ORIGINAL ARTICLE





A new and unusual species of *Hericium* (Basidiomycota: Russulales, Hericiaceae) from the Dja Biosphere Reserve, Cameroon

Blaise Jumbam¹ · Danny Haelewaters¹ · Rachel A. Koch¹ · Bryn T. M. Dentinger² · Terry W. Henkel³ · M. Catherine Aime¹

Received: 2 May 2019 / Revised: 25 September 2019 / Accepted: 28 September 2019 © German Mycological Society and Springer-Verlag GmbH Germany, part of Springer Nature 2019

Abstract

Tropical rainforests form the most species-rich biome on the earth. The Dja Biosphere Reserve (DBR) in Cameroon is a biodiverse tropical forest characterized in part by upland monodominant stands of the ectomycorrhizal (ECM) *Gilbertiodendron dewevrei* and ECM *Uapaca* spp. scattered along river banks. This mostly primary Guineo-Congolian evergreen forest harbors natural populations of large megafauna and numerous plant and fungal species. Studies have indicated that some ECM fungal groups of the large order Russulales are abundant in certain localities in the tropics, including the DBR. However, currently, other predominantly wood-decaying families of Russulales are poorly represented in Africa. For example, only three records of the saprotrophic genus *Hericium* (Russulales, Hericiaceae) are known from the African continent. Here, we describe a new species of *Hericium* recently collected from the DBR. Morphological characteristics and molecular phylogenetic analyses support placement of the Cameroonian collection in *Hericium* and its recognition as a new species within a larger *H. coralloides* species complex. The new species, *H. bembedjaense*, differs from *H. coralloides* in its smaller basidiospores (2.6– 3.0×1.7 – 2.2μ m compared to 3.5– 5.0×2.8 – 4.2μ m) and longer basidia (up to 27.0μ m compared to 15.0μ m). It differs from all other described *Hericium* species in the production of pleurocystidia. This is the first species of Hericiaceae known from sub-Saharan lowland tropical evergreen forests. This study highlights the need to increase fungal sampling in species-rich tropical forests such as those of the Congo Basin.

Keywords Africa · rDNA systematics · Russulales · Taxonomy · Wood rot fungi

Introduction

Tropical rainforests form the most species-rich biome on earth, harboring over 50% of species on just 7% of the land area (Hill and Hill 2001; Wilson 1988). The Dja Biosphere Reserve (DBR) in the Central African region covers an area of more than 500,000 km² (Carson et al. 2018) and is an integral part of the dense Guineo-Congolian forest encompassing the

Section Editor: Zhu-Liang Yang

Blaise Jumbam jumbam.blaise@gmail.com

- ² Natural History Museum of Utah & School of Biological Sciences, University of Utah, Salt Lake City, UT, USA
- ³ Department of Biological Sciences, Humboldt State University, Arcata, CA 95521, USA

Congo Basin. The DBR is exceptionally biodiverse (Hill and Hill 2001) with more than 90% of the forest area still in a natural state (Betti 2004). It consists mostly of primary evergreen forest that supports natural populations of large megafauna as well as various plant and fungal species (Sonké and Couvreur 2014; Verbeken et al. 2008). The reserve is surrounded by 36 villages spread around the buffer zones. More than 6000 people live in these villages including the indigenous Baka (Carson et al. 2018). Within the reserve are patches of forests dominated by a few ectomycorrhizal (ECM) tree species—*Gilbertiodendron dewevrei* (Fabaceae subfam. Detarioideae) and some *Uapaca* spp. (Phyllanthaceae)— scattered along the river banks (Castellano et al. 2016).

Various studies have been conducted to document fungal diversity within tropical forests around the world (e.g., Berndt 2012; Cornejo et al. 1994; Henkel et al. 2012; Piepenbring et al. 2012). Some of these studies have indicated that, locally, the Russulaceae (Russulales) can be the most abundant group of ECM macrofungi (Smith et al. 2017; Verbeken and Walleyn 2010; Zhou and Dai 2013). Verbeken et al. (2008)

¹ Department of Botany and Plant Pathology, Purdue University, West Lafayette, IN 47907, USA

revealed that *Lactifluus* (Pers.) Roussel and *Russula* Pers. (Russulaceae) were the dominant ECM macrofungal genera in a *G. dewevrei* monodominant Guineo-Congolian rainforest of Central Africa. In the Guiana Shield, the Russulaceae were also abundant in a long-term study in monodominant forests of ECM *Dicymbe* (Henkel et al. 2012; Miller et al. 2012; Smith et al. 2017). In contrast, few tropical studies have revealed representatives of saprotrophic Russulales. In temperate regions, saprotrophic species such as members of Hericiaceae can be important both during wood decay and as causal agents of white rot of hardwood and coniferous trees (Boddy et al. 2011; Das et al. 2011; Hallenberg et al. 2013).

Hericium Pers. (Hericiaceae) is a dentate and coralloid basidiomycete genus. Ecologically, members are white rotters. But, importantly, many species within the genus are important as sources of food (Hallenberg et al. 2013) and medicinals (e.g., Mori et al. 2008; Pegler 2003; Thongbai et al. 2015) that have a long history of traditional use (e.g., Khan et al. 2013; Ramberg et al. 2010). For example, several species such as H. erinaceus (Bull.) Pers., H. flagellum (Scop.) Pers., and H. coralloides (Scop.: Fr) Pers. are cultivated for food and production of beneficial secondary metabolites. Active compounds (hericenones, hericene, hericerine, erinacines, enzymes, etc.) isolated from members of the genus are useful in therapeutic treatments because they have negligible side effects in patients, unlike chemotherapeutic medication (Thongbai et al. 2015). These extracts also contain antibacterial and anti-aging properties (Kim et al. 2000, 2012; Wittstein et al. 2016; Xu et al. 2010) as well as the ability to prevent the Crohn's disease (Abdulla et al. 2008; Wong et al. 2013). Hericium compounds are being used in the prevention and treatment of diabetes and various types of cancers (Kim et al. 2011, 2013; Ma et al. 2012; Yang et al. 2003). In cancer patients, Hericium secondary compounds enhance immune responses by increasing their CD4 T cells, which are cytotoxic to tumor cells (Liu et al. 2000) and seem to increase the life span (Ying et al. 1987). Many supplements for cognitive brain function and memory improvement contain compounds from Hericium (Obara and Nakahata 2002; Rupcic et al. 2018) and could be used in the treatment of Alzheimer's disease (Allen and Dawbarn 2006; Prine et al. 2014). Finally, Hericium is a model for bio-transforming active plant material (Thongbai et al. 2015).

Among species of *Hericium*, variations of micromorphological characters can be very subtle, even when considering specimens from different geographic regions (Hallenberg et al. 2013). Consequently, most species have been differentiated based on a combination of additional features including substratum preference, geographic origin, and molecular data (Ginns 1985; Hallenberg et al. 2013). In terms of phylogenetic analyses, thus far, only the internal transcriber spacer (ITS) region of the ribosomal DNA has been used for species delimitation in

the genus (Das et al. 2011, 2013; Hallenberg et al. 2013). Most of the known species of *Hericium* have been described from higher latitude ecosystems of the Americas and Eurasia. Presently, there are 26 accepted species of *Hericium* (Index Fungorum 2019), all documented from temperate North and South America, Asia, Europe, Australia, and Africa (Tunisia alone) (Boddy et al. 2011; Fraiture and Otto 2015; Ginns 1985; Hallenberg et al. 2013; Kalucka and Olariaga Ibarguren n.d.; Ouali et al. 2018). Thus far, no reports are known from the sub-Saharan lowland tropical evergreen forests.

Here, we describe a new species of *Hericium* from the Dja Biosphere Reserve in Cameroon. We provide morphological, molecular phylogenetic, ecological, and geographic data to support recognition of the new species.

Materials and methods

Field collections

Basidiomata were collected in Cameroon during the April-May early rainy season of 2018 from the Dja Biosphere Reserve, Northwest Sector, near the village of Somalomo. Specifically, the study site is in the Upper Dja River Basin, within a 2-km radius of a base camp located at 3° 21' 29.8" N 12° 43' 46.9" E, 650 m a.s.l., in forests dominated by Gilbertiodendron dewevrei (Peh et al. 2014). Descriptions of macromorphological features were made from freshly collected basidiomata in the field. Colors were compared with plates in the Online Auction Color Chart (Online Auction Color Chart Co 2004). Fresh specimens were photographed in situ and in the field camp. Basidiomata were dried in the field using silica gel. The holotype collection is deposited at PUL (Kriebel Herbarium, Purdue University); an isotype is deposited at YA (National Herbarium of Cameroon, Yaoundé). Photomicrographs were taken with an Olympus SC30 camera mounted on an Olympus BH2 bright field compound microscope (Olympus Co., Tokyo, Japan) using cellSens 1.18 imaging software.

Micromorphological features were observed from rehydrated sections of specimens. For basidia, cystidia, basidiospores, sterigmata, and hyphal features, rehydrated tissue was mounted in water, 3% KOH or Melzer's reagent, and at least 20 individuals were measured. Line drawings of basidiospores were made using tracing paper from images taken with the cellSens camera mounted to an Olympus BH2 microscope mainly at × 1000 magnification. Drawings of other micromorphological structures (basidia, cystidia, gloeocystidia, etc.) were made from images taken at × 400 magnification. Drawings were edited with Adobe Photoshop Elements 6 ver. 6.0 (Adobe, San Jose, CA, USA). Basidium length excludes sterigmata and basidiospore dimensions exclude the dimensions of the ornamentations and the hilar appendix. Basidiospores were randomly selected for measurement in side view and their sizes are given as $Lx-Lz-Ly \times Wx-Wz-Wy$ where Lx = minimum value for length of the measured basidiospores, Ly = maximum value for length of the measured pores, Lz = mean value for the length of measured basidiospores, Wx = minimum value for the width of measured basidiospores, Wy = maximum value for the width of measured basidiospores, and Wz = mean value for the width of measured basidiospores. The quotient indicates the length by width ratio (Q = L/W) and is given as Qx-Qz-Qy where Qx = minimum quotient value of the measured basidiospores, Qy = maximum quotient value of the measured basidiospores, and Qz = mean quotient value of the measured basidiospores.

DNA isolation, PCR amplification, and sequencing

Total genomic DNA was extracted from basidioma tissue using the Wizard® Genomic DNA Purification kit (Promega Co., Madison, WI, USA), following the manufacturer's protocols. Both the internal transcribed spacer (ITS) DNA barcode region (Dentinger et al. 2011; Schoch et al. 2012) and the large subunit (28S) of the ribosomal DNA (rDNA) were amplified with polymerase chain reaction (PCR) using the primer sets ITS1F/ITS4B for ITS (Gardes and Bruns 1993) and LR0R/LR6 for 28S (Moncalvo et al. 2000; Vilgalys et al. 1994; Vilgalys and Hester 1990). PCR reactions consisted of 12.5 µL of Promega 2× PCR Master Mix, 1.25 μ L of each 10 μ M primer, 9.0 μ L of H₂O, and 1.0 μ L of template DNA. All amplifications were done in an Eppendorf Mastercycler ep Thermal Cycler (Hauppauge, New York, USA) with initial denaturation at 94 °C for 3:00 min; followed by 35 cycles of denaturation at 94 °C for 1:00 min, annealing at 50 °C for 0:45 min and extension at 72 °C for 1:30 min; and final extension at 72 °C for 10:00 min. PCR products were sent to Genewiz (South Plainfield, NJ, USA) for purification and sequencing. Raw sequence reads were assembled and edited using Sequencher v5.2.3 (Gene Codes Co., Ann Arbor, MI, USA) software. Sequences were deposited at the National Center for Biotechnology Information (NCBI) Genbank database, under accession numbers MK683483 and MK683482.

Sequence alignment and phylogenetic analysis

The newly generated sequences were queried against the NCBI GenBank database using the "megablast" algorithm to search for closest relatives (http://blast.ncbi.nlm.nih.gov/Blast.cgi). Resulting ITS and 28S sequences of previously described *Hericium* spp. were downloaded. Sequences were aligned using Muscle v3.7 (Edgar 2004). Ambiguously

aligned regions and uninformative regions were removed with TrimAl v1.3 on the command line (Capella-Gutiérrez et al. 2009) with gt = 0.60 and cons = 0.50. We also constructed a combined ITS+28S dataset using MEGA7 (Kumar et al. 2015). Maximum likelihood (ML) analyses were done using IQ-TREE (Nguyen et al. 2015), of both individual datasets and a smaller concatenated ITS+28S dataset. Appropriate models of nucleotide substitution were selected under the Akaike Information Criterion corrected for small sample size (AICc) using jModelTest2 on XEDE (Darriba et al. 2012) on the CIPRES Science Gateway (Miller et al. 2010). For the ITS dataset, the HKY+G model was selected (-lnL = 2657.2323); for 28S, the TrN+I+G model (-lnL = 3332.2045). The models selected for the concatenated datasets were TrN+G for ITS $(-\ln L = 1998.2828)$ and TrN+I+G for 28S $(-\ln L = 1863)$. 5439). ML was inferred for each individual dataset, as well as for the concatenated ITS+28S dataset under partitioned models (Chernomor et al. 2016). Rapid bootstrapping was inferred under 1000 replicates (Hoang et al. 2017).

Results

Over 4 years of plot-based sampling in DBR, we have vouchered thousands of ECM and saprotrophic taxa. Only a single collection of Hericium has ever been observed during this period. BLASTn searches of ITS and 28S sequences of this collection shared the closest identity with other Hericium species in GenBank. The final alignment of the Hericium ITS rDNA dataset contained 38 sequences and 619 positions of which 116 were parsimony-informative. In the ITS topology resulting from ML inference (Fig. 1), H. bembedjaense is part of a clade including 13 specimens of H. coralloides sensu lato. Hericium bembedjaense is sister to a strain annotated as H. coralloides from Argentina (FCUG 3209, Hallenberg et al. 2013), but these share only 90.70% sequence identity. Furthermore, H. bembedjaense shares only 89.09% sequence identity with H. coralloides FCUG 1229, the specimen that is believed to most closely represent H. coralloides sensu stricto (Larsson and Larsson 2003). The 28S rDNA alignment contained 48 sequences and 920 positions, of which 113 were parsimony-informative. The topology resulting from ML inference of the 28S dataset (not shown) revealed that this locus is not informative for Hericium at the species level. We also constructed a concatenated ITS+28S dataset, including 26 sequences (Table 1) and 1538 positions, of which 140 were parsimony-informative. The phylogenetic reconstruction of the two-locus dataset (Fig. 2) also places H. bembedjaense within the H. coralloides species complex. In both analyses (Figs. 1 and 2), taxa in several clades (e.g., H. alpestre and H. erinaceus) in addition to the H. coralloides complex are unresolved.



Fig. 1 Phylogeny of *Hericium*, reconstructed from the ITS dataset. The topology is the result of maximum likelihood inference performed with IQ-TREE under partitioned models. Only rapid bootstrapping support values of \geq 70 are shown. Countries are shown (if known) for isolates

lection from the same locale as the neotype of *H. coralloides*. The new species from Cameroon is highlighted in bold

Taxonomy

Hericium bembedjaense Jumbam and Aime, sp. nov.

Figures 3, 4, and 5

MycoBank number: MB 830806

Type: Cameroon, East region, Dja biosphere reserve, 3° 21' 29.80" N, 12° 43' 46.90" E, alt. 650 m a.s.l., on dead fallen log of *Gilbertiodendron dewevrei* in a monodominant forest, 25 Apr 2018, B. Jumbam JB 41 (HOLOTYPE:

🖄 Springer

deposited and preserved as dried specimen in the Kriebel Herbarium, PUL F25402; isotype YA) GenBank accession nos. MK683483 (ITS) and MK683482 (28S).

Etymology: Referring to "bembe," the indigenous Baka vernacular name of the host tree (*Gilbertiodendron dewevrei*) and "dja" for the type locality of the new species.

Diagnosis: Different from other species of *Hericium* in the production of pleurocystidia; different from *H. coralloides* in

 Table 1
 List of ITS and 28S sequences used for molecular phylogenetic analysis, with voucher/isolate, country of collection (when available), accession numbers, and references

Species	Isolate/voucher	Country	ITS	28S	Reference(s)
Dentipellis fragilis	Dai 9009	N/A	JQ349108	JQ349094	Zhou and Dai 2013
Dentipellis leptodon	CBS:125879	New Zealand	MH864083	MH875541	Vu et al. 2019
Hericium abietis	CBS:125851	N/A	MH863807	MH875271	Vu et al. 2019
Hericium abietis	CBS:243.48	Canada	AY534579	MH867882	Park et al. 2004; Vu et al. 2019
Hericium abietis	HMJAU:23283	China	JF430070		Wang et al. 2011
Hericium abietis	K:107270	UK	EU784259		Brock et al. 2009
Hericium abietis	NH6990	N/A	AF506456	AF506456	Larsson and Larsson 2003
Hericium alpestre	DSMZ:108284	Germany	MK491173	MK491173	E. Büttner and H. Kellner unpubl.
Hericium alpestre	FCUG 1555	Romania	JQ716936		Hallenberg et al. 2013
Hericium alpestre	NH13240	N/A	AF506457	AF506457	Larsson and Larsson 2003
Hericium americanum	AFTOL-ID 469	USA: Massachusetts	DQ206987	DQ411538	Matheny et al. 2007
Hericium americanum	CBS:129.40	N/A	MH856062		Vu et al. 2019
Hericium americanum	CBS:493.63	USA: New York	AY534581		Park et al. 2004
Hericium americanum	DAOM:21467	N/A	AF506458	AF506458	Larsson and Larsson 2003
Hericium bharengense	CBS:kd10658E	India	JN185603		Das et al. 2013
Hericium cirrhatus	F794		AF506385	AF506385	Larsson and Larsson 2003
Hericium cirrhatus	K:125827	Europe	EU784260		Brock et al. 2009
Hericium cirrhatus	K:135658	Europe	EU784261		Brock et al. 2009
Hericium coralloides	ATCC:52480	Canada	AY534584		Park et al. 2004
Hericium coralloides	FCUG 3209	Argentina	JQ716934		Hallenberg et al. 2013
Hericium coralloides	FCUG 426	France	JO716935		Hallenberg et al. 2013
Hericium coralloides	HMJAU:23285	China	JF430072		Wang et al. 2011
Hericium coralloides	HMJAU:23287	China	JF430074		Wang et al. 2011
Hericium coralloides	HMJAU:4368	China	JF430062		Wang et al. 2011
Hericium coralloides	HMIAU-4990	China	JF430064		Wang et al. 2011
Hericium coralloides	IFO 7716	USA	AY 534582		Park et al 2004
Hericium coralloides	K·104978	Furone	FU784262		Brock et al. 2009
Haricium coralloidas	K:61470		EU784262		Brock et al. 2009
Hariaium conalloidas	R.01470	Swadan	A E 506450	1506450	Larsson and Larsson 2002
Hericium coralloides	NVRG:0011	USA: Missouri	KV432832	AI'500459	B Bomanz unnubl
Hericium erinaceus	B2	Slovenia	AM981220		D Jurc et al unpubl
Hericium erinaceus	CB1	China	GU584100		Vin and Chi 2015
Hericium erinaceus	CBS:202.31	The Netherlands	MH855186	MH866638	Vu et al. 2019
Hericium erinaceus	CBS:260.74	The Netherlands	DO185922	MH872587	Park et al 2004 · Vu et al 2019
Hericium erinaceus	CBS:200.71	Czech Republic	DQ185922	11110/2007	Park et al. 2004
Horicium orinacous	CBS:447.85	Czech Republic	DQ185927		Park et al. 2004
Hariaium aringaaus	CDS:447.05	Czech Republie	DQ185026		Park et al. 2004
Horicium orinaceus	DAOM:10644	Canada	DQ103920	DIC 40245	Siälwist et al. 2012
Hericium erinaceus	DAOM.19044	Eurono	JIN049343	JIN049343	Brock et al. 2000
	K.02494	Karra	EU/64203		Drock et al. 2009
Hericium erinaceus	NUME 1055	NJIA	DQ183919	1 50(4(0	
Hericium erinaceus	NH12103 7b001	N/A Tunicio	AF506460	AF506460	Cureli et al. 2018
		Tullisia Dalama	K1055905	K1055904	M Knigeneles et al annuchl
	N/A	Poland	MG649451	N (17 CO2 402	M. Kujawska et al. unpubl.
Hericium bembedjaense	JB41 ECUC CD1007	Cameroon	MK083483	MK083482	I his study
nericium rajchenbergii	FCUG GK1997	Argentina	JA403943		Hallenberg et al. 2013
петісіцт rajchenbergu	FCUG GK2041	Argentina	JQ/16939	D/055024	Hallenberg et al. 2013
Hericium yumthangense	BSHC:KD-11-146	India	JX855033	JX855034	Das et al. 2013
Laxitextum bicolor	CBS:412:34	N/A	MH855587	MH867097	Vu et al. 2019

N/A not available

smaller basidiospores, longer and narrower basidia, and presence of pleurocystidia.

Description: Basidioma solitary, thick, fleshy, pendant, 120×70 mm, pale yellow (oac816) throughout, unchanging, branching up to six times from the main stipe attached to the underside of the host log, thicker primary branches diverging downward into progressively thinner secondary, tertiary, and

quaternary branches giving rise to numerous spines; *spines* \sim 3 mm long, irregularly distributed laterally, clustered terminally, tapering apically, concolorous with the branches, drying to become orange brown (oac740–oac741). *Exposed context* wet, unchanging. *Odor* fragrant, reminiscent of hibiscus. *Taste* indistinct to slightly sweet. *Hyphal system* monomitic; *contextual hyphae* generative, 3.0–8.3 µm wide, branching

Fig. 2 Phylogeny of *Hericium*, reconstructed from the concatenated ITS+28S rDNA dataset. The topology is the result of maximum likelihood inference performed with IQ-TREE under partitioned models. Only rapid bootstrapping support values of \geq 70 are shown. The asterisk (*) denotes collection from the same locale as the neotype of *H. coralloides*. The new species from Cameroon is highlighted in bold



frequently, walls up to 0.4 µm wide; *hymenial tramal hyphae* 3.5–4.0 µm wide, hyaline in KOH, branching, walls < 0.4 µm wide; *gloeopleurous hyphae* 4.5–6.7 µm wide, abundant with dense yellowish-green content, aseptate, apex rounded to somewhat clavate. *Basidiospores* (2.6–)2.8(– 3.0) × (1.7–)2.0(– 2.2) µm; Q = (1.0–)1.35(– 1.70), subglobose to broadly ovate, hyaline, amyloid, smooth to slightly roughened; *hilar appendix* 0.44 µm long. *Basidia* 13.5–27.0 × 3.5–4.5 µm, subclavate to clavate, 2- to 4-sterigmate; *sterigmata* 3.4–4.5 × 1.0–1.5 µm. *Gloeocystidia* 3.4–6.7 µm wide, cylindrical to aciculate, extending beyond



Fig. 3 Field photograph of *Hericium bembedjaense* at the Dja Biosphere Reserve, showing the irregularly branched basidiomata freshly collected from a fallen *Gilbertiodendron dewevrei* tree trunk. Photo: Bryn T.M. Dentinger

the hymenial palisade, with dense content. *Pleurocystidia* 13.5–24.7 × 3.4–4.5 μ m including the acuminate tip, ventricose–rostrate to mucronate–acuminate. *Hymenium* inamyloid; *subhymenial hyphae* thin-walled, up to 4.35 μ m wide. *Clamp connections* abundant on hyphae of all tissues.

Discussion

An integrative taxonomic approach using multiple properties including morphology, ecology, host specificity, molecular phylogenetic data, and/or mating behavior is increasingly being employed for accurate delimitation of fungal species (e.g., Aime 2004; Araújo et al. 2015; Haelewaters et al. 2018; Sochorová et al. 2019), and has been applied to some species in Hericium, although accurate delimitations are far from resolved in this genus (Hallenberg et al. 2013). A contributing factor to this situation is the relative paucity of Hericium collections. Some species have been collected so infrequently that they are considered locally rare and added to regional Red Lists. This is the case for two taxa in some European countries: H. coralloides and H. erinaceus (Boddy et al. 2011; Kalucka and Olariaga Ibarguren n.d.). Other factors such as seasonal fruiting phenology may contribute to the low rate of Hericium encounters. In Cameroon, we found a single Hericium basidioma during a field survey from 21

Fig. 4 Microscopic features of Hericium bembedjaense (Jumbam 41, holotype). a Pleurocystidia. b Basidia. c Gloeocystidia. d Basidiospores. Scale bars = \mathbf{a} - \mathbf{b} = 10 µm, c = 20 µm, d = 2.5 µm





Fig. 5 Microscopic features of *Hericium bembedjaense* (Jumbam 41, holotype). **a** Tramal hyphae. **b** Thick-walled contextual hyphae. **c** Gloeopleurous hyphae. Scale bars = $20 \ \mu m$

Apr to 3 May 2018. Three previous expeditions conducted at the same site between Aug and Oct in 2015–2017 yielded no *Hericium* collections. This absence of fruiting body observations may be due, at least in part, to interspecific variations in fruiting seasons, leading to the possibility of missing individual fungal species during short periods of fieldwork (De Crop et al. 2019).

Hericium coralloides is believed to be a complex containing cryptic species (Hallenberg et al. 2013). Our Cameroonian species, H. bembedjaense, falls within this complex (Figs. 1 and 2). Hericium coralloides (Scop.) Pers. was designated as the type species for the genus (Persoon 1794) and the species was neotypified by Hallenberg (1983) using a specimen collected in 1948 from Femsjö (Småland Province) in Sweden that was growing on Fagus silvatica. No sequences are available for the neotype, though we included in our analyses a sequence from a more recent Swedish specimen (indicated by * in Figs. 1 and 2), collected in Östergötland Province, Åby, growing on a dead coniferous tree, culture FCUG 1229, GenBank accession no. AF506459 (Larsson and Larsson 2003). The neotype and FCUG 1229, collected in neighboring provinces in the southern part of Sweden (Götaland), are presumed to be conspecific and so FCUG 1229 can be considered representative of H. coralloides sensu stricto. In both of our analyses, H. bembedjaense appears in a separate lineage from all northern temperate collections,

including FCUG 1229 (Figs. 1 and 2). *Hericium bembedjaense* and FCUG 1229 share only 89.09% sequence identity at the ITS locus, well below the threshold recommended for delimiting fungal species (e.g., Blaalid et al. 2013; Garnica et al. 2016; Niu et al. 2015).

Hericium bembedjaense differs from all other described species of Hericium in the presence of pleurocystidia (Fig. 4a). Additionally, H. bembedjaense differs from H. coralloides in several macro- and micromorphological features (fide Koski-Kotiranta and Niemela 1988), including shorter spines (~ 5 mm); smaller basidiospores $(3.5-5.0 \times$ 2.8–4.2 μ m vs. 2.6–3.0 × 1.7–2.2 μ m in *H. bembedjaense*); and longer, more narrow basidia up to $15.0 \times 5 \mu m$. Apart from these morphological features, H. bembedjaense can be differentiated from other members of the H. coralloides complex by different substratum preferences (G. dewevrei for H. bembedjaense vs. Fagaceae spp. for H. coralloides) and geographic ranges (tropical Central Africa for H. bembedjaense vs. temperate North America and Eurasia for H. coralloides). Hericium bembedjaense is the first taxon after H. coralloides sensu stricto to receive a formal description in the *H. coralloides* species complex.

Hericium bembedjaense likely causes white rot of G. dewevrei and potentially other Congo Basin hardwoods, similar to rots caused by other members of Hericium on temperate hardwoods and conifers. From the African continent, only a few records of *Hericium* are known; H. erinaceus was recently reported from Tunisia (Ouali et al. 2018) and one (unvouchered) observation from Algeria has been submitted to the citizen-science platform iNaturalist (https://www.inaturalist.org/observations/ 22251773). Both of these countries are floristically part of the Mediterranean province of the Boreal floristic kingdom (Good 1974), where the fungi are more likely to share biogeographic connections with Europe. A single unvouchered observation in Madagascar is also present on iNaturalist (https://www.inaturalist.org/observations/ 10099211), but its affinities cannot be determined due to the absence of DNA data and micromorphology.

Conclusion

In this study, we present the first *Hericium* species from the sub-Saharan African tropical evergreen forest using data from morphology, DNA sequences, and ecology. Thus far, basidiomata of *Hericium* have been very rarely collected on the African continent. Most countries, especially in the Central African sub-region, are mycologically poorly explored because of a scarcity of trained African mycologists (Gryzenhout et al. 2012), political instability, and challenging field work conditions (De Crop et al. 2019). In addition, the timing of sampling around rainy seasons can be critical but

logistically difficult. Many *Hericium* species are important as sources of food and secondary metabolites; the documentation of a new species—the first from sub-Saharan Africa—highlights the importance of efforts to document tropical fungal diversity for potential future application.

Acknowledgments We are grateful to Dr. Ngo Ngwe Florence, Head of The National Herbarium of Cameroon (Institute of Agricultural Research for Development, IRAD), for providing logistical assistance. The Conservator of the Dja Biosphere Reserve, Mr. Mengamenya Goue Achille, and his staff greatly assisted the fieldwork in the Dja. Logistical, herbarium, and laboratory assistance was provided by Olivier Sene, Eric Ngangsop, Emerson Jeesh, Kirk Rumple, and members of the Aime Lab. We also thank Karl-Henrik Larsson (Natural History Museum, University of Oslo) for providing us with specimen details for collection RD282. Field assistance in Cameroon was provided by Emerson Arehart, Alamane Gabriel (a.k.a. Sikiro), Aziem Jean Aime, Essambe Jean-Pierre (a.k.a. Papa Chef), and Mama Tutu. Research permits were granted by the Cameroon Ministry of Scientific Research and Innovation (MINRESI) and Ministry of Forestry and Wildlife (MINFOF).

Funding information Funding for this work was made available by the National Science Foundation DEB-1556412 to MCA, and NSF DEB-1556338 to TWH.

References

- Abdulla MA, Noor SM, Sabaratnam V, Abdullah N, Wong KH, Ali HM (2008) Effect of culinary medicinal lion's mane mushroom, *Hericium erinaceus* (bull.: Fr.) Pers. (Aphyllophoromycetideae) on ethanol induced gastric ulcers in rats. Int J Med Mushrooms 10:325–330
- Aime MC (2004) Intercompatibility tests and phylogenetic analysis in the *Crepidotus* Sphaerula group complex: concordance between ICGs and nuclear rDNA sequences highlight phenotypic plasticity within Appalachian species. In: Cripps CL (ed) Fungi in forest ecosystems: systematics, diversity, and ecology. New York Botanical Gardens, NY, pp 71–80
- Allen SJ, Dawbarn D (2006) Clinical relevance of the neurotrophins and their receptors. Clin Sci (Lond) 110:175–191
- Araújo JPM, Evans HC, Geiser DM, Mackay WP, Hughes DP (2015) Unravelling the diversity behind the *Ophiocordyceps unilateralis* (Ophiocordycipitaceae) complex: three new species of zombie-ant fungi from the Brazilian Amazon. Phytotaxa 220:224–238. https:// doi.org/10.11646/phytotaxa.220.3.2
- Berndt R (2012) Species richness, taxonomy and peculiarities of the neotropical rust fungi. Are they more diverse in the neotropics? Biodivers Conserv 21:2299–2322. https://doi.org/10.1007/s10531-011-0220-z
- Betti JL (2004) Impact of forest logging in the Dja Biosphere Reserve, Cameroon. Unpublished Context Study Report, Ministry of Environment and Forestry, Cameroon, 1–13. https://www.cbd.int/doc/case-studies/for/cs-ecofor-cm-01-en. pdf. Accessed 11 April 2019
- Blaalid R, Kumar S, Nilsson RH, Abarenkov K, Kirk PM, Kauserud H (2013) ITS1 versus ITS2 as DNA metabarcodes for fungi. Mol Ecol Resour 13:218–224. https://doi.org/10.1111/1755-0998.12065
- Boddy L, Crockatt ME, Ainsworth AM (2011) Ecology of *Hericium cirrhatum*, *H. coralloides* and *H. erinaceus* in the UK. Fungal Ecol 4:163–173. https://doi.org/10.1016/j.funeco.2010.10.001

- Brock PM, Doring H, Bidartondo MI (2009) How to know unknown fungi: the role of a herbarium. New Phytol 181:719–724. https://doi.org/10.1111/j.1469-8137.2008.02703.x
- Capella-Gutiérrez S, Silla-Martinez JM, Gabaldon T (2009) trimAl: a tool for automated alignment trimming in large-scale phylogenetic analyses. Bioinformatics 2009:1971–1973
- Carson SL, Kentatchime F, Nana ED, Njabo KY, Cole BL, Godwin HA (2018) Indigenous peoples' concerns about loss of forest knowledge: implications for forest management. Conserv Soc 16:431– 440. https://doi.org/10.4103/cs.cs 17 105
- Castellano MA, Dentinger BTM, Séné O, Elliott TF, Truong C, Henkel TW (2016) New species of *Elaphomyces* (Elaphomycetaceae, Eurotiales, Ascomycota) from tropical rainforests of Cameroon and Guyana. IMA Fungus 7:59–73. https://doi.org/10.5598/ imafungus.2016.07.01.05
- Chernomor O, von Haeseler A, Minh BQ (2016) Terrace aware data structure for phylogenomic inference from supermatrices. Syst Biol 65:997–1008. https://doi.org/10.1093/sysbio/syw037
- Cornejo FH, Varela A, Wright SJ (1994) Tropical forest litter decomposition under seasonal drought: nutrient release, fungi and bacteria. Oikos 70:183–190. https://doi.org/10.2307/3545629
- Darriba D, Taboada GL, Doallo R, Posada D (2012) jModelTest 2: more models, new heuristics and parallel computing. Nat Methods 9:772. https://doi.org/10.1038/nmeth.2109
- Das K, Stalpers J, Eberhardt U (2011) A new species of *Hericium* from Sikkim Himalaya (India). Cryptogam Mycol 32:285–293. https:// doi.org/10.7872/crym.v32.iss3.2011.285
- Das K, Stalpers JA, Stielow JB (2013) Two new species of hydnoid-fungi from India. IMA Fungus 4:359–369. https://doi.org/10.5598/ imafungus.2013.04.02.15
- De Crop E, Lescroart J, Njouonkou AL, De Lange R, Van de Putte K, Verbeken A (2019) *Lactifluus bicapillus* (Russulales, Russulaceae), a new species from the Guineo-Congolian rainforest. MycoKeys 39: 25–39. https://doi.org/10.3897/mycokeys.45.29964
- Dentinger BTM, Didukh MY, Moncalvo J-M (2011) Comparing COI and ITS as DNA barcode markers for mushrooms and allies (Agaricomycotina). PLoS One 6:e25081. https://doi.org/10.1371/ journal.pone.0025081
- Edgar RC (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Res 32:1792–1797
- Fraiture A, Otto P (2015) Distribution, ecology and status of 51 macromycetes in Europe: results of the ECCF Mapping Programme. Scripta Bot Belg 53:1–247
- Gardes M, Bruns TD (1993) ITS primers with enhanced specificity for basidiomycetes-application to the identification of mycorrhizae and rusts. Mol Ecol 2:113–118. https://doi.org/10.1111/j.1365-294X. 1993.tb00005.x
- Garnica S, Schön EM, Abarenkov K, Riess K, Liimatainen K, Niskanen T, Dima B, Soop K, Frøslev TG, Jeppesen TS, Peintner U, Kuhnert-Finkermagel R, Brandrud TE, Sar G, Oertel B, Ammirati JF (2016) Determining threshold values for barcoding fungi: lessons from *Cortinarius* (Basidiomycota), a highly diverse and widespread ectomycorrhizal genus. FEMS Microbiol Ecol 92:fiw045. https:// doi.org/10.1093/femsec/fiw045
- Ginns J (1985) *Hericium* in North America: cultural characteristics and mating behavior. Can J Bot 63:1551–1563. https://doi.org/10.1139/ b85-215
- Good R (1974) The geography of flowering plants, 3rd edn. Longman, White Plains
- Gryzenhout M, Jefwa JM, Yorou NS (2012) The status of mycology in Africa: a document to promote awareness. IMA Fungus 3:99–102. https://doi.org/10.5598/imafungus.2012.03.01.11
- Haelewaters D, De Kesel A, Pfister DH (2018) Integrative taxonomy reveals hidden species within a common fungal parasite of ladybirds. Sci Rep 8: 15966. https://doi.org/10.1038/s41598-018-34319-5

- Hallenberg N (1983) *Hericium coralloides* and *H. alpestre* (Basidiomycetes) in Europe. Mycotaxon 18:181–189
- Hallenberg N, Nilsson RH, Robledo G (2013) Species complexes in *Hericium* (Russulales, Agaricomycota) and a new species -*Hericium rajchenbergii* - from southern South America. Mycol Prog 12:413–420. https://doi.org/10.1007/s11557-012-0848-4
- Henkel TW, Aime MC, Chin MML, Miller SL, Vilgalys R, Smith ME (2012) Ectomycorrhizal fugal sporocarp diversity and discovery of new taxa in *Dicymbe* monodominant forests of the Guiana Shield. Biodivers Conserv 21:2195–2220. https://doi.org/10.1007/s10531-011-0166-1
- Hill JL, Hill RA (2001) Why are tropical rain forests so species rich? Classifying, reviewing and evaluating theories. Prog Phys Geogr 25:326–354. https://doi.org/10.1177/030913330102500302
- Hoang DT, Chernomor O, von Haeseler A, Minh BQ, Vinh LS (2017) UFBoot2: improving the ultrafast bootstrap approximation. Mol Biol Evol 35:518–522. https://doi.org/10.1093/molbev/msx281
- Index Fungorum (2019) Search Index Fungorum. http://www. indexfungorum.org/Names/Names.asp. Accessed 24 April 2019.
- Kalucka IL, Olariaga Ibarguren I (n.d.) *Hericium erinaceus* (Bull.) Pers. The Global Fungal Red List Initiative. http://iucn.ekoo.se/iucn/ species view/356812. Accessed 15 April 2019
- Khan MA, Tania M, Liu R, Rahman MM (2013) *Hericium erinaceus*: an edible mushroom with medicinal values. J Complement Integr Med 10:253–258
- Kim DM, Pyun CW, Ko HG, Park WM (2000) Isolation of antimicrobial substances from *Hericium erinaceum*. Mycobiology 28:33–38
- Kim SP, Kang MY, Kim JH, Nam SH, Friedman M (2011) Composition and mechanism of antitumor effects of *Hericium erinaceus* mushroom extracts in tumor-bearing mice. J Agric Food Chem 59:9861–9869
- Kim SP, Moon E, Nam SH, Friedman M (2012) Hericium erinaceus mushroom extracts protect infected mice against Salmonella typhimurium-induced liver damage and mortality by stimulation of innate immune cells. J Agric Food Chem 60:5590–5596
- Kim SP, Nam SH, Friedman M (2013) *Hericium erinaceus* (Lion'sMane) mushroom extracts inhibit metastasis of cancer cells to the lung in CT-26 colon cancer-transplanted mice. J Agric Food Chem 61: 4898–4904
- Koski-Kotiranta S, Niemela T (1988) Hydnaceous fungi of the Hericiaceae, Auriscalpiaceae and Climacodontaceae in northwestern Europe. Karstenia 27:43–70. https://doi.org/10.29203/ka.1987.253
- Kumar S, Stecher G, Tamura K (2015) Molecular Evolutionary Genetics Analyses version 7.0 for bigger datasets. Mol Biol Evol 33:1870–1874
- Larsson E, Larsson KH (2003) Phylogenetic relationships of russuloid basidiomycetes with emphasis on aphyllophoralean taxa. Mycologia 95:1037–1065. https://doi.org/10.1080/15572536.2004.11833020
- Liu C, Gao P, Qian J, Yan W (2000) Immunological study on the antitumor effects of fungus polysaccharides compounds. Wei Sheng Yan Jiu 29:178–180
- Ma BJ, Ma JC, Ruan Y (2012) Hericenone L, a new aromatic compound from the fruiting bodies of *Hericium erinaceum*. Chin J Nat Med 10: 363–365
- Matheny PB, Wang Z, Binder M, Curtis JM, Lim YW, Nilsson RH, Hughes KW, Hofstetter V, Ammirati JF, Schoch CL, Langer E, Langer G, McLaughlin DJ, Wilson AW, Froslev T, Ge ZW, Kerrigan RW, Slot JC, Yang ZL, Baroni TJ, Fischer M, Hosaka K, Matsuura K, Seidl MT, Vauras J, Hibbett DS (2007) Contributions of rpb2 and tef1 to the phylogeny of mushrooms and allies (Basidiomycota, Fungi). Mol Phylogenet Evol 43:430–451. https://doi.org/10.1016/j.ympev.2006.08.024
- Miller M, Pfeiffer WT, Schwartz T (2010) Creating the CIPRES Science Gateway for inferences of large phylogenetic trees. Proc Gateway Comp Environ Workshop 14:1–8. https://doi.org/10.1109/GCE. 2010.5676129

- Miller SL, Aime MC, Henkel TW (2012) Russulaceae of the Pakaraima Mountains of Guyana 2 New species of Russula and Lactifluus. Mycotaxon 121:233–253. https://doi.org/10.5248/121.233
- Moncalvo JM, Lutzoni FM, Rehner SA, Johnson J, Vilgalys R (2000) Phylogenetic relationships of agaric fungi based on nuclear large subunit ribosomal DNA sequences. Syst Biol 49:278–305. https:// doi.org/10.1093/sysbio/49.2.278
- Mori K, Obara Y, Hirota M, Azumi Y, Kinugasa S, Inatomi S, Nakahata N (2008) Nerve growth factor-inducing activity of *Hericium erinaceus* in 1321N1 human astrocytoma cells. Biol Pharm Bull 31:1727–1732. https://doi.org/10.1248/bpb.31.1727
- Nguyen LT, Schmidt HA, von Haeseler A, Minh BQ (2015) IQ-TREE: a fast and effective stochastic algorithm for estimating maximum likelihood phylogenies. Mol Biol Evol 32:268–274. https://doi.org/10. 1093/molbev/msu300
- Niu L, Song X, He S, Zhang P, Wang N, Li Y, Huang D (2015) New insights into the fungal community from the raw genomic sequence data of fig wasp *Ceratosolen solmsi*. BMC Microbiol 15:27. https:// doi.org/10.1186/s12866-015-0370-3
- Obara Y, Nakahata N (2002) The signaling pathway of neurotrophic factor biosynthesis. Drug News Perspect 15:290–298
- Online Auction Color Chart Co (2004). The online auction color chart: the new language of color for buyers and sellers. Palo Alto Calif. Online Auction Color Chart Co.
- Ouali Z, Sbissi I, Boudagga S, Rhaiem A, Hamdi C, Venturella G, Saporita P, Jaouani A, Gargano ML (2018) First report of the rare tooth fungus *Hericium erinaceus* in North African temperate forests. Plant Biosyst. https://doi.org/10.1080/11263504.2018.1549604
- Park HG, Ko HG, Kim SH, Park WM (2004) Molecular identification of Asian isolates of medicinal mushroom *Hericium erinaceum* by phylogenetic analysis of the nuclear ITS rDNA. J Microbiol Biotechnol 14:816–821
- Pegler DN (2003) Useful fungi of the world: the monkey head fungus. Mycologist 17:120-121. https://doi.org/10.1017/ S0269915X03003069
- Peh KS, Sonké B, Séné O, Djuikouo MN, Nguembou CK et al (2014) Mixed-forest species establishment in a monodominant forest in central Africa: implications for tropical forest invasibility. PLoS One 9:e97585
- Persoon CH (1794) Neuer Versuch einer systematischen Einteilung der Schwämme. Römer Neues Mag Bot 1:63–128
- Piepenbring M, Hofmann TA, Unterseher M, Kost G (2012) Species richness of plants and fungi in western Panama—towards a fungal inventory in the neotropics. Biodivers Conserv 21:2181–2193. https://doi.org/10.1007/s10531-011-0213-y
- Prine M, Albanese E, Guerchet M, Prina M (2014) World Alzheimer report 2014 - dementia and risk reduction an analysis of protective and modifiable factors, p.1–104.
- Ramberg JE, Nelson ED, Sinnott RA (2010) Immunomodulatory dietary polysaccharides: a systematic review of the literature. Nutr J 9:54
- Rupcic Z, Rascher M, Kanaki S, Köster RW, Stadler M, Wittstein K (2018) Two new Cyathane Diterpenoids from mycelial cultures of the medicinal mushroom *Hericium erinaceus* and the rare species, *Hericium flagellum*. Int J Mol Sci 19(3):1–12. https://doi.org/10. 3390/ijms19030740
- Schoch CL, Seifert KA, Huhndorf S, Robert V, Spouge JL, Levesque CA, Chen W, Fungal Barcoding Consortium (2012) Nuclear ribosomal internal transcribed spacer (ITS) region as a universal DNA barcode marker for Fungi. Proc Natl Acad Sci U S A 109:6241–6246. https:// doi.org/10.1073/pnas.1117018109
- Sjökvist E, Larsson E, Eberhardt U, Ryvarden L, Larsson KH (2012) Stipitate stereoid basidiocarps have evolved multiple times. Mycologia 104:1046–1055. https://doi.org/10.3852/11-174
- Smith ME, Henkel TW, Williams GC, Aime MC, Fremier AK, Vilgalys R (2017) Investigating niche partitioning of ectomycorrhizal fungi

in specialized rooting zones of the monodominant leguminous tree *Dicymbe corymbosa*. New Phytol 215:443–453. https://doi.org/10. 1111/nph.14570

- Sochorová Z, Döbbeler P, Sochor M, van Rooy J (2019) Octospora conidiophora (Pyronemataceae) – a new species from South Africa and the first report of anamorph in bryophilous Pezizales. MycoKeys 54:49–76. https://doi.org/10.3897/mycokeys.54.34571
- Sonké B, Couvreur TLP (2014) Tree diversity of the Dja Faunal Reserve, southeastern Cameroon. Biodivers Data J 2:e1049. https://doi.org/ 10.3897/BDJ.2.e1049
- Thongbai B, Rapior S, Hyde KD, Wittstein K, Stadler M (2015) *Hericium* erinaceus, an amazing medicinal mushroom. Mycol Prog 14:1–23. https://doi.org/10.1007/s11557-015-1105-4
- Verbeken A, Walleyn R (2010) Fungus flora of tropical Africa. Volume 2. Monograph of *Lactarius* in tropical Africa. National Botanic Garden of Belgium, Meise.
- Verbeken A, Stubbe D, Nuytinck J (2008) Two new *Lactarius* species from Cameroon. Cryptogam Mycol 29:137–143
- Vilgalys R, Hester M (1990) Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. J Bacteriol 172:4238–4246. https://doi.org/10.1128/jb.172. 8.4238-4246.1990
- Vilgalys R, Hopple JS, Hibbett DS (1994) Phylogenetic implications of generic concepts in fungal taxonomy: the impact of molecular systematic studies. Mycol Helv 6:73–91
- Vu D, Groenewald M, De Vries M, Gehrmann T, Stielow B, Eberhardt U, Al-Hatmi A, Groenewald JZ, Cardinali G, Houbraken J, Boekhout T, Crous PW, Robert V, Verkley GJM (2019) Large-scale generation and analysis of filamentous fungal DNA barcodes boosts coverage for kingdom fungi and reveals thresholds for fungal species and higher taxon delimitation. Stud Mycol 92:135–154. https://doi.org/ 10.1016/j.simyco.2018.05.001
- Wang J, Bau T, Gao X (2011) The molecular systematics research of Hericium in China. Edible Fungi of China 4.
- Wilson EO (1988) The current state of biological diversity. In: Wilson EO, Peters FM (eds) Biodiversity. National Academy Press, Washington, pp 3–18
- Wittstein K, Rascher M, Rupcic Z, Löwen E, Winter B, Köster RW, Stadler M (2016) Corallocins A–C, nerve growth and brainderived neurotrophic factor inducing metabolites from the mushroom *Hericium coralloides*. J Nat Prod 79:2264–2269
- Wong JY, Abdulla MA, Raman J, Phan CW, Kuppusamy UR, Golbabapour S, Sabaratnam V (2013) Gastroprotective effects of lion's mane mushroom *Hericium erinaceus* (Bull.:Fr.) Pers. (Aphyllophoromycetideae) extract against ethanol-induced ulcer in rats. Evid Based Complement Alternat Med 52:66–71
- Xu H, Wu PR, Shen ZY, Chen XD (2010) Chemical analysis of *Hericium* erinaceum polysaccharides and effect of the polysaccharides on derma antioxidant enzymes, MMP-1 and TIMP-1 activities. Int J Biol Macromol 47:33–36
- Yang BK, Park JB, Song CH (2003) Hypolipidemic effect of an exobiopolymer produced from a submerged mycelial culture of *Hericium erinaceus*. Biosci Biotechnol Biochem 67:1292–1298
- Yin L, Chi Y (2015) Cloning and bioinformatics analysis of MnP1 cDNA gene from *Hericium erinaceum*. Sci Silvae Sin 2015(5):68–77
- Ying J, Mao X, Ma Q, Zong Y, Wen H (1987) Icons of medicinal fungi from China (translated, Yuehan X). Science Press, Beijing, p 575
- Zhou LW, Dai YC (2013) Taxonomy and phylogeny of wood-inhabiting hydnoid species in Russulales: two new genera, three new species and two new combinations. Mycologia 105:636–649. https://doi. org/10.3852/12-011

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.