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Revision of *Kneiffiella* with segregation of *Egonia* gen. nov. (*Hymenochaetales*, *Agaricomycetes*): how similar morphology can hide taxonomic diversity in the molecular era

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Key words

Hyphodontia
multi-gene-based phylogeny
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13 new species

Abstract DNA-based phylogenetic inference has shown that many morphological traits, once considered taxonomically relevant, are the result of convergent evolution. In this study, we analyze *Kneiffiella*, a genus of corticioid and polyporoid wood-inhabiting basidiomycetes in the order *Hymenochaetales*. A multi-gene-based phylogeny demonstrates that *Kneiffiella* is polyphyletic, and the new genus *Egonia* is established for *K. cineracea* and its relatives, despite their morphological similarity to other *Kneiffiella* species. Additionally, we present the best resolved phylogram of the *Hymenochaetales* to date. A revised circumscription of *Kneiffiella* is presented, as well as an overview of the 29 species accepted in the genus, including 10 new species. Three new species of *Egonia* are described, and *H. subefibulata* is placed in synonymy with *K. subglobosa*. A key to the species of *Kneiffiella* and *Egonia* is presented.

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INTRODUCTION

Recent molecular data has challenged fungal taxonomy that is based traditionally on morphology, revealing that traits once considered taxonomically important, such as basidiocarp habit and hymenophore configuration, are the result of convergent evolution. Nevertheless, many taxonomic groups characterized solely on morphology have survived. Example of such a group is Patouillard's (1900) *Série des Igniaries*, proposed for genera of basidiomycetes with prominent brown basidiocarps and unique cystidial elements called setae. This group of polyporoid and corticioid fungi is currently recognized as the family *Hymenochaetaceae*, which constitutes the core of the order *Hymenochaetales*. The rest of the order is composed of genera with different morphologies and trophic modes (summarized in Larsson (2007)); most were proposed before the introduction of molecular methods. Efforts to organize these traditional genera into natural families are ongoing and challenging because unrelated but morphologically similar species are often included together in the same genus. One such example is *Hyphodontia* s.lat., as conceived, a groups of light-coloured corticioid fungi.

Despite being readily recognizable due to characteristic hyphal features, basidial morphology, and other microscopic characters, *Hyphodontia* s.lat. include species with varied cystidial morphologies. Early studies of *Hyphodontia* by Parmasto (1968) and Langer (1994) placed particular emphasis on the cystidia. Continuing in the same mode, Hjortstam & Ryvarden (2002, 2007, 2009) and Hjortstam et al. (2005) elevated Parmasto's sections to generic rank and reintroduced a number of older genera previously synonymized with *Hyphodontia* s.lat. Thus, *Hyphodontia* s.lat. species were segregated into smaller, morphologically uniform genera such as *Kneiffiella*, *Lyomyces*, and *Xylodon*.

At approximately the same time, Langer (2002) and Larsson et al. (2006) demonstrated by molecular evidence that *Hyphodontia* s.lat. is polyphyletic. Their results favored the division of *Hyphodontia* s.lat. into these morphologically characterized genera with some exceptions such as *Lagarobasidium* (see Viner et al. 2018, 2023). Among the *Hyphodontia* segregates, only the compact *Hyphodontia* s.str., with lagenocystidia, appeared to have a consistent kind of cystidial elements.

Kneiffiella was resurrected by Hjortstam & Ryvarden (2002) to accommodate corticioid species with characteristic thick-walled cystidia arising from the subiculum (i.e., tubular cystidia). Although subsequent DNA-based studies (Riebesehl & Langer 2017, Yurchenko et al. 2020) showed that three genera with thin-walled cystidia: *Alutaceodontia*, *Chaetoporellus*, and *Deviodontia* were synonyms of *Kneiffiella*, the current concept of the core of *Kneiffiella*, characterized by tubular cystidia, remains unchallenged. Given that similarly shaped cystidia are found in at least two other genera of the *Hymenochaetales*, *Tubulicrinis* (e.g., *T. angustus*) and *Xylodon* (e.g., *X. ussuriensis*), there is a need for revision of the systematics of the core *Kneiffiella*.

This study was prompted by DNA sequences from fresh material of *K. cineracea* s.str. with tubular cystidia. Initial analysis of its LSU locus placed it far from published sequences labeled as *K. cineracea* and other *Kneiffiella* species. Surprisingly, the closest hits to our new sequences of *K. cineracea* were

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taxa in the *Trichaptum* clade, an assemblage of polypore and corticioid genera, some of which have been assigned to the families *Neoantrodiellaceae* and *Nigrofomitaceae*. Our sequences of *Jacksonomyces phlebioides*, the generic type of *Jacksonomyces*, and *J. subulatus* were also among the close hits. To resolve these findings, we created a comprehensive *Hymenochaetales* dataset that includes long stretches of four unlinked loci: mtSSU, *RPB1*, *RPB2*, and *EF-1α* into a concatenated dataset. This dataset includes *Kneiffiella* s.lat. with both tubular and thin-walled cystidia and all major clades of the *Hymenochaetales*. Based on our results, we establish a new genus, *Egonia*, describe 13 new species, propose one new combination, and relegate one species to synonymy. A key to the 29 species of *Kneifiella* and four of *Egonia* (as accepted on 2 Feb. 2024) is presented

MATERIAL AND METHODS

Morphological study

Type specimens and other collections from herbaria BJFC, BLS, BO, BPI, CFMR, DAOM, GB, H, KAS, O, PC, S, SNP, TAA, TUF, UBC, and UPS were studied. Herbarium acronyms are given according to Thiers (continuously updated). Microscopic methods were described in Miettinen et al. (2006). All measurements were made in Cotton Blue (CB, Merck 1275; Kenilworth, New Jersey) with phase contrast illumination (1250×), whose benefits over bright-field microscopy are explained in Stein (1969). The following abbreviations were used in microscopic descriptions: L – mean spore length; W – mean spore width; Q – mean L/W ratio; n – number of elements (basidiospores, basidia, cystidia, and hyphae) measured. We excluded 5 % of measurements from each end of the range representing variation of basidia, basidiospores, conidia, conidiophores, and 20 % for cystidia. Excluded extreme values were indicated in parentheses when they strongly differed from the lower or higher 95 % percentile. Hyphae in the focal group are typically so variable that the 5 % tails were not informative so we reported their full range.

DNA isolation and sequencing

For protocols of DNA extraction, PCR, and sequencing of the target loci see Viner et al. (2021a) and references therein. In this study, we used standard primers to amplify complete nuc rDNA ITS1-5.8S-ITS2 (ITS) and LSU (Table 1). Deciphering and assembling of chromatograms was performed as described in Viner et al. (2021b). Additional sequences (including all mtSSU, *RPB1*, *RPB2*, and *EF-1α* loci) used in the analyses were retrieved from partial genomes as described in Spirin et al. (2022). All newly produced sequences of acceptable quality (even if not utilized in the phylogenetic analyses) have been deposited in GenBank (Table 2).

Taxon sampling for phylogenetic analyses

In addition to our newly produced data, we retrieved relevant sequences from GenBank (Benson et al. 2018) and UNITE (Kõljalg et al. 2013). We also used published (Korotkin et al. 2018) and unpublished genomes (with the permission of the rightful holders) from the Fungal Genomics Resource (https://mycocosm.jgi.doe.gov) and GenBank as of 17 January 2023 (Table 3). Alignments were calculated through the MAFFT 7.429 online server (https://mafft.cbrc.jp/alignment/server/) using the L-INS-I strategy (Katoh et al. 2017). They were then manually adjusted in the fragments where the machine-derived alignment clearly violated homology principles. The resulting alignments after removing unalignable fragments are summarized in Table 4.

To determine the proper generic placement for the *Kneiffiella* taxa studied, we constructed a comprehensive order-level dataset, utilizing 5 unlinked DNA loci (LSU, mtSSU, *RPB1*, *RPB2*, and *EF-1α*). We conducted independent analyses of these loci to corroborate the complementarity of the datasets. Except for the LSU locus, all well-supported clades of the resulting topologies (not shown here) were resolved similarly or left unresolved depending on the locus. The deviance of the LSU locus was particularly pronounced in *Coltricia* and to a greater extent in *Kurtia*. The latter situation has already been reported by Kolařík & Vohník (2018). Conveniently, the use of relatively extensive fragments of mtSSU, *RPB1*, *RPB2*, and *EF-1α* in the concatenated dataset yielded phylogenetic signal sufficient to produce a fairly resolved *Hymenochaetales* tree, even without the LSU locus. Therefore, we omitted the LSU locus from the multigene dataset. The outgroup taxa (*Phlebia subcretacea* and *Xenasmatella tulasnelloidea*) were chosen according to the Joint Genome Institute's MycoCosm genome tree (https://mycocosm.jgi.doe.gov/mycocosm/species-tree/tree;YCJTN5?organism=basidiomycota).

The ITS variability in the newly proposed genus *Egonia* is suitable for constructing a reliable all-inclusive alignment without violating phylogenetic homology principles. Conversely, we found the ITS locus in the *Kneiffiella* clade to be overly variable so we discarded poorly aligned fragments in ITS1 and ITS2, which resulted in a loss of phylogenetic signal. To overcome this, we supplemented the shortened ITS fragments with a fragment of LSU that includes domains D1–D3. For certain focal species, namely *K. subefibulata*, *K. perlongispora*, and *K. trichophora*, an LSU sequence was not available. Therefore, we utilized reliably aligned ITS datasets to provide phylogenetic resolution for the corresponding *Kneiffiella* clades. Additionally, this approach enabled us to make full use of available ITS data from public databases and provided better phylogenetic context for species grouped around *K. subalutacea*, *K. alutacea*, and *K. subglobosa* (all datasets are listed in Table 4). The outgroups were selected based on the highest pairwise similarity to the focal clades to sequences in public databases. The full alignments

Table 1 Primers used in this study.

Primer name	Sequence	Target DNA locus	Binding site	Direction	Reference
ITS5	GGAAGTAAAAGTCGTAACAAGG	ITS, ITS1	18S	fwd	White et al. 1990
ITS2	GCTGCGTTCTTCATCGATGC	ITS1	5.8S	rev	White et al. 1990
ITS3	GCATCGATGAAGAACGCAGC	ITS2	5.8S	fwd	White et al. 1990
ITS4	TCCTCCGCTTATTGATATGC	ITS, ITS2	28S	rev	White et al. 1990
LR22	CCTCACGGTACTTGTTCGCT	ITS	28S	rev	Vilgalys lab, Duke University (https://sites.duke.edu/vilgalyslab/files/2017/08/rDNA-primers-for-fungi.pdf)
JS1	CGCTGAACTTAAGCATAT	28S	28S	fwd	Landvik 1996
LR7	TACTACCACCAAGATCT	28S	28S	rev	Hopple & Vilgalys 1994
LR5	TCCTGAGGGAAACTTCG	28S	28S	rev	Hopple & Vilgalys 1994

Table 2 GenBank accession numbers for DNA loci of specimens sequenced in this study.

Species	Specimen	ITS	28S	12S	*rpb1*	*rpb2*	*tef1*
Alloclavaria purpurea	*Miettinen* 18831	ON188807	ON188807	ON228494	**OQ776825**	**OQ776864**	**OQ776787**
Asterodon ferruginosum	*Hakala* T192i	–	–	**OQ831465**	**OQ776826**	**OQ776865**	**OQ776788**
Basidioradulum radula	*Miettinen* 16070	–	–	**OQ831466**	**OQ776827**	MT333824	MT333807
Coltricia insularis	*Miettinen* 22083	–	–	**OQ831467**	**OQ776828**	**OQ776866**	**OQ776789**
Coltricia sp.	*Miettinen* 17670	–	–	**OQ831468**	**OQ776829**	**OQ776867**	**OQ776790**
Cyanotrama gypsea	*Miettinen* 10640	–	–	**OQ831476**	**OQ776851**	**OQ776889**	**OQ776812**
Egonia cineracea	*Miettinen* 11988.2	**OQ913419**	–	**OQ831469**	**OQ776830**	**OQ776868**	**OQ776791**
	Hjorstam 19108	**OQ913417**	**OQ913417**	–	–	–	–
	Larsson 13593	**OQ913418**	**OQ913418**	–	–	–	–
	Larsson 17236	**OQ913420**	**OQ913420**	–	–	–	–
	Spirin 14490	**OQ913421**	**OQ913421**	–	–	–	–
	Spirin 7886	**OQ913422**	–	–	–	–	–
Egonia heremita	*Spirin* 7547	**OQ913425**	**OQ913425**	–	–	–	–
	Spirin 9225	**OQ913426**	–	–	–	–	–
	Spirin 9240	**OQ913427**	–	–	–	–	–
	Spirin 9243	**OQ913430**	–	–	–	–	–
Egonia occidentalis	*Spirin* 8452	**OQ913423**	**OQ913423**	**OQ831470**	**OQ776831**	**OQ776869**	**OQ776792**
	Spirin 8486	**OQ913424**	**OQ913424**	–	–	–	–
Egonia turgida	*Miettinen* 24509.1	**OQ913428**	**OQ913428**	–	–	–	–
	Viner 2019_183	**OQ913429**	**OQ913429**	–	–	–	–
	Viner 2019_234	**OQ913430**	**OQ913430**	–	–	–	–
Fasciodontia bugellensis	*Larsson* 13832	OK273855	OK273855	ON228480	**OQ776832**	**OQ776870**	**OQ776793**
Fibricium rude	*Hakala* T231i	–	–	**OQ831471**	**OQ776833**	**OQ776871**	**OQ776794**
Hastodontia halonata	Finn Oldervik	ON188810	ON188810	ON228482	**OQ776834**	**OQ776872**	**OQ776795**
Hastodontia hastata	*Larsson* 14646	MH638232	MH638232	ON228492	**OQ776835**	**OQ776873**	**OQ776796**
Hyphodontia alutaria	*Miettinen* 13500.2	ON188811	ON188811	ON228488	**OQ776836**	**OQ776874**	**OQ776797**
Hyphodontia subdetritica	*Savchenko* TU114869	OP620786	OP620786	OP620780	**OQ776837**	**OQ776875**	**OQ776798**
Jacksonomyces subulatus	*Miettinen* 22811	–	–	**OQ831472**	**OQ776838**	**OQ776876**	**OQ776799**
Kneiffiella abdita	*Miettinen* 22165	ON188809	ON188809	ON228493	**OQ776839**	**OQ776877**	**OQ776800**
Kneiffiella abieticola	*Miettinen* 24321.1	**OQ913431**	**OQ913431**	–	–	–	–
Kneiffiella aff. *alutacea*	*Spirin* 5643	**OQ913459**	–	–	–	–	–
	Kotiranta 26191	**OQ913460**	–	–	–	–	–
Kneiffiella aff. *eucalypticola*	*Spirin* 8039	**OQ913434**	**OQ913434**	–	–	–	–
Kneiffiella aff. *frondosarum*	*Spirin* 5694	**OQ913435**	–	–	–	–	–
Kneiffiella aff. *tetraspora*	*Miettinen* 14344	**OQ913448**	**OQ913448**	**OQ831474**	**OQ776846**	**OQ776884**	**OQ776807**
Kneiffiella alienata	*Miettinen* 22764	**OQ913449**	**OQ913449**	–	–	–	–
	Viner 2021_13	**OQ913450**	**OQ913450**	–	–	–	–
	Miettinen 17319	**OQ913466**	–	–	–	–	–
Kneiffiella alutacea	*Miettinen* 21701	ON188808	ON188808	ON228491	**OQ776840**	**OQ776878**	**OQ776801**
Kneiffiella amplipora	*Miettinen* 16323	**OQ913458**	**OQ913458**	–	–	–	–
Kneiffiella barba-jovis	*Spirin* 10622	ON188812	ON188812	ON228489	**OQ776841**	**OQ776879**	**OQ776802**
Kneiffiella conidiophora	*Spirin* 14670	**OQ913461**	**OQ913461**	–	–	–	–
	Spirin 15680	**OQ913462**	–	–	–	–	–
Kneiffiella curvispora	*Pennanen* 4040	OP620787	OP620787	OP620781	**OQ776842**	**OQ776880**	**OQ776803**
Kneiffiella efibulata	*Kotiranta* 23202	**OQ913432**	**OQ913432**	–	–	–	–
Kneiffiella fabiformis	*Miettinen* 18884	**OQ913451**	**OQ913451**	**OQ831473**	**OQ776843**	**OQ776881**	**OQ776804**
Kneiffiella floccosa	*Spirin* 10728	**OQ913433**	**OQ913433**	–	–	–	–
Kneiffiella frondosarum	*Miettinen* 15378	**OQ913436**	–	–	–	–	–
	Miettinen 17175.1	**OQ913437**	–	–	–	–	–
	Miettinen 22674	**OQ913438**	**OQ913438**	–	–	–	–
	Miettinen 24523	**OQ913439**	–	–	–	–	–
	Spirin 15752	**OQ913440**	**OQ913440**	–	–	–	–
Kneiffiella macra	*Miettinen* 16455	**OQ913455**	**OQ913455**	–	–	–	–
Kneiffiella microspora	*Miettinen* 11418	OP620788	OP620788	OP620782	**OQ776844**	**OQ776882**	**OQ776805**
Kneiffiella ornamentata	*Miettinen* 16379	**OQ913452**	**OQ913452**	–	–	–	–
Kneiffiella pilaecystidiata	*Helo* 1517	OP620789	OP620789	OP620783	**OQ776845**	**OQ776883**	**OQ776806**
Kneiffiella similis	*Spirin* 8141	**OQ913453**	**OQ913453**	–	–	–	–
	Spirin 8315	**OQ913454**	**OQ913454**	–	–	–	–
Kneiffiella subaltaica	*Miettinen* 15592.2	**OQ913465**	–	–	–	–	–
Kneiffiella subalutacea	*Kokaeva* LYK2021_23	**OQ913441**	–	–	–	–	–
	Spirin 12575	**OQ913442**	**OQ913442**	–	–	–	–
	Spirin 16280	**OQ913443**	**OQ913443**	–	–	–	–
	Spirin 8759	**OQ913444**	–	–	–	–	–
	Spirin 8752a	**OQ913445**	–	–	–	–	–
	Spirin 7727	**OQ913446**	–	–	–	–	–
Kneiffiella subglobosa	*Miettinen* 23605	**OQ913447**	**OQ913447**	–	–	–	–
Kneiffiella thermophila	*Miettinen* 10251.1	**OQ913456**	**OQ913456**	–	–	–	–
	Miettinen 11424b	**OQ913457**	**OQ913457**	–	–	–	–
	Miettinen 10313.2	**OQ913464**	–	–	–	–	–
Kneiffiella trichophora	*Ryvarden* 12735	**OQ913463**	–	–	–	–	–

Table 2 (cont.)

Species	Specimen	ITS	28S	12S	*rpb1*	*rpb2*	*tef1*
Lawrynomyces etruriae	*Antunes* LISU254474	–	–	**OQ831475**	**OQ776847**	**OQ776885**	**OQ776808**
Lyomyces crustosus	*Spirin* 12630	OK273832	OK273832	ON228478	**OQ776848**	**OQ776886**	**OQ776809**
Lyomyces pruni	*Spirin* 12682	OK273833	OK273833	ON228483	**OQ776849**	**OQ776887**	**OQ776810**
Lyomyces sambuci	*Miettinen* 11705	OK273852	OK273852	ON228487	**OQ776850**	**OQ776888**	**OQ776811**
Oxyporus populinus	L-11146	–	–	**OQ831477**	**OQ776852**	**OQ776890**	**OQ776813**
Peneophorella martinii	*Miettinen* 22048	–	–	**OQ831478**	**OQ776853**	**OQ776891**	**OQ776814**
Peniophorella tsugae	*Spirin* 12469	–	–	**OQ831479**	**OQ776854**	**OQ776892**	**OQ776815**
Poriodontia subvinosa	*Miettinen* 10493.1	–	–	**OQ831480**	**OQ776855**	**OQ776893**	**OQ776816**
Schizocorticium sp.	*Miettinen* 17849.1	–	–	**OQ831481**	**OQ776856**	**OQ776894**	**OQ776817**
Trichaptum durum	*Miettinen* 14249	–	–	**OQ831482**	**OQ776857**	**OQ776895**	**OQ776818**
Trichaptum laricinum	*Hottola* 4100	–	–	**OQ831483**	**OQ776858**	**OQ776896**	**OQ776819**
Tsugacorticium kenaicum	*Burdsall* 17333	–	–	**OQ831484**	**OQ776859**	**OQ776897**	**OQ776820**
Tubulicrinis borealis	*Miettinen* 20469.2	–	–	**OQ831485**	**OQ776860**	**OQ776898**	**OQ776821**
Tubulicrinis chaetophorus	*Spirin* 12616	ON188814	ON188814	ON228495	**OQ776861**	**OQ776899**	**OQ776822**
Xylodon paradoxus	*Oivanen* PO109	–	–	ON228474	**OQ776862**	**OQ776900**	**OQ776823**
Xylodon quercinus	*Spirin* 12030	OK273841	OK273841	ON228469	**OQ776863**	**OQ776901**	**OQ776824**

* New sequences are in **bold**.

Table 3 Genomic assemblages used as the source of 12S, *rpb1*, *rpb2*, and *tef1* for the order-level phylogenetic analyses.

Species	Specimen	Source
Coniferiporia weirii	FP-133613	GenBank
Fuscoporia viticola	PhevitSig-SM15	Fungal Genomics Resource
Kurtia argillacea	*Miettinen* 21477	Fungal Genomics Resource
Onnia scaura	P-53A	Fungal Genomics Resource
Phellinidium ferrugineofuscum	SpK3Phefer14	Fungal Genomics Resource
Phellinidium pouzarii	DSM 108285	GenBank
Phellinus igniarius	CCBS 575	Fungal Genomics Resource
Phlebia subcretacea	*Miettinen* 11972.1	Fungal Genomics Resource
Porodaedalea pini	BCRC 35384	GenBank
Pyrrhoderma lamaoense	FFPRI 411162	GenBank
Pyrrhoderma noxium	KPN91	GenBank
Resinicium bicolor	*Miettinen* 11775.1	Fungal Genomics Resource
Rickenella fibula	*Korotkin* 330	Fungal Genomics Resource
Rickenella mellea	SZMC22713	Fungal Genomics Resource
Rigidoporus microporus	ED310	GenBank
Sanghuangporus vaninii	CFCC81183	GenBank
Sidera vulgaris	*Miettinen* 21893	Fungal Genomics Resource
Xenasmatella tulasnelloidea	*Miettinen* 20453	Fungal Genomics Resource
Xylodon ovisporus	KUC8140	Fungal Genomics Resource

Table 4 Summary of DNA sequence alignments used in the analyses.

Dataset	12S + rpb1 + rpb2 + tef1 *Hymenochaetales*	ITS + LSU *Kneiffiella*	ITS *K. alutaceodontia*	ITS *K. subalutacea*	ITS *K. subglobosa*	ITS *Egonia*
Specimens (alignment rows)	62	43	17	45	11	17
Length of the original allignment	11052	2587	2380	2338	2151	2394
Length of the allignment after editing	5351	1100	509	507	580	672
Parsimony informative characters	2714	252	77	91	93	176
ITS model		GTR + G + I	HKY + G	HKY + G	HKY	HKY + G
LSU model		GTR + G + I				
12S model	GTR + G + I					
rpb1 model intron	SYM + G					
rpb1 model exon position 1–2	GTR + G + I					
rpb1 model exon position 3	SYM + G + I					
rpb2 model exon position 1–2	GTR + G + I					
rpb2 model exon position 3	GTR + G + I					
tef1 model exon position 1–2	HKY + G + I					
tef1 model exon position 3	SYM + G					

with annotation of the excluded characters were deposited at TreeBASE (TB2:S30827).

We inferred rooted phylogenetic trees with maximum likelihood (ML) and Bayesian Inference (BI). Nucleotide substitution models for BI (Table 4) were chosen with ModelTest-NG 0.2.0 (Darriba et al. 2020) based on the Bayesian information criterion (BIC). Altogether we set 8 partitions for the order-level alignment (mtSSU, *RPB1*, *RPB2*, and *EF-1α*). While mtSSU was treated as a separate partition, exons of the protein-coding genes were further divided into 1–2 vs 3 codon positions. All introns were discarded from further analyses except for a fragment of the long *RPB1* intron between conserved amino acid motifs A and B (as designated in Stiller & Hall (1997)). We performed BI using MrBayes 3.2 (Ronquist et al. 2012). In these analyses, three parallel runs with four chains each and other default parameters were run for one million generations. A burn-in of 25 % was used in the final analyses. The average standard deviation of split frequencies had reached < 0.01 for all data sets. When depicting phylograms, the support for nodes is indicated when posterior probabilities are ≥ 0.90. For ML analyses, IQ-TREE 1.2.2 (Nguyen et al. 2015) with the best-fitted model option was used. Bootstrapping was performed using the standard nonparametric bootstrap algorithm with the number of replicates set to 1 000. Support for nodes is indicated with bootstrap values ≥ 80.

RESULTS

Phylogenetic placement and limits of Kneiffiella

The results of both BI and ML analyses on the concatenated dataset of mtSSU, *RPB1*, *RPB2*, and *EF-1α* returned the same topology (Fig. 1), which was further confirmed by the concordant genomics-based *Hymenochaetales* tree available on the MycoCosm webpage (https://mycocosm.jgi.doe.gov/mycocosm/species-tree/tree;YCJTN5?organism=basidiomycota) as of 23 October 2023. *Kneiffiella* species were recovered in two distant clades within the *Hymenochaetales* with *K. cineracea* resolved distant from all other *Kneiffiella* species. This clade,

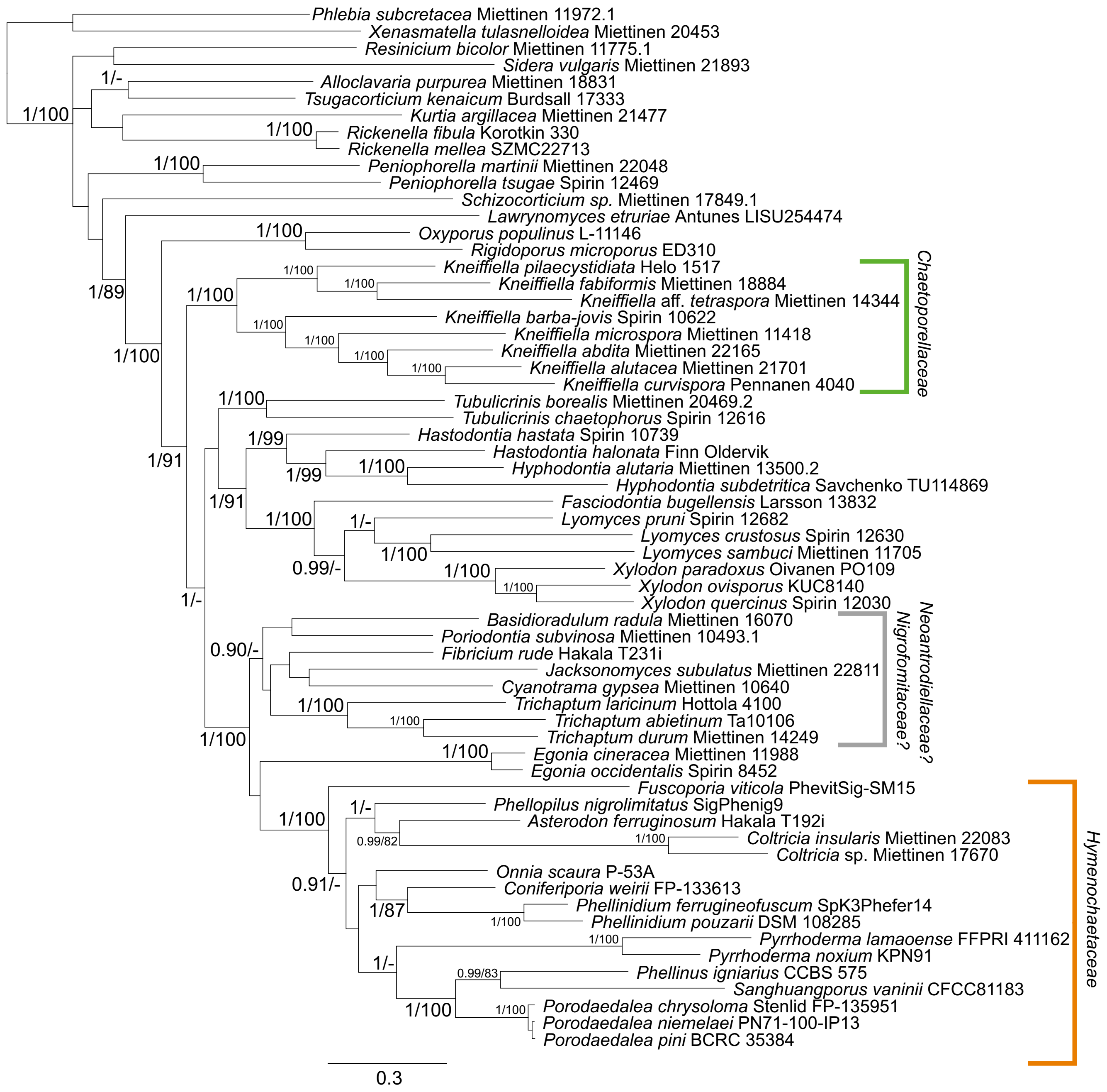

Fig. 1 Phylogenetic relationships of the *Hymenochaetales* inferred from the mtSSU + *RPB1* + *RPB2* + *EF-1α* concatenated dataset using BI analysis. Bayesian posterior probabilities followed by ML bootstrap values are shown at nodes; branch lengths reflect estimated number of changes per site.

called the *Egonia* clade henceforth, nested together with the *Hymenochaetaceae* and the *Trichaptum* clade. The other *Kneiffiella* species formed a monophyletic lineage referred to as the *Kneiffiella* clade. This clade includes the generic type of *Kneiffiella*, *K. barba-jovis*, along with *K. alutacea*, *K. abdita*, and *K. pilaecystidiata* – the generic types of *Alutaceodontia*, *Chaetoporellus*, and *Deviodontia*, respectively. *Kneiffiella* species with thick-walled tubular cystidia did not form a monophyletic clade; instead, on the tree, they were interspersed with clades representing species with thin-walled cystidia.

Phylogeny of the core Kneiffiella clade based on ITS + LSU dataset

The ITS+LSU-based phylogeny of the *Kneiffiella* clade (Fig. 2) was congruent to the multigene phylogeny in Fig. 1. The *Kneiffiella* clade was divided into two main subclades, both of which contained *Kneiffiella* species with thick-walled tubular cystidia and thin-walled cystidia. One of them formed a species-rich monophyletic clade that contained generic types of both *Chaetoporellus* and *Alutaceodontia*. Another species with thin-walled cystidia, *K. pilaecystidiata* clustered with *Kneiffiella* with tubular cystidia viz. two newly introduced species *K. ornamentata* and *K. fabiformis*, and *K.* aff. *tetraspora* and *K. alienata*. It is noteworthy that other easily definable morphological groupings of *Kneiffiella* were also found to be polyphyletic. For instance, all three simple-septate *Kneiffiella*, which were used in this analysis (*K.* aff. *tetraspora*, *K efibulata*, and *K. subglobosa*), ended up in different clades together with clamped species. *Kneiffiella* with polyporoid fruit bodies (e.g., *K. abdita*, *K. amplipora*, *K. macra*, and *K. thermophila*) were divided into three clades that were interspersed with taxa with corticioid hymenophores.

Reassessing the Kneiffiella subalutacea s.lat. clade based on ITS

Our ITS analyses resolved several highly supported clades (Fig. 3). These included *K. subalutacea* as well as newly proposed species: *K. frondosarum*, *K. perlongispora*, and *K. similis*. The *K. frondosarum* clade showed geographical structuring, with all Asian sequences (*Spirin* 5694, KUC20130726-11, and Zhou 20170816-9) confined to a single supported subclade.

Reassessing the Kneiffiella subglobosa clade based on ITS

The newly described *K. trichophora* was found to be clearly distinct from both *K. subglobosa* and *K. subefibulata* (Fig. 4).

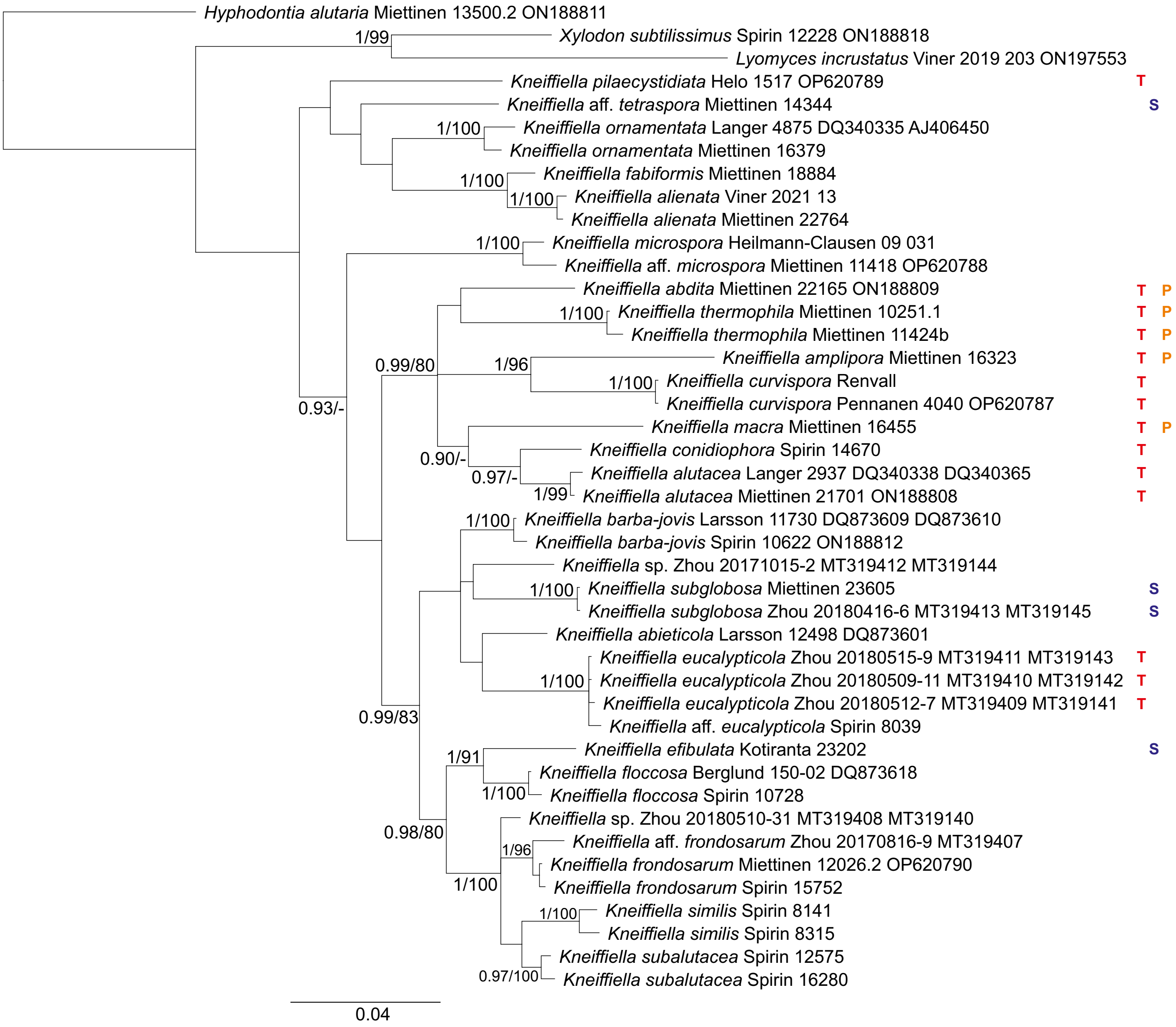

Fig. 2 Phylogenetic relationships of *Kneiffiella* inferred from the ITS + LSU dataset using BI analysis. Bayesian posterior probabilities followed by ML bootstrap values are shown at nodes; branch lengths reflect estimated number of changes per site. **P** indicates species with polyporoid basidiocarps, **S** indicates species with simple-septate hyphae, and **T** indicates species with thin-walled cystidia.

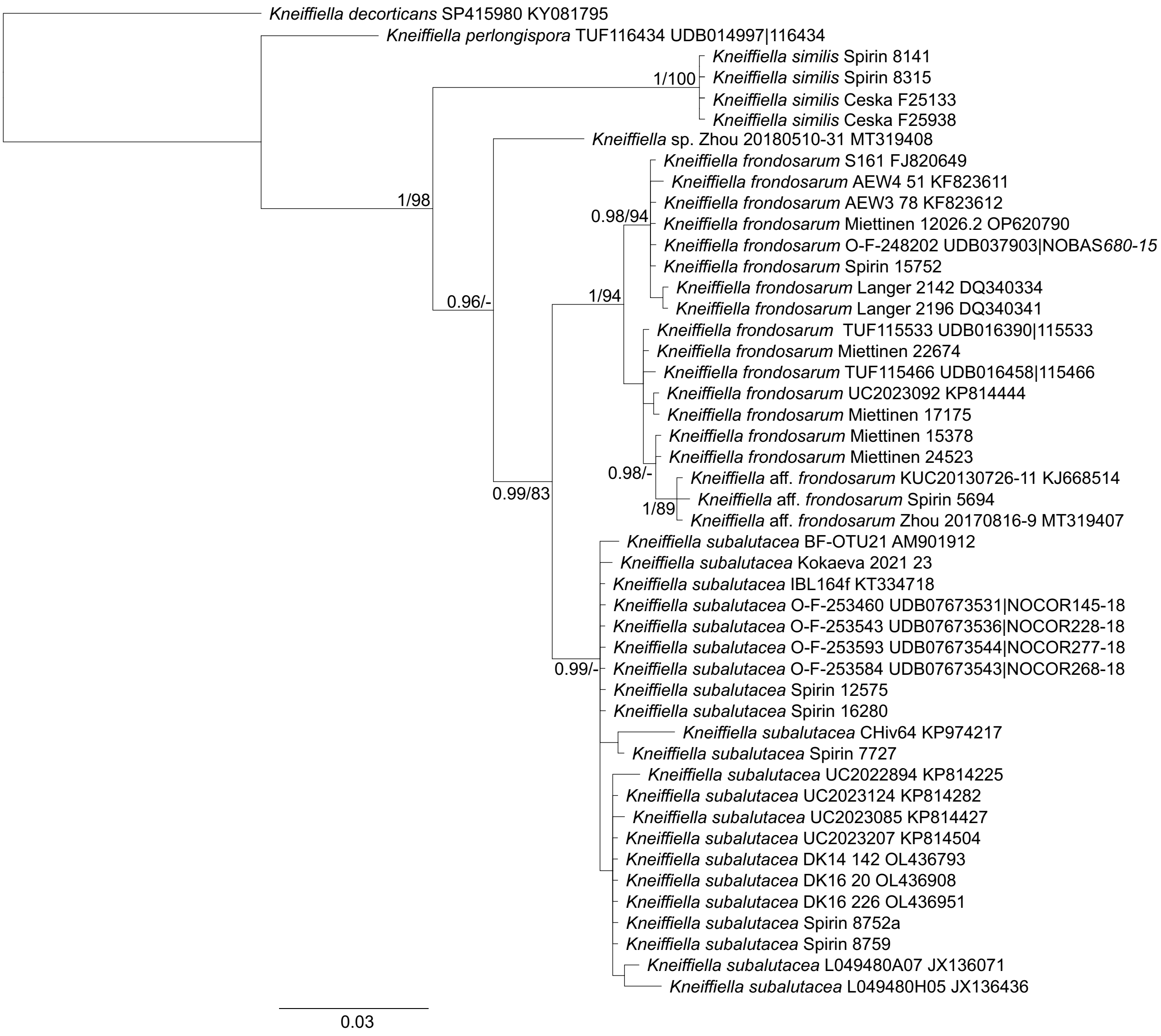

Fig. 3 Phylogenetic relationships of the *Kneiffiella subalutacea* clade inferred from the ITS dataset using BI analysis. Bayesian posterior probabilities followed by ML bootstrap values are shown at nodes; branch lengths reflect estimated number of changes per site.

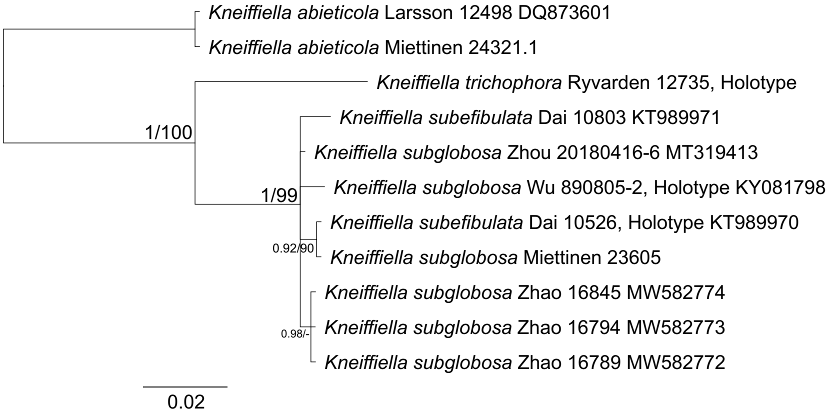

Fig. 4 Phylogenetic relationships of the *Kneiffiella subglobosa* clade inferred from the ITS dataset using BI analysis. Bayesian posterior probabilities followed by ML bootstrap values are shown at nodes; branch lengths reflect estimated number of changes per site.

However, the last two species were not resolved as monophyletic. The holotype and paratype of *K. subefibulata* were interspersed with sequences identified as *K. subglobosa*, including the holotype of the latter.

Reassessing the Alutaceodontia *clade based on ITS*

The ITS analyses resolved two highly supported clades corresponding to *K. alutacea* and *K. conidiophora* (Fig. 5). The *K. alutacea* clade consists of several subclades and suggests that this may represent a species complex since slight morphological differences among the subclades were observed (see notes under *K. alutacea* below).

Phylogeny of the Egonia clade based on ITS

Our ITS analyses identified four highly supported clades that correspond to *E. cineracea* and three newly proposed species, viz. *E. heremita*, *E. occidentalis*, and *E. turgida* (Fig. 6). We included in the analyses one environmental sequence from a Brazilian soil sample that could be credibly aligned with *Egonia* sequences. This sequence of aff. *Egonia* sp. resolved at the deepest split of the *Egonia* clade and appears to be a distinct taxon but lacks a physical voucher. In addition, sequences for more DNA loci are desirable to confirm its placement in *Egonia*.

Alternative taxonomic treatments of Kneiffiella s.lat.

We did not find any morphological features that unequivocally differentiate *K. cineracea* from other *Kneiffiella* with thick-walled tubular cystidia in the core *Kneiffiella* clade. However, we reject the idea of treating all of them, including *K. cineracea*, as a monophyletic genus. If they were all placed in one genus, *Kneiffiella* would automatically lose its priority to older *Xylodon* or *Coltricia* and thus would utterly blur the lines between many traditionally accepted *Hymenochaetales* genera with vastly different basidiocarp types and trophic modes. Therefore, we propose the new genus, *Egonia*, to accommodate *K. cineracea* and its relatives.

The phylogenetic analyses of the core *Kneiffiella* clade in Fig. 2 demonstrate that hyphal septation, cystidial wall thickness, and hymenophore configuration are plastic and variable characters without phylogenetic value. Although extending the generic concept of *Kneiffiella* by adding polyporoid and corticioid species with thin-walled cystidia makes it hard to define *Kneiffiella* vs other *Hyphodontia* s.lat., the alternative solution would be more problematic. By restoring *Chaetoporellus* and *Deviodontia*, *Kneiffiella* species with tubular cystidia would be divided into at least three monophyletic clades, and require the establishment of two new genera. The genera would be nearly impossible to differentiate morphologically among *Hyphodontia* s.lat. and against each other. Therefore, we accept a broadly circumscribed *Kneiffiella* that includes *Alutaceadontia*, *Chaetoporellus*, and *Deviodontia* as synonyms.

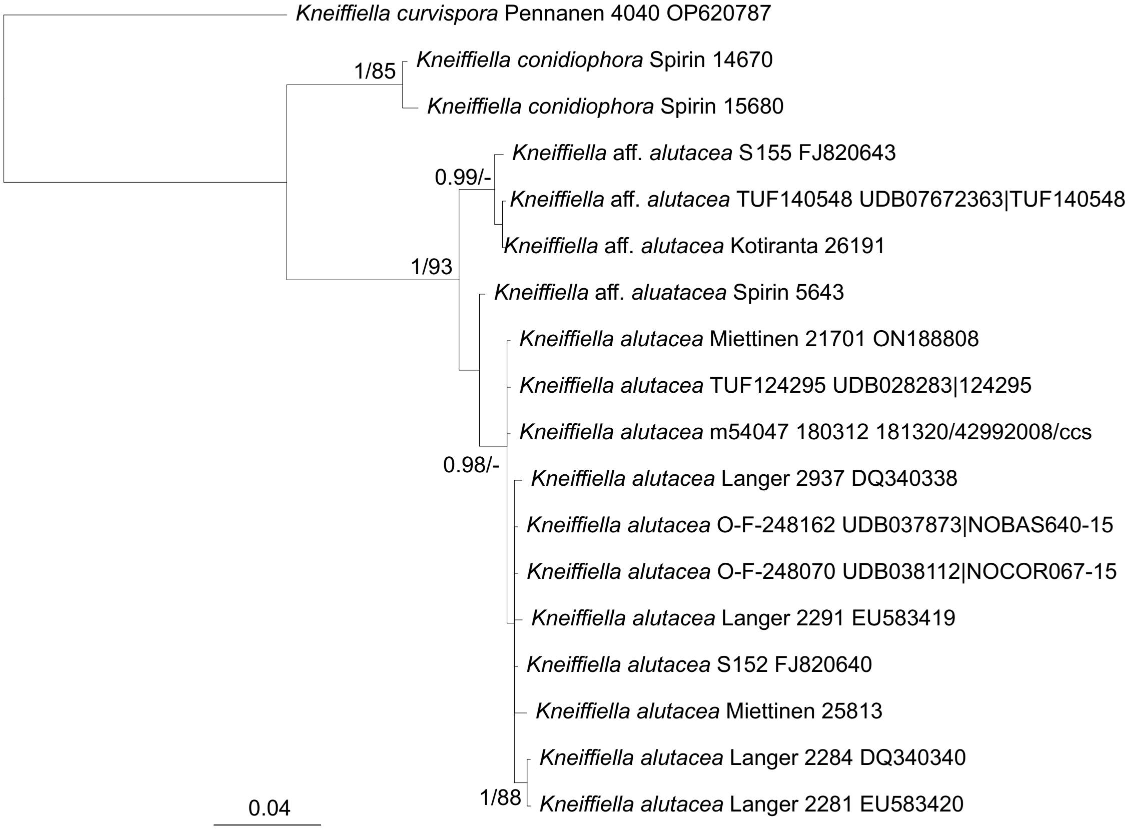

Fig. 5 Phylogenetic relationships of the *Alutaceodontia* clade inferred from the ITS dataset using BI analysis. Bayesian posterior probabilities followed by ML bootstrap values are shown at nodes; branch lengths reflect estimated number of changes per site.

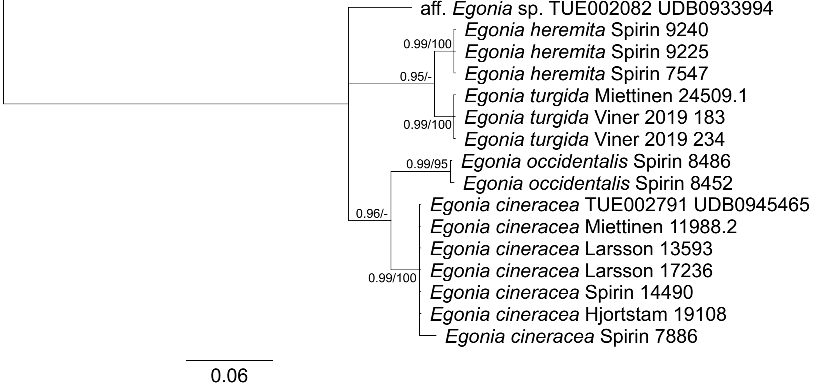

Fig. 6 Phylogenetic relationships of *Egonia* inferred from the ITS dataset using BI analysis. Bayesian posterior probabilities followed by ML bootstrap values are shown at nodes; branch lengths reflect estimated number of changes per site.

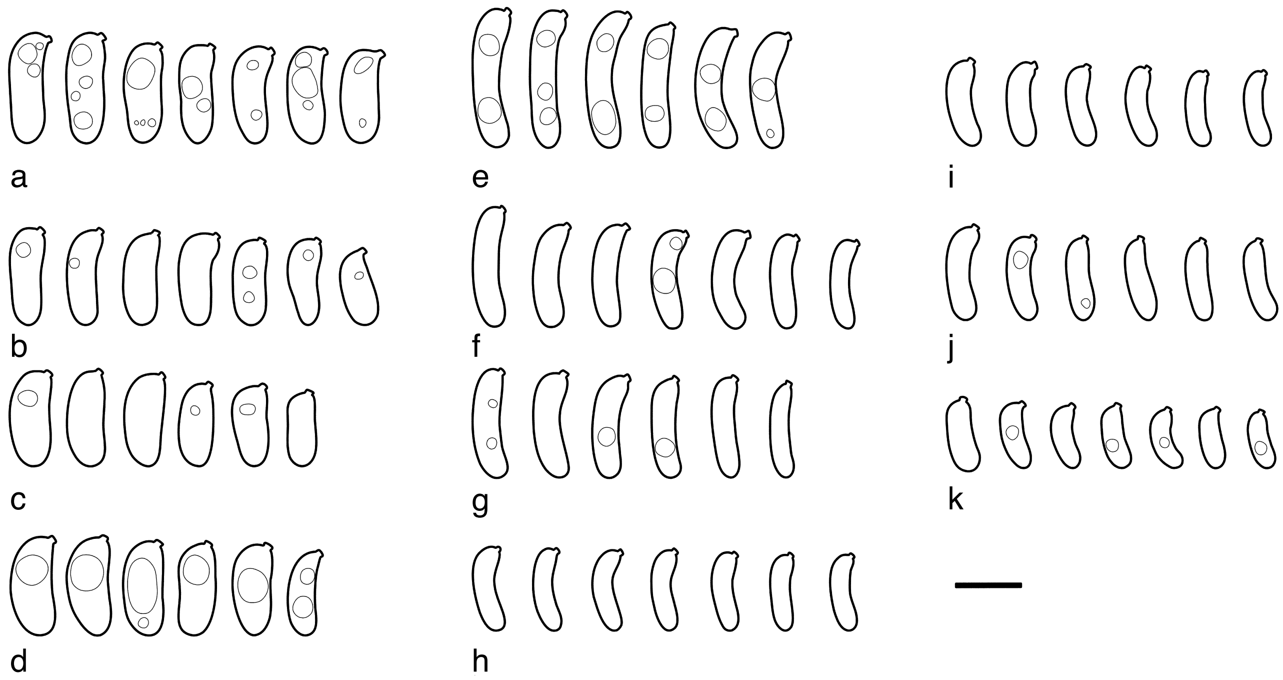

Fig. 7 Basidiospores in *Egonia* and similar-looking *Kneiffiella* in CB. a. *Egonia heremita* (holotype); b. *E. cineracea* (*Miettinen* 11988.2); c. *E. occidentalis* (holotype); d. *E. turgida* (holotype); e. *K. perlongispora* (holotype); f. *K. frondosarum* (holotype); g. *K. subalutacea* (lectotype); h. *K. similis* (holotype); i. *K. floccosa* (*Berglund* 150-02); j. *K. subaltaica* (*Miettinen* 15592.2); k. *K. altaica* (holotype). — Scale bar = 5 µm.

Jacksonomyces and the limits of the Trichaptum clade

The genera *Basidioradulum*, *Cyanotrama*, *Fibricium*, *Nigrofomes*, *Poriodontia*, and *Trichaptum* are usually placed in the proximity of the *Hymenochaetaceae* (e.g., Wang et al. 2021, 2023). In Fig. 1, this clade received moderate support (BI 0.9). We report for the first time that *Jacksonomyces*, represented by *J. subulatus* (also known as *Phlebia subulata*), is also in this clade.

TAXONOMIC PART

Egonia K.H. Larss., Miettinen & Viner, *gen. nov.* — MycoBank MB 848842

Etymology. After Kurt Egon Hjortstam, a major specialist in this group, who first pointed to the affinity of the generic type to *Hyphodontia*.

Type. Peniophora cineracea (Bourdot & Galzin) Sacc. & Trotter, Syll. Fung. (Abellini) 23: 536. 1925.

Basidiocarps resupinate, effused; *hymenophore* smooth, under the lens minutely floccose, no distinct margin. *Hyphal system* monomitic, thin- to slightly thick-walled, acyanophilous to slightly cyanophilous. Hyphae with small distinct clamps richly branched with branches originating near septa or on clamps. *Subhymenium* typically composed of clusters of short, often isodiametric hyphae. *Cystidia* numerous, tubular, originating in subiculum/subhymenium, projecting. *Basidia* broadly clavate, cylindrical or utriform, with 4 sterigmata and a basal clamp. *Spores* smooth, thin-walled, slightly curved to fusiform, hyaline, IKI-, acyanophilous.

Ecology & Distribution — On dead wood in the boreal and temperate zones of the Northern hemisphere.

Notes — All *Egonia* species fall within the traditional concept of *K. cineracea* that is often mistaken for several *Kneiffiella* species that are characterized by slightly curved to cylindrical spores, tubular cystidia, and a more or less smooth hymenophore. In addition to macromorphology, they can be distinguished by spore morphology and size, particularly the Q value and spore width (Fig. 7). The characteristic subhymenium of *Egonia*, often composed of short-celled hyphae, may also be helpful in identification. Among similar-looking *Kneiffiella*, *K. altaica* is most often confused with *Egonia* not least because of their similar macromorphology. However, *K. altaica* has smaller spores (Fig. 7) and noticeably smaller basidia (Fig. 8).

The following taxa are accepted species of *Egonia* based on their phylogenetic relatedness.

Egonia cineracea (Bourdot & Galzin) K.H. Larss., Spirin & Viner, *comb. nov.* — MycoBank MB 848856; Fig. 7, 8

See also Eriksson & Ryvarden (1976) f. 299–300 and Langer (1994) f. 34.

Basionym. Peniophora glebulosa subsp. *cineracea* Bourdot & Galzin, Bull. Soc. Mycol. France 28 (4): 387. 1913.

Type material studied. France, Occitania, Aveyron, on *Erica arborea* wood, 9 Aug. 1910, coll. *A. Galzin* 6704 (*H. Bourdot* 8012) (PC 0085021, lectotype, designated here MycoBank Typification MB 10013439).

Basidiocarps effused, adnate, 0.1–0.3 mm thick, up to 15 cm in the widest dimension, under the lens porose and pilose by the projecting cystidia; *hymenophore* smooth or under the lens finely minutely floccose, no distinct margin. Basidiocarp colour

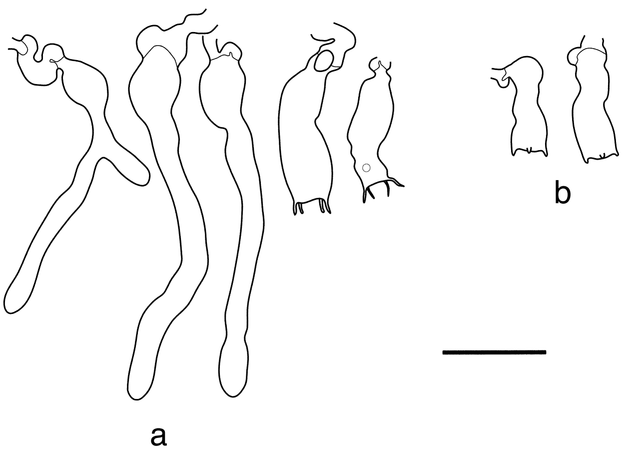

Fig. 8 Basidia and hyphidia in a. *Egonia cineracea* (*Miettinen* 15592.2) and basidia in b. *Kneiffiella altaica* (holotype) in CB. — Scale bar = 10 µm.

varied from ochraceous to grayish white. *Hyphal structure* monomitic, hyphae clamped and frequently branched. *Subicular hyphae* thin to slightly thick-walled, loosely intertwined, 1.7–3.7 µm diam (n = 121). *Subhymenium* composed of clusters of short hyphae, hyphae thin-walled, densely intertwined, (1.4–) 1.8–3.7 µm diam (n = 135). *Cystidia* (41–)70–220(–360) × (5–)6–9.5(–10.5) µm (n = 224), frequent, tubular with thin-walled apical part projecting, especially thick-walled at the base (up to 2.9 µm), hyaline, acyanophilous to distinctly cyanophilous, except for the thin-walled apical part, often with adventitious septa. *Hyphidia* swollen at the base 31–45 × 4–5 µm, not abundant. *Basidia* four-sterigmate, broadly clavate to subcylindrical or utriform, sometimes slightly thick-walled at the base 11–18(–29) × (3.5–)4–6 µm (n = 114). *Basidiospores* smooth, thin-walled, cylindrical to slightly curved or even fusiform, (4–)5.4–7.8(–8.3) × (1.7–)2–2.4(–2.9) µm (n = 335), L = 6.7, W = 2.1, Q = 3.2, guttules few small ones in the protoplasm of some spores, apiculus prominent.

Ecology & Distribution — On deciduous and coniferous wood in temperate and boreal Eurasia.

Additional material studied. Austria, Tirol, Schattwald, Vilstal, Pfrontener Wald, Zwersberg, on *Picea abies* wood, 15 Sept. 1989, coll. *E. Langer* 2067 (KAS). – Finland, Uusimaa, Helsinki, Ultuna, *Juniperus communis* (fallen stem), 15 Oct. 2022, coll. *V. Spirin* 15870. – France, Occitania, Boutes, on *Erica arborea* wood, June 1910, coll. *A. Galzin* 6446 (*H. Bourdot* 7407) (GB). – Norway, Telemark, Drangedal, Spirdalen, clearcut, on *Pinus sylvestris* log, 10 Oct. 2007, coll. *O. Miettinen* 11988.2 (H); Vestfold og Telemark, Drangedal, brook valley W of Vassenden, on *Pinus sylvestris* log, 11 Oct. 2007, coll. *K.H. Larsson* 13593 (GB). – Russia, Khabarovsk reg., Verkhnebureinskii dist., Dublikan Nat. Res. on *Picea ajanensis* log, 20 Aug. 2014, coll. *V. Spirin* 7886 (H 7028609). – Slovenia, Ribnica, Gorenje Podpoljane, *Fagus sylvatica* (fallen branch), 16 Aug. 2021, coll. *V. Spirin* 14490 (H). – Sweden, Öland, Långlöt, Ismantorp, on *Juniperus*, 19 Sept. 2006, coll. *K. Hjortstam* 19108 (GB 0207479); Västergötland, Skepplanda parish, south of L. Mulsjön, on conifer wood, 26 Sept. 2015, coll. *K.H. Larsson* 17236 (GB); Småland, Femsjö par., Dullaberget, on conifer fence, 11 Aug. 1937, coll. *S. Lundell* 5157 (GB 0096709).

Notes — Although this is the only *Egonia* species recorded from a deciduous substrate, specimens from conifers may be confused with other *Egonia*. Spore size statistics and characteristic thin-walled hyphidia separate conifer collections of *E. cineracea* from species with an overlapping distribution, *E. heremita* and *E. turgida*.

Weresub (1961) typified *P. glebulosa* subsp. *cineracea* with original material, *Galzin* 6731 (*Bourdot* 8015), that agreed with the protologue. The specimen she examined was obtained from the personal collection of Marinus Anton Donk, but she did not indicate the herbarium where this specimen was deposited, rendering her typification ineffective (Art. 8.1). We select *Galzin* 6704 (*Bourdot* 8012) from the original material in PC as lectotype that also agrees with the protologue.

Previously published sequences of this species (Sequence GenBank ID: DQ340336 and AJ406450) refer to *Langer* 4958 and *Langer* 4875 from Réunion. They are treated as paratypes of a new *Kneiffiella* species, *K. ornamentata* described herein.

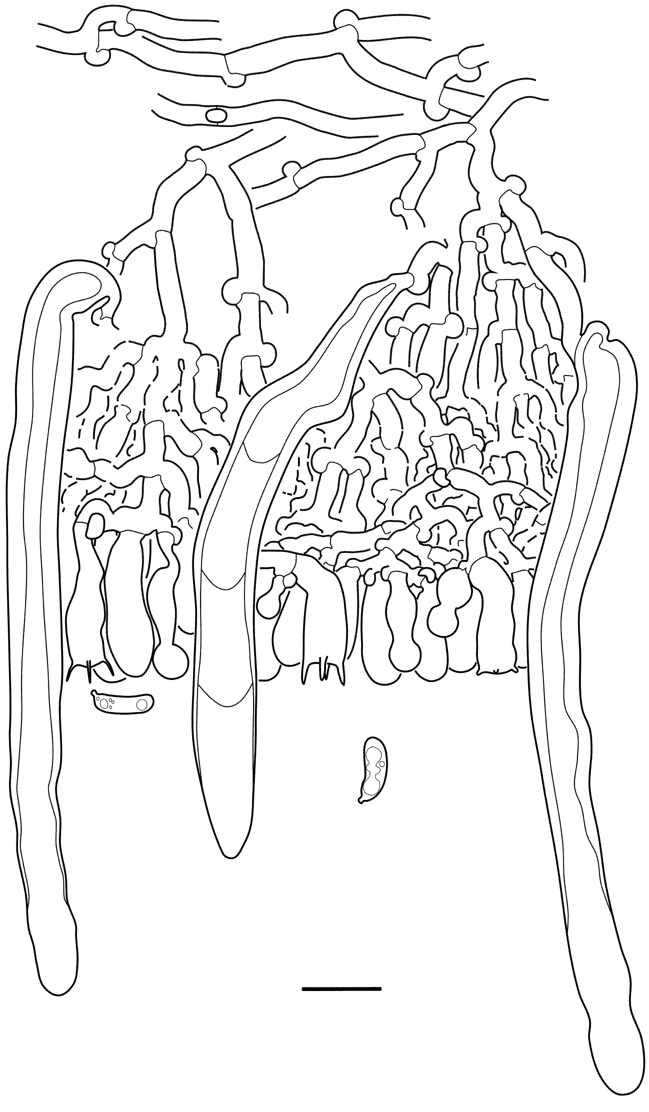

Fig. 9 Microscopic structures of *Egonia heremita* (holotype) in CB. — Scale bar = 10 µm.

Egonia heremita Viner, Langer & Spirin, *sp. nov.* — MycoBank MB 848843; Fig. 7, 9

Etymology. *Heremita* (Latin), hermit, in reference to the locus classicus Staraya Pustyn, which translates from Russian as Old Hermitage.

Type. Russia, Nizhny Novgorod Oblast, Arzamas dist., Pustynsky Nat. Res., near Staraya Pustyn settlement, sparse old-growth grass-herb pine forest, N55.6759 E43.5791, *Juniperus communis* (dry standing stem), 13 Aug. 2015, coll. *V. Spirin* 9240 (H, holotype). GenBank: ITS = OQ913427.

Basidiocarps effused, adnate, 0.1–0.3 mm thick, up to 5 cm in widest dimension, under the lens porose and pilose by the projecting cystidia; *hymenophore* smooth or under the lens minutely floccose, no distinct margin. Basidiocarp colour varies from white to grayish white. *Hyphal structure* monomitic, hyphae clamped and frequently branched. *Subicular hyphae* thin to slightly thick-walled, loosely intertwined, 1.8–4 µm diam (n = 70). *Subhymenium* is characteristically composed by clusters of short hyphae, although it may not always be observed in most microscope preparation. Hyphae thin-walled, densely intertwined, 1.8–4 µm diam (n = 70). *Cystidia* 55–115(–130) × (5–)6–9 µm (n = 120); frequent, tubular with a thin-walled apical part, especially thick-walled at the base (up to 2 µm), projecting, hyaline, acyanophilous to distinctly cyanophilous; often with adventitious septa; some are bi-rooted. Thin-walled capitate cystidia 15–17 × 4–4.5 µm are also present in the hymenium but not abundant. *Basidia* four-sterigmate, clavate to subcylindrical or utriform (11–)12–16(–18) × (3–)3–5.5(–6) µm (n = 60). *Basidiospores* smooth, thin-walled, cylindrical to slightly curved or even fusiform, (5.2–)7–8.9(–9.7) × (1.8–)2–2.8(–3) µm (n = 181), L = 7.8, W = 2.4, Q = 3.5, usually with conspicuous round or amorphous guttules occupying most of the protoplasm, apiculus prominent.

Ecology & Distribution — On conifer wood in temperate and boreal Eurasia.

Additional material studied. Russia, Kemerovo oblast, Shorski Nat. Park, Medny, Mrasu river, on *Abies* branch, 26 Aug. 2011, coll. *H. Kotiranta* 28350 (H 7044013); Khabarovsk reg., Verkhnebureinskii dist., Hegdy, on *Picea ajanensis* branch, 18 Aug. 2014, coll. *V. Spirin* 7547 (H 7028284); Nizhny Novgorod Oblast, Arzamas dist., Pustynsky Nat. Res. on *Juniperus communis* stem, 13 Aug. 2015, coll. *V. Spirin* 9243 (H 7051289); coll. *V. Spirin*

9225 (H 7051222). – Slovenia, Kranjska Gora, Zelenci, *Picea abies* (hanging dead branch), 25 Sept. 2019, coll. *V. Spirin* 13181.

Notes — Conifer collections of *E. cineracea* are similar to *E. heremita*. The two species can be distinguished based on spore measurement statistics and the shape of sterile hymenial elements (capitate cystidia vs hyphidia swollen at the base in *E. cineracea*). Conspicuous guttule bodies in the spore protoplasm of *E. heremita* are also characteristic. Another conifer-dwelling species, which *E. heremita* might be confused with, is *E. turgida.* The latter has shorter spores and, as a rule, short cylindrical to broadly clavate basidia.

Egonia occidentalis Viner & Spirin, *sp. nov*. — MycoBank MB 848844; Fig. 7, 10

Etymology. *Occidentalis* (Latin), western, in reference to the western distribution of this species.

Type. USA, Washington, Pend Oreille County, Sullivan Creek, old-growth coniferous (*Tsuga heterophylla* and *Thuja plicata*) forest, N48.8615 E-117.1592, on *Thuja plicata* branch, 13 Oct. 2014, coll. *V. Spirin* 8452 (H 7047490, holotype). GenBank: ITS+28S = OQ913423.

Basidiocarps effused, adnate, 0.1–0.3 mm thick, up to 5 cm in widest dimension, under the lens porose and pilose by the projecting cystidia; *hymenophore* smooth or under the lens minutely floccose, no distinct margin, grayish white. *Hyphal structure* monomitic, hyphae clamped, frequently branched. *Subicular hyphae* thin to slightly thick-walled, loosely intertwined, 1.8–3.2 µm diam (n = 31). *Subhymenium* is characteristically composed by clusters of short hyphae, although it may not always be observed in most microscope preparation. Hyphae thin-walled, densely intertwined, 1.7–3.2 µm diam (n = 31). *Cystidia* (42.5–)57.6–83.1(–90) × (5.5–)6–8.5(–9) µm (n = 40); frequent, tubular, with a thin-walled apical part, thick-walled at the base only, up to 1 µm, projecting, hyaline, acyanophilous to distinctly cyanophilous; rarely with one adventitious septum. Thin-walled capitate cystidia 7–17 × 3–4 µm with cyanophilous granulation in the protoplasm are also present in the hymenium but not abundant. *Basidia* four-sterigmate, broadly clavate to subcylindrical or utriform 11–17 × 3–5.5 µm (n = 20). *Basidiospores* smooth, thin-walled, cylindrical to slightly curved, (5–)5.2–7.7(–8) × 1.8–3 µm (n = 60), L = 6.5, W = 2.2, Q = 3, without guttules or with a few small droplets in the protoplasm, apiculus prominent.

Ecology & Distribution — So far collected twice from *Thuja plicata* branches. The known distribution area covers the American Northwest. There are no confirmed findings of other *Egonia* species from North America, which likely does not reflect reality. Further studies may uncover richer *Egonia* diversity in this region.

Additional material studied. USA, Idaho, Bonner County, Trapper Creek, on *Thuja plicata* branch, 14 Oct. 2014, coll. *V. Spirin* 8486 (H 7047536).

Notes — Although there is no other known species of *Egonia* from North America that could be confused with *E. occidentalis*, this species can be distinguished by its delicate tubular cystidia, having the thinnest cell walls and being the shortest in the genus.

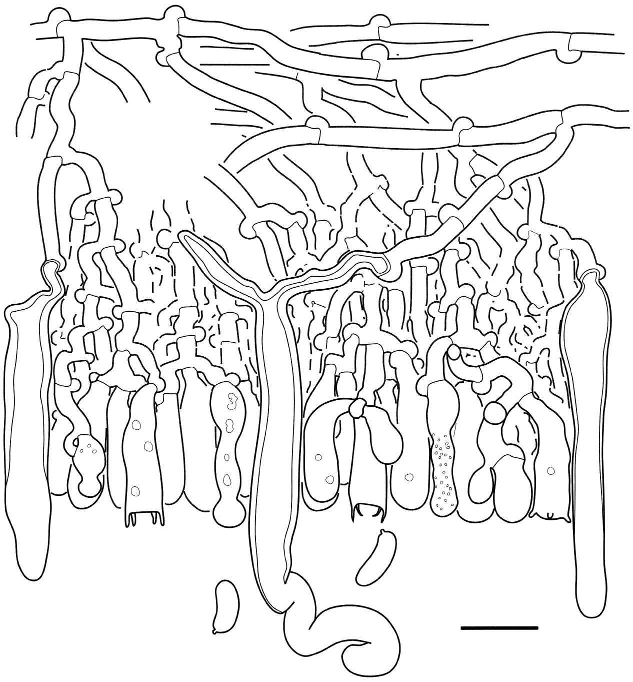

Fig. 10 Microscopic structures of *Egonia occidentalis* (holotype) in CB. — Scale bar = 10 µm.

Egonia turgida Viner & Miettinen, *sp. nov*. — MycoBank MB 848845; Fig. 7, 11, 12

Etymology. *Turgida* (Latin), turgid, in reference to the broadly clavate swollen-like basidia.

Type. Finland, Uusimaa, Helsinki, Talinranta, Tali, a patch of several old *Picea abies* on the edge of the park, N60.209694 E24.852000, on *Picea abies* branch, 16 Oct. 2019, coll. *I. Viner* 2019_183 (H 6080367, holotype). GenBank: ITS + LSU = OQ913429.

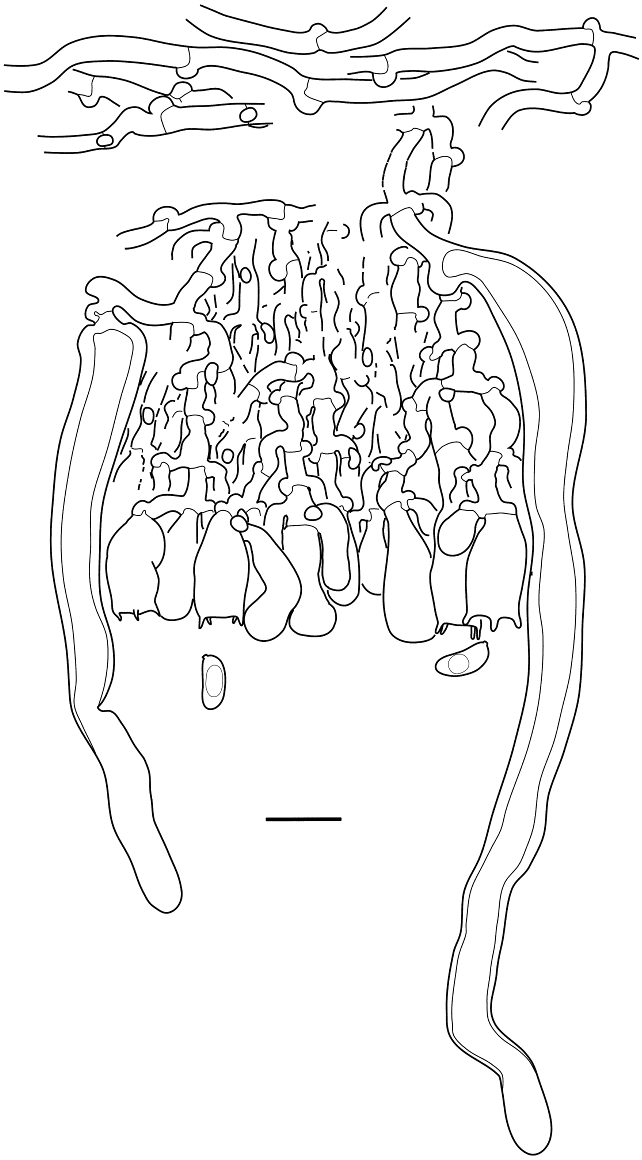

Fig. 11 Microscopic structures of *Egonia turgida* (holotype) in CB. — Scale bar = 10 µm.

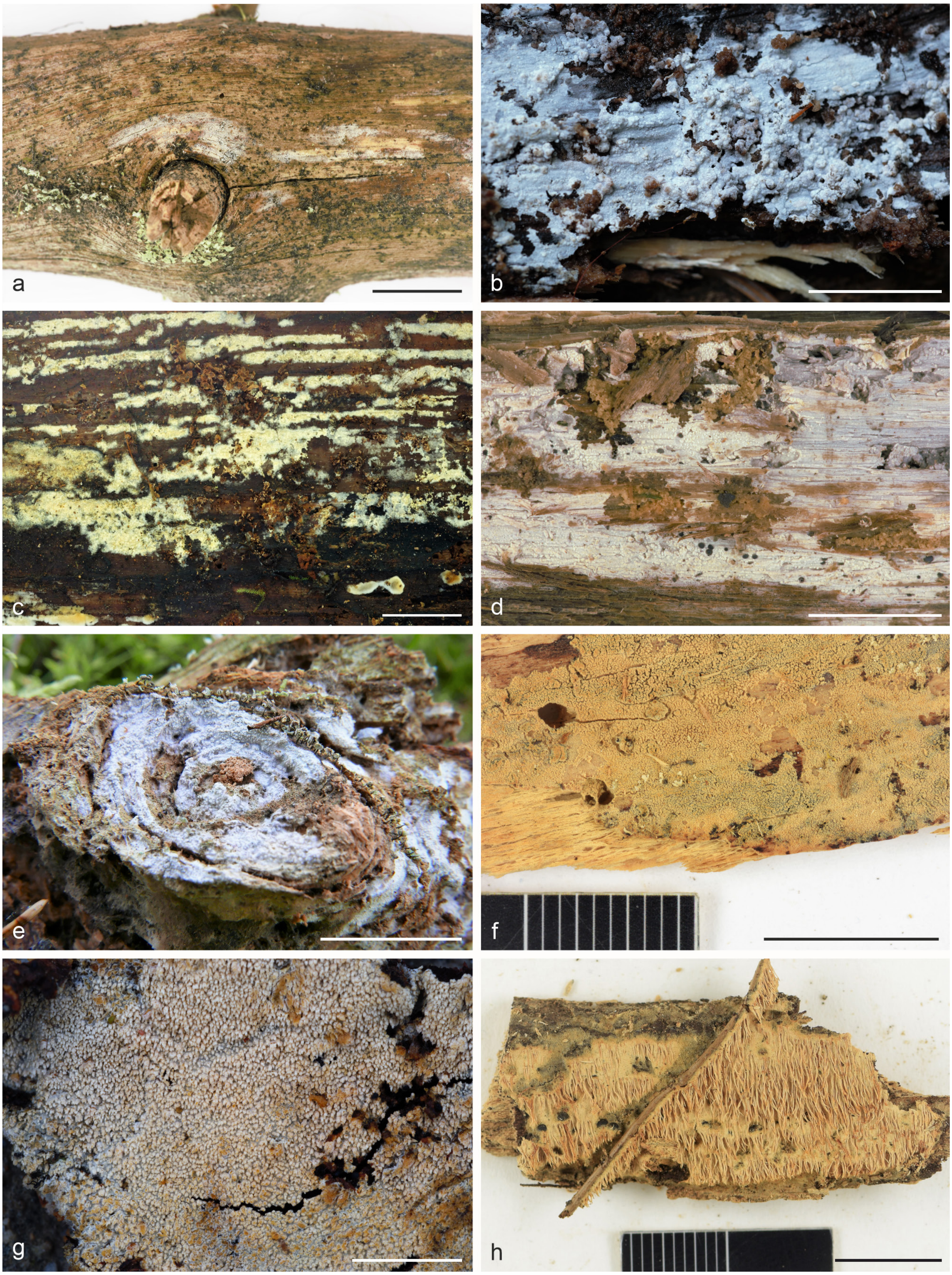

Fig. 12 Basidiocarps in *Egonia* and *Kneiffiella*. a. *Egonia turgida* (*Miettinen* 24509); b. *K. frondosarum* (*Miettinen* 17175.1); c. *K. alienata* (*Miettinen* 22764); d. *K. subalutacea* (*Miettinen* 24523); e. *K.* aff. *alutacea* (*Miettinen* 23979); f. *K. floccosa* (*Berglund* 150-02); g. *K. alutacea* (*Miettinen* 14615); h. *K. trichophora* (holotype); i. *K. abdita* (*Viner* 2019_117); j. *K. thermophila* (*Miettinen* 17887.1); k. *K. macra* (holotype); l, m, n. *K. amplipora* (holotype). — Scale bars: = 1 cm. — Photo by: b–e, g, j–n. O. Miettinen; a, f, h–i. I. Viner.

Fig. 12 (cont.)

Basidiocarps effused, adnate, 0.1–0.3 mm thick, up to 5 cm in widest dimension, under the lens porose and pilose by the projecting cystidia; *hymenophore* smooth or under the lens minutely floccose, no distinct margin, whitish. *Hyphal structure* monomitic, hyphae clamped, frequently branched. *Subicular hyphae* thin to slightly thick-walled, loosely intertwined, 1.9–3.2 µm diam (n = 40). *Subhymenium* is typically composed by clusters of short and even isodiametric hyphae, although it may not always be observed in every microscope preparation. Hyphae thin-walled, densely intertwined, 1.5–3.3 µm diam (n = 46). *Cystidia* (75–)84.7–165.8(–190) × 7–9(–9.5) µm (n = 60); frequent, tubular with a thin-walled apical part, especially thick-walled at the base (up to 1.2 µm), projecting, hyaline, acyanophilous; rarely with one adventitious septum. *Basidia* four-sterigmate, short cylindrical to broadly clavate (8–)9.9–16.2(–19) × 5.5–7.1(–8) µm (n = 30). *Basidiospores* smooth, thin-walled, ellipsoid to cylindrical and sometimes slightly curved, (5.2–)6–8(–8.2) × (2.1–)2.3–3.4(–3.8) µm (n = 91), L = 7, W = 2.8, Q = 2.5, often with large guttules in the protoplasm, apiculus prominent.

Ecology & Distribution — So far, it is known exclusively from Southern Finland but likely has a wider distribution, at least in boreal Europe. All collections came from conifer branches.

Additional material studied. Finland, Uusimaa, Helsinki, Haltiala, Rocky outcrop, *Pinus mugo* thicket, on *Pinus mugo* branch, 13 Dec. 2020, coll. *O. Miettinen* 24509.1 (H); Viikki, Viikin kalliot, on *Pinus sylvestris* branch, 6 Nov. 2019, coll. *I. Viner* 2019_234 (H 6080799).

Notes — Spore measurements statistics in combination with short cylindrical to broadly clavate basidia in *E. turgida* makes it distinguishable from other *Egonia* species treated here.

Kneiffiella P. Karst., Bidrag Kannedom Finlands Natur och Folk 48: 371. 1889

Type. *Hydnum barba-jovis* Bull., Herb. France 10 (109–120): t. 481, f. 2. 1790.

Basidiocarps resupinate, adnate; *hymenophore* varied, pruinose, smooth, floccose, tuberculoid, hydnoid, odontioid, labyrinthoid or poroid. *Hyphal system* monomitic, hyphae thin- to thick-walled, acyanophilous to strongly cyanophilous; septa usually clamped, in a few species with rare or even completely without clamps. The branching point of hyphae in most cases located close to septa or on clamps themselves. Together with a rich hyphal branching, these features constitute a characteristic hyphal pattern intrinsic to all *Hyphodontia* s.lat. *Cystidia* numerous, often tubular. In species with thin-walled cystidia, they are of subhymenial origin, obtuse to pestle-shaped, i.e., widening both at the distal and proximal part. *Basidia* can be cylindrical to clavate or utriform, with 2 or 4 sterigmata with or without a basal clamp. *Basidiospores* smooth, most often thin-walled, from ellipsoid and cylindrical to slightly or strongly curved, hyaline, IKI-, acyanophilous to slightly cyanophilous. Ovoid to subellipsoid *conidia* are found in three species. *Conidiophores* are of hymenial origin, subulate (sometimes branched) with a basal clamp.

Notes — As treated here, *Kneiffiella* is not uniform in terms of morphology. It contains forms with basidiocarps ranging from pruinose to hydnoid or even poroid. This variation in hymenophore types is not unusual among other genera of wood-inhabiting fungi, and indeed among *Hyphodontia* s.lat. At least two other currently recognized genera of *Hyphodontia* derivatives have both corticioid and polyporoid representatives: *Hyphodontia* s.str. itself (e.g., *H. borbonica* vs *H. pallidula*) and *Xylodon* (e.g., *X. nongravis* vs *X. quercinus*). While *Hyphodontia* s.str. remains a morphologically definable genus thanks to its characteristic lagenocystidia, *Kneiffiella*, as circumscribed here, is conceptually similar to *Xylodon*. Both genera are inclusive to the point where their morphological concepts overlap with other genera of *Hyphodontia* s.lat.: differentiating *Kneiffiella* against *Egonia* and *Xylodon* against *Lyomyces* (see the discussion section in Viner et al. (2023)) may be difficult without precise knowledge of species identification. However, this does not mean that assigning an unknown *Hyphodontia* s.lat. specimen to the correct genus would always require in-depth taxonomic expertise; in most cases it does not. For *Hyphodontia* s.lat. specimens with suballantoid to cylindrical spores and tubular cystidia, species with spores below 2 μm in width can be classified in *Kneiffiella*, while those with wider spores are likely *Egonia*. The exceptions are two species with a distribution, which does not overlap with any known *Egonia* species: South American *K. decorticans* and *K. tubuliformis* described from Taiwan. *Kneiffiella decorticans* has been confirmed to be a member of *Kneiffiella* through molecular evidence (Riebesehl & Langer 2017), while *K. tubuliformis* develops grandinioid to odontioid hymenophore not typical to *Egonia*. Below, we present a list of all taxa that can be classified within the genus *Kneiffiella* (as accepted on 2 Feb. 2024) based on either molecular data or a close resemblance to other known *Kneiffiella* species, even if molecular barcodes are not currently available. We omit citations for type specimens if none of the authors of this paper has studied them.

Kneiffiella abdita Riebesehl & Langer, Mycol. Progr. 16(6): 647. 2017 — Fig. 12, 13, 14

See also Eriksson & Ryvarden (1976) f. 261 and Langer (1994) f. 61.

Obligate synonym. *Poria latitans* Bourdot & Galzin, Bull. Trimestriel Soc. Mycol. France 41(2): 226. 1925.

Type material studied. France, Aveyron, Causse Noir, on *Pinus* wood, 4 Dec. 1910, coll. *A. Galzin* (in Hym. De France Nr. 698) (*H. Bourdot* 29007) (PC, lectotype selected by Langer (1994); S, isolectotype).

Basidiocarp resupinate, effuse, adnate, 1–2 mm thick, at first whitish then cream to buff sometimes with violet tints, soft, when dried firm and friable; *hymenophore* poroid with rounded pores 2–5 per mm (n = 72) or, especially on vertical substrate, with irregularly lacerate or labyrinthine pores; subiculum very thin; margin indistinct, pruinose. *Hyphal structure* monomitic, hyphae with somewhat thickened walls, clamped, frequently branched, distinctly cyanophilic. *Tramal hyphae* are more or less parallel 1.9–3.7 μm diam (n = 80), in older parts of the hymenophore filled with oily material and in this case completely acyanophilic. *Subicular hyphae* irregularly intertwined, 1.9–3.7 μm (n = 80), subhymenial hyphae densely packed, rather thin-walled, 1.8–3.2 μm diam (n = 80). *Cystidia* of hymenial origin 12–26.1(–34) × 3–5(–6) μm (n = 140); numerous, slightly projecting, mostly cylindrical or slightly fusiform, somewhat constricted, thin-walled, obtuse, naked. *Basidia* small, four-sterigmate, cylindrical, (5–)5.5–8(–10) × 2.5–3.5(–4) μm (n = 70). *Basidiospores* smooth, thin-walled, allantoid, strongly curved, (2.4–)2.9–3.9(–4.2) × 0.5–0.8(–1) μm (n = 210), L = 3.4, W = 0.7, Q = 5.1, without guttules.

Ecology & Distribution — On conifer and deciduous wood in North Eurasia.

Additional material studied. Finland, South Savo, Sulkava, Lohikoski, Lohilahti, on *Picea abies* log, 30 Aug. 2006, coll. *J. Pennanen* 30.08.2006 (H 6055818); Uusimaa, Helsinki, Haltiala, on *Salix caprea* log, 5 June 2019, coll. *O. Miettinen* 22165 (H 6014642). – Georgia, Imereti, Kutaisi, near the Tskaltsitela river, on *Fagus* log, 19 Dec. 2021, coll. *I. Viner* 2021_341 (H 7075607). – Russia, Primorsky Krai, Ussuriyskiy dist., Ussuriyskiy Nat. park, Peishula, Suvorovskiy kordon, on *Fraxinus* branch, 1 Aug. 2018, coll. *H. Kotiranta* 28788 (H 7046844); Volgograd Oblast, Novoanninsky dist., near Novoanninsky, on *Pinus sylvestris* wood, 5 July 2015, coll. *I. Viner* 2015_44 (H 7069887); Yakutia, Churapchinsky dist., Telei village, near the Lena river, on *Larix* log, 22 Aug. 2016, coll. *H. Kotiranta* 27805 (H 7036239).

Notes — *Poria latitans* was transferred to *Kneiffiella* by Riebesehl & Langer (2017) based on molecular data. To address the nomenclatural issue with the preoccupied name *Kneiffiella latitans*, they have introduced the replacement name *K. abdita*.

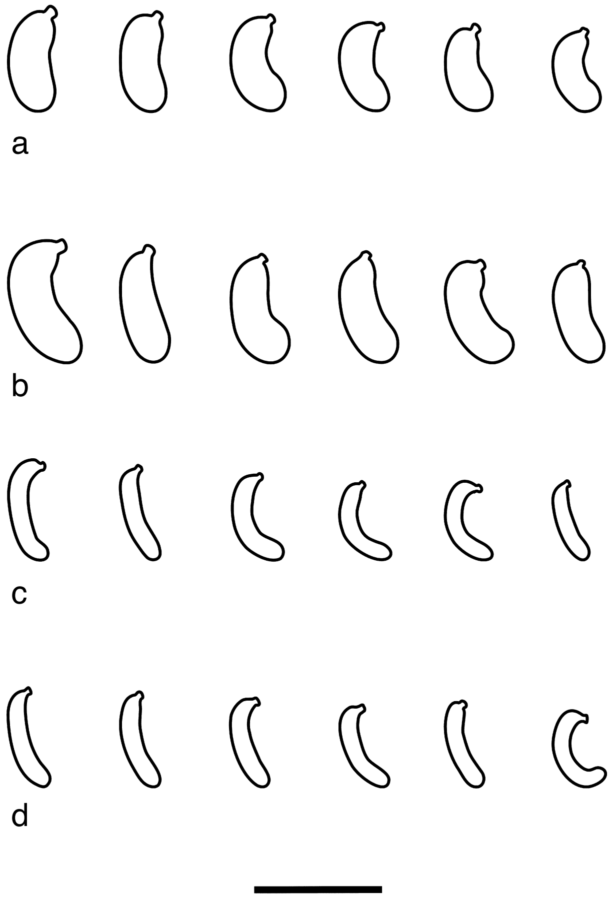

Fig. 13 Basidiospores of *Kneiffiella* with polyporoid basidiocarps in CB. a. *Kneiffiella macra* (holotype); b. *K. amplipora* (holotype); c. *K. abdita* (*Pennanen* 30.08.2006); d. *K. thermophila* (holotype). — Scale bar = 5 μm.

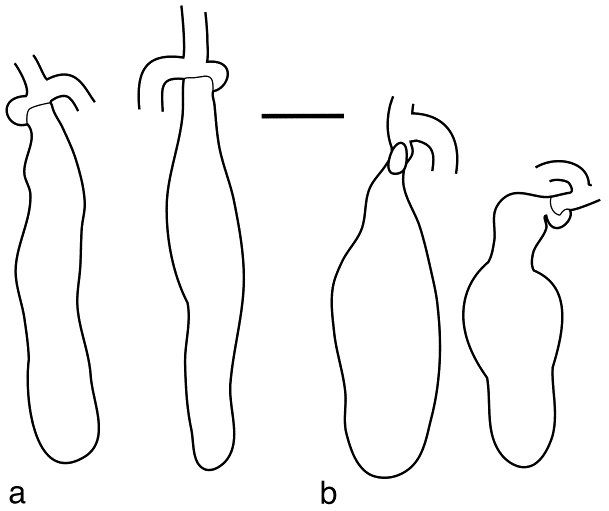

Fig. 14 Cystidial elements in a. *Kneiffiella abdita* (*Pennanen* 30.08.2006) and b. *K. thermophila* in CB: (holotype). — Scale bar = 5 µm.

Notably, our similar-looking collections from the tropics represent another species, *K. thermophila*. The latter can be distinguished from *K. abdita* by its slightly broader cystidia (Fig. 14). According to information available, their distribution areas do not overlap, allowing for straightforward identification.

Kneiffiella abieticola (Bourdot & Galzin) Jülich & Stalpers, Verh. Kon. Ned. Akad. Wetensch., sect. 2, 74: 130. 1980

For the description and illustrations, refer to Eriksson & Ryvarden (1976) f. 272–274 and Langer (1994) f. 2.

Basionym. Odontia barba-jovis subsp. *abieticola* Bourdot & Galzin, Hymenomyc. France (Sceaux): 426. 1928.

Type material studied. France, Vosges, Corcieux, Rue du Galtz, on *Picea* wood, 8 Nov. 1904, coll. *A. Galzin* 409 (*H. Bourdot* 4141 A ¢) (PC, lectotype designated here MycoBank Typification MB 10013440).

Ecology & Distribution — All sequenced *K. abieticola* were collected from conifers in Europe and the American Northwest (Sequence UNITE ID: UDB039493).

Additional material studied. Finland, Helsinki, Haltiala, middle-aged mixed forest, on *Picea abies* log, 18 Oct. 2020, coll. *O. Miettinen* 24321.1 (H).

Notes — Weresub (1961) attempted to establish the typification of *O. barba-jovis* subsp. *abieticola* using original material, *Maire* 492 (*Bourdot* 24478), that appeared to be in agreement with the protologue. The specimen she examined was obtained from the personal collection of Marinus Anton Donk, but she did not indicate the herbarium where this specimen was deposited, rendering her typification ineffective (Art. 8.1). We have chosen to select *Galzin* 409 (*Bourdot* 4141 A ¢) from the original material in PC, which is also in agreement with the protologue and our sequenced material.

Kneiffiella alienata (S. Lundell) Jülich & Stalpers, Verh. Kon. Ned. Akad. Wetensch., sect. 2, 74: 130. 1980 — Fig. 15

For the description and additional illustrations, refer to Eriksson & Ryvarden (1976) f. 275, 277 and Langer (1994) f. 13.

Basionym. Peniophora alienata S. Lundell, Fungi Exsicc. Suecici 21–22 (Sched.): 28. 1941.

Type material studied. Sweden, Västergötland, St. *Änggården*, Nature park, on *Alnus glutinosa* branch, 6 June 1940, coll. *T. Nathorst-Windahl* (UPS, holotype; GB, isotype).

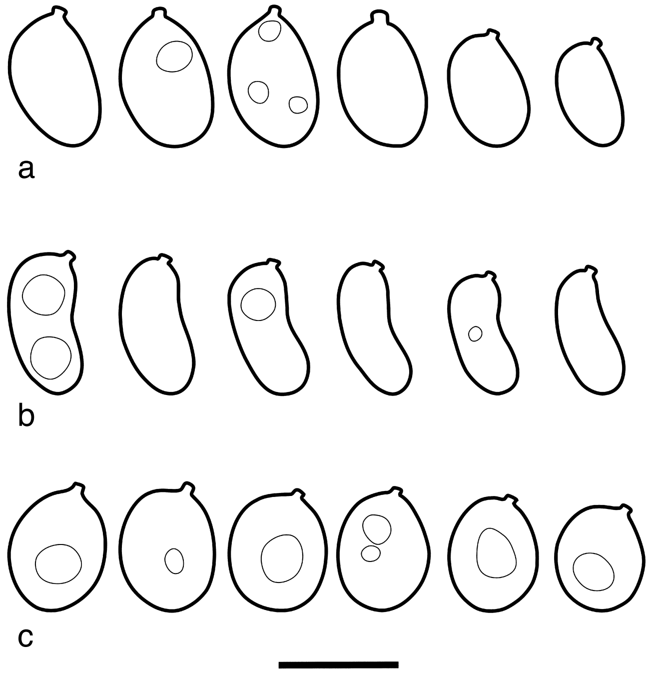

Fig. 15 Basidiospores of *Kneiffiella alienata* and similar-looking species in CB. a. *Kneiffiella alienata* (*Viner* 2021_13); b. *K. fabiformis* (holotype); c. *K. ornamentata* (holotype). — Scale bar = 5 µm.

Additional material studied. Poland, Podlasie, Hajnówka, Białowieża National Park, Mixed, swampy old-growth forest, on *Alnus glutinosa* wood, 23 Sept. 2019, coll. *O. Miettinen* 22764 (H). – Russia, Sochi, Krasnaya Polyana, near Beshenka creek, on *Carpinus* wood, 2 May 2021, coll. *I. Viner* 2021_13 (H). – USA, Massachusetts, Paxton, Boynton Park, Slope of a moist, fertile valley, aging deciduous forest, on angiosperm wood, 12 Oct. 2013, coll. *O. Miettinen* 17319 (H).

Ecology & Distribution — All DNA-confirmed *K. alienata* were collected in Europe and the American Northeast from both conifer and angiosperm wood.

Kneiffiella altaica (Parmasto) Hjortstam & Ryvarden, Syn. Fungorum (Oslo) 26: 42. 2009 — Fig. 7

For the description and additional illustrations, refer to Eriksson & Ryvarden (1976) f. 301, Langer (1994) f. 14, and Langer et al. (2022) f. 5–8.

Basionym. Hyphodontia altaica Parmasto, Consp. System. Corticiac. (Tartu): 211. 1968.

Type material studied. Russia, Altai, Telezkoie, on *Abies sibirica* wood, 21 Aug. 1959, coll. *E. Parmasto* 8576 (TAAM, holotype).

Additional material studied. Russia, Leningrad Reg., Boksitogorsk Dist., Kolp’, on *Picea abies* wood, 21 July 2011, coll. *I. Sorokina* 2011 (H); Podporozhie Dist., Kutka, on *Pinus sylvestris* wood, 1 Oct. 2013, coll. *V. Spirin* 6786 (H).

Notes — *Kneiffiella altaica* has been collected exclusively from conifers. All sequenced specimens are limited to Europe (Langer et al. 2022), however, its type originates from the Asiatic part of Russia. The sequenced material from Nothern Asia would allow confirming its identity.

Kneiffiella alutacea (Fr.) Jülich & Stalpers, Verh. Kon. Ned. Akad. Wetensch., sect. 2, 74: 134. 1980 — Fig. 12, 16, 17

See also Langer (1994) f. 15–16.

Basionym. Hydnum alutaceum Fr., Syst. Mycol. (Lundae) 1: 417. 1821.

Type material studied. Sweden, Småland, Femsjö par., S of Dröplastigen, slope towards a mire, on *Pinus* log, 2 Sept. 1949, coll. *S. Lundell* 6044 and *J. Stordal* (GB, neotype of *Hydnum alutaceum* selected by Hjortstam (1984)).

Synonym. Kneiffia stenospora P. Karst., Hedwigia 25: 231. 1886.

Type material studied. Finland, Southwest Finland, Merimasku, on *Pinus sylvestris* log, 16 May 1859, coll. *P.A. Karsten* 3005 (H 6011825, lectotype designated here MycoBank Typification MB 10013441).

Basidiocarps effused, adnate, 0.5–1.3 mm thick, at first minutely floccose or furfuraceous, then odontioid with small (usually less than 1 mm long) conical aculei, cream to sordidly ochraceous. When old, aculei are aggregated into coralloid-like pegs. Margin pruinose, indistinctly thinning out. Hymenium between the aculei porose-reticulate, in older basidiocarps, only disjoined clusters of basidia present. *Hyphal structure* monomitic, hyphae clamped, frequently branched, and cyanophilic, in the centre of the aculei more or less parallel with clearly thickened walls and only sparse ramifications, 3–5 µm diam (n = 70). *Subicular hyphae* thin- to thick-walled, 2.9–4.5 µm diam (n = 71), *subhymenial hyphae* thin-walled, densely intertwined, 2–4.5 µm diam (n = 70). *Cystidia* (12–)22–51.2(–69) × 4–6(–8.5) µm (n = 100); scarce to numerous, thin-walled, projecting or enclosed, cylindrical, obtuse, often with a few or several constrictions. *Basidia* four-sterigmate, subclavate to cylindrical, or utriform, varying greatly in length (7–)9–20.3(–34) × (3.5–)4–5.5 µm (n = 40). *Basidiospores* smooth, thin-walled, allantoid, (5.4–)5.9–8.8(–9.8) × (1.4–)1.6–2(–2.2) µm (n = 156), L = 7.5, W = 1.8, Q = 4.2, usually without guttules, apiculus prominent.

Ecology & Distribution — All confirmed specimens of *K. alutacea* s.str. were collected on both conifer and deciduous wood in Europe and Western Canada.

Additional material studied (*Kneiffiella alutacea* s.str.). Canada, British Columbia, North Vancouver, Lynn Creek, on conifer wood, 20 May 2023, coll. *O. Miettinen* 25813 (H). – Finland, Uusimaa, Helsinki, Kuusiluoto, on *Picea abies* (?) log, 3 Sept. 2018, coll. *O. Miettinen* 21701.2 (H 6014360). – Norway, Akershus, Nesodden, Røerskogen, on angiosperm wood, 18 Sept. 2014, coll. *K.H. Larsson* (O O-F-248162); Østfold, Aremark, Tjøstøl, on *Picea abies* wood, 24 Oct. 2011, coll. *S. Svantesson* 1003 (O O-F-248070).

Additional material studied (*Kneiffiella* aff. *alutacea*). Estonia, Valga County, Otepää commune, Otepää parish, Otepää looduspark, Hobusemägi, on conifer wood, 26 Mar. 2020, coll. *I. Sell* (TUF 140548). – Finland, Lapland, Sodankylä, Kolholaki, *Picea abies* log, 3 Sept. 2020, coll. *O. Miettinen* 23979 (H 6014850). – Russia, Khabarovsk reg., Khabarovsk dist., Ulun, on *Picea ajanensis* log, 26 Aug. 2012, coll. *V. Spirin* 5643 (H 7022785); Khabarovsk reg., Solnechnyi dist., Razlivnaya, on *Picea ajanensis* log, 22 Aug. 2011, coll. *V. Spirin* 4254 (H 7022688); 22 Aug. 2011, coll. *V. Spirin* 4248 (H 7022663); Krasnoyarsk Krai, Evenk Autonomous District, Central Siberian res., the Podkamennaya Tunguska river, on *Picea obovata* log, 12 Aug. 2013, coll. *H. Kotiranta* 26191 (H 7024921).

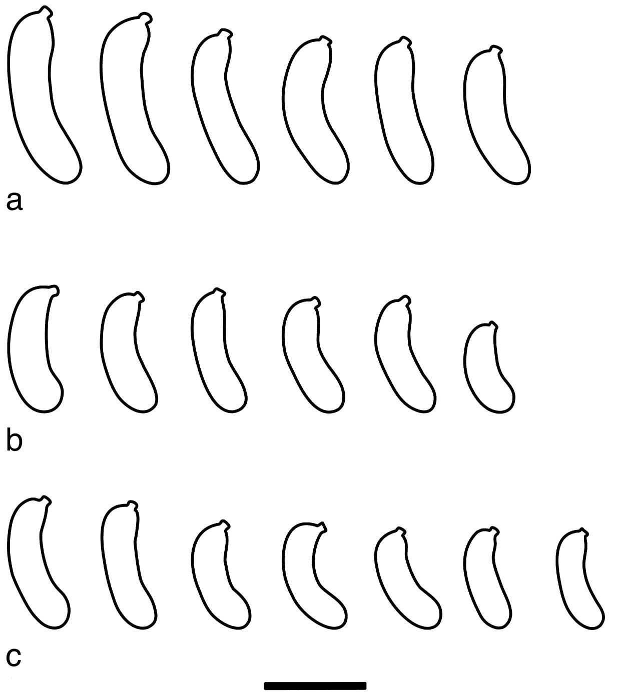

Fig. 16 Basidiospores of the *Alutaceodontia* clade in CB. a. *Kneiffiella alutacea* (neotype); b. *K.* aff. *alutacea* (*Kotiranta* 26191); c. *K. conidiophora* (holotype). — Scale bar = 5 µm.

Notes — After its description, two varieties of *H. alutaceum* were introduced. These are *Hyphodontia alutacea* var. *mamillicrinis* and *Odontia alutacea* var. *dubia*. The latter was later elevated to the species level as *Odontia dubia*, but this name has not been widely used since. Rick's protologue refers to a species with ellipsoid spores and stresses its similarity to *Hyphodontia arguta*, which, according to the same text, Rick himself confused with *O. alutacea* var. *dubia*. As reported by Baltazar et al. (2016), the name is of unknown application.

Hyphodontia alutacea var. *mamillicrinis* was introduced by Eriksson & Hjortstam (1969) for specimens with cystidia with multiple constrictions and a conidial stage. However, later this variety was abandoned, and consequently, the concept of *H. alutacea* was broadened to include specimens with varying shapes of cystidia and the optional presence of conidiophores (Eriksson & Ryvarden 1976). Our data suggests that *K. alutacea* s.str. can vary in the shape and abundance of cystidia but never forms a conidial stage. Although we were unable to examine the original material of *H. alutacea* var. *mamillicrinis* during the preparation of our manuscript, we believe that it belongs to a separate species, *K. conidiophora*, described below.

Judging by the strongly structured phylogenetic clade of *K. alutacea*, it likely represents a species complex that includes one or two species in Northern Eurasia (designated as *K.* aff. *alutacea* in Fig. 5, 12, 16, 17). This hypothesis is further supported by mating tests with European strains of *K. alutacea* (Hallenberg 1988) and morphological differences that we found in the studied material (Fig. 12, 16, 17). Specimens of *K.* aff. *alutacea* have shorter spores and hyphae in the core of the aculei are not as thick-walled as those observed in *K. alutacea*, resulting in a less conspicuous contrast with thin-walled hyphae in the subhymenium. Formal recognition of *K.* aff. *alutacea* as new species requires additional genetic data for improved phylo-

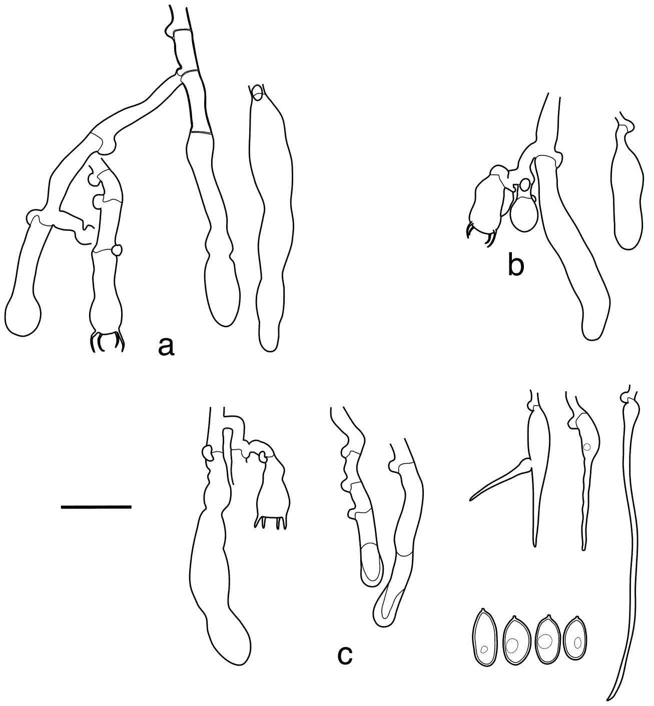

Fig. 17 Microscopic structures of the *Alutaceodontia* clade in CB. a. Basidia and cystidial elements in *Kneiffiella alutacea* (neotype); b. basidia and cystidial elements in *K.* aff. *alutacea* (*Kotiranta* 26191); c. *K. conidiophora* (holotype) from left to right: basidia together with cystidial elements, terminal hyphal cells in the hymenium with thick-walled tips, conidia and conidiophores. — Scale bar = 10 µm.

genetic resolution. *Kneiffiella* aff. *alutacea* occurs in Northern Asia, and therefore might refer to *Hyphodontia alutacea* f. *salicis*, which is based on a Siberian collection from *Salix* wood.

Although Legon et al. (2005) listed *Hydnum melleum* from Wales as a synonym of *K. alutacea*, we follow unpublished notes of Kurt Hjortstam who studied the corresponding type and identified it as *Dacryobolus sudans.*

Kneiffiella amplipora Viner & Miettinen, *sp. nov.* — MycoBank MB 848846; Fig. 12, 13, 18

Etymology. *Amplipora* (Latin), with wide pores, in reference to the largest pores among all polyporoid *Kneiffiella*.

Type. Malaysia, Sabah, Ranau, Kinabalu Park, Kiau view trail, lower montane rainforest, N6.04723 E116.5949, alt. 1600 m, on a fallen dicot tree crown (45 cm diam, decay stage 3/5), 17 June 2013, coll. *O. Miettinen* 16323 (SNP 33576, holotype; H 7200685, isotype). GenBank: ITS + 28S = OQ913458.

Basidiocarp resupinate, effuse, adnate, 0.2–3 mm thick, around 40 cm in the longest dimension, ochraceous, when mature cream, soft also when dried; *hymenophore* poroid with angular pores 1–2 per mm (n = 12) to irregularly lacerate or labyrinthiform; subiculum very thin; margin indistinct. *Hyphal structure* monomitic, clamped, frequently branched, cyanophilic. *Tramal hyphae* interwoven, 1.7–4.2 µm diam (n = 20) with slightly thickened walls (up to 0.7 µm). *Subicular hyphae* irregularly intertwined, 2–3 µm diam (n = 20) thin- to slightly thick-walled, strongly cyanophilic. *Subhymenial hyphae* thin-walled, 2–4 µm diam (n = 20). *Cystidia* of hymenial and sometimes of tramal origin 15–38 × (4–)4.5–8(–9) µm (n = 21); numerous, slightly projecting, broadly fusoid to cylindrical, thin-walled, naked. Large cystidia originating in trama may have 1–2 additional septa with clamps. *Basidia* small, four-sterigmate, broadly clavate to broadly cylindrical (6–)6.5–9.6(–10) × 3.5–4 µm (n = 10). *Basidiospores* smooth, thin-walled, allantoid, strongly curved, (3.3–)3.9–5 × (1.2–)1.4–1.8 µm (n = 31), L = 4.4, W = 1.6, Q = 2.8, without guttules.

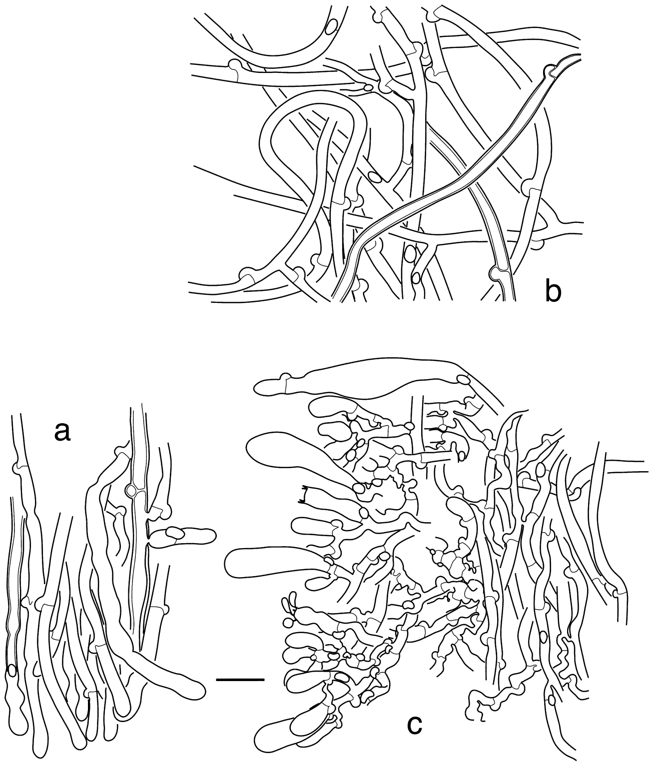

Fig. 18 Microscopic structures of *Kneiffiella amplipora* (holotype) in CB. a. Hyphal ends in lower trama; b. subiculum; c. dissepiment in vertical section. — Scale bar = 10 µm.

Ecology & Distribution — So far known exclusively from angiosperm wood in Borneo.

Notes — *Kneiffiella amplipora* has conspicuous basidiocarps and is readily recognizable for its pores are much larger than in other polyporoid *Kneiffiella* species. *Kneiffiella macra*, also from Borneo, lacks proper pores and has a labyrinthic to hydnoid hymenophore and sturdier basidiocarp. Microscopically, *K. macra* has smaller spores, larger basidia, significantly wider tramal hyphae, and heavily incrusted cystidia.

Kneiffiella barba-jovis (Bull.) P. Karst. (as '*barba-jobi*'), Bidrag Kannedom Finlands Natur Folk 48: 371. 1889

For the description and illustrations, refer to Eriksson & Ryvarden (1976) f. 292–295 and Langer (1994) f. 23–24.

Basionym. Hydnum barba-jovis Bull. (as '*barba-jobi*'), Herb. France (Paris) 11: t. 481, f. 2. 1791.

Synonym. Kneiffia irpicoides P. Karst., Bidrag Kannedom Finlands Natur Folk 48: 368. 1889.

Synonym. Hydnum nyssae Berk. & M.A. Curtis, Grevillea 1 (no. 7): 100. 1873.

Specimen studied. Russia, Nizhny Novgorod Oblast, Lukoyanov dist., Razino, *Padus avium* (fallen log), 10 Aug. 2016, coll. *V. Spirin* 10622 (H); Rep. North Osetia-Alania, Vladikavkaz, Dendrarium, on conifer wood, 5 Aug. 2021, coll. *L. Kokaeva* LYK2021_8 (H).

Notes — Our records show that *K. barba-jovis* grows on both conifer and angiosperm wood. All known specimens of *K. barba-jovis* that have been sequenced are from Europe. However, its synonym *H. nyssae* originates from North America. Obtaining sequences of *K. barba-jovis* from North America is necessary to determine whether it is a species complex.

Both MycoBank and Index Fungorum list *Odontia lanceolata* and *Peniophora prominens* as synonyms of *K. barba-jovis*. However, we have doubts about their conspecific status. Weresub (1961) compared *P. prominens* with *Tubulicrinis* species, although she was uncertain about its phylogenetic placement. According to unpublished notes of Kurt Hjortstam, *P. prominens* is related to *Hypochnicium*. As far as we could trace, Jülich & Stalpers (1980) were the first to list *P. prominens* under *K. barba-jovis*, but with a question mark.

When describing *O. lanceolata*, Furukawa (1974) mentioned the presence of thin-walled septate cystidia arranged in bundles at the top of aculei, which are features not characteristic of *K. barba-jovis*. He referred to *Dacryobolus sudans* as the most similar species to his new taxon. In the same paper, Furukawa provided a correct description of *K. barba-jovis* based on his Japanese collection, which indicates his familiarity with the morphological concept of the latter. Later, Maekawa (1993) studied the type and suggested that it is the same as *K. barba-jovis* without dwelling into any details. The revision of the type specimen is clearly needed.

Kneiffiella conidiophora Viner & Spirin, *sp. nov.* — MycoBank MB 848847; Fig. 16, 17

Etymology. *Κόνις* plus -φόρος (Ancient Greek), bearing conidia.

Type. Slovenia, Kočevje, Borovec pri Kočevski Reki, Krokar Forest Reserve, virgin beech-fir (*Fagus sylvatica* and *Abies alba*) forest, N45.5389 E14.7657, *Abies alba* (fallen log), 18 Aug. 2021, coll. *V. Spirin* 14670 (H, holotype). GenBank: ITS+28S = OQ913461.

Basidiocarps effused, adnate, 0.5–1 mm thick, at first minutely floccose or furfuraceous, then odontioid with small (usually less than 1 mm long) conical aculei, cream to sordidly ochraceous. Margin pruinose, indistinctly thinning out. Hymenium between the aculei porose-reticulate, in older basidiocarps. *Hyphal structure* monomitic, hyphae clamped, frequently branched, and cyanophilic, in the centre of the aculei more or less parallel with thickened walls and only sparse ramifications, 2.5–5 µm diam (n = 42). *Subicular hyphae* thin- to thick-walled, 2.5–4.2 µm diam (n = 41). *Subhymenial hyphae* thin-walled, densely intertwined, 2.7–5 µm diam (n = 41). Some terminal hyphal cells in the hymenium have thick-walled tips. *Cystidia* 20–58(–65) × 4–7(–7.5) µm (n = 62); from very few to numerous, thin-walled, projecting or enclosed, cylindrical, obtuse, often with a few or several constrictions, some cystidia have distinctly thickened walls in their proximal part. *Basidia* four-sterigmate, subclavate to cylindrical or utriform 7–18.5(–20) × 3.5–5.5 µm (n = 31). *Basidiospores* smooth, thin-walled, allantoid, (4.2–)5–7.5(–8) × 1.3–1.9(–2.1) µm (n = 91), L = 5.9, W = 1.6, Q = 3.8, usually without guttules, apiculus prominent. *Conidia* (4.5–)5.2–8(–9) × (2.5–)2.8–3.5(–5) µm (n = 41), L = 6.9, W = 3.2, Q = 2.2, vary in shape from ovoid to subellipsoid, tapering towards the base, thick-walled. They develop in the hymenium from subulate (sometimes branched) *conidiophores*, (15–)19.9–28.1(–44) × (0.8–)1.5–3(–3.3) µm (n = 40), with a basal clamp. Cell walls of both conidia and conidiophores are strongly cyanophilous (much more intense than all other elements), which makes them easy to spot in microscope preparations.

Ecology & Distribution — On conifers with confirmed distribution in southern Europe.

Additional material studied. France, Lozère, Aubrac, Les Salces, *Pinus sylvestris* (fallen log), 30 June 2022, coll. *V. Spirin* 15680 (H).

Notes — The presence of strongly cyanophilous conidiophores and conidia make *K. conidiophora* readily identifiable. Eriksson & Ryvarden (1976) reported similar conidiophores in *K. floccosa* (*Bourdot* 6487). In addition, we found a single conidiophore in *K.H. Larsson* O-F-248202, a specimen of *K. frondosarum* described below. Unlike in *K. conidiophora*, the conidiophores and conidia in both specimens are only slightly cyanophilous and extremely rare, making them difficult to find.

Eriksson & Hjortstam (1969) described *Hyphodontia alutacea* var. *mamillicrinis* from Southern Sweden. Unfortunately, the original material was not accessible for comparison but f. 280 in Eriksson & Ryvarden (1976) and f. 26 in Eriksson & Hjortstam (1969) most likely represent *K. conidiophora*. See also taxonomic notes under *K. alutacea.*

Kneiffiella crassispora (P. Roberts) Hjortstam & Ryvarden, Syn. Fungorum (Oslo) 15: 15. 2002

For the description and illustration see Roberts (2000) f. 2.

Basionym. Botryodontia crassispora P. Roberts, Kew Bull. 55(4): 806. 2000.

Notes — *Kneiffiella crassispora* was originally described from Cameroon. To ascertain its phylogenetic position within *Kneiffiella*, sequenced material from West Africa is required.

Kneiffiella curvispora (J. Erikss. & Hjortstam) Jülich & Stalpers, Verh. Kon. Ned. Akad. Wetensch., sect. 2, 74: 134. 1980

For the description and illustrations, refer to Eriksson & Ryvarden (1976) f. 260 and Langer (1994) f. 39–40.

Basionym. Hyphodontia curvispora J. Erikss. & Hjortstam, Svensk Bot. Tidskr. 63(2): 224. 1969.

Type material studied. Sweden, Dalarna, Hamra par., Börningsberget, spruce forest, on fallen trunk of *Picea abies*, 24 Sept. 1966, coll. *Eriksson* 14.09.1966 (GB, holotype).

Ecology & Distribution — All sequenced *K. curvispora* were collected from conifers in Europe (Běťák et al. 2021).

Kneiffiella decorticans (Gresl. & Rajchenb.) Hjortstam & Ryvarden, Syn. Fungorum (Oslo) 26: 43. 2009

For the description and illustrations, refer to Greslebin & Rajchenberg (1997) f. 1–6.

Basionym. Hyphodontia decorticans Gresl. & Rajchenb., Mycotaxon 65: 205. 1997.

Notes — *Kneiffiella decorticans* was described from Argentina. Its phylogenetic placement was confirmed in *Kneiffiella* through molecular evidence by Riebesehl & Langer (2017).

Kneiffiella efibulata (J. Erikss. & Hjortstam) Jülich & Stalpers, Verh. Kon. Ned. Akad. Wetensch., sect. 2, 74: 129. 1980

For the description and illustrations, refer to Eriksson & Ryvarden (1976) f. 305–306 and Langer (1994) f. 44–45.

Basionym. Hyphodontia efibulata J. Erikss. & Hjortstam, Svensk Bot. Tidskr. 63(2): 226. 1969.

Type material studied. Sweden, Västergötland, Bälinge par., W of Torp railway station, on fallen trunk of *Salix* sp., 1 Sept. 1968, coll. *Hjortstam* 01.09.1968 (GB, holotype).

Ecology & Distribution — All sequenced *K. efibulata* were collected from *Salix* wood in Fennoscandia.

Kneiffiella eucalypticola Xue W. Wang & L.W. Zhou, in Wang, May, Liu & Zhou, Journal of Fungi 7 (no. 478): 20. 2021

For the description and illustrations, refer to Wang et al. (2021) f. 8–9.

Notes — An Australian species described based on sequenced material.

Kneiffiella fabiformis Viner & Miettinen, *sp. nov.* — MycoBank MB 848848; Fig. 15, 19

Etymology. *Fabiformis* (Latin), bean-shaped, in reference to its reniform spores with clearly concave adaxial side.

Type. USA, Idaho, Boundary County, Upper Priest River, trailhead, rd 1013, N48.8978 E116.9685, pristine conifer forest dominated by *Tsuga* and *Thuja*, on a fallen crown of *Tsuga heterophylla* (42 cm diam, decay stage 4/5), 16 Oct. 2014, coll. *O. Miettinen* 18884 (H 7009524, holotype). GenBank: ITS + LSU = OQ913451.

Basidiocarps effused, pruinose, arid, 0.1 mm thick, no distinct margin. *Hyphal structure* monomitic, hyphae clamped, frequently branched, strongly cyanophilic. *Subicular hyphae* thick-walled loosely intertwined, 2.2–5 µm diam (n = 21), often with large guttules, subhymenial hyphae thin- to thick-walled, intertwined, 2–4 µm diam (n = 20). *Cystidia* (30–)36.7–97.4(–105) × 4–6(–6.5) µm (n = 20); numerous, slightly thick-walled (up to 0.5 µm) in the proximal part, projecting, somewhat fusiform, without strong incrustation, originating from basal hyphae and only slightly differentiated from these. *Basidia* four-sterigmate, broadly utriform 13–20 × (4–)4.5–5.5 µm (n = 10), thin-walled. *Basidiospores* smooth, thin-walled, reniform, (4.1–)4.6–6.7 × 2–2.5 µm (n = 30), L = 5.7, W = 2.2, Q = 2.6, with clearly concave adaxial side and a few small guttules, apiculus prominent.

Ecology & Distribution — Described based on a single specimen collected from *Tsuga heterophylla* wood in Idaho, USA.

Notes — *Kneiffiella alienata* is the closest match to *K. fabiformis* in both phylogenetic (Fig. 2) and morphological terms. Our DNA-confirmed specimen of *K. alienata* (*Miettinen* 17319) was collected from Massachusetts: the opposite side of North America from the locus classicus of *K. fabiformis*. Although there is no evidence of overlapping distribution of these two species, the following characteristics would be useful for identification: *K. fabiformis* has cystidia with thinner walls, which are somewhat more tapered towards the apex and not encrusted.

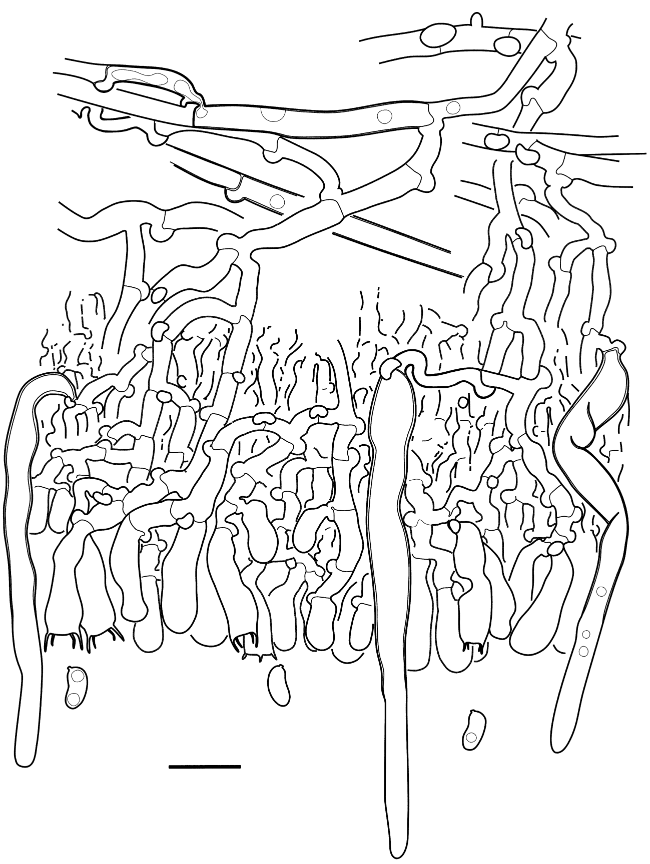

Fig. 19 Microscopic structures of *Kneiffiella fabiformis* (holotype) in CB. — Scale bar = 10 µm.

Additionally, the spores of *K. fabiformis* are more concave compared to those of *K. alienata* (Fig. 15).

Kneiffiella floccosa (Bourdot & Galzin) Jülich & Stalpers, Verh. Kon. Ned. Akad. Wetensch., sect. 2, 74: 130. 1980 — Fig. 7, 20

For additional illustrations, refer to Langer (1994) f. 102–103.

Basionym. Odontia alutacea subsp. *floccosa* Bourdot & Galzin, Hymenomyc. France (Sceaux): 423. 1928.

Type material studied. France, Auvergne-Rhône-Alpes, Lyon, on *Pinus* wood, 11 July 1925, coll. *M. Josserand* (*H. Bourdot* 39600) (PC, lectotype selected by Langer (1994)).

Synonym. Hyphodontia intermedia (Bourdot & Galzin) Parmasto, Consp. System. Corticiac. (Tartu): 125. 1968.

Type material studied. France, Haute-Marne, Andelot-Blancheville, on *Pinus*?, Oct. 1919, coll. *L. Maire* 1264 (*H. Bourdot* 28326) (UPS, lectotype selected by Langer (1994); GB, isolectotype).

Basidiocarps 0.1–0.3 mm thick, effused, adnate, soft, at first minutely floccose or furfuraceous, then odontioid with small conical aculei, cream to ochraceous. Margin pruinose indistinctly thinning out. Hymenium between the aculei porose-reticulate. *Hyphal structure* monomitic, hyphae clamped, frequently branched, and more or less cyanophilic. *Subicular hyphae* slightly thick-walled, loosely intertwined, 2–4.7 µm (n = 100), *subhymenial hyphae* thin-walled, densely intertwined, 1.9–3.2 µm (n = 102). *Cystidia* often aggregated in the distal part of aculei, (38–)65–150(–255) × 5–8(–10) µm (n = 162), from very few to numerous, tubular, thick-walled (up to 3 µm at the proximal part) up to the very tip but sometimes along the entire length, projecting, sometimes with a few constrictions, often with adventitious septa. *Basidia* four-sterigmate, subclavate to cylindrical, or utriform (9–)9.6–16(–19) × 3.5–5 µm (n = 73). *Basidiospores* smooth, thin-walled, allantoid, (4.9–)5.3–7.9 (–8.8) × 1.3–1.9(–2.2) µm (n = 210), L = 6.5, W = 1.6, Q = 4, without guttules, apiculus prominent. One examined specimen, Galzin (*Bourdot* 6487) has conidia 7 × 3 µm (n = 3), which vary in shape from ovoid to subcylindrical. They develop from subulate conidiophores in the hymenium, 30 × 3.5 µm (n = 2), with basal clamps but are not abundant.

Fig. 20 Tubular cystidia in *Kneiffiella floccosa* (*Berglund* 150-02) in CB. — Scale bar = 5 µm.

Ecology & Distribution — *Kneiffiella floccosa* is a conifer-dwelling species. All our collections have been found in northern Eurasia. However, this species also occurs in North America: UC2022902 from Minnesota (Sequence GenBank ID: KP814441) perfectly matches the European sequences of *K. floccosa*); f. 5c–d in Larsen (1964) depicts an American specimen of *K. floccosa* (*Gilbertson* 3787 SY-F), with cystidia similar to its European counterparts.

Additional material studied. France, Auvergne-Rhône-Alpes, Vernusse, on *Pinus* branch, 11 Aug. 1905, coll. *A. Galzin* (*H. Bourdot* 6487) (PC); bois de la Pouge pres St. Priest, on *Pinus sylvestris* wood, 11 July 1905, coll. *H. Bourdot* 6485 (GB). – Russia, Khabarovsk reg., Solnechnyi dist., Igdomi, on *Picea ajanensis* log, 1 Sept. 2014, coll. *V. Spirin* 10728 (H 7046493). – Sweden, Lapland, Norrbotten County, Gällivare Municipality, Muddus National park, on *Picea abies* log, 23 Sept. 1947, coll. *J. Eriksson* 2266 (GB 0094556); Gällivare parish, Granlandet nature reserve, on dead wood, 2002, coll. *H. Berglund* 150-02 (GB).

Notes — Prior to our study, representatives of *K. subalutacea* (including newly described *K. frondosarum*) had been differentiated from the morphologically similar *K. floccosa* based primarily on the latter's more robust hydnoid hymenophore and tubular cystidia that are aggregated in the distal part of aculei. However, we discovered that micromorphologically similar *Kneiffiella* species can also have aculeate and even hydnoid hymenophores. And, vice versa, *K. floccosa* at its initial stages of development typically has minutely floccose hymenophore. Based on our examination of both the original material and fresh ITS-confirmed specimens, we propose new traits for distinguishing *K. floccosa* from other similar looking *Kneiffiella* with an overlapping distribution.

In general, basidiocarps of *K. floccosa* are indeed more robust than the vast majority of *K. subalutacea* and *K. frondosarum* studied by us (Fig. 12). However, this feature is not reliable for identification of East Asian material. For instance, *Spirin* 5694, a specimen of *K.* aff. *frondosarum*, is as robust as fully developed *K. floccosa*. We find the combination of two other traits more useful in identification of this species:

1 Most tips of tubular cystidia in similar-looking *Kneiffiella* species from the Northern Hemisphere taper to a thin-walled condition at a much lower point (10–25 µm from the tip) then in *K. floccosa*. In the latter, most cystidia are thick-walled up to the very tip and sometimes along the entire length. It should be noted that f. 308 in Eriksson & Ryvarden (1976) and f. 32 in Eriksson (1958) depict *K. floccosa* s.str., specimens Galzin (*Bourdot* 6487) and *Eriksson* 2266, respectively, but incorrectly convey their tubular cystidia in a manner more typical for *K. subalutacea*;
2 The spores of *K. floccosa* are significantly smaller compared to those of *K. subalutacea* and *K. frondosarum*, two species that are most commonly mistaken for *K. floccosa* (Fig. 7).

Given the high similarity between *K. floccosa* and *K. subalutacea*, it is not surprising that there was confusion about the taxonomic status of intermediate specimens. For example, *Odontia alutacea* subsp. *intermedia* was classified as a synonym of *K. floccosa* in Eriksson & Ryvarden (1976), a synonym of *K. subalutacea* in Langer (1994), and as a species of its own in Nikolajeva (1961). In our opinion, both the macro- and micromorphology of the type of *O. alutacea* subsp. *intermedia* indicate that it belongs to *K. floccosa*. This specimen was illustrated by Langer (1994) f. 102–103, who accurately conveys the character of its tubular cystidia.

Kneiffiella frondosarum Viner, Spirin & Miettinen, *sp. nov.* — MycoBank MB 848849 — Fig. 7, 12

Etymology. *Frondōsus* plus *-arum* (Latin), belonging to a frondous tree, in reference to the substrate preferences.

Type. FINLAND, Uusimaa, Helsinki, Paloheinä, N60.2551 E24.9431 on a decayed splinter of *Betula* (?) log (20 cm diam, decay stage 4/5), 24 Dec. 2020, coll. *O. Miettinen* 24523 (H 6200077, holotype). GenBank: ITS = OQ913439.

Basidiocarps 0.1–0.5 mm thick, effused, adnate, at first porose-reticulate to furfuraceous, from cream to lurid yellow, darkening to ochraceous or tan when old. Margin pruinose, indistinctly thinning out. *Hyphal structure* monomitic, hyphae clamped, frequently branched and more or less cyanophilic. *Subicular hyphae* thin- to slightly thick-walled, irregularly intertwined, 1.8–3.3 µm (n = 82), *subhymenial hyphae* thin-walled, densely intertwined, 1.3–3.5 µm (n = 80). *Cystidia* (41–)48–120 (–132) × (4–)5–7.5(–8) µm (n = 141); numerous, projecting, tubular, thin-walled in the distal part and sometimes somewhat widening, especially thick-walled (up to 1.2 µm) at the base, rarely with a few constrictions and (or) adventitious septa. *Basidia* four-sterigmate, subclavate to cylindrical or utriform (8–)9–17(–23) × 3.5–5 µm (n = 70). *Basidiospores* smooth, thin-walled, allantoid, (5.5–)6.5–8.9(–10.5) × (1.3–)1.4–1.9 (–2.3) µm (n = 212), L = 7.7, W = 1.6, Q = 4.9, without guttules, apiculus prominent.

Ecology & Distribution — *Kneiffiella frondosarum* is distributed in temperate and boreal Europe and the American Northeast. All studied material and sequences used in phylogenetic analyses are associated with angiosperm wood except for one sequence, which refers to *Langer* 2142 (Sequence GenBank ID: DQ340334). According to our field notes, that specimen was collected from conifer substrate. Unfortunately, it is lost so we are not able to ascertain if its substrate was in fact conifer wood.

Additional material studied. FINLAND, Uusimaa, Helsinki, Haltialan aarnialue, on *Betula* log, 3 June 2012, coll. *O. Miettinen* 15378 (H 6013357). – FRANCE, Lozère, Aubrac, Saint Germain du Teil, *Castanea sativa* (fallen branch), 30 June 2022, coll. *V. Spirin* 15752 (H). – NORWAY, Akershus, Nesodden, Røerskogen, on *Salix*, 18 Sept. 2014, coll. *K.H. Larsson* (O O-F-248202); Vestfold, Tønsberg, Jarlsberg, Gullkronen nature reserve, on angiosperm wood, 11 Oct. 2007, coll. *O. Miettinen* 12026.2 (H 7200286). – POLAND, Podlasie, Hajnówka, Białowieża National Park, mixed, swampy old-growth forest, on *Quercus robur*, 21 Sept. 2019, coll. *O. Miettinen* 22674 (H). – ROMANIA, Arad, Runcu, on *Quercus petraea* wood, 15 Sept. 2021, coll. *V. Spirin* 15008 (H). – USA, New York, Essex Co, Harris Lake N, Mixed, aging forest, on *Betula* log, 23 Sept. 2013, coll. *O. Miettinen* 17175.1 (H).

Notes — Apart from substrate preferences, the only noticeable feature distinguishing *K. frondosarum* from *K. subalutacea* are the slightly thicker walls of cystidia in the latter. It should be noted though that this characteristic may be influenced by the developmental stage of the basidiocarp, and therefore, may not be reliable for identification purposes. As for similar-looking species growing on deciduous substrate and sharing distribution range with *K. frondosarum*, *K. subaltaica* is noteworthy. Previously only known from the holotype collected in Michigan, our DNA-confirmed specimen of *K. subaltaica* (*Miettinen* 15592.2) extends its known distribution to New York where it co-occurs with *K. frondosarum*. The two species can be distinguished by the smaller spores in *K. subaltaica* (Fig. 7).

Hallenberg (1984, 1988, 1991) conducted mating experiments with strains of *K. subalutacea* and identified two European incompatibility groups that were found exclusively on angiosperms. One of these groups is widespread in the Nordic countries, particularly Finland, whence the holotype of *K. frondosarum* originates. Our sequence data on *K. frondosarum* fully matches this geographic range, indicating that these groups may coincide. Since we were unable to examine Hallenberg's specimens during the preparation of this manuscript, the second incompatibility group reported by Hallenberg (a single strain from Scotland) has yet to be addressed. In this context, it is worth noting that *K.* aff. *frondosarum* from the Russian far east, *Spirin* 5694, is morphologically distinct from *K. frondosarum*, with a more robust odontioid basidiocarp and amorphous dark orange matter in the subhymenium. To the naked eye, this matter appears as brown dots on the hymenophore. *Spirin* 5694 forms a highly supported subclade with two other East Asian sequences (Fig. 3), suggesting that it may be a separate species. Additional material and DNA loci are required to confirm whether it constitutes a distinct taxon or not. Accordingly, we do not include this specimen among the paratypes of *K. frondosarum*.

Kneiffiella macra Viner & Miettinen, *sp. nov.* — MycoBank MB 848850; Fig. 12, 13, 21

Etymology. *Μακρά* (Ancient Greek), large, in reference to prominent basidiocarps.

Type: MALAYSIA, Sabah, Ranau, Kinabalu Park, Mesilau, upper mountain primary forest with gymnosperms, N6.04723 E116.5949, alt. 2200 m, on an uprooted tree (20 cm diam, decay stage 2/5), 18 June 2013, coll. *O. Miettinen* 16455 (SNP 35206, holotype; H 7200686, isotype). GenBank: ITS + LSU = OQ913455.

Basidiocarp resupinate, effuse, adnate, 3–6 mm thick, around 30 cm in the longest dimension, ochraceous, when mature cream, sturdy; *hymenophore* labyrinthiform to irregularly lacerate and hydnoid; subiculum prominent (0.5–1 mm); margin indistinct. *Hyphal structure* monomitic, hyphae clamped and frequently branched, cyanophilic. *Tramal hyphae* more or less parallel, noticeably wider than hyphae in both subhymenium and subiculum but sometimes narrowing and becoming skeletal-like, 1.7–5.9 µm (n = 25), distinctly thick-walled (up to 1.2 µm). *Subhymenial hyphae* densely packed, less thick-walled, 2.5–4.2 µm (n = 20). *Subicular hyphae* irregularly intertwined, 2–3.3 µm (n = 20), slightly thick-walled, strongly cyanophilic. *Cystidia* of hymenial origin 20–60.3(–65) × 4.5–6.5 µm (n = 20); numerous, slightly projecting, broadly fusoid to cylindrical, sometimes with cyanophilous contents, thin-walled, naked or when cylindrical covered by coarse crystals. *Basidia* four-sterigmate, broadly clavate to broadly cylindrical, (8–)8.6–13.5(–14) × 3.5–4 µm (n = 12). *Basidiospores* smooth, thin-walled, allantoid, curved, 3–4(–4.3) × 1.4–1.8 µm (n = 30), L = 3.6, W = 1.6, Q = 2.3, without guttules.

Notes — *Kneiffiella macra* has conspicuous basidiocarps and should be easily recognized thanks to its labyrinthic hymenophore. *Kneiffiella amplipora*, another polyporoid *Kneiffiella* from Borneo, is readily distinguishable due to both micro- and macro-morphology (see notes to this species).

Kneiffiella microspora (J. Erikss. & Hjortstam) Jülich & Stalpers, Verh. Kon. Ned. Akad. Wetensch., sect. 2, 74: 130. 1980

For the description and illustrations, refer to Eriksson & Ryvarden (1976) f. 315–316 and Langer (1994) f. 62.

Basionym. Hyphodontia microspora J. Erikss. & Hjortstam, Cortic. N. Eur., 4 (Oslo): 651. 1976.

Type material studied. Sweden, Dalsland, Ödsköłt, near Uleviken, on *Betula* branch, 24 Aug. 1974, coll. *E. Hangström* 24.08.1974 (GP, holotype).

Additional material studied. Indonesia, Papua, Merauke, Wasur National Park, savanna, on a fallen branch, 20 Jan. 2007, coll. *O. Miettinen* 11418 (H).

Notes — *Kneiffiella microspora* specimens with ITS region almost identical to the holotype from Sweden have been found as far southeast as Taiwan (*Langer* 3456, Sequence GenBank ID: DQ340333). The northernmost and easternmost confirmed DNA record of this species is from the Kolyma Lowland in Siberia, strain VKM FW-785, was isolated as a growing mycelium in a permafrost hole at a depth of 27 meters (Sequence GenBank ID: FJ609295). If it is not a species complex, *K. microspora* exhibits remarkable ecological plasticity compared to all other known species of *Hyphodontia* s.lat. See also notes under *K. palmae*.

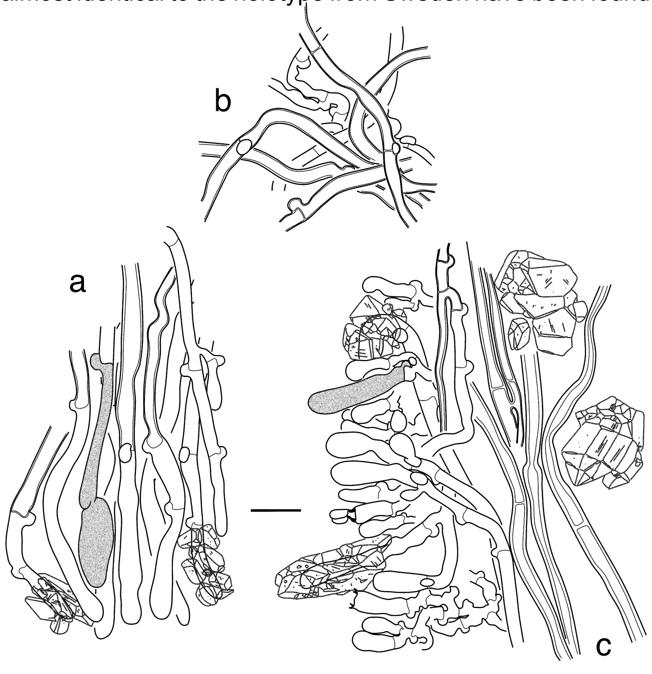

Fig. 21 Microscopic structures of *Kneiffiella macra* (holotype) in CB, grey colour represents cyanophilous content. a. Hyphal ends in lower trama; b. subiculum; c. dissepiment in vertical section. — Scale bar = 10 µm.

Kneiffiella ornamentata Viner, Miettinen & Langer, *sp. nov.* — MycoBank MB 848851; Fig. 15, 22

Etymology. *Ornamentata* (Latin), ornamented, in reference to the characteristic cystidia covered by a grainy crust of crystals.

Type. Malaysia, Sabah, Ranau, Kinabalu Park, Mesilau, N6.04723 E116.5949, alt. 2000 m, montane primary forest, on a fallen tree crown (23 cm diam, decay stage 2/5); 18 June 2013; coll. *O. Miettinen* 16379 (SNP 33608, holotype; H 7200688, isotype). GenBank: ITS + LSU = OQ913452.

Basidiocarps effused, pruinose, arid, 0.1 mm thick, no distinct margin. *Hyphal structure* monomitic, hyphae clamped, frequently branched, strongly cyanophilic. *Subicular hyphae* slightly thick-walled, loosely intertwined, 2–4.3 µm (n = 62). *Subhymenial hyphae* thin- to slightly thick-walled, intertwined, 2.2–5 µm (n = 65). *Cystidia* (50–)64–105(–120) × (4–)4.6–7(–7.5) µm (n = 104); numerous, slightly thick-walled (up to 0.5 µm) in the proximal part, projecting, somewhat fusiform, covered by a thin grainy crust of crystals similar to *Hypochnicium polonense*. The cystidia originate from basal hyphae and are only slightly differentiated from these. *Basidia* four-sterigmate, broadly utriform 9–13.4(–17) × 4–5.5 µm (n = 52), thin-walled. *Basidiospores* smooth, thin-walled, ellipsoid, (4.1–)4.3–5.3(–5.7) × 3–4(–4.2) µm (n = 151), L = 5, W = 3.5, Q = 1.4, with a few small guttules, apiculus prominent.

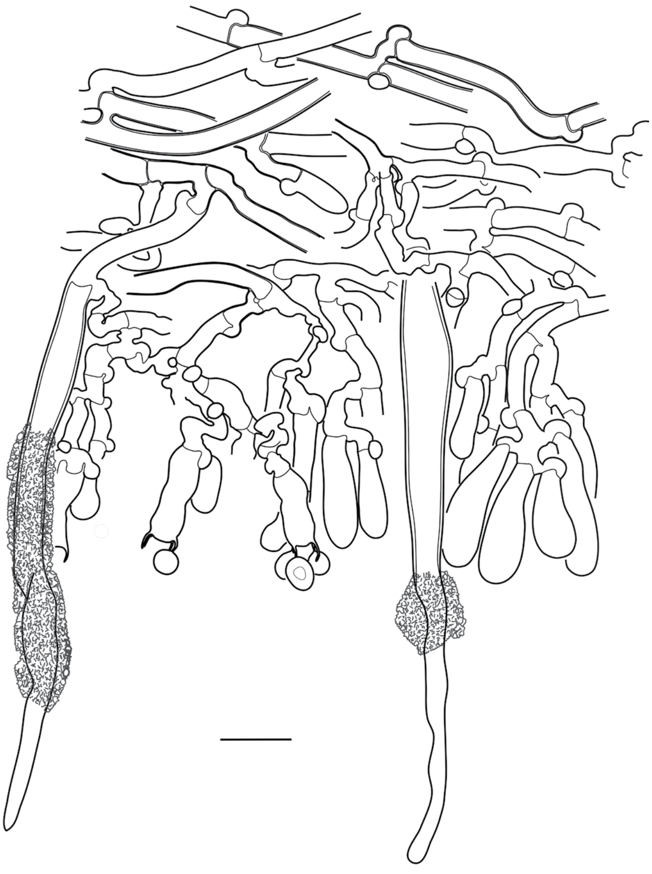

Fig. 22 Microscopic structures in *Kneiffiella ornamentata* (holotype) in CB. — Scale bar = 10 µm.

Ecology & Distribution — *Kneiffiella ornamentata* is a Paleotropical species. ITS varies between our specimens from Réunion and Borneo, which leaves open the possibility that *K. ornamentata* is a species complex. More sequenced collections and additional DNA loci are required to properly address this question.

Additional material studied. France, Réunion, Bourg-Murat, around the parking lot near Col de Bellevue and La Source Reilhac, 17 Mar. 1998, coll. *E. Hennen*, *G.* and *E. Langer* 4875 (KAS); Route forestière Bébour-Bélouve, la Petit Plaine, *Cryptomeria*-forest, 1190 m alt., on *Cryptomeria japonica* log, 20 Mar. 1998, coll. *E. Hennen*, *G.* and *E. Langer* 4957 (KAS); *E. Hennen*, *G.* and *E. Langer* 4958 (KAS); coll. *E. Hennen*, *G.* and *E. Langer* 4959 (KAS).

Notes — Hyphal pattern and the presence of fusiform cystidia brings in mind *K. alienata* and *K. fabiformis*, but the characteristic crystalline cover of cystidia and spore shape in *K. ornamentata* makes it easy to identify. One New Zealand sequence (Sequence GenBank ID: MN103593), which is close to our material (17–20 bp differences), is apparently also morphologically similar, as it is incorrectly identified as *H. polonense*.

Kneiffiella perlongispora Viner, *sp. nov.* — MycoBank MB 848852; Fig. 7, 23

Etymology. *Per-* plus *longus* plus *spora* (Latin), very long spored, in reference to the spores longer than in any other *Kneiffiella* known to us.

Type. Argentina, Río Negro, San Carlos de Bariloche, N41.262300 E71.298300, on angiosperm wood, 2013, coll. *L. Tedersoo* (TUF 116434, holotype). UNITE: ITS = UDB014997|116434.

Basidiocarps 0.1–0.3 mm thick, effused, adnate, porose-reticulate, smooth, grayish white. Margin pruinose, indistinctly thinning out. *Hyphal structure* monomitic, hyphae clamped, frequently branched, more or less cyanophilic. *Subicular hyphae* thin- to slightly thick-walled irregularly intertwined, 1.3–3 µm (n = 30). *Subhymenial hyphae* thin-walled, densely intertwined, 1.6–3 µm (n = 31). *Cystidia* (50–)60–126 × 5.5–8 µm (n = 41); numerous, projecting, tubular with a thin-walled distal part, especially thick-walled at the base (up to 1.2 µm). *Basidia* four-sterigmate, subclavate to cylindrical or utriform 11–15 (–15.5) × (4–)4.5–6 µm (n = 20). *Basidiospores* smooth, thin-walled, allantoid, (8.2–)8.8–10.8(–11.5) × 1.7–2.1 µm, L = 9.7, W = 2, Q = 4.9 (n = 60), with two guttules, apiculus prominent.

Ecology & Distribution — Known only from angiosperm wood in Argentina.

Additional material studied. Argentina, Tierra del Fuego, Dpto. Rio Grande, Ea. Indiana, on *Nothofagus antarctica* wood, 7 Nov. 1998, coll. *M. Rajchenberg* 11779 (BLS).

Notes — *Kneiffiella perlongispora* exhibits the longest spores in comparison to all other known *Kneiffiella* species, reaching up to 11.5 µm in length. This distinct feature facilitates its identification. *Kneiffiella decorticans*, another South American species, also displays long spores (up to 10 µm), but they are considerably wider (2.5–3 µm) than in *K. perlongispora* (1.7–2 µm).

Kneiffiella pilaecystidiata (S. Lundell) Jülich & Stalpers, Verh. Kon. Ned. Akad. Wetensch., sect. 2, 74: 132. 1980

For the description and illustrations, refer to Eriksson & Ryvarden (1976) f. 320–322.

Basionym. *Odontia pilaecystidiata* S. Lundell, Fungi Exsicc. Suecici 43–44 (Sched.): 24. 1953.

Synonym. *Hyphodontia mongolica* Min Wang, Yuan Y. Chen & B.K. Cui, Phytotaxa 309 (1): 50. 2017.

Notes — All sequenced *K. pilaecystidiata* were collected from *Salix* and *Populus* wood in Northern Eurasia.

Fig. 23 Microscopic structures in *Kneiffiella perlongispora* (holotype) in CB. — Scale bar = 10 µm.

Kneiffiella similis Viner & Spirin, *sp. nov.* — MycoBank MB 848853; Fig. 7

Etymology. *Similis* (Latin), similar, in reference to the similarity to *K. subalutacea*.

Type. USA, Washington, Clallam County, Sol Duc, old-growth coniferous (*Pseudotsuga menziesii* and *Tsuga heterophylla*) forest, N47.9323 E123.7700, on *Tsuga heterophylla* log, 6 Oct. 2014, coll. *V. Spirin* 8141 (H 7047219, holotype). GenBank: ITS+28S = OQ913453.

Basidiocarps 0.1 mm thick, effused, adnate, at first smooth to tuberculate, yellowish cream. Margin pruinose, indistinctly thinning out. *Hyphal structure* monomitic, hyphae clamped, frequently branched, cyanophilic. *Subicular hyphae* thin-walled, irregularly intertwined, 2–4 µm (n = 50). *Subhymenial hyphae* thin-walled, densely intertwined, 1.4–2.7 µm (n = 50). *Cystidia* (25–)39–124(–150) × 5–8(–9) µm (n = 84); numerous, projecting, tubular with thin-walled distal part often slightly widening in apical direction, especially thick-walled (up to 1.1 µm) at the base, often with two or more constrictions. *Basidia* four-sterigmate, utriform 11–16(–19) × 3–5 µm (n = 40), slightly thick-walled at the base. *Basidiospores* smooth, thin-walled, allantoid, (4.3–)5–7.1(–7.7) × 1.4–2 µm (n = 120), L = 6.2, W = 1.7, Q = 3.8, without guttules, apiculus prominent.

Ecology & Distribution — On both conifer and deciduous substrates in the American Northwest and Western Canada.

Additional material studied. Canada, Victoria, Saanich Peninsula, Observatiory Hill, margin of the mixed forest, on rotten wood of *Arbutus menziesii*, 20 May 2013, coll. *O. Ceska* (UBC F25938); southern slope above the main gate, mixed forest, on rotting wood, 17 July 2011, coll. *O. Ceska* (UBC F25133). – USA, Washington, Jefferson County, Port Townsend, on *Arbutus menziesii* branch, 9 Oct. 2014, coll. *V. Spirin* 8315 (H 7047351).

Notes — *Kneiffiella similis* has an overlapping distribution with *K. subalutacea*, a conifer-dwelling specialist. Smaller spores in *K. similis* can help in the identification of conifer-derived material from the American Northwest.

Kneiffiella stereicola (Bres.) Nakasone, Cryptog. Mycol. 29(3): 252. 2008

For the description and illustrations, refer to Langer (1994) f. 75–77.

Basionym. Odontia stereicola Bres., Stud. Trent., Classe II, Sci. Nat. Econ. 7(1): 60. 1926.

Synonym. Irpex furfuraceovelutinus Rick, Iheringia 5: 188. 1959.

Synonym. Hyphodontia orasinusensis Gilb. & M. Blackw., Mycotaxon 33: 382. 1988.

Type material studied. USA, Louisiana, Burden Farm, Black Woods, Baton Rouge, on *Celtis lavigata*, 20 Oct. 1983, coll. *M. Blackwell* 2141 (BPI, holotype).

Notes — The only known sequence of this species is from the holotype of *H. orasinusensis* (Sequence GenBank ID: KY081797) collected in Louisiana, whereas types of both *I. furfuraceovelutinus* and *K. stereicola* are from Brazil. In order to determine whether *K. stereicola* is a species complex, additional sequences of this species from South America are required.

See also notes under *K. crassa*.

Kneiffiella subaltaica Riebesehl & Langer, in Langer, Běťák, Holec, Klug & Riebesehl, Nova Hedwigia 115(1–2): 218. 2022 — Fig. 7

For the description and additional illustrations, refer to Langer et al. (2022) f. 9.

Type material studied. USA, Michigan, Cheboygan County, Pellston, The Gorge, Univ. Michigan Biological Station, on decorticated wood of *Tsuga*, 16 Sept. 2016, coll. *H.H. Burdsall* 20039 (CFMR, holotype).

Additional material studied. USA, New York, Essex Co, Huntington Wildlife Forest, Wolf Lake N, mixed old-growth forest, on *Acer* wood, 15 Aug. 2012, coll. *O. Miettinen* 15592.2 (H 7009468).

Notes — *Kneiffiella subaltaica* is described based on the single collection from Michigan. Our collection of *K. subaltaica* from New York is the second report of this species, which expands the known geographic distribution of *K. subaltaica* to the east. It also suggests that this species may grow on both coniferous and hardwood substrates.

Kneiffiella subalutacea (P. Karst.) Jülich & Stalpers, Verh. Kon. Ned. Akad. Wetensch., sect. 2, 74: 131. 1980 — Fig. 7, 12

Basionym. Corticium subalutaceum P. Karst., Meddeland. Soc. Fauna Fl. Fenn. 9: 65. 1883.

Type material studied. Finland, Kanta-Häme, Tammela, Mustiala, on *Pinus sylvestris* log, 13 Sept. 1872, coll. *P.A. Karsten* 1237 (H 6049969, lectotype selected by Eriksson & Ryvarden (1976), FH isolectotype).

Basidiocarps 0.1–1 mm thick, effused, adnate, at first porose-reticulate to furfuraceous, from whitish to cream, darkening to ochraceous or tan when old. Margin pruinose indistinctly thinning out. *Hyphal structure* monomitic, hyphae clamped, frequently branched, more or less cyanophilic. *Subicular hyphae* thin- to slightly thick-walled, irregularly intertwined, 1.8–3.3 µm (n = 111). *Subhymenial hyphae* thin-walled, densely intertwined, 1.8–3.4 µm (n = 113). *Cystidia* (40–)51.5–155.5(–250) × (4–)5–7.8(–8) µm (n = 210); numerous, projecting, tubular, with thin-walled distal part somewhat widening in apical direction, especially thick-walled (up to 2.5 µm) at the base, rarely with a few constrictions and (or) several adventitious septa. *Basidia* four-sterigmate, subclavate to cylindrical or utriform (8–)10–16(–19) × (3–)3.5–5(–5.5) µm (n = 101). *Basidiospores* smooth, thin-walled, allantoid, (5.3–)6–9(–9.7) × 1.4–2(–2.7) µm (n = 306), L = 7.3, W = 1.7, Q = 4.2, sometimes with two guttules, apiculus prominent.

Ecology & Distribution — On coniferous wood throughout temperate and boreal Eurasia and North America.

Additional material studied. France, Aveyron, Millau, Larzac, on *Pinus sylvestris* (fallen branch), 14 Nov. 2022, coll. *V. Spirin* 16280 (H). – Russia, Khabarovsk reg., Solnechnyi dist., Suluk-Makit, on *Picea ajanensis* log, 17 Aug. 2011, coll. *V. Spirin* 4150 (H 7022607); Verkhnebureinskii dist., Dublikan Nat. Res., on *Picea ajanensis* log, 21 Aug. 2014, coll. *V. Spirin* 7727 (H 7028527); Rep. North Osetia-Alania, Zei, Abaytykau, on *Pinus* branch, 13 Aug. 2021, coll. *L. Kokaeva* LYK2021_23 (H). – Slovenia, Bohinj, Krnica, *Picea abies* (fallen log), 26 Sept. 2019, coll. *V. Spirin* 13248 (H); Kranjska Gora, Vršič, *Pinus mugo* (fallen branch), 5 June 2019, coll. *V. Spirin* 12575 (H). – Sweden, Dalsland, Dalskog par., SW of the lake Bergatjärn, on decorticated *Picea abies*, 23 Sept. 1972, coll. *K. Hjortstam* 5861 (GB 0097309). – USA, Washington, Clallam County, Hurricane Ridge, on *Abies lasiocarpa* log, 19 Oct. 2014, coll. *V. Spirin* 8746 (H 7047796); coll. *V. Spirin* 8759 (H 7047833); coll. *V. Spirin* 8752a (H 7047831).

Notes — *Kneiffiella subalutacea* has a distribution that overlaps with several similar species. Noticeably larger spores allow separating it from *K. altaica*, *K. similis*, *K. subaltaica*, and *K. floccosa*. The latter species is also distinguished by more robust hydnoid basidiocarps and tubular cystidia that are thick-walled up to the very tip (Fig. 20, see also notes under *K. floccosa*). Inconveniently, there are no handy morphological traits that distinguish *K. subalutacea* from *K. frondosarum* except for their substrate preferences: *K. subalutacea* grows exclusively on conifers while *K. frondosarum* is an angiosperm-dwelling species.

Relying solely on morphological observations, Eriksson & Ryvarden (1976) hypothesized that *K. subalutacea* constitutes a species complex. In this study, we have restricted the concept of this species to a conifer-dwelling specialist. Nonetheless, the actual diversity of conifer-dwelling *K. subalutacea* exceeds the species we have addressed in this paper. Hallenberg (1984, 1988, 1991) conducted mating tests with *K. subalutacea* strains from the Northern hemisphere and identified at least four incompatibility groups of conifer-dwelling *K. subalutacea*. One of Hallenberg's incompatibility groups was reported as widespread in Nordic countries, particularly Finland (the locus classicus of *K. subalutacea*), and was also found in western North America. Our sequence data on *K. subalutacea* s.str. fully match this geographical range, so it is likely that this group corresponds to *K. subalutacea* s.str. Unfortunately, we were unable to examine Hallenberg's specimens during the preparation of this manuscript, so the three remaining incompatibility groups have yet to be addressed.

Kneiffiella subglobosa (Sheng H. Wu) Hjortstam, in Hjortstam & Ryvarden, Syn. Fungorum (Oslo) 15: 16. 2002

For the description and illustrations, refer to Langer (1994) f. 105–107.

Basionym. Hyphodontia subglobosa Sheng H. Wu, Acta Bot. Fenn. 142: 106. 1990.

Type material studied. Taiwan, Taichung, Tunghai University, on a stump of cut *Acacia confusa*, 5 Aug. 1989, coll. *S.H. Wu* 890805-2 (TAI, holotype; GB, H, TAAM, isotypes).

Synonym. Hyphodontia subefibulata Jia J. Chen & L.W. Zhou, in Chen, Zhou, Ji & Zhao, Phytotaxa 269(1): 7. 2016.

Additional material studied. Singapore, Bukit Timah Nature Reserve, old secondary forest hillside, on angiosperm wood, 19 Mar. 2020, coll. *O. Miettinen* 23605 (H).

Notes — Our phylogenetic analyses did not resolve *H. subefibulata* as a monophyletic clade; the sequences of the type material were interspersed with those of *K. subglobosa* (Fig. 4). Furthermore, *K. subglobosa* from Singapore is morphologically concordant with the holotype of *K. subglobosa* but has an ITS sequence that is fully identical to the holotype of *H. subefibulata*. Based on these results, we treat *H. subefibulata* as a synonym of *K. subglobosa*.

Kneiffiella tetraspora (S.S. Rattan) Hjortstam & Ryvarden, Syn. Fungorum (Oslo) 15: 16. 2002

For the description and illustrations, refer to Langer (1994) f. 109.

Basionym. Hyphodontia efibulata f. *tetraspora* S.S. Rattan, Biblioth. Mycol. 60: 335. 1977.

Type material studied. India, Himachal Pradesh, Jaggat Sukh, Kulu, on *Picea smithiana* wood, 14 Sept. 1971, coll. *S.S. Rattan* 1237 (K, holotype; BPI, DAOM, PAN, TENN, isotypes).

Ecology & Distribution — *Kneiffiella tetraspora* was originally described from Himachal Pradesh in northern India based on a single specimen collected from *Picea smithiana*.

Additional material studied (*Kneiffiella* aff. *tetraspora*). Indonesia, Papua, Barat, Manokwari Reg., Amberbaken, Tamuk near Saukorem, Hilly primary forest with palms, on fallen *Octomeles sumatranus*, decay stage 4, 110 cm diam, 2 Nov. 2010, coll. *O. Miettinen* 14344 (H).

Notes — Our specimen of *K.* aff. *tetraspora* from Papua (*Miettinen* 14344) conforms entirely to the type description of *K. tetraspora* as given in Langer (1994). To ascertain its phylogenetic position within *Kneiffiella*, sequenced material from northern India is required.

Kneiffiella thermophila Viner & Miettinen, *sp. nov*. — MycoBank MB 848854; Fig. 12, 13, 14

Etymology. *Θερμός* plus –φιλος (Ancient Greek), loving warm, in reference to distribution in warm regions.

Type. China, Yunnan, Xishuangbanna, Xishuangbanna Primeval Forest Park near Jinghong, N22.0321 E100.8847, alt. 800 m, streamside valley with somewhat altered natural forest, on angiosperm log (70 cm diam, decay stage 3/5), 13 Aug. 2005, coll. *O. Miettinen* 10251.1 (H 7200687, holotype; BJFC, isotype). GenBank: ITS + 28S = OQ913456.

Basidiocarp resupinate, effuse, adnate, 1–2 mm thick, at first whitish, when mature cream, soft, when dried firm and friable; *hymenophore* poroid with rounded pores 3–6(–7) per mm (n = 80) or especially on vertical substrate with irregularly lacerate or labyrinthine pores; subiculum very thin; margin indistinct, pruinose. *Hyphal structure* monomitic, hyphae with somewhat thickened walls, clamped, frequently branched, distinctly cyanophilic. *Tramal hyphae* are more or less parallel 1.5–3.5 µm (n = 94), in older parts of the hymenophore filled with oily material and in this case completely acyanophilic. *Subicular hyphae* irregularly intertwined, 1.9–3.2 µm (n = 91). *Subhymenial hyphae* densely packed, less thick-walled, 1.8–3.1 µm (n = 91). *Cystidia* of hymenial origin 10–20(–25) × (4.5–)5–6.5(–7) µm (n = 162); numerous, slightly projecting, mostly cylindrical or slightly fusiform, somewhat constricted, thin-walled, obtuse, naked. *Basidia* small, four-sterigmate, cylindrical (3.5–)4–7(–8) × (2–)2.3–3.2 µm (n = 80). *Basidiospores* smooth, thin-walled, allantoid, strongly curved, (2.1–)2.6–3.9(–4.3) × 0.5–0.9 µm (n = 240), L = 3.3, W = 0.7, Q = 4.5, without guttules inside.

Ecology & Distribution — On angiosperm wood in tropical and subtropical regions. All our material came from Asia except for one Floridian collection.

Additional material studied. China, Yunnan, Xishuangbanna, Mandian Water Fall surroundings near Jinghong, on angiosperm wood, 15 Aug. 2005, coll. *O. Miettinen* 10313.2 (H). – Indonesia, Riau, Indragiri Hulu, Bukit Aluran Babi, secondary open forest on angiosperm wood, 30 June 2004, coll. *O. Miettinen* 8764.1 (BO, H); Kampar, Bulu Cina, old riparian secondary forest, on angiosperm wood, 6 Sept. 2013, coll. *O. Miettinen* 16594 (BO, H); Rokan Hilir, Sungai Majo, burned forest clearing on peat, on angiosperm wood, 8 Sept. 2004, coll. *O. Miettinen* 8839.2 (BO, H). – USA, Florida, Alachua County, Gainesville, San Felasco Hammock Preserve, rather old forest with *Carya*, *Quercus*, and *Ostrya*, on angiosperm wood (probably *Quercus*), 24 Nov. 2013, coll. *O. Miettinen* 17887.1 (H).

Notes — To our current knowledge, the distribution range of *K. thermophila* does not overlap with that of the similar *K. abdita*, which is found further north in Eurasia. In GenBank, there are two sequences that actually belong to *K. thermophila* (Sequence GenBank ID: ON063639 and AJ537400). The latter refers to the specimen Zhou 20150802-9, which was apparently misidentified in Wang et al. (2023) as *Echinoporia hydnophora*. We compared our collections of *K. thermophila* with the type specimen of *E. hydnophora* and found them to be distinctly dissimilar. For instance, *E. hydnophora* has ellipsoid spores while they are allantoid in *K. thermophila.*

Kneiffiella trichophora Viner, *sp. nov.* — MycoBank MB 848855; Fig. 12, 24, 25

Etymology. *Τρίχᾰ* plus -φόρος (Ancient Greek), hair-bearing, in reference to narrow aculei.

Type. Ghana, Ashanti Region, Bobiri Forest Reserve, 30 km E of Kumasi, on angiosperm wood, 18 Apr. 1974, coll. *L. Ryvarden* 12735, (H holotype; O, isotype). GenBank: ITS = OQ913463.

Basidiocarps effused, attached by a loose subiculum, hymenial aculei dense, mostly 3–4 mm long, narrow (around 0.3 mm), cylindrical, apically conical and tapering to the subulate sterile apex; ochraceous in dry condition; subiculum cream, cottony, constituting the sterile margin, which indistinctly thins out to the periphery. Hymenium forms a dense layer along aculei except for the apex, while there are only disjoined clusters of basidia between the aculei. *Hyphal structure* monomitic, hyphae without clamps, frequently branched, often cyanophilic. *Tramal hyphae* more or less parallel, some of them noticeably wider than hyphae in both subhymenium and subiculum but sometimes narrowing and becoming skeletal-like especially in the core of aculei, 3.1–5.5 µm (n = 21), thin- to distinctly thick-walled (up to 1 µm). *Subicular hyphae* thin- to thick-walled, irregularly intertwined, 2–4.8 µm (n = 20). *Subhymenial hyphae* thin-walled, densely intertwined, 2–3 µm (n = 20). *Cystidia* (50–)65.3–160 × 5–8 µm (n = 24); frequent along and between aculei but occur rarely closer to their apex; projecting, tubular, with thin-walled distal part often somewhat widening in apical direction, especially thick-walled (up to 1.5 µm) at the base, rarely with a few constrictions and (or) several adventitious septa. *Basidia* four-sterigmate, rounded to broadly utriform 9–13 × 5–6 µm (n = 10). *Basidiospores* smooth, subglobose to ellipsoid, 3.7–4.9(–5.5) × (2.8–)3–3.8 µm (n = 30), L = 4.4, W = 3.2, Q = 1.4, with one guttule inside, apiculus prominent.

Ecology & Distribution — Described based on a single specimen collected from angiosperm wood in Ghana.

Notes — This species is a relative of Asian *K. subglobosa*. They can be distinguished by aculei no longer than 1 mm in the latter and non-overlapping distribution.

Kneiffiella tubuliformis (Sheng H. Wu) Hjortstam & Ryvarden, Syn. Fungorum (Oslo) 26: 47. 2009

For the description and illustrations, refer to Wu (2006) f. 1.

Basionym. Hyphodontia tubuliformis Sheng H. Wu, Mycotaxon 95: 185. 2006.

Ecology & Distribution — Described from Taiwan based on a single specimen collected from *Pinus* branch. To ascertain its phylogenetic position within *Kneiffiella*, sequenced material from Taiwan is required.

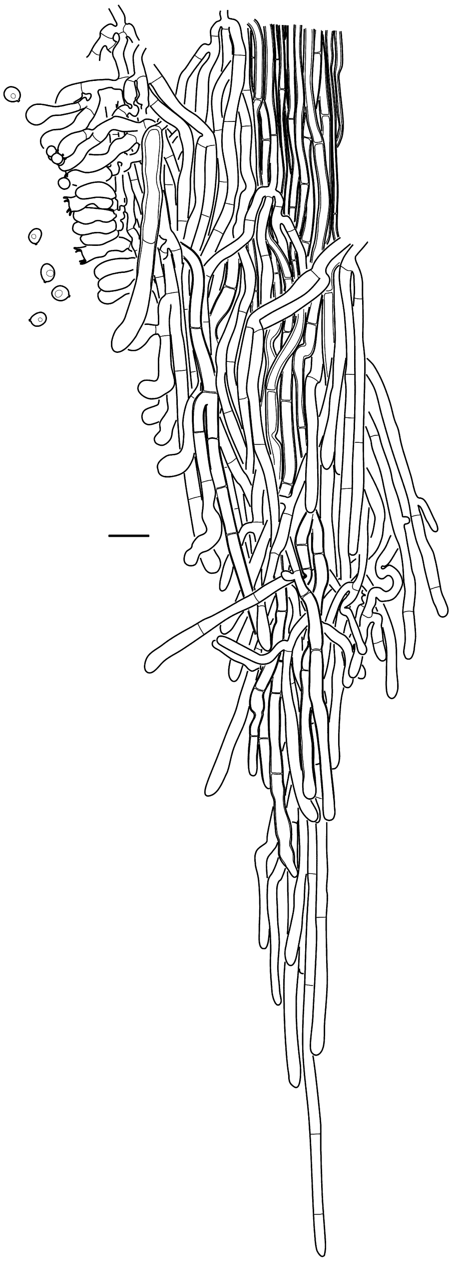

Fig. 24 Part of aculeal apex of *Kneiffiella trichophora* (holotype) in CB. — Scale bar = 10 µm.

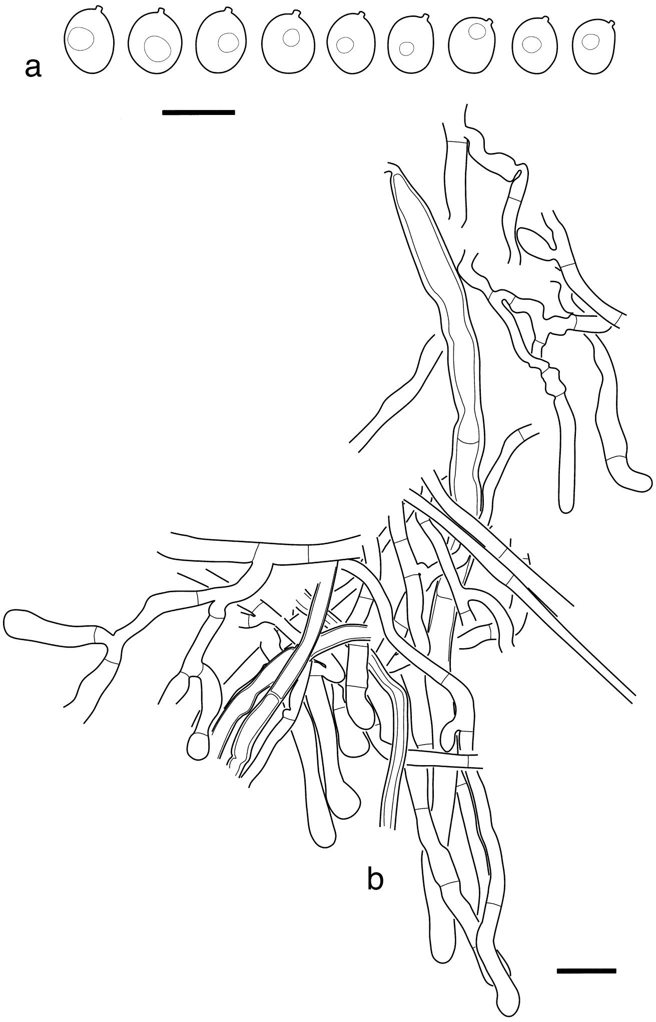

Fig. 25 Microscopic structures in *Kneiffiella trichophora* (holotype) in CB. a. Basidiospores; b. section through the part of the fruit body between aculei with tubular cystidia. — Scale bars: a = 5 µm; b = 10 µm.

IDENTIFICATION KEY

The following key includes all *Kneiffiella* (29 species) and *Egonia* (four species) as accepted on 2 Feb. 2024

1\. Basidiocarps prominent with poroid, semiporoid, labyrinthiform to raduloid hymenophore, cystidia thin-walled 2
1\. Hymenophore otherwise 6

2\. Cystidia pestle-shaped (both capitate and basally widened), Northern Eurasia . . . . *K. pilaecystidiata*
2\. Cystidia otherwise, never pestle-shaped 3

3\. Basidiospores up to 1 µm wide 4
3\. Basidiospores wider than 1 µm 5

4\. Cystidia up to 7 µm wide. — Indonesia, Southern China, and Florida . . . . *K. thermophila*
4\. Cystidia slightly narrower usually no wider than 5 µm. — Northern Eurasia . . . . *K. abdita*

5\. Basidiospores 3.9–5 µm in length, cystidia naked . . . . *K. amplipora*
5\. Basidiospores 3–4 µm in length, heavily incrusted cystidia frequent . . . . *K. macra*

6\. Entirely without clamp connections 7
6\. Most hyphae with clamp connections 11

7\. Most basidia with two sterigmata . . . . *K. efibulata*
7\. Most basidia with four sterigmata 8

8\. Basidiospores longer than 5 µm, slightly thick-walled. — West Africa . . . . *K. crassispora*
8\. Basidiospores shorter than 5 µm. 9

9\. Cystidia cylindrical apically incrusted cystidia; basidiospores narrowly ellipsoid, 3–5 × 2–2.5 µm *K. tetraspora*
9\. Cystidia naked, basidiospores ≥ 3 µm in width, on hardwood 10

10\. Aculei up to 1 mm long. — East and South-East Asia. . . . . *K. subglobosa*
10\. Aculei up to 4 mm long. — Ghana . . . . . . *K. trichophora*

11\. Cystidia pestle-shaped (both capitate and basally widened) . . . . *K. pilaecystidiata*
11\. Cystidia otherwise, never pestle-shaped 12

12\. Basidiospores ellipsoid to subglobose. 13
12\. Basidiospores otherwise 19

13\. Simple-septate in subiculum and aculeus core. — Western Hemisphere . . . . *K. stereicola*
13\. All hyphae with clamp connections 14

14\. Cystidia often covered with a thin grainy crust of crystals similar to *Hypochnicium polonense* . . . . . *K. ornamentata*
14\. Cystidia otherwise 15

15. Basidiospores up to 3.5 µm long and less than 3 µm wide . . . . *K. microspora*
15. Basidiospores larger 16

16. Cystidia covered with clusters of coarse crystals, often somewhat fusiform, hymenium smooth . . . . . . *K. alienata*
16. Cystidia otherwise, fruit body is not smooth when fully developed 17

17. Aculei up to 3 mm long, basidiospores ellipsoid to subglobose (both sides convex) . . . . *K. barba-jovis*
17. Aculei up to 1 mm, basidiospores subellipsoid (one side might be slightly concave), ellipsoid to ovoid 18

18. Conifer-dwelling species known from Northern Hemisphere, basidiospores often slightly broader towards the base . . . . *K. abieticola*
18. Angiosperm-dwelling species known only from Australia, basidiospores otherwise . . . . *K. eucalypticola*

19. Cystidia of subhymenial origin clearly thin-walled throughout the entire length 20
19. Most cystidia of subicular origin, clearly thick-walled at least closer to the proximal part (tubular cystidia) 22

20. Most basidiospores strongly curved, less than 1 µm wide . . . . *K. curvispora*
20. Basidiospores allantoid but not strongly curved, more than 1 µm wide 21

21. Some terminal hyphal cells in the hymenium are differentiated by having strongly thick-walled (up to 2.5 µm) tips. Strongly cyanophilous conidiophores and ovoid to subellipsoid conidia present . . . . *K. conidiophora*
21. Terminal hyphal cells otherwise. Conidiophores and conidia absent . . . . *K. alutacea*

22. Basidiospores reniform Q = 2.6 with clearly concave adaxial side, cystidia slightly thick-walled (up to 0.5 µm), somewhat fusiform. — Northwestern United States . . . . *K. fabiformis*
22. Basidiospores and cystidia otherwise 23

23. Basidiospores < 2 µm wide on average 24
23. Basidiospores ≥ 2 µm wide on average 30

24. Most cystidia thick-walled up to the very tip and sometimes along the entire length . . . . *K. floccosa*
24. Cystidia otherwise 25

25. Basidiospores > 10 µm, up to 11.5 µm, always with at least two guttules. — South American species . . . . *K. perlongispora*
25. Basidiospores shorter, only occasionally with guttules 26

26. Basidiospore average Q ≤ 3.5 27
26. Basidiospore average Q ≥ 4.2 28

27. Most basidia typically ≤ 10 µm, cystidia up to 10 µm in width. — Northern Eurasia . . . . *K. altaica*
27. Most basidia typically ≥ 10 µm, cystidia up to 7 µm in width. — North America . . . . *K. subaltaica*

28. Basidiospores 5.5–7.2 µm in length. — American Northwest . . . . *K. similis*
28. Basidiospores 6–9 µm in length. — Northern Eurasia and North America 29

29. On conifer wood . . . . *K. subalutacea*
29. On angiosperm wood . . . . *K. frondosarum*

30. Cystidia robust up to 15 µm in width, walls up to 6 µm thick. — South America . . . . *K. decorticans*
30. Cystidia thinner (≤ 10 µm), walls up to 3 µm thick. — Eurasia and North America 31

31. Hymenophore grandinioid to odontioid. — Taiwan . . . . *K. tubuliformis*
31. Hymenophore more or less smooth, never odontioid. — Northern Eurasia and North America (*Egonia*) 32

32. Cystidia never reaching 100 µm in length with walls thickened up to 1 µm. — American Northwest *E. occidentalis*
32. Cystidia more robust. — Northern Eurasia 33

33. Thin-walled capitate cystidia present in the hymenium, on conifers . . . . *E. heremita*
33. Thin-walled capitate cystidia typically absent 34

34. Thin-walled hyphidia swollen at the base 31–45 × 4–5 µm present in the hymenium, basidiospores 2–2.4 µm in width on average, without oil drops or with only a few small ones, on both conifer and angiosperm wood . . . . *E. cineracea*
34. Basidiospores 2.3–3.4 µm in width on average, with prominent guttules, on conifers. . . . . *E. turgida*

EXCLUDED AND INSUFFICIENTLY KNOWN TAXA

Kneiffiella byssoidea (H. Furuk.) Hjortstam & Ryvarden (as '*byssoideus*'), Syn. Fungorum (Oslo) 26: 42. 2009

Basionym. Odontia byssoidea H. Furuk., Bull. Govt. Forest Exp. Stn Meguro 261: 18. 1974.

Notes — It appears that Hjortstam & Ryvarden (2009) relied only on the original description when introducing this combination, as there are no indications that they studied the type. According to the protologue, *K. byssoidea* has lanceolate cystidia of subicular origin that are thick-walled throughout their entire length. This feature is unique in the genus. Sequences of this taxon from East Asia is necessary to accurately determine its generic placement.

Kneiffiella crassa (Rick) Hjortstam & Ryvarden, Syn. Fungorum (Oslo) 15: 14. 2002

Basionym. Odontia crassa Rick, Egatea 17: 279. 1932.

Notes — *Kneiffiella crassa* has not been properly typified to date. Rick (1932) did not designate a type when describing the species. Hjortstam & Ryvarden (1982) returned to the matter of typification of *O. crassa*. They studied eight specimens labeled as *O. crassa* by Rick, with collection dates ranging between 1930 and 1939 (Rick (1959) provides the complete lists of specimens he labelled as *O. crassa*). Hjortstam & Ryvarden (1982) attempted to designate Rick 19888, collected in 1933, as a type. Since this specimen dates after the protologue, it should be considered a neotype. However, since the original material available for a lectotype exists (predating the publication of the species), their typification cannot be considered effective (Art. 9.8). To properly reinstate this name, the original material needs to be revisited, and a lectotype should be selected from it.

Nakasone (2008) considered *K. crassa* synonymous with *K. stereicola*. She based her judgement on the neotype selected by Hjortstam & Ryvarden (1982). We consider this issue – identity of *K. stereicola* vs *K. crassa*, unresolved until proper typification.

Kneiffiella palmae Rick ex Hjortstam & Ryvarden, Syn. Fungorum (Oslo) 26: 45. 2009

Notes — *Odontia palmae* Rick was published in Rick (1959) as an illegitimate name because the type was not indicated (Art. 40.1). In an attempt to validate it, Langer (1994) introduced *Hyphodontia palmae* Rick ex Langer with the lectotype Rick 22701. However, he did not indicate the single fungarium, where this specimen is stored, instead referring to two herbaria (PACA and O) simultaneously. Therefore, the criterion for lectotypification was not fulfilled (Art. 40.7). Later, Hjortstam & Ryvarden (2002) mistakenly considered *Hyphodontia palmae* Rick ex Langer as a validated taxon and cited Rick 22701 in PACA as the holotype. If made before 1 January 2001, such typification would be a correctable error, and Rick 22701 (PACA) would be the lectotype automatically. However, after that date, the code plainly requires the use of the word ‘lectotypus’ or its equivalent term for lectotypification (Art. 9.21). This means that both *O. palmae* and based on it *K. palmae* remain invalid names. Although Hjortstam & Ryvarden (1982) indicated the close affinity of Rick 22701 to *K. microspora*, we refrain from selecting it as a lectotype and thus validating *O. palmae* to avoid the use of a problematic name without molecular reference.

Kneiffiella parvispora Rick, in Rambo (ed.), Iheringia, Sér. Bot. 4: 111. 1959

Notes — *Kneiffiella parvispora* was not validly published for a type was not indicated (Art. 40.1).

Kneiffiella sinensis (H.X. Xiong, Y.C. Dai & Sheng H. Wu) Riebesehl & Langer, Mycol. Progr. 16(6): 650. 2017

Basionym. Hyphodontia sinensis H.X. Xiong, Y.C. Dai & Sheng H. Wu, Mycologia 102(4): 921. 2010.

Notes — Riebesehl & Langer (2017) introduced this combination based on thin-walled cystidia in *K. sinensis* that are similar to those of *K. alutacea*, *K. curvispora*, and *K. abdita*. However, when combined with other traits of *K. sinensis*, such as thick-walled ellipsoid basidiospores and the presence of thick-walled, apically inflated cystidia, no *Kneiffiella* known to us appear to be related. Later, these authors abandoned this combination in *Kneiffiella*, and compared it with the genus *Fasciodontia* (Yurchenko et al. 2020). In our opinion, the aforementioned morphological traits are reminiscent of taxa such as *Xylodon calongei* and *X. ussuriensis*. Sequences of *H. sinensis* from East Asia is necessary to accurately determine the generic placement of this species.

Kneiffiella sparsa Rick, in Rambo (ed.), Iheringia, Sér. Bot. 4: 112. 1959

Notes — *Kneiffiella sparsa* was not validly published for no type specimen was indicated (Art. 40.1).

DISCUSSION

Traits that were once thought to be synapomorphic and used to define taxa are often found to be the result of independent evolution (for examples in corticioid fungi see Larsson & Larsson (2003), and Spirin et al. (2019, 2021); in both corticioid and polyporoid fungi see Miettinen et al. (2012)). In this study, we segregated *Egonia* from *Kneiffiella*, despite their remarkably similar morphology, including characteristic tubular cystidia that is shown to be a homoplasic character. Although the two genera are morphologically definable only through a combination of quantitative characters (see notes under *Egonia*), they are phylogenetically distantly related within the *Hymenochaetales*.

The function of sterile elements in basidiocarps of aphyllophoroid fungi is generally unknown with few exceptions such as stephanocysts and echinocysts in *Peniophorella* that are involved in nutrition and capturing invertebrates (Hallenberg 1990). Tubular (or similar) cystidia are in four genera of the *Hymenochaetales* (*Kneiffiella*, *Egonia*, *Tubulicrinis*, and *Xylodon*) as well as in other orders of the Agaricomycetes, for instance the *Auriculariales* (e.g., *Protomerulius dubius*), *Corticiales* (e.g., *Vuilleminia macrospora*), *Jaapiales* (e.g., *Jaapia argillacea*), *Polyporales* (e.g., *Crustoderma dryinum*, *Dacryobolus karstenii*), and *Gloeophyllales* (e.g., *Chaetodermella luna*). Their function is unknown, and their development may simply be a consequence of undiscovered genetic traits that predisposes certain lineages to develop such structures. Further studies in ecology, genomics, and developmental biology may elucidate the function and value of cystidia. From a taxonomic perspective, this highlights the need to reevaluate accepted morphologically uniform genera, particularly those with limited DNA barcoding coverage, to ensure accurate classification of morphologically similar taxa. Indubitably, micromorphology is still important and informative for fungal taxonomy at the species level, but molecular data is less subjective and provides a more informative means of supraspecific classification.

Our analyses place *Egonia* and *Jacksonomyces* in a highly supported clade that encompasses at least three available families: *Hymenochaetaceae*, *Neoantrodiellaceae*, and *Nigrofomitaceae*. If *Egonia* in fact resolves at the base of the *Hymenochaetaceae* (as shown in Fig. 1), two options become available: 1) the erection of a separate family for *Egonia*; or 2) its inclusion within the *Hymenochaetaceae.* In its current state, the *Hymenochaetaceae* is a well-defined family of macromycetes characterized by robust, dark-coloured basidiocarps with a xanthochroic reaction and simple-septate hyphae. With the addition of *Egonia*, with its inconspicuous, whitish basidiocarps and clamped hyphae, the morphological boundaries between the *Hymenochaetaceae* and other families of the order would be significantly blurred. Such a taxonomic re-arrangement would also call into question the necessity of a separate family for the *Trichaptum* clade, for which the names *Nigrofomitaceae* and *Neoantrodiellaceae* are available. On the other hand, the family placement of the remaining *Kneiffiella* clade seems to be straightforward if our order-level phylogeny is correct. We are not aware of any available family names for it except for *Chaetoporellaceae*, which currently would be a monotypic family. Notwithstanding these arguments, we believe that a revision of family limits within the *Hymenochaetales* is clearly premature without more comprehensive sampling, both in terms of generic types and DNA loci. Therefore, we refrain from assigning *Egonia* and *Jacksonomyces* to any existing family.

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