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ORIGINAL ARTICLE

Two new *Agaricomycetes* related to post-fire mosses

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Abstract
The very hot summers of recent years have led to an increase in the number of large forest fires in Europe. We investigated four large fire sites in Brandenburg and Saxony (Germany) up to 4 years after the fires with a focus on studying the post-fire fungal communities. In this context, we documented two species of *Agaricomycetes* associated with mosses, which are common but particularly emerge on burnt areas, i.e., *Arrhenia bryophthora* sp. nov. and *Bryopistillaria clavarioides* sp. nov. The former is an agaric with omphalinoid habit that causes the dieback of the common moss *Ceratodon purpureus*; the latter is a clavarioid fungus associated with either *Ceratodon purpureus* or another common moss, *Funaria hygrometrica*. Both fungal species appear to be restricted to recently burnt areas and have otherwise not been observed on or in close vicinity of these mosses. Herein, we describe these fungi macro- and micromorphologically as well as on a molecular basis and discuss their taxonomic position and potential lifestyles.

Keywords Bryophily · *Arrhenia bryophthora* · *Bryopistillaria clavarioides* · Forest fire · *Ceratodon purpureus* · *Funaria hygrometrica*

Introduction

Burnt areas represent special, spatially and temporally limited habitats that are colonized by a specialized fungal community (Dix and Webster 1995). These species are generally considered to be highly adapted but weak in competition (El-Abyad and Webster 1968b). After a fire, the topsoil in particular is poor in microorganisms and alkalinized to a certain extent (El-Abyad and Webster 1968a). The rapid colonization mechanisms of fire sites by phoenicoid fungi have been intensely documented and discussed since the second half of the twentieth century and four general hypotheses have so far been proposed: dispersal hypothesis, dormancy hypothesis, heat tolerance hypothesis, and body snatchers hypothesis (Matheny et al. 2018). However, none of these hypotheses has been sufficiently verified, and it seems plausible that fungi can pursue different strategies (Matheny et al. 2018; Filialuna and Cripps 2021).

In the absence of freshly burnt areas, certain species of the genera *Sphaerosporella*, *Wilcoxinia*, *Geopyxis*, and *Peziza* s.l. are endophytically associated and/or form mycorrhizas with different tree species and may only fruit after their host is damaged by wildfires (Hughes et al. 2020; Pulido-Chavez et al. 2021). The rather common species *Pholiota carbonaria* and *Plicaria carbonaria* follow a typical saprotrophic lifestyle as decomposers of dead plant biomass (Matheny et al. 2018; Kouki and Salo 2020). However, it was shown that the range of trophic lifestyles is broader than originally assumed (Raudabaugh et al. 2020). In addition to saprotrophy, *P. carbonaria* can interact with *Polytrichum commune*, a moss that also occurs on burnt areas (Raudabaugh et al. 2021). In the case of *Plicaria* spp., it has recently been reported that they have endophytic phases in mosses (Raudabaugh et al. 2020). Moreover, members of the genera *Anthracobia*, *Geopyxis*, *Peziza*, *Tricharina*, *Psathyrella*, and *Cotylidia* seem to be endophytically associated with various bryophytes as well (Raudabaugh et al. 2020; Korotkin et al. 2018).

Thus, many groups of fungi are dependent on post-fire mosses quickly colonizing burnt areas. Due to the perfect

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light and nutrient situation on such areas, these bryophytes can reach high abundancies of individuals, for example, *Funaria hygrometrica* and *Ceratodon purpureus* (Esposito et al. 1999; Sim-Sim et al. 2004).

In addition to phoenicoid fungi, bryophilic associations are not uncommon in some fungal families. For instance, the *Hygrophoraceae* (*Agaricales*) show a broad spectrum of interactions with phototrophic partners. They range from species that form lichens (*Dictyonema*, *Lichenomphalia*) to ectomycorrhizal species that live in mutualistic symbiosis with trees (*Hygrophorus*); others are endophytic biotrophs in grasslands (*Hygrocybe* s. l.) or develop strong associations with bryophytes as in the case of *Arrhenia* (Halbwachs et al. 2018; Redhead et al. 2002b; Lodge et al. 2014; Lawrey et al. 2009). The *Rickenellaceae* (*Hymenochaetales*) consist of various genera that are strictly associated with mosses (as parasites, commensals, or symbionts), e.g., *Bryopistillaria*, *Muscinupta*, *Sphagnomphalia*, *Rickenella*, and *Loreleia* (Redhead et al. 2002a; Korotkin et al. 2018).

Until the recent major forest fires in the Northern Hemisphere, such exceptional habitats could only rarely be studied, especially in Europe (Moser 1949; Butin and Kappich 1980). One reason for this is the strict forest fire policy of European countries, which leads to the removal of dead wood and prohibits the development of smaller fire areas in the wild. For this reason, phoenicoid fungi have only rarely been found in European countries (Knudsen and Vesterholt 2012; Dämmrich et al. 2016). On the other hand, after the great fires of the last years, it can be assumed that still undiscovered species live in these specific and (so far) underrepresented habitats. Against this background, we have mycologically examined four large forest fire areas in Germany (Brandenburg and Saxony) over the last 6 years. Among the collected fungi, two members of the *Agaricomycetes*, *Hygrophoraceae* and *Rickenellaceae*, are described herein.

Material and methods

Morphological study

The basis of this study is the investigation of large forest fire events in Saxony and Brandenburg, Germany (for details see the examined samples below). The fires took place in the years 2018, 2019, and 2022 (Brandenburg) and 2022 (Saxony). Sampling was carried out from 2019 on in periods of higher precipitation and in the winter half-year, when the weather was favorable for fungal fruiting.

Fresh specimens were photographed in the field, collected, morphologically examined and documented, and finally, dried and stored. In addition, the surrounding plants and mosses were recorded. The microscopic examination and documentation of the morphological characteristics of fresh and dried specimens were done with a Zeiss AXio1 light microscope with × 100, × 400, and × 1000 magnification in combination with a Canon EOS 60D, digital camera, or a Bresser microscope equipped with a Toupcam SPCMOS05000KPA. The microscopic measurement was done manually with a measuring eyepiece (Zeiss, Germany) or digitally in CorelDRAW2019 or in ToupView. Microscopic drawings are based on real microscopic photographs traced in CorelDRAW2019. Type specimen are deposited at Herbarium Senckenbergianum Görlitz (GLM).

Molecular genetic study and phylogenetic reconstruction

DNA of the samples was extracted using the E.Z.N.A.® Plant DNA Kit or the REDExtract-N-Amp Kit (Sigma-Aldrich) in 1:5 dilution. The primer pairs ITS1F/ITS4, ITS1F/ITS4B, and LR6/LR0R (White et al. 1990; GARDES and BRUNS 1993) and the DreamTaq Green PCR Master Mix (2x, Thermo Scientific™) or YourTaqPolymerase (in case of Touchdown PCR) were used to amplify and sequence the partial 28 s rDNA (large subunit, LSU) and internal transcribed spacer (ITS) barcoding region. The polymerase chain reaction was setup in an Eppendorf 5341 Mastercycler. The reaction involved initial denaturation at 95 °C for 2 min, followed by 35 cycles in series of denaturation at 95 °C for 0.5 min, annealing at 52 °C for 0.5 min, and extension at 72 °C for 1 min, with a final step of one cycle at 72 °C for 10 min to final extension. Subsequently, the PCR products were purified using the PCR Purification Kit-Column Kit (Jena BioScience) or sent directly to Eurofins (Germany) for further processing. The purified PCR products were sequenced in both directions at LGC Genomics GmbH (Berlin) or at Eurofins Genomics. The resulting chromatograms were quality-checked and edited in Geneious Prime 2023.2 (Kearse et al. 2012).

The newly generated sequences (ITS and LSU) were compared and identified with entries in GenBank using a blastn search (Altschul et al. 1990). Selected sequences of related species from GenBank and UNITE (Nilsson et al. 2019) and own generated sequences were concatenated and aligned using Clustal Omega 1.2.2 (Sievers and Higgins 2021) implemented in Geneious 2023.2. The alignments were carefully checked and edited manually; ambiguous regions were masked and not used for phylogenetic analysis. All newly gathered sequences were submitted to GenBank under accession numbers OR912523–OR912545 (or listed in Table 1).

Maximum Likelihood (ML) phylogenetic analysis was performed using RAxML 8.2.11 (Stamatakis 2014) implemented in Geneious 2023.2, applying the rapid bootstrapping algorithm with 1000 replicates. Four nucleotide partitions (ITS1, 5.8S, ITS2, 28S) were set, and the GTR

Table 1 Sequences from GenBank and newly created sequences (bold) used in this manuscript

Species	GenBank description	Voucher	ITS acc. number	LSU acc. number	Reference
Alloclavaria purpurea		Strain M. Korhonen 10305	MF319044	MF318895	Korotkin et al. 2018
A. purpurea		Strain H6047663	MF319055	MF318905	Korotkin et al. 2018
A. purpurea		Strain T. Niskanen 01–053	MF319053	MF318894	Korotkin et al. 2018
A. purpurea		Strain M. Korhonen 10411	MF319054	MF318893	Korotkin et al. 2018
A. purpurea		Strain T. Niskanen 01–044	MF319052	MF318904	Korotkin et al. 2018
A. purpurea		Voucher NAMA 2017–341	MH979233		Korotkin et al. 2018
A. purpurea		Voucher DBG:F-018950	OM859366	OM859366	
A. cf. *purpurea* (sp. 1)	*Alloclavaria purpurea*	Voucher Miettinen 18831 (H)	ON188807		
Amylocorticium cebennense		CFMR:HHB-2808	GU187505	GU187561	Binder et al. 2010
Arrhenia auriscalpium			AAU66428	AAU66428	Lutzoni 1997
Arrhenia bigelowii		Voucher S-F277532	MH198190		Voitk et al. 2022
A. bigelowii		Voucher S-F277529	MH198192		Voitk et al. 2022
A. bigelowii		Voucher TU117583	MH198219		Voitk et al. 2022
A. bigelowii	*Arrhenia* sp. EL-2019a	Isolate FNL:05.06.15.av01	MH473347	MH473347	Voitk et al. 2022
A. bigelowii	*Arrhenia* sp. EL-2019a	Isolate FNL:04.07.05.av03	MH473348	MH473347	Voitk et al. 2022
Arrhenia bryophthora		GLM-F137751 Type	**OR912530**	**OR912545**	Herein
A. bryophthora		IHI-23Arr2-KS48	**OR912527**	**OR912542**	Herein
A. bryophthora		IHI-23Arr3-KS49	**OR912526**	**OR912541**	Herein
A. bryophthora		IHI-23Arr4-KS52	**OR912525**	**OR912540**	Herein
A. bryophthora		IHI-23Arr1-KS2	**OR912528**	**OR912543**	Herein
A. bryophthora		20201007-V312	**OR912537**		Herein
A. bryophthora		20201125-U913	**OR912536**		Herein
A. bryophthora		20210310-J209	**OR912535**		Herein
A. bryophthora		20210311-F607	**OR912534**		Herein
A. bryophthora		20210317-D614	**OR912533**		Herein
A. bryophthora		20210512-V903	**OR912532**		Herein
Arrhenia epichysium	*Omphalina epichysium*	Redhead 5223 (ITS), Redhead 3140 (LSU)	OEU66442	OEU66442	Lutzoni 1997
A. epichysium		Isolate S.D. Russell iNaturalist # 23163045	ON245256		
A. epichysium		Strain G1952		MK277599	Varga et al. 2019
Arrhenia gerardiana		Isolate FNL:05.07.03.av02	MH473355	MH473355	Voitk et al. 2022
A. gerardiana		Isolate FNL:07.07.23.av02	MH473356	MH473356	Voitk et al. 2022
Arrhenia griseopallida	*Phaeotellus griseopallidus*	Lutzoni & Lamoure 910824–4	PGU66436	PGU66436	Lutzoni 1997
A. griseopallida	*Arrhenia* sp.	Voucher O50445	MT967298		Voitk et al. 2020

Table 1 (continued)

Species	GenBank description	Voucher	ITS acc. number	LSU acc. number	Reference
Arrhenia lobata			ALU66429	ALU66429	Lutzoni 1997
A. lobata		Voucher WU_38079	MW113698		Voitk et al. 2020
Arrhenia obscurata	*Omphalina obscurata*	Lamoure L73-101	OOU66448	OOU66448	Lutzoni 1997
A. obscurata		Voucher TU117230	MT967333		Voitk et al. 2020
A. obscurata		Voucher NSK 1017176	OP725689		
Arrhenia obatra		O-F-74283, G. Gulden	UDB036133		
A. obatra		O-F-304993, TE Brandrud	UDB037771		
A. obatra		Gro Gulden, François M. Lutzoni	UDB07674020		
A. obatra		O-F-260135, A. Molia	UDB036442		
Arrhenia philonotis	*Omphalina philonotis*	Lutzoni 930804–5	OPU66449	OPU66449	
A. philonotis		Voucher TU117359	MH198197		Voitk et al. 2022
A. philonotis		Voucher TU117360	MH198198		Voitk et al. 2022
Arrhenia retiruga		Voucher EL 76/03 (GB)	EU118604		Larsson 2007
A. retiruga			MT967340		
Arrhenia rustica	*Omphalina rustica*	Strain KH72	GU234093	GU234144	Geml et al. 2012
A. rustica		Voucher 0728–17	MW748470		
A. rustica	*Arrhenia obatra*	O-F-301204, Oyvind Weholt	UDB037751		
Arrhenia spathulata		Voucher TAAM172553	MT967342		Voitk et al. 2020
A. spathulata		Voucher TAAM172613	MT967343		Voitk et al. 2020
Arrhenia telmatiaea		NY 12555, Type specimen	NR_184964		Voitk et al. 2022
A. telmatiaea	*Omphalina sphagnicola*	Lutzoni 930810–1	OSU66453	OSU66453	Lutzoni 1997
A. telmatiaea	*Arrhenia fusconigra*	Voucher H6057157	MH198185		Voitk et al. 2022
A. telmatiaea	*A. fusconigra*	Voucher M-0276632	MH198193		Voitk et al. 2022
A. telmatiaea	*A. fusconigra*	Voucher TAAM147228	MH198215		Voitk et al. 2022
A. telmatiaea	*A. fusconigra*	Voucher TAAM144086	MH198216		Voitk et al. 2022
A. telmatiaea	*A. fusconigra*	Voucher TAAM145308	MH198217		Voitk et al. 2022
Arrhenia velutipes	*Omphalina velutipes*	Lamoure L77-166h11Xh4	OVU66455	OVU66455	Lutzoni 1997
A. velutipes		Voucher WU_28855	MW113696		Voitk et al. 2020
A. velutipes		Voucher WU_22371	MW113697		Voitk et al. 2020
A. velutipes		NSK 1017148	OQ216550		
***Arrhenia* sp. 1**	uncultured *Agaricales*		LR864676		
A. sp. 1	uncultured fungus	Clone 3993_3202	MW216197		Marčiulynienė et al. 2021
A. sp. 1	uncultured *Tricholomataceae*	Clone OTU_4114-phylogroup Tricholom_6	KX115646		Voyron et al. 2017
***Arrhenia* sp. 2**	*Arrhenia* cf. *obatra*	MICH56269, A. Smith	UDB07672073		

Table 1 (continued)

Species	GenBank description	Voucher	ITS acc. number	LSU acc. number	Reference
Blasiphalia pseudogrisella	*Rickenella pseudogrisella*	Lutzoni 930728–3	RPU66437	RPU66437	
B. pseudogrisella	*Rickenella pseudogrisella*	Strain P. Hoijer 4393	MF319048	MF318899	Korotkin et al. 2018
B. pseudogrisella	*Rickenella pseudogrisella*	Strain P. Hoijer 4118	MF319047	MF318898	Korotkin et al. 2018
Bryopistillaria clavarioides		GLM-F137752-Type	**OR912529**	**OR912544**	Herein
B. clavarioides		IHI-23RClav2-KS29	**OR912523**	**OR912538**	Herein
B. clavarioides		IHI-23RClav1-KS30	**OR912524**	**OR912539**	Herein
B. clavarioides		20230328-KF27	**OR912531**		Herein
B. clavarioides	*Globulicium* sp.	Isolate OTU83	MK019009		Gao et al. 2020
B. clavarioides	uncultured *Basidiomycota*	Isolate soil 3051	MF484257		
B. clavarioides	uncultured fungus		MH451219		Hahn et al. 2018
Bryopistillaria sagittiformis	*Rickenellaceae* sp.	IO.14.164 (S)	MT232349	MT232303	Olariaga et al. 2020
B. sagittiformis	uncultured fungus	Clone 3993_1832	MW215649		Marčiulynienė et al. 2021
B. sagittiformis	*Rickenellaceae* sp.	Voucher IO.15.41		MT232301	Olariaga et al. 2020
B. sagittiformis	*Rickenellaceae* sp.	Voucher IO.15.85		MT232302	Olariaga et al. 2020
Cantharocybe gruberi		Voucher AH24539	JN006420	JN006422	Esteve-Raventós et al. 2011
C. gruberi		AFTOL-ID 1017	DQ200927	DQ234540	Matheney et al. 2007
Cantharocybe virosa		Voucher D214	MH827010	MH820128	Parnmen et al. 2019
C. virosa		Voucher D298	MH827021	MH820139	Parnmen et al. 2019
C. virosa		Voucher D297	MH827020	MH820138	Parnmen et al. 2019
Cantharellopsis prescotii		Strain HRL2135	MF319049	MF318900	Korotkin et al. 2018
C. prescotii		Strain I. Kytovuori 08–0808	MF319050	MF318901	Korotkin et al. 2018
C. prescotii		Strain H6059300	MF319051	MF318903	Korotkin et al. 2018
Chromosera citrinopallida		Voucher D. Boertmann 2006/2 (CFMR DEN-29)	KF291072	KF291073	Lodge et al. 2014
C. citrinopallida	*Hygrocybe citrinopallida*	Lutzoni 930731–1	HCU66435	HCU66435	Lutzoni 1997
C. citrinopallida		Strain G0152		MK277690	Varga et al. 2019
C. citrinopallida		Isolate SAT-22–244-06	OQ987863		
Chrysomphalina chrysophylla		A. H. Smith 76299 (ITS), S. A. Redhead 7700 (LSU)	CCU66430	CCU66430	Lutzoni 1997
Chrysomphalina chrysophylla		Voucher iNaturalist # 9986321	MH256117		
Chrysomphalina chrysophylla		Voucher K(M):233320	MZ159640		
Chrysomphalina grossula	*Omphalina grossula*	Gulden 417/75	OGU66444	OGU66444	Lutzoni 1997
Chrysomphalina grossula		Voucher OSC 113667	EU644703	EU652372	
Chrysomphalina grossula		Voucher OSC 113683	EU644704	EU652373	
Contumyces rosellus		Strain MGW1462	MF319059	MF318912	Korotkin et al. 2018

Table 1 (continued)

Species	GenBank description	Voucher	ITS acc. number	LSU acc. number	Reference
C. rosellus		Strain NK1887 isolate FBT2530	OL771755	OL771796	
C. rosellus		Voucher JLF9262 iNaturalist # 72620806	OQ799963		
C. cf. *rosellus* (sp. 2)	*Contumyces rosellus*	Voucher HFRG_JD201004_1	OQ133543		
C. cf. *rosellus* (sp. 2)	*C. rosellus*	Voucher HFRG_JE201104_1	OQ133600		
C. cf. *rosellus* (sp. 1)	*Omphalina rosella*	Redhead 7501	ORU66452	ORU66452	Lutzoni 1997
Cotylidia carpatica		Strain HRL1319	MF319060	MF318914	Korotkin et al. 2018
Cotylidia diaphana		Strain DAOM182136		AF261459	Moncalvo et al. 2002
C. diaphana		Strain HRL1509		MF318915	Korotkin et al. 2018
C. cf. *diaphana* (sp. 1)	*Cotylidia* sp. MB5	Isolate AFTOL-ID 700	AY854079	AY629317	Lutzoni et al. 2004
C. cf. *diaphana* (sp. 2)	*C. diaphana*	Isolate S.D. Russell ONT NAMA2022 iNaturalist # 137771754	OP743618		
Cotylidia undulata		Strain V. Haikonen 25824	MF319061	MF318916	Korotkin et al. 2018
C. undulata		Strain HRL0625	MF319062	MF318917	Korotkin et al. 2018
C. undulata		Strain V. Haikonen 26475	MF319063	MF318918	Korotkin et al. 2018
Ginnsia viticola	*Phanerochaete viticola*	Strain Wu0010-29 clone Wu0010-29–1		GQ470670	Wu et al. 2010
G. viticola	*Phanerochaete viticola*	Strain Wu0010-29 clone Wu0010-29–4		GQ470671	Wu et al. 2010
G. viticola	*Phanerochaete viticola*	Strain FCUG 3001		GQ845003	Wu et al. 2010
G. viticola		Wu 0010–29	MN123802		Wu et al. 2021
G. viticola		Dai 22775		OL473615	
Globulicium hiemale		Isolate 5444b	DQ873595	DQ873595	Larsson et al. 2006
G. hiemale		Voucher KHL 961221 (GB)	EU118626		Larsson 2007
G. hiemale		Strain G0514		MK278091	Varga et al. 2019
Haasiella venustissima	*H. splendidissima*	Voucher E.C. 08191	JN944393	JN944394	Vizzini et al. 2012
H. venustissima	*H. splendidissima*	Voucher Herbarium Roux n. 3666	JN944398	JN944399	Vizzini et al. 2012
H. venustissima	*H. splendidissima*	Voucher Herbarium Roux n. 4044	JN944400	JN944401	Vizzini et al. 2012
H. venustissima		Voucher A. Gminder 971488 (STU)	KF291092	KF291093	Lodge et al. 2014
Kneiffiella pilaecystidiata		Voucher Helo_1517	OP620789	OP620789	Viner et al. 2023
Kneiffiella subalutacea		Voucher Miettinen_12026.2	OP620790	OP620790	Viner et al. 2023
Leifia flabelliradiata		Isolate 1367	DQ873635	DQ873635	Larsson et al. 2006
Lichenomphalia alpina	*Omphalina luteovitellina*	Lutzoni 930816–8	OLU66447	OLU66447	Lutzoni 1997
L. alpina		Lutzoni 930812–2	AY293962		Zoller and Lutzoni 2003
L. alpina		Strain GAL1550	GU810973		Geml et al. 2012
L. alpina		Strain GAL2126	GU810974		Viner et al. 2023

Table 1 (continued)

Species	GenBank description	Voucher	ITS acc. number	LSU acc. number	Reference
Lichenomphalia grisella	*Omphalina grisella*	Lutzoni 930822–6	OGU66443	OGU66443	Lutzoni 1997
Lichenomphalia hudsoniana	*Omphalina hudsoniana*	Lutzoni 920728-4a	OHU66446	OHU66446	Lutzoni 1997
Lichenomphalia meridionalis		S-270-FB1	LC428308	LC428307	Masumoto and Degawa 2020
L. meridionalis		Strain A1368	MT035854	MT032349	Nagy et al. 2020
Lichenomphalia oreades		Isolate MON3953	KY495791		Lücking et al. 2017
L. oreades		FH 00543609, Type scpecimen	NR_158521		Lücking et al. 2017
Lichenomphalia umbellifera	*Omphalina ericetorum*	Lutzoni 930817–2	OEU66445	OEU66445	Lutzoni 1997
Lichenomphalia velutina		Voucher 11–32289 (KUN-L)	KY435924		Liu et al. 2018
L. velutina		Voucher O-L-200004	MK811822		Marthinsen et al. 2019
L. velutina		Lutzoni 930812–1	OVU66454	OVU66454	Lutzoni 1997
Muscinupta laevis		Strain P. Salo 9493	MF319072	MF318928	Korotkin et al. 2018
M. laevis		Strain R. Saarenoksa 43385	MF319067	MF318922	Korotkin et al. 2018
M. laevis		Strain V. Haikonen 19745	MF319066	MF318921	Korotkin et al. 2018
M. laevis		Strain R. Saarenoksa 25994	MF319065		Korotkin et al. 2018
M. laevis	*Cyphellostereum laeve*	Voucher JJ 020909 (GB)	EU118621		Larsson 2007
M. laevis	*C. laeve*	Voucher UBCF20365	KC581335		
Odonticium romellii		Isolate 1514b	DQ873639	DQ873639	Larsson 2007; Larsson et al. 2006
O. romellii		Strain H. Murdoch 38	MF319073	MF318929	Korotkin et al. 2018
Rickenella danxiashanensis		Voucher GDGM45576	MF326426		Zhang et al. 2018
R. danxiashanensis		Voucher GDGM45513	MF326424		Zhang et al. 2018
R. danxiashanensis		Voucher GDGM45529	MF326425		Zhang et al. 2018
Rickenella fibula		Strain I. Kytovuori 96–071	MF319092	MF318948	Korotkin et al. 2018
R. fibula		Strain I. Kytovuori 93–040	MF319089	MF318945	Korotkin et al. 2018
R. fibula		Strain P. Salo 1882	MF319088	MF318949	Korotkin et al. 2018
R. fibula		Strain I. Kytovuori 94–482	MF319090	MF318946	Korotkin et al. 2018
R. fibula		PBM 2503 (WTU)	DQ241782	AY700195	Lutzoni et al. 2004
R. fibula		Strain HBK014	MF319082	MF318942	Korotkin et al. 2018
R. fibula		Strain HBK330-10	OL957172	OL957172	
Rickenella mellea		Culture CBS:579.87	MH862106	MH873795	Vu et al. 2019
R. mellea		Strain SZMC22713	OL898502	OL898502	
R. mellea		Strain CBS:581.87	MH862107	MH873796	Vu et al. 2019
R. mellea		Lamoure 74-20 h 1/9.91	RMU66438	RMU66438	Lutzoni 1997
R. mellea		iNat89558967	ON975049		

Table 1 (continued)

Species	GenBank description	Voucher	ITS acc. number	LSU acc. number	Reference
Rickenella indica		K 190585 – Type specimen	NR_137857		Latha et al. 2015
Rickenella. minuta		Strain MES1965	KY559321	MF318963	Korotkin et al. 2018
R. minuta		Strain MES1950	KY559314	MF318964	Korotkin et al. 2018
R. minuta		Strain MES2110	KY559318	MF318960	Korotkin et al. 2018
R. minuta		Strain TFB8528	KY352654		Korotkin et al. 2018
Rickenella swartzii		Strain HRL1399	MF319112	MF318977	Korotkin et al. 2018
R. swartzii		*swartzii* strain MGW1341	MF319114	MF318980	Korotkin et al. 2018
R. swartzii	*Rickenella setipes*	Strain P. Salo 4860	MF319109		Korotkin et al. 2018
R. swartzii	*R. setipes*	Strain GG119_88	GU234136		Geml et al. 2012
R. swartzii	*R. setipes*	Strain I. Kytovuori 93–032	MF319111		Korotkin et al. 2018
Serpulomyces borealis		CFMR:L-8014	GU187512	GU187570	Binder et al. 2010
R. swartzii	*R. setipes*	Strain R. Saarenoksa 06978	MF319110	MF318968	Korotkin et al. 2018
Sphagnomphalia brevibasidiata	*Omphalina brevibasidiata*	Lutzoni 930826–1	OBU66441	OBU66441	Lutzoni 1997
S. brevibasidiata		Strain P. Hoijer 1610	MF319117		Korotkin et al. 2018
S. brevibasidiata		Strain H6055490	MF319118		Korotkin et al. 2018
S. brevibasidiata	*Gyroflexus brevibasidiatus*	Voucher MQ18R160-QFB30676	MN992165		
S. brevibasidiata		Voucher IO.14.230	MT232351	MT232305	Olariaga et al. 2020

GAMMA I substitution model was applied, in addition to one binary partition (indel characters) that was set to default. The Bayesian Inference (BI) phylogeny was carried out using MrBayes 3.2.6 (Huelsenbeck and Ronquist 2001) implemented in Geneious 2023.2. Four gamma categories were used with the GTR substitution model and the invgamma rate variation. The Markov Chain Monte Carlo were set to 1,000,000 generations, sampling every 1000th generation. The first 20% of the trees was discarded as burn-in. For the remaining trees, a 50% majority rule consensus phylogram with posterior probabilities as nodal supports was computed. Clades with bootstrap support above 95% for ML and 0.95 for BI are considered highly supportive. Phylogenetic trees were edited in Geneious 2023.2 and in Corel Draw (v21.0.0.593 Corel Corporation).

Results

Phylogenetic analysis

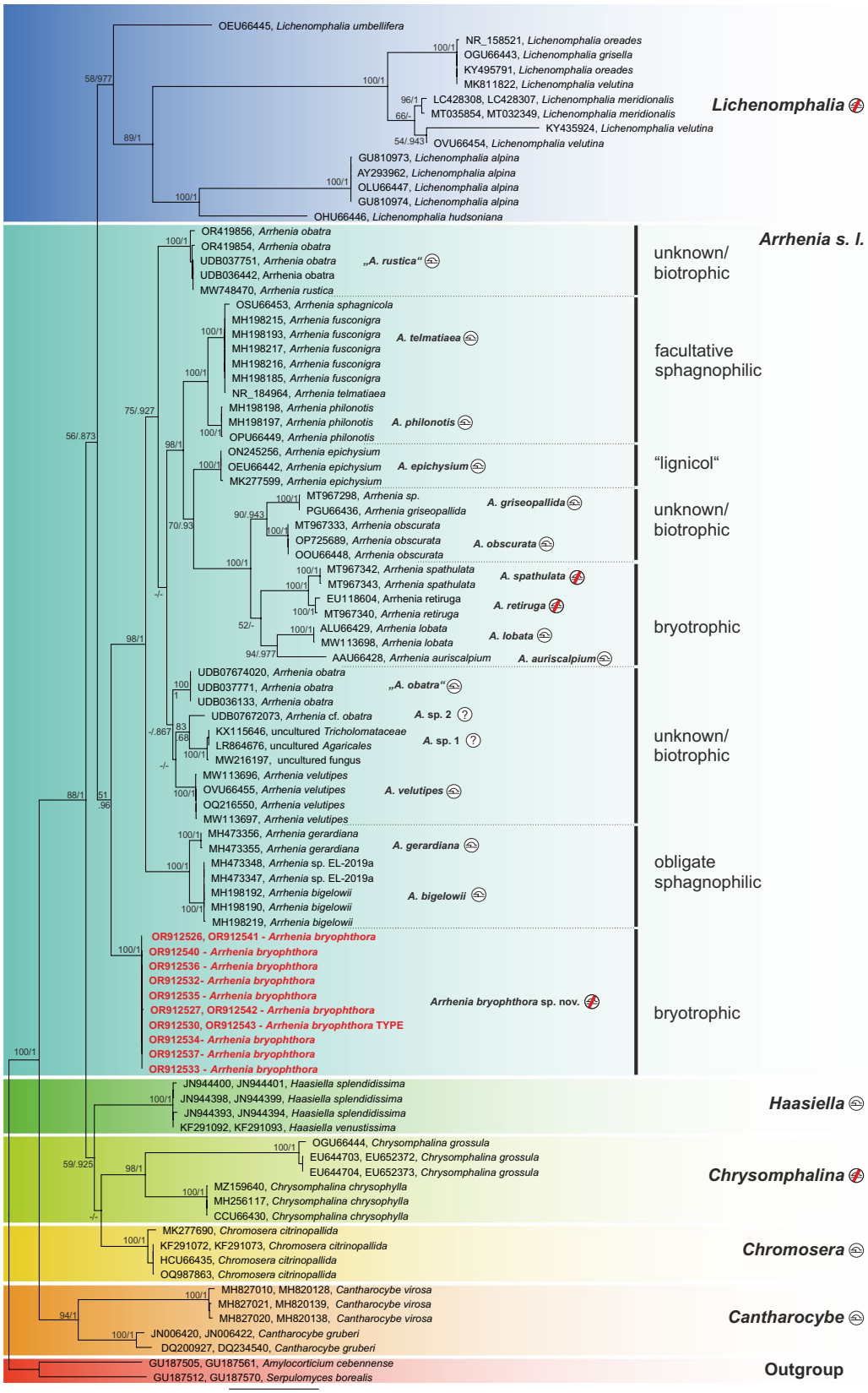
Result of the phylogenetic analysis based on sequences of the ITS and 28S rDNA (LSU) region from *A. bryophthora* and members of the *Hygrophoraceae* Lotsy selected from GenBank and UNITE is depicted as RAxML tree in Fig. 1. *Serpulomyces borealis* and *Amylocorticium cebennense* were selected as outgroup.

The aligned matrix contained 1814 unique nucleotide position features (262 ITS1, 157 5.8S, 353 ITS2, and 1041 28S) for the entire dataset of 93 specimens. Generated phylogenetic ML and BI trees had similar topological structures (compare Fig. 1 and S1).

The genera of *Hygrophorineae*, i.e., *Cantharocybe Chromosera*, *Chrysomphalina*, *Haasiella*, and *Lichenomphalia*, each form statistically well-validated clades. Sequences of *Arrhenia bryophthora* cluster in a statistically well-validated clade (BP/BI: 100/1) that is basally located in *Arrhenia* s.l., indicating that this species belongs to that monophyletic clade. However, this clade is only moderately supported statistically (BP/BI: 51/0.96).

Arrhenia s.l. comprises species with different ecological affiliations. These are categorized as follows: The *gerardiana/bigelowii* clade and the *telmatiaea/philonotis* clade include facultative or obligate sphagnophilic species and one lignicolous species. The *obatra/velutipes* clade (plus two unknown and possibly undescribed species), the *rustica*

Fig. 1 RAxML tree combining selected ITS and LSU-sequences ▶ from the *Hygrophorineae* Aime, Dentinger & Gaya including *A. bryophthora* BP and BI values less than 50 and 0.75, respectively, are omitted. Bold lettering indicates species' sequences generated in this study, and red font indicates the newly described species. Pictograms mark presence or absence of clamps


OEU66445, Lichenomphalia umbellifera
NR_158521, Lichenomphalia oreades
OGU66443, Lichenomphalia grisella
KY495791, Lichenomphalia oreades
MK811822, Lichenomphalia velutina
LC428308, LC428307, Lichenomphalia meridionalis
MT035854, MT032349, Lichenomphalia meridionalis
KY435924, Lichenomphalia velutina
OVU66454, Lichenomphalia velutina
GU810973, Lichenomphalia alpina
AY293962, Lichenomphalia alpina
OLU66447, Lichenomphalia alpina
GU810974, Lichenomphalia alpina
OHU66446, Lichenomphalia hudsoniana
Lichenomphalia
Arrhenia s. l.
OR419856, Arrhenia obatra
OR419854, Arrhenia obatra
UDB037751, Arrhenia obatra
„A. rustica“
UDB036442, Arrhenia obatra
MW748470, Arrhenia rustica
unknown/ biotrophic
OSU66453, Arrhenia sphagnicola
MH198215, Arrhenia fusconigra
MH198193, Arrhenia fusconigra
A. telmatiaea
MH198217, Arrhenia fusconigra
MH198216, Arrhenia fusconigra
MH198185, Arrhenia fusconigra
NR_184964, Arrhenia telmatiaea
MH198198, Arrhenia philonotis
MH198197, Arrhenia philonotis
A. philonotis
OPU66449, Arrhenia philonotis
facultative sphagnophilic
ON245256, Arrhenia epichysium
OEU66442, Arrhenia epichysium
A. epichysium
MK277599, Arrhenia epichysium
“lignicol“
MT967298, Arrhenia sp.
PGU66436, Arrhenia griseopallida
A. griseopallida
MT967333, Arrhenia obscurata
OP725689, Arrhenia obscurata
A. obscurata
OOU66448, Arrhenia obscurata
unknown/ biotrophic
MT967342, Arrhenia spathulata
A. spathulata
MT967343, Arrhenia spathulata
EU118604, Arrhenia retiruga
A. retiruga
MT967340, Arrhenia retiruga
ALU66429, Arrhenia lobata
A. lobata
MW113698, Arrhenia lobata
AAU66428, Arrhenia auriscalpium
A. auriscalpium
bryotrophic
UDB07674020, Arrhenia obatra
UDB037771, Arrhenia obatra
„A. obatra“
UDB036133, Arrhenia obatra
UDB07672073, Arrhenia cf. obatra
A. sp. 2
KX115646, uncultured Tricholomataceae
LR864676, uncultured Agaricales
A. sp. 1
MW216197, uncultured fungus
MW113696, Arrhenia velutipes
OVU66455, Arrhenia velutipes
A. velutipes
OQ216550, Arrhenia velutipes
MW113697, Arrhenia velutipes
unknown/ biotrophic
MH473356, Arrhenia gerardiana
MH473355, Arrhenia gerardiana
A. gerardiana
MH473348, Arrhenia sp. EL-2019a
MH473347, Arrhenia sp. EL-2019a
MH198192, Arrhenia bigelowii
A. bigelowii
MH198190, Arrhenia bigelowii
MH198219, Arrhenia bigelowii
obligate sphagnophilic
OR912526, OR912541 - Arrhenia bryophthora
OR912540 - Arrhenia bryophthora
OR912536 - Arrhenia bryophthora
OR912532- Arrhenia bryophthora
OR912535 - Arrhenia bryophthora
OR912527, OR912542 - Arrhenia bryophthora
OR912530, OR912543 - Arrhenia bryophthora TYPE
OR912534- Arrhenia bryophthora
OR912537- Arrhenia bryophthora
OR912533 - Arrhenia bryophthora
Arrhenia bryophthora sp. nov.
bryotrophic
JN944400, JN944401, Haasiella splendidissima
JN944398, JN944399, Haasiella splendidissima
JN944393, JN944394, Haasiella splendidissima
KF291092, KF291093, Haasiella venustissima
Haasiella
OGU66444, Chrysomphalina grossula
EU644703, EU652372, Chrysomphalina grossula
EU644704, EU652373, Chrysomphalina grossula
MZ159640, Chrysomphalina chrysophylla
MH256117, Chrysomphalina chrysophylla
CCU66430, Chrysomphalina chrysophylla
Chrysomphalina
MK277690, Chromosera citrinopallida
KF291072, KF291073, Chromosera citrinopallida
HCU66435, Chromosera citrinopallida
OQ987863, Chromosera citrinopallida
Chromosera
MH827010, MH820128, Cantharocybe virosa
MH827021, MH820139, Cantharocybe virosa
MH827020, MH820138, Cantharocybe virosa
JN006420, JN006422, Cantharocybe gruberi
DQ200927, DQ234540, Cantharocybe gruberi
Cantharocybe
GU187505, GU187561, Amylocorticium cebennense
GU187512, GU187570, Serpulomyces borealis
Outgroup
0.6

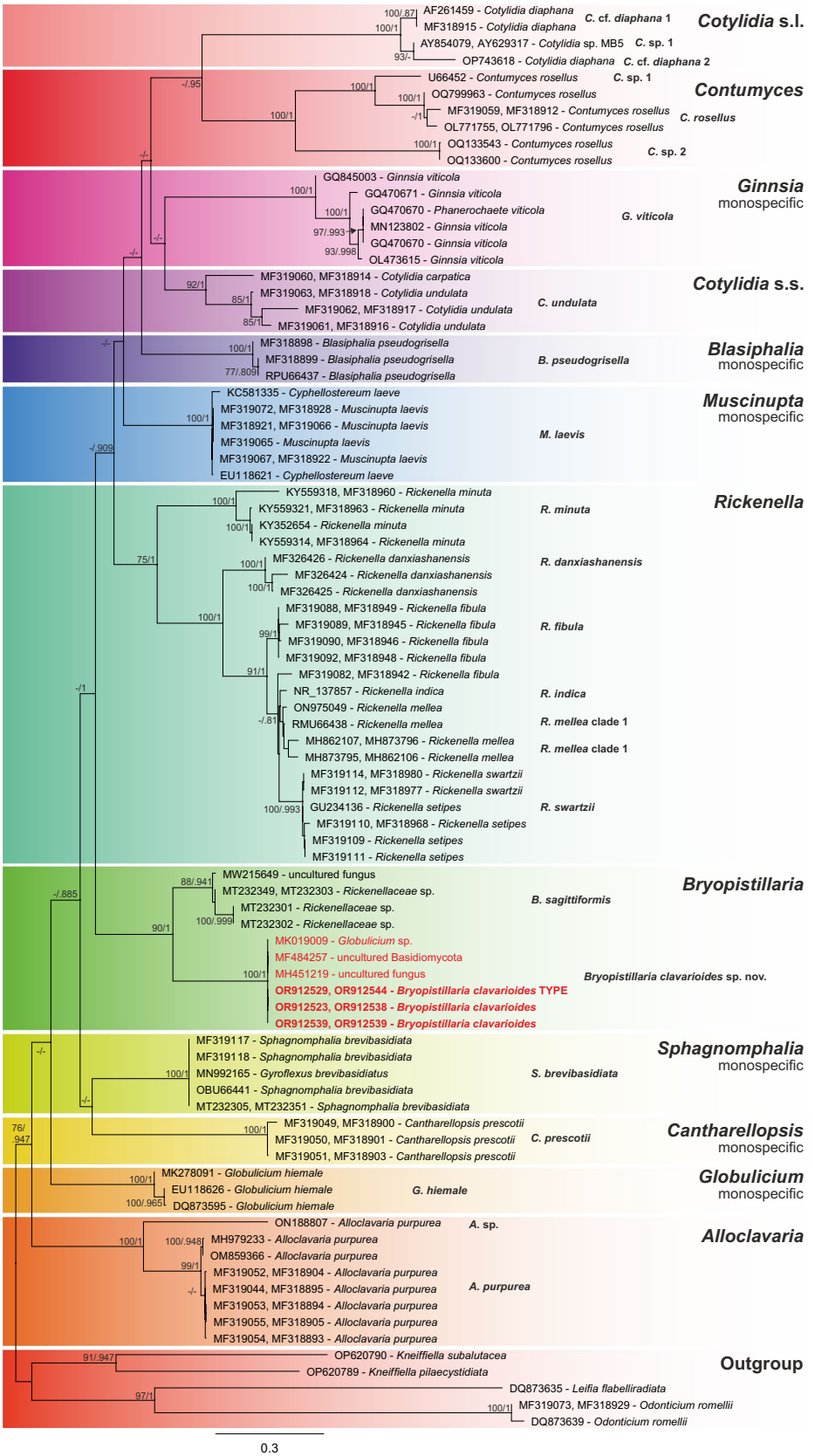


Fig. 2 RAxML tree combining selected ITS and LSU-sequences of the *Rickenellaceae* Vizzini (*Hymenochaetales*) related to *B. clavarioides.* BP and BI values less than 75 and 0.75, respectively, are omitted. Bold lettering indicates species' sequences generated in this study, and red font indicates the newly described species

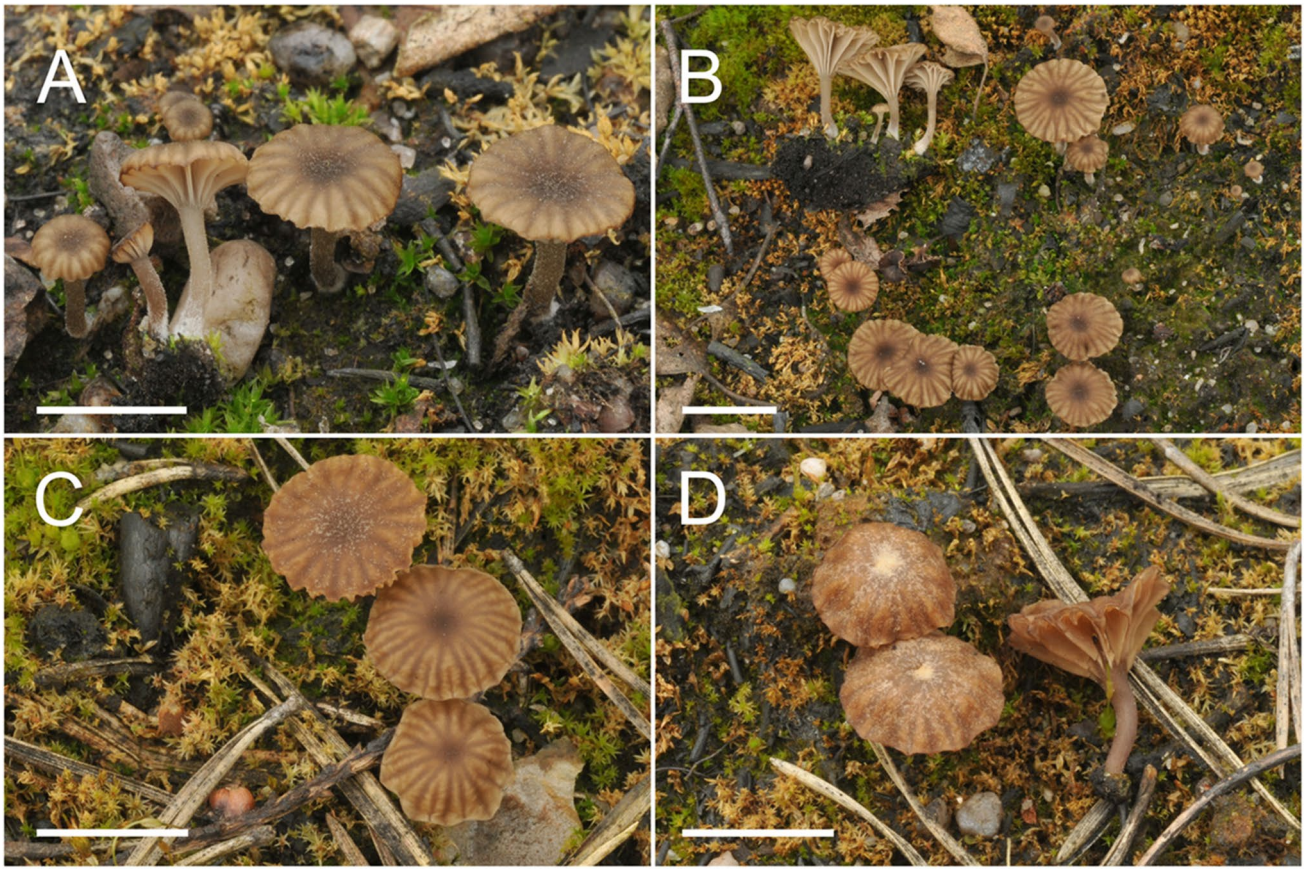


Fig. 3 In situ photographs of *Arrhenia bryophthora*; IHI-23Arr4-KS52 (**A**), IHI-23Arr1-KS2 (**B**), and GLM-F137751—type (**C**, **D**), scale bars 1 cm. Photos A. Karich

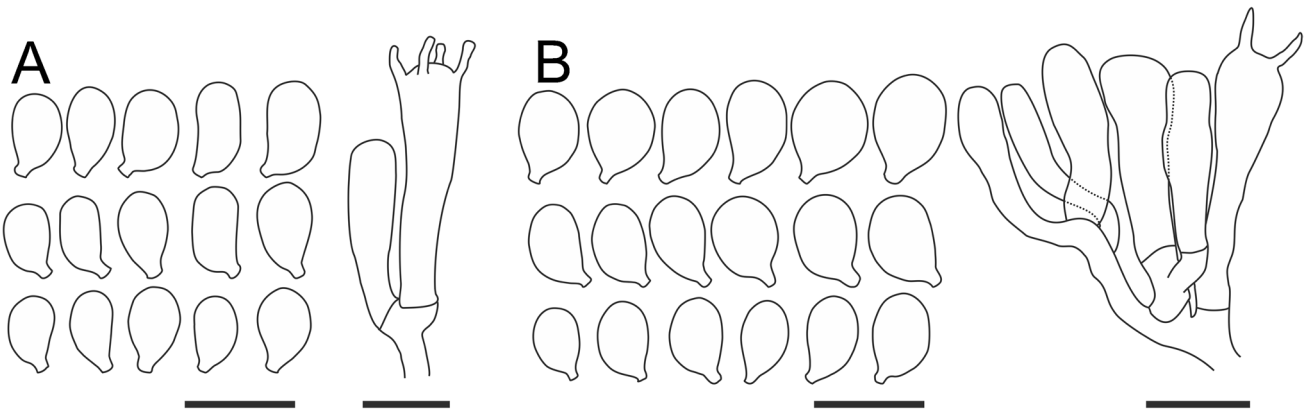


Fig. 4 Typical (GLM-F137751—type (**A**)) and exceptional (IHI-23Arr1-KS2 (**B**)) basidiospores and basidia of *Arrhenia bryophthora*; scale bars 10 µm

clade, and the *obscurata/acerosa* clade include species with unknown but possibly biotrophic ecology. Bryotrophic species are represented by the *bryophthora* clade and species within *Arrhenia* sensu stricto (including the type species of the genus *A. auriscalpium*).

A RaxML tree based on ITS and LSU sequences from *B. clavarioides* and allied sequences of representatives from the *Rickenellaceae* in GenBank and UNITE is depicted in Fig. 2. The aligned matrix contained 2322 unique nucleotide position features (267 ITS1, 163 5.8S, 247 ITS2, and 1645

28 s) for the entire dataset of 86 specimens. Generated phylogenetic ML and BI trees had similar topological structures (compare Fig. 2 and S2).

Sequences of *Bryopistillaria clavarioides* generated in this study and three additional sequences of environmental samples form a distinct and well-supported clade that is closely related to specimen-sequences of *Bryopistillaria sagittiformis* from Olariaga et al. (2020) displaying sequence similarities in ITS sequences from 89.25 to 90.42%. Sequences of both species form a well-supported clade in the *Rickenellaceae* RaxML tree (BP/I: 90/1).

The RAxML tree contains six monospecific genera, i.e., *Globulicium*, *Canthrarellopsis*, *Sphagnomphalia*, *Muscinupta*, *Blasiphalisa*, and *Ginnsia*. Together with the genera *Contumyces* and *Alloclavaria*, all these clades are well supported (BP/BI:100/1). Samples of the genus *Cotylidia* form two separate clades, each being well supported (BP/BI: 100/1). One includes *C. undulata*, the genus' type species, and hence is accounted as *Cotylidia* sensu stricto. And the second phylogenetically separate clade groups around *Cotylidia diaphana*. These results indicate that *Cotylidia* is polyphyletic and should be divided. However, this is beyond the scope of this work.

Moss-associated species of the genus *Rickenella* form a well-supported clade. *R. minuta*, that was recently discovered to have an ectomycorrhizal relation to *Notofagaceae* in Argentina builds a sister clade to those *Rickenella* with strict bryophilic relation (Korotkin et al. 2018). The entire *Rickenella* clade is only moderately well supported (BP/BI:75/1).

Taxonomy

***Arrhenia bryophthora* Karich, Jarling, R. Ullrich, sp. nov.**

Mycobank number: 851246

Type: GLM-F137751 – Germany, Zeithain, Gohrischheide, Plot 3, 13,33206 E 51,43189 N, 95 m asl., fire site in forest with *Pinus sylvestris* and *Betula pendula*, on and in between post fire moss *Ceratodon purpureus* and possibly *Funaria hygrometrica* and causing their dieback, 23rd of March 2023, leg. A. Karich, R. Ullrich and R. Erlacher.

Etymology: From ancient Greek βρύον (brúon, "moss") and φθορά (phthorá, "destruction").

Diagnosis: Small brown agaric with omphalinoid habit growing on old fire sites in association with *Ceratodon purpureus* and causing its dieback. Being distinct from other similar species in *Arrhenia* s.l. by the absence of clamp connections.

Macromorphology (Fig. 3a–d): Basidiocarps small, omphalinoid. Cap 4–10 mm broad, distinctly translucently striate when fresh, striae and in the center dark, chestnut to coffee brown (RAL 040 40 30 and RAL 040 30 20, respectively), between striae lighter, maple syrup brown (RAL 060 60 40), strongly hygrophanous when drying, glabrous to slightly scaly when young (scales hygrophanous), margin crenulate. Lamellae falcate-decurrent, distant, L = 14–18 with 1–2 lamellulae, maple syrup brown. Stem 6–12 × 1–1.5 mm, of cap color, finely pruinose in fresh specimen, turning glabrous at age, basally with whitish mycelium when young. No specific smell and taste. Spore print white.

Micromorphology (Fig. 4a, b): Basidia solely four-spored to predominantly two-spored, 25–30 × 6–8 µm, clampless. Basidiospores heteromorphic, cylindrical, dacryoid to subglobose, with distinct apiculus, (6)6.5–8(9) × 3.5–5(5.5) µm, ave. 7.1–8.1 × 3.7–4.1 µm, Q = 1.4–2.4 ave. 1.8–2.0 an exceptional specimen bearing sublobose to globose spores with deviating measurements, 7–9 × 4.5–7.5(8) µm ave. 7.9 × 5.7 µm, Q = 1.1–1.7(1.8) ave. 1.4 (IHI-23Arr1-KS2). Trama and cutis in pileus and stipe composed of 3–9 µm broad hyphae with partially fine to distinct incrusting pigmentation. Lamellar trama irregular, hyphae 2–9 µm broad, frequently distinctly incrusted and often branched. No cystidia observed. No structures amyloid or dextrinoid. No clamps observed.

Habitat (Fig. 5a–e): Growing on old fire sites (0.5 to 4 years postfire) solitarily or in clusters in between the dioicous moss *Ceratodon purpureus*, also observed near *Funaria hygrometrica* and *Marchantia polymorpha*, causing the dieback of the surrounding *C. purpureus*, being evident by brownish, circular, about 15 cm diameter large spots on the moss surface (compare Fig. 5). Fruit body formation was observed from September to May, mainly in November and March.

Distribution: So far, only known from four localities in Brandenburg and Saxony, Germany.

Additional specimens examined:

20201007-V312 – Germany, west of Luckenwalde, Felgentreu, Plot V3, 13.041819 E, 52.087368 N, 65 m asl., fire site on former *Pinus sylvestris* forest with few *Betula pendula*, on and between post fire moss *Ceratodon purpureus* causing its dieback, 7th of October 2020, leg. J. Neuendorf, T. Pilz-Hunter.

20201125-U913 – Germany, west of Luckenwalde, Felgentreu, Plot U9, 13.039827 E, 52.089232 N, 65 m asl., fire site on former *Pinus sylvestris* forest with few *Betula pendula*, on and between post fire moss *Ceratodon purpureus* and possibly *Funaria hygrometrica* causing their dieback, 25th of November 2020, leg. W. Linder, A. Schaepe, S. Hutter.

20210310-J209 – Germany, east of Treuenbrietzen, Frohnsdorf, Plot J2, 12.936418 E, 52.043814 N, 95 m asl., *Populus-Betula* succession on fire site on former *Pinus sylvestris* forest, cleared, plowed, and reafforested with *Pinus sylvestris*, on and between post fire moss *Ceratodon purpureus*, causing its dieback, and healthy *Polytrichum piliferum*, 10th of March 2021, leg. W. Linder, A. Schaepe.

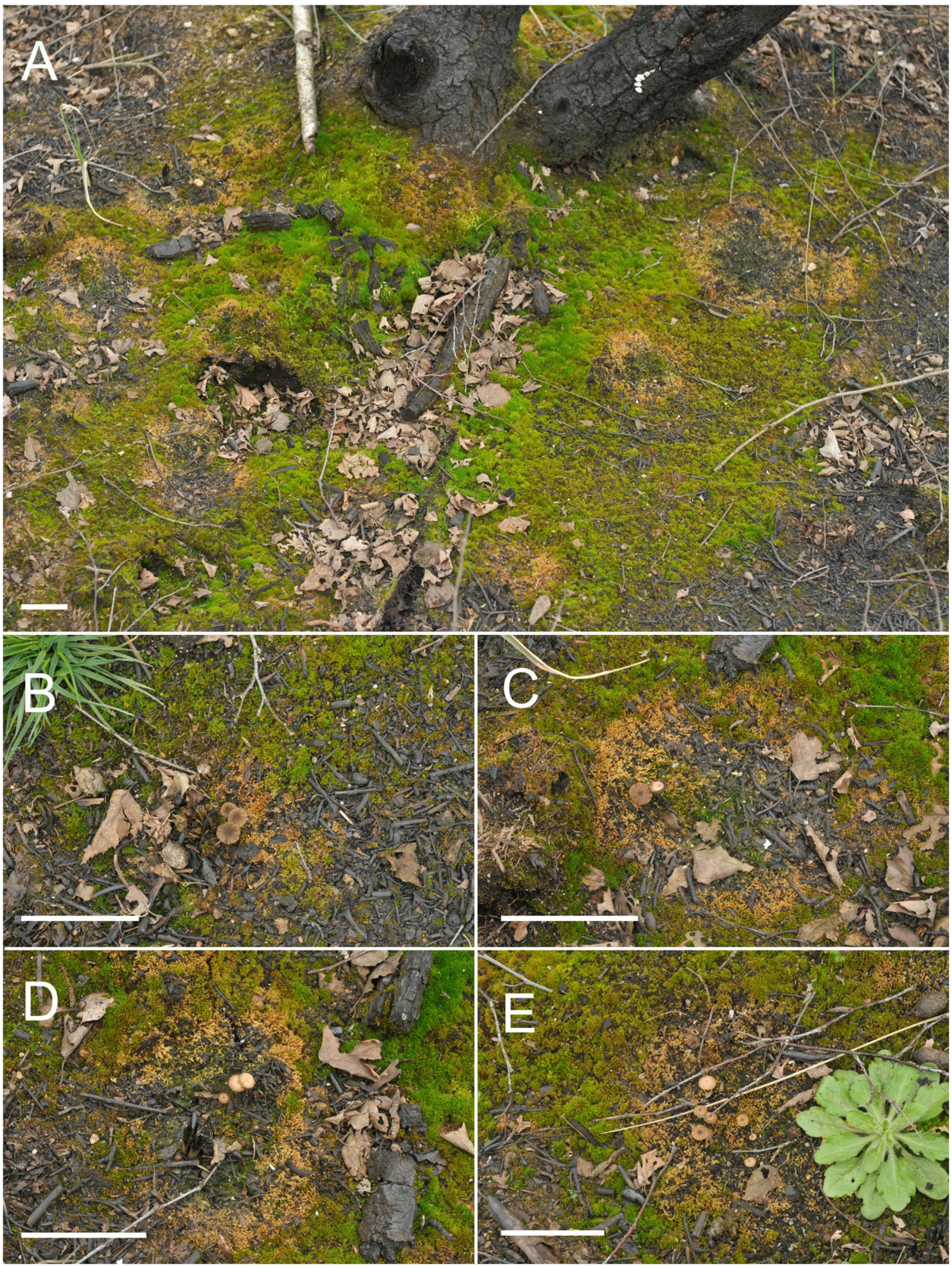


Fig. 5 Brownish circular spots on the moss surface of *Ceratodon purpureus* caused by *Arrhenia bryophthora* (**A**); basidiocarps of *A. bryophthora* (IHI-23Arr3-KS49) constantly growing inside these spots (**B**–**E**); scale bars 5 cm. Photos A. Karich

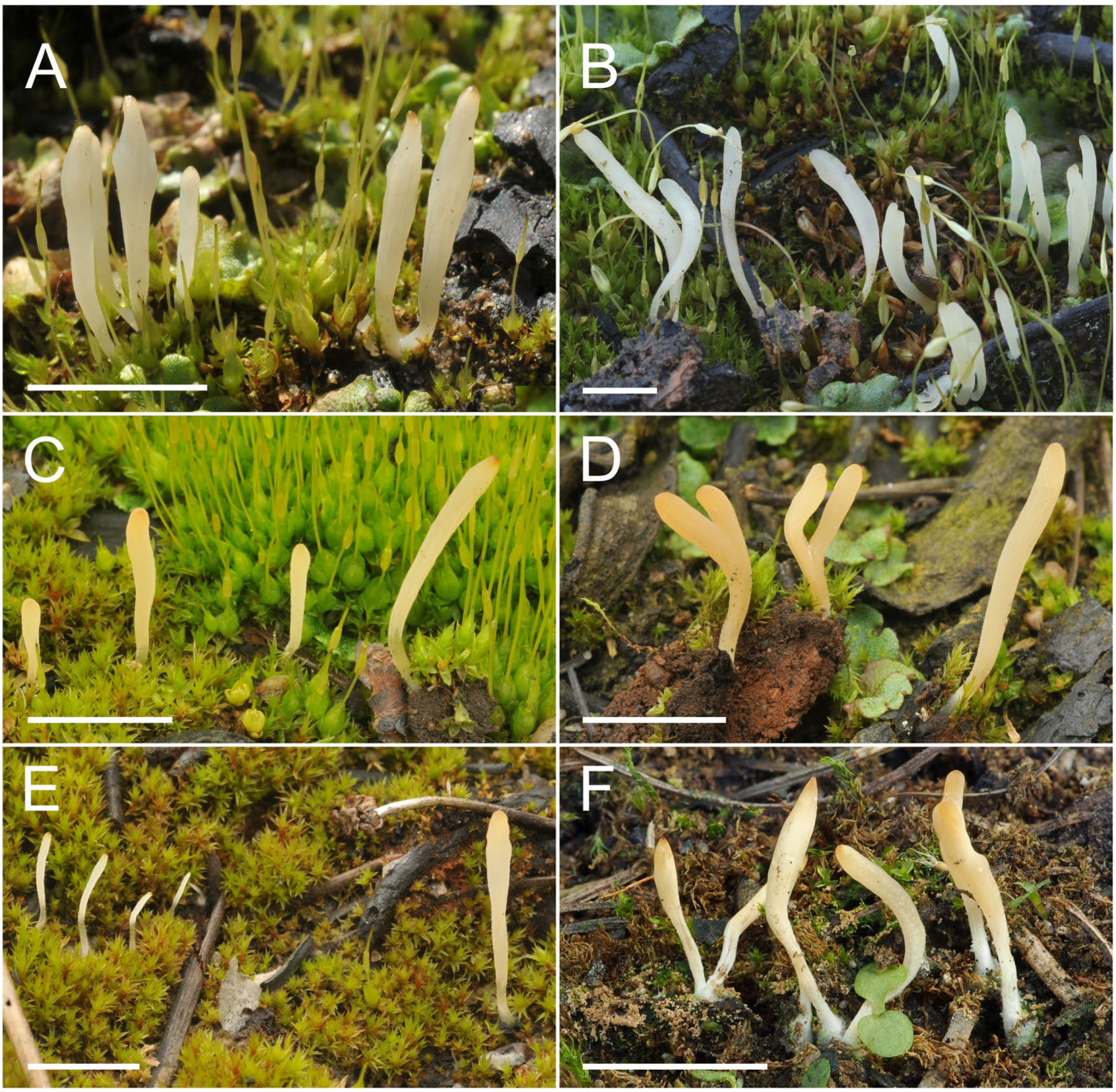


Fig. 6 In situ photographs of *Bryopistillaria clavarioides*; IHI-23RClav1-KS2 (**A**, **B**), GLM-F137752 – type (**C**), IHI-23RClav2-KS29 (**D**, **E**), 20190906–002 (**F**); scale bars 1 cm. Photos R. Ullrich (**B**) and J. Ehrich (**F**), others by A. Karich

20210311-F607 – Germany, east of Treuenbrietzen, Frohnsdorf, Plot F6, 12.918541 E, 52.042959 N, 95 m asl., *Populus-Betula* succession on fire site on former *Pinus sylvestris* forest, partly cleared and reafforested with *Quercus petraea* and *Pinus sylvestris*, on and between post fire moss *Ceratodon purpureus* and possibly *Funaria hygrometrica* causing their dieback, 11th of March 2021, leg. J. Ehrich, J. Seelbach.

20210317-D614 – Germany, east of Treuenbrietzen, Frohnsdorf, Plot D6, 12.915415 E, 52.039248 N, 95 m asl., *Populus-Betula* succession on fire site on former *Pinus sylvestris* forest, partly cleared, on and between post fire moss *Ceratodon purpureus* causing its dieback, 17th of March 2021, leg. J. Ehrich, T. Röthling.

20210512-V903 – Germany, west of Luckenwalde, Felgentreu, Plot V9, 13.041126 E, 52.088145 N, 65 m asl., fire site on former *Pinus sylvestris* forest with few *Betula pendula*, on and between post fire mosses *Ceratodon purpureus*, *Funaria hygrometrica*, and *Marchantia polymorpha*, possibly causing their dieback, 12th of May 2021, leg. J. Ehrich, J. Seelbach.

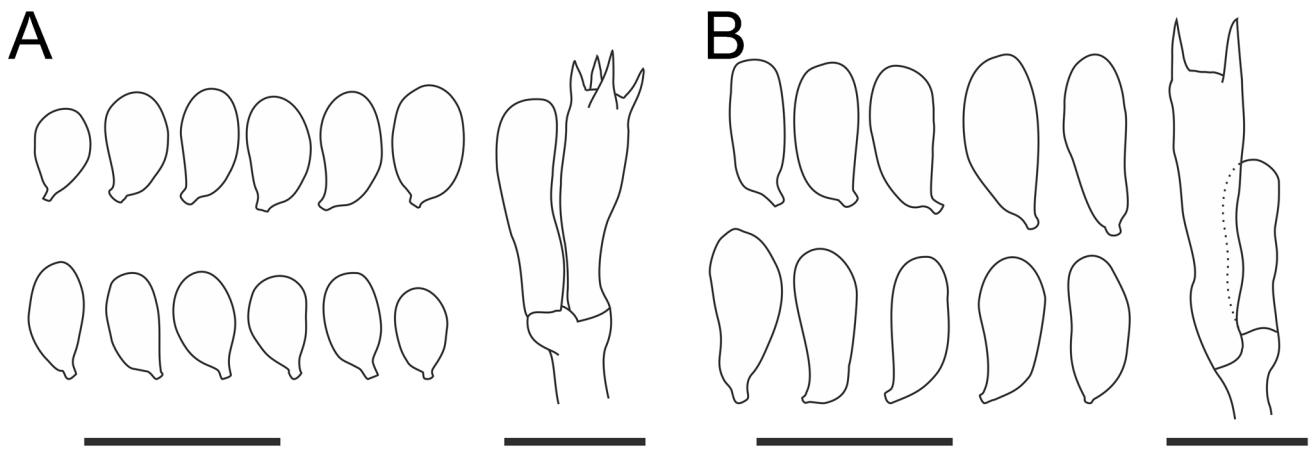


Fig. 7 Basidiospores and basidia of *Bryopistillaria clavarioides*; GLM-F13775 – type (**A**) and IHI-23RClav1-KS2 (**B**); scale bars 10 µm

IHI-23Arr1-KS2 – Germany, Nationalpark Sächsische Schweiz, Richterschlüchte—Krinitzgrab, fire site in forest with *Picea abies*, *Larix decidua*, *Pinus sylvestris*, and *Fagus sylvatica*, 14.27467 E, 50.89607 N, 450 m asl. on and in between post fire moss *Ceratodon purpureus* and possibly *Funaria hygrometrica* and causing their dieback, 4th of April 2023, leg. A. Karich, R. Ullrich and R. Erlacher.

IHI-23Arr2-KS48 – Germany, Zeithain, Gohrischheide, fire site in forest with *Pinus sylvestris* and *Betula pendula* (fire in summer 2022), Plot 1, 13.33253 E, 51.41907 N, 95 m asl., on and in between post fire moss *Ceratodon purpureus* and possibly *Funaria hygrometrica* and causing their dieback, 23rd of March 2023, leg. A. Karich, R. Ullrich and R. Erlacher.

IHI-23Arr3-KS49 – Germany, Zeithain, Gohrischheide, fire site in forest with *Pinus sylvestris* and *Betula pendula* (fire in summer 2022), Plot 4, 13.33253 E, 51.41907 N, 95 m asl., on and in between post fire moss *Ceratodon purpureus* and possibly *Funaria hygrometrica* and causing their dieback, 23rd of March 2023, leg. A. Karich, R. Ullrich and R. Erlacher.

IHI-23Arr4-KS52 – Germany, Zeithain, Gohrischheide, fire site in forest with *Pinus sylvestris* and *Betula pendula* (fire in summer 2022), Plot 4, 13.33148 E, 51.4124 N, 95 m asl., on and in between post fire moss *Ceratodon purpureus* and possibly *Funaria hygrometrica* and causing their dieback, 23rd of March 2023, leg. A. Karich, R. Ullrich and R. Erlacher.

Bryopistillaria clavarioides **Karich, Jarling & R. Ullrich, sp. nov.**

= *Clavaria tenuipes* ss. Kajan & Grauwinkel 1987

Non *Clavaria tenuipes* Berk. & Broome 1848

Mycobank number: 851247

Type: GLM-F137752 – Germany, Zeithain, Gohrischheide, Plot 2, 13,33372 E 51,42659 N, 95 m asl., fire site in forest with *Pinus sylvestris* and *Betula pendula* (fire in summer 2022), on and in between post fire mosses *Funaria hygrometrica* and *Ceratodon purpureus*, 23rd of March 2023, leg. A. Karich, R. Ullrich and R. Erlacher.

Etymology: Referring to the macromorphological similarity with species of the genus *Clavaria* L.

Diagnosis: Small to medium sized club shaped fruit body with whitish to cream color. Occurring on old fire sites in association with *Funaria hygrometrica* and *Ceratodon purpureus*. Distinct from other clavarioid fungi by its phylogenetical association to *Bryopistillaria sagittiformis*. Distinct from the later by its larger size and different habit and lifestyle.

Macromorphology (Fig. 6a–f): Basidiocarps clavarioid (club shaped) 10–25(30) × 1–3 mm, whitish to yellowish-crème (RAL 9003 to RAL 1012) to almost pale yolk-yellow (RAL 1002). Sterile stem about 1/5 to 1/4 (1/3) of entire club, glabrous and with somewhat glassy surface, demarcated from fertile head which is broadened, glabrous or wrinkled with age and with a dull surface, tips tan when drying. No specific smell and taste. Spore print white.

Micromorphology (Fig. 7a, b): Basidia 16–26 × 5–6 µm, four or two (one) spored, clampless. Basidiospores subglobose, ellipsoid to oblong dacryoid, often adhering to each other in packages of two or four, with distinct apiculus, inamyloid, (4.5)5.0–6.0(6.5) × 2.5–3.5 µm, ave. 5.6 × 3.0 µm, Q = (1.4)1.7–2.2 ave. 1.90 in typical predominantly four spored specimens (GLM-F13775/IHI-23RClav2-KS29), and 7.5–9.0(9.5) × (2.5)3.0–3.5(4) µm, ave. 8.1 × 3.3 µm, Q = 2.1–3.2 ave. 2.5 µm in predominantly two spored specimens (IHI-23RClav1-KS2). Stipiticutis consisting of 4–7 µm broad cylindric and parallel directed hyphae. Trama in stipe and hymenium consisting of 5–20 µm wide,

subirregularly directed hyphae, often constricted at the septa. No cystidia observed. All structures without iodine reactions. All septa clampless.

Habitat: Growing on up to two years old fire sites in between *Funaria hygrometrica* and *Ceratodon purpureus*. Sometimes, the mosses concomitant dieback was observed. Fruiting observed in spring and autumn. Attempts to obtain cultures from shed spores and fresh basidiocarps unsuccessful.

Distribution: Known from Europe and two soil samples from North America.

Additional collections examined:

IHI-23RClav1-KS2 – Germany, Nationalpark Sächsische Schweiz, Richterschlüchte—Krinitzgrab, 14,27467 E 50,89607 N, 450 m asl., fire site in forest with *Picea abies*, *Larix decidua*, *Pinus sylvestris*, and *Fagus silvatica* (fire in summer 2022), on and in between post fire mosses *Funaria hygrometrica* and *Ceratodon purpureus*, 4th of April 2023, leg. A. Karich, R. Ullrich, F. Salzsieder and R. Erlacher.

IHI-23RClav2-KS29 – Germany, Zeithain, Gohrischheide, Plot 1, 13,33253 E 51,41907 N, 95 m asl., fire site in forest with *Pinus sylvestris* and *Betula pendula* (fire in summer 2022), on and in between post fire mosses *Funaria hygrometrica* and *Ceratodon purpureus*, 23rd of March 2023, leg. A. Karich, R. Ullrich and R. Erlacher.

20190906–002 – Germany, east of Treuenbrietzen, Frohnsdorf, 12.905322 E, 52.037015 N, 95 m asl. *Populus-Betula* succession on fire site on former *Pinus sylvestris* forest (fire in summer of 2018), on and between post fire moss *Ceratodon purpureus* causing its dieback, September 6th 2019, leg. R. Jarling, J. Ehrich.

20201118-F618 – Germany, east of Treuenbrietzen, Frohnsdorf, Plot F6, 12.918541 E, 52.042959 N, 95 m asl., *Quercus*-plantation with *Populus*-succession on fire site (fire in summer of 2018) on former *Pinus sylvestris* forest, on and between post fire moss *Ceratodon purpureus* causing its dieback, 18th of November 2020, leg. A. Schaepe, W. Linder.

20201118-FF39 – Germany, east of Treuenbrietzen, Frohnsdorf, Site F, 12.917358 E, 52.042550 N, 95 m asl., *Quercus*-plantation with *Populus*-succession on fire site (fire in summer of 2018) on former *Pinus sylvestris* forest, on and between post fire mosses *Ceratodon purpureus* and *Funaria hygrometrica* causing their dieback, 18th of November 2020, leg. A. Schaepe, W. Linder.

20201119-D126 – Germany, east of Treuenbrietzen, Frohnsdorf, Plot D1, 12.916197 E, 52.040119 N, 95 m asl., *Populus*-succession on fire site (fire in summer of 2018) on former *Pinus sylvestris* forest, on and between post fire moss *Ceratodon purpureus* causing its dieback, 19th of November 2020, leg. P. Mohr, N. Scharnofski.

20230328-KF27 – Germany, east of Treuenbrietzen, Frohnsdorf, 12.914158 E, 52.037606 N, 95 m asl., *Populus*-succession on fire site (after two fires, 2018 & 2022) on former *Pinus sylvestris* forest, on and between post fire mosses *Ceratodon purpureus* and *Funaria hygrometrica* causing their dieback, 28th of March 2023, leg. R. Jarling, J. Ehrich.

Discussion

Arrhenia-species are either obligatory bryophiles, e.g., *A. retiruga* and *A. lobata*, others are lichenophiles, e.g., *A. peltigerina*, still others are not strictly moss-bound at all, such as species of the *acerosa*-complex (Voitk et al. 2020, 2022). Recently, Voitk et al. (2022) have shown that the species diversity of sphagnophilous *Arrhenia* is much greater than originally thought and that some are obligate and others facultative sphagnophiles, i.e., *A. bigelowii*, *A. gerardiana*, *A. telmatiaea*, and *A. philonotis*, respectively. *A. bryophthora* appears to be closely associated with *Ceratodon purpureus* and possibly *Funaria hygrometrica*, both dioicous mosses common on recent to old burnt areas. However, unlike the sphagnophilous and most other moss-dwelling *Arrhenia*, *A. bryophthora* causes a necrosis on its host and must therefore be considered a true parasite (Voitk et al. 2022). To our knowledge, a similarly destructive lifestyle is only known from the lichenophilic *A. peltigerina* (Diederich et al. 2022), which is macroscopically similar, but microscopically distinct by the presence of clamp connections and phylogenetically related to species of the *auriscalpium/spathulata* complex (Voitk et al. 2020).

Morphologically similar applies to *A. velutipes*, but this species has a faint odor of pelargonium, abundant clamp connections in all tissues and also differs in its molecular data (Bas et al. 1995; Vesterholt 2012). *Arrhenia obatra* and *Arrhenia obscura* can be macroscopically confused with *A. bryophthora*, as well, but both bare clamp connections (Bas et al. 1995; Vesterholt 2012).

Specimens of *Arrhenia bryophthora* were so abundant in late autumn, winter and early spring after the fire in all the areas studied (sometimes with hundreds of fruiting bodies on a few square meters) that it seems incredible to us that this species is not found in the literature (Moser 1983; Bas et al. 1995; Ludwig 2001; Vesterholt 2012). Ludwig (2001) mentioned in his comment on *Omphalina velutina* (=*Lichenomphalia velutina*) that it can occur after fires. Unfortunately, it is not clear where this information comes from. However, that species belongs to another linage of omphalinoid agarics that are lichenized (Redhead et al. 2002b). Vesterholt (2012) remarks on *A. velutipes* that it can also occur on old fire places. It is noteworthy that these two species can have a distinct pubescent stipe, as we have seen in many young specimens of *A. bryophthora*. Therefore, we believe that confusion with *A. velutipes* or *L. velutina* may have occurred in the past.

In the phylogenetic tree based on ITS and LSU sequences (Fig. 1), all specimens of *A. bryophthora* group in the same moderately supported clade that is the most basal one of all sequences assigned to *Arrhenia* specimens. Considering the phylogenetic results presented in Fig. 1 and in the literature (Voitk et al. 2020, 2022; Zhang et al. 2022) and the fact that the current understanding of the genus *Arrhenia* includes species with facultative and obligate bryophilous, lichenophilous, and saprotrophic lifestyles as well as cyphelloid, pleurotoid, and omphalinoid habitus; it is plausible that this taxonomic group should be revised and studied in more detail in the future. This includes careful morphological and phylogenetic studies based on multi-locus sequencing and comprehensive sampling. Thus, we believe that *Arrhenia* s.l. will be split into further genera and consequently, *A. bryophthora* will be recombined into another, perhaps new, genus. However, in view of the critical discussions on the establishment of new genera (Vellinga et al. 2015), we consider it best not to establish a new monospecific genus for *A. bryophthora* at this point, but to include it in the current understanding of *Arrhenia* s.l.

Bryopistillaria clavarioides has been confused with *Clavaria tenuipes* Berk. & Broome in the past. That fact is caused by a description of *C. tenuipes* by Rea (1922), which was later accepted by Corner (1950). Rea was the first who included old charcoal heaps in the substrate range of *C. tenuipes*. This obviously wrong information was later adopted in keys to the genus *Clavaria*, even until recent times (Pilát 1958; Jülich 1984; Knudsen et al. 2012;). Schild (1981) described clavarioid specimens growing on recently burnt sites, but was convinced that these were related to another collection that came from a flowerpot in the garden of the Geobotanical Institute of ETH Zurich (Switzerland). Therefore, he concurred with Corner's opinion on *C. tenuipes* and grouped all these specimens under this taxon. Kajan (1986) and Kajan and Grauwinkel (1987) were the first to recognize that *C. tenuipes* Berk. & Broome and clavarioid specimens growing on recently burnt sites are not conspecific. They, however, incorrectly applied the taxon *C. tenuipes* to specimens growing exclusively on burnt sites (=*B. clavarioides*), and in turn established a new taxon, namely, *C. krieglsteineri*, for non-phoenicoid specimens.

Apart from the divergent ecology, the macroscopic description of *C. tenuipes* Berk. & Broome does not seem to correspond to *B. clavarioides*. Features like the pale clay-color and the up to 7 mm swollen head rather suggest a relation to *C. daulnoyae* Quel., or alike. In view of this and the fact that the type specimen is in poor condition (Schild 1981), we leave the clarification of what is to be understood as *C. tenuipes* to further studies.

All specimens of *B. clavarioides* discussed in this publication grew near or among the common fire mosses *Funaria hygrometrica* or *Ceratodon purpureus*. The same applies to the specimens presented in Kajan and Grauwinkel (1987). According to these authors, *B. clavarioides* is not uncommon on burnt areas in the spring and autumn after a fire up to 2.5 years. At this point, it must be noted that although the clubs grew along and between *Funaria*, the moss always appeared healthy and fresh, without any necrosis (which neither we nor other authors have observed before). However, we could observe the dieback of *Ceratodon purpureus* growing in the vicinity of *B. clavarioides*. Whether this was actually caused by the *Bryopistillaria* is not clear to us.

Bryophily is common among members of the *Rickenellaceae*. *Muscinupta laevis* and *Bryopistillaria sagittiformis* grow biotrophically on mosses, but it is still controversial whether they also live facultatively saprotrophically (Olariaga et al. 2020). *Rickenella* spp., *Loreleia* spp., and *Blasiphalia pseudogrisella* (=*R. pseudogrisella*) and *Cantharellopsis prescotii* are strictly associated with various mosses and therefore cannot be found separately from their partner. Dentinger and McLaughlin (2006) who erected *Alloclavaria* as the first clavarioid taxon within the *Hymenochaetaceae*[1] suggested to test whether *A. purpurea* is bryophilic, because it is frequently found among mosses. However, later results suggested that it represents a new linage of ectomycorrhizal fungi within the *Hymenochaetales* (Korotkin et al. 2018). The authors of the latter study also pointed out that *L. marchantiae* or *Blasiphalia pseudogrisella*, *Muscinputa laevis*, and *Rickenella swartzii* belong to the same ectomycorrhizal (ECM) cluster and can thus be classified as ECM or rather ECM-like. They specifically ruled out a parasitic lifestyle, but mentioned that a possible commensalism should not be dismissed unless the benefit to the fitness of their bryophytic partners will have been proven (Korotkin et al. 2018). Especially on our plots studied, we can exclude true ECM because most of the plant partners, i.e., *Pinus sylvestris* and *Betula pendula*, died in the fires, and other potential partners were missing. Therefore, a commensal (bryophilic) or even bryotrophic lifestyle of *B. clavarioides* is plausible.

Some representatives of the *Rickenellaceae* have hymenial cystidia or setae (*Rickenella*/*Alloclavaria* etc.); others do not (*Muscinupta laevis*, *B. sagittiformis*). Thus, it is not surprising that *B. clavarioides* has no cystidia, although it is assigned to the *Hymenochaetales*.

It is interesting that the spores of *B. clavarioides* often stick together in clusters (tetrads or more), which was also observed for *Bryopistillaria sagittiformis* (Olariaga et al. 2020) and *Rickenella* spp. (Ludwig 2001). Furthermore, it is remarkable that the latter author mentioned a high variability in spore size of *R. swartzii*, a fact that also applies to *B. clavarioides*.

[1] Note: later proposed by Vizzini (2010) to be placed in the *Rickenellaceae.*

Looking at the macro-morphology of *B. clavarioides* and *B. sagittiformis*, it is strange at first to place them in the same genus. While the club-shaped basidiocarps of *B. sagittiformis* are only up to 1.2 mm in size (Olariaga et al. 2020), *B. clavarioides* can form clubs that are up to 30 times larger. However, despite some little differences, their microscopic features match well; the spores are about of same size and lack an iodine reaction in both species (Olariaga et al. 2020). The RaxML-tree based on ITS and LSU loci (Fig. 2), the sequences of *B. clavarioides* and *B. sagittiformis* form a strongly supported clade. *B. sagittiformis* is biotrophic in/on various mosses and additionally can follow a saprotrophic lifestyle (Olariaga et al. 2020). The fact that *B. clavarioides* seems specific to its hosts, on the other hand, argues for a separate genus. Nevertheless, based on the available data, we do not consider it advisable to establish a new genus in this case and therefore follow the recommendation of Vellinga et al. (2015).

Finally, one question remains to be answered regarding the ecology of the two fungal species discussed here. Both are obviously associated with the mosses *Ceratodon purpureus* and/or *Funaria hygrometrica*. The mosses, for their part, prefer to grow on older burnt areas, but can also thrive outside former forest fire sites (fire-disturbed habitats). However, it has never been observed that the fungi were associated with the mosses when were no such sites. This phenomenon is remarkable and should be studied in more detail in the future.

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Data Availability Alignements available at figshare https://doi.org/10.6084/m9.figshare.24763770 and https://doi.org/10.6084/m9.figshare.25249969.

Declarations

Competing interests The authors declare no competing interests.

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