosa canina</i> (Rosaceae), base of dead branches	PP851524	—	PP853739	This study
	France	MJ-HL21-018-CL2	<i>Rosa canina</i> (Rosaceae), base of dead branches	PP851525	—	PP853740	This study
	France	CD-CA-01	<i>Ulex europaeus</i> (Fabaceae), base of living trunk	PP851526	PP853927	PP853741	This study
<i>P. ribis</i> (f. on <i>Ulex europaeus</i> )	Portugal	MUCL 56411 / CBS 579.50	<i>Ulex europaeus</i> (Fabaceae), base of living trunk	MN240818	PP853928	PP853742	Jerusalem <i>et al.</i> (2019), this study
	France	LY 7445	<i>Ulmus minor</i> (Ulmaceae), base of living trunk	PP851528	PP853929	PP853743	This study
<i>P. ribis</i> (f. on <i>Ulmus minor</i> )	Gabon	MJ-GA19-025	<i>Rinorea</i> sp. (Violaceae), living branches or twigs	PP851529	PP853930	PP853744	This study
<i>P. rinoreae</i>	Gabon	MJ-GA19-029	<i>Rinorea</i> sp. (Violaceae), living branches or twigs	PP851530	PP853931	PP853745	This study
	Gabon	MJ-GA19-032	<i>Rinorea</i> sp. (Violaceae), living branches or twigs	PP851531	PP853932	PP853746	This study



Table 1. (Continued).

(Genera) / Species	Country	Collection reference	Substrate / host	GenBank Accession No.			References
				LSU	RPB2	TEF-1 $\alpha$	
<i>P. rzedowskii</i>	Gabon	MUCL 56283 (HT)	<i>Rinorea</i> sp. ( <i>Violaceae</i> ), living branches or twigs	MN243144	PP853933	PP853747	Jerusalem <i>et al.</i> (2019), this study
	Gabon	MUCL 57328	<i>Rinorea</i> sp. ( <i>Violaceae</i> ), living branches or twigs	MN243146	PP853934	PP853748	Jerusalem <i>et al.</i> (2019), this study
	Mexico	MUCL 52859	<i>Hybanthus mexicanus</i> ( <i>Violaceae</i> ), living branches	HM635673	PP853935	PP853749	Valenzuela <i>et al.</i> (2011), this study
	Mexico	MUCL 52860 (PT)	<i>Hybanthus mexicanus</i> ( <i>Violaceae</i> ), living branches	HM635674	PP853936	PP853750	Valenzuela <i>et al.</i> (2011), this study
	Mexico	MUCL 52861	<i>Hybanthus mexicanus</i> ( <i>Violaceae</i> ), living branches	HM635675	PP853937	PP853751	Valenzuela <i>et al.</i> (2011), this study
<i>P. solicola</i>	Brazil	JRF145 (HT)	Ground, associated with roots	MG738815	—	—	Wu <i>et al.</i> (2019)
<i>Phylloporia</i> sp.	Ecuador	EC22-01	Unidentified angiosperm, liana	PP851537	PP853938	PP853752	This study
	Ecuador	EC22-02	Unidentified angiosperm, liana	PP851538	PP853939	PP853753	This study
	Ecuador	EC22-03	Unidentified angiosperm, liana	PP851539	PP853940	PP853754	This study
	Ecuador	EC22-04	Unidentified angiosperm, liana	PP851540	PP853941	PP853755	This study
	Ecuador	EC22-05	Unidentified angiosperm, liana	PP851541	PP853942	PP853756	This study
	Ecuador	EC22-12	Unidentified angiosperm, base of living trunk	PP851542	PP853943	PP853757	This study
	Ecuador	EC22-13	Unidentified angiosperm, base of living trunk	PP851543	PP853944	PP853758	This study
	Ecuador	EC22-14	Unidentified angiosperm, base of living trunk	PP851544	PP853945	PP853759	This study
	Ecuador	EC22-17	Ground, probably associated with roots	—	PP853946	PP853760	This study
	Ecuador	EC22-18	Ground, probably associated with roots	PP851545	PP853947	PP853761	This study
	Ecuador	EC22-19	Ground, probably associated with roots	PP851546	PP853948	PP853762	This study
	Ecuador	EC22-20	Ground, probably associated with roots	PP851547	PP853949	PP853763	This study
	Ecuador	EC22-21	Ground, probably associated with roots	PP851548	—	PP853764	This study
	Ecuador	EC22-22	Ground, probably associated with roots	PP851549	—	PP853765	This study
	Ecuador	EC22-23	Ground, probably associated with roots	PP851550	PP853950	PP853766	This study
	French Guiana	FG10-238	Unidentified angiosperm, living trunk	KY349159	PP853951	PP853767	Yombiyeni & Decock (2017), this study
	French Guiana	FG10-321	Unidentified angiosperm, trunk	KJ743277	PP853952	PP853768	Yombiyeni <i>et al.</i> (2015), this study
	French Guiana	FG11-462	Ground, probably associated with roots	KC136228	PP853953	PP853769	Decock <i>et al.</i> (2013), this study
	French Guiana	FG11-506	Ground, probably associated with roots	KC136227	PP853954	PP853770	Decock <i>et al.</i> (2013), this study
	French Guiana	FG12-522	Ground, probably associated with roots	KJ743259	PP853955	—	Decock <i>et al.</i> (2013), this study
	French Guiana	FG12-523	Ground, probably associated with roots	KJ743260	PP853956	PP853771	Decock <i>et al.</i> (2013), this study
	French Guiana	FG13-670	Unidentified angiosperm, trunk	KJ743262	PP853957	PP853772	Yombiyeni <i>et al.</i> (2015), this study
	French Guiana	FG13-671	Ground, among mosses, probably associated with roots	PP851558	PP853958	PP853773	This study
	French Guiana	FG13-721	Unidentified angiosperm, trunk	KJ743263	PP853959	PP853774	Yombiyeni <i>et al.</i> (2015), this study
	French Guiana	FG13-722	Unidentified angiosperm, trunk	KJ743264	PP853960	PP853775	Yombiyeni <i>et al.</i> (2015), this study
	French Guiana	FG13-726	Ground, probably associated with roots	KJ743279	PP853961	PP853776	Yombiyeni <i>et al.</i> (2015), this study

Table 1. (Continued).

(Genera) / Species	Country	Collection reference	Substrate / host	GenBank Accession No.			References
				LSU	RPB2	TEF-1 $\alpha$	
	French Guiana	FG13-749	Ground, probably associated with roots	KJ743280	PP853962	PP853777	Yombiyeni <i>et al.</i> (2015), this study
	French Guiana	FG13-754	Ground, probably associated with roots	KJ743281	PP853963	PP853778	Yombiyeni <i>et al.</i> (2015), this study
	French Guiana	FG14-850	Unidentified angiosperm, living liana	—	PP853964	PP853779	This study
	French Guiana	FG14-855	Unidentified angiosperm, living trunk	PP851564	PP853965	PP853780	This study
	French Guiana	FG15-929	Ground, probably associated with roots	PP851565	PP853966	PP853781	This study
	French Guiana	FG15-930	Ground, probably associated with roots	KY363574	PP853967	PP853782	Yombiyeni & Decock (2017), this study
	French Guiana	FG15-931	Ground, probably associated with roots	PP851567	PP853968	PP853783	This study
	French Guiana	FG15-932	Ground, probably associated with roots	KY363573	PP853969	—	Yombiyeni & Decock (2017), this study
	French Guiana	FG15-959	Ground, probably associated with roots	KY349157	PP853970	PP853784	Yombiyeni & Decock (2017), this study
	French Guiana	FG15-961	Ground, probably associated with roots	KY349158	PP853971	PP853785	Yombiyeni & Decock (2017), this study
	French Guiana	FG15-965	Ground, probably associated with roots	PP851571	PP853972	PP853786	This study
	French Guiana	FG15-966	Ground, probably associated with roots	PP851572	PP853973	PP853787	This study
	Gabon	GA-RABI-01	Unidentified angiosperm, living liana	PP851573	PP853974	PP853788	This study
	Brazil	ISA 352	Unknown substrate	KJ743267	PP853975	PP853789	Yombiyeni <i>et al.</i> (2015), this study
	Martinica	MA15-96	Ground, among mosses, probably associated with roots	KY349149	PP853976	PP853790	Yombiyeni & Decock (2017), this study
	Martinica	MA15-97	Ground, among mosses, probably associated with roots	KY349150	PP853977	PP853791	Yombiyeni & Decock (2017), this study
	Martinica	MA15-115	Unidentified angiosperm, living liana	PP851577	PP853978	—	This study
	Martinica	MA15-126	Soil, among mosses, probably associated with roots	KY349151	PP853979	PP853792	Yombiyeni & Decock (2017), this study
	Martinica	MA15-127	Soil, among mosses, probably associated with roots	KY349152	PP853980	—	Yombiyeni & Decock (2017), this study
	Martinica	MA15-CL1	Soil, among mosses, probably associated with roots	PP851580	PP853981	PP853793	This study
	Martinica	MA15-CL2	Soil, among mosses, probably associated with roots	PP851581	PP853982	PP853794	This study
	Martinica	MA16-130	Ground, probably associated with roots	PP851582	PP853983	PP853795	This study
	Martinica	MA16-131	Ground, probably associated with roots	PP851583	PP853984	PP853796	This study
	Martinica	MA16-133	Ground, probably associated with roots	PP851584	PP853985	PP853797	This study
	Martinica	MA16-137	Ground, probably associated with roots	PP851585	PP853986	PP853798	This study
	Martinica	MA16-150	Unidentified angiosperm, living trunks	PP851586	PP853987	PP853799	This study



Table 1. (Continued).

(Genera) / Species	Country	Collection reference	Substrate / host	GenBank Accession No.			References
				LSU	RPB2	TEF-1 $\alpha$	
	Martinica	MA16-158	Unidentified angiosperm, living trunks	PP851587	PP853988	PP853800	This study
	Martinica	MA16-165	Unidentified angiosperm, living trunks	PP851588	PP853989	PP853801	This study
	Martinica	MA16-174	Ground, among mosses, probably associated with roots	PP851589	PP853990	PP853802	This study
	Martinica	MA16-186	Ground, probably associated with roots	PP851590	PP853991	PP853803	This study
	Martinica	MA16-193	Ground, probably associated with roots	PP851591	PP853992	PP853804	This study
	Martinica	MA16-194	Ground, probably associated with roots	PP851592	PP853993	PP853805	This study
	Martinica	MA16-197	Ground, probably associated with roots	PP851593	PP853994	PP853806	This study
	Martinica	MA16-199	Ground, probably associated with roots	PP851594	PP853995	PP853807	This study
	Martinica	MA16-209	Ground, among mosses, probably associated with roots	PP851595	—	—	This study
	Martinica	MA16-211	Ground, among mosses, probably associated with roots	PP851596	PP853996	PP853808	This study
	Martinica	MA16-217	Unidentified angiosperm, living liana	PP851597	PP853997	PP853809	This study
	Martinica	MA16-218	Unidentified angiosperm, living trunks	PP851598	PP853998	PP853810	This study
	Martinica	MA16-219	Unidentified angiosperm, living trunks	PP851599	PP853999	PP853811	This study
	Martinica	MA16-223	Unidentified angiosperm, living trunks	PP851600	PP854000	—	This study
	Martinica	MA16-228	Ground, among mosses, probably associated with roots	PP851601	PP854001	PP853812	This study
	Martinica	MA16-234	Ground, among mosses, probably associated with roots	PP851602	PP854002	PP853813	This study
	Martinica	MA16-235	Ground, among mosses, probably associated with roots	PP851603	PP854003	PP853814	This study
	Martinica	MA16-236	Ground, among mosses, probably associated with roots	PP851604	PP854004	PP853815	This study
	Martinica	MA16-237	Ground, among mosses, probably associated with roots	PP851605	PP854005	PP853816	This study
	Martinica	MA19-PL1	Unidentified liana	PP851606	PP854006	PP853817	This study
	Martinica	MA19-PP1	Unidentified angiosperm, living trunks	—	PP854007	PP853818	This study
	Martinica	MA19-PS1	Ground, among mosses, probably associated with roots	—	PP854008	PP853819	This study
	Martinica	MA19-PS2	Ground, among mosses, probably associated with roots	PP851607	PP854009	PP853820	This study
	Martinica	MA19-PS3	Ground, among mosses, probably associated with roots	PP851608	PP854010	PP853821	This study
	Martinica	MA19-PS4	Ground, among mosses, probably associated with roots	PP851609	PP854011	PP853822	This study



Table 1. (Continued).

(Genera) / Species	Country	Collection reference	Substrate / host	GenBank Accession No.			References
				LSU	RPB2	TEF-1 $\alpha$	
Martinica	Martinica	MA19-PS5	Ground, probably associated with roots	PP851610	PP854012	PP853823	This study
Martinica	Martinica	MA19-PS8	Ground, probably associated with roots	PP851611	PP854013	PP853824	This study
Martinica	Martinica	MA19-PS10	Ground, probably associated with roots	PP851612	PP854014	PP853825	This study
Martinica	Martinica	MA19-PS16	Ground, probably associated with roots	PP851613	PP854015	PP853826	This study
Martinica	Martinica	MA19-PS17	Ground, among mosses, probably associated with roots	PP851614	PP854016	—	This study
Martinica	Martinica	MA19-PS18	Ground, probably associated with roots	PP851615	PP854017	PP853827	This study
Martinica	Martinica	MA19-PX2	Ground, probably associated with roots	PP851616	PP854018	PP853828	This study
Martinica	Martinica	MA19-PX3	Ground, probably associated with roots	PP851617	PP854019	PP853829	This study
Martinica	Martinica	MA19-PX4	Ground, probably associated with roots	—	PP854020	PP853830	This study
Cuba	Cuba	MUCL 43733	Unknown substrate	KJ743278	PP854021	—	Yombiyeni <i>et al.</i> (2015), this study
Cuba	Cuba	MUCL 45062	Unidentified angiosperm, trunk	KJ743284	PP854022	PP853831	Yombiyeni <i>et al.</i> (2015), this study
Ecuador	Ecuador	MUCL 52864	Ground, probably associated with roots	HM635676	—	—	Valenzuela <i>et al.</i> (2011)
Mexico	Mexico	MUCL 53433	Unidentified angiosperm	KC136231	PP854023	PP853832	Decock <i>et al.</i> (2013), this study
Brazil	Brazil	MUCL 54226	Unidentified liana	KJ743270	PP854024	PP853833	Yombiyeni <i>et al.</i> (2015), this study
Brazil	Brazil	MUCL 54263	Unidentified angiosperm, dead trunk	PP851622	PP854025	PP853834	This study
Brazil	Brazil	MUCL 54288	Unknown substrate	KJ743268	PP854026	PP853835	Yombiyeni <i>et al.</i> (2015), this study
Brazil	Brazil	MUCL 54295	Unknown substrate	KJ743269	PP854027	PP853836	Yombiyeni <i>et al.</i> (2015), this study
Mexico	Mexico	MX 01	Unknown substrate	PP851625	PP854028	PP853837	This study
Mexico	Mexico	MX 02	Unknown substrate	PP851626	PP854029	PP853838	This study
Gabon	Gabon	PY-SN3	Unknown substrate	PP851627	—	—	This study
Gabon	Gabon	PY-SN5	Unknown substrate	PP851628	PP854030	PP853839	This study
Gabon	Gabon	PY-SN6	Unknown substrate	PP851629	PP854031	PP853840	This study
Argentina	Argentina	Robledo 351	Ground, probably associated with roots	KC136226	—	—	Decock <i>et al.</i> (2013), this study
Argentina	Argentina	Robledo 526	<i>Allophylus edulis</i> (Sapindaceae), living twigs	KJ651914	PP854032	PP853841	This study
Argentina	Argentina	Robledo 527	<i>Allophylus edulis</i> (Sapindaceae), living twigs	KJ651915	PP854033	—	Decock <i>et al.</i> (2015), this study
Argentina	Argentina	Robledo 968	<i>Allophylus edulis</i> (Sapindaceae), living twigs	KJ651916	—	PP853842	Decock <i>et al.</i> (2015), this study
Argentina	Argentina	Robledo 1220	Unidentified angiosperm, living trunk	KC136225	—	MK265758	Decock <i>et al.</i> (2013)
Argentina	Argentina	Robledo 1467	Ground, probably associated with roots	KJ651918	—	PP853843	Unpublished GenBank sequences and this study
Argentina	Argentina	Robledo 1790	Ground, probably associated with roots	KJ651921	—	PP853844	Unpublished GenBank sequences and this study
Argentina	Argentina	Robledo 2984	Unknown substrate	MG457809	—	MK265757	Unpublished GenBank sequences
Thailand	Thailand	TH04-83	Unknown substrate	PP851635	PP854034	PP853845	This study



Table 1. (Continued).

(Genera) / Species	Country	Collection reference	Substrate / host	GenBank Accession No.			References
				LSU	RPB2	TEF-1 $\alpha$	
	DRC	Thoen 4902	<i>Englerophytum magalismontanum</i> (Sapotaceae), living branches	PP851636	PP854035	—	This study
	Argentina	Urcelay 625	Ground, probably associated with roots	PP851637	—	MG470837	Ferreira Lopes <i>et al.</i> (2016) and unpublished GenBank sequences
	Argentina	Urcelay 626	Ground, probably associated with roots	KT223570	—	PP853847	Ferreira Lopes <i>et al.</i> (2016) and unpublished GenBank sequences
	Argentina	Urcelay 628	Unknown substrate	MG457810	—	MG470834	Unpublished GenBank sequences
	Brazil	WI 117	Unknown substrate	KJ743271	PP854036	PP853848	Yombiyeni <i>et al.</i> (2015), this study
	Brazil	WI 333	Unknown substrate	KJ743272	PP854037	PP853849	Yombiyeni <i>et al.</i> (2015), this study
	Brazil	WI 555	Unknown substrate	KJ743274	PP854038	PP853850	Yombiyeni <i>et al.</i> (2015), this study
<i>P. cf. spathulata</i>	Mexico	Chay 456	Apocynaceae, root	AF411822	—	—	Wagner & Ryvarden (2002)
<i>P. subpulla</i>	China	Cui 5251	Tree, unidentified angiosperm	KU904468	—	—	Wu <i>et al.</i> (2019)
	China	Dai 9627	Tree, unidentified angiosperm	KU904469	—	—	Wu <i>et al.</i> (2019)
<i>P. sumacoensis</i>	Ecuador	JV2109-73 (HT)	Unidentified living liana	ON006468	—	—	Zhou <i>et al.</i> (2022)
<i>P. tamilnadensis</i>	India	MUCL 57837	<i>Catunaregam spinosa</i> (Rubiaceae), living branches	MN525279	PP854039	—	Jerusalem <i>et al.</i> (2019), this study
	India	MUCL 57838 (HT)	<i>Catunaregam spinosa</i> (Rubiaceae), living branches	MN525278	PP854040	—	Jerusalem <i>et al.</i> (2019), this study
<i>P. terrestris</i>	China	He 2359	Soil	MH165869	MH161220	—	Unpublished GenBank sequences
<i>P. tiliae</i>	China	Yuan 5491 (HT)	<i>Tilia</i> sp. (Tiliaceae), living trunks	KJ787805	—	—	Zhou (2015)
<i>P. ulloai</i>	Mexico	MUCL 52866	Unidentified living liana	HM635677	PP854041	PP853851	Valenzuela <i>et al.</i> (2011), this study
	Mexico	MUCL 52867 (HT)	Unidentified living liana	HM635678	PP854042	PP853852	Valenzuela <i>et al.</i> (2011), this study
	Mexico	MUCL 52870	Unidentified living liana	HM635679	PP854043	PP853853	Valenzuela <i>et al.</i> (2011), this study
<i>P. verae-crucis</i>	Mexico	F19-159	Ground, probably associated with roots	PP851647	PP854044	PP853854	This study
<i>P. warneckeicola</i> sp. nov.	Gabon	GA12-813	Living trunk, <i>Warneckea floribunda</i> (Melastomataceae)	KJ743253	PP854045	PP853855	Yombiyeni <i>et al.</i> (2015), this study
	Gabon	GA12-814	Living trunk, <i>Warneckea floribunda</i> (Melastomataceae)	KJ743256	PP854046	PP853856	Yombiyeni <i>et al.</i> (2015), this study
	Gabon	GA12-815	Living trunk, <i>Warneckea floribunda</i> (Melastomataceae)	KJ743257	PP854047	PP853857	Yombiyeni <i>et al.</i> (2015), this study
	Gabon	GA12-816	Living trunk, <i>Warneckea floribunda</i> (Melastomataceae)	KJ743255	PP854048	PP853858	Yombiyeni <i>et al.</i> (2015), this study
	Gabon	GA12-830	Living trunk, <i>Warneckea floribunda</i> (Melastomataceae)	PP851652	PP854049	—	This study
	Gabon	GA12-846	Living trunk, <i>Warneckea floribunda</i> (Melastomataceae)	KJ743254	PP854050	PP853859	Yombiyeni <i>et al.</i> (2015), this study

Table 1. (Continued).

(Genera) / Species	Country	Collection reference	Substrate / host	GenBank Accession No.			References
				LSU	RPB2	TEF-1 $\alpha$	
<i>P. yuchengii</i>	Gabon	MJ-GA19-017	Living trunk, <i>Warneckea floribunda</i> (Melastomataceae)	PP851654	PP854051	—	This study
	Gabon	MJ-GA19-020	Living trunk, <i>Warneckea floribunda</i> (Melastomataceae)	PP851655	PP854052	—	This study
	Gabon	MJ-GA19-048	Living trunk, <i>Warneckea floribunda</i> (Melastomataceae)	PP851656	PP854053	—	This study
	Gabon	MJ-GA19-055	Living trunk, <i>Warneckea floribunda</i> (Melastomataceae)	PP851657	PP854054	—	This study
	Gabon	MJ-GA19-069	Living trunk, <i>Warneckea floribunda</i> (Melastomataceae)	PP851658	PP854055	PP853860	This study
	Gabon	MJ-GA19-088	Living trunk, <i>Warneckea floribunda</i> (Melastomataceae)	PP851659	PP854056	PP853861	This study
	Gabon	MJ-GA19-092	Living trunk, <i>Warneckea floribunda</i> (Melastomataceae)	PP851660	PP854057	PP853862	This study
	Uzbekistan	YG 051 (HT)	Unidentified angiosperm, dead trunk	KM264325	—	—	Gafforov <i>et al.</i> (2014)

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 v. 4.0 (Maddison & Maddison 2005) and then compared with several annotated *Phylloporia* sequences available on GenBank (MK265749, MK265747, MK265763, MH167425, MH167437, MH167433).

Phylogenetic analyses were performed separately for each individual and concatenated loci using Bayesian inference (BI) as implemented in MrBayes v. 3.2 (Ronquist *et al.* 2012) and Maximum likelihood (ML) as implemented in RAXML v. 7.0.4 (Stamatakis 2006, Stamatakis *et al.* 2008).

*Fulviformes rimosus* MUCL 38440 and MUCL 38446 were designated as outgroups following the results in Jérusalem *et al.* (2019). Models of evolution for BI were estimated using the Akaike information criterion (AIC) as implemented in Modeltest v. 3.7 (Posada & Crandall 1998). In order to facilitate the data partitioning by codon position, the three clade specific, confidently alignable introns, present in the *TEF-1 $\alpha$*  partition and the one at the end of the *RPB2* partition were excised and analysed as a distinct partition. In order to reduce possible errors resulting from over-parameterization, the most appropriate partitioning scheme and substitution models for the combined dataset were determined with the program PartitionFinder v. 1.10 (Lanfear *et al.* 2012) under the AIC, using the “greedy” search option.

Therefore, the dataset was subdivided into six partitions: (LSU) (*RPB2* codons 1+2) (*RPB2* codon 3) (*TEF-1 $\alpha$*  codons 1+2) (*TEF-1 $\alpha$*  codon 3) (*TEF-1 $\alpha$*  introns, *RPB2* intron) (Table 2).

The best-fit models for each partition were implemented as partition-specific models within partitioned mixed-model analyses of the combined dataset (Table 2) and all parameters were unlinked across partitions. The combined dataset Bayesian analyses were implemented with four independent runs, each with four simultaneous independent chains for 120 M generations, starting from random trees, and keeping one tree every 1000th generation.

All trees sampled after convergence (av. standard deviation of split frequencies < 0.01) and confirmed using Tracer v. 1.4 (Rambaut & Drummond 2007) were used to reconstruct a 50 % majority-rule consensus tree (BC) and to calculate Bayesian posterior probabilities (PP). The 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. 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 ML BS values of 75 % or greater were considered supported by the data.

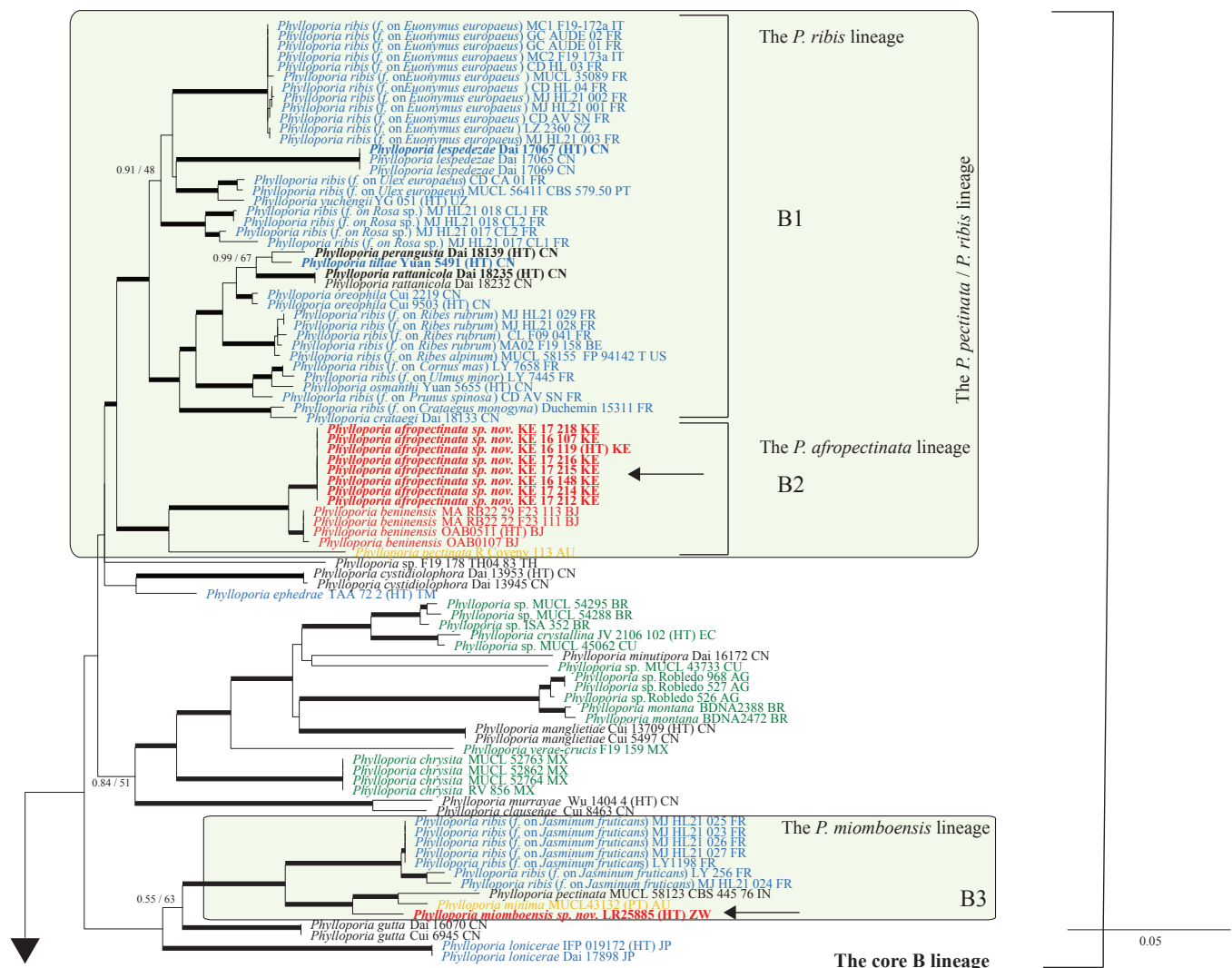
Nucleotide sequences are phylogenetically informative until they reach the substitution saturation, especially in coding sequences, saturation will be more pronounced in the rapidly evolving third codon position. At this point, it is no longer possible to deduce whether an observed similarity between a pair of sequences results from their common ancestry or



whether this has occurred by chance (Jeffroy *et al.* 2006). To detect the possible bias from substitution saturation, we tested the first, second and the third codon position of the coding region studied (*RPB2* and *TEF-1 $\alpha$* ) as well as the non-coding loci (*LSU*, *TEF-1 $\alpha$*  and *RPB2* introns) by using Xia's test (Xia *et al.* 2003, Xia & Lemey 2009), as implemented in DAMBE (Xia & Xie 2001). Because the critical index substitution saturation (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 perform the test for each subset to see if substitution saturation exists for these subsets of sequences. To confirm the results of the Xia's method we also plotted transitions and transversions at the first, second, and third codon positions against Tamura-

Nei genetic distances with the aid of the DAMBE package, with an asymptotic relationship indicating the presence of saturation.

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 & Kellogg 1996, Lutzoni *et al.* 2004, Reeb *et al.* 2004) compared with the software *compat.py* (Kauff & 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.



**Fig. 1.** Phylogenetic relationships of *Phylloporia* species inferred from partial *nucLSU* rDNA, partial *tef1- $\alpha$*  and *rbp2* genes sequences. Thickened branches represent bootstrap value (ML BS) and PP value greater than 75 % / 0.95. Names of specimens are highlighted following their biogeographical realms, according to Udvardy's system (blue: Holarctic region; red: Afrotropical region; black: Indomalayan/ Tropical Asia region; green: Neotropical region; yellow: Australasian region). Coloured boxes represent supported lineages whose members share common morpho-ecological traits. Boxes with dashed lines represent supported lineages whose members share a common biogeographic domain. The new African species described in this study are highlighted in bold. Abbreviations used. AG = Argentina; AU = Australia; BE = Belgium; BJ = Benin; BR = Brazil; CD = Democratic Republic of Congo; CL = Chile; CM = Cameroon; CN = China; CU = Cuba; CZ = Czech republic; EC = Ecuador; FG = French Guiana; FR = France; GA = Gabon; IN = India; IT = Italy; JP = Japan; KE = Kenya; MA = Martinique; MX = Mexico; PK = Pakistan; PT = Portugal; TH = Thailand; TM = Turkmenistan; TW = Taiwan; US = United States of America; UZ = Uzbekistan; ZW = Zimbabwe. (HT) = Type specimen.



## RESULTS

### Phylogenetic analysis

Sequences from 296 collections (288 LSU sequences, 214 *TEF-1α* and 214 *RPB2*) were used in our phylogenetic inferences. Missing *TEF-1α* and *RPB2* sequences concerned essentially Asian and South American collections recovered from GenBank. The final combined DNA sequence alignments of these three loci, including gaps, resulted in 2961 characters (LSU: 995 characters; *TEF-1α*: 1113 characters, of which 888 in the exon partition and 225 in the combined introns partition; *RPB2*: 853 characters, of which 786 in the exon partition and 67 in the combined introns partition). Summary statistics of sequence data, best-fit models and tests of substitution saturation for each dataset are provided in Table 2. 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 test of substitution saturation (Table 2) showed that the observed index of substitution saturation (Iss) for the *TEF-1α*, *RPB2* and introns partitions, was significantly lower than the corresponding Iss.c, indicating that there was little saturation in our sequences ( $P < 0.001$ ). On the other hand, the LSU partition showed signs of substitution saturation, indicating the unsuitability of these data for phylogenetic analysis. Nevertheless, re-analysing the LSU partition with DAMBE, after the exclusion of the 167 sites (18 % of a total of the original 995 sites)

retained by Gblocks, the substitution saturation test revealed an Iss value that was significantly ( $P < 0.001$ ) lower than the Iss.c (Table 2), indicating the suitability of this data for further phylogenetic analysis. We therefore included the LSU partition, excluding the ambiguous positions identified by Gblocks, in the combined dataset. In the ML searches, the combined dataset showed 1885 distinct patterns with a proportion of gaps and undetermined characters of 27.51 %, while the LSU only alignment had 612 distinct patterns with a proportion of gaps and undetermined characters of 15 %.

The two Bayesian runs converged to stable likelihood values after 87010000 generations; 32990 stationary trees from each analysis were used to compute a 50 % majority rule consensus tree and to calculate posterior probabilities (PP).

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, regarding the recovery and the relative positions of the different genera of *Hymenochaetaceae* included, were almost identical whatever the phylogenetic methodology and in accordance with previous results (Decock *et al.* 2013, 2015, Yombiyeni & Decock 2017). The *Phylloporia* lineage is very well supported in the multigene phylogeny (Fig. 1). The terminal clades also received significant support whereas most of the deeper internodes were variably supported (Fig. 1).

The phylogenetic analyses recovered several specimens of *Phylloporia* from tropical Africa as twelve additional distinct terminal clades or branches (Fig. 1), viz. the

**Table 2.** Summary of data sets used for phylogenetic inferences.

Properties	<i>TEF-1α</i>	<i>TEF-1α</i>	LSU	<i>RPB2</i>	<i>RPB2</i>	Introns
	1 <sup>st</sup> & 2 <sup>nd</sup>	3 <sup>rd</sup>		1 <sup>st</sup> & 2 <sup>nd</sup>	3 <sup>rd</sup>	
Alignment size	592	296	995	524	262	292
Excluded characters	—	—	167	—	—	—
Model selected	GTR+I+G	GTR+G	GTR+I+G	HKY+I+G	GTR+I+G	GTR+I+G
-Likelihood score	3.250.915	66.952.549	158.480.479	22.536.924	55.748.057	57.160.884
Base frequencies						
Freq. A	0.3087	0.1481	0.2381	0.2930	0.2577	0.2337
Freq. C	0.2099	0.2839	0.1629	0.2224	0.2145	0.2105
Freq. G	0.2783	0.3013	0.3245	0.2613	0.2669	0.2110
Freq. T	0.2031	0.2667	0.2745	0.2233	0.2610	0.3448
Proportion of invariable sites	0.5357	—	0.3963	0.6198	0.0689	0.1118
Gamma shape	0.5344	32.455	0.6493	0.7747	91.620	46.204
Test of substitution saturation <sup>1</sup>						
Iss	0.484	0.501	0.711	0.241	0.379	0.618
Iss.cSym	0.712	0.683	0.802	0.705	0.682	0.724
P (Sym)	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
Iss.cAsym	0.384	0.354	0.442	0.378	0.465	0.769
P (Asym)	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001

<sup>1</sup> 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).

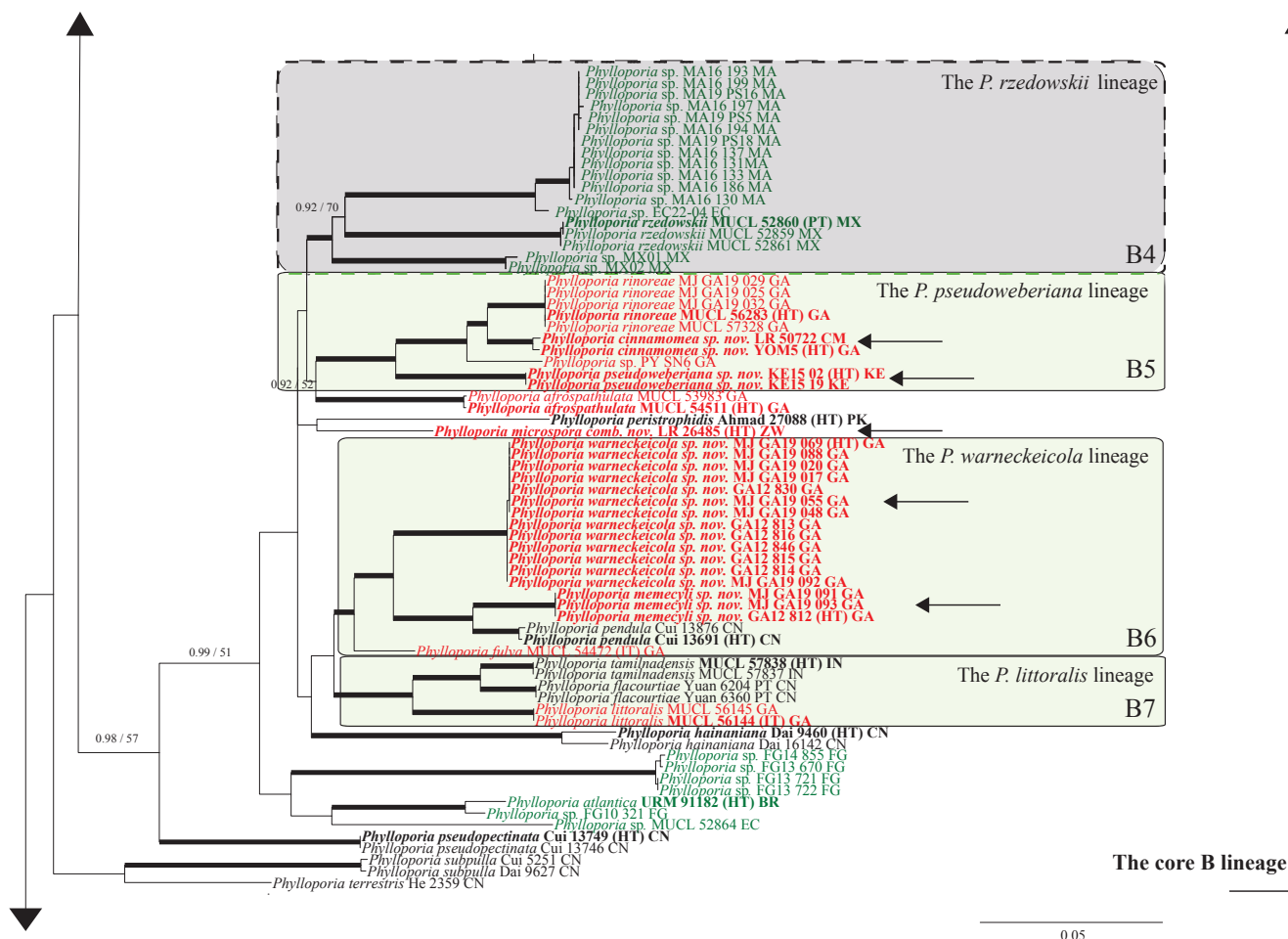


Fig. 1. (continued)

clade *P. afropectinata*, *P. cinnamomea*, *P. memecyli*, *P. pseudoweberiana*, and *P. warneckeicola*, as well as the branches *P. microspora*, *P. miomboensis* and *Phylloporia* spp. GA-RABI-01, PY-SN3, PY-SN5, PY-SN6, and Thoen 4902. These species clades are distant from all other species clades shown to date (Fig. 1, e.g., Jerusalem *et al.* 2019, Wu *et al.* 2019, 2020a).

### Morphological and ecological characteristics

Each of these terminal phylogenetic clades, which voucher specimens originated from tropical Africa, showed also a unique combination of morphological (although sometimes subtle) and autecological characters, including substrate and host affinities. They differ from their closest phylogenetic relatives in morphology, ecology, and habitat.

Based on the results of both phylogenetic inferences, morphological studies, and considering the autecological parameters, we described below six new species, viz. *Phylloporia afropectinata*, *P. cinnamomea*, *P. memecyli*, *P. miomboensis*, *P. pseudoweberiana*, and *P. warneckeicola*. The new combination *Phylloporia microspora* (basonym: *Inonotus microsporus*) is also proposed, and the species is redescribed.

### Taxonomy

***Phylloporia afropectinata*** Decock, Jerusalem, Amalfi & Castillo, *sp. nov.* MycoBank MB 851871. Figs 2, 3.

**Etymology:** “*afropectinata*” (Latin) is referring to the morphological resemblance with *P. pectinata*.

**Typus:** Kenya, Trans Nzoia Province, Mount Elgon National Park, ~N1°2'42.30", E34°47'18.18", elev. ~ 2130 masl, trunk of living tree, *Turraea* cf. *holstii* (Meliaceae), 31 Mar. 2016, C. Decock, KE-16-119 (**holotype** MUCL 58359; **isotype** NMK/E).

**Diagnosis:** *Phylloporia afropectinata* resemble *P. pectinata* sensu Corner (1991) by the combination of sessile, variably sized, compound, merismatoid basidiomes, with downward proliferation of imbricated pilei, but differs in having larger pores, 8–9 / mm vs 10–12 / mm, ellipsoid vs broadly ellipsoid to subglobose basidiospores (3.5–)3.8–4.3(–4.5) × (2.7–)3.0–3.5 µm vs 2.7–3.5 × 2–2.5 µm, host plant (*Turraea* cf. *holstii*, Meliaceae, vs *Timonius flavescens*, Rubiaceae), and inhabiting Afromontane middle elevation forest vs Southeast Asian rainforest.

**Description:** Basidiomes pileate, sessile, perennial, emerging solitary or simultaneously in small number, superposed; individual basidiomata attached by a small dorsal circular point, first semicircular, applanate in section, then becoming compound, merismatoid by successive downward proliferations of new and larger, imbricating pilei, the all compound basidiome triquetrous, triangular in transversal section, then ungulate, projecting mostly downward 3–8(–10) mm, 20–250 mm wide at the last growth, the margin outline of the last formed pileus semicircular to ellipsoid, with a general



oak brown]; pores small, regular, mostly round to ellipsoid, occasionally fused, 8–9/mm, 90–115(–120)  $\mu\text{m}$  diam. (av. = 101  $\mu\text{m}$  diam.); dissepiments thin, 20–65  $\mu\text{m}$  thick (av. = 40  $\mu\text{m}$ ); context very thin to almost absent, up to 500  $\mu\text{m}$  thick, homogeneous, dense, greyish brown, with a thin upper black line subtending an upper thin tomentum, up to 2.5 mm thick, tufted near the margin, progressively agglutinating toward the base, golden brown (5D7) to yellowish brown (5E8) in



section; tube layer up to 10 mm deep at the base, greyish brown. Hyphal system pseudodimitic (intermediate sensu Pegler 1996); generative hyphae simple septate, thin- to slightly thick-walled, hyaline to faintly yellowish, branched, with a constriction at the branching point, 1.3–2.5  $\mu\text{m}$  diam.; lower context, dominated by thick-walled (sclerified) generative, mostly parallel to long axis, tightly packed, arising from a generative hyphae, 3.0–4.0  $\mu\text{m}$  wide (av. = 3.4  $\mu\text{m}$ ), golden brown, darker (brown) in alkali, thick-walled but with the lumen wide, mostly aseptate throughout, or with few secondary septa near the apices; tomentum with prostrate to erected hyphae, mostly unbranched, thick-walled with widely open lumen, septate with both true and secondary septa, the apices rounded to open, yellowish to brown, mostly 3.5–4  $\mu\text{m}$  diam.; hymenophoral trama dominated by thick-walled (sclerified) generative, supporting hyphae, subparallel to the tube main axis, arising from a generative hyphae or a mediate hyphae, mostly terminal of limited growth, ending thin-walled, or intercalary, septate at both ends, apically reversing into slightly thick-walled generative hyphae, measured from 115  $\mu\text{m}$  to 350  $\mu\text{m}$  long, 1.5–2.5  $\mu\text{m}$  diam. at the basal septa to (2.5–)3.0–3.5  $\mu\text{m}$  diam. (av. = 3.2  $\mu\text{m}$ ) in the main part, mostly straight, occasionally geniculate, occasionally locally constricted, or inflated (up to 5–7  $\mu\text{m}$ ), with a few secondary septa, golden brown, darker brown in alkali. Hymenium: *Basidioles* slightly pyriform to broadly clavate, 6.0–7.0  $\times$  3.0–4.0  $\mu\text{m}$ ; mature basidia few, barrel-shaped to broadly clavate, with four sterigmata; *cystidioles* few, fusoid to lageniform, thin-walled; *basidiospores* broadly ellipsoid to subglobose, appearing somewhat angular on drying, thick-walled, smooth, pale yellowish in KOH, without reaction in Melzer's reagent, (3.5)–3.8–4.3(–4.5)  $\times$  (2.7–)3.0–3.5  $\mu\text{m}$  (av. = 4.0  $\times$  3.2  $\mu\text{m}$ ),  $R = 1.1\text{--}1.4$  (ave<sub>Q</sub> = 1.2).

**Phylogenetic affinities:** The species, hitherto, is related to *P. beninensis*, known from Benin (Western Africa), and to a specimen of *P. cf. pectinata* from Australia (Fig. 1).

**Ecology** (substrate, host, habitat): On surfacing roots, trunks, and lower branches, small-stemmed *Turraea* cf. *holstii* (Meliaceae), understory compartment, Afromontane forest (elev. ~ 2000 masl).

**Geographic distribution:** Currently known from a single spot of Afromontane Forest, at Mount Elgon, Kenya.

**Additional specimens examined.** **Kenya**, Trans Nzoia Province, Mount Elgon National Park, ~ N01°2'40.84", E034°34'9.4", elev. ~ 2170 masl, on trunks of living trees, *Turraea* cf. *holstii* (Meliaceae), 31 Mar. 2016, C. Decock, KE-16-105, KE-16-107, KE-16-108, KE-16-109, KE-16-113, KE-16-118, KE-16-119 & KE-16-120; *ibid.*, ~ N01°2'25.33", E034°47'13", elev. ~ 2160 masl, on trunks of living trees, *Turraea* cf. *holstii* (Meliaceae), 2 Apr. 2016, C. Decock, KE-16-148, KE-16-154 & KE-16-159; *ibid.*, ~ N01°2'54.9", E034°46'22.4", elev. ~ 2296 masl, on trunk of a living tree, *Turraea* cf. *holstii* (Meliaceae), 3 Apr. 2016, C. Decock KE-16-168; *ibid.*, ~ N01°2'54.9", E034°46'22.4", elev. ~ 2296 masl, on trunk of a living tree, *Turraea* cf. *holstii* (Meliaceae), 4 Apr. 2016, C. Decock, KE-16-187, KE-16-191 & KE-16-192; *ibid.*, ~ N01°2'54.9", E034°46'22.4", elev. ~ 2296 masl, on

trunk of a living tree, *Turraea* cf. *holstii* (Meliaceae), 26 Feb. 2017, C. Decock, M. Jérusalem & G. Castillo, KE-17-212, MJ-KE17-002, MJ-KE17-003, MJ-KE17-004, MJ-KE17-005, MJ-KE17-006, MJ-KE17-007, MJ-KE17-008, MJ-KE17-009, MJ-KE17-010, MJ-KE17-011, MJ-KE17-012 & MJ-KE17-013; *ibid.*, ~ N01°2'54.9", E034°46'22.4", elev. ~ 2296 masl, on trunk of a living tree, *Turraea* cf. *holstii* (Meliaceae), 1 Nov. 2017, C. Decock, KE-17-275.

**Notes:** *Phylloporia afropectinata* is characterised by perennial, merismatoid basidiomes with multiple downward proliferations of imbricated pilei (Fig. 2), variably sized, and reaching, based on our observations, up to 25 cm wide. It is so far the species producing the largest merismatoid basidiomes in *Phylloporia*. Corner (1991) provided likely the best modern description of the development of the merismatoid basidiomes in *Phylloporia*, and our description are, partly, adapted from him.

The hyphal system is of uncertain classification. In the classification scheme of Corner (1991), it would be best described as dimitic of the second degree (d2), with sclerified hyphae, as in *P. weberiana* and *P. chrysites*, both *sensu* Corner (1991). However, dimitism of the d2 degree is not entirely satisfactory by omitting the intercalary, very thick-walled hyphae. The sclerified hyphae of limited length originate from a generative hyphae, occasionally from a mediate hyphae, and are either terminal or intercalary, then reversing to slightly thick-walled, generative hyphae (Fig. 3). It could be also considered as intermediate dimitic, following Pegler (1996), or with sclerified, supporting hyphae following Cléménçon (2012), as adopted by Ferreira Lopes (2018), e.g., in *P. pectinata* *sensu stricto* or in *P. ribis* *sensu stricto*.

*Phylloporia afropectinata*, hitherto, is known exclusively from a small-stemmed *Meliaceae*, *Turraea* sp., in a single spot of mid-elevation (~2000 masl) Afromontane Forest (Kindt *et al.* 2014), at Mount Elgon, Western Kenya. The identification of the host could not be confirmed *in situ*, nor by DNA sequence data. It is referred to as *Turraea* cf. *holstii*. The basidiomes emerge from different tree organs, from surfacing roots to, and predominantly, trunks and the main lower branches (Fig. 2). Locally, the species is widely distributed, concomitantly to its host; it infects almost every individual tree present in an immediate neighbourhood. This might be linked to the locally gregarious habit of the host, forming small patches. Its distribution range in tropical Africa is still unknown. The species could follow its host over the Eastern Mountain range, where it is widely distributed, although it may depend also on other ad hoc environmental parameters.

In a phylogenetic perspective, the closest relative of *P. afropectinata* is shown to be, hitherto, the western African *P. beninensis*, that is only known to date from Benin (Olou *et al.* 2021). Both are related to a specimen originating from Australia and tentatively identified as *P. pectinata* (Australia, New South Wales, Kurrajong, R. Coveny 113, on *Rhodamnia rubescens*, Myrtaceae, O, CANB, Wagner & Ryvarden 2002). These three species form a well-supported clade (Fig. 1).

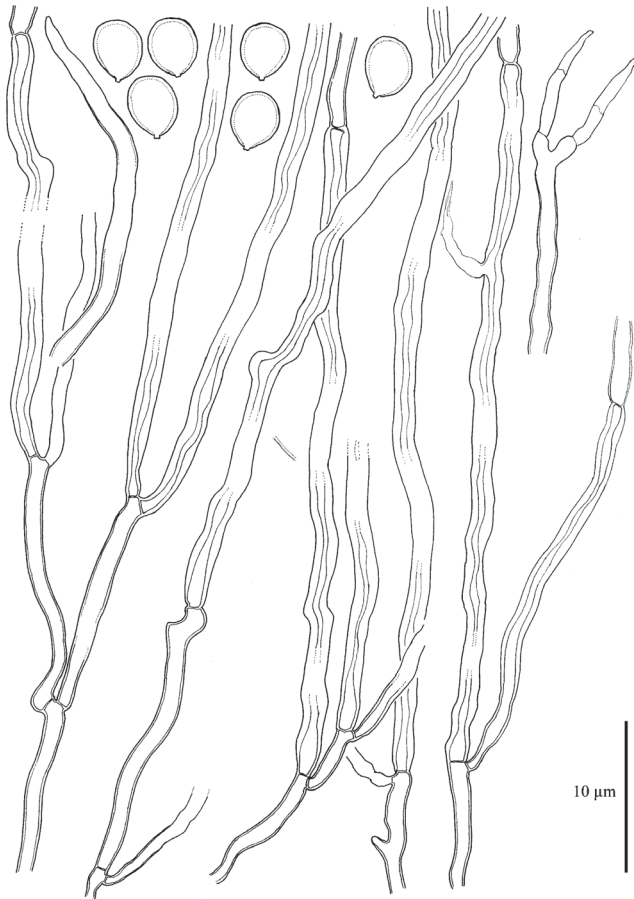
*Phylloporia afropectinata* shares with *P. beninensis* the imbricate basidiomes, the substrate, and the host family (Meliaceae). *Phylloporia beninensis* (Olou *et al.* 2021) differs in having an annual (fide Olou *et al.* 2021) basidiome, more cylindrical oblong basidiospores (mostly 3.3–4.3  $\times$  2.4–3.3





**Fig. 2.** Basidiomata of *Phylloporia afropectinata* in situ: **A.** KE 17 212-216, bottom view. **B, F.** KE 16-119 (holotype), general view. **C, E, G.** KE 17 212-216, upper view. **D.** KE 17 212-216 view of the pores surface. Scale bars: A–G = 3 cm.





**Fig. 3.** Microscopic structures of *Phylloporia afropectinata*, from the holotype KE-16-119 (MUCL 58359): Vegetative hyphae from the hymenophoral trama and basidiospores.

µm, av.  $3.8 \times 2.8$  µm vs  $3.8\text{--}4.3\text{--}(4.5) \times 3.0\text{--}3.5$  µm, av. =  $4.0 \times 3.2$  µm), growing on *Trichilia emetica* (vs *Turraea* cf. *holstii*), and a different habitat.

*Phylloporia afropectinata* should be compared also to *P. pectinata* sensu Ryvarden *et al.* (2022) (or under *Phellinus pectinatus*; Ryvarden & Johansen 1980), reported from East Africa, from Ethiopia Northward, Southward to Malawi. However, the identity of *P. pectinata* sensu Ryvarden *et al.* (2022) is uncertain. Considering its main characters, including compound basidiomes, small pores (8–10/mm), and a distribution in East Africa, *P. afropectinata* could be equated, at least pro parte, to *P. pectinata* sensu Ryvarden & Johansen (1980).

*Phylloporia memecyli*, *P. miomboensis*, and *P. warneckeicola* (cf. below) could be morphologically compared also to *P. afropectinata*. *Phylloporia miomboensis* was tentatively identified as *P. pectinata* (identification by L. Ryvarden, herbarium label, O!). They differ in having much smaller basidiomes and a dimittic hyphal system with skeletal hyphae of restricted growth. *Phylloporia memecyli* and *P. warneckeicola* also differ in their reproduction strategy, with the simultaneous emergence in dense clusters of multiple basidiomes. Both species inhabit the lowland western edge of the Guineo-Congolian phytochorion and grow from two species of *Melastomataceae*, respectively *Memecylon viride* and *Warneckea floribunda*, both absent from the East African montane range. *Phylloporia miomboensis* differs also as inhabiting the Lowland Zambezian dry open forest.

Outside Africa, *P. pectinata* sensu Corner (1991) is the taxon most comparable to *P. afropectinata*, with respect to its biology, macro- and micromorphology, autecological parameters such as substrate relationships, and local distribution. Both species share the compound, merismatoid basidiomes, reaching up to 15 cm wide in *P. pectinata* sensu Corner (1991). They both grow from small-stemmed trunks, and have a very comparable pattern of occurrence at a local scale. While *P. pectinata* sensu Corner (1991) was found on “almost every tree” of the small-stemmed, understory *Timonius flavescens* (*Rubiaceae*) at the ridge forest of Gunong Panti (Southeast of Johor, Malaysia), *P. afropectinata* was emerging from almost every individual of *Turraea* cf. *holstii* growing in an immediate neighbourhood at Mount Elgon, Kenya. *Phylloporia pectinata* sensu Corner (1991) and *P. afropectinata* differ by their pore size (60–90 µm diam., ~10–12 / mm vs 90–115 µm, 8–9 / mm), ellipsoid vs broadly ellipsoid to subglobose basidiospores ( $2.7\text{--}3.5 \times 2\text{--}2.5$  µm vs  $3.8\text{--}4.3 \times 3.0\text{--}3.5$  µm), host plant (*Timonius flavescens* vs *Turraea* cf. *holstii*), and habitat (Southeast Asian rainforest vs Afromontane middle elevation forest).

***Phylloporia cinnamomea*** Decock, Yombiy., & Amalfi, *sp. nov.* MycoBank MB 851872. Figs 4A–C, 5.

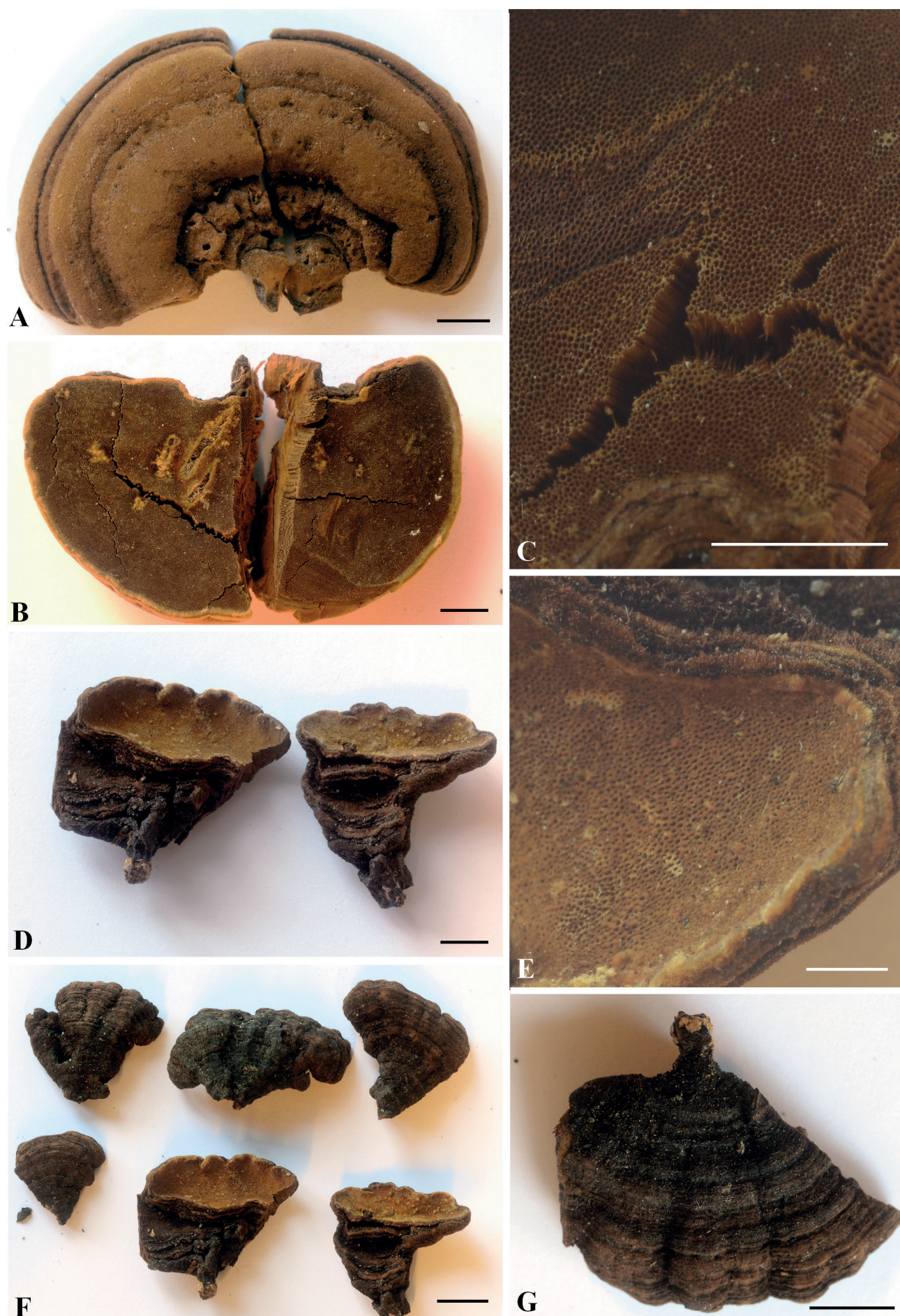
**Etymology:** “*cinnamomea*” (Latin) in reference to the colour of the pileus.

**Typus:** **Cameroon**, East Provinces, Dja Biosphere Reserve, NW sector, 3 km South of Somalomo, ~ N03°01'31", E12°59'59", elev. ~ 675 masl, on an unidentified tree, 12–25 Sep. 2019, L. Ryvarden, LR 50722 (**holotype** O).

**Diagnosis:** *Phylloporia cinnamomea* is similar to *P. rinorea* by the small, pileate, dimidiate basidiomes, roughly sulcate pilei, in cinnamon brown shade, presenting in section a comparatively thin, homogeneous context covered by a thin black line, subtending a comparatively thicker tomentum but differs in having slightly larger pores 8–9 / mm, (80–)85–124(–130) µm wide (vs 9–10 / mm, 85–100 µm wide), and smaller basidiospores mostly  $3.5\text{--}4.0 \times 2.2\text{--}2.5$  µm (vs  $4.0\text{--}4.5 \times 2.5\text{--}3.0$  µm).

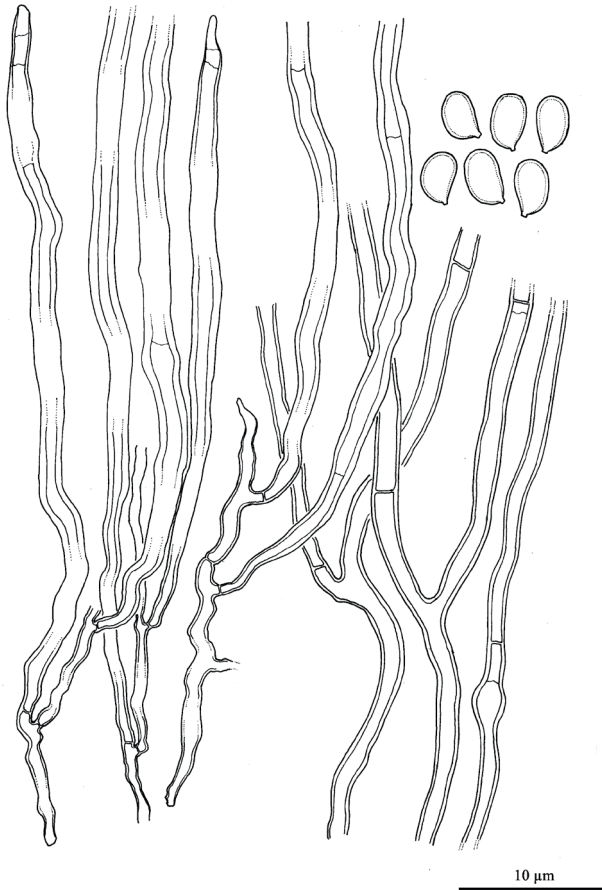
**Description:** *Basidiomes* solitary, seasonal, pileate, sessile, semi-circular to dimidiate first, attached by the vertex, applanato-convex in section, bent downward toward the margin, projecting 7–15 mm long, 10–20 mm wide, from 0.5–1 mm thick at the very margin up to 5–7 mm at the base or the attachment point (vertex); pileus surface tomentose, spongy, velvety to the touch, broadly sulcate with a few (1–4) deep furrows near the base, more narrowly and densely sulcate near the margin, dull, mostly uniformly light brown to brown when dry [cinnamon to cocoa brown, 6(D–E)6, 6E(6–7)] (no data from fresh basidiomes but likely slightly darker), progressively darker near the margin (dark brown, 6F6); margin well-marked, forming a well-defined narrow rim, entire, regular in outline, greyish orange on drying; pore surface plane to mostly concave, the pore field starting immediately behind the very margin, mostly light brown when dry [5D(3–4) up to 5(D–E)6, honey yellow, oak brown, mustard brown]; pores regular, mostly round, 8–9 / mm,





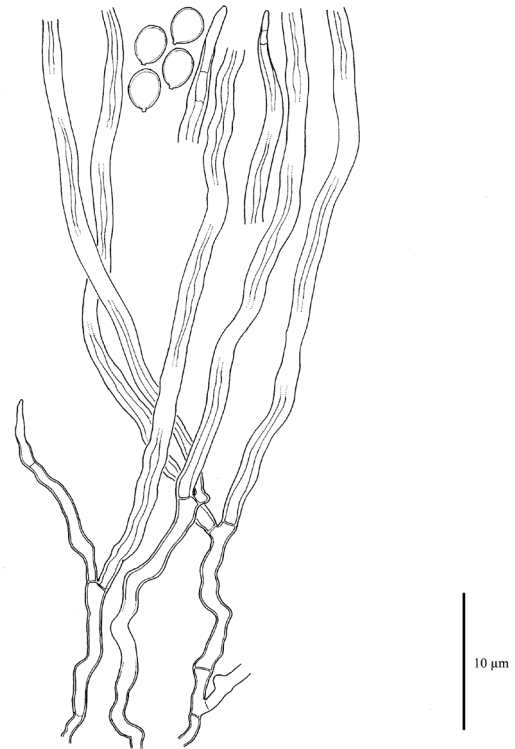
**Fig. 4.** A–C. Dried Basidiomata of *Phylloporia cinnamomea* and (D–G) of *Phylloporia miomboensis*. A. LR 50722 (holotype), upper surface. B. LR 50722, pore surface. C. LR 50722 details of the pores surface. D, E. LR 25885 (holotype), general view. F. LR 25885, details of the pores surface. G. LR 25885, upper surface. Scale bars: A–G = 1 cm.





**Fig. 5.** Microscopic features of *Phylloporia cinnamomea* drawn from the holotype LR 50722: Vegetative hyphae from the hymenophoral trama and basidiospores.

(80–)85–124(–130) µm wide (av. = 103.5 µm wide) when round, 110–130 × 90–100 µm when ellipsoid; dissepiments thin, entire, agglutinated, 20–50 µm thick (av. = 32 µm); in section, tomentum spongy, loose, brown, from 1 mm thick at the margin to 3 mm thick at the thickest part; context 0.2–1.0 mm thick toward the base or the attachment point, gradually thinning to the margin where it is very thin to absent, hard corky, shiny, light brown to brown, topped with a thin, dense black line, up to 100 µm thick, subtending the tomentum; tube layer up to 0.5–1.0 mm deep, light brown to brown; all parts darkening in alkali 3 %. Hyphal system dimitic in the context and hymenophoral trama, monomitic in the tomentum; generative hyphae simple septate, thin- to slightly thick-walled, hyaline to yellowish, scarcely ramified, the branches constricted at their emergence point, 1.5–3.0 µm diam. (Fig. 5). In the tomentum, next to the black line, hyphae horizontal, with a near parallel orientation, soon variably mixed, horizontal to predominantly erected (vertical) and loosely packed, near the margin slightly incurving backward; individual hyphae mostly straight, rarely geniculated, locally with local swelling, mostly unbranched, or with a dichotomy, ending rounded, slightly thick-walled to thick-walled, the lumen > wall thickness, with both primary and secondary septa, hyaline first then yellowish to golden brown, from 2.5–3.0 µm diam. near the base gradually enlarging up to 3.5–5.5(–6.0) µm (av. = 4.2 µm diam.), swelling locally up to 7.5 µm; in the context, skeletal hyphae horizontal, with a near parallel orientation, golden brown, darker in KOH, moderately thick-walled with the lumen widely open, (2.5–)3.5–4.0 µm diam.



**Fig. 6.** Microscopic structures of *Phylloporia miomboensis* holotype LR 25885: Vegetative hyphae from the hymenophoral trama and basidiospores.

(av. = 3.6 µm); in the hymenophoral trama, skeletal hyphae, born from a generative hyphae straight, of limited growth, 200–300 µm long, measured up to 350 µm, ending rounded, golden brown, darker in KOH, with an interwoven disposition, moderately thick-walled, the lumen ≤ wall thickness, aseptate or with occasional secondary septa, from 1.5–2.3 µm at the basal septum to 2.5–3.5 µm diam. (av. = 2.9 µm) in the main part, occasionally, locally inflated (up to 5 µm). Hymenium: *Basidioles* slightly pyriform to clavate; mature basidia mostly clavate, 12.5 × 4.5 µm, with four sterigmata; *cystidioles* rare, fusiform; *basidiospores* oblong to elliptical (to broadly elliptical) in face view, the abaxial side straight to faintly incurved in side view, appearing slightly angular on drying, thick-walled, smooth, pale yellowish in KOH, without reaction in Melzer's reagent, 3.5–4.0(–4.2) × (2.0–)2.2–2.5(–2.5) µm (av. = 3.9 × 2.3 µm),  $R = (1.4–)1.5–1.8(–2.0)$  (ave<sub>R</sub> = 1.7).

**Phylogenetic affinities:** The species, hitherto, is closely related to *P. rinoreae*, also known from the Guineo-Congolian rainforest in Western Gabon. Both species are affine to an unnamed species (*Phylloporia* sp. PY-SN6), and to *P. pseudoweberiana* (Fig. 1).

**Ecology** (substrate, host, habitat): Unknown plant organ, unidentified angiosperm, Guineo-Congolian rainforest.

**Geographic distribution:** Currently known from two spots of Guineo-Congolian rainforest, in Gabon (Ipassa-Makokou Biosphere Reserve, ~ N00°31'18", E12°45'24", elev. ~ 540 masl) and Cameroon (Dja Biosphere Reserve, ~ N03°01'31", E12°59'59", elev. ~ 675 masl).

**Additional specimen examined:** **Gabon**, Ogooue Ivindo Province, Ivindo National Park, Ipassa-Makokou Biosphere

Reserve, Ipassa Biological Station, ~ N0°31'18", E12°45'24", elev. ~ 540 masl, small stem of unidentified angiosperm, Oct. 2016, *P. Yombiyeni*, YOM 5 (BE).

**Notes:** *Phylloporia cinnamomea* is characterised by solitary basidiomes, a pileus in cinnamon brown shade, a thin, homogeneous, brown context and a comparatively thicker tomentum, both separated by a thin black line. In a morphological and phylogenetic perspective, *P. cinnamomea* is closely related to *P. rinoreae*. Both species share also the habitat, which is the Guineo-Congolian rainforest (Jerusalem *et al.* 2019). These two species differ by their pore size, slightly smaller in *P. rinoreae*, basidiospores size, slightly shorter and narrower in *P. cinnamomea* ( $3.5\text{--}4.0 \times 2.2\text{--}2.5$ , av. =  $3.9 \times 2.3 \mu\text{m}$  and  $4.0\text{--}4.5 \times 2.5\text{--}3.0 \mu\text{m}$ , av. =  $4.3 \times 2.7 \mu\text{m}$ ). The host plant is unknown for *P. cinnamomea*.

*Phylloporia cinnamomea* and *P. rinoreae* could be compared also to *P. pseudoweberiana*, which belongs to the same clade (see notes under this species). These species share the basidiome anatomy and substrate affinities. *Phylloporia cinnamomea* and *P. rinoreae* have smaller basidiomes, up to 20 mm wide, whereas they are 20–80 mm wide in *P. pseudoweberiana*.

***Phylloporia memecyli*** Jerusalem, Yombiy., Amalfi & Decock, *sp. nov.* MycoBank MB 851908. Figs 9A–D, 10.

**Etymology:** “*memecyli*” (Latin) is referring to the host tree, a species of *Memecylon*.

**Typus:** **Gabon**, Ogooue Maritime Province, CTFS-ForestGEO Rabi forest monitoring Plot, ~ S01°55'28.5", E09°52'48", elev. ~ 30–60 m, on the trunk of a small-stemmed living tree (10–15 cm diam.), *Memecylon* cf. *viride* (*Melastomataceae*), 7 Apr. 2012, C. Decock & P. Yombiyeni, GA-12-812 (**holotype** BR; **isotype** NY).

**Diagnosis:** *Phylloporia memecyli* is similar to *P. warneckeicola*, by the combination of small (projecting horizontally mostly 3–12 mm, 3–22 mm wide), sessile basidiomes, emerging gregariously in clusters, closely, very finely, densely sulcate, light brown to brown pilei but differs in having a brown pore surface, larger pores, 10–11 / mm, (70–)78–100(–105)  $\mu\text{m}$  diam., and growing on *Memecylon viride* (*Melastomataceae*) in the Lower Guineo-Congolian rainforest.

**Description:** *Basidiomata* perennial, pileate, sessile, gregarious, emerging simultaneously in clusters of up to 80 individuals, mostly superposed; individual basidiomata mostly turbinate, pendant, attached by a small apical/subapical vertex, very closely to the bark of the host, hence appearing a first sight broadly attached, projecting firstly downward then horizontally, 3–12(–23) mm, 3–22(–34) mm wide, slightly flabelliform then mostly semicircular in outline, in transversal section, first slightly triquetrous when very young, then progressively thinly applanate, the pores surface concave (incurved inside), with a general hard corky consistency; pileus surface finely, densely concentrically sulcate, with numerous fine growth zones, up to 10–12 / cm, shortly velutinous, mainly homogeneously light brown (6D6, cinnamon), to brown (6E6, cocoa brown), to dark brown on aging (6F6, burnt amber), slightly lighter toward the margin, slightly glistening; margin

entire, thinly rounded, forming a well-defined narrow rim next to the pore surface, especially in young basidiomes, greyish yellow when fresh, pale cork-coloured on drying; pore surface plane to mostly concave (incurved inside), first homogeneous, then regrowth homogeneous or heterogeneous, in confluent patches, dark brown (6F6 burnt amber); pores small, regular, round to slightly ellipsoid, 10–11 / mm, (70–)78–100(–105)  $\mu\text{m}$  diam. (av. = 87  $\mu\text{m}$  diam.); dissepiments thin, (20–)25–55(–85)  $\mu\text{m}$  thick (av. = 36  $\mu\text{m}$ ); context homogeneous, fibrous, 0.5–1.5 mm thick at the base, very thin to the margin, cinnamon brown to brown [6(D–E)6], topped by a thin black line subtending a thin upper trichoderm; trichoderm 125–250  $\mu\text{m}$  thick, shortly velutinous (under the lens), agglutinating from the base, golden brown (5D7) to yellowish brown (5E8); tube layer 0.5–1.5 mm deep, concolourous with the lower trama. Hyphal system dimitic; generative hyphae simple septate, thin- to slightly thick-walled, hyaline to faintly yellowish, scarcely branched, with a constriction at the branching point, 1.5–2.3  $\mu\text{m}$  diam.; lower context, dominated by skeletal hyphae, descending, parallel to long axis, tightly packed, arising from a generative hyphae and of limited growth, measured up to 400  $\mu\text{m}$  long, 2.0–2.5  $\mu\text{m}$  wide at the basal septa, progressively widening to 3.0–4.5(–4.8)  $\mu\text{m}$  wide (av. = 3.7  $\mu\text{m}$ ), golden brown, darker (brown) in alkali, thick- to very thick-walled with the lumen wide to narrow, mostly aseptate throughout, or with few secondary septa near the apices; trichoderm with prostrate to erected hyphae, mostly unbranched, thick-walled with widely open lumen, septate with both true and secondary septa, the apices rounded to open, yellowish to brown, mostly 4–6(–8)  $\mu\text{m}$  diam., the apices 6–8  $\mu\text{m}$  wide; hymenophoral trama dominated by skeletal hyphae, subparallel to the tube main axis, arising from a generative hyphae or a mediate hyphae, terminal, of limited growth, measured from 115  $\mu\text{m}$  to 350  $\mu\text{m}$  long, 2.0–2.3  $\mu\text{m}$  diam. at the basal septa to 2.5–3.5  $\mu\text{m}$  diam. (av. = 3.0  $\mu\text{m}$ ) in the main part, occasionally geniculated in the basal lower third to, and mostly, straight in the main part, occasionally locally constricted or inflated (up to 4–5  $\mu\text{m}$ ), slightly thick-walled at the basal septa, progressively thick- to very thick-walled, the lumen opening then narrow, locally lenticular, ending thin-walled, aseptate throughout but with a few secondary septa near the apices, golden brown, darker brown in alkali. Hymenium: *Basidioles* slightly pyriform to broadly clavate,  $6.0\text{--}7.0 \times 3.0\text{--}4.0 \mu\text{m}$ ; mature basidia few, barrel-shaped to broadly clavate, with four sterigmata; *cystidioles* absent; *basidiospores* mostly ellipsoid, bean-shaped in side view, appearing somewhat angular on drying, thick-walled, smooth, hyaline to pale yellowish in KOH, without reaction in Melzer's reagent,  $3.5\text{--}4.0(–4.2) \times 2.2\text{--}2.5(–2.7) \mu\text{m}$  (av. =  $3.7 \times 2.3 \mu\text{m}$ ),  $R = 1.4\text{--}1.8$  (ave<sub>0</sub> = 1.6).

**Phylogenetic affinities:** The species, hitherto, is related to a group of morphologically similar and ecologically related species, including *P. warneckeicola*, *P. fulva*, and *P. pendula* (Fig. 1).

**Ecology** (substrate, host, habitat): On small-stemmed, living trunks, *Memecylon viride* (*Melastomataceae*), understory compartment, Lower Guineo-Congolian rainforest.

**Geographic distribution:** Currently known from the CTFS-ForestGEO Rabi forest monitoring Plot in South-western Gabon (~ S01°55'28.5", E09°52'48", elev. ~ 30–60 m).



**Additional specimen examined.** **Gabon**, Ogooue Maritime Province, CTFS-ForestGEO Rabi forest monitoring Plot, ~ S 01°55'28.5", E09°52'48", elev. ~ 30–60 m, on the trunk of a small-stemmed living tree, *Memecylon viride* (Melastomataceae), 7 May 2019, M. Jérusalem & P. Yombiyeni, MJ-GA19-091 & MJ-GA19-093 (in herb.BR).

**Notes:** See below under *P. warneckeicola*.

***Phylloporia microspora*** (Ryvarden) Decock & Amalfi, **comb. nov.** MycoBank MB 851909. Figs 7, 8.

**Basionym:** *Inonotus microsporus* Ryvarden, *Kew Bull.* **54**(3): 803. 1999. MB 459949.

**Typus:** **Zimbabwe**, Matebeleland North Province, Victoria Falls, Miombo forest behind the statue of D. Livingstone, ~ S17°55'22", E25°50'49", on dead trunk, *Colophospermum mopane* (Fabaceae), 23 Jan. 1989, L. Ryvarden, Ryvarden 26485 (**holotype** O; **isotype** K).

**Description:** *Basidiomata* annual, pileate, sessile, gregarious, emerging simultaneously in clusters, with "a hundreds of pilei covering 1.5 m of standing trunk" (fide Ryvarden 1999) (in the type, the cluster of basidiomes is 70 mm high, 75 mm wide); individual pilei mostly superposed, emerging from a common base, closely imbricated, with adjacent pilei in rows frequently laterally fused to form wavy, compound pilei, individually slightly spatulate to broadly attached, projecting horizontally, slightly downward (10–)15–25(–30) mm, 15–30 mm wide, from 0.5 mm thick at the very margin up to 6 mm the thickest part near the base, mostly applanate in section; pileus surface smooth, or radially very faintly wrinkled on drying, brownish orange [5C(3–4)] near the margin progressively nearly mostly uniformly light brown when dry [5D(6–7), golden brown], slightly darker at the base [6D(5–6), light brown, cinnamon brown]; margin thin to thick, rounded, entire, mostly regular in outline, rarely slightly wavy, likely white when fresh, drying whitish, pale yellowish grey, cork-coloured [4A(2–3) to 5C3], extending below 0.5–1.5 mm wide; pore surface plane, the pore field starting at about 0.5–1.5 mm behind the very margin, leaving a pale greyish yellow sterile zone, the pore field mostly greyish to pale greyish orange, pale greyish orange to yellowish brown (5[B–C]3 to 5D5, honey yellow, oak brown, mustard brown), slightly glancing; pores mostly round to angular, overall 5–6(–7) / mm when dry, (110–)120–170(–180)  $\mu$ m wide (av. = 146  $\mu$ m wide), occasionally radially ellipsoid to oblong, 190–220  $\times$  140–160  $\mu$ m, or lobed up to 250  $\times$  200  $\mu$ m; dissepiments thin to moderately thick, (25–)32–60(–65)  $\mu$ m thick (av. = 45  $\mu$ m), not agglutinated, with free hyphal tips, appearing slightly lanose under the lens; context homogeneous, without black line, shiny, 1–6.0 mm thick at the base [5(C–D)6], brownish orange to light brown; tube layer up to 1.2 mm deep, concolourous or slightly darker than the context, light brown [6D(5–6)]; context and tube layer discolouring to reddish brown in 3 % KOH, then pale brown. Hyphal system monomitic, both in the context and hymenophoral trama; generative hyphae simple septate, thin- to slightly thick-walled, hyaline, yellowish to light golden brown, darker in KOH, scarcely ramified, except at the very basal segment, the branches constricted at their emergence point, soon growing parallel to the mother hyphae; in the context, hyphae with a parallel to subparallel (synclinal) orientation, mostly moderately thick-walled with the lumen widely open,

septate, but with long aseptate segments, 2.0–2.5  $\mu$ m at the very basal segment, (3.0–)3.3–5.2(–5.4)  $\mu$ m diam. (av. = 4.4  $\mu$ m); pileus surface with prostrate hyphae, mostly unbranched, identical to the contextual hyphae; in the hymenophoral trama hyphae with a subparallel disposition, thin- to slightly thick-walled, the lumen widely open, septate, but with long aseptate segments or with occasional with secondary septa, little branched, except at the very basal segment, 2.0–2.3  $\mu$ m at the very base (2.3–)2.6–4.7(–5.0)  $\mu$ m diam. (av. = 3.2  $\mu$ m). Hymenium: *Basidioles* slightly pyriform to broadly clavate, 6.0–9.0  $\times$  3.5–4.5  $\mu$ m; mature basidia broadly clavate, with four sterigmata, 9–11  $\times$  4–5  $\mu$ m; *cystidioles* few, fusoid, thin-walled; *basidiospores* ellipsoid to slightly ovoid, or shortly oblong, appearing somewhat angular on drying, thick-walled, smooth, hyaline to pale yellowish in KOH, without reaction in Melzer's reagent, (3.0–)3.2–3.8  $\times$  2.0–2.5  $\mu$ m (av. = 3.5  $\times$  2.2  $\mu$ m), R = 1.3–1.4–1.8(–1.9) (ave<sub>0</sub> = 1.5).

**Phylogenetic affinities:** The species, hitherto, has no close relative within the current *Phylloporia* lineage (Fig. 1).

**Ecology** (substrate, host, habitat): On dying, standing trunk, *Colophospermum mopane* (locally known as Mopane) (Fabaceae), in seasonally dry, open woodlands.

**Geographic distribution:** Currently known from a single locality, the Victoria Falls, in Southwestern Zimbabwe.

**Notes:** *Phylloporia microspora* is characterised by seasonal, multiple, gregarious, basidiomes, arising simultaneous from a common base, small- to medium-sized (up to 15–25(–30) mm long  $\times$  15–30 mm wide), slightly spatulate to broadly attached with smooth, mostly uniformly light brown pilei (Fig. 7), and 5–6 pores / mm. The hyphal system is homogeneously monomitic. The basidiospores are narrowly ellipsoid to shortly oblong, 3.2–3.8  $\times$  2.0–2.5  $\mu$ m (Fig. 8). Its sole known habitat for the time being is the low altitude, low rainfall, seasonally dry Zambebian open forest and perhaps, more specifically, the Mopane Forest that should be the local native vegetation in the neighbourhood of Victoria Falls, in Zimbabwe (White 1983, Mapaure 1994).

*Phylloporia microspora* has no close morphological relative in its known habitat of occurrence nor, hitherto, in tropical Africa or out of Africa. In a phylogenetic perspective, it stands on an isolated branch (Fig. 1).

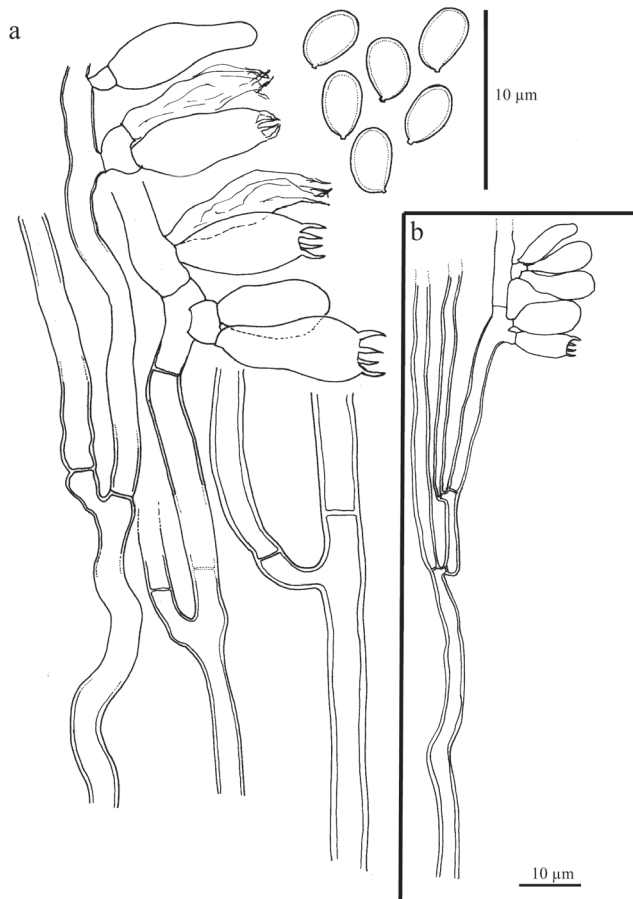
To some extent, but superficially, *P. microspora* reminds of *P. flabelliformis* and *P. gabonensis* (Decock *et al.* 2015, Ryvarden 2019). These three species share the reproduction strategy with multiple, simultaneous, gregarious emergence of short-living (seasonal) basidiomes, light-coloured pileus, the monomitic hyphal system, and the growth from trunks of small-stemmed trees (Decock *et al.* 2015). These similitudes are only superficially comparable, however. The basidiomes of *P. microspora* emerge from a common base whereas, inversely, in both *P. flabelliformis* and *P. gabonensis*, the basidiomes emerge individually from the trunk. *Phylloporia microspora* also differs from both above-mentioned species in having denser, hard corky basidiomes, which are much softer, fragile when dry in the two other species. In an ecological context, *P. microspora* was found growing from *Colophospermum mopane* (Fabaceae), a markedly xeric species found in the low altitude, low rainfall areas, seasonally





**Fig. 7.** Dried basidiomata of *Phylloporia microspora* (LR 26485, holotype). **A.** General view. **B.** Details of the pores surface. **C, E, F.** Bottom view. **D.** Upper view. Scale bars: A–F = 1 cm.





**Fig. 8.** Microscopic features of *Phylloporia microspora* drawn from LR 26485 (holotype): hyphae from the hymenium, basidioles, basidia and basidiospores.

dry Zambezian open forest, in Zimbabwe (White 1983, Mapaire 1994). *Phylloporia gabonensis* and *P. flabelliformis* were found growing on two *Euphorbiaceae* (*Dichostemma glaucescens* and *Anthostema aubryanum*) in the Western edge of Central Africa, in Gabon, or in biogeographical term, the Lower Guinean rainforest (White 1983), which is a humid to very humid, moisture-buffered, closed forest.

***Phylloporia miomboensis*** Decock & Amalfi, *sp. nov.*  
Mycobank MB 851910. Figs 4D–G, 6.

**Etymology:** “*miomboensis*” (Latin) is referring to the phytocorion, the Miombo woodland.

**Typus:** **Zimbabwe**, Mashonaland West Province, in the vicinity of the Kariba Lake, ~ S17°08'23", E27°50'30", elev. ~ 480 masl, on the trunk of a small-stemmed living trunk, unidentified angiosperm, 10 Jan. 1989, L. Ryvarden, LR 25885 (**holotype** O F-306030).

**Diagnosis:** *Phylloporia miomboensis* is similar to *P. memecyli* and *P. warneckeicola* by a combination of perennial, small basidiomes, projecting downward 10–20 mm, 8–30 mm long, 5–10 mm wide, attached by a narrow back point (vertex), mostly pendant, the pileus surface finely concentrically sulcate, but differs by the larger pores 8–9 pores / mm, 80–120 µm diam., and growing on a bushy plant in the Zambezian / Miombo open forest.

**Description:** *Basidiomata* perennial, pileate, sessile (rarely with a stipe-like elongated base), mostly solitary or 2–3 imbricated; individual basidiomata attached by a small apical or subapical, dorsal vertex, turbinate, pendant when young, but very closely to the bark, hence appearing a first sight semicircular to broadly attached, projecting downward 10–20 mm, conical flattened, enlarging toward the margin, then elliptical, elongated, crescent-shaped in outline at the margin, 8–30 mm long × 5–10 mm wide, in longitudinal section slightly triquetrous when very small, then thinly conical, with the pores surface concave (incurved inside), with a general hard corky consistency; pileus surface shortly velutinous, finely, densely concentrically sulcate, with numerous fine sulcations, up to 10–12 very narrow concentric zones/cm, sometimes radially furrowed, mainly brown (6E5, cocoa brown) to dark brown on aging (6F6, burnt amber), slightly lighter toward the margin (cinnamon brown); margin entire, thinly rounded, forming a well-defined narrow rim especially in young basidiomes or surrounding patchy regrowth of pore field, greyish yellow when fresh, pale cork-coloured on drying; pore surface (mostly) concave (incurved inside), light brown [cinnamon, 5E(4–5) to 5F5, bronze, sooty brown, Havana brown]; pores small, regular, mostly round, sometimes slightly ellipsoid, (7–)8–9 / mm, 80–120 µm diam. (av. = 98 µm diam.); dissepiments thin, 25–50 µm thick (av. = 34 µm); context almost absent to very thin, up to 0.5 mm thick at the base homogeneous, dense, compact, cinnamon brown to brown [6(D–E)6], topped by a hard, horny black line subtending an upper trichoderm; trichoderm 125–250 µm thick, shortly velutinous (under the lens), with agglutinated tufts of hyphae, dark brown (5D7) to yellowish brown (5E8); tube layer 0.5–1.5 mm deep, concolourous with the lower trama. Hyphal system dimitic; generative hyphae simple septate, thin- to slightly thick-walled, hyaline to faintly yellowish, scarcely branched, with a constriction at the branching point, 1.3–2.5 µm diam.; context dominated by skeletal hyphae, tightly packed parallel to long axis, arising from a generative hyphae and of limited growth, measured from 90 to 220 µm long (av. = 153 µm), 2.0–2.5 µm wide at the basal septa, progressively widening to (2.5–)3.2–4.0(–4.5) µm wide (av. = 3.4 µm), yellowish to yellowish brown, darker (brown) in alkali, thick- to very thick-walled with the lumen wide to narrow, mostly aseptate throughout, or with few secondary septa near the apices; trichoderm with mostly prostrate tufts of mostly unbranched hyphae, thick-walled with widely open lumen, septate with both true and secondary septa, the apices rounded to open, yellowish to brown, mostly 4–6 (–8) µm diam., the apices 6–8 µm wide; hymenophoral trama dominated by skeletal hyphae, descending, parallel to long axis, tightly packed, arising from a generative hyphae and of limited growth, measured from 100 to 220 µm long (av. = 153 µm), 2.0–2.5 µm wide at the basal septa, progressively widening to 2.8–3.3 µm wide (av. = 3.0 µm), yellowish to yellowish brown, darker (brown) in alkali, thick- to very thick-walled with the lumen wide to narrow, mostly aseptate throughout, or with few secondary septa near the apices, mostly straight in the main part, occasionally locally slightly inflated, or subapically constricted once or twice (slightly moniliform), slightly thick-walled at the basal septa, progressively thick-walled, ending thin-walled, aseptate throughout but with a few secondary septa near

the apices, golden brown, darker brown in alkali. Hymenium: *Basidioles* slightly pyriform to broadly clavate,  $\sim 10 \times 4.0 \mu\text{m}$ ; mature basidia few, barrel-shaped to broadly clavate,  $\sim 10\text{--}12 \times 4.0\text{--}5.0 \mu\text{m}$ , with four sterigmata; *cystidioles* not seen; *basidiospores* ellipsoid to slightly oblong ellipsoid, appearing somewhat angular on drying, thick-walled, smooth, hyaline to pale yellowish in KOH, without reaction in Melzer's reagent,  $3.0\text{--}3.5 \times 2.2\text{--}2.6 \mu\text{m}$  (av. =  $3.3 \times 2.4 \mu\text{m}$ ),  $R = 1.2\text{--}1.5\text{--}1.6$  (ave<sub>Q</sub> = 1.38).

**Phylogenetic affinities:** The species, hitherto, is related to *P. minima* (Wu *et al.* 2021), known from North-eastern Australia, *P. cf. pectinata* CBS 58.123, from India, and the form *jasmini* of *P. ribis* (or *P. pectinatus* var. *jasmini*, Quélet 1891) (Bourdot & Galzin 1928) (Fig. 1).

**Ecology** (substrate, host, habitat): Unidentified bushy plant, seasonally dry, Zambezian open forest (cf. Miombo woodland).

**Geographic distribution:** Currently known from a single spot of North-western Zimbabwe.

**Notes:** *Phylloporia miomboensis* is known from a single specimen, growing from an unidentified bushy angiosperm in Kariba Lake area, North-western Zimbabwe, without indication of the plant organ. The local vegetation is the seasonally dry Zambezian open forest and perhaps, more specifically, the Miombo woodland (White 1983).

The gross morphology of *P. miomboensis*, including the small basidiome with narrowly concentrically sulcate pileus, a black line subtending a trichoderm, and small pores reminds much of *P. warneckeicola* and *P. memecyli*. These species also share their hyphal system, vegetative hyphae differentiation, and basidiospores shape and size. *Phylloporia miomboensis* differs in having slightly larger pores (8–9 pores / mm vs 10–11 and 11–13) and different autecological parameters, including the botanical host, the substrate (plant organ), and the habitat. The host of *P. miomboensis* is unknown. Nonetheless, it is not a species of *Warneckeia* (host of *P. warneckeicola*) or *Memecylon* (host of *P. memecyli*), nor a *Melastomataceae*; there is no representative of this family in the vegetation at the type locality of *P. miomboensis*. The habitat of *P. warneckeicola* and *P. memecyli* is the humid Lower Guinean rainforest, drastically different from the seasonally dry Zambezian open forest (White 1983, Kindt *et al.* 2014, Marshall *et al.* 2021).

In a phylogenetic perspective, *P. miomboensis* is also distantly related from *P. warneckeicola* and *P. memecyli* (Fig. 1) and has, hitherto, no known relative in tropical Africa. It is however related to the Australian *P. minima*, the mediterranean *Ph. pectinatus* var. *jasmini*, and an Indian specimen of *P. cf. pectinata* (Fig. 1).

***Phylloporia pseudoweberiana*** Decock, *sp. nov.* MycoBank MB 851916. Figs 12, 13.

**Etymology:** “*pseudoweberiana*” (Latin) is referring to the similarity with *P. weberiana*.

**Typus:** Kenya, Western Province, Kakamega Forest National Reserve, N00°17'30", E034°51'22", elev.  $\sim 1500$  masl, on

the living trunk of the small-stemmed tree, *Rawsonia lucida* (Achariaceae), 16 Feb. 2015, C. Decock, KE-15-02 (**holotype** MUEL 58350; **isotype** NMK).

**Diagnosis:** *Phylloporia pseudoweberiana* is similar to *P. weberiana* sensu Ryvarden & Johansen (1980), characterised by the combination of sessile, perennial basidiomes emerging solitary, a sulcate pileus covered by a tomentum in brown to dark brown shade, a context absent to very reduced covered by a thin black line subtending a comparatively thicker tomentum, and a dimitic hyphal system but differs in having broadly ellipsoid to obovoid, larger basidiospores ( $3.0\text{--}3.2\text{--}4.0 \times (1.8\text{--})2.5\text{--}3.0 \mu\text{m}$  (av. =  $3.5 \times 2.5 \mu\text{m}$ ) and smaller pores, 9–11 / mm, 80–100  $\mu\text{m}$  diam., and occurring on *Rawsonia lucida* (Achariaceae) in the Eastern edge of the Guineo-Congolian rainforest, in Kenya.

**Description:** *Basidiomes* pileate, sessile, solitary, perennial; primordia nodulous, rounded; mature basidiomes dimidiate, attached to the substrate only by a narrow circular area at the back but so close to the substrate that appearing at first sight broadly attached, occasionally pendant, then attached by a small apical/subapical vertex, projecting horizontally 10–45 mm, 20–80 mm wide at the margin, from 8 mm thick at the margin up to 20 mm thick at the base, semicircular to dimidiate in face view, the margin outline regular to slightly lobed, mostly applanate in transversal section, the pores surface slightly concave (slightly incurved inside) or slightly decurrent; overall with a corky consistency when fresh, hard corky to woody on drying; pileus covered by a tomentum in 2–5 concentric, broad, rounded, distant bands separated by well-marked furrows, wearing off from the base with weathering, exposing then a narrowly, finely sulcate pileal surface, overall dark brown (6F7, dark brown, chestnut brown), darker on weathering toward the base when the tomentum wears off, paler toward the margin [6E(6–7), cocoa brown, leather brown]; very margin beneath the pileus, forming a thin, but well-delimited, slightly rounded ring, whitish yellow when fresh, pale cork-coloured on drying; pore surface plane to slightly concave (slightly incurved inside), light brown to brown [6(D–E)4, 6E6, camel, greyish brown, cocoa brown], slightly glancing; pores small, regular, mostly round, 9–11/mm, (80–)85–105(–120)  $\mu\text{m}$  diam. (av. = 96  $\mu\text{m}$  diam.); dissepiments thin, (15–)20–60(–75)  $\mu\text{m}$  thick (av. = 34  $\mu\text{m}$ ), agglutinated; context very reduced to almost absent, up to 0.5 mm thick layer between the tube layer and a thin black line subtending the comparatively thicker tomentum, homogeneous, dense, dark brown (6E6); tomentum 4–15 mm, soft corky when fresh, drying hard corky, light brown (6D6, cinnamon) near the base to brown (6E6, cocoa brown), agglutinating with weathering and wearing off from the base, soft corky when fresh, hard corky on drying; tube layer indistinctly stratified, 0.5–14 mm deep, concolourous with the context (6E6, cocoa brown), gradually paler near the pore surface (6D6, cinnamon). Hyphal system dimitic in the context and hymenophoral trama, monomitc in the tomentum; generative hyphae simple septate, thin- to slightly thick-walled, hyaline to faintly yellowish, scarcely branched, with a constriction at the branching point, 2.0–4.0  $\mu\text{m}$  diam.; lower context, dominated by skeletal hyphae, parallel to black line, tightly packed, arising from a generative hyphae and of limited growth, 2.0–2.5  $\mu\text{m}$  wide at the basal septa,



progressively widening to 3.0–4.5  $\mu\text{m}$  wide (av. = 3.6  $\mu\text{m}$ ), golden brown, darker (brown) in alkali, thick- to very thick-walled with the lumen wide to narrow, mostly aseptate throughout, or with few secondary septa near the apices; tomentum monomitic with hyphae first disposed parallel to the black-line, then progressively erected, then arranged in a fan-shaped, mostly unbranched or Y-branched, thick-walled with widely open lumen, occasionally locally constricted or inflated, septate with both true and secondary septa, the apices rounded to open, yellowish to brownish, mostly (3.5–)3.8–6.0(–6.5)  $\mu\text{m}$  diam. (av. = 4.7  $\mu\text{m}$ ); hymenophoral trama dominated by skeletal hyphae, mostly subparallel to the tube main axis, arising from a generative hyphae or a mediate hyphae, mostly terminal, of limited growth, measured from 115  $\mu\text{m}$  to 250  $\mu\text{m}$  long (av. = 185  $\mu\text{m}$ ), 2.0–2.5  $\mu\text{m}$  diam. at the basal septa to (2.3–)2.8–3.3(–3.5)  $\mu\text{m}$  diam. (av. = 3.30  $\mu\text{m}$ ) in the main part, mostly straight in the main part, occasionally locally constricted or inflated (up to 4–5  $\mu\text{m}$ ), slightly thick-walled at the basal septa, progressively thick- to very thick-walled, the lumen opening then narrow, locally lenticular, ending thin-walled, aseptate throughout but with a few secondary septa near the apices, golden brown, darker brown in alkali. Hymenium: *Basidioles* slightly pyriform to broadly clavate, 6.0–7.0  $\times$  3.0–4.0  $\mu\text{m}$ ; mature basidia few, barrel-shaped to broadly clavate, with four sterigmata; *cystidioles* absent or very few, fusoid to lageniform, thin-walled; *basidiospores* (ellipsoid), mostly broadly ellipsoid to slightly ovoid, appearing somewhat angular on drying (oblong), thick-walled, smooth, pale yellowish in KOH, without reaction in Melzer's reagent, 3.0–3.7(–4.0)  $\times$  (1.8–)2.2–3.0  $\mu\text{m}$  (av. = 3.4  $\times$  2.5  $\mu\text{m}$ ),  $R = 1.1\text{--}1.5(1.9)$  (ave<sub>0</sub> = 1.4).

**Phylogenetic affinities:** The species, hitherto, is related to *P. rinoreae*, *P. cinnamomea*, and *Phylloporia* sp. PY-SN6, known from the Guineo-Congolian rainforest in Gabon and Cameroon (Fig. 1).

**Ecology** (substrate, host, habitat): On small-stemmed, living trunks and lower branches, *Rawsonia lucida* (*Achariaceae*), understorey compartment, Lake Victoria transitional rain forest (which is an easternmost relict fragment of the Guineo-Congolian rainforest, White 1983, Kindt *et al.* 2014).

**Geographic distribution:** Currently known from the Kakamega Forest National Reserve, in Western Kenya.

**Additional specimen examined:** **Kenya**, Western Province, Kakamega Forest National Reserve, N00°17'30", E34°51'22", elev. ~ 1500 masl, on the living trunk of a small-stemmed tree (15 cm diam.), *Rawsonia lucida* Harv. & Sond. (*Achariaceae*), 16 Feb. 2015, C. Decock, KE-15-19 (MUCL 58351).

**Notes:** *Phylloporia pseudoweberiana* is characterised by solitary, perennial, deeply sulcate basidiomes (Fig. 12) with a very thin context underneath a comparatively thicker tomentum, both separated by a thin black line. The tomentum wears off with age from the base, exposing then the black line. The hyphal system is dimittic in the context and the hymenophoral trama. The basidiomes emerge from trunk and lower branches (Fig. 12) of the small understory tree *Rawsonia lucida* (*Achariaceae*), so far the only known and, a

priori, exclusive host. *Phylloporia pseudoweberiana* is known, hitherto, from the Lake Victoria transitional rainforest (sensu Kindt *et al.* 2014), at Kakamega Forest National Reserve, in Western Kenya. The Lake Victoria transitional rainforest is the easternmost reminiscence in Kenya of the Equatorial rainforest (Guineo-Congolian rainforest) that stretched from the Atlantic Ocean (Guinea) to the Indian Ocean (Kenya).

In a phylogenetic perspective, *P. pseudoweberiana* is closely related to *P. rinoreae*, *P. cinnamomea*, and *Phylloporia* sp. PY-SN6 (Fig. 1), currently known from the Western edge of Guineo-Congolian rainforest, in Central and Western Gabon (Jerusalem *et al.* 2019) and Cameroon.

In tropical Africa, *P. pseudoweberiana* should be compared to *P. weberiana* sensu Ryvarden & Johansen (1980) or Ryvarden *et al.* (2022). However, the very identity of *P. weberiana* and, a fortiori, of *P. weberiana* sensu Ryvarden & Johansen (1980) or Ryvarden *et al.* (2022) was uncertain (Caberroí Hernández *et al.* 2019). Decock *et al.* (2024) lectotypified and redefined *P. weberiana* s.s. In that sense, *P. weberiana* sensu Ryvarden & Johansen (1980) differs from *P. weberiana* s.s. and *P. pseudoweberiana* in having much larger pores, mostly 5–6 / mm (Ryvarden & Johansen 1980) vs 12–13 / mm (Decock *et al.* 2024) and 9–11 / mm, respectively.

*Phylloporia rinoreae* and *P. cinnamomea* share with *P. pseudoweberiana* solitary basidiomes, a pileus covered by a broadly sulcate tomentum, comparatively thicker than the underlying context, and both separated by a thin black line, and small pores (> 9 / mm). *Phylloporia rinoreae* and *P. cinnamomea* differ in having smaller basidiomes, not exceeding 20 mm wide, 7 mm thick, and larger basidiospores, respectively, mainly 4.0–4.5  $\times$  2.5–3.0  $\mu\text{m}$  (av. = 4.3  $\times$  2.7  $\mu\text{m}$ ) and 3.5–4.0  $\times$  2.2–2.5 (av. = 3.9  $\times$  2.3  $\mu\text{m}$ ). *Phylloporia rinoreae* also has a distinct substrate affinity and host relationship, growing from narrow, apical twigs of the shrubby *Violaceae*, *Rinorea* sp. (Jerusalem *et al.* 2019). The host tree and substrate of *P. cinnamomea* are unknown.

Out of Africa, *P. weberiana* sensu Corner (1991) and *P. alyxiae* (Wu *et al.* 2020a) are comparable, in both a morphological and ecological context; both share with *P. pseudoweberiana* the basidiome habit and anatomy, the tomentum in deeply sulcate, rounded zones, small pores, a dimittic hyphal system, basidiospores similar in shape and size, and some of their autecological parameters (growing from living understorey trees).

*Phylloporia weberiana* sensu Corner (1991) differs in having a context comparatively thicker (2.5–18 mm) than the overlying tomentum (4–6 mm, fide Corner 1991), an anatomy which is inverted in *P. pseudoweberiana* (cf. above), and slightly larger pores, viz. 110–200  $\mu\text{m}$  (fide Corner 1991) vs 85–105  $\mu\text{m}$  (cf. above). Corner (1991) reported four specimens of *P. weberiana* from Malaysia and the Philippines, but identified the host tree (*Diospyros* sp., *Ebenaceae*) for only one collection. *Phylloporia alyxiae* differs from *P. pseudoweberiana* in having larger pores [6–8 (fide Wu *et al.* 2020a) vs 9–11 pores / mm], its host (*Alyxia insularis*, an endemic *Apocynaceae* from Taiwan, vs *Rawsonia lucida*, *Achariaceae*), and distribution range.

***Phylloporia warneckeicola*** Jerusalem, Yombiy., Amalfi & Decock, **sp. nov.** MycoBank MB 851917. Figs 9C, E, F, 11.





**Fig. 9.** **A, B, D.** Moist basidiomata of *Phylloporia memecyli* and **(E, F)** basidiomata of *Phylloporia warneckeicola*. **A.** GA12-812 (holotype), bottom view. **B.** GA12-812, upper view. **C.** Comparative view of the colour of the pore surface of *P. warneckeicola* (MJ-GA19-017, above) and *P. memecyli* (MJ-GA19-091, below) when fresh. **D.** GA12-812, general view. **E.** GA12-813, bottom and upper view. **F.** MJ-GA19-017 (holotype), general view. Scale bars: A–F = 1 cm.





**Fig. 10.** Microscopic structures of *Phylloporia memecyli* holotype (GA12-812): vegetative hyphae from the tube trama and basidiospores.



**Fig. 11.** Microscopic structures of *Phylloporia warneckeicola*: generative/skeletal/sclerified hyphae from the tube trama, basidia, basidioles and basidiospores.

**Etymology:** “warneckeicola” (Latin) is referring to the host tree genus (*Warneckea* Gilg.).

**Typus:** **Gabon**, Ogooue Maritime Province, CTFS-ForestGEO Rabi forest monitoring Plot, ~ S1°55'28.56", E9°52'48", elev. ~ 30–60 masl, on the trunk of a small-stemmed living trunk, *Warneckea floribunda* (*Melastomataceae*), 2 May 2019, *M. Jerusalem* & *P. Yombiyeni*, MJ-GA19-017 (**holotype** BR; **isotype** NY).

**Diagnosis:** *Phylloporia warneckeicola* is similar to *P. memecyli* by the combination of small basidiomes (projecting 5–16 mm, 5–22 mm wide) emerging gregariously in clusters, mostly sessile, attached by a narrow dorsal point but closely following the substrate than appearing semicircular or broadly attached, and a densely, finely, concentrically sulcate pileus surface, but differs by a pore surface with a distinct greenish hue when fresh, smaller 11–13 pores / mm, 60–80 µm diam., and growing on *Warneckea floribunda* (*Melastomataceae*) in the understory of the Lower Guineo-Congolian rainforest.

**Description:** *Basidiomes* perennial, pileate, sessile (rarely with a stipe-like elongated base), gregarious, emerging simultaneously in clusters of up to 40 individuals, superposed, mostly solitary or 2–5 individuals imbricated; individual basidiome attached by a small apical or subapical, dorsal vertex, turbinate, pendant when young, but very closely to the bark, hence appearing a first sight semicircular to broadly attached, projecting firstly downward then horizontally, 5–16 mm, 3–22 mm wide, mostly semicircular or ellipsoid in outline, first slightly triquetrous when very small, progressively thinly applanate in transversal section, with the pores surface concave (incurved inside), with a general hard corky consistency; pileus surface shortly velutinous, finely, densely concentrically sulcate, with numerous fine sulcations (up to 10–12 very narrow concentric zones / cm), mainly brown (6E5, cocoa brown) to dark brown on aging (6F6, burnt amber), slightly lighter toward the margin (cinnamon brown); margin entire, thinly rounded, forming a well-defined, narrow rim especially in young basidiomes or surrounding patchy regrowth of pore field, greyish yellow





**Fig. 12.** Moist specimens of *Phylloporia pseudoweberiana* in situ. **A.** KE15-02 (holotype), details of the pores surface. **B.** KE15-19, view of the pores surface. **C.** KE15-19, upper view. **D.** KE15-02, general view. Scale bars: A–D = 1 cm.

when fresh, pale cork-coloured on drying; pore surface plane to mostly concave (incurved inside), first homogeneous, then with homogeneous or heterogeneous regrowth, in confluent, variably sized patches, brown or with a distinct greenish, olive green hue when very fresh, drying yellowish brown [5E(4–5) to 5F5, bronze, sooty brown, Havana brown]; pores small, regular, mostly round, sometimes slightly ellipsoid, 11–13(–14) / mm, (50–)60–80(–90)  $\mu\text{m}$  diam. (av. = 69  $\mu\text{m}$  diam.); dissepiments thin, (15–)20–50(–60)  $\mu\text{m}$  thick (av. = 31  $\mu\text{m}$ ); context homogeneous, dense, compact, 0.5–1.5 mm thick at the base, very thin to the margin, cinnamon brown to brown [6(D–E)6], topped by a thin black line subtending a thin upper trichoderm; trichoderm 125–250  $\mu\text{m}$  thick, shortly velutinous (under the lens), agglutinating from the base, brown to dark brown (5E8); tube layer 0.5–1.5 mm deep, concolourous with the lower trama. Hyphal system dimitic; generative hyphae simple septate, thin- to slightly thick-walled, hyaline to faintly yellowish, scarcely branched, with a constriction at the branching point, 1.3–2.5  $\mu\text{m}$  diam.; lower context, dominated by skeletal hyphae, parallel to long axis, tightly packed, arising from a generative hyphae and of limited

growth, measured up to 250  $\mu\text{m}$  long, 2.0–2.5  $\mu\text{m}$  wide at the basal septa, progressively widening to (2.7–)3.2–4.0(–4.3)  $\mu\text{m}$  wide (av. = 3.5  $\mu\text{m}$ ), golden brown, darker (brown) in alkali, thick- to very thick-walled with the lumen wide to narrow, mostly aseptate throughout, or with few secondary septa near the apices; trichoderm with prostrate to erected hyphae, mostly unbranched, thick-walled with widely open lumen, septate with both true and secondary septa, the apices rounded to open, yellowish to brown, mostly 4–6(–8)  $\mu\text{m}$  diam., the apices 6–8  $\mu\text{m}$  wide; hymenophoral trama dominated by skeletal hyphae, mostly subparallel to the tube main axis, arising from a generative hyphae or a short mediate hyphae, mostly terminal, of limited growth, measured from 115  $\mu\text{m}$  to 250  $\mu\text{m}$  long, 1.8–2.5  $\mu\text{m}$  diam. at the basal septa to (2.7–)3.2–4.0(–4.3)  $\mu\text{m}$  wide (av. = 3.5  $\mu\text{m}$ ) in the main part, occasionally geniculated in the basal lower third to mostly straight in the main part, occasionally locally inflated (up to 5–7  $\mu\text{m}$ ), or subapically constricted once or twice (slightly moniliform), slightly thick-walled at the basal septa, progressively thick- to very thick-walled, the lumen opening then narrow, locally lenticular, ending thin-walled, aseptate





**Fig. 13.** Microscopic structures of *Phylloporia pseudoweberiana* (KE-15-02, holotype): hyphae from the tube trama and basidiospores.

throughout but with a few secondary septa near the apices, golden brown, darker brown in alkali. Hymenium: *Basidioles* slightly pyriform to broadly clavate,  $6.0\text{--}7.0 \times 3.0\text{--}4.0 \mu\text{m}$ ; mature basidia few, barrel-shaped to broadly clavate, with four sterigmata; *cystidioles* not seen; *basidiospores* ellipsoid to broadly ellipsoid, appearing somewhat angular on drying, thick-walled, smooth, hyaline to pale yellowish in KOH, without reaction in Melzer's reagent,  $(3.0\text{--})3.2\text{--}3.5\text{--}(3.8) \times 2.2\text{--}2.5\text{--}(2.8) \mu\text{m}$  (av. =  $3.4 \times 2.4 \mu\text{m}$ ),  $R = 1.3\text{--}1.5\text{--}(1.6)$  (ave<sub>Q</sub> = 1.4).

**Phylogenetic affinities:** The species, hitherto, is related to a group of morphologically and ecologically similar species, including *P. warneckeicola*, *P. fulva*, and *P. pendula* (Fig. 1).

**Ecology** (substrate, host, habitat): On living trunk, small-stemmed *Warneckea floribunda* (*Melastomataceae*), understory compartment, Lower Guineo-Congolian rainforest.

**Geographic distribution:** Currently known from the CTFS-ForestGEO Rabi forest monitoring Plot, South-western Gabon.

**Additional specimens examined:** **Gabon**, Ogooue Maritime Province, CTFS-ForestGEO Rabi forest monitoring Plot, ~ S01°55'28.56", E09°52'48", elev. ~ 30–60 masl, on the trunk of a small-stemmed living tree, *Warneckea floribunda* (*Melastomataceae*), 15 Apr. 2012, C. Decock & P. Yombiyeni, GA-12-657; *ibid.*, 2 May 2019, M. Jerusalem & P. Yombiyeni

MJ-GA19-020; 3 May 2019, M. Jerusalem & P. Yombiyeni MJ-GA19-048, MJ-GA19-049, MJ-GA19-050, MJ-GA19-055; 4 May 2019, M. Jerusalem & P. Yombiyeni MJ-GA19-057, MJ-GA19-064, MJ-GA19-069, MJ-GA19-070; 5 May 2019, M. Jerusalem & P. Yombiyeni MJ-GA19-072, MJ-GA19-073; 7 May 2019, M. Jerusalem & P. Yombiyeni MJ-GA19-088, MJ-GA19-089, MJ-GA19-092.

**Notes:** *Phylloporia warneckeicola* is closely related to *P. memecyli*, whatever the perspective. Both are related also to *P. fulva*, described from the same phytochorion in Gabon; these species belong to the same well-supported lineage (Fig. 1). They also share most of their biology, including reproduction strategy, morphology, and some of their autecological parameters. They produce perennial, gregarious basidiomes, emerging in dense clusters (Fig. 9), rather small (mostly around 10 mm radius, 1–3 mm thick at the base), mostly applanate, densely and very finely concentrically sulcate, shortly velutinous pilei (Fig. 9), and small pores (~ 10–13 / mm). Their hyphal system, in the hymenophoral and context trama, could be considered as dimitic, with skeletal hyphae originating from a generative hyphae, occasionally from a mediate hyphae, and of a limited growth (Figs 10, 11), what is especially obvious in the hymenophoral trama. In the classification scheme of Corner (1991), it would be described as dimitic of the fifth degree (d5). The basidiospores are mostly ellipsoid, ~  $3.2\text{--}3.5 \times 2.2\text{--}2.5 \mu\text{m}$ , av.  $3.4 \times 2.4 \mu\text{m}$ , ~  $3.5\text{--}4.0 \times 2.2\text{--}2.5$ , av.  $3.7 \times 2.3$ , and ~  $3.0\text{--}3.5 \times (2.2\text{--})2.5\text{--}2.8 \mu\text{m}$ , av.  $3.2 \times 2.7 \mu\text{m}$ , respectively. They also share the substrate affinities and habitat: they grow from trunks of small-stemmed understory trees, which belong to the *Melastomataceae* in the case of *P. warneckeicola* and *P. memecyli*, and they inhabit the lower Guinean rain forest, at the westernmost edge of the larger Guineo-Congolian phytochorion. *Phylloporia warneckeicola* and *P. memecyli* are sympatric at least at the CTFS-ForestGEO Rabi plot in Gabon, an area of the Guineo-Congolian rainforest (Anderson-Teixeira *et al.* 2014).

*Phylloporia warneckeicola* is abundant at a local scale, depending on the density of its host tree, *W. floribunda*. In the 25 Ha of the CTFS-ForestGEO Rabi plot, *W. floribunda*, with a density of ~ 110 individuals / Ha, represents the 14<sup>th</sup> most abundant tree (Memiaghe *et al.* 2016). Most of the individual trees present in an immediate neighbourhood are often hosting *P. warneckeicola*. Locally, *P. memecyli* is much less abundant, in parallel to its host tree, *Memecylon viride*, which is not reported amongst the locally abundant understory tree (Memiaghe *et al.* 2016).

*Phylloporia warneckeicola* and *P. memecyli* differ marginally by their pore surface colour, pores size, and basidiospores size; the pores surface in *P. warneckeicola* has a marked greenish brown tint (brown with greenish hue, bronze on drying), what is best seen in fresh, actively growing basidiomes, whereas it is mostly dark brown in *P. memecyli* (Fig. 9C); the pores are, respectively, mostly 11–13 vs 10–11 pores / mm; the basidiospores are slightly smaller in *P. warneckeicola*,  $3.2\text{--}3.5 \times 2.2\text{--}2.5 \mu\text{m}$ , av.  $3.4 \times 2.4 \mu\text{m}$ , vs  $3.5\text{--}4.0 \times 2.2\text{--}2.5 \mu\text{m}$ , av.  $3.7 \times 2.3 \mu\text{m}$ . The two species also differ in their host relationships, growing respectively from *W. floribunda* and *M. viride*. *Phylloporia fulva* differs in having a paler pileus colour, greyish orange to pale cinnamon. Its host tree is unknown.

*Phylloporia miomboensis* (cf. discussion under this species) is similar in gross basidiome morphology but differs in having solitary basidiomes, and inhabiting a very distinct ecosystem. It is also phylogenetically distant (Fig. 1).

Out of Africa, both *P. warneckeicola* and *P. memecyli* should be compared to *P. pendula*, which is biologically, morphologically, ecologically (Chen *et al.* 2017), and phylogenetically related (Fig. 1). *Phylloporia pendula* differs from both African species in having larger pores, 7–9 / mm (Chen *et al.* 2017). Its geographic distribution and, pending confirmation, its host, could also differentiate it. *Phylloporia pendula* is known so far from Eastern, subtropical to tropical, continental and insular China but its host was not recorded (Chen *et al.* 2017).

The macro- and the micromorphology of the basidiomes of *P. warneckeicola* and *P. memecyli* also point toward *P. pulla* (Yombiyeni *et al.* 2015) and *P. subpulla* (Wu *et al.* 2019). Yombiyeni *et al.* (2015) redescribed *P. pulla* based on examination of the type specimen, originating from Indonesia on an unidentified host. *Phylloporia pulla* is also, in literature (Wu *et al.* 2019), reported from an unidentified host in Thailand. The species is represented, for the time being, by a single LSU sequence, from the above-mentioned Thai specimen (GenBank accession: MG738809), but the LSU-based phylogenetic inferences did not allow identifying any close relative (Wu *et al.* 2019). This species differs from *P. warneckeicola* and *P. memecyli* in having broadly ellipsoid to subglobose basidiospores, mostly 2.8–3.5 × 2.3–2.8 µm (av. 3.0 × 2.6 µm).

*Phylloporia subpulla* was described from tropical, continental and insular China (Wu *et al.* 2019). It differs from *P. warneckeicola* and *P. memecyli* in having smaller pores, 13–16 / mm (vs ≤ 13 / mm in both African taxa), and smaller basidiospores, av. 2.7 × 2.0 µm (Wu *et al.* 2019). Its phylogenetic affinities also are unknown (Fig. 1, Wu *et al.* 2019).

## DISCUSSION

*Phylloporia* has been continuously surveyed worldwide since the monographic work of Wagner & Ryvarden in 2002 (e.g., Yombiyeni & Decock 2017, Wu *et al.* 2019, 2020a, Chamorro-Martínez *et al.* 2022, Zhou *et al.* 2022), although with an unequal geographic coverage. China and, to a lesser extent, the Neotropics have been especially well covered (see e.g., Valenzuela *et al.* 2011, Ferreira-Lopes *et al.* 2016, Wu *et al.* 2019, Chamorro-Martínez *et al.* 2022, Zhou *et al.* 2022).

In tropical Africa, the revision of *Phylloporia* has started to be implemented through several works (Decock *et al.* 2015, Yombiyeni *et al.* 2015, Yombiyeni & Decock 2017, Jerusalem *et al.* 2019, Olou *et al.* 2021, 2023) and currently, with the addition of *P. afropectinata*, *P. cinnamomea*, *P. memecyli*, *P. microspora*, *P. miomboensis*, *P. pseudoweberiana*, and *P. warneckeicola*, 22 named species are reported. Their main differentiating characters are summarised in the identification key below.

### Key to the species of *Phylloporia* reported in tropical Africa

- 1 Basidiomes (laterally) stipitate; emerging from underground roots of (small) trees or bushes ..... 2
- 1 Basidiomes sessile, emerging from aboveground organs (surfacing roots, trunks, branches, twigs, petioles, or leaves) of small trees, bushes, or liana ..... 4
- 2 Pileus surface with silvery concentric lines; context with a black line; pores 10–11 / mm; basidiospores ellipsoid 3.4–4.0 × 2.2–2.7 µm ..... ***P. afrospathulata***  
Known from the Guineo-Congolian phytochorion in Gabon. Description in Yombiyeni *et al.* (2015).  
***Phylloporia spathulata***, identified in literature from Central Africa (e.g., Cameroon) as are keyed out here.
- 2 Pileus surface homogeneously coloured; context with or without black line; pores 6–9 / mm ..... 3
- 3 Context without black line; stipe thinning toward the pileus, down 1 mm diam., bulbous at the base; pores 7–9 / mm; basidiospores mostly 2.0–3.0 × 2.5 µm ..... ***P. minutispora***  
Known from the Eastern side of the Guineo-Congolian phytochorion, at medium elevation forest of the Albertine rift, Democratic Republic of Congo and Uganda. Description in Ipulet & Ryvarden (2005).
- 3 Context with a black line; stipe stout all over, up to 1 cm thick; pores 6–8 / mm; basidiospores mostly 2.7–3.8 × 2.0–2.9 µm, av. 3.2 × 2.4 µm ..... ***P. mutabilis***  
Known from Benin, in dry forest. Description in Olou *et al.* (2023).
- 4 Basidiomes emerging from the abaxial side of living leaves; circular, button-shaped, shortly pendant, centrally attached ..... ***P. parasitica***  
This species in tropical Africa should be considered as *sensu auctores*. It is reported in tropical East Africa (Tanzania) by Ryvarden & Johansen (1980). Description in Ryvarden & Johansen (1980).
- 4 Basidiomes emerging from trunks, branches, twigs, petioles; distinctly pileate ..... 5
- 5 Pileus with a tomentum thicker than the underlying context ..... 6
- 5 Pileus without tomentum, smooth or with a trichoderm much thinner than the underlying context ..... 11
- 6 Black line absent between the context and the tomentum ..... 7
- 6 Black line present between the context and the tomentum ..... 8



- 7 Pileus pale brown, cork-coloured; pores surface cork-coloured; pores 3–5 / mm ..... ***P. littoralis***  
Known from an open, coastal forest in Gabon, on *Nichallea* sp. (*Rubiaceae*), and from Benin (unidentified host).  
Description in Yombiyeni & Decock (2017).
- 7 Pileus golden yellow to rusty brown; pores surface cinnamon to rusty brown; pores 2–4 / mm ..... ***P. fruticum sensu auct.***  
Specimens from tropical Africa identified as *P. fruticum* (Ryvarden & Johansen 1980, Ryvarden *et al.* 2022) should be taken as *sensu auctores* and not *sensu stricto*. Description in Ryvarden *et al.* (2022).
- 8 Pores 5–6 / mm; hyphal system monomitic; basidiomes 3–10 cm wide ***P. weberiana sensu Ryvarden & Johansen (1980).***  
This species is reported in tropical Africa by Ryvarden & Johansen (1980), but it should be considered as *sensu auctores*. Description in Ryvarden & Johansen (1980).
- 8 Pores 9–11 / mm; hyphal system dimitic ..... 9
- 9 Basidiomes 2–8 cm wide; on trunk and branches of *Rawsonia lucida* ..... ***P. pseudoweberiana***  
Known from Kakamega Forest, on *Rawsonia lucida* (*Achariaceae*), Kenya. Description above
- 9 Basidiomes up to 2 cm wide ..... 10
- 10 Basidiospores 4.0–4.5 × 2.5–3.0 µm, av. = 4.3 × 2.7 µm; pores 9–10 / mm, 85–100 µm wide;  
on twigs of *Rinorea* sp. (*Violaceae*) ..... ***P. rinoreae***  
Known from Lower Guinean rainforest in Gabon. Description in Jerusalem *et al.* (2019).
- 10 Basidiospores 3.6–4.0 × 2.2–2.5 µm, av. = 3.9 × 2.3; 8–9 / mm, 85–124(–130) µm wide;  
unidentified angiosperm ..... ***P. cinnamomea***  
Known from an unidentified angiosperm tree in Cameroon and Gabon, Guineo-Congolian rainforest. Description above.
- 11 Pileus with a trichoderm lying over a thin black line; hyphal system dimitic / pseudodimitic ..... 12
- 11 Pileus without trichoderm; context without black line; hyphal system monomitic ..... 17
- 12 Basidiomes wider than 2 cm, solitary to pectinate ..... 13
- 12 Basidiomes smaller, up to 2 cm wide, solitary, but emerging in large numbers ..... 14
- 13 Basidiomes medium to large-sized, > 3 cm long, up to 25 cm wide; basidiospores 3.8–4.3 (–4.5) × 3.0–3.5 µm, av. = 4.0 × 3.2 µm, on *Turraea* cf. *holstii* (*Meliaceae*) ..... ***P. afropectinata***  
Known from Elgon Mountain, from roots, trunk or branches. Description above.  
***Phylloporia pectinata*** sensu Ryvarden & Johansen (1980) or Ryvarden *et al.* (2022) are keyed out here.
- 13 Basidiomes up to 3 cm long, 5 cm wide, 1 cm thick; basidiospores 3.3–4.3 × 2.4–3.3 µm, av. 3.8 × 2.8 µm;  
on *Trichilia emetica* (*Meliaceae*) ..... ***P. beninensis***  
Known from Benin in West Africa. Description in Olou *et al.* (2021).
- 14 Pileus black, finely, densely sulcate; basidiomes emerging from small branches of bushy tree; Zambezian  
phytochorion (Miombo); basidiospores ellipsoid, oblong ellipsoid ..... ***P. miomboensis***  
Known from an unidentified bushy tree in Zimbabwe. Description above.
- 14 Pileus greyish orange, light to dark brown, blackish; basidiomes emerging mostly from trunk; understorey of the  
Guineo-Congolian rainforest; basidiospores ellipsoid to broadly ellipsoid ..... 15
- 15 Pileus greyish orange, light brown; basidiomes pendant, flabelliform, conical, thin ..... ***P. fulva***  
Known from the very humid rainforest at Mont de Crystal, in Gabon; host unknown; description in Yombiyeni *et al.* (2015).
- 15 Pileus darker, brown to black; basidiomes semi-circular, applanate ..... 16
- 16 Pore surface with greenish tint; pores 11–13 / mm; on *Warneckea floribunda* (*Melastomataceae*) ..... ***P. warneckeicola***  
Known from the Lower Guinean rainforest in Gabon. Description above.
- 16 Pore surface dark brown; pores 10–11 / mm; on *Memecylon* cf. *viride* (*Melastomataceae*) ..... ***P. memecyli***  
Known from the Lower Guinean rainforest in Gabon. Description above.
- 17 Basidiomes solitary; pores 2–3 / mm; basidiospores oblong ellipsoid, 4.5–5.5 × 2.0–2.5 µm ..... ***P. inonotoides***  
Known from Lower Guinean rainforest in Gabon on trunks of *Crotonogyne manniana* (*Euphorbiaceae*). Description in Yombiyeni *et al.* (2015).
- 17 Basidiomes gregarious (10–100); pores 5–6 / mm; basidiospores on average < 4 µm long ..... 18
- 18 Basidiomes emerging from a common base; basidiospores narrowly ellipsoid to oblong; open (Zambezian)  
woodland ..... ***P. microspora***  
Known from Zimbabwe, on the trunk of *Colophospermum mopane* (*Fabaceae*). Description above.
- 18 Basidiomes emerging individually; basidiospores broadly ellipsoid; Lower Guinean rainforest ..... 19
- 19 Basidiomes > 1.5 thick; pileus dull; margin irregular, incised ..... ***P. gabonensis***  
Known from *Euphorbiaceae* in the humid Lower Guinean rainforest in Gabon. Description in Decock *et al.* (2015).
- 19 Basidiomes ≤ 1.5 mm thick; pileus shining; margin regular, entire ..... ***P. flabelliformis***  
Known from *Euphorbiaceae* in the humid Lower Guinean rainforest in Gabon. Description in Decock *et al.* (2015).



Nonetheless, 22 named *Phylloporia* species in tropical Africa represent an underestimated figure. The Mycota of the forests of the plant-rich Guineo-Congolian centre of endemism (or the forests of the Congo basin) remains largely understudied (Cheek *et al.* 2020). Given the local botanical diversity and presumed host specificity of *Phylloporia* species, additional undescribed taxa can be expected from this phytochorion. Our studies already show the existence of four additional phylogenetic species from its western edge in Gabon, that await formal description in the Linnean scheme (Fig. 1, GA-RABI-01, PY-SN3, PY-SN5, and PY-SN6). Other African phytochoria could also harbour additional species, such as the Miombo forest, which is the habitat of the species represented by the specimen Thoen 4902 (Fig. 1).

It must also be kept in mind that the reports in tropical Africa of several species that were originally described from other continents are highly questionable. Those presumed pantropical, multiple host taxa, represent undoubtedly collective species, hiding a taxonomic diversity whose level is arguably as diverse as their host plant diversity. It concerns *P. fruticum*, *P. parasitica*, *P. pectinata*, *P. spathulata*, and *P. weberiana* (Ryvarden & Johansen 1980, Ryvarden *et al.* 2022).

In tropical Africa, *P. fruticum* is reported from Kenya, Tanzania, the Democratic Republic of the Congo, and Madagascar (Ryvarden & Johansen 1980). The species was originally described from Cuba, growing on small twigs of an unidentified bushy plant (Berkeley & Curtis 1869). Castro Hernandez (2020) tentatively identified the host of *P. fruticum* as *Espadaea amoena* (Goetzeaceae), a Cuban native species. In that sense, *P. fruticum* is interpreted as a Greater Antilles endemic, and therefore absent from Africa.

Its closest African morphological relative to date is *P. littoralis*, originally described from coastal areas in South-western Gabon (Yombiyeni & Decock 2017), also reported from Benin (Olou *et al.* 2021). Both species share the soft, spongy basidiome, large pores, a monomitic hyphal system, elliptical basidiospores, and substrate affinities, viz. small (terminal) branches of bushy plants (Yombiyeni & Decock 2017). However, *P. littoralis* and a specimen tentatively identified as *P. cf. fruticum* are phylogenetically distant (Fig. 1).

*Phylloporia parasitica* was originally described from Colombia, on living leaves of an unidentified *Bignoniaceae* (Murrill 1904). In tropical Africa, it is only known from a single specimen from East Africa [Tanzania, Pangani dist., Msubugwe forest, 19 June 1956, (growing on) Tanner 2919, K, *fide* Wagner & Ryvarden 2002]. The specimen Tanner 2919 corresponds to the host plant, and was identified as *Whitfieldia orientalis* Vollesen (*Acanthaceae*, Grall & Darbyshire 2021). *Phylloporia parasitica* is here considered absent in tropical Africa and the Tanzanian specimen growing on Tanner 2919 should represent a morphologically related but distinct taxon that needs re-evaluation.

*Phylloporia pectinata* was described originally as *Polyporus pectinatus* Kl. from an imprecise locality of Southern India and growing on an unidentified host (Klotzsch 1833). The type specimen, as well as type specimens of some presumed synonyms from both the Paleo- and the Neotropics, were revised by Ferreira Lopes (2018) who redefined *P. pectinata* s.s. morphologically, and circumscribed its distribution range from Southern India to Southeast Asia, suggesting that it may also extend to Australia. The present results confirm that *P.*

*pectinata* sensu Ryvarden & Johansen (1980) or Ryvarden *et al.* (2022) in tropical Africa encompasses several species. It includes *P. afropectinata*, *P. beninensis* (Olou *et al.* 2021), *P. fulva* (Yombiyeni *et al.* 2015), *P. memecyli*, *P. miomboensis*, *P. warneckeicola*, and as a yet undescribed taxon, *Phylloporia* sp. (Thoen 4902, annotated as *P. pectinata* on the herbarium label by L. Ryvarden, BR, Fig. 1).

*Phylloporia spathulata* has been recorded several times from the Lowland Guineo-Congolian rainforests in Cameroon (Hjortstam *et al.* 1993, Wagner & Ryvarden 2002, Roberts & Ryvarden 2006). The species was originally described from a medium elevation forest in the Ecuadorian Andes (Kunth 1822) and is considered absent from the Guineo-Congolian rainforests. In tropical Africa, *P. spathulata* sensu Ryvarden & Johansen (1980) is represented so far by *P. afrospathulata*, known from the Western edge of the Guineo-Congolian rainforest in Gabon (Yombiyeni *et al.* 2015), *P. minutispora* in its Eastern edge, in Western Uganda and Eastern Democratic Republic of the Congo (Ipuleit & Ryvarden 2005, Yombiyeni *et al.* 2015), and *P. mutabilis*, from dense, dry forest in Benin (Olou *et al.* 2023).

*Phylloporia weberiana* was described originally as *Fomes weberianus* from the Southern Pacific Island of Samoa (Saccardo 1891). The interpretation of this species has been long debated (cf. Steyaert 1972, Ryvarden 1972, Cabarro Hernández *et al.* 2019) and its recognition within *Phylloporia* dates back from Ryvarden (1972). Decock *et al.* (2024) lectotypified and redescribed *P. weberiana* sensu stricto. The species has been widely reported in tropical Africa, from Western (Ghana), Central (Cameroon, Democratic Republic of Congo, Nigeria, Uganda), and Eastern areas (Kenya, Tanzania), down to insular Madagascar (Ryvarden & Johansen 1980, Ryvarden *et al.* 2022). Given its wide distribution in Africa (Ryvarden & Johansen 1980, Ryvarden *et al.* 2022), covering different vegetation types and a rich and differentiated botanical diversity, *P. weberiana* sensu Ryvarden (Ryvarden *et al.* 2022) is likely a collective species, encompassing several additional taxa. In the Guineo-Congolian phytochorion, it includes so far *P. cinnamomea*, *P. pseudoweberiana*, *P. rinoreae*, and *Phylloporia* sp. PY-SN6.

## Insights into the preliminary phylogenetic structure of *Phylloporia*

Until now, phylogenetic inferences within *Phylloporia* have been based mainly on LSU DNA sequence data (e.g., Jerusalem *et al.* 2019, Wu *et al.* 2019, 2020a, 2022, Chamorro-Martínez *et al.* 2022). Olou *et al.* (2021, 2023) proposed a “multilocus” phylogenetic analysis of *Phylloporia*, including data from LSU and ITS (Olou *et al.* 2021) and LSU, ITS, and partial *TEF-1α* (Olou *et al.* 2023). However, in these “multilocus” phylogenetic analysis, the number of ITS and partial *TEF-1α* sequences included is low or very low (Olou *et al.* 2023) comparatively to the LSU sequences. The ITS is represented by 38 sequences and the *TEF-1α* by 20 sequences, or ~30 % and ~15 % of the LSU dataset. ITS and *TEF-1α* are also scattered in the dataset. De facto, the phylogenetic signal of LSU predominates in the tree reconstruction, with a very restricted or insignificant input of the ITS and more obviously of the *TEF-1α*. Furthermore, as noted by Decock *et al.* (2015) and Wei *et al.* (2024), the ITS sequences of *Phylloporia* species proved to be difficult to align





unambiguously. They present also indels of variable length. For instance, Decock *et al.* (2015) showed presence of two indels of 85 and 13 bp long in the ITS1 and ITS2 regions of *P. flabelliformis* and *P. gabonensis* compared to *P. parasitica*. The way these indels and the ambiguous alignments were treated by Olou *et al.* (2021, 2023) is not discussed at all by these authors.

Phylogenetic inferences based on the LSU alone do not reveal any structure within *Phylloporia* as currently accepted (e.g., Wu *et al.* 2019, 2020a, 2022). Wu *et al.* (2019) did report four lineages within *Phylloporia* (A–D), described as “neutral term groups”, but none were substantiated, regardless of the phylogenetic hypothesis tested. Each of these “neutral term groups” also encompassed species from various morpho-ecological types and geographic origins, without any structuring features, whether it concerns the basidiome habit, hyphal system, substrate and host preference, or geographic origins. Alternatively, based on the most comprehensive LSU dataset available by then and an unbalanced LSU-ITS dataset, Olou *et al.* (2021) recognized two well-supported lineages within *Phylloporia*, that they noted A and B, without any further discussion.

Our phylogenetic inferences based on the most comprehensive LSU data set (data not shown) showed the same overall unresolved topology, without statistically supported internal lineages but the two above mentioned lineages A and B (Olou *et al.* 2021) and the terminal taxon clades. Our current multilocus phylogenetic inferences, based on a reduced set of species, confirmed the results of the LSU-based inferences, as far as phylogenetic species are concerned. It also confirmed the core A lineage and a well-supported basal B lineage (Fig. 1) and resolved, within the core A lineage, several well-supported lineages.

### The basal B lineage (Fig. 1)

The basal B lineage comprises hitherto four named and two unnamed species clades. They are *P. boldo* (Rajchenberg *et al.* 2019), *P. dependens* (Liu *et al.* 2015), *P. mori* (Wu *et al.* 2020a), *P. moricola* (Wu *et al.* 2021), *Phylloporia* sp. MUCL 54263 (Brazil), and *Phylloporia* sp. PY-SN3 (Gabon). This lineage is pantropical in distribution.

The basidiome, hyphal system, hyphal differentiation (dimitic with skeletal hyphae or monomitic, fide Y.C Dai in Liu *et al.* 2015), and basidiospores of the species of the B lineage do not differ significantly from those of several species of the core A lineage as e.g., species of the *P. warneckeicola* lineage (Fig. 1, A3). However, noteworthy, *P. mori* has the unique characteristic of possessing hymenial setae, whereas all other *Phylloporia* species of lineages A and B known to date lack any setae. Furthermore, the sequenced portion of the *TEF-1α* gene of *Phylloporia* sp. MUCL 54263 (Brazil) and *Phylloporia* sp. PY-SN3 (Gabon) differs also from the homologous sequences of the other species of the core A lineage in terms of the number of spliceosomal introns. Furthermore, while the introns were easily alignable across the whole core A lineage, they strongly diverged from the two available sequences of the basal B lineage, making the alignment problematic and suggesting a different evolutionary history. There are no available *TEF-1α* sequences of the other species of the lineage B to date.

The ecology of these six species, including their trophic relationships, is still little documented so far, except for the host plants of *P. boldo* (*Peumus boldus*, *Monimiaceae*, Rajchenberg *et al.* 2019), *P. mori* (*Morus* sp., *Moraceae*; Wu *et al.* 2020a), and *P. moricola* (*Morus* sp., *Moraceae*; Wu *et al.* 2021).

Rajchenberg *et al.* (2019) questioned the taxonomic placement of *P. boldo* in relation to *Phylloporia*. This lineage B may well deserve recognition at its own taxonomic rank.

### The core A lineage (Fig. 1)

The core A lineage contains most of the known, named *Phylloporia* species but also a significant number of unnamed taxa (Fig. 1). It embraces the morphological and ecological heterogeneity of the genus, synthesised by morpho-ecological types (Yombiyeni *et al.* 2015) and its geographic distribution, although some areas remain little explored. The structuring nature of these morpho-ecological types were questioned, together with independent, sympatric or allopatric, morphological and ecological convergences (Yombiyeni *et al.* 2015).

The current multilocus phylogenetic inferences (Fig. 1) do not resolve any backbone structure within the core lineage. No primary structuring feature is shown, either in terms of e.g., basidiome habit, ecology, or geographic distribution. For instance, the basidiome habit, stipitate vs sessile, is not an overall phylogenetically structuring element for the genus. The stipitate habit, with basidiomes emerging from underground roots, represents a homoplastic trait, dispersed into several unrelated lineages or branches in distant geographic areas (viz. the various Neotropical lineages, as well as the clades *P. minutispora* and *P. afrospathulata*, Fig. 1). Nor is the biogeographic domain a primary structuring element within lineage B. The multilocus-based phylogenies showed that neotropical and paleotropical species are dispersed into multiple, (hitherto) unrelated lineages (Fig. 1). For example, neotropical taxa are not monophyletic, while e.g., they are in the *Fomitiporia* core clade (Chen & Cui 2017, Alves *et al.* 2020b).

Notwithstanding, several well-supported lineages, encompassing multiple species, are globally homogeneous in what concerns their geographic range, either neotropical, paleotropical, or Northern pantemperate-Eurasian. They are the *P. ribis* lineage in the Northern pantemperate-Eurasian area; the *P. afropectinata* lineage, two independent *P. pectinata*-like lineages (*P. miomboensis* and *P. warneckeicola* lineages), the *P. pseudoweberiana*, and *P. littoralis* lineages (Fig. 1) in the Paleotropics; and the *P. rzedowskii* lineage, *P. solicola* lineage, *P. sumacoensis* lineage, and *P. elegans* lineage in the Neotropics (Fig. 1).

### The pantemperate lineage

The pantemperate *P. ribis* lineage (Fig. 1, A1) gathers taxa spanning over Eurasia (Europe and Central to East Asia) and North America. The species has been declined into multiple host specific forms (Bourdote & Galzin 1928, Pilát 1942, Bondartsev 1971). These forms are distributed into as many terminal clades as host plants (Fig. 1, A1). In the current dataset, it comprises 15 species-level or potential species-level clades or branches, grouped into two variably supported sublineages.

The first, and well-supported sublineage, comprises *P. ribis* s.s. (*f. ribis*) and the forms *corni*, *f. crataegi*, *f. pruni-spinosae*, and *f. ulmi* (*Xanthochrous ribis f. crataegi*, *f. pruni-spinosae*, and *f. ulmi*, Bourdot & Galzin 1928, or *Phellinus ribis f. corni*, *f. crataegi*, *f. pruni-spinosae*, and *f. ulmi*, Pilát 1942, Bondartsev 1971). It includes also *P. crataegi*, *P. oreophila*, *P. osmanthi*, *P. perangusta*, and *P. tiliae* (Zhou & Dai 2012, Zhou 2013, 2015b, Wu *et al.* 2019). The second sublineage, which support is uncertain (0.87/35), includes three additional forms of *P. ribis*, viz. *f. euonymi*, *f. rosae*, and *f. ulicis* (*Xanthochrous ribis f. euonymi*, *f. rosae*, and *f. ulicis* or *Phellinus ribis f. euonymi*, *f. rosae*, and *f. ulicis*, Pilát 1942). It comprises also *P. lespedezae* and *P. yuchengii*, both known from central and temperate East Asia (Gafforov *et al.* 2014, Ren & Wu 2017). These taxa constitute the *P. ribis* morpho-ecological type, characterised by merismatoid basidiomes emerging from the very bases of living, (mostly) small-stemmed trees or bushes. Some of these forms (e.g., *f. euonymi*, *f. ulicis*, *f. pruni-spinosae*, etc.), if not all, deserve to be recognized at species level.

Nevertheless, two exceptions are worth discussing. They concern *Phylloporia rattanicola* (Wu *et al.* 2019) and the *f. jasmini* of *P. ribis*.

*Phylloporia rattanicola* nests in the *P. ribis* lineage. However, this placement is surprising, given the host, substrate affinities, and distribution. *Phylloporia rattanicola* was collected in subtropical China on rattans (*Calamoideae*, *Arecaceae*), which are tropical monocotyledonous high-climbing vines. This would therefore be the only *Phylloporia* described (to date) from a monocot, and a (sub)tropical species belonging to a globally northern pantemperate clade.

The specific form of *P. ribis* on *Chrysojasminum fruticans* (L.) Banfi (*Oleaceae*; *Phellinus pectinatus* var. *jasminii*, Quélet 1891; *X. ribis f. jasmini*, Bourdot & Galzin 1928) is also a remarkable exception. It does not belong to the *P. ribis* lineage but to the distant *P. miomboensis* lineage (cf. below, Fig. 1, lineage B3). It also differs from *P. ribis* in that the basidiomes emerge mainly from aerial branches, mostly in rows, and not just from the base of the stem.

### The paleotropical lineages

The paleotropical lineages are, to date, morphologically and ecologically homogeneous. Each is characterised by a combination of morphological and ecological traits and, in that sense, each represents a morpho-ecological type (MET, Yombiyeni *et al.* 2015). The pantemperate – Eurasian *P. ribis* lineage also corresponds to a MET. The MET is a descriptive element for these lineages.

The *P. afropectinata* / *P. ribis* lineage (Fig. 1, A1 and A2) – Ferreira Lopes (2018) morphologically redefined *P. pectinata* s.s., based on type studies, and circumscribed its putative geographical distribution. There is no ascertained DNA sequence of *P. pectinata* s.s. to date, impeding to infer its phylogenetic affinities.

Two collections tentatively identified as *P. pectinata* and collected in its hypothetical distribution range (cf. Ferreira Lopes 2018), R. Coveny 113 (K) (Wagner & Ryvarden 2002, Wu *et al.* 2019) and CBS 445.76, were included in the current phylogenetic inferences. R. Coveny 113 was collected in Southern Australia (Kurrajong / New South Wales, growing on the *Myrtaceae* *Rhodamnia rubescens*) whereas CBS 445.76

is a culture isolated from a voucher specimen collected in India, without additional precision. These two collections represent two species, which are phylogenetically distant. The specimen R. Coveny 113 belongs to the well-supported *P. afropectinata* / *P. beninensis* lineage (Fig. 1, A2). *Rhodamnia rubescens* is absent in the type locality of *P. pectinata* in Southern India (<https://www.gbif.org/fr/species/3186016>). From this perspective, it certainly does not represent *P. pectinata* s.s. CBS 445.76 belongs to the well-supported *P. miomboensis* / *P. minima* / *Ph. pectinatus* var. *jasminii* lineage (Fig. 1, lineage B3). *Phylloporia miomboensis* (Fig. 4) and *P. minima* (Walters 1969) are characterised by a dimitic hyphal system with skeletal hyphae, which differentiates them from *P. pectinata* s.s. characterised by sclerified generative hyphae (Ferreira Lopes 2018). In that sense, assuming that the species from the *P. miomboensis* lineage are homogeneous in terms of hyphal system and hyphal differentiation, CBS 445.76 would neither represent *P. pectinata* s.s.

The *P. afropectinata* lineage (Fig. 1, A2) is here interpreted as the *P. pectinata* s.s. lineage. This is supported by similar hyphal differentiation in *P. afropectinata* and *P. pectinata* s.s. (Ferreira Lopes 2018). This is also supported by the phylogenetic and morphological affinities with species of the Northern temperate, Eurasian *P. ribis* lineage (A1 & A2, Fig. 1, see above). The *P. afropectinata* and *P. ribis* lineages are sister clades (Fig. 1). These species share the same hyphal system and hyphal differentiation (Ferreira Lopes 2018).

Historically, the affinities between *P. pectinata* and *P. ribis* had been suggested very early. Bresadola (1912) related *P. ribis* and *P. pectinata* (under *Fomes pectinatus*), whereas Lloyd (1915) noted that “*Fomes pectinatus* is in reality the tropical form of *Fomes ribis*”. Bourdot & Galzin (1928) commented also that the *f. ephedra-nebrodenensis* of *P. ribis* (under *Xanthochrous ribis f. ephedra-nebrodenensis*) would be the *P. pectinata* closest taxon.

The *P. pectinata*-like lineages (Fig. 1, A3 & A6) – Other species would have agreed with the wide morphological (historical) circumscription of *P. pectinata* s.l. (e.g., sensu Ryvarden & Johansen 1980, Corner 1991, Ryvarden *et al.* 2022). It includes, in our dataset, members of the *P. miomboensis* lineage (Fig. 1, B6), members of the *P. warneckeicola* lineage (Fig. 1, B6), and the African specimen *P. pectinata* Thoen 4902 (identification on the herbarium label by Ryvarden). Species of these lineages are characterised by a dimitic hyphal system with skeletal hyphae of limited length, in which feature they differ also from *P. pectinata* s.s. (Ferreira Lopes 2018). Thoen 4902 stands hitherto on an isolated branch (Fig. 1), but only the LSU sequence is available, and more DNA sequences are necessary to resolve its affinities.

The *P. miomboensis* lineage (Fig. 1, A3) – This well-supported lineage gathers four additional *P. pectinata*-like species from the paleotropics and the European Mediterranean area: *P. miomboensis*, *P. minima* (Walters 1969, Wu *et al.* 2022), *Phellinus pectinatus* var. *jaminii* Quélet (Quélet 1891), and *Phylloporia* sp. (cf. *P. pectinata*, CBS 445.76). The basidiomes of *Phylloporia miomboensis*, and *P. minima* (Walters 1969, Wu *et al.* 2022) are morphologically similar to the basidiomes of members of e.g., the *P. memecyli* clade, but differ in solitary vs gregarious emergence, and substrate affinity. The basidiome of *P. miomboensis* (cf. description above) and of *P. minima* (Walters 1969) emerge solitary from branches of bushy plants or twigs of scrub vines.



The substrate (plant organ) of *P. cf. pectinata* CBS 445.76 is unknown. The basidiomes of *Ph. pectinatus* var. *jaminii* emerge in rows from stems of the bushy *Chrysojasminum fruticans* (*Oleaceae*).

This lineage is heterogeneous in terms of habitat and geographic distribution. The species of this lineage have their origin in very distinct ecosystems in distant biogeographical domains, viz. the (Mediterranean) scrubby vegetation for *Ph. pectinatus* var. *jaminii*, the Miombo woodland (Zambezian open forest phytocorion) for *P. miomboensis*, and the Northeastern rainforest of Australia for *P. minima*. The locality (except India) and habitat of *P. cf. pectinata* CBS 445.76 are unknown. These species have no known close relatives to date in their native range.

The *P. warneckeicola* lineage (Fig. 1, A6) – This lineage gathers four *P. pectinata*-like species from the Paleotropics, *P. fulva*, *P. memecylii*, *P. pendula*, and *P. warneckeicola*. It is morphologically and ecologically homogeneous, characterised by gregarious, perennial basidiomes, emerging in large numbers from trunks of small-stemmed trees. The basidiomes are small, applanate to conical, with a dimitic hyphal system dominated by skeletal hyphae of limited growth (dimitism d5 according to Corner 1991). They share also the substrate affinity (trunks of small-stemmed trees). In that sense, the combination of life cycle, mitism, hyphal differentiation, and substrate affinities, defining MET, represent also a structuring feature of this lineage. *Phylloporia fulva*, *P. memecylii*, and *P. warneckeicola* inhabit and are known so far only from the western edge of the Guineo-Congolian Lowland rainforest, whereas *P. pendula* originate from tropical China.

The *P. littoralis* lineage (Fig. 1, A7) – *Phylloporia littoralis* (Yombiyeni & Decock 2017), *P. tamilnadensis* (Sridhar *et al.* in Crous *et al.* 2021), and *P. flacourtiae* (Zhou 2015b) form a well-supported, paleotropical clade. This clade corresponds to a MET characterised by solitary, seasonal, pileate, sessile basidiomes growing on thin branches or terminal stems of their host. Their basidiomes are anatomically very similar with a thin homogeneous context covered by a spongy tomentum, with or without an intermediate, separating layer of melanized hyphae (or a black line). Their hyphal system is monomitic. These species originate, respectively, from coastal areas in Southwestern Gabon and Benin, Southeastern India, and Southwestern China. *Phylloporia littoralis* and *P. tamilnadensis* both grow on *Rubiaceae*, *Nichallea* sp. and *Catunaregam spinosa*, respectively, whereas *P. flacourtiae* grows on the *Salicaceae*, *Flacourtia* sp.

*Phylloporia bibulosa* was originally described from Singapore (Lloyd 1924). The species was best described by Corner (1991), based on various collections, from several hosts, including two *Rubiaceae*, *Nauclea subdita* and *Ixora kingstonii*. It shares most of the morphological characters of *P. littoralis*, *P. tamilnadensis*, and *P. flacourtiae*. There is an LSU sequence available at GenBank referred to as *P. bibulosa* (Wagner & Ryvarden 2002). However, this sequence was obtained from the lectotype of *Inonotus peristrophidis*, from Pakistan. Although once considered as a synonym of *P. bibulosa* (Wagner & Ryvarden 2002), this species is nowadays accepted as *Phylloporia peristrophidis* (Wu *et al.* 2022). Its phylogenetic affinities, based on a single LSU available sequence, are uncertain (Fig. 1). The absence of confirmed sequences of *P. bibulosa* impedes confirmation

that the morphological affinities with *P. littoralis* and a paleotropical distribution underpin phylogenetic affinities.

The *P. pseudoweberiana* lineage (Fig. 1, A5) – *Phylloporia cinnamomea*, *P. pseudoweberiana*, *P. rinoreae*, and *Phylloporia* sp. PY SN6 belong to a very-well supported lineage. These four species share also the main morphological characteristics, including a sessile basidiome, a tomentum comparatively thicker than the underlying context, both separated by a thin layer of melanized hyphae (or a black line), a dimitic hyphal system, and the habitat, which is the Guineo-Congolian rainforest. *Phylloporia cinnamomea*, *P. rinoreae*, and *Phylloporia* sp. PY SN6 inhabit the western edge of this phytocorion whereas *P. pseudoweberiana* inhabits its easternmost limit in Kenya, at the Lake Victoria transitional rainforest (Kindt *et al.* 2014). This lineage corresponds to a morpho-ecological type known so far only in the Guineo-Congolian phytocorion. Several species may well be related, such as *P. weberiana* s.s. (Decock *et al.* 2024), *P. weberiana* sensu Corner (1991), or *P. alyxiae* (Wu *et al.* 2020a). These taxa are morphologically and ecologically related to *P. pseudoweberiana*, but DNA sequences are lacking or insufficient, which prevents the assessment of their phylogenetic affinities.

The *P. flabelliformis* / *P. gabonensis* lineage (Fig. 1, B9) – *Phylloporia flabelliformis* and *P. gabonensis* are very closely related, whatever the perspective, morphological, ecological, and phylogenetic. Both species are characterised by seasonal, short-living, soft, basidiomes, emerging simultaneously in large clusters of up to hundreds of individuals, from trunks of *Euphorbiaceae*, and a little differentiated monomitic hyphal system (Decock *et al.* 2015). They were described from and are to date known only from the western edge of the Guineo-Congolian rainforest in Gabon (Decock *et al.* 2015). They form a well-supported two-species clade (Fig. 1), which has no confirmed relative so far in Africa nor elsewhere.

### The Neotropical lineages

The majority of the Neotropical species included in our phylogenetic inferences are distributed into four lineages (Fig. 1, A4, A8–A10). These neotropical lineages are not strictly modelled by MET but include species encompassing different basidiome habits (sessile vs stipitate) and ecological traits. In these lineages, the main structuring feature that has been highlighted so far is the biogeographical distribution.

*Phylloporia parasitica* – The *Phylloporia* type species, *P. parasitica*, is missing from most previous (e.g., Wu *et al.* 2019, 2020a, 2022) and from our own phylogenetic inferences (Fig. 1), impeding to infer its phylogenetic affinities and, consequently, the definition of the type lineage. The species is known from very few specimens and only one single confirmed ITS sequence is available to date (GenBank KU198361, Argentina, L. Ryvarden 19483, OI, Decock *et al.* 2015). A partial ITS sequence (5.8S, ITS2, GenBank MT596135), based on environmental DNA from soil in Japan and obtained through metagenomics, was identified also to this species, but this identification is doubtful. Olou *et al.* (2023) used the unique ITS sequence KU198361 available (Decock *et al.* 2015) in their phylogenetic studies, but the affinities of *P. parasitica* were little supported.

A blast search at GenBank (06 January 2024) showed that the ITS sequences most similar to that of *P. parasitica*



KU198361 are to date *Phylloporia* sp. ON180506 and ON180504 (186/203), from Florida, followed by *P. cf. spathulata* MG489957 from Argentina (213/234), and several paleotropical species including *P. beninensis* MW244094 (269/301), *P. radiata* (MH151198 (298/334), and *P. flabelliformis* NR154332 (308/349). Nonetheless, a quick ITS-based RAxML analysis (data not shown) showed that the closest relatives of *P. parasitica* would be *P. amplexens* (based on specimens from Florida, USA, FLAS-F-61316, FLAS-F-61317, FLAS-F-61603), *P. cf. fruticum*, from Mexico (MX11, KU198363, Decock *et al.* 2015), and *Phylloporia* sp. (based on specimens from Florida FLAS-F-67305, MUOB:377247).

*Phylloporia amplexens* and *P. fruticum* are two morphologically and ecologically closely related species. They share with *P. parasitica* the basidiome anatomy and hyphal system and, to a certain level, affinities for terminal organs of the plant (small upper twigs up to petioles and leaves) but differ in having basidiomes with a thicker tomentum.

The basidiome of *P. parasitica* is usually defined as resupinate (e.g., Ryvarden & Johansen 1980, Wagner & Ryvarden 2002, Wu *et al.* 2019, 2022). However, it is in fact shortly pendant, hanging from a small central vertex, hence pileate, with the pileus extending laterally, closely parallel to the leaf surface (C. Decock, pers. obs.). The flat, button-like basidiome as present in *P. parasitica* may represent an extremely reduced form that could be shaped by the substrate. Inversely, the basidiome of *P. amplexens* or *P. fruticum* could represent an expanded form of the *P. parasitica* basidiome on different terminal organs.

On this basis, *P. parasitica* would belong to a hypothetical *P. parasitica* / *P. fruticum* / *P. amplexens* Neotropical lineage, within the core A lineage, and corresponding to a MET. This would represent *Phylloporia* s.s.

The *P. rzedowskii* lineage (Fig. 1, A4) – This lineage comprises, hitherto, four species including *P. rzedowskii*, known from Mexico (Valenzuela *et al.* 2011), and three unnamed taxa, known from Ecuador, Martinica (lesser Antilles), and Mexico. This lineage is heterogeneous regarding the basidiome habit. *Phylloporia rzedowskii* and *Phylloporia* spp. (MX-01, MX-02) have both sessile basidiomes emerging from twigs or small-stemmed trunks. *Phylloporia* sp. EC-22-04 and *Phylloporia* sp. [MA#] are sister clades, and both have stipitate basidiomes.

The *P. solicola* lineage (Fig. 1, A8) – This is the second most species-diverse clade shown to date (Fig. 1), and the most diverse in terms of species with stipitate basidiomes. It potentially includes eleven or twelve species, ten or eleven of which have a stipitate basidiome. The species with a stipitate habit includes *P. solicola*, known from Brazil (Wu *et al.* 2019), and nine or ten yet undescribed species, known from the Martinica (lesser Antilles), French Guiana, and Ecuador. *Phylloporia solicola* is known by two LSU sequences (MG738815, OL901672). These sequences differ in 3 to 4 positions from our sequences of a set of 8 collections originating from Martinica (e.g., MA-15-97, MA-16-236, MA-19-PS3, Fig. 1). Whether this could be considered as intraspecific variability within *P. solicola*, or would indicate distinct taxa remains uncertain to date. It should be confirmed by morphological comparison, and additional DNA markers from the type. This lineage comprises also *P. nouraguensis*, a species with sessile basidiomes emerging from small apical

twigs of a bushy *Myrtaceae*, so far known only from French Guiana (Decock *et al.* 2013).

The *P. sumacoensis* lineage (Fig. 1, A9) – This is the third most species-diverse lineage shown to date, with 11 species clades. It includes *P. ulloai*, known from Mexico (Valenzuela *et al.* 2011), *P. sumacoensis*, known from Ecuador (Zhou *et al.* 2022), and potentially nine undescribed taxa, known from Argentina, Brazil, Ecuador, French Guiana, Martinique, and Mexico. The species of this lineage are characterised by either sessile or stipitate basidiomes, mixing two morpho-ecological types. *Phylloporia* sp. (Robledo 2984, 351, Urcelay 628), *Phylloporia* sp. (Robledo 1220; G. Robledo, pers. com.), and *P. cf. spathulata* (Chay 456) have stipitate basidiomes.

Six species with sessile basidiomes are known only from liana, either the main stem or surfacing roots. They are *P. sumacoensis*, *Phylloporia* sp. (MA-19 PL, MUCL 54226), *Phylloporia* sp. (MA-19-PX2, PX3, PX4), *Phylloporia* sp. (WI117, I333, I555, EC-22-05), *Phylloporia* sp. (EC-22-02), and *Phylloporia* sp. (EC-22-03, FG-14-850). *Phylloporia sumacoensis*, *Phylloporia* sp. (MA-19 PL, MUCL 54226), *Phylloporia* sp. (WI117, 333, 555, EC-22-05), and *Phylloporia* sp. (EC-22-02) have a basidiome anatomy of the *P. weberianum* type, sessile, with an upper tomentum covering a comparatively thinner context.

The *P. elegans* lineage (Fig. 1, A10) – This lineage comprises three additional Neotropical species with a stipitate basidiome, including *P. elegans*, known from Southeastern Brazil and Northeastern Argentina (Ferreira Lopes *et al.* 2016), and two unnamed species clades, known from the Amazonian rainforest in Ecuador (Yasuni National Park) and French Guiana (Reserve naturelle nationale des Nouragues).

The species of the *P. spathulata* morpho-ecological type has stipitate basidiomes, emerging from soil, with a subterranean, likely intra-radical mycelial phase (Yombiyeni *et al.* 2015). There is no DNA sequence data from *P. spathulata* s.s. and its phylogenetic affinities are unknown. DNA sequences attributed to *P. spathulata* are available at GenBank but they are dispersed in the phylogenetic analyses (Fig. 1). They should be considered as *sensu auctores*. The *P. spathulata* MET is dispersed into several Neotropical but also paleotropical lineages, which indicates multiple independent emergences.

The Neotropics are so far the most diverse area in terms of species with a stipitate basidiome. Eight named species are known from this area (Ryvarden 2004, Ferreira Lopes *et al.* 2016, Wu *et al.* 2019, Chamorro-Martínez *et al.* 2022) and fifteen to sixteen additional species, not yet named in the Linnaean system, are shown by the current multilocus phylogenetic inferences (Fig. 1). The French Lesser Antilles, French Guiana, and the western Amazon in Ecuador are particularly well represented in our sampling, and rich in species with stipitate basidiome.

In comparison, the *P. spathulata* morpho-ecological type in tropical Africa is represented to date by only three species. They are *P. afrospathulata*, known from the western edge of the central African, Lowland Guineo-Congolian rainforest (Yombiyeni *et al.* 2015), *P. minutispora* in its eastern edge (Ipulet & Ryvarden 2005, Yombiyeni *et al.* 2015), and *P. mutabilis* in Benin, West Africa (Olou *et al.* 2023). These species are phylogenetically independent from each other (Fig. 1). In tropical Asia, four species are reported. They are *Polyporus cumingii* (Corner 1991), for which no DNA



sequence is available, and *Phylloporia terrestris* and *P. vietnamensis* that are two phylogenetically distant species (Zhou 2015c, Wei *et al.* 2024). Corner (1991) also reported *P. spathulata* from Southeast Asia that he distinguished from *Polyporus cumingii*. Corner's (Corner 1991) concept of *P. spathulata* should be revised, however.

## CONCLUSIONS

*Phylloporia* is becoming a very large - it comprises 86 species to date - and complex genus. Olou *et al.* (2021), using model-based methods for species delimitation and relying mostly on the variability of LSU sequences data available to them, estimated the number of putative species ranging from 82 to 100. The current phylogenetic inferences showed numerous phylogenetic species, unnamed to date, originating mainly from the Neotropics but also, to a lesser degree, from tropical Africa and the North temperate area. That will raise the number of species to about 125. However, this number is probably still an underestimate. As indicated above, several pantropical taxa presumed to have multiple hosts undoubtedly represent collective species, whose taxonomic diversity is undoubtedly as varied as that of their host plants. Furthermore, sampling suffers from geographical gaps; Southeast Asia and Australia are under-represented.

As the number of described species increases, species definition will become more difficult for *Phylloporia*, as for many other groups of *Hymenochaetales* (Cao *et al.* 2021). The constant addition of species will render ineffective the few available morphological characters used to distinguish species within morpho-ecological types, whether phylogenetically related or distant. Today, the delimitation of species is increasingly based, firstly, on phylogenetic data and then, a posteriori, on various morphological characters that are already no longer very reliable. The criteria to delimit and identify species are likely to evolve to integrate the host and substrate specificity and the intraspecific/interspecific genetic variation, as is the case for other phytopathogenic fungi (Cai *et al.* 2011). It is strongly recommended that the host plants of any new collection of *Phylloporia* species are accurately identified, as this will represent an essential characteristic that is too often overlooked.

Our multilocus dataset has highlighted various lineages within *Phylloporia* and made it possible to discuss the relevance of morpho-ecological types for describing these lineages but only on local scales. Limitations still prevent us from obtaining a supported, comprehensive structure of the *Phylloporia* core clade. Firstly, many species are to date only known by their LSU sequence, which provides poor resolution at internal nodes. The ITS1 and 2 are relevant at species level, but it has proven difficult to align between species of distant lineages (Decock *et al.* 2015, Wei *et al.* 2024). The addition of taxa from throughout the distribution range and of additional house-keeping genes could contribute to a better resolution of the internal nodes within the main lineage (Rokas & Carroll 2005, Li *et al.* 2021).

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