The genus Fomitopsis (Polyporales, Basidiomycota) reconsidered

V. Spirin^{1,2,*}, K. Runnel³, J. Vlasák⁴, I. Viner¹, M.D. Barrett⁵, L. Ryvarden⁶, A. Bernicchia⁷, B. Rivoire⁸, A.M. Ainsworth⁹, T. Grebenc¹⁰, M. Cartabia¹¹, T. Niemelä¹, K.-H. Larsson^{12, 13}, O. Miettinen¹

¹Botany Unit (Mycology), Finnish Museum of Natural History, P.O. Box 7, FI-00014 University of Helsinki, Finland; ²Department of Biological and Environmental Sciences, University of Gothenburg, Box 461, 40530 Gothenburg, Sweden; ³Institute of Ecology and Earth Sciences, University of Tartu, J. Liivi 2, 50409 Tartu, Estonia; ⁴Biology Centre, Academy of Sciences of the Czech Republic, Branišovská 31, CZ 37005, České Budějovice, Czech Republic; ⁵Australian Tropical Herbarium, Sir Robert Norman Building, James Cook University Cairns Campus, McGregor Road, Smithfield, QLD 4878, Australia; ⁶Institute of Biological Sciences, University of Oslo, P.O. Box 1045, Blindern, N-0316 Oslo, Norway; ⁷Via Alessandro Guidotti 39, I-40134 Bologna, Italy; ⁸Société Linnéenne de Lyon, 33 rue Bossuet, 69006 Lyon, France; ⁹Jodrell Laboratory, Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AE UK; ¹⁰Slovenian Forestry Institute, Večna pot 2, 1000 Ljubljana, Slovenia; ¹¹Via Lazio 19, 21100 Varese, Italy; ¹²Natural History Museum, University of Oslo, P.O. Box 1172, Blindern, 0318 Oslo, Norway; ¹³Gothenburg Global Biodiversity Centre, University of Gothenburg, Box 461, 40530 Gothenburg, Sweden

*Corresponding author: V. Spirin, viacheslav.spirin@helsinki.fi, spirin.viacheslav@bioenv.gu.se

Abstract: Based on seven- and three-gene datasets, we discuss four alternative approaches for a reclassification of *Fomitopsidaceae (Polyporales, Basidiomycota)*. After taking into account morphological diversity in the family, we argue in favour of distinguishing three genera only, *viz. Anthoporia, Antrodia* and *Fomitopsis*. *Fomitopsis* becomes a large genus with 128 accepted species, containing almost all former *Fomitopsis* spp. and most species formerly placed in *Antrodia, Daedalea* and *Laccocephalum*. Genera *Buglossoporus, Cartilosoma, Daedalea, Melanoporia, Neolentiporus*, alongside twenty others, are treated as synonyms of *Fomitopsis*. This generic scheme allows for morphologically distinct genera in *Fomitopsidaceae*, unlike other schemes we considered. We provide arguments for retaining *Fomitopsis* and suppressing earlier (*Daedalea, Caloporus*) or simultaneously published generic names (*Piptoporus*) considered here as its synonyms. Taxonomy of nine species complexes in the genus is revised based on ITS, ITS + *TEF1* + *RPB1* and ITS + *TEF1* + *RPB2* datasets. In total, 17 species are described as new to science, 26 older species are reinstated and 26 currently accepted species names are relegated to synonymy. A condensed identification key for all accepted species in the genus is provided.

Key words: brown-rot fungi, new taxa, phylogeny, polypores, taxonomy.

Taxonomic novelties: New species: Fomitopsis algumicola Grebenc & Spirin, F. caseosa Vlasák & Spirin, F. cupressicola Vlasák, J. Vlasák Jr. & Spirin, F. derelicta Vlasák & Spirin, F. dollingeri Vlasák & Spirin, F. fissa Vlasák & Spirin, F. lapidosa Miettinen & Spirin, F. lignicolor Vlasák & Spirin, F. maculosa Miettinen & Spirin, F. pannucea Runnel & Spirin, F. perhiemata Viner & Spirin, F. purpurea Spirin & Ryvarden, F. retorrida Spirin & Kotiranta, F. solaris Rivoire, A.M. Ainsworth & Vlasák, F. tristis Miettinen & Spirin, F. tunicata Miettinen & Spirin, F. visenda Miettinen & Spirin. New combinations: Fomitopsis aculeata (Cooke) Spirin & Miettinen, F. aethalodes (Mont.) Spirin, F. alaskana (D.V. Baxter) Spirin & Vlasák, F. albidoides (A. David & Dequatre) Bernicchia & Vlasák. F. amygdalina (Berk. & Ravenel) Spirin & Vlasák, F. angusta (Spirin & Vlasák) Spirin & Vlasák, F. atypa (Lév.) Spirin & Vlasák, F. caespitosa (Murrill) Spirin & Miettinen, F. calcitrosa (Spirin & Miettinen) Spirin & Miettinen, F. circularis (B.K. Cui & Hai J. Li) Spirin, F. concentrica (G. Cunn.) M.D. Barrett, F. cyclopis (Miettinen & Spirin) Miettinen & Spirin, F. dickinsii (Berk. ex Cooke) Spirin, F. elevata (Corner) Spirin & Miettinen, F. eucalypti (Kalchbr.) Spirin, F. ferrea (Cooke) Spirin & Viner, F. flavimontis (Vlasák & Spirin) Vlasák & Spirin, F. foedata (Berk.) Spirin & Miettinen, F. gilvidula (Bres.) Spirin & Miettinen, F. glabricystidia (Ipulet & Ryvarden) Miettinen & Ryvarden, F. globispora (Ryvarden & Aime) Spirin, F. hartmannii (Cooke) M.D. Barrett & Spirin, F. hyalina (Spirin, Miettinen & Kotir.) Spirin & Miettinen, F. hypoxantha (Bres.) Spirin & Miettinen, F. incana (Lév.) Spirin & V. Malysheva, F. infirma (Renvall & Niemelä) Miettinen & Niemelä, F. juniperina (Murrill) Spirin & Vlasák, F. kuzyana (Pilát ex Pilát) Spirin & Vlasák, F. leioderma (Mont.) Spirin & Vlasak, F. leucaena (Y.C. Dai & Niemelä) Spirin & Miettinen, F. luzonensis (Murrill) Spirin & Miettinen, F. maculatissima (Lloyd) Spirin, F. madronae (Vlasák & Ryvarden) Vlasák & Ryvarden, F. malicola (Berk. & M.A. Curtis) Spirin, F. marchionica (Mont.) Spirin & Miettinen, F. marianii (Bres.) Spirin, Vlasák & Cartabia, F. mellita (Niemelä & Penttilä) Niemelä & Miettinen, F. microcarpa (B.K. Cui & Shun Liu) Spirin, F. micropora (B.K. Cui & Shun Liu) Spirin, F. modesta (Kuntze ex Fr.) Vlasák & Spirin, F. monomitica (Yuan Y. Chen) Spirin & Viner, F. morganii (Lloyd) Spirin & Vlasák, F. moritziana (Lév.) Spirin & Miettinen, F. neotropica (D.L. Lindner, Ryvarden & T.J. Baroni) Vlasák, F. nigra (Berk.) Spirin & Miettinen, F. nivosella (Murrill) Spirin & Vlasák, F. oboensis (Decock, Amalfi & Ryvarden) Spirin, F. oleracea (R.W. Davidson & Lombard) Spirin & Vlasák, F. philippinensis (Murrill) Spirin & Vlasák, F. primaeva (Renvall & Niemelä) Miettinen & Niemelä, F. psilodermea (Berk. & Mont.) Spirin & Vlasák, F. pulverulenta (Rivoire) Rivoire, F. pulvina (Pers.) Spirin & Vlasák, F. pulvinascens (Pilát ex Pilát) Niemelä & Miettinen, F. quercina (L.) Spirin & Miettinen, F. ramentacea (Berk. & Broome) Spirin & Vlasák, F. renehenticii (Rivoire, Trichies & Vlasák) Rivoire & Vlasák, F. roseofusca (Romell) Spirin & Vlasák, F. sagraeana (Mont.) Vlasák & Spirin, F. sandaliae (Bernicchia & Ryvarden) Bernicchia & Vlasák, F. sclerotina (Rodway) M.D. Barrett & Spirin, F. serialiformis (Kout & Vlasák) Vlasák, F. serialis (Fr.) Spirin & Runnel, F. serrata (Vlasák & Spirin) Vlasák & Spirin, F. squamosella (Bernicchia & Ryvarden) Bernicchia & Ryvarden, F. stereoides (Fr.) Spirin, F. subectypa (Murrill) Spirin & Vlasák, F. substratosa (Malençon) Spirin & Miettinen, F. tropica (B.K. Cui) Spirin, F. tumulosa (Cooke) M.D. Barrett & Spirin, F. tuvensis (Spirin, Vlasák & Kotir.) Spirin & Vlasák, F. uralensis (Pilát) Spirin & Miettinen, F. ussuriensis (Bondartsev & Ljub.) Spirin & Miettinen, F. variiformis (Peck) Vlasák & Spirin, F. yunnanensis (M.L. Han & Q. An) Spirin, Daedaleopsis candicans (P. Karst.) Spirin, Megasporoporia eutelea (Har. & Pat.) Spirin & Viner, Neofomitella hemitephra (Berk.) M.D. Barrett, Pseudophaeolus soloniensis (Dubois) Spirin & Rivoire, P. trichrous (Berk. & M.A. Curtis) Vlasák & Spirin. New synonyms: Antrodia bondartsevae Spirin, A. huangshanensis Y.C. Dai & B.K. Cui, A. taxa T.T. Chang & W.N. Chou, A. wangii Y.C. Dai & H.S. Yuan, Antrodiella subnigra Oba, Mossebo & Ryvarden, Antrodiopsis Audet, Boletus quercinus Schrad., Brunneoporus Audet, Buglossoporus Kotl. & Pouzar, Buglossoporus eucalypticola M.L. Han, B.K. Cui & Y.C. Dai, Caloporus P. Karst., Cartilosoma Kotlaba & Pouzar, Coriolus clemensiae Murrill, C. cuneatiformis Murrill, C. hollickii Murrill, C. parthenius Hariot & Pat., C. rubritinctus Murrill, Daedalea Pers., Daedalea allantoidea M.L. Han, B.K. Cui & Y.C. Dai, D. americana M.L. Han, Vlasák & B.K. Cui, D. radiata B.K. Cui & Hai J. Li, D. rajchenbergiana Kossmann & Drechsler-Santos, D. sinensis Lloyd, Daedalella B.K. Cui & Shun Liu, Dentiporus Audet, Flavidoporia Audet, Fomes subferreus Murrill, Fomitopsis cana B.K. Cui, Hai J. Li & M.L. Han, F. caribensis B.K. Cui & Shun Liu, F. cystidiata B.K. Cui & M.L. Han, F. ginkgonis B.K. Cui & Shun Liu, F. iberica Melo & Ryvarden, F. incarnata K.M. Kim, J.S. Lee & H.S. Jung, F. subfeei B.K. Cui & M.L. Han, F. subtropica B.K. Cui & Hai J. Li, Fragifornes B.K. Cui, M.L. Han & Y.C. Dai, Leptoporus epileucinus Pilát, Melanoporia Murrill, Neoantrodia Audet, Neolentiporus Rajchenb., Nigroporus macroporus Ryvarden & Iturr., Niveoporofomes B.K. Cui, M.L. Han & Y.C. Dai, Pilatoporus Kotl. & Pouzar, Piptoporus P. Karst., Polyporus aurora Ces., P. durescens Overh. ex J. Lowe, P. griseodurus

© 2024 Westerdijk Fungal Biodiversity Institute. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/bync-nd/4.0/).

Lloyd, Poria incarnata Pers., Pseudoantrodia B.K. Cui, Y.Y. Chen & Shun Liu, Pseudofomitopsis B.K. Cui & Shun Liu, Ranadivia Zmitr., Rhizoporia Audet, Rhodofomes Kotl. & Pouzar, Rhodofomitopsis B.K. Cui, M.L. Han & Y.C. Dai, Rhodofomitopsis pseudofeei B.K. Cui & Shun Liu, R. roseomagna Nogueira-Melo, A.M.S. Soares & Gibertoni, Rubellofomes B.K. Cui, M.L. Han & Y.C. Dai, Subantrodia Audet, Trametes fulvirubida Corner, T. lignea Murrill, T. lusor Corner, T. pseudodochmia Corner, T. subalutacea Bourdot & Galzin, T. supermodesta Ryvarden & Iturr., T. tuberculata Bres., Tyromyces multipapillatus Corner, T. ochraceivinosus Corner, T. palmarum Murrill, T. singularis Corner, T. squamosellus Núñez & Ryvarden, Ungulidaedalea B.K. Cui, M.L. Han & Y.C. Dai. Lectotypes: Hexagonia sulcata Berk., Polyporus castaneae Bourdot & Galzin, Poria incarnata Pers., Trametes subalutacea Bourdot & Galzin, Ungulina substratosa Malençon. Neotypes: Agaricus soloniensis Dubois, Boletus pulvinus Pers.

Citation: Spirin V, Runnel K, Vlasák J, Viner I, Barrett MD, Ryvarden L, Bernicchia A, Rivoire B, Ainsworth AM, Grebenc T, Cartabia M, Niemelä T, Larsson K-H, Miettinen O (2024). The genus *Fomitopsis (Polyporales, Basidiomycota)* reconsidered. *Studies in Mycology* **107**: 149–249. doi: 10.3114/sim.2024.107.03 Received: 26 July 2023; Accepted: 10 November 2023; Effectively published online: 22 February 2024 Corresponding editor: R.A. Samson

INTRODUCTION

The transition from the traditional morphology-based classification to one supported by molecular phylogenetics heralded the beginning of a new era in fungal taxonomy. Within the past two decades the new methods (phylogenetic analyses) and evidence (genetic markers) have largely replaced the morphology-based phenetic systematics that guided fungal taxonomy for centuries. The challenge now lies in connecting the old and new types of evidence. As a rule, contemporary phylogenetic studies maintain safe links to traditional morphology-based systems, but often with little critical overview. This becomes evident when reviewing modern genus-level taxonomy wherein many newly detected smallscale clades in old morphology-based genera have been raised to generic rank. This approach fulfils some of the criteria necessary for solid genus delimitation while overlooking others. Notably, whereas the criterion of monophyly (cf. Vellinga et al. 2015) is fulfilled, alternative formal classifications to the multiple new genera are rarely discussed. This may be due to limitations in the data: such discussions would require analysis of the deeper nodes of the phylogenetic clades, which is difficult because it requires both extensive global sampling and the use of multiple genetic markers. Further complication is that the type material, a benchmark in the morphology-based systematics, is often very old and difficult (or impossible) to sequence and connect to recent material. This could be partly compensated with critical morphological analysis but is sufficiently carried out in a few recent studies only. Combined, these issues have brought about many cases of unstable phylogeny. It is particularly problematic when associated with well-known fungal groups that perform crucial functions in ecosystems and serve as flagships in fungal conservation.

Polypores constitute one such well-known group among the wood-inhabiting basidiomycetes. Before the advent of modern DNA methods, taxonomy of wood-inhabiting basidiomycetes in general and polypores in particular relied on two main cornerstones: the type of wood decay and anatomical traits of basidiocarps. Depending on wood-decay characteristics, these fungi were traditionally divided in two groups - brown- and white-rot producing species. The type of rot was recognized as a taxonomically significant character sufficient for rearranging morphologically similar species into separate genera or supra-generic units after the studies by Nobles (1958, 1971), David (1980) and Gilbertson (1980). In addition to wood-decay features, hyphal structure (hyphal system) has been regarded as one of the most profound characters for taxonomy of polypores (Corner 1935, 1953, Cunningham 1954). The morphology-based genus division of brown-rot polypores, that until recently prevailed in taxonomic literature, widely corresponded to Corner's concept of hyphal systems: species with monomitic hyphal structure (all hyphae

more or less uniform, clamped) were placed in the genus Postia (= *Oligoporus*), species with dimitic structure (possessing fibrous, thick-walled and nonclamped 'skeletal' hyphae alongside thinwalled and clamped ones) referred to Antrodia, and predominantly trimitic species (with branched 'binding' hyphae, in addition to the two previous hyphal types) gathered in Fomitopsis. Additionally, a few genera of brown-rot polypores had been characterized via hymenophore configuration (Daedalea), specific basidiocarp colour (Melanoporia), basidiospore morphology (Sarcoporia, Jahnoporus), presence of peculiar cystidia (Amylocystis, Auriporia) or absence of clamp connections (Laetiporus, Pycnoporellus). In general, hyphal structure was regarded as correlating with basidiocarp type and, consequently, with the life strategy of a species: monomitic taxa possess ephemeral, usually soft basidiocarps, dimitic ones have sturdier, seasonal fruitbodies, while trimitic taxa produce tough, as a rule perennial basidiocarps (Ryvarden 1991).

The first attempts to reconsider this simplistic approach were undertaken by Kotlaba and Pouzar (1957, 1990, 1993, 1998) in several publications dealing with the genus Fomitopsis. They stressed the high morphological diversity of Fomitopsis spp. and argued for further splitting of this genus based on consistency and pigmentation of basidiocarps, as well as thickness of the basidiospore wall. Ryvarden (1991) criticized their reclassification, pointing out the lack of data regarding the value of the aforementioned characters in dismantling Fomitopsis sensu lato. Most of the polypore manuals published between 1990 and 2010 treated Fomitopsis in a wide sense (e.g., Ryvarden & Gilbertson 1993, Bernicchia 2005, Niemelä 2005) while a few authors supported ideas by Kotlaba and Pouzar (Vampola 1996, Spirin & Zmitrovich 2003, Spirin et al. 2006). Eventually, it became apparent that no good solution could be proposed for a redefinition of Fomitopsis and allied genera with the use of traditional criteria only.

Applying the molecular phylogenetic methods generated considerable turbulence in the generic definition of Fomitopsis but has not yet resulted in solutions that would satisfy the taxonomic community as well as the broader audience. Kim et al. (2005) were the first to show that Fomitopsis is polyphyletic by applying DNA methods to investigate the phylogenetic relationships of this genus and other brown-rot polypores. Ortiz-Santana et al. (2013) obtained the same result with a much broader set of taxa. Neither of these studies, however, resulted in taxonomic conclusions. Justo et al. (2017) proposed a comprehensive family-level reclassification of the Polyporales based on a three-gene dataset. They reinstated the family Fomitopsidaceae to encompass Fomitopsis spp. (except F. officinalis considered incertae sedis), Antrodia sensu stricto (as redefined by Spirin et al. 2013a), most of the residual Antrodia species (after Ortiz-Santana et al. 2013, Spirin et al. 2013b, 2016), and Anthoporia (Karasiński & Niemelä 2016). The three included

Fomitopsis species formed a strongly supported clade with residual Antrodia spp., as well as Daedalea guercina (generic type of Daedalea) and Piptoporus betulinus (generic type of Piptoporus). Nevertheless, Justo et al. (2017) refrained from giving an explicit interpretation for delimiting genera in the Fomitopsidaceae. A year before, Han et al. (2016) detected representatives of Fomitopsis in nine different clades, of which eight belonged to Fomitopsidaceae sensu Justo et al., which were described or re-introduced as separate genera. These results were based on a six-gene dataset including sequences of 26 Fomitopsis sensu lato species, i.e. nearly half of all species accepted in the genus at that time. Audet (2017) and Zmitrovich (2018) proposed eight new genera to name unranked clades containing residual Antrodia/Daedalea spp. in the Fomitopsidaceae, basing their suggestions on already published data. Finally, Liu et al. (2022) published an all-encompassing revision of brown-rot taxa in the Polyporales grounded on a partial seven-gene dataset. Their study resulted in introducing four more genera in the family. However, there is still a need for studies of deep nodes in the Fomitopsidaceae with a sufficiently wide taxon sampling and, consequently, there has been a lack of discussions regarding other options for translating the phylogenetic trees into formal taxonomic units.

In this study, we aimed to redefine the genus *Fomitopsis* by combining thorough type studies with multigene analyses in the *Fomitopsis* clade containing residual *Antrodia* spp., along with *Daedalea/Piptoporus/Fomitopsis* spp. in the *Fomitopsidaceae* sensu Justo et al. (2017). First, we compiled comprehensive multigene datasets to show the position and limits of *Fomitopsidaceae* within *Polyporales*, and among other brownrotting families. Simultaneously, we revised 133 type specimens and sequenced at least two genetic markers for 80 species assigned to the genus *Fomitopsis* below. As *Fomitopsis sensu lato* encompasses dozens of described species all over the world, we aimed for a wide geographic coverage, to include many species not hitherto sequenced.

Our earlier studies in brown-rot polypores showed that an apparent morphological dissimilarity does not necessarily imply evolutionary remoteness. When redefining the genus *Antrodia*, we showed it embraces not only sturdy dimitic poroid species but also monomitic or nearly monomitic poroid and corticioid taxa; the latter ones were previously classified among widely different genera, *i.e. Postia* and *Phlebia* (Spirin *et al.* 2013a, Runnel *et al.* 2019). The same is true for *Fomitopsis* as redefined in the present study: we show it should encompass several members of such traditional polypore genera as *Dichomitus*, *Gloeophyllum*, *Junghuhnia*, *Laccocephalum*, *Nigroporus*, *Skeletocutis*, *Trametes*, and *Tyromyces*, which were not included in phylogenetic studies of brown-rot polypores before. We assign 128 species to the genus *Fomitopsis* and describe seventeen species as new. Twenty-six names in use are proposed as synonyms of already described taxa.

MATERIAL AND METHODS

Morphological study

Type specimens and other collections from herbaria H, O, S, PC, K, PRM, TUF, LY, LE, UPS, L, HUBO, NY, BPI, MICH, FH, GB, W, LJF, MCF, MJ, C, MPU, MG, BO, BORH, DNA, MEL, and PERTH were studied. Herbarium acronyms are given according to Thiers (2021). Morphological study (i.e., pore and spore measuring techniques) follows Miettinen et al. (2018). All structures were measured from microscopic mounts in Cotton Blue (henceforth CB), using phase contrast and oil immersion lenses (Leitz Diaplan microscope, ×1 250 magnification). In total, 20-30 basidiospores, 20 subhymenial / tramal and subicular / context hyphae (skeletal hyphae for dimitic species, generative hyphae for monomitic ones), and at least 10 basidia were measured per specimen studied. The following abbreviations are used in morphological descriptions: L - mean basidiospore length, W - mean basidiospore width, Q' length / width ratio, Q - mean length / width ratio, n - number of measurements per specimens measured.

While describing hyphal structures in *Fomitopsis* spp., we apply the term 'monomitic' to the species having clamps throughout and 'dimitic' to those with unclamped, aseptate, thick-walled (skeletal) hyphae, regardless of the degree of branching in the skeletal hyphae. We follow proposals of Rajchenberg (1986) and Hattori (2005) and avoid describing hyphal structure in the genus as trimitic because all species treated below do not have differentiated binding hyphae characteristic for the representatives of *Polyporaceae* (e.g., *Funalia, Trametes, Ganoderma*) (see Results for further discussion on this subject). Basidiospores are described as thin-walled if the spore wall is visible in phase contrast as an outer contour, having a distinct wall if the wall thickness is at the measurable minimum (*i.e.* $0.1-0.2 \mu m$ thick), and slightly thick-walled if the spore wall is $0.3-0.4 \mu m$ thick.

DNA isolation and sequencing

DNA extraction, PCR, and sequencing of the target loci for this study (ITS, LSU, RPB1 and TEF1) followed protocols described by Spirin et al. (2013b), Tamm and Põldmaa (2013), and Liimatainen and Ainsworth (2018). The ITS region was amplified using primers ITS1F and ITS4B (Gardes & Bruns 1993), and/or ITS2, ITS4, ITS5 (White et al. 1990), 58A1F (Martin & Rygiewicz 2005), LR22 (Vilgalys lab, Duke University) (https://sites.duke.edu/vilgalyslab/files/2017/08/ rDNA-primers-for-fungi.pdf)), and the D1-D2 domains of the LSU region using primers CTB6 (Garbelotto et al. 1997) and LR7 (Vilgalys & Hester 1990). The area between conserved domains A and C of RPB1 (c. 1 400 bp) was amplified using primers RPB1gAf and RPB1-fCr (Stiller & Hall 1997, Matheny et al. 2002). The TEF1 region was amplified using primers EF983F and EF2218R (Matheny et al. 2007). Amplification products were sequenced at the Genomics Laboratory of the Biology Centre, Academy of Sciences of the Czech Republic (České Budějovice, Czech Republic), Macrogen Europe (Netherlands), Eurofins Genomics (Germany), and the Jodrell Laboratory, Royal Botanic Gardens (Kew, UK). Deciphering and assembling of chromatograms were performed as described in Viner et al. (2021). Data for the studied specimens and the GenBank accession numbers of ITS, LSU, RPB1, RPB2 and TEF1 sequences are presented in Table 1 and Suppl. Table S1.



Sancion	Constitute / species-level	Drivingenies (newly gen	ובו מובח אבלתבוורב		nave). Mb / LINITE 2000	notanina noton		Doformana(a)
ohecies	opecifien (curue) /	Arrigini (rao coue)		Celloo				Reletence(s)
	repository		LSU	ITS	RPB1	RPB2	TEF1	
Amylocystis lapponica	FP-105131-Sp (CFMR)	US-CO	КҮ948879	KY948805	KY 948973	I	I	Justo et al. (2017)
Amyloporia carbonica	Zabel-40-GLN (CFMR)	US-NY	KC585065	KC585243	KY949013	I	Ι	Ortiz-Santana et al. (2013); Justo et al. (2017)
A. sinuosa	FP-105386-Sp (CFMR)	HN-SU	KC585066	KC585244	KY949018	I	Ι	Ortiz-Santana et al. (2013); Justo et al. (2017)
A. xantha	DAOM 16570	CA-BC	KC585076	KC585254	KY949016	Ι	I	Ortiz-Santana et al. (2013); Justo et al. (2017)
Anthoporia albobrunnea	Spirin 4665 (H)	RU-LEN	КҮ948880	КҮ 948808	KY949020	Ι	I	Justo <i>et al.</i> (2017)
Antrodia griseoflavescens	Spirin 11175 (H)	RU-LEN	MK119762	MK119762	MK134850	Ι	I	Runnel <i>et al.</i> (2019)
A. heteromorpha	HHB-140162 (CFMR)	US-AK	KC585279	KC585279	KY949010	I	I	Ortiz-Santana <i>et al.</i> (2013); Justo <i>et al.</i> (2017)
А. тарра	Spirin 4605 (H)	RU-VLG	MK119770	MK119770	MK134844	I	I	Runnel <i>et al.</i> (2019)
A. multiformis	Vlasak 1209/76 (PRM)	US-AZ	KT381618	KT381618	MK134846	I	Ι	Kout <i>et al.</i> (2017); Runnel <i>et al.</i> (2019)
A. serpens	Vampola 20.09.1990 (MJ)	SK	KC543143	KC543143	KY949012	I	I	Spirin <i>et al.</i> (2013a); Justo <i>et al.</i> (2017)
A. tenerifensis	Kout 1412/2 (PRM)	ES	KY446066	KY446066	MK134848	I	I	Kout <i>et al.</i> (2017); Runnel <i>et al.</i> (2019)
Crustoderma corneum	HHB-5685-Sp (CFMR)	US-MT	KC585143	KC585318	КҮ949037	I	Ι	Ortiz-Santana et al. (2013); Justo et al. (2017)
Dacryobolus karstenii	Miettinen 18685 (H)	US-WA	КҮ948900	КҮ948743	КҮ948955	Ι	OQ789530	Justo <i>et al.</i> (2017)
Daedalea nyvardeniana	FLOR41052	BR	Ι	OP526845	Ι	Ι	I	Cristaldo <i>et al.</i> (2022)
D. ryvardeniana	URM80515	BR	Ι	OP526846	Ι	Ι	Ι	Cristaldo <i>et al.</i> (2022)
Fibroporia gossypium	Rajchenberg 11443	AR	КҮ948897	KY948811	КҮ949029	I	I	Justo <i>et al.</i> (2017)
F. vaillantii	FP-90877-R (CFMR)	US-NJ	KC585170	KC585345	KY949035	Ι	I	Ortiz-Santana et al. (2013); Justo et al. (2017)
Fomitopsis abieticola	Cui 10521 (BJFC)	CN	Ι	MN148231	Ι	Ι	MN161746	Liu <i>et al.</i> (2021)
F. abieticola	Cui 10532 (BJFC)	CN	Ι	MN148230	I	MN158174	MN161745	Liu <i>et al.</i> (2021)
F. aculeata	CSIRO (M) E7436	ID-KI	I	AJ536655	I	I	I	GenBank
	CSIRO (M) E7381	ID-KI	I	AJ542522	I	I	I	GenBank
	CSIRO (M) E7393	ID-KI	Ι	AJ542530	Ι	Ι	I	GenBank
	Cui 8624 (BJFC)	CN	Ι	JQ314348	I	Ι	I	Li & Cui (2013)
	Cui 8487 (BJFC)	CN	Ι	JQ314349	I	Ι	I	Li & Cui (2013)
	Yuan 3629 (BJFC)	CN	Ι	JQ314350	I	I	I	Li & Cui (2013)
	Miettinen 8674 (H)	ID-RI	ON970637	ON970637	Ι	Ι	Ι	This study
F. aethalodes	Campi 70 (FACEN 004306)	PΥ	I	OP526843	I	I	I	Cristaldo <i>et al.</i> (2022)
F. africana	Kout 1408/K9 (H)	TH	ON924667	ON994669	OP022430	I	Ι	This study
	Mossebo 13* (MUCL42384)	CM	I	DQ491422	I	I	I	Kim <i>et al.</i> (2008)
	isolate 6565	Z	I	MG430333	I	I	I	GenBank
	isolate 6566	Z	Ι	MG430334	I	Ι	Ι	GenBank
	isolate 6537	Z	Ι	MG430342	I	Ι	Ι	GenBank
	Miettinen 15198 (H)	ID-RI	I	ON970652	I	I	Ι	This study
F. albidoides	Bernicchia 5672	Π	KC543147	KC543147	I	I	I	Spirin <i>et al.</i> (2013a)

SPIRIN ET AL.

species . algumicola	Specimen (culture) / repository Bemicchia 7224 (HUBO) MCF MAK 01/2095 MCF MAK 07/8020 MCF MAK xx/771	Origin (ISO code) IT MK MK	 	GenB: ITS KC543114 FM872461 FM872462 FM872463 FM872463	ink / UNITE acce: <i>RPB1</i> OP022431 	ssion number RPB2 	TEF1 	
: amygdalina : atypa	MCF MAK 00/4578 MCF MAK 07/8293 Vlasák 1707/9J (H) TFRI 781 TFRI 782	MK MK CR CR CR	— — — — — — —	FM872465 FM872465 MN318452 EU232191 EU232192				
	Cui 8355 (BJFC) Dai 7857 (BJFC) Cui 8515 (BJFC) Cui 10151 (BJFC) Cui 10124 (BJFC) Cui 10124 (BJFC) ZD16091109 Dunaev 27.1.2019 (H) Ryvarden 17588 (O)			CC207398 KC907399 KP171204 KP171205 KR605291 MN523241 ON970658 ON994670				
betulina caespitosa	L-15603-Sp (CFMR) CIRM-BRFM1772 Cui 10140 (BJFC) Cui 10154 (BJFC) Cui 10181 (BJFC) Miettinen 5486 (H) Miettinen 1307 (H) Miettinen 13076 (H)	US-N D-RI D-RI SB SB SB SB SB SB SB SB SB SB SB SB SB	KC585202	KC585373 CIRM- BRFM1772 JQ067651 JQ067652 JQ067653 KC595913 KC595910 KC595911 KC595912	KY949005			יסססביבי אי
cajanderi	Dunaev w/n (H) KUN 1123 (H) KUN 2874 (H) Miettinen 8823.3 (H) CBS 127.24 HOU 10773 Cui 9888 (BJFC) Spirin LE213630 Vlasák 0410/14 (JV)	LK MY MY ID-RI US-RU-PRI RU-NIZ US-VA		ON934671 ON970655 ON970656 ON970632 DQ491407 DQ491413 KC507156 KC595915 KC595915				HAT HIN KALL

www.studiesinmycology.org

. (Continued).	Specimen (culture) / repository	Origin (ISO code)	1	GenBa	ank / UNITE acces	ssion number	100	Reference(s)
	Ichoaitory		LSU	ITS	RPB1	RPB2	TEF1	
	Spirin 4089 (H)	RU-KHA		ON994672		I	I	This study
	FP-133692 (CFMR)	US-OR	KC585127	KC585303	КҮ 948998	I	Ι	Ortiz-Santana et al. (2013); Justo et al. (2017)
	Miettinen 13120.1 (H)	ID-SB	Ι	KC595916	I	Ι	I	Ortiz-Santana <i>et al.</i> (2013)
	BBH 40441	Ħ	Ι	KX421865	Ι	Ι	Ι	GenBank
	Miettinen 15115.2 (H)	ID-RI	ON924668	ON924668	Ι	Ι	Ι	This study
	Dai 18551 (BJFC)	MA	Ι	MW377283	I	I	I	Liu <i>et al.</i> (2022)
	Dai 18562 (BJFC)	MA	I	MW377284	I	I	I	Liu <i>et al.</i> (2022)
	Dai 17823 (BJFC)	SG	Ι	MW377285	I	I	I	Liu <i>et al.</i> (2022)
	UOC MINNP M18	LK	I	KP780437	I	I	I	GenBank
	Vlasák 1504/28 (PRM)	CR	ON994673	ON994673	I	I	I	This study
	Vlasák 1504/36J (H)	CR	ON924669	ON994674	OP022433	I	I	This study
	Cui 8488 (BJFC)	CN	I	JQ314351	I	I	I	Li & Cui (2013)
	Cui 10134 (BJFC)	CN	I	JQ314352	I	I	I	Li & Cui (2013)
	Cui 10125 (BJFC)	CN	I	JQ780411	I	I	I	GenBank
	Dai 13062 (BJFC)	CN	I	KP171200	I	I	I	Han <i>et al.</i> (2016)
	Barrett F197/11 (PERTH)	AU	ON691651	ON691651	ON667940	I	I	This study
	Vlasák 1312/E15 (PRM)	CR	KT156690	KT156690	OP022434	I	I	Vlasák <i>et al.</i> (2016); this study
a	AN49	BR	I	MF589756	I	I	I	Soares <i>et al.</i> (2017)
	NM692	BR	Ι	MF589757	Ι	Ι	Ι	Soares et al. (2017)
	NM710	BR	Ι	MF589758	Ι	Ι	Ι	Soares et al. (2017)
	JMB34	BR	Ι	MF589760	Ι	Ι	Ι	Soares et al. (2017)
	NM731	BR	I	MF589761	I	I	Ι	Soares et al. (2017)
	PS2013-01	BR	I	MF772343	I	I	I	Soares <i>et al.</i> (2017)
	Kout 0610/K4 (H)	BZ	I	ON994675	I	I	I	This study
	Vlasák 1908/81 (H)	GF	Ι	ON994676	Ι	Ι	Ι	This study
a	Dollinger 778 (H)	US-FL	Ι	ON994677	Ι	Ι	Ι	This study
	Vlasák 1706/7J (H)	US-NJ	Ι	ON994678	Ι	Ι	Ι	This study
	Vlasák 1706/9J (H)	US-NJ	I	ON994679	I	I	I	This study
	Vlasák 1710/21	US-NJ	I	ON994680	I	I	I	This study
	Ryvarden 45191 (CFMR)	BZ	I	FJ403211	I	I	I	Lindner <i>et al.</i> (2011)
	Vlasák 2104/2J (H)	US-TX	I	ON994681	I	I	I	This study
	NBRC4979	Ъ	I	AB733158	I	I	I	GenBank
	NBRC31163	Ъ	Ι	AB733161	Ι	Ι	I	GenBank
	strain 027	CN	Ι	EU661878	Ι	Ι	Ι	GenBank
	Ryvarden 21710	CN	Ι	FJ403210	I	I	I	Lindner <i>et al.</i> (2011)
	strain xsd08139	CN	I	FJ481049	I	I	Ι	GenBank

																																		1				
	Reference(s)		GenBank	GenBank	GenBank	GenBank	GenBank	Li & Cui (2013)	GenBank	GenBank	Han <i>et al.</i> (2015)	Han <i>et al.</i> (2015)	Han <i>et al.</i> (2016)	GenBank	GenBank	GenBank	This study	This study	This study	This study	Ortiz-Santana <i>et al.</i> (2013)	Liu <i>et al.</i> (2022)	Liu <i>et al.</i> (2022)	Liu <i>et al.</i> (2022)	Liu <i>et al.</i> (2019)	Liu <i>et al.</i> (2019)	Liu <i>et al.</i> (2019)	Han & Cui (2015)	Han & Cui (2015)	Soares et al. (2017)	This study	This study	Soares <i>et al.</i> (2017)	Han & Cui (2015); this stud	Yuan <i>et al.</i> (2020)	Yuan <i>et al.</i> (2020)	Yuan <i>et al.</i> (2020)	This study
		TEF1	1	I	I	I	I	I	Ι	Ι	I	Ι	I	Ι	I	I	OP019459	I	Ι	I	Ι	I	Ι	I	MK900483	I	MK900484	I	I	Ι	OP019460	OP215805	Ι	I	I	Ι	Ι	I
	ssion number	RPB2	1	I	I	I	I	I	Ι	Ι	I	Ι	Ι	Ι	I	Ι	Ι	I	Ι	I	Ι	I	Ι	Ι	Ι	I	I	I	I	Ι	Ι	Ι	Ι	Ι	I	Ι	Ι	I
	ink / UNITE acce	RPB1	1	I	I	I	I	Ι	Ι	Ι	Ι	Ι	Ι	Ι	I	Ι	Ι	OP022432	Ι	I	Ι	I	Ι	Ι	Ι	I	I	I	I	Ι	Ι	OP022435	Ι	Ι	I	Ι	Ι	I
	GenBa	ITS	FJ810145	FJ810167	FJ810173	FJ810178	JN182911	JQ314353	KC505574	KJ668556	KP171201	KP171202	KR605790	MG712332	MK172824	MN823154	ON970657	ON994682	ON994683	ON994684	KC595917	MW377280	MW377281	MW377282	MK852560	MK852561	MK852562	KC844850	KC844851	KX423689	ON970659	ON994685	KX423688	KF999924	MK461952	MK461953	MK461954	ON970630
		LSU		I	Ι	Ι	Ι	Ι	Ι	Ι	Ι	Ι	Ι	Ι	Ι	Ι	Ι	ON924670	Ι	ON924671	Ι	Ι	Ι	Ι	Ι	Ι	I	I	I	Ι	Ι	ON924673	Ι	ON924672	I	Ι	Ι	ON970630
	Drigin (ISO code)		N	N	N	N	N	N	N	ß	N	N	N	N	N	R	Z	JS-FL	D-RI	D-RI	NU NU	N N	N	N	Ń	NU NU	N N	Έ	ßR	ßR	Z	JS-CA	R	'n	N N	Ń	'n	D-PA
	Specimen (culture) / C	repository	strain dd08028 C	strain dd08028 C	strain dd08076 C	strain dd08089 C	isolate 143 C	Cui 6825 (BJFC) C	HE2730 C	KUC20130903A-13 K	Yuan 2685 (BJFC) C	Yuan 2707 (BJFC) C	Yuan 1090 (BJFC) C	450526MF0259 C	MHHNU 8317 C	strain KMCC04903 K	Dunaev 7.II.2019 (H)	Dollinger 56 (H)	Miettinen 8692 (H) II	Miettinen 20529 (H) II	Schigel 5234 (H) A	Cui 16748 (BJFC) A	Cui 16773 (BJFC) A	Cui 16786 (BJFC) A	Cui 16594 (BJFC) A	Cui 16595 (BJFC) A	Cui 16598 (BJFC) A	Ryvarden 37603 (O) V	Oinonen 60119006 (H) B	URM 86162 B	Dunaev 26.1.2019 (H) It	Vlasák 0407/13J (H) U	URM 89405 B	Uotila 42928 (H) A	Cui 16794 (BJFC) A	Cui 16803 (BJFC) A	Cui 16807 (BJFC) A	Miettinen 11466 (H) II
Table 1. (Continued).	Species																F. dochmia	F. dollingeri	F. elevata		F. eucalypti				F. eucalypticola			F. feei			F. ferrea	F. fissa	F. flabellata	F. foedata				
¥	FUN FUN DIV IN S	GALBI ERSIT TITUT	к 0 Ү Е	WV	/W.S	stud	iesi	nmy	colo	ogy.	org																										15	5

Table 1. (Continued).								
Species	Specimen (culture) /	Origin (ISO code)		GenBa	ink / UNITE acces	sion number		Reference(s)
	repository		LSU	ITS	RPB1	RPB2	TEF1	
F. fragilis	Cui 10919 (BJFC)	CN	KF937286	KF937286	I	I	I	Han <i>et al.</i> (2016)
F. gilvidula	Miettinen 20535 (H)	ID-RI	ON924674	ON994686	Ι	Ι	Ι	this study
F. glabrocystidia	Ipulet 378 (O)	NG	ON970633	ON970633	OQ789528	I	Ι	this study
F. globispora	C5	Ι	Ι	JX434660	Ι	Ι	Ι	GenBank
	Fomitopsis sp. S-20	MX	Ι	KR135353	Ι	Ι	Ι	GenBank
	Aime 3413 (O)	BZ	Ι	KC017760	Ι	Ι	I	GenBank
F. hartmannii	Dai 13660 (BJFC)	CN	Ι	KR605808	Ι	Ι	I	Han <i>et al.</i> (2016)
	Núñez 554 (O)	ЧL	OQ701091	Ι	Ι	Ι	Ι	This study
	Núñez 679 (O)	Ъ	ON924675	ON994687	I	I	I	This study
F. hengduanensis	Cui 16259 (BJFC)	CN	Ι	MN148232	Ι	MN158175	MN161747	Liu <i>et al.</i> (2021)
	Cui 17056 (BJFC)	CN	Ι	MN148233	Ι	MN158176	MN161748	Liu <i>et al.</i> (2021)
F. hyalina	Spirin 2772 (H)	RU-NIZ	JQ700283	JQ700283	КҮ949007	I	Ι	Spirin et al. (2013b); Justo et al. (2017)
F. hypoxantha	Cui 8951 (BJFC)	CN	Ι	KC507164	Ι	Ι	Ι	GenBank
	Dai 5983 (H)	CN	Ι	KC595924	Ι	I	I	Ortiz-Santana <i>et al.</i> (2013)
	Cui 8969 (BJFC)	CN	Ι	KR605785	Ι	Ι	I	Han <i>et al.</i> (2016)
	KA12-1397	KR	Ι	KR673596	Ι	Ι	Ι	Kim <i>et al.</i> (2015)
	Zhao 2241	CN	Ι	MH114658	I	Ι	I	GenBank
F. incana	Dai 13612A (BJFC)	CN	Ι	KR605795	Ι	Ι	I	Han <i>et al.</i> (2016)
	LE 313649	Z	ON787634	ON787633	I	I	I	This study
F. juniperina	FP 105489-Sp (CFMR)	US-MD	Ι	KC585282	Ι	Ι	I	Ortiz-Santana <i>et al.</i> (2013)
	FP 71540 (CFMR)	US-MD	Ι	KC585283	Ι	Ι	I	Ortiz-Santana <i>et al.</i> (2013)
	SRM 403 (CFMR)	US-NE	KC585109	KC585285	КҮ948991	I	I	Ortiz-Santana <i>et al.</i> (2013); Justo <i>et al.</i> (2017)
	FP97452-T (CFMR)	ET	I	AY966454	I	I	I	GenBank
	WM-284-T (CFMR)	US-PA	I	EU232212	I	Ι	Ι	GenBank
	E. Larsson 15-11 (GB)	ES	Ι	KC543112	I	I	I	Spirin <i>et al.</i> (2013a)
	Dai 17104 (BJFC)	NZ	I	KX958182	I	I	I	Yuan <i>et al.</i> (2017)
	Dai 17105 (BJFC)	NZ	Ι	KX958183	I	Ι	I	Yuan <i>et al.</i> (2017)
	Vlasák 0310/1J (H)	US-PA	Ι	MG787606	Ι	Ι	Ι	GenBank
	CBS 117.40	US-MD	Ι	MH856056	Ι	Ι	I	Vu <i>et al.</i> (2019)
	CBS 639.75	TZ	Ι	MH860961	Ι	Ι	Ι	Vu <i>et al.</i> (2019)
	CBS 105824	ET	I	ON970645	I	I	I	This study
	H7068514	US-AR	I	ON994688	I	I	I	This study
	Vlasák 0709/154 (H)	US-VA	I	ON994689	I	I	I	This study
	Vlasák 1209/14 (H)	US-AZ	I	ON994690	I	I	I	This study
	Vlasák 1711/13J (H)	US-AZ	Ι	ON994691	I	I	Ι	This study
F. kenyensis	O F-915372	KE	I	KP171196	I	I	I	Han <i>et al.</i> (2016)

	Reference(s)		Liu <i>et al.</i> (2021)	Liu <i>et al.</i> (2021)	Spirin et al. (2016); this study	Spirin <i>et al.</i> (2013b); Justo <i>et al.</i> (2017)	Spirin et al. (2016); this study	This study	This study	This study	Vlasák <i>et al.</i> 2016; this study	This study	Kim <i>et al.</i> (2008)	Kim <i>et al.</i> (2008)	Han <i>et al.</i> (2016)	Ortiz-Santana et al. (2013); Justo et al. (2017); this study	Dimetindomoti of of /0000	Rungjinaamal et al. (2003)	Ortiz-Santana <i>et al.</i> (2013)	Ortiz-Santana <i>et al.</i> (2013)	Han <i>et al.</i> (2016)	This study	This study	This study	This study	This study	This study	This study	GenBank	GenBank	GenBank	This study	This study	Vlasák et al. (2012); this study	GenBank	This study	GenBank	This study
		TEF1	MN161749	MN161750	Ι	I	Ι	Ι	Ι	I	Ι	Ι	I	Ι	Ι			I	I	I	KR610686	I	OP215806	OP019457	Ι	Ι	Ι	Ι	I	Ι	Ι	Ι	I	I	I	I	MJIM0100001	OP215807
	ession number	RPB2	MN158177	MN158178	Ι	I	Ι	Ι	Ι	Ι	Ι	Ι	Ι	Ι	Ι	I		I	Ι	I	I	Ι	Ι	Ι	I	I	I	I	I	I	Ι	Ι	I	I	I	I	24 —	I
	nk / UNITE acc	RPB1	I	Ι	OP022437	КҮ948992	OP022436	Ι	Ι	I	OP022438	Ι	I	Ι	Ι	КҮ949006, Ори22439	01 044340	I	I			I	OP022440	Ι	Ι	Ι	Ι	Ι		Ι	Ι	Ι	Ι	OP022441		Ι	MJIM010002	OP022442
	GenBa	ITS	MN148234	MN148235	ON994693	JQ700282	ON994692	ON994694	ON994695	ON994754	KT156689	OQ673257	DQ491400	DQ491403	KR605773	KC595920	1070501	FJ31 2004	KC595918	KC595919	KR605779	ON970642	ON994696	ON970638	ON970639	ON970640	ON970646	ON970650	I	JX090121	JX090122	OQ701093	0Q701092	JN592494	MK991847	ON994699	MJIM01000216	ON754045
		LSU	I	I	Ι	JQ700282	Ι	ON924676	Ι	Ι	ON924677	Ι	Ι	I	Ι	KC595920		I	Ι	I	I	ON970642	Ι	ON970638	ON970639	ON970640	Ι	I	AF518632	I	I	OQ701093	OQ701092	JN592494	I	I	I	ON924678
	Origin (ISO code)		٨N	NN	FR	RU-NIZ	RU-NIZ	ID-PB	GF	ML	CR	VE	CR	AU	AU	ID-PB	ΠL		ID-PB	ID-PB	CN	ID-RI	ID-RI	ID-RI	ID-RI	ID-PB	ID-RI	ID-RI	AR	AR	AR	ID-BA	ID-BA	US-OR	US-OR	ID-PA	JP	CZ
	Specimen (culture) /	repository	Cui 16437 (BJFC)	Cui 16466 (BJFC)	Rivoire 3574 (LY)	Spirin LE208476	Spirin 6771 (H)	Miettinen 21981 (H)	Vlasák 1908/82 (H)	Ryvarden 41624 (O)	Vlasák 1312/A4 (H)	Kout 0402/M1	CBS 236.87	CBS 422.84	Schigel 5193 (H)	Miettinen 14311 (H)	D////22200	BUUZ3330Z	Miettinen 11573 (H)	Miettinen 14417 (H)	Vlasák 0509/52-X (JV)	Miettinen 5678 (H)	Miettinen 11224 (H)	Miettinen 13163 (H)	Miettinen 13162 (H)	Miettinen 14261 (H)	Miettinen 15222 (H)	Miettinen 23504 (H)	Rajchenberg 158 (BAFC)	CIEFAP92	CIEFAP93	Miettinen 12230 (H)	Miettinen 12233.1 (H)	Vlasák 0709/117 (PRM)	JLF 3745	Miettinen 11454 (H)	ATCC 62978	Běták 10/743 (JV)
Table 1. (Continued).	Species		F. kesiyae		F. kuzyana			F. lapidosa	F. leioderma	F. lignea	F. lignicolor		F. lilacinogilva			F. luzonensis													F. maculatissima			F. maculosa		F. madronae		F. marchionica	F. marianii	
¥	WES FUN DIV IN S	GALBI GALBI ERSIT TITUT	к 0 Ү Е	wv	/W.S	tud	iesi	nmy	/col	ogy.	org																										15	7

Table 1. (Continued).								
Species	Specimen (culture) /	Origin (ISO code)		GenBa	nk / UNITE acces	sion number		Reference(s)
	repository		LSU	ITS	RPB1	RPB2	TEF1	1
	Spirin LE209783	RU-NIZ	1	JQ700276	1	I	I	Spirin <i>et al.</i> (2013b)
	Dai 6613 (H)	CN	I	JQ700277	I	I	I	Spirin <i>et al.</i> (2013b)
	Cui 5525 (BJFC)	CN	I	JQ837942	I	I	I	Cui (2013)
	Cui 7597 (BJFC)	CN	Ι	KP171213	Ι	Ι	KR610687	Han <i>et al.</i> (2015, 2016)
	Cui 7615 (BJFC)	CN	I	KR605780	Ι	Ι	KR610688	Han <i>et al.</i> (2016)
	MS 48 (CFMR)	IM-SU	I	KC585352	I	I	Ι	Ortiz-Santana <i>et al.</i> (2013)
	Vampola s.n. (H)	CZ	Ι	KC595930	Ι	Ι	Ι	Ortiz-Santana <i>et al.</i> (2013)
	Fo6	П	I	KF615756	Ι	I	I	Roccotelli et al. (2014)
	TYP-6137 (CFMR)	ЧŲ	Ι	KJ995920	Ι	Ι	Ι	GenBank
	O F010808	AU	I	KR605770	I	I	KR610675	Han <i>et al.</i> (2016)
	O F10810	PT	I	KR605771	I	I	I	Han <i>et al.</i> (2016)
	O F10811	Г	I	KR605772	I	I	I	Han <i>et al.</i> (2016)
	Cui 16871 (BJFC)	US-PR	I	MK852559	I	I	MK900482	Liu <i>et al.</i> (2019)
	Cui 17170 (BJFC)	CN	I	MK852563	I	I	MK900485	Liu <i>et al.</i> (2019)
	Cui 17171 (BJFC)	CN	I	MK852564	I	I	MK900486	Liu <i>et al.</i> (2019)
	Dollinger 836 (H)	US-FL	ON924679	ON754046	OP022443	I	OP215808	This study
	Gilbertson 14757 (O)	US-LA	I	ON754047	I	I	OP215809	This study
	MJ 4157	SK	Ι	ON754048	OP022444	Ι	OP215810	This study
	MJ 4158	HR	Ι	ON754049	Ι	Ι	OP215811	This study
	MJ 4606	CZ	Ι	ON754050	Ι	Ι	OP215812	This study
	Rivoire 6563 (LY)	FR	Ι	ON754051	OP022445	Ι	OP215813	This study
	Spirin 5175 (H)	RU-KHA	I	ON754052	I	I	I	This study
	Spirin 5176 (H)	RU-KHA	Ι	ON754053	Ι	I	OP215814	This study
	Spirin 5302 (H)	RU-KHA	Ι	ON754054	Ι	Ι	OP215815	This study
	Spirin 9267 (H)	RU-NIZ	Ι	ON754055	Ι	Ι	Ι	This study
	Spirin 10503 (H)	RU-NIZ	Ι	ON754056	Ι	Ι	Ι	This study
	Spirin 10575 (H)	RU-NIZ	Ι	ON754057	Ι	Ι	I	This study
	Spirin 11249 (H)	RU-NIZ	Ι	ON754058	Ι	Ι	OP215816	This study
F. massoniana	Cui 2848 (BJFC)	CN	Ι	MN148236	Ι	Ι	MN161751	Liu <i>et al.</i> (2021)
	Cui 9058 (BJFC)	CN	Ι	MN148237	Ι	Ι	MN161752	Liu <i>et al.</i> (2021)
	Cui 11288 (BJFC)	CN	Ι	MN148238	Ι	MN158179	MN161753	Liu <i>et al.</i> (2021)
	Cui 11304 (BJFC)	CN	Ι	MN148239	Ι	Ι	MN161754	Liu <i>et al.</i> (2021)
F. meliae	FP-105065 (CFMR)	SM-SU	I	KC585350	I	I	I	Ortiz-Santana <i>et al.</i> (2013)
	SRM 209 (CFMR)	US-NE	Ι	KC585351	I	I	I	Ortiz-Santana <i>et al.</i> (2013)
	Roberts GA863 (K)	NG	Ι	KR605775	I	I	KR610682	Han <i>et al.</i> (2016)
	Ryvarden 16863 (O)	co	Ι	KR605776	I	I	KR610681	Han <i>et al.</i> (2016)

																						il. (2017)		il. (2017)													
	Reference(s)		Vlasák & Dollinger (2017); this study	GenBank	GenBank	GenBank	GenBank	GenBank	GenBank	GenBank	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study	Ortiz-Santana <i>et al.</i> (2013); Justo <i>et</i> a	Han <i>et al.</i> (2016)	Ortiz-Santana <i>et al.</i> (2013); Justo <i>et</i> :	Cristaldo <i>et al.</i> (2022)	Cristaldo <i>et al.</i> (2022)	This study	This study	This study	This study	Chen & Wu (2017)	Chen & Wu (2017)	This study	This study	GenBank	Haight <i>et al.</i> (2016)	Haight <i>et al.</i> (2016)
		TEF1	-	MW590292	MW590290	MW590291	MW590293	MW590294	MW590295	MW590296	OP215817	OP215818	I	OP215819	OP215820	OP215821	OP215822	Ι	I	Ι	Ι	Ι	I	I	Ι	I	I	I	Ι	Ι	Ι	I	I	I	AY885152	KF178346	KF178347
	ession number	RPB2	I	Ι	Ι	Ι	I	Ι	I	I	I	Ι	I	Ι	I	I	Ι	Ι	Ι	Ι	Ι	I	I	Ι	Ι	I	I	I	I	Ι	I	I	I	I	AY786056	KF169690	KF169691
	3ank / UNITE acc	RPB1	I	Ι	Ι	Ι	Ι	Ι	Ι	Ι	I	Ι	Ι	Ι	OP022446	OP022447	Ι	Ι	Ι	Ι	Ι	KY948994	I	KY948993	Ι	I	I	I	I	Ι	Ι	I	I	I	AY864874	I	I
	Genl	ITS	KY264030	MW221272	MW567238	MW567239	MW567240	MW567241	MW567242	MW567243	ON994700	ON994701	ON994702	ON994703	ON994704	ON994705	ON994706	ON994707	ON994708	ON994709	ON994710	KC543139	KR605777	KC595898	OP526847	OP526848	ON994711	ON994712	ON994713	ON994714	KY421732	KY421733	ON970661	ON970653	AY 854083	KF169621	KF169622
		LSU	1	I	Ι	Ι	I	Ι	I	I	I	Ι	I	Ι	I	I	Ι	Ι	I	Ι	Ι	KC543139	KR605716	KC595898	I	I	I	I	I	I	I	I	I	I	AY684164	I	I
	Origin (ISO code)		US-TX	US-AZ	US-AZ	US-AZ	US-AZ	US-AZ	US-AZ	US-AZ	US-FL	US-FL	PE	NG	GP	CR	CR	MQ	GF	GF	GF	RU-LEN	AR	RU-NIZ	BR	BR	CR	CR	CR	GF	CN	CN	RU-PRI	MA	NS	US-WA	US-OR
	Specimen (culture) /	repository	Vlasák 1109/40J (H)	isolate FM1C20	isolate FM1C7	isolate FM1C11	isolate FM1C21	isolate FM1C22	isolate FM1C30	isolate FM1C33	Dollinger 989 (H)	Dollinger 991 (H)	Hormia 2109 (H)	Vlasák 1511/24J (JV)	Vlasák 1612/22J (JV)	Vlasák 1704/61 (H)	Vlasák 1704/78J (H)	Vlasák 1712/27 (JV)	Vlasák 1808/33 (JV)	Vlasák 1808/81 (JV)	Vlasák 1808/82 (JV)	Spirin 3315 (H)	Rajchenberg 10661 (BAFC)	Spirin 2680 (H)	FLOR70928	FLOR70929	Vlasák 1312/A7-J (JV)	Vlasák 1407/90 (H)	Vlasák 1504/21 (H)	Vlasák 1808/87 (H)	Dai 10630 (BJFC)	Dai 16894 (BJFC)	Viner KUN2550 (H)	Miettinen 11662 (H)	AFTOL-770	32TT (CFMR)	CS-1 (CFMR)
Table 1. (Continued).	Species																					F. mellita	F. minutispora	F. minutula	F. modesta						F. monomitica			F. moritziana	F. mounceae	F. mounceae	F. mounceae
¥	FUN DIV INS	GALBI ERSIT TITUT	K D Y E	WV	vw.s	stud	iesi	nmy	/col	ogy.	.org																									1	59

Table 1. (Continued).								
Species	Specimen (culture) /	Origin (ISO code)		GenBa	ink / UNITE acces	sion number		Reference(s)
	repository		LSU	ITS	RPB1	RPB2	TEF1	
	DR-301 (CFMR)	IM-SU	1	KF169623	I	KF169692	KF178348	Haight <i>et al.</i> (2016)
	DR-366 (CFMR)	IM-SU	Ι	KF169624	Ι	KF169693	KF178349	Haight <i>et al.</i> (2016)
	DR-472 (CFMR)	IM-SU	Ι	KF169625	Ι	KF169694	KF178350	Haight <i>et al.</i> (2016)
	JAG-08-19 (CFMR)	US-ID	Ι	KF169626	Ι	KF169695	KF178351	Haight <i>et al.</i> (2016)
	JAG-08-20 (CFMR)	US-ID	Ι	KF169627	Ι	KF169696	KF178352	Haight <i>et al.</i> (2016)
	JAG-08-25 (CFMR)	US-ID	Ι	KF 169628	Ι	KF169697	KF178353	Haight <i>et al.</i> (2016)
	JEH-78 (CFMR)	CA-AB	Ι	KF169629	Ι	KF169698	KF178354	Haight <i>et al.</i> (2016)
	JEH-82 (CFMR)	CA-AB	Ι	KF169630	I	KF169699	KF178355	Haight <i>et al.</i> (2016)
	JEH-86 (CFMR)	CA-AB	Ι	KF169631	Ι	KF169700	KF178356	Haight <i>et al.</i> (2016)
	JEH-146 (CFMR)	IM-SU	Ι	KF169632	Ι	KF169701	KF178357	Haight <i>et al.</i> (2016)
	JEH-147 (CFMR)	IM-SU	I	KF169633	I	KF169702	KF178358	Haight <i>et al.</i> (2016)
	KM-1 (CFMR)	US-OR	I	KF169634	Ι	KF169703	KF178359	Haight <i>et al.</i> (2016)
	LT-5 (CFMR)	US-AK	Ι	KF169635	Ι	KF169704	KF178360	Haight <i>et al.</i> (2016)
	MJL-112-Sp (CFMR)	US-NY	I	KF169636	I	KF169705	KF178361	Haight <i>et al.</i> (2016)
	FP-105760-T (CFMR)	US-ID	I	KF169637	I	KF169706	KF178362	Haight <i>et al.</i> (2016)
	FP-133890-T (CFMR)	US-MT	Ι	KF169638	Ι	KF169707	KF178363	Haight <i>et al.</i> (2016)
	FP-125086-T (CFMR)	HN-SU	Ι	KF169639	Ι	KF169708	KF178364	Haight <i>et al.</i> (2016)
	MB_03_036 (CFMR)	US-CA	Ι	MH086259	Ι	MK208855	MK236353	Haight <i>et al.</i> (2019)
	Niemelä 2530 (H)	CA-QC	Ι	MN148240	I	I	MN161755	Liu <i>et al.</i> (2021)
	Ahti 60351 (H)	CA	Ι	MN148241	Ι	Ι	MN161756	Liu <i>et al.</i> (2021)
	Miettinen 18782 (H)	US-ID	Ι	MN148242	I	I	MN161757	Liu <i>et al.</i> (2021)
	Spirin 8367 (H)	US-WA	Ι	MN148243	Ι	I	MN161758	Liu <i>et al.</i> (2021)
F. neotropica	DLC04-74 (CFMR)	BZ	Ι	FJ403216	I	I	Ι	Lindner <i>et al.</i> (2011)
	DLC04-80 (CFMR)	BZ	I	FJ403217	I	I	Ι	Lindner <i>et al.</i> (2011)
	DLC04-100 (CFMR)	BZ	Ι	FJ403218	I	I	Ι	Lindner <i>et al.</i> (2011)
	DLC04-174 (CFMR)	BZ	Ι	FJ403219	I	I	I	Lindner et al. (2011)
	Vlasák 1312/E18-J (JV)	CR	Ι	KT156688	I	I	I	Vlasák <i>et al.</i> (2016)
F. nigra	Davidson-Wester (CBS 341.63)	US-DC	KC543172	KC543172	OP114093	Ι	Ι	Spirin <i>et al.</i> (2013a); this study
	Vlasák 1410/10J (JV)	US-PA	Ι	KT156694	OP022448	Ι	Ι	Vlasák <i>et al.</i> (2016); this study
F. niveomarginata	Cui 10108 (BJFC)	CN	KR605717	KR605778	Ι	Ι	Ι	Han <i>et al.</i> (2016)
F. nivosella	PCO 43	CO	Ι	HQ248222	Ι	Ι	Ι	GenBank
	Ryvarden 41410 (O)	VE	I	KF937292	I	I	KR610669	Han <i>et al.</i> (2016)
	Overholts 4215 (BPI)	HO-SU	I	KF937293	I	I	I	Han <i>et al.</i> (2016)
	de Jesus OF 10833	BR-AM	I	ON994715	I	I	I	This study
	de Meijer 3465 (O)	BR-PR	I	ON994716	Ι	I	I	This study

																																				al. (2017)		
	Reference(s)		This study	Haight <i>et al.</i> (2016)	Liu <i>et al.</i> (2021)	Liu <i>et al.</i> (2021)	Liu <i>et al.</i> (2021)	This study	Ortiz-Santana <i>et al.</i> (2013); Justo <i>et</i>	GenBank	Ortiz-Santana <i>et al.</i> (2013)																											
		TEF1	OP215823	KF178313	KF178314	KF178315	KF178316	KF178317	KF178318	KF178319	KF178320	KF178322	KF178323	KF178324	KF178326	KF178327	KF178329	KF178330	KF178331	KF178332	KF178333	KF178334	KF178336	KF178337	KF178338	KF178339	KF178341	KF178342	KF178343	KF178344	KF178345	MN161759	MN161760	MN161761	OP215824	I	I	Ι
	ession number	RPB2	I	KF169657	KF169658	KF169659	KF169660	KF169661	KF169662	KF169663	KF169664	KF169666	KF169667	KF169668	KF169670	KF169671	KF169673	KF169674	KF169675	KF169676	KF169677	KF169679	KF169680	KF169681	Ι	KF169683	KF169685	KF169686	KF169687	KF169688	KF169689	I	I	I	I	I	I	Ι
	Bank / UNITE acc	RPB1	I	Ι	I	Ι	Ι	I	I	Ι	Ι	I	Ι	Ι	I	I	Ι	I	Ι	Ι	Ι	Ι	Ι	I	Ι	I	I	I	I	I	I	I	I	I	I	КҮ948987	I	Ι
	Gen	ITS	ON994717	KF169588	KF169589	KF169590	KF169591	KF 169592	KF169593	KF169594	KF169595	KF169597	KF169598	KF169599	KF169601	KF169602	KF169604	KF169605	KF169606	KF169607	KF169608	KF169610	KF169611	KF169612	KF169613	KF169614	KF169616	KF169617	KF169618	KF169619	KF169620	MN148244	MN148245	MN148246	ON994718	KC585293	EU232198	KC585290
	e)	LSU	I	Ι	Ι	Ι	Ι	I	I	Ι	Ι	I	I	I	I	I	I	I	Ι	Ι	Ι	Ι	Ι	I	I	I	I	I	I	I	I	I	I	I	ON924680	KC585117	I	Ι
	Origin (ISO cod		US-PR	NM-SU	NM-SU	HN-SU	US-AK	US-TN	US-TN	US-TN	IM-SU	US-AK	US-AK	US-AK	US-AK	US-AK	CA-AB	CA-AB	CA-AB	CA-AB	CA-AB	CA-BC	CA-AB	CA-AB	US-VT	US-AK	US-AK	US-AK	US-AK	CA-NL	NM-SU	US-WA	US-WA	US-WA	US-UT	US-AZ	US-NC	IM-SU
	Specimen (culture) /	repository	Kout 1807/19 (H)	DLL-3 (CFMR)	DLL-4 (CFMR)	FP-125083-T (CFMR)	HHB-17661 (CFMR)	HHB-19667 (CFMR)	HHB-19670 (CFMR)	HHB-19692 (CFMR)	HHB-3331-Sp (CFMR)	JEH-12E (CFMR)	JEH-12F (CFMR)	JEH-13A (CFMR)	JEH-13D (CFMR)	JEH-37 (CFMR)	JEH-79 (CFMR)	JEH-80 (CFMR)	JEH-81 (CFMR)	JEH-83 (CFMR)	JEH-85 (CFMR)	JEH-87 (CFMR)	JEH-88 (CFMR)	JEH-91 (CFMR)	KTS-28 (CFMR)	LT-12 (CFMR)	LT-18 (CFMR)	LT-19 (CFMR)	LT-17 (CFMR)	TRTC48800	CFMR: PEL-Lk-6-1	Miettinen 18568 (H)	Miettinen 18673 (H)	Spirin 8165 (H)	Vlasák 1811/13J (JV)	HHB-5988-Sp (CFMR)	RLG-3818-Sp (CFMR)	FP-48282-R (CFMR)
Table 1. (Continued).	Species			F. ochracea																																F. oleracea		
¥	WES FUN DIV INS	GALBI ERSIT TITUT	к 0 Ү Е	WW	/W.S	studi	iesir	וmy	colo	ogy.	org																										16	1

www.studiesinmycology.org

lable 1. (Continued).								
Species	Specimen (culture) /	Origin (ISO code)		GenBa	nk / UNITE access	sion number		Reference(s)
	repository		rsu	ITS	RPB1	RPB2	TEF1	
	FP-70890-Sp (CFMR)	US-GA	I	KC585291	I	I	I	Ortiz-Santana <i>et al.</i> (2013)
	HHB-3543-Sp (CFMR)	IN-SU	I	KC585292	I	Ι	I	Ortiz-Santana <i>et al.</i> (2013)
	Mad-497 (CFMR)	US-TX	I	KC585295	I	I	I	Ortiz-Santana <i>et al.</i> (2013)
	MD-177 (CFMR)	IW-SU	I	KC585296	I	I	I	Ortiz-Santana <i>et al.</i> (2013)
	CBS 388.51	IM-SU	Ι	MH856911	I	Ι	Ι	Vu <i>et al.</i> (2019)
	strain KRT_lso_3	US-KY	Ι	MN430923	I	Ι	Ι	GenBank
	Vlasák 1009/31 (H)	US-PA	Ι	ON994719	Ι	Ι	I	This study
F. ostreiformis	Dai 9611 (BJFC)	CN	Ι	JX435776	I	Ι	Ι	Li <i>et al.</i> (2013)
	Cui 6239 (BJFC)	CN	I	JX435777	I	Ι	I	Li <i>et al.</i> (2013)
	Miettinen 10071 (H)	CN	I	KC595914	OP022449	I	OP215825	Ortiz-Santana <i>et al.</i> (2013); this study
	Dai 10035 (BJFC)	CN	Ι	KR605774	Ι	Ι	KR610683	Han <i>et al.</i> (2016)
	Dämmrich 2003 (H)	LK	ON970641	ON970641	Ι	Ι	I	This study
	Miettinen 8854.1 (H)	ID-RI	ON970636	ON970636	I	I	I	This study
	Miettinen 11629 (H)	ID-PB	Ι	ON994720	OP022450	Ι	OP215826	This study
	Miettinen 21986 (H)	ID-RI	Ι	ON970649	Ι	Ι	Ι	This study
	Miettinen 23532 (H)	SG	Ι	ON970651	Ι	Ι	Ι	This study
F. palustris	Dollinger 782 (PRM)	US-FL	Ι	ON994721	OP022451	Ι	OP215827	This study
	Lowe 4092 (PRM)	US-GE	Ι	ON994722	I	Ι	OP215828	This study
	Ryvarden 44439 (O)	BZ	Ι	ON994723	Ι	Ι	I	This study
	Vlasák 1904/1J (H)	US-FL	I	ON994724	OP022452	Ι	I	This study
F. pannucea	Runnel 824 (TUF)	GF	UDB035620	UDB035620	UDB07672434	Ι	Ι	This study
F. perhiemata	Viner 2021/35 (H)	RU-KDA	I	099076NO	I	I	I	This study
F. philippinensis	JZ36	Z	I	MG719293	Ι	I	I	GenBank
	Kout 1408/K2 (H)	TH	Ι	ON994725	I	Ι	Ι	This study
	Ryvarden 17840 (CBS 426.84)	TH	I	DQ491401	I	I	I	Kim <i>et al.</i> (2008)
F. pinicola	GR9-4	SE	MPVS00000000	MPVS000000000	MPVS01000315	MPVS01000002	MPVS01000007	GenBank
	LT-323 (CFMR)	EE	Ι	KF169651	I	KF169720	KF178376	Haight <i>et al.</i> (2016)
	LT-319 (CFMR)	EE	Ι	KF169652	Ι	KF 169721	KF178377	Haight <i>et al.</i> (2016)
	FCUG2056	SE	Ι	KF169653	Ι	KF169722	KF178378	Haight <i>et al.</i> (2016)
	Kotiranta 19330 (H)	RU-SVE	Ι	KF169654	Ι	KF169723	KF178379	Haight <i>et al.</i> (2016)
	TS-Fp-24 (CFMR)	RU-MOW	Ι	KF169655	I	KF169724	KF178380	Haight <i>et al.</i> (2016)
	FCUG2034	SE	I	KF169656	I	KF169725	KF178381	Haight <i>et al.</i> (2016)
	Kotiranta 15815 (H)	RU	I	KU171406	I	MK236364	MK236361	Haight <i>et al.</i> (2019)
	Kotiranta 27183 (H)	RU-CHU	I	ON994726	I	I	OP215829	This study
	Spirin 4111 (H)	RU-KHA	Ι	ON994727	Ι	I	OP215830	This study

	Reference(s)		This study	This study	This study	GenBank	Kim <i>et al.</i> (2008)	GenBank	Han <i>et al.</i> (2016); this study	Han <i>et al.</i> (2016)	Han <i>et al.</i> (2016)	GenBank	Spirin <i>et al.</i> (2013b); Justo et al (2017)	Han & Cui (2015)	Han & Cui (2015)	Lindner <i>et al.</i> (2011)	Binder <i>et al.</i> (2013)	Ortiz-Santana <i>et al.</i> (2013)	Ortiz-Santana <i>et al.</i> (2013)	Ortiz-Santana <i>et al.</i> (2013)	Justo <i>et al.</i> (2017)	GenBank	GenBank	GenBank	GenBank	GenBank	GenBank	This study	Ortiz-Santana et al. (2013); Justo et al. (2017)	Spirin <i>et al.</i> (2013a)	This study	This study	Rivoire et al. (2015); this study	Rivoire et al. (2015); this study	Zibarova <i>et al.</i> (2019)	Zibarova <i>et al.</i> (2019)	Zibarova et al. (2019)	Zibarova <i>et al.</i> (2019)
		TEF1	OP215831	I	Ι	Ι	I	Ι	Ι	I	Ι	Ι	Ι	I	Ι	Ι	I	Ι	Ι	Ι	Ι	Ι	I	Ι	Ι	Ι	I	I	I	I	OP215832	OP215833	OP215834	OP215835	I	I	I	I
	sion number	RPB2	I	Ι	Ι	Ι	Ι	Ι	Ι	Ι	Ι	Ι	Ι	Ι	I	Ι	Ι	Ι	Ι	Ι	Ι	I	Ι	Ι	Ι	Ι	Ι		Ι	Ι	I	Ι	Ι	I	Ι	I	I	Ι
	ink / UNITE acces	RPB1	I	Ι	Ι	Ι	Ι	I	OP022453	Ι	Ι	Ι	KY948995	Ι	Ι	Ι	Ι	Ι	Ι	Ι	KY948989	Ι	Ι	Ι	Ι	Ι	I	I	KY949002	Ι	Ι	Ι	Ι	I	I	I	I	I
	GenBa	ITS	ON994728	OQ701094	Ι	MG787587	DQ491419	KM411464	KR605800	KR605801	KR605799	MT939446	JQ700286	KF999921	KC507155	FJ403214	JX109855	KC585335	KC585336	KC585337	KY948809	MH277957	MK532776	MK607490	MK991837	MN596945	MZ159711	ON994729	KC595903	KC543138	ON994730	ON994731	KM068100	KM068101	MK558724	MK558725	MK558726	MK558727
		LSU	ON924681	OQ701094	OQ701097	I	I	I	ON924682	Ι	I	Ι	JQ700286	I	I	I	I	Ι	Ι	I	KY948883	I	I	Ι	Ι	Ι	I	I	KC595903	I	Ι	I	I	I	I	I	I	I
	Drigin (ISO code)		Z	D-PB	D-PB	R	ЭЕ	SU	JS-PA	Z	R	US-NJ		Ζ.	Ζ.	IM-SL		JS-GA	HN-Sr	JS-MD	JS-PE	JS-OR	NI-Sſ	NI-Sſ	JS-OR	٩G	38	JS-GA	SIN-NIZ	01	Z	ĸ	R	Т	Z	Z	Z	Z
	Specimen (culture) / 0	repository	Vlasák 1905/1 (H) 0	Miettinen 14284 (H)	Miettinen 14373.1 (H) II	Vlasák 1504/34 (H) C	CBS 858.72 E	LE287547 F	Vlasák 0906/15J (JV)	Vlasák 1406/1 (PRM) 0	Rivoire 2030 (LY) F	Bigelow w/n	Pennanen 1532 (H) F	Ryvarden 10118 (O) 7	O F915519 T	HHB-8735 (CFMR)	Miettinen 12662 (H) F	FP103364-T (CFMR)	FP125063-T (CFMR)	OKM-3802-Sp (CFMR)	FP56429 (CFMR)	JLF3791 L	Russell MycoMap 7714 L	Grootmyers 4.X.2015 L	JLF1738 U	FFUI-4	K(M) 250617 C	Vlasák 0404/2-J (H)	Spirin 2540 (H) F	Marstad 274-09 (O)	Kout 1001/1 (H) C	David 3182 (LY) F	Rivoire 4111 (LY) F	Bernicchia 8142 (HUBO) I	PRM 951454 C	PRM 944766 C	Kout 1709/7 (KBI) C	PRM 951086 C
Table 1. (Continued).	Species			F. pseudopetchii		F. psilodermea	F. pulvina						F. pulvinascens	F. purpurea		F. quercina													F. ramentacea				F. renehenticii					
¥	WES FUN DIV INS	GALBI ERSIT TITUT	к 0 Ү Е	WW	/w.s	stud	iesiı	nmy	col	ogy.	org																										16	3

Table 1. (Continued).								
Species	Specimen (culture) /	Origin (ISO code)		GenBar	nk / UNITE acces	sion number		Reference(s)
	repository		LSU	ITS	RPB1	RPB2	TEF1	
	Rivoire 3059 (LY)	FR	1	ON994732	I	I	OP215836	This study
	Rivoire 6274 (LY)	FR	I	ON994733	I	I	I	This study
	Rivoire 7347 (LY)	FR	Ι	ON994734	I	I	I	This study
F. renehenticii × solaris	Rivoire 6356 (LY)	FR	Ι	ON994735	Ι	Ι	OP215837	This study
F. retorrida	Kotiranta 28979 (H)	RU-SAK	ON924683	ON994736	OP022454	Ι	I	This study
F. rosea	RLG-6954 (CFMR)	US-AZ	KC585181	KC585353	КҮ949003	I	I	Ortiz-Santana et al. (2013); Justo et al. (2017)
	DLL2009-166 (CFMR)	NM-SU	I	JQ673050	I	I	I	Brazee et al. (2012)
	Oivanen 118 (H)	FI	Ι	KC595923	I	Ι	I	Ortiz-Santana <i>et al.</i> (2013)
	Vlasák 1110/9 (JV)	CZ	I	KR605783	I	I	I	Han <i>et al.</i> (2016)
	FIAPH485-13	FI	Ι	ON970648	Ι	Ι	I	This study
F. roseofusca	Ryvarden 42363 (O)	VE	ON970634	ON970634	Ι	Ι	I	This study
	Vlasák 1908/83 (H)	GF	ON924684	ON994737	OR703809	Ι	I	This study
F. sagraeana	Vlasák 1512/3J (H)	CR	ON924685	ON994738	OP022455	Ι	I	This study
	CBS 424.84	MX	Ι	DQ491402	Ι	Ι	I	Kim <i>et al.</i> (2008)
	Kout 0610/K9 (JV)	MX	Ι	KF999922	Ι	Ι	I	Han & Cui (2015)
	Lopez 1324 (O 14115)	CR	Ι	KF999923	Ι	Ι	I	Han & Cui (2015)
	Vlasák 1412/5J (H)	CR	Ι	ON994739	Ι	Ι	Ι	This study
	Vlasák 1512/2J (H)	CR	Ι	ON994740	Ι	Ι	I	This study
	Vlasák 0904/39 (H)	US-FL	Ι	ON994741	Ι	Ι	I	This study
	Vlasák 1707/27J (H)	US-FL	Ι	ON994742	Ι	Ι	I	This study
F. sandaliae	HUBO 7083	Ц	JN592495	JN592495	Ι	Ι	Ι	Vlasák <i>et al.</i> (2012)
F. scalaris	Vlasák 1808/50 (JV)	GF	ON924686	ON994743	Ι	Ι	I	This study
	Vlasák 1909/66 (H)	GF	Ι	ON994744	OP022456	Ι	I	This study
F. schrenkii	FP-58527 (CFMR)	US-SD	I	FP-58527 SS1	I	AEHC02000126	AEHC02000044	JGI; GenBank
	FP-105881-R (CFMR)	NS-CO	I	KF169641	I	KF160710	KF178366	Haight <i>et al.</i> (2016)
	JEH-121A (CFMR)	NN-SU	I	KU169355	I	MK208856	MK236354	Haight <i>et al.</i> (2019)
	JEH-142-ss12 (CFMR)	NN-SU	I	KF169642	I	KF160711	KF178367	Haight <i>et al.</i> (2016)
	JEH-142-ss14 (CFMR)	NN-SU	Ι	KF169643	Ι	KF160712	KF178368	Haight <i>et al.</i> (2016)
	JEH-142-ss5 (CFMR)	NN-SU	I	KF169644	I	KF160713	KF178369	Haight <i>et al.</i> (2016)
	JEH-142-ss6 (CFMR)	NN-SU	I	KF169645	I	KF160714	KF178370	Haight <i>et al.</i> (2016)
	JEH-144 (CFMR)	NN-SU	Ι	KU169364	Ι	MK208857	MK236355	Haight <i>et al.</i> (2019)
	JEH-150 (CFMR)	US-SD	I	KU169365	I	MK208858	MK236356	Haight <i>et al.</i> (2019)
	JEH-152 (CFMR)	US-SD	I	KU169367	I	MK208859	MK236357	Haight <i>et al.</i> (2019)
	JW24-525-0-sap (CFMR)	US-CO	Ι	KF169646	I	KF160715	KF178371	Haight <i>et al.</i> (2016)
	JW24-549B-1-sap (CFMR)	NS-CO	I	KF169647	Ι	KF160716	KF178372	Haight <i>et al.</i> (2016)

									et al. (2017)																											
	Reference(s)		Haight <i>et al.</i> (2016)	Haight <i>et al.</i> (2016)	Haight <i>et al.</i> (2016)	Liu <i>et al.</i> (2021)	Liu <i>et al.</i> (2021)	This study	Ortiz-Santana <i>et al.</i> (2013); Justo	JGI	Spirin <i>et al.</i> (2017); this study	GenBank	Rajchenberg <i>et al.</i> (2011)	This study	- - - -	I his study	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study	This study	Kim <i>et al.</i> (2008)	Han <i>et al.</i> (2016)	GenBank	GenBank	GenBank	Genbank	GenBank	GenBank
		TEF1	KF178373	KF178374	KF178375	MN161763	MN161762	Ι	Ι	Ι	Ι	Ι	Ι	OP215838		I	Ι	I	I	Ι	Ι	Ι	OP215839	Ι	OP215840	OP215841	I	I	I	I	Ι	Ι	Ι	I	Ι	I
	ssion number	RPB2	KF160717	KF160718	KF160719	Ι	MN158180	Ι	Ι	Ι	Ι	Ι	Ι	I		I	Ι	I	I	Ι	Ι	Ι	Ι	Ι	I	I	Ι	I	I	I	Ι	Ι	Ι	I	Ι	Ι
	ank / UNITE acce	RPB1	I	I	I	Ι	Ι	ON667941	KY949000	Sig1Antser10	OP022457	Ι	I	I		I	Ι	I	I	I	Ι	Ι	I	I	I	I	I	OP022458	I	I	I	Ι	Ι	I	Ι	Ι
	GenB	ITS	KF169648	KF169649	KF169650	MN148248	MN148247	ON691652	KC585302	Sig1Antser10	KT995120	KT334658	JF713082	ON994745		ON808966	ON808967	ON808968	ON808965	ON808964	ON808969	ON808963	ON994746	ON994747	ON994748	ON994749	ON970644	ON994750	DQ491406	KR605784	KY777368	MG663257	MK571181		MK575221	MK575222
		rsu	I	I	Ι	Ι	Ι	ON691652	KC585126	Sig1Antser10	Ι	Ι	I	I		I	Ι		Ι	Ι	Ι	Ι	Ι	Ι	I	Ι	Ι	ON924687	I	Ι	Ι	Ι	Ι	I	Ι	I
	Origin (ISO code)		US-CO	US-CO	US-AZ	JS	US-AZ	AU	US-MD	NO	CZ	Ъ	AR	УC		GB	GB	GB	GB	GB	GB	Щ	CA-NT	CA-NT	FR	_	JS-TN	JS-NY	HO-SL	R	NT-SL	US-TN	JS-NC	NI-OD	NI-SL	NI-SL
	Specimen (culture) /	repository	JW18-240-1-sap (CFMR)	J.J. Worrall w/n (CFMR)	RLG-10752-Sp (CFMR)	Ahonen 58 (H)	Vlasák 1209/61J (BJFC)	Syme 2967 (PERTH)	FP-105717 (CFMR)	Sig1Antser10 (O)	Vlasák 1509/5 (JV)	isolate IBL104f	MR 11937	Boertmann 2013-501446	(C)	K(M) 84579	K(M) 85251	K(M) 137688	K(M) 153625	K(M) 169193	K(M) 180117	K(M) 191007	Niemelä 3058 (H)	Niemelä 3061 (H)	Rivoire 4732 (LY)	Zmitrovich 2008 (H)	Ryvarden 46569 (H)	Vlasák 1608/14J (JV)	CBS 365.64	Rivoire 4638 (LY)	TENN069504	TENN065680	Mushroom Observer	S.D. Kussell Mycomap 6609	S.D. Russell Mycomap 73	S.D. Russell Mycomap 1318
Table 1. (Continued).	Species							F. sclerotina	F. serialiformis	F. serialis		F. solaris															F. spraguei									
¥	WES FUN DIV INS	GALBIO ERSIT TITUTI	K D Y E	ww	/W.S	tud	iesiı	nmy	colo	ogy.	org																									165

Table 1. (Continued).								
Species	Specimen (culture) /	Origin (ISO code)		GenB	ank / UNITE acce	ssion number		Reference(s)
	repository		LSU	ITS	RPB1	RPB2	TEF1	
	S.D. Russell Mycomap 105	NI-SN	I	MK575223	I	I	I	GenBank
	W. Langer 348	NI-SU	I	OM972619	I	I	I	GenBank
F. squamosella	Bernicchia 7690-03	F	ON924688	ON994751	OP022459	I	I	This study
F. stereoides	O 10551	ET	I	FJ403215	Ι	I	I	Lindner e <i>t al.</i> (2011)
F. subectypa	Vlasák 0312/24.7 J (JV)	US-FL	I	KP171197	I	I	I	Han <i>et al.</i> (2015)
	Vlasák 0904/19 (H)	US-FL	I	KP171198	I	I	I	Han <i>et al.</i> (2015)
	Vlasák 0904/20 (BJFC)	US-FL	I	KP171199	I	I	I	Han <i>et al.</i> (2015)
	Vlasák 1408/3 (JV)	CR	I	ON994752	I	I	I	This study
	Vlasák 1704/107J (JV)	CR	I	ON994753	I	I	I	This study
F. subpinicola	Cui 9836 (BJFC)	CN	I	MN148249	I	I	MN161764	Liu <i>et al.</i> (2021)
	Cui 9819 (BJFC)	CN	I	MN148250	I	I	MN161765	Liu <i>et al.</i> (2021)
	Dai 11101 (BJFC)	CN	I	MN148251	I	MN158182	MN161766	Liu <i>et al.</i> (2021)
	Dai 11206 (BJFC)	CN	Ι	MN148252	Ι	MN158183	MN161767	Liu <i>et al.</i> (2021)
	Dai 13480 (BJFC)	CN	I	MN148253	I	MN158184	MN161768	Liu <i>et al.</i> (2021)
	Yuan 4912 (BJFC)	CN	Ι	MN148254	I	Ι	MN161769	Liu <i>et al.</i> (2021)
F. substratosa	Cui 9229 (BJFC)	CN	Ι	KR605789	Ι	Ι	Ι	Han <i>et al.</i> (2016)
F. sulcata	Kout 1408/K5 (H)	TH	OR702646	OR702647	Ι	Ι	I	This study
F. tianshanensis	Wei 1568 (BJFC)	CN	Ι	MN148255	Ι	Ι	MN161770	Liu <i>et al.</i> (2021)
	Wei 1473a (BJFC)	CN	Ι	MN148256	Ι	Ι	MN161771	Liu <i>et al.</i> (2021)
	Wei 1462a (BJFC)	CN	Ι	MN148257	Ι	Ι	MN161772	Liu <i>et al.</i> (2021)
	Cui 16821 (BJFC)	CN	Ι	MN148258	Ι	Ι	MN161773	Liu <i>et al.</i> (2021)
	Cui 16823 (BJFC)	CN	Ι	MN148259	Ι	I	MN161774	Liu <i>et al.</i> (2021)
	Cui 16825 (BJFC)	CN	Ι	MN148260	Ι	Ι	MN161775	Liu <i>et al.</i> (2021)
	Cui 16828 (BJFC)	CN	Ι	MN148261	Ι	Ι	MN161776	Liu <i>et al.</i> (2021)
F. tristis	Miettinen 14263 (H)	ID-PB	OQ701095	OQ701095	Ι	Ι	Ι	This study
F. tropica	Dai 13434 (BJFC)	CN	KX958185	KX958181	Ι	Ι	I	Yuan <i>et al.</i> (2017)
F. tumulosa	CBS 332.49	AU	MH856544	MH856544	Ι	Ι	I	Vu <i>et al.</i> (2019)
F. tunicata	Miettinen 8579 (H)	ID-RI	ON970631	ON970631	OQ789527	Ι	Ι	This study
	Miettinen 13050 (H)	ID-SB	ON970635	ON970635	OQ789527	Ι	I	This study
F. uralensis	Cui 3705 (BJFC)	CN	Ι	FJ627258	Ι	Ι	Ι	GenBank
	Dai 6082 (BJFC)	CN	Ι	JQ837943	Ι	Ι	Ι	Cui (2013)
	Dai 6118 (BJFC)	CN	I	KC951178	I	I	I	Cui & Dai (2013)
	Cui 10277 (BJFC)	CN	I	KX958178	Ι	I	I	Yuan <i>et al.</i> (2017)
	Spirin 5399 (H)	RU-KHA	ON970647	ON970647	Ι	Ι	OP019458	This study

Reference(s)		This study	Kim <i>et al.</i> (2008)	Kim <i>et al.</i> (2008)	GenBank	GenBank	This study	Han <i>et al.</i> (2020)	Ortiz-Santana <i>et al.</i> (2013); Justo <i>et al.</i> (2017	This study	This study	Lindner & Banik (2008); Justo <i>et al.</i> (2017)	This study	This study	Ortiz-Santana <i>et al.</i> (2013); Justo <i>et al.</i> (2017)	Justo <i>et al.</i> (2017)	Liu <i>et al.</i> (2022)	Liu <i>et al.</i> (2022)	This study	Ortiz-Santana <i>et al.</i> (2013); Justo <i>et al.</i> (2017)	Ortiz-Santana <i>et al.</i> (2013); Justo <i>et al.</i> (2017)	Ortiz-Santana <i>et al.</i> (2013); Justo <i>et al.</i> (2017)	Justo et al. (2017)	Miettinen & Larsson (2011)	Ortiz-Santana <i>et al.</i> (2013); Justo <i>et al.</i> (2017)	This study	Ortiz-Santana et al. (2013); Justo et al. (2017
	TEF1	OP215842	I	I	I	Ι	Ι	I	Ι	Ι	I	I	I	I	I	I	I	I	I	I	Ι	I	I	I	I	I	I
ssion number	RPB2	I	I	I	Ι	Ι	Ι	Ι	I	Ι	I	I	Ι	Ι	Ι	Ι	I	Ι	Ι	I	Ι	Ι	I	Ι	Ι	Ι	Ι
ank / UNITE acce	RPB1	I	I	I	Ι	Ι	Ι	Ι	КҮ948997	Ι	ON667941	KY949025	OP022460	Ι	КҮ948974	KY948978	I	Ι	OP022461	KY949040	KY949028	KY949022	KY948982	Ι	KY949023	Ι	KY949026
GenB	ITS	ON994756	DQ491409	DQ491411	EU232200	KJ668548	ON970643	MT497885	KC585309	OQ701096	ON691653	EU402565	ON994757	ON970654	KC585358	KY948814	MG787601	MG787602	ON994758	KC585385	KC585390	KC585393	I	FN907916	KC987580	ON994759	KC585400
	LSU	I	Ι	I	Ι	Ι	ON970643	MT497887	KC585134	OQ701096	ON691653	EU402532	ON924689	Ι	KC585187	KY948885	Ι	Ι	OQ660486	KC585218	KC585223	KC585226	Ι	FN907916	KF053407	Ι	KC585234
Origin (ISO code)		RU-KHA	KR	KR	ML	KR	CN-JL	CN	US-CO	ID-JA	AU	US-CT	RU-SA	OM	GB	PL	CN	CN	CR	US-CA	US-CA	US-NY	US-NY	FI	US-ID	MA	US-KY
Specimen (culture) /	repository	Spirin 10946 (H)	SNU m-05072501	SFC04010313	BCRC 35447	KUC20130725-21	Dai 3023 (H)	Zhao 4566 (SWFC)	FP-104442 (CFMR)	Miettinen 6223 (H)	Barrett F17/09 (DNA D0268068)	CT-1	Kotiranta 27358 (H)	Razmadze 2202/9 (H)	FP-135372-Sp (CFMR)	Kinnunen 5087 (H)	Dai 10828 (BJFC)	Dai 13381 (BJFC)	Vlasák 2203/5 (H)	CA-20(Ta)	Dietz7E	L-14910-Sp (CFMR)	L-15957-Sp (CFMR)	Miettinen 9472 (H)	OKM4756 (CFMR)	PRM842893	CS635913
Species			F. ussuriensis					F. yunnanensis	F. variiformis	F. visenda	<i>Fomitopsis</i> sp. Darwin (M.D. Barrett F17/09)	Laetiporus sulphureus	Laricifomes officinalis	Megasporoporia eutelea	Postia balsamea	Postia cyanescens	Pseudoantrodia monomitica	P. monomitica	Pseudophaeolus trichrous	Pycnoporellus fulgens	Rhodonia placenta	Sarcoporia polyspora	Skeletocutis chrysella		Sparassis radicata	Trametes junipericola	Wolfiporia dilatohypha
	Species Species Specimen (culture) / Origin (ISO code) GenBank / UNITE accession number Reference(s)	Species Specimen (culture) / Origin (ISO code) GenBank / UNITE accession number Reference(s) repository LSU ITS RPB1 RPB2 TEF1	Species Specimen (culture) / Origin (ISO code) GenBank / UNITE accession number Reference(s) repository LSU ITS RPB1 RPB2 TEF1 Spirin 10946 (H) RU-KHA - ON994756 - OP215842 This study	Species Specimen (culture) / Origin (ISO code) GenBank / UNITE accession number Reference(s) repository repository LSU ITS RPB1 RPB2 TEF1 Spirin 10946 (H) RU-KHA - ON994756 - OP215842 This study F. ussuriensis SNU m-05072501 KR - DQ491409 - - Kim et al. (2008)	Species Specimen (culture) / repository Origin (ISO code) GenBank / UNITE accession number Reference(s) Repository repository LSU ITS RPB1 RPB2 TEF1 Spirin 10946 (H) RU-KHA - ON994756 - OP215842 This study F. ussuriensis SNU m-05072501 KR - DQ491409 - - OP215842 This study SFC04010313 KR - DQ491411 - - - Kim et al. (2008)	Species Specimen (culture) / repository Origin (ISO code) GenBank / UNITE accession number Reference(s) Repository LSU ITS RPB1 RPB2 TF1 Repository Spirin 10946 (H) RU-KHA - ON994756 - - OP215842 This study F. ussuriensis SNU m-05072501 KR - DQ491409 - - 0 - - C083 BCRC 35447 TW - EU232200 - - - CBBank	Species Specimen (culture) / repository Origin (ISO code) GenBank / UNITE accession number Reference(s) repository repository LSU ITS RPB1 RPB2 TEF1 repository Spirin 10946 (H) RU-KHA - ON994756 - - 0 F. ussuriensis Snu m-05072501 KR - ON994756 - - 0 F. ussuriensis Snu m-05072501 KR - DQ491409 - - 0 -	Species Specimen (culture) / repository Origin (ISO code) GenBank / UNITE accession number Reference(s) repository Egository LSU ITS RPB1 RPB2 TEF1 repository Spirin 10946 (H) RU-KHA — ON994756 — — PC Spirin 10946 (H) RU-KHA — ON994756 — — PC Spirin 10946 (H) RU-KHA — ON994756 — — PC Spirin 10946 (H) RU-M-05072501 KR — ON994756 — — PC Spirin 10946 (H) RU — DQ491410 — — PC PC Spirin 10313 KR — — DQ491411 — — — — PC PC	Species Specimen (culture) / repository Origin (ISO code) GenBank / UNITE accession number Reference(s) Repository Repository LSU ITS RPB1 RPB2 TEF1 Spirin 10946 (H) RU-KHA - ON934756 - - 0 Spirin 10946 (H) RU-KHA - ON934756 - - 0 Spirin 10946 (H) RU-KHA - ON934756 - - 0 Spirin 10946 (H) RU- DQ491410 - - 0 0 - - 0 0 - - 0 0 -	Species Specimen (culture) / repository Origin (ISO code) GenBank / UNITE accession number Reference(s) Repository EJU ITS RPB1 RPB2 TEF1 Reference(s) Fuszviensis Spin 10946 (H) RU-KHA - ON994756 - - OP215842 This study F. ussviensis SNU m-05072501 KR - ON994756 - - OP215842 This study F. ussviensis SNU m-05072501 KR - DQ491409 - - OP215842 This study RuC20130725-21 KR - DQ491411 - - - CenBank RuU220130725-21 KR - - DQ491411 - - - CenBank Dai 3023 (H) CN-LL ON970643 ON970643 - - - CenBank F. vunnanensis FP-10442 (CFMR) US-CO KC585309 KY94897 - - - - CenBank - - -	Species Specimen (culture) / repository Origin (ISO code) GenBank / UNITE accession number Reference(s) Repository LSU IS BP1 RPB1 RPB2 TEF1 Repository Spin 10946 (H) RU-KHA - Ov994756 - - 0<215842	Species Specimen (culture) / repository Origin (ISO code) GenBank / UNITE accession number Reference(s) Repository Evolution / repository LSU ITS RPB1 RPB2 TEF1 Repository Spin 10946 (H) RU-KHA E ON994756 E P P Returnelisis Spin 10946 (H) RU-KHA E ON994756 E P P Store Spin 10946 (H) RU-KHA E ON994756 E P P P Store SNU m-05072601 KR E ON994766 E P	Specime (ulture) / origin (ISO code) GenBank / UNITE accession number Reference(s) repository LSU ITS RPB1 RPB1 Reference(s) repository Spin 10946 (H) RU-HKHA - On994756 - - P F usuriensis Snu 10946 (H) RU-m.65072501 KR - ON994756 - - P P - P - P -	Species Specimen (cutture) / regin (ISO code) GenBank / UNITE accession number Reference(s) Repository LSU ITS RPB1 RPB2 TEF1 Reference(s) Repository Spin 10946 (H) RU-KHA — ON994756 — — PC Rundown Spin 10946 (H) RU-KHA — ON994756 — — PC PC Spin 10946 (H) RU-KHA — ON994756 — — PC PC	Species Specimen (cutture) / torigin (ISO code) GenBank / UNITE accession number Reference(s) repository Evo ISU ITS RPB1 RPB2 IEF1 Reference(s) spont torigin (ISO code) EV ISU ITS RPB1 RPB2 IEF1 Reference(s) spont torigin (ISO code) EV ON994756 ON994756 Code) IEF1 Reference(s) Struth model EV NU m-65075601 KR DQ491411 C OP215842 This study Struth model EV NU m-65075501 KR DQ491411 C OP215842 This study Record a Mitternensis EV NU m-65075501 KR C	Species Specimen (culture) / Origin (ISO code) GenBank / UNITE accession number Reference(s) repository LSU TS APB1 APB2 TEF1 Reference(s) repository Spin 10946 (H) RU-HHA ON994756 C	Species Specimen (culture) / erigin (ISO code) GenBank / UNITE accession number Reference(s) repository Exu TS AP91 RP81 RP82 TE/1 Reference(s) spoint 0346 (H) RU-HXHA — ON994756 — O 0 TE/1 Reference(s) Synin 0346 (H) RU-HXHA — ON994756 — O 0 Te/1 Reference(s) Synin 0346 (H) RU RU R05075501 KR — O 0431439 — — O PE/1 Reference(s) Synin 0346 (H) RU — DQ431439 — — O PE/1 PE/1 <td>Species Specimen (culture) / Origin (ISO code) CentBank / UNITE accession number Reference(s) repository Spin (1956 (cil) RU-KHA — Origin (ISO code) EU Repository Spin (1956 (cil) RU-KHA — Origin (ISO code) EU Reference(s) Reference(s) Spin (1956 (cil) RU-KHA — Op34758 — — OP21582 TE/F Mis study SFCud010313 KR — — DQ491419 — — — Mis study SFCud010315-21 KR — DQ491419 — — — Mis study RU-misors Excussion number Mis study — — — — — — — — = (2003) = = … Min et al. (2003) = = … E E E E E E E E E E E E E E E E E E E</td> <td>SpecineSpecime (culture) /Orgin (ISO code)GenBank / UNITE accession numberReference(s)repositionyRpositionyFU-KHALCun946 (H)RU-KHAEUCon146 (H)RP32TEF1Reference(s)spin 10946 (H)RU-KHAHCode)RP31RP31RP31RP31Reference(s)spositionySpin 10946 (H)RU-KHAHCode)Con1491409HHHspositionySpin 10946 (H)RU-KHAHCode)Code)HHHspositionySpin 10946 (H)RU-KHAHCode)Code)HHHspositionySpin 10946 (H)RU-KHAHCode)HHHHHbackCode103725-21KRHHH<t< td=""><td>Species Specimen (culture) / repository Origin (ISO code) ComBank / UNITE accession number Reference(s) repository RUKHA - ON94758 - - OP15842 This study Fuscrinensis Slimi (1966 (H) RUKHA - ON94758 - O OP15842 This study Fuscrinensis SUM (1057) 261 KR - ON94740 - - OP15842 This study Fuscrinensis SUM (1073) KR - OV49410 - - OP15842 Terr - - OP15842 Terr -</td><td>Specie Specient (ulture) (Origin (ISO code) CanBank (UNITE accession number Reference(s) repository Spin (1904 (i)) RUX (1004 (i)) RUX (1004 (i)) RUX (1004 (i)) Reference(s) Reference(s) repository Spin (1904 (i)) RUX (1004 (i)) RUX (1004 (i)) RUX (1004 (i)) Reference(s) Reference(s) repository Spin (1904 (i)) RUX (1) - ON94736 - - O Nux (1) Spin (1904 (i)) RUX (1) RUX (1) - ON94736 - - O Nux (1) Nux (1)</td><td>Specifies Specifies Specifies Specifies Application Application Reference(s) Reference(s) Reference(s) Fuszwinsis Symin 1994(H) RUH(A) - 0093436 - - 0023437 TEr/ Reference(s) Simin 1994(H) RUH(A) - 0093436 - - 0021430 Reference(s) Strond 00313 KR - 0093436 - - 0021430 Reference(s) Strond 00313 KR - 0049441 - 0049441 - - 0021400 Reference(s) Reference(s) Strond 00313 KR - 0049441 - - 0049441 -</td><td>Species Specient (ollure) Crigin (SO code) Geneant (UNITE accession number Reference(s) Reference(s) Fuscine Spin (1946 (H) RU-HAI — =</td><td>Species Specient (ulture) / Origin (S0 code) Geneant / UNITE accession number Reference(s) Fuszminests Spin (1946 (H) R.U.H.M. -</td><td>Spectrame turbure in the second mumber Additional accession number Reference(s) Fusurination for additional accession number Spectrame turbure in the second model (i) Origin (SO code) Centabart in the second model (i) Reference(s) Fusurination for additional accession number SUN mode/T3d(i) KR </td><td>Species Species Application Control (IS) Coold) Control (IS) Coold) Control (IS) Coold) Control (IS) Coold) Reference(s) F ussuritants Sivi (196.ft) RH H4 -</td><td>Species Species Species Advances <t< td=""></t<></td></t<></td>	Species Specimen (culture) / Origin (ISO code) CentBank / UNITE accession number Reference(s) repository Spin (1956 (cil) RU-KHA — Origin (ISO code) EU Repository Spin (1956 (cil) RU-KHA — Origin (ISO code) EU Reference(s) Reference(s) Spin (1956 (cil) RU-KHA — Op34758 — — OP21582 TE/F Mis study SFCud010313 KR — — DQ491419 — — — Mis study SFCud010315-21 KR — DQ491419 — — — Mis study RU-misors Excussion number Mis study — — — — — — — — = (2003) = = … Min et al. (2003) = = … E E E E E E E E E E E E E E E E E E E	SpecineSpecime (culture) /Orgin (ISO code)GenBank / UNITE accession numberReference(s)repositionyRpositionyFU-KHALCun946 (H)RU-KHAEUCon146 (H)RP32TEF1Reference(s)spin 10946 (H)RU-KHAHCode)RP31RP31RP31RP31Reference(s)spositionySpin 10946 (H)RU-KHAHCode)Con1491409HHHspositionySpin 10946 (H)RU-KHAHCode)Code)HHHspositionySpin 10946 (H)RU-KHAHCode)Code)HHHspositionySpin 10946 (H)RU-KHAHCode)HHHHHbackCode103725-21KRHHH <t< td=""><td>Species Specimen (culture) / repository Origin (ISO code) ComBank / UNITE accession number Reference(s) repository RUKHA - ON94758 - - OP15842 This study Fuscrinensis Slimi (1966 (H) RUKHA - ON94758 - O OP15842 This study Fuscrinensis SUM (1057) 261 KR - ON94740 - - OP15842 This study Fuscrinensis SUM (1073) KR - OV49410 - - OP15842 Terr - - OP15842 Terr -</td><td>Specie Specient (ulture) (Origin (ISO code) CanBank (UNITE accession number Reference(s) repository Spin (1904 (i)) RUX (1004 (i)) RUX (1004 (i)) RUX (1004 (i)) Reference(s) Reference(s) repository Spin (1904 (i)) RUX (1004 (i)) RUX (1004 (i)) RUX (1004 (i)) Reference(s) Reference(s) repository Spin (1904 (i)) RUX (1) - ON94736 - - O Nux (1) Spin (1904 (i)) RUX (1) RUX (1) - ON94736 - - O Nux (1) Nux (1)</td><td>Specifies Specifies Specifies Specifies Application Application Reference(s) Reference(s) Reference(s) Fuszwinsis Symin 1994(H) RUH(A) - 0093436 - - 0023437 TEr/ Reference(s) Simin 1994(H) RUH(A) - 0093436 - - 0021430 Reference(s) Strond 00313 KR - 0093436 - - 0021430 Reference(s) Strond 00313 KR - 0049441 - 0049441 - - 0021400 Reference(s) Reference(s) Strond 00313 KR - 0049441 - - 0049441 -</td><td>Species Specient (ollure) Crigin (SO code) Geneant (UNITE accession number Reference(s) Reference(s) Fuscine Spin (1946 (H) RU-HAI — =</td><td>Species Specient (ulture) / Origin (S0 code) Geneant / UNITE accession number Reference(s) Fuszminests Spin (1946 (H) R.U.H.M. -</td><td>Spectrame turbure in the second mumber Additional accession number Reference(s) Fusurination for additional accession number Spectrame turbure in the second model (i) Origin (SO code) Centabart in the second model (i) Reference(s) Fusurination for additional accession number SUN mode/T3d(i) KR </td><td>Species Species Application Control (IS) Coold) Control (IS) Coold) Control (IS) Coold) Control (IS) Coold) Reference(s) F ussuritants Sivi (196.ft) RH H4 -</td><td>Species Species Species Advances <t< td=""></t<></td></t<>	Species Specimen (culture) / repository Origin (ISO code) ComBank / UNITE accession number Reference(s) repository RUKHA - ON94758 - - OP15842 This study Fuscrinensis Slimi (1966 (H) RUKHA - ON94758 - O OP15842 This study Fuscrinensis SUM (1057) 261 KR - ON94740 - - OP15842 This study Fuscrinensis SUM (1073) KR - OV49410 - - OP15842 Terr - - OP15842 Terr -	Specie Specient (ulture) (Origin (ISO code) CanBank (UNITE accession number Reference(s) repository Spin (1904 (i)) RUX (1004 (i)) RUX (1004 (i)) RUX (1004 (i)) Reference(s) Reference(s) repository Spin (1904 (i)) RUX (1004 (i)) RUX (1004 (i)) RUX (1004 (i)) Reference(s) Reference(s) repository Spin (1904 (i)) RUX (1) - ON94736 - - O Nux (1) Spin (1904 (i)) RUX (1) RUX (1) - ON94736 - - O Nux (1) Nux (1)	Specifies Specifies Specifies Specifies Application Application Reference(s) Reference(s) Reference(s) Fuszwinsis Symin 1994(H) RUH(A) - 0093436 - - 0023437 TEr/ Reference(s) Simin 1994(H) RUH(A) - 0093436 - - 0021430 Reference(s) Strond 00313 KR - 0093436 - - 0021430 Reference(s) Strond 00313 KR - 0049441 - 0049441 - - 0021400 Reference(s) Reference(s) Strond 00313 KR - 0049441 - - 0049441 -	Species Specient (ollure) Crigin (SO code) Geneant (UNITE accession number Reference(s) Reference(s) Fuscine Spin (1946 (H) RU-HAI — =	Species Specient (ulture) / Origin (S0 code) Geneant / UNITE accession number Reference(s) Fuszminests Spin (1946 (H) R.U.H.M. -	Spectrame turbure in the second mumber Additional accession number Reference(s) Fusurination for additional accession number Spectrame turbure in the second model (i) Origin (SO code) Centabart in the second model (i) Reference(s) Fusurination for additional accession number SUN mode/T3d(i) KR	Species Species Application Control (IS) Coold) Control (IS) Coold) Control (IS) Coold) Control (IS) Coold) Reference(s) F ussuritants Sivi (196.ft) RH H4 -	Species Species Species Advances Advances <t< td=""></t<>

Taxon sampling for phylogenetic analyses

We compiled 22 datasets for phylogenetic analyses (Table 2). Datasets were aligned in the online version of MAFFT v. 7 (Katoh *et al.* 2019) using the E- or G-INS-I algorithm or PRANK (Löytynoja & Goldman 2010) followed by manual adjustment in AliView (Larsson 2014) or PhyDE (Müller *et al.* 2010). Each marker was aligned separately. GBlocks (Castresana 2000) followed by manual curation was used to select those regions of the sequences that were confidently aligned to be included in the family- and genus-level analyses. The number of included taxa, as well as length of aligned datasets with and without the excluded regions are given in Table 2 and Suppl. Table S1.

The first and second datasets used seven markers: nrDNA 18S (SSU), ITS, 28S (LSU), mtDNA 16S (mtSSU), RPB1, RPB2 and TEF1. Taxa were selected to this dataset after Liu et al. (2022) and other available sequences including genomes, so that at least LSU and two additional markers were present. In the first dataset (the seven-gene Polyporales dataset), we aimed to cover all families in the Polyporales with emphasis on the brown-rotters. Outgroups were Thelephora (Thelephorales) and Heterobasidion (Russulales), in accordance to Miyauchi et al. (2020). For Pseudophaeolus soloniensis, we excluded mtSSU (GenBank OM039220) from the analysis, since it is nearly identical with Fomitopsis pinicola and has either a wrong identity or is in severe phylogenetic conflict with the rest of the data. The final dataset represented 124 species (Suppl. Table S2). In the second dataset (the seven-gene Fomitopsidaceae dataset), we focused on the Fomitopsidaceae and allied taxa subsampling from the first dataset. The outgroup for the Fomitopsidaceae included Amyloporia, Rhodonia, and Ryvardenia, and was selected based on the results of the analyses of the seven-gene *Polyporales* dataset. The final dataset represented 50 species.

The seven-gene *Polyporales* and seven-gene *Fomitopsidaceae* datasets, while maximizing the number of markers, had a significant amount of missing data (Suppl. Table S2). In the seven-gene *Polyporales* dataset, in total 160 out of 875 single markers (18 %) were lacking across all taxa and all markers. In the seven-gene *Fomitopsidaceae* dataset, in total 94 out of 350 single markers (27 %) were lacking across all taxa and all markers. For this reason, we compiled additional datasets with fewer markers but a full matrix of high-quality markers.

The third dataset (the three-gene brown-rotter dataset), had the aim of showing the position and limits of *Fomitopsidaceae* among other brown-rotting families in the so-called antrodia clade in the *Polyporales* (Ortiz-Santana *et al.* 2013, Justo *et al.* 2017). It contained a selection of combined ITS + LSU + *RPB1* sequences representing all major groups in this clade including *Fomitopsidaceae*, amyloporia/fibroporia clade, *Dacryobolaceae* and *Laetiporaceae*. *Skeletocutis chrysella*; a representative of the neighbouring '*Skeletocutis/Tyromyces*' clade (Justo *et al.* 2017), was used as an outgroup. The final dataset represented 58 species (32 taxa from *Fomitopsidaceae*, six taxa from the neighbouring *Antrodia sensu stricto*, *Antrodia* (*Anthroporia*) *albobrunnea* and two to four taxa from each of the other larger groups in the antrodia clade).

The fourth and fifth datasets assessed phylogenetic relationships of species in the 'Daedalea – Fomitopsis clade'. Both datasets consisted of sequences representing the members of Fomitopsis sensu lato in Fomitopsidaceae, Daedalea and Piptoporus spp. and residual Antrodia spp. (after Han et al. 2016, Justo et al. 2017, Runnel et al. 2019 and Liu et al. 2022).

Table 2. Datasets compiled for the present stu	ıdy.			
Dataset	Figure number	Number of sequences	Alignment length	Number of parsimony informative sites
ITS + LSU + <i>RPB1</i> brown-rot Polyporales	1	58	1 913	338
Seven-gene Fomitopsidaceae	2	50	1 997	170
ITS + LSU + RPB1 Fomitopsis	3, 4	59	1 997	231
ITS Daedalea clade	5	88	438	136
ITS Pilatoporus clade	6	106	401	58
ITS + TEF1 F. marianii complex	7	28	1 046	58
ITS + TEF1 F. meliae complex	8	23	1 016	139
ITS + TEF1 + RPB1 Pilatoporus clade	9	12	2 408	261
ITS + TEF1 + RPB2 F. pinicola clade	10	75	1 244	92
ITS <i>F. feei</i> clade	11	60	481	174
ITS F. rosea clade	12	25	488	71
TEF1 F. ramentacea clade	13	13	526	18
ITS + TEF1 F. ramentacea clade	14	13	1 072	50
ITS F. spraguei clade	15	21	548	23
Seven-gene Polyporales	S1	124	3 990	190
ITS + LSU Fomitopsis	S2	65	1 218	121
TEF1 F. marianii complex	S3	22	452	40
TEF1 F. meliae complex	S4	22	427	67
ITS + TEF1 F. pinicola clade	S5	104	711	50
ITS F. ramentacea clade	S6	35	546	34
ITS <i>F. juniperina</i> clade	S7	21	574	29
ITS Buglossoporus clade	S8	20	680	168

Two representatives of the closely related *Antrodia sensu stricto* (Runnel *et al.* 2019) were used as an outgroup. The fourth dataset (the *Fomitopsis* ITS+LSU+*RPB1* dataset), mainly contained combined ITS+LSU+*RPB1* sequences (in total, 44), but in addition 15 samples represented only by ITS+LSU were included to position the key taxa in *Fomitopsis* clade that lacked the *RPB1* marker. The total number of sequences in the second dataset was 59. The fifth dataset (*Fomitopsis* ITS+LSU dataset) was limited to the combined

ITS+LSU region and included five additional taxa that were only represented with ITS sequences (totalling 65 taxa).

Seventeen additional datasets were compiled to justify species concepts in several lineages within the *Daedalea – Fomitopsis* group (Table 2, Suppl. Table S2). In each case, the outgroup selection was guided by the three-gene phylogenies of the brownrot *Polyporales* and *Fomitopsis* clade (see Figs 1 and 3).



0.07

Fig 1. Phylogenetic placement of the *Daedalea – Fomitopsis* clade (box) within the "antrodia clade" (including all taxa shown other than outgroups) based on Maximum Likelihood of the ITS + LSU + *RPB1* dataset. Numbers on nodes represent bootstrap values > 70 % and Bayesian Inference posterior probabilities > 0.85. The scale bar indicates the number of expected substitutions per site. Two-letter codes in the parentheses denote the country of origin.



Phylogenetic analyses

We conducted Maximum Likelihood (ML) and Bayesian inference (BI) for all datasets. The ITS and LSU regions and introns and exons of protein coding markers were partitioned separately. ModelTest-NG (Darriba et al. 2020) was used to select models for the order- and family-level analyses, using AICc as the selection criterion. The same models were used in ML and BI analyses (Suppl. Table S1). For these datasets, we used RAxML-NG v. 1.1.0 (Kozlov et al. 2019) to search for the highest likelihood tree with 50 parsimony and 50 random starting trees, coupled with 1 000 bootstrap replicates. MrBayes v. 3.2.7a was run with three parallel runs 8 chains each for 10-40 million generations, sampling every 10 000 generations (Suppl. Table S1). Good convergence (SD of split frequencies < 0.01) was reached in all cases except seven-gene Polyporales dataset (SD still over > 0.2 after 40 million generations) and the Fomitopsis ITS+LSU dataset (moderate convergence of SD ≈0.02). These computations were run at the CSC – IT Centre for Science (Espoo, Finland) computing environment.

For the phylogenetic analyses of species complexes within Fomitopsis, we used IQ-TREE v. 1.2.2 (Nguyen et al. 2015) with 1 000 bootstrap (bs) replicates and the 'best-fitted model' for searching the ML tree. MrBayes v. 3.2.6 (Ronquist et al. 2012) was used for BI analyses at the CIPRES Science Gateway (Miller et al. 2010). Nucleotide substitution models for the species level BI datasets were chosen with TOPALI v. 2.5 (Milne et al. 2008) based on the Bayesian information criterion (BIC). Two parallel MCMC analyses were run, each consisting of four chains, initiated from random starting trees. The analyses were run for 3-10 million generations, sampling every 1 000 generations (Suppl. Table S2). The first 25 % of the trees were discarded as the burn-in ensuring the average standard deviation of split frequencies had reached < 0.01 for all datasets, after which posterior probability (pp) values were calculated. Analyses for the Buglossoporus clade, three-gene Fomitopsis palustris group and F. juniperina group datasets were conducted as described for the family-level analyses. Results were also analysed in Tracer v. 1.6.0 (Rambaut et al. 2018). Posterior probabilities were calculated from the remaining trees in all cases.

The final alignments for all datasets as well as the input data for the phylogenetic analyses (nexus blocks) and phylograms are stored in the PlutoF web platform, at https:// dx.doi.org/10.15156/ BIO/2483943.

RESULTS

Phylogenetic placement and structure of the *Fomitopsidaceae*

We undertook an order-wide, seven-gene analysis of the *Polyporales* with a focus on brown-rot fungi, at most parts mirroring the one of Liu *et al.* (2022). We used this dataset to assess the monophyly and placement of the *Fomitopsidaceae* (*sensu* Justo *et al.* 2017). The Bayesian analysis of this dataset could not be concluded satisfactorily, since runs of the Bayesian analysis (Suppl. Fig. S1) did not converge. We suggest this is partly due to missing marker data and availability of only short fragments for some markers (*RPB2*, *TEF1*), but notwithstanding these issues this set of markers is probably still too small to recover the complex branching history in the order. We studied topologies of consensus trees of different runs and high-probability stationary states individually as

well as the ML tree (Suppl. Fig. S1), and while they differ in the case of many deeper nodes without support, they agreed on some aspects.

Monophyly of brown-rot fungi was never supported, but the recognized families *Dacryobolaceae*, *Laetiporaceae* and *Sparassidaceae* appeared with varying support. *Fomitopsidaceae* was consistently present in all the consensus trees (ML bs = 95 %, overall Bayesian pp = 0.9). In all analyses *Amyloporia* was placed as its sister clade, except in some runs when it was the sister of a *Fomitopsidaceae – Laricifomes – Ryvardenia* clade. Monophyly of *Amyloporia – Fibroporia* clade earlier introduced by Justo *et al.* (2017) was not supported. A big clade of brownrot fungi with *Fomitopsidaceae*, *Amyloporia, Laricifomes – Ryvardenia, Fibroporia, Pseudophaeolus, Sparassis, Crustoderma – Pycnoporellus* and *Laetiporaceae* was also consistent in all the trees, albeit not always with good support (bs = 34 %, pp = 0.88).

Next, we conducted a partially overlapping analysis of a threegene brown-rotter dataset, which represents a sample of brown-rot families in the antrodia clade, but with no missing marker data. This analysis showed that *Fomitopsidaceae* (*sensu* Justo *et al.* 2017) resolves as highly supported (bs = 98 %, pp = 1) (Fig. 1). Based on these results, we are fairly confident in the circumscription of *Fomitopsidaceae*. Its closest relatives include other dimitic brownrot polypores traditionally placed in *Antrodia* or *Fomitopsis*, such as *Amyloporia*. Additionally, our data assert that *Fomitopsis officinalis* should be excluded from *Fomitopsidaceae* and treated under *Lariciformes*, for which it is the type species (Fig. 1), in accordance with the previous results of Liu *et al.* (2022).

The three-gene brown-rotter analysis split *Fomitopsidaceae* in three well-supported clades (Fig. 1): (1) *Antrodia albobrunnea* clade (= *Anthoporia*) represented by a single species; (2) *Antrodia sensu stricto* clade as redefined by Runnel *et al.* (2019) (bs = 100 %, pp = 1) with several poroid and one corticioid species; (3) a large *Daedalea – Fomitopsis* clade (bs = 97 %, pp = 1). Our third phylogeny, based on the seven-gene dataset of *Fomitopsidaceae* and satellite taxa (Fig. 2), corroborates monophyly of the *Daedalea – Fomitopsis* clade (bs = 98 %, pp = 1). Justo *et al.* (2017) first recognized the *Daedalea – Fomitopsis* group as a strongly supported clade and our expanded datasets confirm that result.

Three subclades can be defined in the *Daedalea – Fomitopsis* clade, detected in our seven-gene analyses (Suppl. Fig. S1, Fig. 2) and the three-gene brown-rotter analysis (Fig. 1):

- the *Buglossoporus* subclade containing the effusedreflexed *Antrodia madronae*, stipitate terrestrial sclerotiaforming *Laccocephalum* spp. and semistipitate wood-inhabiting *Neolentiporus squamosellus* and *Buglossoporus quercinus*;

- a single-species lineage represented by an undescribed species, *Fomitopsis* sp. Darwin (M.D. *Barrett F17/09*) from tropical Australia, which is unusual in *Fomitopsis sensu lato* in having stipitate to substipitate basidiocarps, and lacking clamps at most septa (scattered clamps only);

- the *Fomitopsis* subclade containing the rest (vast majority) of the species.

The Bayesian inference (BI) topology makes it possible to consider the *Fomitopsis spraguei* complex as a separate lineage although this option is not supported in the maximum likelihood (ML) topology (Fig. 1 – represented by *F. spraguei*, Fig. 2 – by *F. hypoxantha*).

Our second three-gene dataset focussed on the *Daedalea* – *Fomitopsis* clade (Fig. 3). This dataset had higher coverage of *Fomitopsis* than the previous analyses but was missing some *RPB1* marker data. Among these taxa, sixteen species are either



0.03

Fig 2. Phylogenetic placement of the Daedalea – Fomitopsis clade (box) within the Fomitopsidaceae and allied taxa (including all taxa shown other than outgroups) based on Maximum Likelihood of the ITS + LSU + SSU + mtSSU + RPB1 + RPB2 + TEF1 dataset. Numbers on nodes represent bootstrap values > 70 % and Bayesian Inference posterior probabilities > 0.85. The scale bar indicates the number of expected substitutions per site. Two-letter codes in the parentheses denote the country of origin.

types of genera or closest relatives of the type species. Most of these genera have been introduced in the last seven years after splitting *Fomitopsis* and *Antrodia sensu lato* (Han *et al.* 2016, Audet 2017, Liu *et al.* 2022). The analyses based on this extended dataset supported the division of the *Daedalea – Fomitopsis* clade to only two subclades (*Buglossoporus* and *Fomitopsis*, the latter containing also *Fomitopsis* sp. Darwin), but the overall topology was broadly

similar to the three- and seven-gene datasets described above. Importantly, the *Daedalea – Fomitopsis* subclade was divided into about 40 supported clades or orphan species, whose relations were unresolved.

Of the taxa that lacked the *RPB1* sequence, *Fomitopsis* niveomarginata formed a long distinct branch within the *Daedalea* – *Fomitopsis* clade in the phylogenetic tree representing the *Daedalea*



0.02

Fig. 3. Phylogenetic relationships of species in the *Daedalea – Fomitopsis* clade based on Maximum Likelihood of the ITS + LSU + *RPB1* dataset. Numbers on nodes represent bootstrap values > 70 % and Bayesian Inference posterior probabilities > 0.85. The species represented with ITS + LSU only are marked with an asterisk (*). The scale bar indicates the number of expected substitutions per site. Two-letter codes in the parentheses denote the country of origin. Names of pink-coloured perennial species are given in red, those of monomitic species are in blue.

- Fomitopsis three-gene dataset (Fig. 3) and the corresponding ITS+LSU dataset (Suppl. Fig. S2). Adding *F. niveomarginata* to the phylogenetic analyses causes a slight change in the inner structure of the *Daedalea* – Fomitopsis clade (Fig. 1 vs. Fig. 3). As a result, the inner structure of the largest subclade containing this species (*i.e.* the Fomitopsis subclade) loses support for the most part.

Alternative treatments of genus level taxonomy in *Fomitopsidaceae*

Taxonomically, the outcome of our phylogenetic analyses can be interpreted in four possible ways:



Fig 4. Three generic concepts for delimiting genera in the *Daedalea – Fomitopsis* clade. A. Microgeneric approach. B. Mesogeneric approach. C. Macrogeneric approach (accepted in the present study). For details about topology, see Fig. 2.

1. The microgeneric approach. Each strongly supported terminal lineage in the *Daedalea – Fomitopsis* group is accepted as a separate genus. This approach was first applied by Han *et al.* (2016) who advocated splitting *Fomitopsis sensu lato* into several smaller genera. However, more extensive taxon sampling makes maintaining this approach problematic for two main reasons. First, even smaller genera become more ill-defined after adding more *Fomitopsis sensu lato / Daedalea / residual Antrodia* spp. to the

dataset. For example, *Antrodia oleracea* makes *Rhodofomitopsis* polyphyletic and *Rubellofomes* does not recover as a single clade (Figs 2, 3). Second, at least 22 new genera in *Daedalea – Fomitopsis* subclade would be necessary (Fig. 4, Suppl. Fig. S2). Of these, at least fifteen would be monotypic, in addition to five single-species genera introduced in the previous publications (Han *et al.* 2016, Audet 2017). Any reliable morphological definition of these potential genera is eventually impossible (we discuss this in

more detail below). If applied further in *Fomitopsidaceae*, it would be natural to split *Antrodia sensu stricto* to many genera as well, causing similar problems.

2. The mesogeneric approach. The Daedalea - Fomitopsis clade is split in two to three genera. Both the analyses of the threegene brown-rotter dataset and the dataset explicitly focussing on the Daedalea - Fomitopsis clade (Figs 2, 3) show three strongly supported subclades which could be interpreted as separate genera: Buglossoporus, Fomitopsis and a single-species genus for the Australian Fomitopsis sp. Darwin (M.D. Barrett F17/09). Being its sister, the latter could also be included in a monophyletic Fomitopsis (two-genera approach). The main problem with such splitting of the Daedalea - Fomitopsis clade is that it could be based only on calculation of support values but would not allow for morphologically identifiable genera. For instance, the Buglossoporus subclade encompasses mainly sappy, semistipitate or stipitate polypores with rather sparse skeletal hyphae in tube trama, but it also contains Antrodia madronae. The latter species, as well as its closest relative A. sandaliae, are morphologically much more similar to some residual Antrodia spp. in the Fomitopsis subclade (e.g., A. infirma, A. oleracea, A. tuvensis) than to Buglossoporus quercinus and its satellites, and therefore they blur any presumed differences between the Buglossoporus subclade and the other lineages in the Daedalea - Fomitopsis clade. For the time being, we do not consider the mesogeneric approach useful.

3. The macrogeneric approach. The whole *Daedalea – Fomitopsis* group is treated as one genus, but *Anthoporia* and *Antrodia sensu stricto* (*sensu* Runnel *et al.* 2019) are retained. Despite their outwardly diverse habit, members of the *Daedalea – Fomitopsis* group share several principal anatomical traits presented below that separate them from *Anthoporia* and *Antrodia sensu stricto*. For the present, we see this approach as the most reasonable taxonomic solution.

4. The monogeneric approach – one family, one genus. All of *Fomitopsidaceae* are placed in one genus, including *Antrodia sensu stricto* and *Anthoporia*. Equating genera and families is a reasonable solution when genetic and morphological variation is small, typically in the case of small isolated genera (*e.g., Ischnoderma*). In contrast, the family *Fomitopsidaceae* shows significant genetic variation and can be divided into morphologically identifiable clades (at least *Anthoporia, Antrodia* and *Fomitopsis* as discussed below). Fusing *Antrodia* and *Fomitopsis* would remove issues with genus identification within the *Fomitopsidaceae*, but *Antrodia sensu lato* species are found in other families of the *Polyporales*, too. This solution would thus not allow easy identification of genera either.

Morphological evidence for maintaining the Daedalea – Fomitopsis clade as one genus

If interpreted taxonomically as one genus, the *Daedalea* – *Fomitopsis* clade can be separated from two other genera of *Fomitopsidaceae*, *i.e. Anthoporia* and *Antrodia sensu stricto*, by the combination of the following features:

1. Branched and coloured skeletal hyphae. In dimitic species of the *Daedalea – Fomitopsis* clade skeletal hyphae are occasionally branched and quite often coloured (brownish to brown or more rarely reddish). Rajchenberg (1986) and Hattori (2005) described and discussed them as a characteristic feature of *Daedalea*

spp. We were able to demonstrate the presence of occasionally branched skeletals in residual *Antrodia* spp. outside *Antrodia* sensu stricto (Spirin et al. 2016, 2017) and now confirm it for the rest of the dimitic species in the whole *Daedalea – Fomitopsis* group. In contrast, all poroid species in *Antrodia* sensu stricto possess unbranched, as a rule hyaline vegetative hyphae (Spirin et al. 2013a, Kout et al. 2017). The single corticioid representative of the latter genus with monomitic basidiocarps, *A. griseoflavescens*, produces skeletal hyphae in culture (Hallenberg 1990). In turn, *Anthoporia albobrunnea* has partly pigmented generative hyphae in the context and uppermost tube trama while skeletal hyphae of this species are unbranched and hyaline (Karasiński & Niemelä 2016).

2. Relatively small basidia and basidiospores. Basidia and basidiospores in the Daedalea - Fomitopsis group are on average smaller than in Antrodia sensu stricto, in almost all species not exceeding 25 µm and 10 µm long, respectively, when considered in combination (both characters found in the same species). Only six of the 128 members of the Daedalea - Fomitopsis clade treated below, i.e. Antrodia albidoides, A. madronae, A. variiformis, Neolentiporus maculatissimus, N. squamosellus and Laccocephalum tumulosum, are exceptions to this rule, i.e. their basidia and basidiospores exceed the aforementioned limits. Of them, the three latter species have stipitate, soft basidiocarps strikingly different from those ones of Antrodia sensu stricto. In turn, A. albidoides possesses well-developed skeletocystidia (if compared with representatives of Antrodia sensu stricto) and its basidiospores show no arcuate depression at the apiculus so characteristic of Antrodia sensu stricto (Spirin et al. 2013a). Antrodia variiformis produces encrusted cystidioles and distinctly coloured hyphae in the uppermost part of context (Spirin et al. 2017); these features rule out Antrodia sensu stricto. Antrodia madronae is a soft, fleshy polypore with hyphae easily dissolving in both KOH and IKI (Vlasák et al. 2012). None of those features fit Antrodia sensu stricto. Nevertheless, these exceptional cases indicate that the length of basidia and basidiospores have limited value as a discriminating character and can be used only in combination with two other morphological traits discussed here. Basidia of Anthoporia albobrunnea are small, comparable with many species of the Daedalea - Fomitopsis complex, but its basidiospores are strikingly different, allantoid to narrowly cylindrical, mostly evenly curved. They are reminiscent more of Amyloporia and Postia than other members of the Fomitopsidaceae.

3. The presence of skeletocystidia and hyphidia. Skeletocystidia and hyphidia are characteristic for truly dimitic representatives of both the *Daedalea – Fomitopsis* clade and *Antrodia sensu stricto*, skeletocystidia occur only occasionally as poorly differentiated blunt endings of skeletal hyphae, and at least some hyphidia are bi- or trifurcate (Spirin *et al.* 2013a, Runnel *et al.* 2019). In the *Daedalea – Fomitopsis* group, all truly dimitic species with pore size equal to dimitic *Antrodia sensu stricto* species (*i.e.* 0.5–3 per mm) possess well-developed skeletocystidia, which are either apically clearly inflated or acute. Only a single representative of the *Daedalea – Fomitopsis* clade, the small-pored *Antrodia sensu stricto* is inflated or acute. Only a single representative of the *Daedalea – Fomitopsis* clade, the small-pored *Antrodia sensu stricto* (Spirin *et al.* 2017), while they are normally unbranched in all other species of the clade.

We illustrate with further examples why the macrogeneric approach is preferable to the microgeneric one. Han et al.

(2016) divided the pink-coloured species of Fomitopsis sensu lato between two genera, Rhodofomes (the Fomitopsis rosea complex) and the newly erected Rhodofomitopsis (the Fomitopsis feei complex). They justified this rearrangement via phylogenetic analyses and indicated the absence of cystidia and cystidioles in Rhodofomitopsis spp. as the only morphological feature separating them from Rhodofomes and similarly coloured Rubellofomes and Daedalea spp. Our observations suggest this is true only for F. feei sensu stricto (as redefined below) while eight other representatives of the F. feei complex have cystidioles and one of them (F. cupreorosea) produces easily detectable skeletocystidia. Moreover, our data show the pink-coloured species of Fomitopsis sensu lato belong to at least nine different lineages in the Daedalea - Fomitopsis group (Fig. 3, Suppl. Fig. S2). We have not found unique morphological traits to justify their acceptance as separate genera. Of course, separation into nine genera is not totally elusive if based on phylogenetic evidence only. However, implementing it would cause a cascade splitting in other parts of the Daedalea -Fomitopsis complex.

The case of *Fomitopsis dochmia* is even more striking. According to our results, its current concept covers six species (*F. dochmia sensu stricto*, *F. elevata*, *F. ferrea*, *F. lapidosa*, *F. lignea*, and *F. philippinensis*) belonging to two very distantly related lineages within the *Daedalea* – *Fomitopsis* group (Figs 3, 5, Suppl. Fig. S2). Morphological differences between them are minimal, however, and these species can be separated with some confidence based only on macroscopic traits of basidiocarps and geographic distribution. *Fomitopsis caseosa*, *F. niveomarginata* and *F. pseudopetchii* can provide another example of the utmost morphological similarity of phylogenetically distant species (Fig. 3, Suppl. Fig. S2).

The merits of the mesogeneric approach, *i.e.* interpreting the Buglossoporus and Fomitopsis subclades as separate genera, deserve further comments. In all published phylogenetic analyses these two lineages are well supported, and at first this division appears to be supported by morphology, making the mesogeneric approach appealing. In fact, Buglossoporus as a genus was included in the earliest versions of this manuscript. Morphologically, all Fomitopsidaceae species with the combination of stipitate, fleshy basidiocarps and nearly monomitic tube trama are found in the Buglossoporus subclade. Two of the ten species we have included in the analyses are effused-reflexed or totally resupinate (Antrodia madronae, A. sandaliae). These species also have a partly monomitic hyphal structure. Additionally, A. madronae has unusually large basidia for Fomitopsis, like several other members of the Buglossoporus subclade. There is no character that is unique for the subclade, however. There are monomitic or nearly monomitic species in several lineages of the Fomitopsis subclade (e.g., A. infirma, A. monomitica, A. oleracea, A. ramentacea). Large hymenial cells are also found in the A. ramentacea complex and a few other species (A. albidoides, A. tuvensis, A. variiformis).

Here, we have defined the large *Fomitopsis* clade through a combination of characters. Applying the same scheme to recognize *Buglossoporus* looks problematic. *Antrodia sandaliae* is difficult to place in *Buglossoporus* even with a combination of characters. A separate genus for it would cause a cascade of splitting, which in essence would mark a return to the microgeneric approach. When two of the ten species do not fit comfortably in a genus, we feel it better to include the whole *Buglossoporus* subclade in one genus with the members of the *Fomitopsis* subclade. Surely, a large portion of species diversity remains undiscovered. Considering the degree of morphological plasticity both in the *Fomitopsis* and



Buglossoporus subclades, that diversity might still significantly alter our understanding of morphological variation. With a deeper understanding of diversity and morphological variation, the mesogeneric approach might become a good option, but for now we consider it is suboptimal to the macrogeneric approach.

Arguments for choosing *Fomitopsis* as a generic name for the *Daedalea* – *Fomitopsis* clade

If the one-genus concept for the whole *Daedalea – Fomitopsis* group is accepted, then the oldest generic name available for it is *Daedalea*, introduced by Persoon (1801) and typified with *Agaricus quercinus* (= *Daedalea quercina*). The three next names in line are *Caloporus* (typified with *Poria incarnata*, see further remarks under *Fomitopsis marianii*) (Karsten 1881a), *Fomitopsis* (typified with *Boletus pinicola* = *Fomitopsis pinicola*) and *Piptoporus* (typified with *Boletus betulinus* = *Piptoporus betulinus*) (Karsten 1881b).

We argue for retaining *Fomitopsis* and suppressing other older (Daedalea, Caloporus) or simultaneously published (Piptoporus) names for the following reasons. First, of the 128 species accepted here in the Daedalea - Fomitopsis generic unit, 33 were already combined or described in Fomitopsis and only 18 in Daedalea. Therefore, applying Fomitopsis will require fewer new combinations than maintaining Daedalea. Second, using Daedalea will necessitate a species epithet change for at least ten species, which would be highly undesirable in the case of two common and well-known species, F. pinicola and P. betulinus (now Fomitopsis betulina). Boletus marginatus for the first species and Agarico-pulpa pseudoagaricon for the second one are available as replacing names, if combination were to be made in Daedalea. Both names are obscure and almost unknown to current mycologists. If Fomitopsis is accepted, only three species (Antrodia minuta, Daedalea africana and Trametes cystidiata) will need new species names. Additionally, two common and well-known polypores. D. quercina and Antrodia serialis, will change their generic affiliation but they will hold their species epithets. Finally, the family name Fomitopsidaceae is in use and retaining the name Fomitopsis in use makes it easier to connect the family name with species. For these reasons, we see more advantages in keeping Fomitopsis as a generic epithet for the Daedalea - Fomitopsis group. A corresponding conservation proposal has been submitted to the Nomenclatural Committee for Fungi.

Reassessing selected species complexes in *Fomitopsis*

We prepared seventeen additional datasets to reconsider species limits in nine selected groups within the genus.

1. Fomitopsis (Daedalea) quercina clade (= Daedalea sensu stricto as redefined by Lindner et al. 2011, Li et al. 2013 and Han et al. 2016). The ML and BI analyses of the ITS dataset resulted in nearly identical topologies with seventeen strongly supported lineages taxonomically interpreted as separate species (Fig. 5). Four of them, Daedalea dickinsii, D. neotropica and D circularis (recombined in *Fomitopsis* below), as well as *Fomitopsis* derelicta *sp. nov.*, are closely related and morphologically similar to *F. quercina*. *Fomitopsis* derelicta is a newly described member of this complex occurring in subtropical – tropical areas of North America. At the same time, *F. quercina* is shown to be widely distributed in Europe and temperate – warm temperate forests of North



Fig 5. Phylogenetic relationships of species in the *Fomitopsis (Daedalea) quercina* clade based on Maximum Likelihood of the ITS dataset. Numbers on nodes represent bootstrap values > 70 % and Bayesian Inference posterior probabilities > 0.85. The scale bar indicates the number of expected substitutions per site. Two-letter codes in the parentheses denote the country of origin.

America (from Oregon to Georgia). The ITS sequence of *Daedalea pseudodochmia* published by Lindner *et al.* (2011) (GenBank FJ403210) is based on a misidentification and belongs to the East Asian *D. dickinsii*. Our data show that *Daedalea pseudodochmia* is not related to the *F. quercina* complex and its phylogenetic position in the genus *Fomitopsis* deserves further study because it is so far represented by the single ITS sequence (Suppl. Fig S2). Hattori (2005) argued that *D. pseudodochmia* is the same species as *Trametes incana*. This viewpoint is not supported by our data. We assert that *Trametes incana* is a member of *F. quercina* complex closely related to *Daedalea allantoidea*. In turn, *D. pseudodochmia* is treated below as *Fomitopsis moritziana* (see Taxonomy section).

Fomitopsis dochmia is proven to be a polyphyletic species complex containing at least six species, of which four (F. dochmia s. str., F. elevata, F. ferrea and F. philippinensis) form a strongly supported lineage in the F. quercina clade. The remaining two (F. lapidosa, F. lignea) do not belong to the F. quercina clade. ITS sequences of Trametes modesta (= Daedalea modesta) are split among two distantly related lineages within the F. quercina clade, in good accordance with their geographic origin and, to a lesser extent, morphological evidence. Sequences of specimens collected in Central and South America represent T. modesta sensu stricto which turns out to be a close relative of Trametes subectypa (= Daedalea americana), another species from subtropical North America. In turn, the Southeast Asian specimens of T. modesta belong to yet another species, for which Polyporus atypus is available as the oldest name. Finally, Polyporus leiodermus, Polystictus aculeatus, Polyporus psilodermeus and Daedalea ryvardeniana are three more members of the F. quercina group; according to our data, they are not closely related to other species in the clade (Fig. 5). Two species, D. africana (= Fomitopsis kenyensis, nom. nov.) and D. aethalodes, ascribed to Daedalea clade by Han et al. (2016), Liu et al. (2022) and Cristaldo et al. (2022), are most distant from the rest of species, and therefore their sequences were used as an outgroup.

2. Fomitopsis (Pilatoporus) palustris complex. Kotlaba and Pouzar (1990) argued that *F. palustris* and its siblings should be treated as members of the separate genus *Pilatoporus*. However, this option was not supported by phylogenetic studies (Kim *et al.* 2005, Ortiz-Santana *et al.* 2013, Han *et al.* 2016), which have shown that *F. palustris* and its sibs are closely related to the generic type of *Fomitopsis*, *F. pinicola*. Our results (Figs 3, 4) do not preclude from recognizing *Pilatoporus* as a separate taxonomic unit, would the microgeneric approach be applied to the reclassification of *Fomitopsidaceae*.

Members of the *F. palustris* group are widely distributed from temperate to tropical zones, and many competing species names, both historical and recently introduced, are available for them. The species concepts proposed here are based on morphological studies of type specimens and newly collected sequenced specimens. They are mostly backed by DNA data, but not fully. This is mainly due to lack of reliable differences between sister species and a rather high variation within the ITS region in some of them.

We could recognize eight species in the complex: *F. caespitosa* (= *F. subtropica*), *F. eucalypticola*, *F. luzonensis* (= *F. ostreiformis* sensu auct., non sensu typi), *F. marianii* (= *F. iberica*), *F. meliae*, *F. nivosella* (= *F. durescens*), *F. ostreiformis* sensu typi (= *F. cana*) and *F. palustris*. ITS-based phylogeny divided the *F. palustris* complex in four strongly supported lineages: *F. eucalypticola*, *F. meliae* – *F. ostreiformis* lineage, *F. caespitosa* and a large group containing *F.*

luzonensis, *F. marianii*, *F. nivosella* and *F. palustris* (henceforth *F. marianii* lineage) (Fig. 6). Further phylogenetic analyses of the *F. marianii* lineage were based on *TEF1* and combined ITS + *TEF1* (+ *RPB1*) datasets.

Both the TEF1 only and the ITS + TEF1 phylogeny split the F. marianii lineage in three strongly supported terminal clades, i.e. Fomitopsis marianii, F. luzonensis - F. nivosella, and F. palustris (Fig. 7, Suppl. Fig. S3). While the F. palustris clade is limited to the single North American species, F. palustris, easily identifiable due to its peculiar morphology (small basidiocarps and rather large basidia and basidiospores) and host species (restricted to warm temperate - subtropical Pinus spp.), the species subdivision of the two other clades is much more problematic. No reliable sequence differences were found between sequences of F. marianii from the temperate - subtropical northern hemisphere and a single specimen of F. hemitephra from New Zealand. However, this sequenced specimen of F. hemitephra seems to be either misidentified or contaminated, since F. hemitephra is a white rot fungus here referred to Neofomitella in the Polyporaceae (see remarks under excluded taxa). Neither the ML nor BI topology show F. luzonensis and F. nivosella forming distinct clades, despite small but stable differences in both ITS and TEF1 regions (3 and 3-4 bp, respectively). For now, we treat them as two different species due to rather clear morphological differences (summarized in Table 3) and different geographic distribution.

The specimen *Dollinger 836* (designated as *F. marianii*) poses one more problem for the species: polymorphism in its ITS and *TEF1* sequences can be interpreted as containing two alleles, one similar to *F. nivosella* and the other identical with *F. marianii*. The *RPB1* sequence does not show this pattern and corresponds to *F. marianii*, thus excluding that this specimen would represent a firstgeneration hybrid between the two species/populations. With only one specimen showing this pattern, no far-reaching conclusions about species delimitation can be drawn, but it indicates there may still be gene flow between the parental species / populations.

The *TEF1* and ITS + *TEF1* phylogenies of the *F. meliae* – *F. ostreiformis* lineage show sequences of the latter species clustering together although they do not form a clade clearly delimited from *F. meliae* (Fig. 8, Suppl. Fig. S4). In the ITS + *TEF1* + *RPB1* phylogram, where these species are represented by two specimens each, they do receive support (Fig. 9). We retain *F. meliae* and *F. ostreiformis* as independent species, based on geographic distribution (subtropical – tropical North America vs. paleotropics), morphological differences (commented under *F. meliae* and summarized in Table 3), and the minor DNA differences. It is evident that the whole group deserves a thorough revision with a much more extensive sampling and the use of additional genetic markers. We consider it quite possible that such a sampling may result in fewer species in this complex (notwithstanding diversity yet undiscovered).

3. Fomitopsis pinicola complex. Haight *et al.* (2019) and Liu *et al.* (2021) have recently described eight new species from North America and Asia in addition to the previously introduced *F. pinicola* and *F. ochracea* (Ryvarden & Stokland 2008). Here, we compiled the most comprehensive dataset for this group published so far, including newly produced sequences and all credible sequences from Haight *et al.* (2019) and Liu *et al.* (2021). Our phylogenetic analyses of the ITS + *TEF1* and ITS + *TEF1* + *RPB2* datasets do not fully support any of the eight newly described species (Fig. 10, Suppl. Fig. S5). Fomitopsis ochracea was resolved at the deepest split of the *F. pinicola* complex, but even recognition of



Fig 6. Phylogenetic relationships of species in *Pilatoporus (Fomitopsis palustris)* group based on Maximum Likelihood of the ITS dataset. Numbers on nodes represent bootstrap values > 70 % and Bayesian Inference posterior probabilities > 0.85. The scale bar indicates the number of expected substitutions per site. Two-letter codes in the parentheses denote the country of origin.





Fig 7. Phylogenetic relationships of species in the *Fomitopsis marianii* complex based on Maximum Likelihood of the ITS + *TEF1* dataset. Numbers on nodes represent bootstrap values > 70 % and Bayesian Inference posterior probabilities > 0.85. The scale bar indicates the number of expected substitutions per site. Two-letter codes in the parentheses denote the country of origin.

this species as a separate lineage is not supported unambiguously in our phylogenetic analyses. However, morphological differences and previous mating tests (Mounce & Macrae 1938, Högberg *et al.* 1999) convinced us to recognize this species. Before division beyond the two species *F. pinicola* and *F. ochracea* is adopted, we call for convincing evidence for their existence through much more solid specimen and gene sampling. For a detailed discussion, consult the Taxonomy section (under *F. pinicola*).

4. Fomitopsis feei clade (= Rhodofomitopsis sensu B.K. Cui et al. in Yuan et al. 2020). Morphologically, the group is highly diverse, encompassing totally effused, soft, monomitic and sturdy, perennial polypores with sessile caps. This makes a morphological definition of the clade eventually impossible. Monomitic porioid species are divided in two groups. One of them contains sequences of *Antrodia oleracea* from North America and *A. monomitica* from East Asia, and another consists of *Pseudoantrodia monomitica* (Fig. 11). Eight remaining species represent sturdy, pileate *Fomitopsis* spp. and they all are redescribed below. ITS sequences of *F. africana, F. carnea* and *F. lilacinogilva* reveal a considerable variation (up to



10 bp in the two latter species), and the taxonomy of these taxa certainly deserves further study.

Trametes marchionica, for a long time considered a synonym of *F. feei*, is morphologically highly similar to the representatives of the *F. feei* complex but phylogenetically very distant from them, here recovered sister to *D. pseudodochmia* (Suppl. Fig. S2). Therefore, we transfer it to *Fomitopsis* as a good species and reintroduce it below.

5. Fomitopsis rosea clade (= Rhodofomes). Kotlaba & Pouzar (1990) introduced Rhodofomes with F. rosea as the type and the sole species. Han et al. (2016) accepted the genus and expanded it with four more species. We compiled an ITS dataset for the F. rosea complex and our analyses confirm seven species in this group (Fig. 12). Of them, F. cupressicola from North America, F. perhiemata from Caucasus and F. purpurea from East Africa are described as new. Nigroporus ussuriensis and Fomitopsis incarnata are proven to be conspecific, and a new combination, F. ussuriensis, is proposed below. Morphological traits of F. rosea and all other pink-coloured species in the genus are summarized in Table 4.

6. Fomitopsis (Antrodia) ramentacea clade. Kotlaba & Pouzar (1958) studied anatomy of *Trametes subsinuosa* (= *Polyporus ramentaceus*) and found that it is a monomitic species with variably thick-walled hyphae (see further notes on miticity in this complex in the next paragraph). This was the main reason for them to place this species in the newly established genus *Cartilosoma*. The genus was accepted in some recent publications (Rivoire *et al.* 2015, Rivoire 2020) while other authors (*e.g.*, Donk 1966,

David & Dequatre 1985, Ryvarden 1991) treated *P. ramentaceus* as a member of *Antrodia*. David and Dequatre (1985) studied cultural characters of *Antrodia ramentacea* and concluded it is a species complex. They introduced *Antrodia subramentacea* as a morphologically indistinguishable but culturally incompatible twin of *A. ramentacea*. Based on DNA data and morphological evidence, Rivoire *et al.* (2015) described another species in the complex, *Cartilosoma renehenticii*.



Fig 8. Phylogenetic relationships of species in the *Fomitopsis meliae* complex based on Maximum Likelihood of the ITS + *TEF1* dataset. Numbers on nodes represent bootstrap values > 70 % and Bayesian Inference posterior probabilities > 0.85. The scale bar indicates the number of expected substitutions per site. Two-letter codes in the parentheses denote the country of origin.



Fig 9. Phylogenetic relationships of species in the *Pilatoporus (Fomitopsis palustris)* group based on Maximum Likelihood of the ITS + *TEF1* + *RPB1* dataset. Numbers on nodes represent bootstrap values > 70 % and Bayesian Inference posterior probabilities > 0.85. The scale bar indicates the number of expected substitutions per site. Two-letter codes in the parentheses denote the country of origin. The tree is midpoint-rooted.



0.02

Fig 10. Phylogenetic relationships of species in the *Fomitopsis pinicola* complex based on Maximum Likelihood of the ITS + *TEF1* +*RPB2* dataset. Numbers on nodes represent bootstrap values > 70 % and Bayesian Inference posterior probabilities > 0.85. The scale bar indicates the number of expected substitutions per site. Two-letter codes in the parentheses denote the country of origin.





Fig 11. Phylogenetic relationships of species in the *Fomitopsis feei* clade based on Maximum Likelihood of the ITS dataset. Numbers on nodes represent bootstrap values > 70 % and Bayesian Inference posterior probabilities > 0.85. The scale bar indicates the number of expected substitutions per site. Two-letter codes in the parentheses denote the country of origin.

Here we show that *Cartilosoma* is a part of the redefined *Fomitopsis* (Figs 2, 3). Three datasets focussing on the *A. ramentacea* group (ITS only, *TEF1* only and combined ITS + *TEF1*) resulted in nearly the same topologies allowing the recognition of four species: *A. ramentacea* (= *A. subramentacea*), *Skeletocutis uralensis* (= *Antrodia huangshanensis*), *C. renehenticii*, and *Fomitopsis solaris*, *sp. nov*. The only exception somehow blurring the species subdivision proposed here is the specimen *Rivoire LY*-

BR 6356 (designated as *F. renehenticii* × solaris in Figs 13, 14 and Suppl. Fig. S6). This specimen is morphologically identical to *C. renehenticii* and its *TEF1* sequence shows no differences from the latter species (Fig. 13). In contrast, its ITS sequence is identical to *F. solaris* (Suppl. Fig. S6). Whether this is a case of incomplete lineage sorting or hybridization between the two species is impossible to tell with our data.



0.02

Fig 12. Phylogenetic relationships of species in the *Fomitopsis rosea* clade based on Maximum Likelihood of the ITS dataset. Numbers on nodes represent bootstrap values > 70 % and Bayesian Inference posterior probabilities > 0.85. The scale bar indicates the number of expected substitutions per site. Two-letter codes in the parentheses denote the country of origin.



Fig 13. Phylogenetic relationships of species in the *Fomitopsis* (*Antrodia*) ramentacea clade based on Maximum Likelihood of the *TEF1* dataset. Numbers on nodes represent bootstrap values > 70 % and Bayesian Inference posterior probabilities > 0.85. The scale bar indicates the number of expected substitutions per site. Two-letter codes in the parentheses denote the country of origin.

7. Fomitopsis spraguei clade (= Niveoporofomes sensu Decock et al. 2022). In addition to three species, *F. spraguei, Niveoporofomes globisporus* and *N. oboensis*, recently recognized via morphology and ITS sequences (Decock et al. 2022), we were able to detect and name one more species in this complex, *Fomitopsis hypoxantha* (Fig. 15).

8. Fomitopsis (Antrodia) juniperina complex. Based on morphological study and ITS dataset, we could recognize only two species in this group, *i.e. F. juniperina* and the newly described *F. algumicola* (Suppl. Fig. S7). Further remarks are given under the latter species and *Antrodia uzbekistanica* (in excluded taxa).



Fig 14. Phylogenetic relationships of species in the *Fomitopsis* (*Antrodia*) ramentacea clade based on Maximum Likelihood of the ITS + *TEF1* dataset. Numbers on nodes represent bootstrap values > 70 % and Bayesian Inference posterior probabilities > 0.85. The scale bar indicates the number of expected substitutions per site. Two-letter codes in the parentheses denote the country of origin.



Fig 15. Phylogenetic relationships of species in *Fomitopsis spraguei* group based on Maximum Likelihood of the ITS dataset. Numbers on nodes represent bootstrap values > 70 % and Bayesian Inference posterior probabilities > 0.85. The scale bar indicates the number of expected substitutions per site. Two-letter codes in the parentheses denote the country of origin. The tree is midpoint-rooted.
Table 3. Morphological, ecological and geographic traits in Fomitopsis palustris complex.							
Species	Geographic distribution / host	Macroscopic characters	Tramal skeletal hyphae	Basidia	Basidiospores		
F. caespitosa	East Asia, Oceania, South America; angiosperms	usually effused- reflexed with large resupinate parts; pores 7–11 per mm	rather densely interwoven, 3.5–7 µm in diam, approaching dissepiment edges	9–12 × 4–5 µm	broadly cylindrical to ellipsoid, 3.0–4.2 × 1.9–2.9 µm; L = 3.58, W = 2.13, Q = 1.68		
F. eucalypticola (fide Liu et al. 2019)	Oceania; angiosperms (<i>Eucalyptus</i> spp.)	sessile or effused- reflexed, pores 3–5 per mm	interwoven, 1.5–3 μm in diam	15–23 × 7–10.5 μm	cylindrical to ellipsoid, 5.8–9.1 × 2.7–5.0 μm; L = 7.52, W = 3.42, Q = 2.23		
F. luzonensis	South-East Asia; angiosperms	sessile or effused- reflexed, pores 8–10 per mm	rather densely interwoven, 2–4.5 μm in diam, approaching dissepiment edges	10–16.5 × 4.5–6.5 μm	cylindrical to fusiform, 5.1–8.1 × 2.0–3.1 μm; L = 6.04, W = 2.66, Q = 2.27		
F. marianii	Eurasia, North America, Oceania (?); angiosperms, very rarely conifers	usually sessile or effused-reflexed, pores 4–6 per mm	rather loosely interwoven, 2–5 μm in diam, absent at dissepiment edges	12.5–21.5 × 4.5–7 μm	cylindrical to fusiform, 5.1–8.7 × 2.0–3.2 μm; L = 6.45, W = 2.60, Q = 2.48		
F. meliae	North America (subtropics – tropics), South America; angiosperms	usually sessile or effused-reflexed, pores 4–7 per mm	rather loosely interwoven, 3–5 μm in diam, approaching dissepiment edges	11–17.5 × 4.5–6 μm	cylindrical to fusiform, 4.2–7.2 × 2.1–2.9 μ m; L = 5.62, W = 2.40, Q = 2.34		
F. nivosella	North and South America; angiosperms	sessile or effused- reflexed, pores 5–6 per mm	rather loosely interwoven, 2–4 µm in diam, approaching dissepiment edges	11–17 × 4–7 μm	cylindrical to fusiform, 5.0–8.0 × 1.8–3.0 μm; L = 6.60, W = 2.50, Q = 2.64		
F. ostreiformis	East Africa, South-East Asia; angiosperms	sessile, effused- reflexed or totally resupinate, pores 5–8 per mm	rather loosely interwoven, 3–4.5 µm in diam, approaching dissepiment edges	10–18 × 4.5–6 µm	cylindrical to fusiform, 4.2–7.3 × 2.1–3.0 μm; L = 5.61, W = 2.55, Q = 2.20		
F. palustris	North America; conifers (<i>Pinus</i> spp.)	sessile, pores 5–7 per mm	loosely interwoven, 3–5 µm in diam, approaching dissepiment edges	14–22 × 5.5–7 μm	cylindrical to fusiform, 6.2–8.2 × 2.4–3.7 μm; L = 7.11, W = 2.95, Q = 2.41		

Table 4. Morphological, ecological and geographic traits in pink-coloured Fomitopsis spp. ¹ .							
Species	Geographic distribution / host	Macroscopic characters	Tramal skeletal hyphae	Skeletocystidia	Basidiospores		
F. africana	Africa, South-East Asia; angiosperms	basidiocarps sessile, hymenophore indistinctly stratified; pores 7–8 per mm	loosely interwoven, brownish, 3–5 μm in diam	not differentiated	cylindrical-subfusiform, 5.8–7.8 × 2.5–3.4 µm; L = 6.53, W = 2.98, Q = 2.21		
F. cajanderi	Holarctic; conifers	basidiocarps sessile or rarely effused-reflexed, hymenophore indistinctly stratified; pores 5–7 per mm	interwoven, reddish- brown, 2.5–4 μm in diam	not differentiated	narrowly cylindrical to subfusiform, 4.2–6.1 × 1.8–2.1 μm; L = 5.24, W = 1.95, Q = 2.69		
F. carnea	South-East Asia; angiosperms	basidiocarps sessile, hymenophore indistinctly stratified; pores 7–9 per mm	densely interwoven, hyaline, yellowish or brownish, 3–4 µm in diam	not differentiated	cylindrical-subfusiform to narrowly ellipsoid, $2.9-4.5 \times 1.9-2.3 \mu m$; L = 3.63, W = 2.07, Q = 1.75		
F. cupreorosea	Neotropics; angiosperms, very rarely conifers	basidiocarps sessile, hymenophore indistinctly stratified; pores 3–5 per mm	densely interwoven, brownish to pinkish- brown, 3–4.5 μm in diam	abundant, normally blunt, slightly projecting	cylindrical-subfusiform, 4.6–6.6 × 2.1–3.0 µm; L = 5.36, W = 2.52, Q = 2.12		
F. cupressicola	North America (eastern part); conifers	basidiocarps sessile, hymenophore indistinctly stratified; pores 6–8 per mm	densely interwoven, brown; 2–3.5 μm in diam	poorly differentiated, obtuse, embedded or slightly projecting	cylindrical to narrowly ellipsoid, 3.7–5.2 × 1.9–2.8 μm; L = 4.31, W = 2.23, Q = 1.96		



```
SPIRIN ET AL.
```

Table 4. (Continued)).				
Species	Geographic distribution / host	Macroscopic characters	Tramal skeletal hyphae	Skeletocystidia	Basidiospores
F. eucalypti	Oceania; angiosperms	sessile or effused- reflexed, hymenophore indistinctly stratified; pores 5–7 per mm	densely interwoven, yellowish, 3–4.5 μm in diam	not differentiated	narrowly ellipsoid to cylindrical, 4.0–6.8 × 2.1–3.0 μm; L = 4.81, W = 2.56, Q = 1.90
F. feei	South America; angiosperms	sessile, hymenophore indistinctly stratified; pores 6–7 per mm	densely interwoven, brownish to reddish- brown, 3–4 μm in diam	not differentiated	cylindrical-subfusiform, 4.0–6.2 × 2.1–2.9 μ m; L = 4.82, W = 2.37, Q = 2.05
<i>F. flabellata</i> (fide Tibpromma et al. 2017)	South America; angiosperms	sessile, hymenophore one-layered, pores 3–4 per mm	interwoven, 3–5 μm in diam	not differentiated	cylindrical, 4–5 × 2–2.5 μm
F. foedata	Oceania; angiosperms	sessile, hymenophore indistinctly stratified; pores 6–8 per mm	densely interwoven, yellowish to reddish- brown, 3–4 µm in diam	not differentiated	cylindrical-subfusiform, 4.0–5.9 × 2.1–3.0 μ m; L = 5.05, W = 2.62, Q = 1.95
F. lilacinogilva	Europe, North America, Oceania; angiosperms	sessile, hymenophore indistinctly stratified; pores 3–5 per mm	interwoven, brownish to reddish-brown, 3–4.5 μm in diam	not differentiated	cylindrical-subfusiform, 5.2–9.2 × 2.6–3.2 µm; L = 6.73, W = 2.97, Q = 2.27
F. marchionica	Oceania; angiosperms	sessile, hymenophore indistinctly stratified; pores 5–7 per mm	densely interwoven, yellowish to brownish, 3–4 μm in diam	not differentiated	cylindrical-subfusiform, 3.2–4.2 × 1.9–2.2 µm; L = 3.63, W = 2.08, Q = 1.75
F. perhiemata	Europe; angiosperms	effused-reflexed, hymenophore indistinctly stratified; pores 5–7 per mm	densely interwoven, brown, 3–4 μm in diam	not differentiated	cylindrical to narrowly ellipsoid, 4.1–5.2 × 2.1–3.0 μm; L = 4.50, W = 2.40, Q = 1.89
F. purpurea	Africa; angiosperms	sessile, hymenophore clearly stratified; pores 6–7 per mm	interwoven, brownish to reddish-brown, 2.5–3.5 μm in diam	not differentiated	cylindrical-subfusiform, 5.0-6.7 × 2.0-2.2 μ m; L = 5.79, W = 2.10, Q = 2.77
F. rosea	Holarctic; conifers, very rarely angiosperms	sessile, hymenophore indistinctly stratified; pores 3–5 per mm	interwoven, brownish to reddish-brown, 3–3.8 μm in diam	not differentiated	cylindrical, 5.0–6.6 × 2.2–2.7 μm; L = 5.80, W = 2.40, Q = 2.40
F. roseofusca	South America; angiosperms	sessile, hymenophore clearly stratified; pores 1–2 per mm	densely interwoven, brownish to brown, 3–5 µm in diam	abundant, acute, slightly projecting	cylindrical-subfusiform, 4.8–6.2 × 1.8–2.8 µm; L = 5.41, W = 2.40, Q = 2.32
F. sagraeana	North America (subtropical – tropical); angiosperms	sessile, hymenophore indistinctly stratified; pores 6–8 per mm	densely interwoven or subparallel, brownish to reddish-brown, 2.5–4 µm in diam	not differentiated	cylindrical-subfusiform, 4.9–7.3 × 2.6–3.9 μ m; L = 5.81, W = 2.99, Q = 1.96
F. scalaris	South America; angiosperms	sessile, hymenophore clearly stratified; pores 6–8 per mm	densely interwoven, brownish to brown, 2–4 μm in diam	poorly differentiated, obtuse, embedded or slightly projecting	cylindrical, 3.1–5.0 × 2.0–2.3 μm; L = 3.70, W = 2.12, Q = 1.75
F. substratosa	North Africa and South- East Asia; conifers	sessile to effused- reflexed, hymenophore clearly stratified; pores 4–7 per mm	densely interwoven, brownish to brown, 2.5–4 μm in diam	not differentiated	cylindrical to narrowly ellipsoid, 3.8–5.1 × 2.0–2.4 µm; L = 4.24, W = 2.16, Q = 1.97
F. ussuriensis	East Asia; angiosperms, very rarely conifers	sessile to effused- reflexed or resupinate, hymenophore clearly stratified; pores 6–7 per mm	densely interwoven, brownish to brown, 2.5–3 μm in diam	not differentiated	cylindrical, 3.7–4.7 × 1.9–2.2 μm; L = 4.07, W = 2.02, Q = 2.02

¹Species occasionally possessing pinkish tints in tubes which quickly disappear in herbarium specimens (*e.g.*, *F. atypa*, *F. gilvidula*, *F. ostreiformis*, *F. sulcata*) or violet-black spots on pileal surface (*F. neotropica*) are not included.

Taxonomy

Fomitopsis P. Karst., Meddeland. Soc. Fauna Fl. Fenn. 6: 9. 1881, *nom. cons.*

Basidiocarps annual, seasonal or perennial, pileate, effusedreflexed or resupinate, or stipitate in a few species, variably coloured. Hymenophore poroid, with angular or regular pores 0.5-10 per mm (in one species concentrically lamellate). Hyphal structure dimitic or (rarely) monomitic; generative hyphae clamped (clamps rare amongst mostly simple septa in one species), skeletal hyphae occasionally branched, in many species lightly tinted. Cystidioles, hymenial cystidia or skeletocystidia present in many taxa. Hyphidia occasionally present, as a rule simple. Basidia clavate, four-spored, normally under 25 µm long; basidia and basidioles becoming slightly thick-walled in senescent hymenium. Basidiospores hyaline, thin-walled or with a distinct wall (in two species slightly thick-walled), cylindrical to ellipsoid, rarely broadly ellipsoid or subglobose, 3-16 × 2-5.5 µm, inamyloid, with occasional small oil droplets, apiculus rather small. Causing brown rot of dead wood of angiosperms and conifers.

Generic type: Boletus pinicola Sw. (= *Fomitopsis pinicola* (Sw.) P. Karst.).

Synonyms:

Antrodiopsis Audet (type Poria oleracea R.W. Davidson & Lombard) Brunneoporus Audet (type Trametes malicola Berk. & M.A. Curtis) Buglossoporus Kotl. & Pouzar (type Boletus quercinus Schrad.) Caloporus P. Karst. (type Poria incarnata Pers.)

Cartilosoma Kotlaba & Pouzar (type *Trametes subsinuosa* Bres.) Daedalea Pers. (type Agaricus quercinus L.)

Daedalella B.K. Cui & Shun Liu (type Daedalella micropora B.K. Cui & Shun Liu)

Dentiporus Audet (type Antrodia albidoides A. David & Dequatre) Flavidoporia Audet (type Poria pulvinascens Pilát)

Fragifomes B.K. Cui, M.L. Han & Y.C. Dai (type *Fomitopsis niveomarginata* L.W. Zhou & Y.L. Wei)

Melanoporia Murrill (type Polyporus niger Berk.)

Neoantrodia Audet (type Polyporus serialis Fr.)

Neolentiporus Rajchenb. (type Polyporus maculatissimus Lloyd)

Niveoporofomes B.K. Cui, M.L. Han & Y.C. Dai (type *Polyporus spraguei* Berk. & M.A. Curtis)

Pilatoporus Kotl. & Pouzar (type *Polyporus palustris* Berk. & M.A. Curtis)

Piptoporus P. Karst. (type Boletus betulinus Bull.)

Pseudoantrodia B.K. Cui, Y.Y. Chen & Shun Liu (type Pseudoantrodia monomitica B.K. Cui, Y.Y. Chen & Shun Liu)

Pseudofomitopsis B.K. Cui & Shun Liu (type Pseudofomitopsis microcarpa B.K. Cui & Shun Liu)

Ranadivia Zmitr. (type Daedalea allantoidea M.L. Han, B.K. Cui & Y.C. Dai)

Rhizoporia Audet (type *Antrodia hyalina* Spirin, Miettinen & Kotir.) *Rhodofomes* Kotl. & Pouzar (type *Boletus roseus* Alb. & Schwein.) Rhodofomitopsis B.K. Cui, M.L. Han & Y.C. Dai (type Polyporus feei Fr.)

Rubellofomes B.K. Cui, M.L. Han & Y.C. Dai (type Fomitopsis cystidiata B.K. Cui & M.L. Han)

Subantrodia Audet (type Agaricus juniperinus Murrill)

Ungulidaedalea B.K. Cui, M.L. Han & Y.C. Dai (type *Fomitopsis fragilis* B.K. Cui & M.L. Han)

As redefined here, the genus Fomitopsis encompasses poroid species only (in two species, A. albidoides and Gloeophyllum concentricum, hymenophore is nearly irpicoid or lamellate), although of a highly diverse habit. Some species formerly addressed to Antrodia sensu lato (e.g., Antrodia infirma, A. oleracea, A. primaeva) produce rather ephemeral, fleshy, predominantly effused basidiocarps. A few sessile or stipitate species previously treated under Laccocephalum and Pilatoporus also possess short-living, sappy basidiocarps easily damaged by insects. However, most Fomitopsis spp. produce long-living seasonal or truly perennial, sturdy basidiocarps. Many of them are able to produce pilei, even though the basidiocarp shape is exceptionally flexible in many species, varying from sessile caps to fully effused. Of macroscopic characters, consistency and colour(s) of basidiocarps, as well as colour change in aged or dried specimens, ability to produce stratified hymenophore and pore size and shape are the most important traits for the species recognition in Fomitopsis.

Anatomically, the genus is much less diverse than it might be expected from the macroscopic range of variation. A small group of Antrodia sensu lato spp. has monomitic hyphal structure. In two species, A. monomitica and A. oleracea, all hyphae are highly uniform, predominantly thin-walled, while in six other species (members of Antrodia ramentacea complex, plus F. fissa and F. retorrida) hyphae possess variably thickened walls and are often densely glued together (Fig. 16A, B). In the A. ramentacea complex, some contextual hyphae are very thick-walled, having a capillary lumen only, and they might be interpreted as skeletal hyphae. However, they have rare septa with clamps (observable in CB and phase contrast), and therefore they likely represent sclerified generative hyphae. The rest of Fomitopsis spp. are dimitic, bearing variably branched skeletal hyphae, and clamped generative hyphae (absent only in *Fomitopsis* sp. Darwin (M.D. Barrett F17/09)). Some species with rather soft, as a rule shortliving basidiocarps have skeletal hyphae located only in context (e.g., Buglossoporus guercinus, Laccocephalum hartmannii) while in others they also occur in tube trama (e.g., Antrodia primaeva, Fomitopsis palustris group). In both cases, variable transitions between sclerified, richly branched generative hyphae and sparsely branched, unclamped skeletal hyphae can be observed, and generative hyphae are either dominating in both context and tubes or present in the same proportion as skeletal hyphae (Fig. 16C). A vast majority of *Fomitopsis* spp. have leathery or corky, persistent basidiocarps consisting mainly of skeletals, which are usually coloured and occasionally branched. In many dimitic species, obtuse or acute endings of skeletal hyphae enter the hymenial layer; we call these structures skeletocystidia (Fig. 16D). Basidia in all *Fomitopsis* spp. treated below are clavate and four-spored, in senescent hymenium often slightly thick-walled and at least partly glued together. Basidiospores vary from narrowly cylindrical to subglobose, and they normally do not exceed 10 µm long, except in the Buglossoporus subclade and a few other species mentioned above.





Fig 16. Anatomical structures (subicular and subhymenial hyphae, hymenial cells and basidiospores) of *Fomitopsis* spp. *F. oleracea* (Miettinen 17902), *F. fissa* (holotype), *F. dollingeri* (holotype), *F. cellularis* (Vlasák 1504/36J). Scale bar = 10 µm.

Morphological diversity in the redefined *Fomitopsis* makes it hardly distinguishable from other poroid brown-rot genera of *Polyporales*. Nevertheless, it is worth mentioning here at least some most important traits differentiating them. Differences between *Fomitopsis* and two other genera of *Fomitopsidaceae*, *Antrodia* and *Anthoporia*, were discussed above. The *Laetiporaceae* (as redefined by Justo *et al.* 2017) encompass sappy pileate (*Laetiporus*) and resupinate (*Wolfiporia*, *Macrohyporia*, *Melanoporella*) polypores which are totally devoid of clamps. Basidiospores of *Laetiporaceae* are ellipsoid or subglobose, bearing a prominent apiculus and usually having oil-rich contents. The genus *Pseudophaeolus* (*incertae sedis*, see notes under excluded taxa and also Fig. 1 and Suppl. Fig. S1) is morphologically highly similar to *Laetiporus* although it has constantly clamped generative hyphae. Both *Laetiporaceae* and *Pseudophaeolus* possess unusually wide (reaching 10–30 µm diam), sclerified hyphae, in the context and (in most taxa) tubes. No such structures are known in *Fomitopsidaceae*.

Wide, variably thick-walled hyphae are characteristic for *Laricifomes officinalis* (= *Fomitopsis officinalis*) and *Gilbertsonia angulipora* which form an isolated monophyletic lineage among the brown-rot *Polyporales* (Ortiz-Santana *et al.* 2013). Unlike *Laetiporaceae* and *Pseudophaeolus*, basidiocarps of *L. officinalis* and *G. angulipora* have a characteristic chalky consistency. Two species of *Ryvardenia* are chalky when dried, too, and they also have wide sclerified hyphae in the context (Rajchenberg 1994). However, the basidiospores of *Ryvardenia* are slightly thick-walled while they are thin-walled in *Laricifomes* and *Gilbertsonia*. The phylogenetic position of *Ryvardenia* among brown-rot polypores

was recently clarified by Liu *et al.* (2022) (see also Suppl. Fig. S1). Three *Fomitopsis* spp. with chalky basidiocarps, *i.e. F. caseosa*, *F. niveomarginata* and *F. pseudopetchii*, differ from *Laricifornes*, *Gilbertsonia* and *Ryvardenia* in having a dark-coloured cap surface, much narrower hyphae and distinctly smaller basidia and basidiospores.

Some Antrodia sensu lato species in the Fibroporia -Amyloporia clade (as defined by Justo et al. 2017), i.e. Antrodia sinuosa and members of the Antrodia crassa complex, have a certain resemblance to Fomitopsis spp. Crumbling basidiocarps consisting of easily breaking, often twisted skeletal hyphae are characteristic for A. crassa and its siblings. In most cases, these hyphae are either amyloid or guickly swelling and partly dissolving in KOH. Moreover, microscopic mounts of species from the A. crassa complex are usually full of resinous droplets (Spirin et al. 2015a). All these features certainly rule out Fomitopsis. Antrodia sinuosa is a much more difficult case because it has slightly coloured, occasionally branched skeletal hyphae and small basidia reminiscent of those in many Fomitopsis spp. However, basidiospores in A. sinuosa are allantoid or narrowly cylindrical and evenly curved; this spore shape is unknown in Fomitopsis. Narrowly cylindrical, curved basidiospores are characteristic for Taiwanofungus spp. as well. Additionally, representatives of the latter genus have brownish skeletal hyphae showing slight amyloid reaction (Wu et al. 2004). According to phylogenetic data, Taiwanofungus is not or very distantly related to Fomitopsidaceae (Ortiz-Santana et al. 2013, Liu et al. 2022; see also Suppl. Fig. S1).

In many respects, monomitic Fomitopsis spp. approach Rhodonia (Amyloporia clade) and some Postia spp. (Dacryobolaceae). Sappy, effused basidiocarps of Rhodonia spp. resemble A. infirma and A. primaeva. However, the two latter species have on average larger, slightly thick-walled basidia and longer, often subfusiform basidiospores. The majority of Postia sensu lato species have allantoid or narrowly cylindrical, curved basidiospores, and therefore they can be differentiated from Fomitopsis spp. based on this character alone. A few species morphologically similar to monomitic Fomitopsis species (e.g., Postia amara, Postia sequoiae) possess unusually wide context hyphae (6-10 µm diam) occasionally bearing double clamps (Gilbertson & Ryvarden 1987); this feature is unknown in Fomitopsis. Laterally stipitate, fleshy basidiocarps of Jahnoporus spp. (Dacryobolaceae) resemble the former species of Laccocephalum (i.e. L. hartmannii and L. tumulosum) transferred to Fomitopsis in this study. However, they can be easily separated due to their different hyphal structure: Jahnoporus spp. are thoroughly monomitic (Spirin et al. 2015b) while L. hartmannii and sibs have true skeletal hyphae at least in the context.

The species below are divided between those that are accepted and those that are excluded or insufficiently known. They are presented in alphabetical order in both sections. For each species, the basionym and type specimen / illustration are indicated. Synonymy is reduced to the newly detected synonyms and taxonomically important names. Further, either a new description (in almost all cases, based on type material and newly sequenced specimens) or a reference to the most modern and reliable source is provided. All additional information is placed under remarks.

Accepted species

Fomitopsis aculeata (Cooke) Spirin & Miettinen, *comb. nov.* MycoBank MB 844877. Figs 17, 18.

Basionym: Polystictus aculeatus Cooke, Grevillea 14 (71): 85. 1886.

Typus: Indonesia, Java, Tjikoya [Cikoya], rotten wood, 1843, *Zollinger* 2055 (holotype PC!).

Synonym: Daedalea radiata B.K. Cui & Hai J. Li, Mycoscience 54: 65. 2013.

Typus: **China**, Yunnan, Mengla, Wangtianshu, hardwood, 16 Sep. 2007, *Yuan* 3629* (**holotype** IFP 13864).

Description: Basidiocarps seasonal, dimidiate or effused-reflexed, projecting up to 2 cm, effused parts up to 8 cm in widest dimension. Upper surface first pale ochraceous, later brownish to brown, hirsute, indistinctly zonate. Pileal edge sharp to rather blunt, concolourous with pileal surface, first sterile, up to 1 mm wide, then fertile. Pore surface first cream-coloured to pale ochraceous, then brownish; pores angular or sinuous, partly fusing together 4–5(–6) per mm, with rather thick, entire or serrate dissepiments. Section: context leathery, ochraceous to brownish, up to 1 mm thick; tubes leathery, one-layered, concolourous with hymenial surface, up to 2 mm thick. Hyphal structure dimitic; hyphae clamped. Context dimitic; skeletal hyphae brownish, interwoven, occasionally branched, (3.9-)4.0-5.2(-5.4) μ m diam (n = 20/1), lumen varying from rather wide to capillary, side branches 2.5-4 µm diam, generative hyphae hyaline, slightly to distinctly thick-walled, 3-4 µm diam. Trama dimitic; skeletal hyphae dominating, brownish to rusty brown, densely interwoven, predominantly dichotomously branched, sometimes twisted and irregularly inflated, (3.0-)3.2-5.0(-5.2) µm diam (n = 40/2), lumen mostly capillary to indistinct, side branches richly ramified, 1.5-2.5 µm diam, generative hyphae rare, thin- to slightly thick-walled, 2-3 µm diam. Subhymenium indistinct. Skeletocystidia present as slightly swollen (up to 4 µm diam), acute or blunt apices of tramal skeletal hyphae, slightly projecting above hymenium. Cystidioles abundant, tapering, often with a long hyphoid neck, 12-17 × 3-3.5 µm. Hyphidia abundant, simple or rarely bifurcate, 1.8-2.2 µm diam at the apex, projecting up to 10 µm. Basidia clavate, (10.7-)10.8-15.2(-19.2) × (4.4-) 4.8-5.3(-5.4) µm (n = 20/1), in senescent hymenium slightly thick-walled and often glued together. Basidiospores thin-walled or with a distinct wall, cylindrical-subfusiform, (4.0-)4.1-5.3(-5.4) × (2.0-) 2.1-2.6(-2.7) µm (n = 30/1), L = 4.81, W = 2.26, Q = 2.13, often with one or a few large oil droplets.

Specimens examined: Indonesia, Riau, Indragiri Hulu, Bukit Aluran Babi, primary rainforest slope, dicot (fallen tree crown), 27 Jun. 2004, *Miettinen* 8674* (H); Sumatera Barat, Padang, Limau Manis, hilly primary forest, dicot, 11 Jul. 2008, *Miettinen* 12960 (H); *ibid.*, 16 Jul. 2008, *Miettinen* 13128.2 (ANDA, H).

Notes: This species was originally described as *Polyporus aculeatus* Lév. (Léveillé 1846). However, this name was illegitimate due to the existence of *P. aculeatus* Mont. (now a member of *Hexagonia*) described six years earlier (Montagne 1840). Cooke (1886) moved Léveillé's species to *Polystictus* and thus mechanically validated it.

Fomitopsis aculeata is distributed in Southeast Asia. It is a distinctive species due to its hirsute, brownish upper surface reminiscent of some *Funalia* spp. Members of the latter genus differ from *F. aculeata* in having harder basidiocarps with trimitic hyphal structure and broader skeletal hyphae, as well as much larger basidiospores. Three sequences of this species in GenBank (AJ542530, AJ536655, AJ542522) are mislabelled as *Funalia trogii*. Another genus that comes into mind macroscopically is *Gloeophyllum* whose representatives are darker-coloured and trimitic and they have distinctly longer basidiospores. See further notes to *F. gilvidula*.





Fig 17. Basidiocarps of Fomitopsis spp. A. Fomitopsis aculeata (Miettinen 8647). B. F. angusta (Spirin 10725). C. F. caespitosa (Miettinen 10227). D. F. cajanderi (Miettinen 22477). E. F. carnea (Miettinen 23610). F. F. caseosa (holotype). G. F. castanea (Spirin 5144). H. F. dickinsii (Niemelä 6435).



Fig 18. Basidiospores of *Fomitopsis* spp. *F. aculeata* (Miettinen 8674); *F. africana* (Kout 1408/K9); *F. algumicola* (holotype); *F. amygdalina* (Vlasák 1707/9J); *F. atypa* (Ryvarden 17588); *F. caespitosa* (Miettinen 8737). Scale bar = 5 µm.

Fomitopsis aethalodes (Mont.) Spirin, *comb. nov.* MycoBank MB 844878.

Basionym: Trametes aethalodes Mont., Ann. Sci. Nat., Bot. 4 (5): 370. 1856.

Typus: **Brazil**, [no locality and collecting date], *Weddell* (**lectotype** PC!) (selected by Ryvarden 1982: 76).

Description: Rajchenberg (1986, as Daedalea aethalodes).

Notes: Rajchenberg (1986) provided a description of morphological and cultural characters of *T. aethalodes*. He proved it is a brownrot fungus and therefore combined it in *Daedalea*. Cristaldo *et al.* (2022) published first DNA sequences of this species and confirmed that it belongs to the *Daedalea* clade of *Fomitopsis* (see also Fig. 5). We studied the type material and concluded that *D. aethalodes* is morphologically most similar to *F. aculeata* redescribed above.

Fomitopsis africana Mossebo & Ryvarden, Sydowia 49 (2): 148. 1997. Fig 18.

Typus: **Cameroon**, Mfoundi, Yaoundé, International Institute of Tropical Agriculture, *Eucalyptus* sp., 2 Jul. 1996, *Mossebo* 13* (**holotype** O).

Description: Basidiocarps perennial, sessile, conchate or ungulate, projecting up to 3 cm. Upper surface first cream-to wood-coloured, sometimes with faint pinkish tint, smooth, later grey to greyishbrown, matt. Pileal edge sharp to rather blunt, concolourous with hymenial surface, fertile. Pore surface pinkish-grey to greyish, sometimes with vinaceous-brown stains; pores roundish to angular, 7–8 per mm, with thick, entire dissepiments. Section: crust (present in old basidiocarps) tough, blackish brown, matt, up to 0.2 mm thick, context soft corky, wood-coloured to brownish, up to 5 mm thick; tubes soft corky, one-layered or indistinctly stratified, concolourous with hymenial surface, up to 8 mm thick. *Hyphal structure* dimitic; hyphae clamped. Context dimitic; skeletal hyphae dominating, yellowish to brownish, interwoven, occasionally branched, $(3.9-)4.2-6.0(-6.2) \mu m$ diam (n = 20/1), lumen mostly narrow to indistinct, side branches 2.5–3.5 µm diam, generative hyphae rare, hyaline, slightly thick-walled, 3–5 µm diam. Trama dimitic; skeletal hyphae dominating, brownish, loosely interwoven, occasionally branched, (2.9–)3.0–5.0(–5.2) µm diam (n = 40/2), lumen wide to capillary, side branches 1.5–2.5 µm diam, generative hyphae thin- to slightly thick-walled, 2–4 µm diam. Subhymenium partly distinct, up to 15 µm thick. Cystidioles infrequent to rather common, tapering, 10–14 × 3.5–5 µm. *Basidia* clavate, (10.2–)10.6–14.8(–14.9) × (4.8–)5.0–6.0(–6.2) µm (n = 20/2), in senescent hymenium slightly thick-walled. *Basidiospores* with a distinct wall, cylindrical-subfusiform, (5.7–)5.8–7.8(–8.1) × (2.4–)2.5–3.4(–3.6) µm (n = 60/2), L = 6.49–6.57, W = 2.97–2.98, Q = 2.19–2.22.

Specimens examined: Indonesia, Riau, Kampar, Serapung, dicot, seasonally flooding village backyard, 6 Dec. 2011, *Miettinen* 15198* (BO, H). Thailand, Sukhotai, Khiri Mat, Ramkamhaeng, 12 Aug. 2014, *Kout* 1408/K9* (JV, TUF).

Notes: Fomitopsis africana was originally described from Cameroon (Mossebo & Ryvarden 1997) and then sequenced by Kim *et al.* (2008). Here we report it from Southeast Asia (Thailand and Sumatra, Indonesia). Two GenBank sequences of *Fomitopsis* sp.' from India (KJ670294, MG430346) belong to *F. africana*. The ITS sequence from the type collection differs in 4 bp from the Southeast Asian ones; for now, it is impossible to decide whether this difference is inter- or infraspecific. Phylogenetically, *F. africana* is related to the *F. feei* complex. Differences between *F. africana* and other members of this group are discussed under *F. carnea*.

Fomitopsis alaskana (D.V. Baxter) Spirin & Vlasák, *comb. nov.* MycoBank MB 844879.

Basionym: Trametes alaskana D.V. Baxter, Pap. Mich. Acad. Sci. 27: 150. 1942.



SPIRIN ET AL.

Typus: **USA**, Alaska, Cordova, *Picea sitchensis*, 21 Aug. 1933, *Baxter* 2-2048 (holotype MICH 12309!).

Description and phylogenetic data: Spirin et al. (2017, as Antrodia alaskana).

Fomitopsis albidoides (A. David & Dequatre) Bernicchia & Vlasák, *comb. nov.* MycoBank MB 844880. *Basionym: Antrodia albidoides* A. David & Dequatre, Mycol. Helv. 1 (6): 361. 1986.

Typus: **France**, Var, Île de Port-Cros, *Phillyrea latifolia*, 31 Oct. 1977, *David* 3495 (**holotype** LY AD-3495!).

Synonyms:

Antrodia subalbidoides A. David & Dequatre, Mycol. Helv. 1 (6): 362. 1986.

Typus: **France**, Var, Le Brusc, *Phillyrea angustifolia*, 1984, *David* 4591 (holotype LY AD-4591!).

Antrodia macrospora Bernicchia & De Dominicis, Polyporaceae sensu lato in Italy: 74. 1990.

Typus: **Italy**, Tuscany, Grosseto, Riserva di Burano, *P. angustifolia*, 29 Sep. 1989, *Bernicchia* 5116 (**holotype** HUBO!).

Description and phylogenetic data: Spirin *et al.* (2013b, as *A. albidoides*), see also Figs 1 and 2.

Specimens examined: **Italy**, Sardinia, Nuoro, Oliena, Strada per Valle di Lanaittu, *Phillyrea* sp., 20 Nov. 1999, *Bernicchia* 7244* (HUBO); Tuscany, Grosseto, Riserva di Burano, *P. angustifolia*, 27 Oct. 1992, *Bernicchia* 5672* (H ex HUBO).

Fomitopsis algumicola Grebenc & Spirin, *sp. nov.* MycoBank MB 844881. Fig 18.

Typus: **North Macedonia**, Resen, Golem Grad Island, 40.87° 20.99°, *Juniperus excelsa* (fallen log), 9 Oct. 2000, *Karadelev* (**holotype** MCF MAK 00/4578*, **isotype** H7200206).

Etymology: Algumicola (Lat., noun) – derived from "algum", the biblical name which seemingly refers to a juniper.

Description: Basidiocarps perennial, effused, up to 15 cm in widest dimension, on sloping substrate with nodulose parts projecting up to 3 cm. Margin sharply delimited, partly detaching, cream-coloured or grevish to ochraceous-brownish, up to 0.5 mm wide, often covered by incomplete pores. Pore surface first cream-coloured to pale ochraceous, then ochraceous-brownish to dark brown, uneven; pores angular to lacerate, 0.5–1.5 per mm, 10–14 per cm, with rather thick, entire or serrate dissepiments. Section: context leathery, cream- to wood-coloured, up to 5 mm thick; tubes leathery, one-layered, concolourous with hymenial surface, up to 15 mm thick. Hyphal structure dimitic; hyphae clamped. Context dimitic; skeletal hyphae brownish, interwoven, occasionally branched, $(3.2-)3.4-4.3(-4.8) \mu m$ diam (n = 20/1), lumen mostly capillary to indistinct, side branches 1.5-2.5 µm diam, generative hyphae rare, hyaline, slightly thick-walled, 3-5 µm diam. Trama dimitic; skeletal hyphae dominating, brownish, interwoven, occasionally branched, (3.8-)3.9-6.3(-8.0) µm diam (n = 60/3), lumen mostly narrow to indistinct, side branches 1.5-2.5 µm diam, generative hyphae thinto slightly thick-walled, 2–4 µm diam. Subhymenium distinct, 20–30 µm thick. Skeletocystidia occasionally present, broadly clavate, up to 7–8 µm diam at the apex. Cystidioles rare, tapering, 15–20 × 3–4 µm; hyphidia rarely present, simple, slightly projecting, 2–2.5 µm diam at the apex. Large rhomboid crystals often present among subhymenial and tramal hyphae, up to 20 µm in widest dimension. *Basidia* clavate, (13.0–)13.2–22.8(–23.1) × (5.1–)5.2–6.4(–6.7) µm (n = 30/3), in senescent hymenium slightly thick-walled and glued together. *Basidiospores* with a distinct wall, broadly cylindrical to subfusiform, occasionally slightly concave at the ventral side, (5.1–)5.2–7.6(–9.8) × (2.3–)2.4–3.3(–3.8) µm (n = 90/3), L = 6.09–6.63, W = 2.83–3.07, Q = 1.98–2.23.

Specimens examined: North Macedonia, Kavadartsi, Tikveš, Tikveška Klisura, Juniperus excelsa, 25 Jul. 1990, Karadelev (H 7042099); Petrovec, Katlanovo, J. excelsa, [no collection date], Karadelev & Rusevska (MCF MAK xx/7771*); Kozhle, J. excelsa, 25 Mar. 2001, Karadelev (MCF MAK 01/2095*); *ibid.*, 19 Oct. 2007, Karadelev & Rusevsca (MCF MAK 07/8020*); Valandovo, Chalakli, J. excelsa, 26 Oct. 2007, Karadelev & Theiss (MCF MAK 07/8293*).

Notes: Fomitopsis algumicola is a close relative of *F. juniperina* distributed in the Balkans (North Macedonia) and inhabiting wood of *Juniperus excelsa* (Suppl. Fig. S7). The latter species differs from *F. algumicola* in having larger pores, 0.5–1 per mm, 8–11 per cm, which could be almost lamellate in fully developed specimens, as well as a usual presence of truly pileate parts. Distribution areas of *F. algumicola* and *F. juniperina* seem not to coincide.

Fomitopsis amygdalina (Berk. & Ravenel) Spirin & Vlasák, *comb. nov.* MycoBank MB 844882. Fig 18.

Basionym: Polyporus amygdalinus Berk. & Ravenel, Ann. Mag. Nat. Hist. 2 (12): 432. 1853.

Typus: **USA**, South Carolina, Newhope, *Quercus* sp., [no collection date], *Ravenel* 1153 (**isotype** NY00730503!).

Description: Basidiocarps annual, spathulate or effused-reflexed, projecting up to 6 cm. Upper surface orange to reddish brownish, azonate, finely velutinous, indistinctly furrowed. Pileal edge rather blunt, concolourous with cap surface, fertile, somewhat undulating. Pore surface pale ochraceous to brownish, slightly concave; pores angular, (4)5–7 per mm, with thin, even or serrate dissepiments. Section: context soft, cream-coloured, up to 25 mm thick; tubes soft, easily cut by a razor blade, one-layered, distinctly paler (cream-coloured) than hymenial surface, up to 3 mm thick, turning reddish-brown after bruising. Smell faint, pleasant (fruit-like) (dry specimen). Hyphal structure monomitic in tube trama and dimitic in context; hyphae clamped. Context dimitic; skeletal hyphae hyaline to yellowish, interwoven, dichotomously branched, (4.2–)4.3–9.2(– 10.4) μ m diam (n = 40/2), lumen mostly indistinct, side branches 3-4 µm diam, generative hyphae infrequent, hyaline, thin-walled, 4–8 µm diam, occasionally with yellowish cyanophilous contents. Trama monomitic; hyphae mostly hyaline, rarely yellowish or greenish, thin-walled, subparallel, (2.3-)2.8-4.2(-4.8) µm diam (n = 40/2), intermixed with hyaline or coloured (greenish or brownish), irregularly inflated hyphae 3-5 µm diam. Cystidia and cystidioles absent. Basidia clavate, hyaline or yellowish greenish, (15.3-) $16.0-37.0(-38.0) \times (5.0-)5.6-7.8(-8.2) \ \mu m \ (n = 25/2), \ sometimes$ pleural. Basidiospores thin-walled, fusiform, longest spores somewhat sigmoid, (5.8–)5.9–9.2(–10.1) × (2.5–)2.6–4.0(–4.1) µm (n = 62/2), L = 6.79–7.54, W = 3.03–3.36, Q = 2.25, cytoplasm often guttulate.

Specimen examined: Costa Rica, Puntarenas, Monteverde, Santa Elena, hardwood, Jul. 2017, Vlasák Jr. 1707/9-J* (JV, TUF).

Notes: Berkeley & Curtis (1853) introduced P. amygdalinus based on a single collection from South Carolina. The identity of the species remained obscure until Lowe & Pegler (1973) studied microscopic traits of the authentic specimen and argued it should be treated under Tyromyces. Ryvarden (1977) accepted P. amygdalinus as a member of Dichomitus. Finally, Gilbertson & Ryvarden (1987) placed it in the synonymy of P. virgatus although the latter species was described from Cuba 16 yr later. We restudied the type of P. amygdalinus. It is still in a good condition and characterized by monomitic tubes and dimitic context. Skeletal hyphae are wide, occasionally branched, usually subsolid; they show neither the cyanophilous reaction nor dichotomous branching so characteristic of Dichomitus and Polyporus spp. Some tramal hyphae become brownish or greenish in KOH, and this feature, combined with longclavate basidia and rather long fusiform basidiospores, pointed to Fomitopsis pulvina (= Buglossoporus quercinus, see below) as a potential closest relative of P. amygdalinus. This suggestion was confirmed by a DNA study of a recent specimen from mountain forest in Costa Rica which we found to be conspecific with the type of P. amygdalinus (Suppl. Fig. S8). Therefore, P. amygdalinus is treated here as a member of Fomitopsis.

Basidiocarps of *F. amygdalina* are strikingly lightweight and show a certain macroscopic similarity to *F. pulvina*; the colour change after bruising typical to the latter species was also noticed in fresh material of *F. amygdalina*. Microscopically, these species are almost indistinguishable except that tapering, narrow cystidia are abundant in the hymenium of *F. pulvina* but not detected in *F. amygdalina*. Among macroscopic traits, tube layer thickness can be used as a character separating the two species: the tubes of *F. amygdalina* are considerably shorter than the pileal context while they are of approximately the same thickness in *F. pulvina*. Additionally, the pores of *F. amygdalina* are smaller than in *F. pulvina*, 5–7 vs. 3–4 per mm although they strongly shrink after drying in both species. So far, *F. amygdalina* is known only from the *locus classicus* and a new locality in Costa Rica.

Fomitopsis angusta (Spirin & Vlasák) Spirin & Vlasák, *comb. nov.* MycoBank MB 844883. Fig 17.

Basionym: Antrodia angusta Spirin & Vlasák, Mycologia 109: 223. 2017.

Typus: **Russia**, Primorie, Krasnoarmeiskii Dist., Valinku, *Picea ajanensis*, 29 Aug. 2013, *Spirin* 6479* (**holotype** H!).

Description and phylogenetic information: Spirin et al. (2017, as A. angusta).

Fomitopsis atypa (Lév.) Spirin & Vlasák, *comb. nov.* MycoBank MB 844884. Fig 18.

Basionym: Polyporus atypus Lév., Ann. Sci. Nat., Bot. 3 (2): 184. 1844.

Typus: **Indonesia**, Java, 'ad truncos', [no collection date and collector] (**holotype** PC!).

Synonyms:

Coriolus cuneatiformis Murrill, Bull. Torrey Bot. Club 34: 467. 1907.

Typus: **Philippines**, Luzon, Lanao River, dead wood, Dec. 1903, *Williams* (holotype NY 00704951!).

Coriolus clemensiae Murrill, Bull. Torrey Bot. Club 35: 394. 1908.

Typus: **Philippines**, Mindanao, Lake Lanao, Camp Keithley, dead wood, Sep.–Oct. 1907, *Clemens* (**holotype** NY 00704945!).

Coriolus rubritinctus Murrill, Bull. Torrey Bot. Club 35: 396. 1908.

Typus: **Philippines**, Mindoro, Mt. Halcon, dead wood, Nov. 1906, *Merrill* 6117 (holotype NY 00704983!).

Coriolus parthenius Hariot & Pat., Bull. Mus. Natn. Hist. Nat. 15: 90. 1909.

Typus: **Gabon**, Cap Lopez, 11 Jul. 1902, *Chevalier* 11478 (**lectotype** FH, **isolectotype** PC!) (selected by Ryvarden 1983: 28).

Antrodia taxa T.T. Chang & W.N. Chou, Mycol. Res. 103: 622. 1999.

Typus: **Taiwan**, Kaohsiung, Liu Kuei, *Taxus mairei*, Nov. 1996, *Chang* (holotype TFRI 781*).

Description: Basidiocarps short-living perennial, sessile, often with a contracted base (fan-shaped), projecting up to 4.5 cm. Upper surface first cream coloured to beige, felty, later pale ochraceous, usually with numerous narrow concentric zones, glabrous, sometimes radially wrinkled. Pileal edge sharp, concolourous with cap surface, first sterile, up to 1 mm wide, then fertile. Pore surface cream-coloured or beige to pale ochraceous, sometimes with a faint pinkish tint, flat or concave; pores roundish to angular, 5-7 per mm, with thin, entire or serrate dissepiments. Section: context corky, cream- to wood-coloured, normally less than 2 mm thick; tubes corky, one-layered, concolourous with hymenial surface, up to 3 mm thick. Hyphal structure dimitic; hyphae clamped. Context dimitic; skeletal hyphae yellowish to brownish, densely interwoven or in subparallel bundles, occasionally or richly branched, (3.0-) 3.6-7.2(-7.3) µm diam (n = 100/5), lumen mostly rather wide, side branches 1.5–3 µm diam, generative hyphae infrequent, hyaline, thin- to moderately thick-walled, 3-5 µm diam. Trama dimitic; skeletal hyphae dominating, hyaline or yellowish to brownish, densely interwoven, occasionally branched, (2.8-)2.9-5.3(-5.4) μ m diam (n = 160/8), lumen mostly narrow to indistinct, side branches 1.5-2.5 µm diam, generative hyphae rather rare, thinto slightly thick-walled, 2-3 µm diam. Subhymenium indistinct. Cystidioles abundant to rather rare, tapering, $11-16 \times 2.5-3.5 \mu m$; hyphidia occasionally present, simple or bi-trifurcate, 1-2 µm diam at the apex. Basidia clavate, (10.3–)11.8–16.2(–16.3) × (4.3–)4.6– 5.7(-5.9) μ m (n = 20/2), occasionally pleural. Basidiospores with a distinct wall, broadly cylindrical to ellipsoid, some slightly concave at the ventral side, $(3.0-)3.2-4.9(-5.0) \times (1.9-)2.0-2.8(-2.9) \mu m$ (n = 80/3), L = 3.89-4.39, W = 2.20-2.47, Q = 1.67-1.83.

Specimens examined: India, Kerala, Idukki, Munnar, Pambumkayam, fallen log, 27 Jan. 2019, *Dunayev** (TUF). Indonesia, Sumatera Barat, Pesisir Selatan, Gunung Sako, dicot, hilly primary forest, 27 Apr. 2002, *Miettinen* 6403 (BO, H). Thailand, Cangwat Chiang Mai, 15 Feb. 1979, *Ryvarden* 17588* (O F508226); *ibid.*, 18 Feb. 1979, *Ryvarden* 18005 (O 12727).

Notes: Fomitopsis atypa is a sibling species of *F. modesta* distributed in the paleotropics. The two species can be distinguished primarily due to their ITS sequences and distribution areas. Morphological differences are subtle: *F. atypa* has pores on average slightly wider than *F. modesta*, and its basidiospores are slightly narrower, occasionally with a somewhat concave ventral side. *Fomitopsis avellanea* (Bres.) Ryvarden, Mycotaxon 33: 304. 1988.

Basionym: Trametes avellanea Bres., Krypt. Exs. Mus. Palat. Vindob. 20: 157. 1910.

Typus: **Madagascar**, [no locality indicated], 'ad truncos', [unkown collection date], *Sikora* (**isotype** H!).

Description: Ryvarden (1988a).

Notes: No phylogenetic data are so far available for this species. *Fomitopsis avellanea* is known only from the type specimen from Madagascar. Macroscopically, it looks like a representative of the *F. feei* complex although the specimen is completely sterile. New collections are highly desirable to infer the relationships of *F. avellanea* with other *Fomitopsis* spp.

Fomitopsis bambusae Y.C. Dai, Meng Zhou & Yuan Yuan, MycoKeys 82: 186. 2021.

Typus: **China**, Hainan, Haikou, Jinniuling Park, *Bambusa* sp., 18 Nov. 2020, *Dai* 22116* (**holotype** BJFC 36008).

Description and phylogenetic data: Zhou et al. (2021).

Fomitopsis betulina (Bull.) B.K. Cui, M.L. Han & Y.C. Dai, Fungal Diversity 80: 359. 2016.

Basionym: Boletus betulinus Bull., Herbier de la France 7: t. 312. 1788.

Typus: Plate 1254 in Flora Danica 21, 1799 (**iconotype**) (selected by Ryvarden 1991: 202).

Synonym: Piptoporus betulinus (Bull.) P. Karst., Meddeland. Soc. Fauna Fl. Fenn. 6: 9. 1881.

Description: Ryvarden et al. (2017, as Piptoporus betulinus).

Notes: Phylogenetic data are available in this paper (Figs 1, 3, Suppl. Fig. S2), in accordance with Kim *et al.* (2005) and Ortiz-Santana *et al.* (2013).

Fomitopsis caespitosa (Murrill) Spirin & Miettinen, *comb. nov.* MycoBank MB 844885. Figs 17, 18.

Basionym: Trametes caespitosa Murrill, Bull. Torrey Bot. Club 34: 473. 1907.

Typus: **Philippines**, Luzon, Bataan, Mt. Mariveles, dead wood, Nov. 1904, *Elmer* 6951 (**holotype** NY00705017!).

Synonyms:

Tyromyces multipapillatus Corner, Beih. Nova Hedwigia 96: 180. 1989.

Typus: **Solomon Islands**, Ysabel, San Jorge, 25 Sep. 1965, *Corner* (holotype E00159594).

Tyromyces ochraceivinosus Corner, Beih. Nova Hedwigia 96: 182. 1989.

Typus: **Singapore**, 'Thompson Road, 9th mile', 23 May 1943, *Corner* (**holotype** E00159597).

Fomitopsis subtropica B.K. Cui & Hai J. Li, Mycol. Progr. 12: 710. 2013.

Typus: **China**, Guangdong, Guangzhou, Tianluhu, *Castanopsis* sp., 19 Aug. 2011, *Cui* 10154* (**holotype** BJFC).

Antrodiella subnigra Oba, Mossebo & Ryvarden, Syn. Fung. 40: 97. 2020.

Typus: **Cameroon**, Mfoundi, Yaoundé, unknown dead hardwood, 25 Oct. 2018, *Mossebo* 1597 (**isotype** O F-76329!).

Description: Basidiocarps annual, effused-reflexed, solitary or in imbricate groups, projecting up to 2 cm, occasionally totally resupinate and then up to 6 cm in widest dimension. Upper surface smooth or scrupose, grevish-ochraceous to mousegrey, sometimes with brownish flecks, azonate. Pileal edge sharp, concolourous with cap surface, usually sterile, margin of resupinate parts cream-coloured to pale ochraceous, compact, adnate or partly detaching, sharply delimited. Pore surface ivory to ochraceous, sometimes with brownish stains; pores roundish to angular, (6-)7-11(-12) per mm, with thin or rather thick, entire dissepiments. Section: context soft corky, white to cream-coloured or pale ochraceous, up to 2 mm thick; tubes corky, one-layered, concolourous with hymenial surface, up to 3 mm thick. Hyphal structure dimitic; hyphae clamped. Context dimitic; skeletal hyphae hyaline to pale ochraceous, densely interwoven, occasionally branched, (3.4–)4.2–7.8(–8.2) µm diam (n = 60/3), lumen varying from narrow to capillary or almost invisible, side branches 2-3.5 µm diam, generative hyphae rare, hyaline, thin- or slightly thickwalled, 3-4 µm diam. Trama dimitic; skeletal hyphae hyaline to pale ochraceous, interwoven to subparallel, some flexuous, occasionally branched, $(3.3-)3.4-6.8(-7.6) \mu m \text{ diam } (n = 100/5)$, lumen capillary to invisible, generative hyphae thin- or slightly thickwalled, 2-3 µm diam, in some places forming subhymenial layer up to 10-15 µm thick, dissepiment edges dimitic, consisting of thinwalled generative hyphae and skeletal hyphae with a wide lumen, apically swollen up to 8 µm diam. Stellate or prismatic crystals occasionally present, incrusting hymenial cells or covering hyphal tips at the dissepiment edges. Cystidioles rare, gradually tapering to the apex, 11-14 × 3-4.5 µm. Basidia short-clavate, (8.8-)8.9- $12.0(-14.3) \times (3.8-)4.0-4.7(-4.8) \mu m$ (n = 30/3), in older hymenium partly glued together and covered by amorphous grainy substance. Basidiospores thin-walled or with a distinct wall, broadly cylindrical to ellipsoid, longest spores subfusiform, (2.7-)3.0-4.2(-4.6) × $(1.8-)1.9-2.9(-3.0) \mu m (n = 150/5), L = 3.35-3.88, W = 2.04-2.25,$ Q = 1.51–1.83.

Specimens examined: Brazil, Para, Paragominas, Mina da Hydro Paragominas, fallen deciduous trunk, 27 Nov. 2014, Runnel 1434* (MG211370). China, Yunnan, Xishuangbanna, 9 Aug. 2005, Miettinen 10120 (H); uprooted tree, 13 Aug. 2005, Miettinen 10227.4 (H); dicot, 15 Aug. 2005, Miettinen 10322 (H). Indonesia, Papua, Jayapura, Cyclop Mountains, steep slope of natural forest, Pometia pinnata, 28 Jan. 2007, Miettinen 11547* (MAN, H); Papua Barat, Manokwari, Amberbaken, Saukorem, dry riverbed in a seaside forest, Terminalia catappa, 31 Oct. 2010, Miettinen 14238 (MAN, H); secondary forest, Pometia pinnata 31 Oct. 2010, Miettinen 14372 (MAN, H); Riau, Indragiri Hulu, Bukit Aluran Babi, dicot, 29 Jun. 2004, Miettinen 8737* (H); felled tree, 2 Jul. 2004, Miettinen 8823* (BO, H); Kampar, Hutan desa Serapung, fallen branch of Syzygium, 4 Dec. 2011, Miettinen 15149.1 (H); Pekanbaru, Rumbai, logged over natural forest, dicot, 2 Apr. 2002, Miettinen 5486* (BO, H); ibid., 18 Jul. 2004, Miettinen 8967 (H); Sumatera Barat, Padang, Limau Manis, dicot, logged over natural forest, 13 Jul. 2008, Miettinen 13019* (ANDA, H); ibid., 15 Jul. 2008, *Miettinen* 13076* (ANDA, H); Pesisir Selatan, Muara Sako, cinnamon plantation, *Durio zibethinus*, 25 Apr. 2002, *Miettinen* 6221 (BO, H). **Malaysia**, Sabah, Ranau, Poring, felled tree (*Sapindales?*), 19 Jun. 2013, *Miettinen* 16417 (SNP, H); Sarawak, Kuching, Bako, fallen logs, 9–13 Feb. 2017, *Dunayev* KUN 1123*, 2874* (BORH, H). **Sri Lanka**, Peradeniya, Kandy Royal Bot. Garden, hardwood, 31 Jan. 2013, *Dunayev** (TUF).

Notes: Fomitopsis caespitosa is widely distributed in Southeast Asia. It is morphologically most similar to *F. luzonensis* and *F. ostreiformis* which have the same geographic distribution. The three species share greyish, tough basidiocarps varying from sessile-imbricate to completely resupinate. Of them, *F. caespitosa* possesses the widest tramal skeletal hyphae and smallest basidiospores (see Table 3). Hattori (2003) reported this species (as *Antrodia multipapillata* (Corner) T. Hattori) as common in temperate forests of Japan. Here we report it for the first time from Africa (Cameroon) and South America (Brazil).

Fomitopsis cajanderi (P. Karst.) Kotl. & Pouzar, Česká Mykol. 11 (3): 157. 1957. Fig 17.

Basionym: Fomes cajanderi P. Karst., Öfversigt af Finska Vetenskaps-Societetens Förhandlingdar 46 (11): 8. 1904.

Typus: **Russia**, Yakutia, Zhigansk, Agrafena, *Larix gmelinii*, 1 Aug. 1901, *Cajander* (herb. Karsten 4320) (**holotype** H 7044546!).

Description: Carranza-Morse & Gilbertson (1986).

Specimens examined: Russia, Khabarovsk Reg., Solnechnyi Dist., Igdomi, *Picea ajanensis*, 4 Aug. 2011, *Spirin* 3760 (H); Gorin, *Larix gmelinii*, 12 Aug. 2011, *Spirin* 4089* (H); Krasnoyarsk Reg., Turukhansk Dist., Lebed', coniferous wood, 23 Aug. 2013, *Kotiranta* 26443* (H).

Notes: Fomitopsis cajanderi is a member of the *F. rosea* complex (Kim *et al.* 2008; see also Fig. 12) distributed in the continental parts of Eurasia and in the cold temperate – boreal area in North America. The differences between *F. cajanderi* and other pink-coloured representatives of the genus are summarized in Table 4.



Fomitopsis calcitrosa (Spirin & Miettinen) Spirin & Miettinen, *comb. nov.* MycoBank MB 844886.

Basionym: Antrodia calcitrosa Spirin & Miettinen, Mycologia 109: 223. 2017.

Typus: **USA**, Washington, Pend Oreille Co., Muskegon Lake, *Picea engelmannii*, 16 Oct. 2014, *Spirin* 8610* (**holotype** H!).

Description and phylogenetic data: Spirin et al. (2017, as A. calcitrosa); see also Fig. 3.

Fomitopsis carnea (Blume & T. Nees) Imazeki, Bull. Tokyo Sci. Mus. 6: 92. 1943. Figs 17, 19.

Basionym: Polyporus carneus Blume & T. Nees, Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 13: 14. 1826.

Typus: Tab. III (*'Polyporus carneus'*) in Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 13, 1826 (**iconotype** designated here, MycoBank MBT 10008288). **Indonesia**, Riau, Kampar Peninsula, loggedover peatswamp forest, *Shorea* (?), 3 Dec. 2011, *Miettinen* 15115.2* (H) (**epitype** designated here, MycoBank MBT 10008289).

Synonym: Polyporus aurora Ces., Atti Accad. Sci. Fis. Mat. Napoli 8: 5. 1879.

Typus: **Malaysia**, Sarawak, [no collection date], *Beccari* (**isotype** BPI US0319608!).

Description: Basidiocarps perennial, sessile, often with a contracted base (fan-shaped), producing large imbricate groups, sometimes fusing together, projecting up to 7 cm. Upper surface smooth, pinkish grey to pinkish buff, sulcate and radially striate. Pileal edge sharp, concolourous with hymenial surface, usually sterile, up to 2 mm wide. Pore surface pink to pinkish grey, usually concave; pores roundish to angular, (6–)7–9 per mm, with thin or moderately thickened, entire dissepiments. Section: context corky, pink or pinkish brownish, normally less than 5 mm thick; tubes corky, one-layered or indistinctly stratified, concolourous



Fomitopsis caseosa

Fomitopsis cupressicola



Fomitopsis dochmia

Fig 19. Basidiospores of *Fomitopsis* spp. *F. carnea* (Miettinen 13120.1); *F. caseosa* (holotype); *F. cupreorosea* (Kout 0610/K4); *F. cupressicola* (holotype); *F. derelicta* (holotype); *F. dochmia* (Dunaev 7.II.2019). Scale bar = 5 µm.



with hymenial surface, up to 3 mm thick. *Hyphal structure* dimitic; hyphae clamped. Context dimitic; skeletal hyphae yellowish to brownish, densely interwoven, occasionally branched, (3.1-)3.3- $5.0(-5.1) \mu m$ diam (n = 40/2), lumen normally capillary to indistinct, side branches 1.5–2 µm diam, generative hyphae rare, hyaline, slightly thick-walled, 2.5-4 µm diam. Trama dimitic; skeletal hyphae dominating, hyaline to yellowish or brownish, densely interwoven, occasionally branched, $(2.8-)2.9-4.2(-4.3) \mu m$ diam (n = 80/4), lumen varying from rather wide to capillary, generative hyphae rare, thin- to slightly thick-walled, 1–2 µm diam. Subhymenium indistinct. Cystidioles abundant to rare, tapering, 8-11 × 3-4 µm. Basidia short-clavate, (8.2–)8.3–13.3(–14.0) × (4.2–)4.7–5.1(–5.2) µm (n = 20/2), in senescent hymenium partly glued together. Basidiospores thin-walled or with a distinct wall, cylindrical-subfusiform to narrowly ellipsoid, occasionally slightly curved, $(2.8-)2.9-4.5(-4.7) \times (1.8-)$ 1.9-2.3(-2.4) µm (n = 150/5), L = 3.29-3.92, W = 2.01-2.11, Q = 1.57-1.86.

Specimens examined: Indonesia, Riau, Indragiri Hulu, Bukit Aluran Bab, selectively logged primary rainforest, dicot, 28 Jun. 2004, *Miettinen* 8700 (H); primary rainforest with *Dipterocarpaceae* and *Dyera costulata*, dicot (fallen tree crown), 29 Jun. 2004, *Miettinen* 8720 (H); half-opened forest, *Pentadesmon* (uprooted tree), 30 Jun. 2004, *Miettinen* 8765.1 (H); Kampar, Balung, heavily logged over natural forest, cut bolt of *Mangifera*, 24 Dec. 2006, *Miettinen* 11249 (BO, H); Sumatera Barat, Padang, Limau Manis, fallen dicot tree crown, 16 Jul. 2008, *Miettinen* 13120.1* (H). Singapore, Botanical Garden, dicot, 6 Jan. 2007, *Miettinen* 11321.1 (H); *ibid.*, 20 Mar. 2020, *Miettinen* 23637 (SING, H); *Shorea* (?), 8 Jul. 2013, *Miettinen* 16605 (H); Bukit Timah, park, cut bolt of dicot, 19 Mar. 2020, *Miettinen* (SING, H). Thailand, Chanwat Chiang Doo, Doo Chiang Doo Nat. Park, 22 Feb. 1979, *Ryvarden* 17979 (O 17742, H).

Notes: Polyporus carneus was originally described from Java (Blume & Nees von Esenbeck 1826). The lack of any surviving type material evidently contributed to the numerous misinterpretations of this species. Here we apply the name *P. carneus* to a relative of *F. feei* widely distributed in Southeast Asia and macroscopically fitting the protologue. An epitype is selected to support our solution.

Phylogenetically, *F. carnea* is closest to *F. eucalypti* from Australia which has larger pores and basidiospores. *Fomitopsis foedata*, distributed in Oceania, differs from *F. carnea* in having thinner, flexible basidiocarps, wider pores and larger basidiospores. *Fomitopsis africana* is one more species of the *F. feei* complex occurring in the same geographic area; it has softer and paler basidiocarps than those of *F. carnea*, as well as wider and more loosely arranged tramal skeletal hyphae, and larger basidiospores. Another morphologically similar but phylogenetically distant species, *F. marchionica*, has more robust basidiocarps with a densely zonate upper surface and wider pores. The latter species is distributed in Oceania (see below). Two previously published sequences of *F. carnea* came from specimens collected in Tanzania (Han & Cui 2015). They belong to *F. purpurea*, a representative of the *F. rosea* complex, which we describe below.

The identity of *F. carnea* from outside the Malay Archipelago deserves further clarification. In our analysis, we detected the ITS sequence of '*F. feei*' (GenBank KP780437) from Sri Lanka as sister to *F. carnea* sequences from Indonesia (Fig. 11). Differences between them were up to 10 bp, and therefore the Sri Lankan specimen may represent a separate species. In the latter case, *Polyporus rubidus* could be a suitable name for it.

Fomitopsis caseosa Vlasák & Spirin, *sp. nov.* MycoBank MB 844887. Figs 17, 19.

Typus: **Costa Rica**, Puntarenas, Golfito, Playa Cacao, abandoned farm, 8.640403° -83.192987°, on a dead stump with a violet core wood (*Peltogyne?*), 19 Apr. 2015, *Vlasák* 1504/28* (**holotype** PRM956227).

Etymology: Caseosus (Lat., adj.) - cheese-like.

Description: Basidiocarps perennial, sessile, ungulate, projecting up to 5 cm. Upper surface brown to brownish-black, smooth, distinctly sulcate, matt. Pileal edge blunt, ochraceous-brownish, sterile, up to 1 mm wide. Pore surface cream-coloured, concave; pores roundish or elongated, 8-9 per mm, with moderately thickened, entire dissepiments. Section: crust brownish-black, matt, 0.5-1 mm thick, context soft corky, brownish, up to 6 mm thick; tubes chalk-like, easily crumbling, clearly stratified, up to 45 mm thick, with up to 10 annual layers 2-4 mm thick, concolourous with hymenial surface, separated by brownish layers of sterile tissue 0.5-2 mm thick. Hyphal structure dimitic; hyphae clamped. Context dimitic; skeletal hyphae hyaline to yellowish or brownish, densely interwoven, occasionally branched, (3.2-)3.3-4.2(-5.0) µm diam (n = 20/1), lumen mostly capillary to indistinct, side branches 2-3 um diam, generative hyphae rare, hyaline, slightly or distinctly thick-walled, 3-4 µm diam. Trama dimitic; skeletal hyphae rather sparse, hyaline, loosely interwoven, occasionally branched, some twisted or irregularly inflated, (2.2-)2.6-3.3(-3.4) µm diam (n = 20/1), lumen varying from wide to capillary or indistinct, generative hyphae abundant, thin- to slightly thick-walled, some sclerified, 2-4 µm diam. Subhymenium not differentiated. Cystidioles abundant, tapering, 9-14 × 3-5 µm. Basidia clavate, (7.1-)7.3-9.7(-9.8) × $(3.9-)4.0-4.2(-4.8) \mu m$ (n = 12/1), in senescent hymenium slightly thick-walled and partly glued together. Basidiospores with a distinct wall, broadly cylindrical to narrowly ellipsoid, $(2.8-)2.9-3.3(-3.7) \times$ $1.9-2.1(-2.2) \mu m$ (n = 20/1), L = 3.14, W = 2.01, Q = 1.57.

Specimen examined: **Costa Rica**, Puntarenas, Golfito, Playa Cacao, the same host as the holotype, 16 Apr. 2017, *Vlasák* 1704/10 (JV).

Notes: Superficially, *F. caseosa* is most similar to the Southeast Asian *F. pseudopetchii*, which has ungulate basidiocarps with a well-developed crust, clearly stratified tubes and small pores 7–10 per mm. Its basidiospore dimensions are very close to those of *F. caseosa* (see below). In contrast to *F. caseosa*, the crust in the well-developed basidiocarps of *F. pseudopetchii* is shining, dark reddish-brown to almost black, reminiscent of some *Ganoderma* spp., while context and tubes are uniformly cream- to woodcoloured. DNA sequences of *F. caseosa* and *F. pseudopetchii* show that these species are not closely related (Suppl. Fig. S2).

Fomitopsis castanea Imazeki, Bull. Gov. Forest Exp. Stn. Tokyo 42: 1. 1949. Fig 17.

Typus: Japan, Kitasaku, Nagano, 9 Oct. 1947, *Imazeki* (holotype TFM F-346).

Synonyms:

Phellinus quercinus Bondartsev & Ljub., Nov. Syst. Pl. non Vasc. 2: 141. 1965.

Typus: **Russia**, Primorie, Shkotovo Dist., Peishula, *Quercus mongolica*, 14 May 1950, *Ljubarksy* (**holotype** LE 22516!).

Melanoporia castanea (Imazeki) T. Hatt. & Ryvarden, Mycotaxon 50: 29. 1994.

Description: Núñez & Ryvarden (2001, as M. castanea).

Specimen examined: Russia, Khabarovsk Reg., Khabarovsk Dist., Ilga, Quercus mongolica, 11 Aug. 2012, Spirin 5144* (H).

Fomitopsis cellularis Vlasák & Spirin, *nom. nov.* MycoBank MB 844888. Fig 16.

Basionym: Trametes cystidiata I. Lindblad & Ryvarden, Mycotaxon 71: 353. 1999.

Typus: **Costa Rica**, Guanacaste, Pitilla, dead deciduous tree, 23 Mar. 1997, *Garcia* 99* (**isotype** O F-450190!).

Etymology: Cellularis (Lat., adj.) – in reference to cellular hymenophore.

Description: Lindblad & Ryvarden (1999, as T. cystidiata).

Specimens examined: **Costa Rica**, Guanacaste, Guanacaste Nat. Park., Pitilla, dead deciduous wood, 1 Feb. 1997, *Lindblad* 2655 (O 19098, H); *ibid.*, 3 Feb. 1997, *Lindblad* 2689 (O 19016, H); Puntarenas, Piedras Blancas Nat. Park, Rio Bonito, 9 May 2000, *Fletes* 1522 (O 14134, H); *ibid.*, 20 Apr. 2015 *Vlasák* Jr. 1504/36J* (JV, TUF).

Notes: Originally described from Costa Rica as a member of *Trametes*, this species proved here to be a member of *Fomitopsis* (Fig. 1). However, it cannot be combined in *Fomitopsis* because the epithet *Fomitopsis cystidiata* is preoccupied by another species described from China (Han *et al.* 2014) (see under *F. sulcata*). Therefore, a new name is introduced for it. Lindblad & Ryvarden (1999) depicted cystidia in the type specimen of *F. cellularis* as finely encrusted; however, they were smooth in all other specimens studied by us.

Fomitopsis circularis (B.K. Cui & Hai J. Li) Spirin, *comb. nov.* MycoBank MB 844889

Basionym: Daedalea circularis B.K. Cui & Hai J. Li, Mycoscience 54: 63. 2013.

Typus: **China**, Yunnan, Mengla, Wangtianshu, hardwood, 2 Nov. 2009, *Cui* 8488* (**holotype** BJFC 6977).

Description and phylogenetic data: Li & Cui (2013, as *D. circularis*); see also Fig. 5.

Fomitopsis concentrica (G. Cunn.) M.D. Barrett, *comb. nov.* MycoBank MB 844890.

Basionym: Gloeophyllum concentricum G. Cunn., Bull. N.Z. Dept. Sci. Industr. Res. 164: 262. 1965.

Typus: **Australia**, Queensland, Cape York Peninsula, Lower Archer River, Mar. 1933, *L.* & *G. Thomson* (**holotype** PDD 12262).

Synonym: Ischnoderma concentricum (G. Cunn.) Corner, Beih. Nova Hedwigia 96: 80. 1989.

Description: Cunningham (1965, as G. concentricum).

Specimen examined: Australia, Western Australia, Theda Station, Kimberley region, *Eucalyptus tetrodonta* (recently fallen branch), 18 May 2011, *Barrett* F197/11* (PERTH).

Notes: Gloeophyllum concentricum is morphologically apomorphic, combining a compound-imbricate basidiocarp, composed of few to



many thin overlapping pilei, and concentrically arranged lamellae. Its placement in *Gloeophyllum* was immediately criticized as "open to serious question" by Reid (1967), due to macroscopic and spore differences. It was later unsatisfactorily moved to *Ischnoderma* by Corner (1989). While reviewing Cunningham's types, Buchanan & Ryvarden (1988) accepted the species in *Gloeophyllum* despite its lack of cystidia typical of that genus, justified by the existence of 'some' *Gloeophyllum* that lack cystidia (although examples were not mentioned). Examination of material *in situ* by one of us (MB) demonstrated that the species produces a brown hear-rot, most commonly on *Eucalyptus* but occasionally on other angiosperms. *Gloeophyllum concentricum* lacks cystidia typical of *Gloeophyllum*. DNA data confirm that it belongs within the concept of *Fomitopsis* accepted here, strongly supported as sister to a clade containing *F. tunicata* and *F. glabricystidia* (Figs 1, 3).

Fomitopsis condensa Ryvarden & Vlasák, *nom. nov.* MycoBank MB 844891.

Basionym: Melanoporia condensa Ryvarden & Vlasák, Syn. Fung. 35: 28. 2016. (invalid under Code Art. 8.1).

Typus: **Costa Rica**, Monteverde, Santa Elena, hardwood, 30 Dec. 2013, *Vlasák* Jr. 1312/E-15-J* (**holotype** PRM 933857!).

Description: Vlasák et al. (2016, as M. condensa).

Notes: Melanoporia condensa was described based on material from Costa Rica (Vlasák *et al.* 2016) although invalidly because the holotype was indicated as stored in three different herbaria. Here we formally validate this species in the genus *Fomitopsis* and designate its holotype. It is closely related to other species formerly included in *Melanoporia* (Fig. 3).

Fomitopsis cupreorosea (Berk.) J. Carranza & Gilb., Mycotaxon 25: 476. 1986. Fig 19.

Basionym: Polyporus cupreoroseus Berk., Hooker's J. Bot. 8: 233. 1856.

Typus: **Brazil**, Panurè, dead trunks, Feb. 1853, *Spruce* 184 (**lectotype** K, **isolectotype** PC!) (selected by Ryvarden 1984: 337).

Description: Basidiocarps perennial, sessile, often with a contracted base (fan-shaped), projecting up to 10 cm. Upper surface first pinkish-ochraceous, often with a brass tint, smooth, even or indistinctly zonate, later pinkish brownish, frequently zonate and radially wrinkled or furrowed, with a silky lustre. Pileal edge sharp to rather blunt, concolourous with hymenial surface, first sterile, up to 2 mm wide, then fertile. Pore surface deep pink to pinkish-ochraceous, flat or concave; pores roundish to angular or sinuous, 3-5 per mm, with thin or moderately thickened, entire or serrate dissepiments. Section: context corky, deep pink or pinkish brownish, normally less than 3 mm thick; tubes corky, onelayered, concolourous with hymenial surface, up to 3 mm thick. Hyphal structure dimitic; hyphae clamped. Context dimitic; skeletal hyphae hyaline to yellowish or brownish, densely interwoven or in subparallel bundles, occasionally branched, (3.4-)3.7-5.3(-6.3) μ m diam (n = 20/1), lumen normally wide, side branches 1.5–3 μ m diam, generative hyphae rare, hyaline, slightly thick-walled, 2.5-4 µm diam. Trama dimitic; skeletal hyphae dominating, brownish to pinkish brown, densely interwoven, occasionally branched, some twisted, (2.8-)2.9-4.7(-5.1) µm diam (n = 40/2), lumen mostly narrow to capillary, generative hyphae rather rare, thinto slightly thick-walled, 2–3.5 µm diam. Subhymenium indistinct. Skeletocystidia present as swollen (up to 5.5 µm diam) apices of tramal skeletal hyphae, slightly projecting above hymenium. Cystidioles infrequent, tapering, $12-15 \times 3-5$ µm. *Basidia* clavate, (10.8–)11.3–17.2(–18.9) × (4.8–)5.0–6.0(–6.3) µm (n = 20/2), occasionally pleural, in senescent hymenium slightly thick-walled and partly glued together. *Basidiospores* with a distinct wall, cylindrical-subfusiform, (4.4–)4.6–6.6(–6.7) × (2.0–)2.1–3.0(–3.1) µm (n = 90/3), L = 5.03–5.75, W = 2.40–2.76, Q = 1.83–2.29.

Specimens examined: Belize, Cayo, Five Sisters, hardwood, 19 Nov. 2001, *Ryvarden* 44394 (O 17632); Stann Creek, Cockscomb Basin, 30 Oct. 2006, *Kout* 0610/K4* (JV, H). Brazil, Bahia, Santa Terezinha, Serra do jibóia, angiosperm tree (fallen trunks), 11 Jan. 2006, *Oinonen* 60111009 & 60111014 (H). French Guiana, Roura, Camp Cayman, 31 Aug. 2019, *Vlasák* 1908/81* (JV, H); Favard, 17 Oct. 2013, *Runnel* 654* (TUF130110).

Notes: Fomitopsis cupreorosea is a member of the *F. feei* complex. It is distributed in tropical forests of Central and South America. *Fomitopsis cupreorosea* is easily distinguishable versus other related species due to its large, irregular pores. ITS sequences of *F. cupreorosea* show considerable variation, but our material is too limited to conclude if several sibling species are hidden under this name.

Fomitopsis cupressicola Vlasák, J. Vlasák Jr. & Spirin, *sp. nov.* MycoBank MB 844892. Fig 19.

Typus: **USA**, New Jersey, Burlington Co., Batsto Village, 39.68764° -74.66108°, *Chamaecyparis thyoides*, 1 Jun. 2017, *Vlasák* Jr. 1706/9-J* (**holotype** H7200201).

Etymology: Cupressicola (Lat., noun) – in reference to *Cupressaceae*.

Description: Basidiocarps perennial, sessile, conchate, projecting up to 4 cm, often fusing together. Upper surface first pinkish greyish to pinkish brownish, smooth, later dark brown to almost black, frequently zonate, matt. Pileal edge sharp to rather blunt, concolourous with hymenial surface, sterile, up to 2 mm wide. Pore surface pinkish-grey to pinkish brownish, concave; pores roundish to angular, 6-8 per mm, with thin or thickened, entire or slightly uneven dissepiments. Section: crust (present in old basidiocarps) exceptionally tough, blackish brown, matt, up to 0.3 mm thick, context hard corky, brown, up to 2 mm thick; tubes corky, one-layered or indistinctly stratified, concolourous with hymenial surface, up to 7 mm thick. Hyphal structure dimitic; hyphae clamped. Context dimitic; skeletal hyphae brown, densely interwoven, mostly unbranched, (2.8–)2.9–3.7(–3.8) μ m diam (n = 20/1), lumen narrow to indistinct, generative hyphae rare, hyaline, thick-walled, 2-2.5 µm diam. Trama dimitic; skeletal hyphae dominating, brown, densely interwoven, rarely branched, (2.0-)2.1-3.6(-3.8) µm diam (n = 60/3), lumen mostly narrow to indistinct, generative hyphae rather rare, thin- to slightly thick-walled, 2–3.5 µm diam. Subhymenium partly distinct, up to 10 µm thick. Skeletocystidia present as slightly swollen (3-4 µm diam) apices of tramal skeletal hyphae, embedded or slightly projecting above hymenium. Cystidioles rather common, tapering, $11-16 \times 3-5 \mu m$. Basidia clavate, (11.0-)11.1-15.4(-16.0) × (4.8-)4.9-6.1(-6.2) µm (n = 20/2), occasionally pleural, in senescent hymenium slightly thick-walled. Basidiospores with a distinct wall, cylindrical to narrowly ellipsoid, longest spores subfusiform or rarely lacrymoid, (3.6-)3.7-5.2(-5.4) × (1.8-)1.9-2.8(-2.9) µm (n = 120/4), L = 3.93-4.74, W = 2.02-2.34, Q = 1.69-2.36.

Specimens examined: **Dominican Republic**, La Vega, Cordillera Central, *Pinus occidentalis*, 18 Feb. 2001, *Paino-Perdomo et al.* 703 (O 14114, H). **USA**, Florida, Manatee Co., Braden River, at the base of an old unknown tree, 8 May 2016, *Dollinger* 778* (JV, H); New Jersey, Burlington Co., Batsto Village, *Chamaecyparis thyoides*, 1 Jun. 2017, *Vlasák* Jr. 1706/7-J* (JV, H).

Notes: Fornitopsis cupressicola is a member of the *F. rosea* complex. It inhabits wood of gymnosperms (predominantly *Cupressaceae*) in the eastern part of North America. Morphologically, *F. cupressicola* is most similar to *F. cajanderi* and *F. substratosa*. The first species is distributed in boreal zone of Eurasia and North America. It differs from *F. cupressicola* in having lighter-coloured, pinkish hymenial surface, as well as longer and narrower basidiospores, $(4.1-)4.2-6.1(-6.2) \times (1.7-)1.8-2.1(-2.2) \mu m (n = 90/3), L = 5.13-5.35, W = 1.94-1.96, Q = 2.62-2.77$. No verified records of *F. cajanderi* from *Cupressaceae* are known to us. As accepted here, *F. substratosa* (= *F. subfeei*) is a species distributed in the northern part of Africa and Southeast Asia. It differs from *F. cupressicola* in having larger pores and narrower basidiospores (see below).

Fomitopsis cyclopis (Miettinen & Spirin) Miettinen & Spirin, *comb. nov.* MycoBank MB 844893.

Basionym: Antrodia cyclopis Miettinen & Spirin, Mycol. Progr. 15 (51): 5. 2016.

Typus: Indonesia, Papua, Kabupaten Jayapura, Sentani, Cyclops Mountains, angiosperm branch, 29 Aug. 2004, *Miettinen* 9166.1* (isotype H!).

Description and phylogenetic information: Spirin et al. (2016, as A. cyclopis).

Fomitopsis derelicta Vlasák & Spirin, *sp. nov.* MycoBank MB 844894. Fig 19.

Typus: **USA**, Texas, Brewster Co., Big Bend, 29.30° -103.356°, *Quercus* sp., 3 Apr. 2021, *Vlasak* Jr. 2104/2J* (**holotype** H7200200).

Etymology: Derelictus (Lat., adj.) - forsaken, desolate.

Description: Basidiocarps perennial, sessile, dimidiate, projecting up to 2.5 cm. Upper surface greyish-ochraceous to brownish, irregularly nodulose, azonate. Pileal edge blunt, concolourous with pileal surface, sterile, up to 5 mm wide. Pore surface pale ochraceous or greyish to brownish, flat or slightly convex; pores angular to sinuous or labyrinthine, (0.5-)1-1.5(-2) per mm, 8-9 per cm, with thick, entire or uneven dissepiments. Section: context fibrous-corky, ochraceous to brownish, up to 15 mm thick; tubes corky, one-layered, concolourous with hymenial surface, up to 10 mm thick. Hyphal structure dimitic; hyphae clamped. Context dimitic; skeletal hyphae brownish, interwoven, occasionally branched, (3.9-)4.0-5.8(-6.0) µm diam (n = 20/1), lumen usually wide, side branches 2–3.5 µm diam, generative hyphae rare, hyaline, slightly thick-walled, 3-5 µm diam. Trama dimitic; skeletal hyphae dominating, hyaline to brownish, interwoven, occasionally branched, (2.1-)2.3-4.1(-4.2) µm diam (n = 20/1), lumen mostly capillary to indistinct, side branches 1.5-2.5 µm diam, generative hyphae thin- to slightly thick-walled, 2-3.5 µm diam. Subhymenium sometimes distinct, up to 20 µm thick. Skeletocystidia present as swollen (up to 6 µm diam), acute or blunt apices of tramal skeletal hyphae, slightly projecting above hymenium. Cystidioles occasionally present, tapering, sometimes sinuous, 16-28 × 3-4 μm. Basidia long clavate, occasionally pleural, $(23-)25-32(-35) \times (5.8-)6.0-7.2(-7.3)$ μm (n = 20/1), in senescent hymenium slightly thick-walled. Basidiospores with a distinct wall, narrowly ellipsoid to ellipsoid or occasionally sigmoid, $(4.6-)4.8-6.8(-7.0) \times (2.7-)2.8-3.9(-4.0)$ μm (n = 32/1), L = 5.60, W = 3.33, Q = 1.69.

Notes: Fomitopsis derelicta is a close relative of *F. quercina* distributed in subtropical – tropical areas of North America. The species is so far known from two collections – one from the southwestern part of Texas, USA and another one from Belize, both from *Quercus* spp. The latter specimen (CFMR BZ-2779) was reported as *Daedalea cf. quercina* by Lindner *et al.* (2011). Macroscopically, *F. derelicta* differs from *F. quercina* in having more regular and smaller pores (0.3–1 per mm, 5–8 per cm in *F. quercina*). In the microscope, the basidiospore shape and size are the main distinguishing characters between the two species. Basidiospores of *F. quercina* are broadly cylindrical or subfusiform and on average narrower than in *F. derelicta*, (4.1–)4.7–6.8(–7.2) × (2.2–)2.3–3.1(– 3.2) µm (n = 60/2), L = 5.52–5.55, W = 2.78–2.80, Q = 1.99–2.00.

According to available sequences and our own data, *F. quercina* is widely distributed in temperate – warm temperate forests of North America, and the southernmost record of this species known to us came from Georgia (Fig. 5). Historical specimens of *F. quercina* from the south-western part of USA should be critically checked to re-define its distribution area on the continent. Another North-American species from this complex is *F. neotropica* (= *Daedalea neotropica*, see below). It can be easily differentiated from *F. derelicta* and *F. quercina* in having much smaller pores, 3–5 per mm, and violet stains on pileal and pore surfaces. The distribution area of *F. neotropica* seems to be limited to tropical forests of Central America (Lindner *et al.* 2011, Vlasák *et al.* 2016).

Fomitopsis dickinsii (Berk. ex Cooke) Spirin, *comb. nov.* MycoBank MB 844895. Fig 17.

Basionym: Trametes dickinsii Berk. ex Cooke, Grevillea 19: 100. 1891.

Typus: **Japan**, [no locality indicated], on trunks, herb. Berkeley (**lectotype** K) (selected by Ryvarden 1988b: 49).

Description: Hattori & Ryvarden (1994, as Daedalea dickinsii).

Specimens examined: **China**, Jilin, Antu Co., Changbaishan Nat. Res., *Quercus mongolica* (fallen log), 20 Sep. 1998, *Niemelä* 6435 (H). **Russia**, Khabarovsk Reg., Khabarovsk Dist., Ilga, *Q. mongolica* (fallen log), 10 Aug. 2012, *Spirin* 5094 (H).

Notes: Lindner *et al.* (2011) provided sequences for this species. Our results confirm its affinity with other species until recently addressed to *Daedalea* (Fig. 5).

Fomitopsis dochmia (Berk. & Broome) Ryvarden, Norw. J. Bot. 19: 231. 1972. Fig 19.

Basionym: Polyporus dochmius Berk. & Broome, J. Linn. Soc., Bot. 14: 50. 1875.

Typus: **Sri Lanka**, Central Province, Dec. 1868, Berkeley's herbarium #970 (lectotype K, isolectotype BPI!) (selected by Ryvarden 1984: 338).

Description: Basidiocarps perennial, sessile, conchate, projecting up to 10 cm. Upper surface first reddish-brown, then darkening to almost black, matt, with distinct annual zones, densely longitudinally cracking, growing margin ochraceous brown. Pileal edge sharp or rather blunt, concolourous with hymenial surface, sterile, up to 1 mm wide. Pore surface pinkish- to reddish-brown, concave; pores roundish, 8-10 per mm, with thick, entire dissepiments. Section: crust dark brown to black, tough, up to 0.5 mm thick, context corky, ochraceous or brownish, up to 5 mm thick; tubes corky, stratified, concolourous with hymenial surface, up to 15 mm thick, sterile tissue often present between annual layers. Hyphal structure dimitic; hyphae clamped. Context dimitic; skeletal hyphae dominating, yellowish- to reddish brownish, densely interwoven, occasionally branched, $(3.2-)3.3-5.8(-6.0) \mu m$ diam (n = 40/2), lumen mostly narrow to indistinct, side branches 2-3 µm diam, generative hyphae rare, hyaline, thin- or slightly thick-walled, 2-3.5 µm diam. Trama dimitic; skeletal hyphae dominating, brownish to reddish-brown, densely interwoven, occasionally branched, (2.8-)2.9-5.0(-5.2) µm diam (n = 40/2), lumen mostly capillary to indistinct, side branches 2–2.5 µm diam, generative hyphae rare, hyaline, thin- or slightly thick-walled, 1.5-3 µm diam. Subhymenium indistinct. Skeletocystidia present as more or less blunt apices of tramal skeletal hyphae, 3-4 µm diam, slightly projecting above hymenium. Cystidioles tapering, 12-20 × 3-4 µm, sometimes with a long hyphoid neck. Hyphidia occasionally present, simple or bifurcate, 1.5-2 µm diam. Basidia clavate, occasionally pleural, rare, $10.4-17.2 \times 3.3-5.1 \mu m$ (n = 8/1). Basidiospores thin-walled or with a distinct wall, cylindrical to broadly cylindrical, occasionally slightly curved, (3.0–)3.1–4.1(–4.2) × (1.8–)1.9–2.3(–2.4) µm (n = 30/1), L = 3.58, W = 2.10, Q = 1.71.

Specimen examined: India, Kerala, Idukki, Munnar, Kannan Devan Hills, fallen log, 7 Feb. 2019, *Dunayev** (TUF).

Notes: To date, F. dochmia was treated as a widely distributed tropical species with a dark, characteristically cracking pileal surface and rather light-coloured, stratified tubes (Carranza-Morse & Gilbertson 1986, Ryvarden 2015). Our data reveal the presence of at least six species covered by the present concept of F. dochmia in two phylogenetically distant lineages in Fomitopsis. Here we reinstate F. dochmia based on the type from Sri Lanka and a newly collected and sequenced specimen from the southern part of India. As accepted here, F. dochmia is most similar to F. philippinensis. The latter species seemingly has a more eastern distribution than F. dochmia, and it is recognizable due to larger pores and strongly fading upper surface of older basidiocarps. Fomitopsis ferrea, originally described from Sri Lanka and up to now considered a synonym of F. dochmia, has somewhat larger pores and lighter-coloured pileal tissues than those of *F. dochmia*. Another look-alike from Southeast Asia is F. elevata (see remarks below). Phylogenetically, these four species form a natural lineage in the genus (Fig. 5).

Two more species, *F. lapidosa* and *F. lignea*, are superficially very similar but not closely related to the *F. dochmia* clade. The first species is strongly reminiscent of *F. ferrea* and *F. elevata* but it has more lightweight basidiocarps and smaller pores than those two species. *Fomitopsis lapidosa* is so far known only from New Guinea. In turn, *F. lignea* possesses somewhat larger pores than *F. dochmia*, and it is distributed in the Caribbean. Anatomical differences between all these species are minimal if any.

Fomitopsis dollingeri Vlasák & Spirin, *sp. nov.* MycoBank MB 844896. Figs 16, 20.

Typus: **USA**, Florida, Collier Co., Copeland, Fahkahatchee Strand, 26.0516° -81.3885°, dry hardwood branch, 15 Jun. 2014, *Dollinger* 56* (holotype H7200204).





Fomitopsis elevata

Fomitopsis ferrea

Fomitopsis fissa

Fomitopsis foedata

Fig 20. Basidiospores of *Fomitopsis* spp. *F. dollingeri* (holotype); *F. elevata* (Miettinen 20529); *F. feei* (Oinonen 60119006); *F. ferrea* (Dunaev 26.1.2019); *F. fissa* (holotype); *F. foedata* (Miettinen 11466). Scale bar = 5 µm.

5 µm

Etymology: After Neil Dollinger, a collector of this species.

Description: Basidiocarps annual, effused, up to 4 cm in widest dimension. Margin adnate, compact, cream-coloured, later ochraceous-brownish, up to 1 mm wide. Hymenial surface even, pale cream-coloured; pores angular, 4-6 per mm, dissepiments uneven. Section: subiculum compact, white, hardly visible, 0.05-0.07 mm thick; tubes soft leathery, white or pale creamcoloured, 0.5-1.5 mm thick. Hyphal structure dimitic; hyphae clamped. Subiculum dimitic; skeletal hyphae hyaline, sparsely arranged, interwoven, occasionally branched, (1.8–)2.1–3.2(–3.3) μ m diam (n = 20/1), lumen wide to rather narrow, generative hyphae dominating, hyaline, thin-walled, 2-3.5 µm diam. Trama dimitic; skeletal hyphae hyaline, sparse, interwoven, occasionally branched, (1.7–)1.8–3.4(–3.7) µm diam (n = 40/2), lumen mostly wide, generative hyphae dominating, hyaline, thin-walled, 2-3 µm diam; dissepiment edges completely monomitic. Cystidioles rather abundant in senescent hymenium, bullet-shaped to fusiform, 12.5-20 × 3-5 µm. Rhomboid or stellate crystals occasionally present in tube trama, up to 10 µm in longest dimension. Basidia clavate, $(13.2-)13.3-17.8(-20.8) \times (5.2-)5.3-6.2(-6.3) \ \mu m \ (n = 20/2).$ Basidiospores thin-walled, broadly cylindrical to narrowly ellipsoid, longest spores subfusiform, (5.1–)5.2–7.2(–7.3) × (2.1–)2.2–3.1(– 3.2) μm (n = 60/2), L =5.86–6.36, W = 2.45–2.81, Q = 2.27–2.40.

Specimen examined: **USA**, Florida, Manatee Co., Parrish, Rye Preserve, hardwood, 27 Mar. 2016, *Dollinger* 700* (H, JV).

Notes: The species was found twice in Florida, USA, inhabiting dry and still corticated branches of angiosperms. It keys out as *Antrodia oleracea* if existing manuals of poroid fungi (Lowe 1966, Gilbertson & Ryvarden 1986) are used for identification. However, *A. oleracea* (= *Fomitopsis oleracea* below) is a completely monomitic species with easily crumbling basidiocarps, and it inhabits decorticated wood of *Quercus* spp. (see description below). *Fomitopsis elevata* (Corner) Spirin & Miettinen, *comb. nov.* MycoBank MB 844897. Figs 20, 21.

Basionym: Trametes elevata Corner, Beih. Nova Hedwigia 97: 98. 1989.

Typus: **Malaysia**, Pahang, Sungei Cheka, 'on the trunk of a small tree', 14 Jun. 1931, *Corner* (**holotype** E00604887).

Description: Basidiocarps perennial, sessile, conchate, sometimes with a contracted base (fan-shaped), solitary or partly fusing together, projecting up to 4 cm. Upper surface blackish brown to bluish-black, with several indistinct annual zones, sometimes longitudinally cracking, growing margin much paler, wood-coloured to ochraceous-brownish, more or less evenly coloured. Pileal edge sharp or rather blunt, concolourous with hymenial surface, first sterile, up to 1 mm wide, then fertile. Pore surface creamcoloured or beige to pale ochraceous, sometimes with scattered blackish-blue stains, even or slightly concave; pores roundish, 6-7 per mm, with very thick, entire dissepiments. Section: crust black, tough, up to 0.5 mm thick, context corky, wood-coloured to pale ochraceous, up to 10 mm thick; tubes corky, indistinctly stratified, concolourous with hymenial surface, up to 5 mm thick. Hyphal structure dimitic; hyphae clamped. Context dimitic; skeletal hyphae dominating, yellowish, densely interwoven, occasionally branched, (3.2–)3.3–5.1(–5.3) µm diam (n = 20/1), lumen capillary to indistinct, side branches 2–3 µm diam, generative hyphae rare, hyaline, thick-walled, 2-3 µm diam. Trama dimitic; skeletal hyphae dominating, yellowish, densely interwoven, occasionally branched, (3.0-)3.1-4.6(-4.8) µm diam (n = 40/2), lumen mostly capillary to indistinct, side branches 2-3 µm diam, generative hyphae rare, slightly thick-walled, 2-3 µm diam. Subhymenium indistinct. No differentiated skeletocystidia seen. Cystidioles abundant, tapering, 10.5-16 × 2.5-3.5 µm. Basidia clavate, (9.3-)10.0-15.1(-15.2) × $(4.0-)4.2-4.9(-5.0) \mu m$ (n = 12/2), in senescent hymenium partly glued together. Basidiospores thin-walled, cylindrical, often slightly



Fig 21. Basidiocarps of Fomitopsis spp. A. F. elevata (Miettinen 8692). B. F. foedata (Miettinen 11466). C. F. gilvidula (Miettinen 20535). D. F. lapidosa (holotype). E. F. leioderma (Vlasák 1908/82). F. F. luzonensis (Miettinen 14311). G. F. maculosa (holotype). H. F. marianii (Spirin 10575).

curved, (3.0–)3.1–4.7(–5.1) × (1.7–)1.8–2.2(–2.3) μ m (n = 60/2), L = 3.60–4.18, W = 1.96–2.05, Q = 1.76–2.13.

Specimens examined: Indonesia, Riau, Indragiri Hulu, Bukit Aluran Bab, selectively logged primary rainforest, dicot (fallen log), 28 Jun. 2004, *Miettinen 8692** (BO, H); Kampar, Balung, logged-over natural forest, dicot, 24 Dec. 2006, *Miettinen 11306.4* (BO, H), Koto Lamo, dicot, 23 Oct. 2016, *Miettinen 20529** (BO, H).

Notes: The species is closely related and morphologically exceptionally similar to *F. ferrea*. It produces on average less robust basidiocarps than the latter species and possesses indistinctly stratified tubes (*vs.* clearly stratose in *F. ferrea*). To date, *F. elevata* has been found in Malaysia and Sumatra, Indonesia. See further notes under *F. ferrea* and *F. philippinensis*.

Fomitopsis eucalypti (Kalchbr.) Spirin, *comb. nov.* MycoBank MB 844898.

Basionym: Polyporus eucalypti Kalchbr. in von Thümen, Grevillea 4 (30): 73. 1875.

Typus: **Australia**, Queensland, Rockhampton, *Eucalyptus* sp., *Thozet* (comm. Müller, ex herb. M.C. Cooke) (holotype K!).

Description: Basidiocarps perennial, sessile or effused-reflexed, often gregarious, projecting up to 4 cm, resupinate part up to 5 cm diam. Upper surface pinkish ochraceous to brown, first felty, indistinctly zonate and radially striate, then almost smooth and fading to pale ochraceous. Pileal edge sharp, concolourous with hymenial surface, usually sterile, up to 1 mm wide. Pore surface pinkish to pinkish-greyish, flat or concave, often fading to almost white; pores roundish to angular, 5-7 per mm, with thin or moderately thickened, entire dissepiments. Section: context corky, pinkish brownish, up to 3 mm thick; tubes corky, one-layered or indistinctly stratified, concolourous with hymenial surface, up to 3 mm thick. Hyphal structure dimitic; hyphae clamped. Context dimitic; skeletal hyphae yellowish, densely interwoven, occasionally branched, $(3.8-)4.0-5.7(-6.0) \mu m$ diam (n = 20/1), lumen narrow to indistinct, side branches 2–3.5 µm diam, generative hyphae rare, hyaline, slightly thick-walled, 2.5-4 µm diam. Trama dimitic; skeletal hyphae dominating, yellowish or brownish to almost hyaline, densely interwoven, occasionally branched, (3.0-)3.2-4.7(-5.0) µm diam (n = 80/4), lumen narrow to indistinct, generative hyphae rare, thinto slightly thick-walled, 2-3.5 µm diam. Subhymenium indistinct. Cystidioles abundant to rather rare, tapering, $10-14 \times 3-4.5 \mu m$. Hyphidia occasionally present, usually simple, 1.8-2.2 µm diam. Basidia clavate, (11.4–)11.8–15.6(–15.8) × (4.9–)5.0–6.2(–6.8) μm (n = 40/4), occasionally pleural, in senescent hymenium partly glued together. Basidiospores with a distinct wall, narrowly ellipsoid to cylindrical-subfusiform, rarely slightly curved, (3.9-)4.0-6.8(-7.2) × $(2.0-)2.1-3.0(-3.1) \mu m (n = 90/3), L = 4.45-5.14, W = 2.50-2.59,$ Q = 1.73–2.02.

Specimens examined: Australia, Queensland, Cairns, Kuranda, angiosperm, 24 Aug. 2006, Schigel 5227 & 5234* (H); Lake Barrine, angiosperm, 19 Aug. 2006, Schigel 5196 & 5204 (H); Lamington Nat. Park, rotting logs, 11 Jul. 2001, Young & Fechner (O 18278, H); *ibid.*, 7 Nov. 2001, Young & Fechner (O 17406, H).

Notes: Polyporus eucalypti was described from Queensland, Australia (Thümen 1875). It was placed to the synonyms of *F. feei* by Lloyd (1915). Here *F. eucalypti* is reinstated as a member of the *F. feei* complex distributed in the northern part of Australia. It differs from *F. foedata* occurring in the same geographic area in having smaller and thinner, often effused-reflexed basidiocarps with a paler hymenophore. Pores of *F. eucalypti* are on average larger than in *F. foedata*. Microscopically, these species are hardly distinguishable, except skeletal hyphae which are less intensively coloured in *F. eucalypti* than in *F. foedata*.

Fomitopsis eucalypticola B.K. Cui & Shun Liu, Mycol. Progr. 18: 1323. 2019.

Typus: **Australia**, Victoria, Dandenong Ranges, *Eucalyptus* sp., 12 May 2018, *Cui* 16598* (**holotype** BJFC).

Description and phylogenetic data: Liu et al. (2019); see also Fig. 6.

Fomitopsis feei (Fr.) Kreisel, Monografias Ciencias Universidad de Habana 16: 83. 1971. Fig 20. *Basionym: Polyporus feei* Fr., Linnaea 5: 518. 1830.

Typus: **Brazil**, [no locality indicated], 1826, comm. Fee (**lectotype** PC 0705341) (selected by Soares *et al.* 2017: 79).

Synonyms:

Polyporus sordidus Lév., Ann. Sci. Nat., Bot. 3 (2): 192. 1844.

Typus: **Guadeloupe**, [no locality and collection date indicated], *L'Herminier* (holotype PC!).

Rhodofomitopsis roseomagna Nogueira-Melo, A.M.S. Soares & Gibertoni, Phytotaxa 331 (1): 78. 2017.

Typus: **Brazil**, Pernambuco, Jaqueira, Mata Caranha, hardwood, Sep. 2012, *Nogueira-Melo* 379* (**holotype** URM 86162).

Description: Basidiocarps perennial, sessile, often with a contracted base (fan-shaped), occasionally effused-reflexed, projecting up to 5 cm. Upper surface pinkish ochraceous to purplish brownish, later fading to pale ochraceous or light greyish, indistinctly zonate and radially furrowed. Pileal edge sharp, concolourous with hymenial surface, usually sterile, up to 2 mm wide. Pore surface deep pink to pinkish brownish, flat or concave; pores roundish to angular, 6-7(-8) per mm, with thin or moderately thickened, entire dissepiments. Section: context corky, deep pink or pinkish brownish, normally less than 2 mm thick; tubes corky, one-layered or indistinctly stratified, concolourous with hymenial surface, usually up to 2 mm thick. Hyphal structure dimitic; hyphae clamped. Context dimitic; skeletal hyphae brownish, densely interwoven, occasionally branched, $(3.1-)3.2-6.1(-6.3) \mu m$ diam (n = 20/1), lumen normally wide, side branches 2-3 µm diam, generative hyphae rather abundant, hyaline, slightly thick-walled, 4-6 µm diam. Trama dimitic; skeletal hyphae dominating, brownish to reddish-brown, densely interwoven, occasionally branched, (2.8-)2.9-4.1(-4.2) μ m diam (n = 40/2), lumen varying from rather wide to capillary, generative hyphae rare, thin- to slightly thick-walled, 2-2.5 µm diam. Subhymenium indistinct. Cystidioles not seen. Basidia shortclavate, (9.4-)10.1-12.8(-13.1) × (4.3-)4.5-6.1(-6.2) µm (n = 20/2), occasionally pleural, in senescent hymenium partly glued together. Basidiospores thin-walled, cylindrical-subfusiform, rarely narrowly ellipsoid, (3.9–)4.0–6.2(–6.7) × (2.0–)2.1–2.9(–3.0) µm (n = 120/4), L = 4.58–5.00, W = 2.33–2.43, Q = 1.98–2.14.

Specimens examined: Brazil, Bahia, Itaberaba, Serra do Orobó, hardwood, 19 Jan. 2006, Oinonen 60119006* (H); Paraná, Iguaçu, decayed

manufactured wood, 3 Jan. 1993, *de Meijer* 2404 (O 13835). **Venezuela**, Bolívar, Las Nieves, hardwood, 12 Jun. 1995, *Ryvarden* 37603* (O 10804); *ibid.*, *Ryvarden* 37901 (O 10802).

Notes: Fomitopsis feei was treated as a species widely distributed in tropical areas of the world. At least five other names were listed among its synonyms (Ryvarden 1991). Of them, *Polyporus sagraeanus*, *P. eucalypti*, *P. foedatus* and *Trametes marchionica* are reinstated here as separate species, while the identity of *P. rubidus* remains uncertain (see remarks to *F. carnea*). Therefore, the name *F. feei* is retained for the species distributed in the tropical zone of South America, from where it was originally described. Another American representative of the *F. feei* complex, *F. sagraeana*, is distributed in the northern and western parts of the Caribbean. It has on average smaller pores and larger basidiospores than *F. feei sensu stricto*. The distribution areas of the two species seem not to overlap.

Fomitopsis ferrea (Cooke) Spirin & Viner, *comb. nov.* MycoBank MB 844910. Fig 20.

Basionym: Fomes ferreus Cooke, Grevillea 14 (69): 21. 1885.

Typus: **Sri Lanka**, Sabaragamuwa, Ratnapura, Adam's Peak, dead wood, Sep. 1844, *Gardner* 104 & 106 (**syntypes** K, **isosyntype** PC!).

Description: Basidiocarps perennial, sessile, conchate, projecting up to 11 cm. Upper surface first greyish brown, indistinctly striate, then darkening to almost black, in older basidiocarps partly eroded and somewhat notched, with distinct annual zones, densely longitudinally cracking, growing margin wood-coloured to greyish. Pileal edge sharp or rather blunt, concolourous with hymenial surface, sterile, up to 1 mm wide. Pore surface wood-coloured or pale ochraceous, occasionally with brownish or blackish stains, concave; pores roundish, 6–8(–10) per mm, with thick, entire dissepiments. Section: crust black, tough, up to 0.5 mm thick, context woodyhard, ochraceous or brownish, up to 7 mm thick; tubes woody-hard, stratified, older layers brownish to brown, sometimes with blackishblue flecks, newer layers concolourous with pore surface, up to 25 mm thick, darker-coloured sterile tissue often present between annual layers. Hyphal structure dimitic; hyphae clamped. Context dimitic; skeletal hyphae dominating, brownish to brown, densely interwoven, occasionally branched, (2.8-)3.0-5.8(-6.3) µm diam (n = 40/2), lumen mostly narrow to capillary, side branches 1.5–2.5 µm diam, generative hyphae rare, hyaline, thin- or slightly thickwalled, 2-4 µm diam. Trama dimitic; skeletal hyphae dominating, yellowish or brownish, densely interwoven, occasionally branched, (2.3-)2.7-5.2(-5.8) µm diam (n = 40/2), lumen mostly capillary to indistinct, side branches 1.5–3 µm diam, generative hyphae rare, thin- or slightly thick-walled, 2–3 µm diam. Subhymenium indistinct. No differentiated skeletocystidia seen. Cystidioles tapering, 8–12.5 × 3-3.5 µm, sometimes with a short side outgrowth. Hyphidia occasionally present, simple or bifurcate, 1-1.5 µm diam. Basidia rare, clavate, 9.2-10.5 × 3.2-4.0 µm (n = 3/1). Basidiospores thinwalled or with a distinct wall, cylindrical to broadly cylindrical or narrowly ellipsoid, (2.8-)2.9-4.1(-4.2) × (1.8-)1.9-2.3 µm (n = 22/1), L = 3.31, W = 2.05, Q = 1.61.

Specimen examined: India, Kerala, Idukki, Munnar, Anakkulam, fallen log, 26 Jan. 2019, *Dunayev** (TUF).

Notes: Fomitopsis ferrea is a close relative of *F. dochmia* distributed in the same geographic region (Sri Lanka and the southern part of India). It can be separated from *F. dochmia* due to its somewhat larger pores, as well as lighter-coloured context and tubes. See further remarks under *F. dochmia*.

Fomitopsis fissa Vlasák & Spirin, *sp. nov.* MycoBank MB 844911. Figs 16, 20.

Typus: **USA**, California, Santa Cruz, Henry Cowell Redwoods St. Park, 37.05377° -122.09830°, dry hardwood branch, 8 Jul. 2004, *Vlasák Jr.* 0407/13-J* (**holotype** H7200197).

Etymology: Fissus (Lat., adj.) - cracked.

Description: Basidiocarps annual, effused, up to 5 cm in widest dimension. Margin adnate, compact, white, up to 2 mm wide. Hymenial surface even, often cracking, white to pale creamcoloured; pores angular, 4-5 per mm, dissepiments uneven. Section: subiculum compact, white, hardly visible, 0.05-0.1 mm thick; tubes soft leathery, white or pale cream-coloured, 0.1-0.5 mm thick. Hyphal structure monomitic; hyphae clamped. Subicular hyphae hyaline, interwoven to subparallel, very thick-walled, $(1.8-)2.2-4.2(-4.3) \mu m$ (n = 20/1). Tramal hyphae hyaline, thin- to distinctly thick-walled, partly glued together, (2.2-)2.3-3.5(-3.8) μ m (n = 20/1). Subhymenium not differentiated. Cystidioles absent. Basidia clavate, (14.2–)17.3–24.3(–24.7) × (6.2–)6.4–7.2(–8.7) μ m (n = 20/1). Basidiospores with a distinct wall, cylindrical, occasionally slightly curved, longest spores subfusiform, (6.3-)6.4- $8.0(-8.7) \times (2.6-)2.7-3.1(-3.2) \ \mu m \ (n = 30/1), \ L = 7.24, \ W = 2.84,$ Q = 2.56.

Notes: Fomitopsis fissa is phylogenetically closely related to the members of the *F. ramentacea* complex. Macroscopically, it is strikingly different from them, possessing soft, irregularly cracking basidiocarps with non-gelatinized hymenophore and rather small pores. However, such anatomical traits as monomitic structure with variably thick-walled hyphae, rather long basidia and long cylindrical basidiospores, as well as the lack of cystidioles point to *F. ramentacea* and its relatives. *Fomitopsis fissa* is so far recorded only in the type locality in California, USA.

Fomitopsis flabellata A.M.S. Soares & Gibertoni, Fungal Diversity 83: 208. 2017.

Typus: **Brazil**, Amapá, Porto Grande, hardwood, Oct. 2014, *Soares* 1794* (holotype URM 89405).

Description and phylogenetic data: Tibpromma et al. (2017).

Fomitopsis flavimontis (Vlasák & Spirin) Vlasák & Spirin, *comb. nov.* MycoBank MB 844912.

Basionym: Antrodia flavimontis Vlasák & Spirin, Mycologia 109: 223. 2017.

Typus: **USA**, Wyoming, Park Co., Yellowstone Nat. Park, *Pinus contorta*, Jul. 2013, *J. Vlasák Jr.* 1307/17* (**holotype** H!).

Description and phylogenetic data: Spirin et al. (2017, as A. flavimontis).

Fomitopsis foedata (Berk.) Spirin & Miettinen, *comb. nov.* MycoBank MB 844913. Figs 20, 21.

Basionym: Polyporus foedatus Berk., J. Linn. Soc., Bot. 16 (1): 41. 1877.



Typus: **Australia**, Queensland, Cape York, Somerset, 1–8 Sep. 1874, '*HMS Challendger Expedition*' (**lectotype** K(M) 264881!) (selected by Cunningham 1965: 171).

Synonym: Rhodofomitopsis pseudofeei B.K. Cui & Shun Liu, Fungal Diversity 104: 138. 2020.

Typus: **Australia**, Queensland, Cairns, Mt. Whitfield Conservation Park, angiosperm, 7 May 2018, *Cui* 16794* (**holotype** BJFC).

Description: Basidiocarps perennial, sessile, often with a contracted base, more rarely effused-reflexed, projecting up to 7 cm, occasionally fusing together. Upper surface first pinkish brown to light brown, felty, then dark brown almost black, smooth and indistinctly zonate. Pileal edge sharp to rather blunt, concolourous with hymenial surface, sterile, up to 2 mm wide. Pore surface pink to pinkish grey, usually concave; pores roundish to angular, 6-8 per mm, with thin or moderately thickened, entire or serrate dissepiments. Section: context leathery, pinkish brownish, up to 10 mm thick; tubes soft-corky, one-layered or indistinctly stratified, concolourous with hymenial surface, up to 2 mm thick. Hyphal structure dimitic; hyphae clamped. Context dimitic; skeletal hyphae yellowish to brownish, rather loosely interwoven, occasionally branched, (3.0–)3.3–5.8(–6.4) µm diam (n = 40/2), lumen varying from wide to narrow, side branches 2-3 µm diam, generative hyphae rare, hyaline, thin- to slightly thick-walled, 2-3 µm diam. Trama dimitic; skeletal hyphae dominating, yellowish to reddishbrown, rather densely interwoven, occasionally branched, (2.8-)2.9-4.0(-4.1) μ m diam (n = 60/3), lumen capillary to indistinct, generative hyphae rare, thin-walled, 2-3.5 µm diam. Subhymenium indistinct. Cystidioles tapering, 8.5-14.5 × 3.5-5.0 µm. Hyphidia occasionally present, as a rule simple, 2-2.5 µm diam. Basidia clavate, (10.3-)10.8-15.4(-17.8) × (5.0-)5.1-6.2(-6.3) µm (n = 30/2). Basidiospores with a distinct wall, narrowly ellipsoid to cylindrical-subfusiform, (3.8–)4.0–5.9(–6.2) × (2.0–)2.1–3.0(–3.1) μm (n = 50/2), L = 4.85–5.24, W = 2.50–2.73, Q = 1.93–1.96.

Specimens examined: Australia, New South Wales: Buladelah, Duck Creek Road, rotting log, 22 Apr. 1990, *Streimann* 43973 (H); Kurrajong, dead wood, 1 Jun. 1985, *Coveny* 108 (O 17744, H); Northern Territory, Darwin, Bicentennial Park, angiosperm, 6 Jun. 1999, *Uotila* 42928* (H); Queensland, Cairns, Kuranda, angiosperm, 24 Aug. 2006, *Schigel* 5219 (H). **Indonesia**, Papua, Merauke, Wasur NP, dry natural forest, *Acacia* (?), 21 Jan. 2007, *Miettinen* 11466* (MAN, H).

Notes: The thin, flexible basidiocarps of *F. foedata* are reminiscent more of *F. cajanderi* than of other species of the *F. feei* complex where it belongs to (Fig. 11). The species is distributed in New Guinea and the northern part of Australia. Its differences from other similar-looking species from Australia, *F. eucalypti* and *F. lilacinogilva*, are discussed under those species.

Fomitopsis fragilis B.K. Cui & M.L. Han, Mycol. Progr. 13: 909. 2014.

Typus: **China**, Hainan, Ledong, Jianfengling, hardwood, 7 Nov. 2012, *Cui* 10919* (**holotype** BJFC).

Description and phylogenetic information: Han et al. (2014).

Fomitopsis gilvidula (Bres.) Spirin & Miettinen, *comb. nov.* MycoBank MB 844914. Figs 21, 22. *Basinnym: Daedalea gilvidula* Bres. Hedwigia 51: 320, 1912

Basionym: Daedalea gilvidula Bres., Hedwigia 51: 320. 1912.

Typus: **Philippines**, Sibuyan, Guiting-Guiting, fallen logs, Apr. 1910, *Elmer* 12327, 12391 (syntypes S F14744!, NY00704678!, NY00704685!).

Synonyms:

Trametes tuberculata Bres., Ann. Mycol. 10: 505. 1912.

Typus: Indonesia, Java, Tjibodas, fallen log, [no collection date], *Höhnel* (holotype S F14738!).

Trametes lusor Corner, Beih. Nova Hedwigia 97: 114. 1989.

Typus: **Malaysia**, Johor, Gunong Panti, 26 Sep. 1966, *Corner* (**holotype** E00430842).

Description: Basidiocarps perennial, sessile, often with a contracted base (fan-shaped) or effused-reflexed, projecting up to 5 cm. Upper surface first pale ochraceous to fawn, smooth or finely pubescent, indistinctly zonate, later greyish to brownish, smooth, more or less clearly and densely zonate, occasionally with a silky lustre. Pileal edge sharp, concolourous with pileal surface, sterile, up to 1 mm wide. Pore surface first cream-coloured to pale ochraceous or pinkish, then discolouring to greyish or almost white, flat or concave; pores angular or sinuous, (1–)1.5–3 per mm, sometimes strongly elongated (almost lamellate) close to the margin, with rather thick, entire or uneven dissepiments. Section: context hard leathery, ochraceous to brownish, up to 2 mm thick; tubes hard leathery, one-layered, concolourous with hymenial surface, up to 2 mm thick. Hyphal structure dimitic; hyphae clamped. Context dimitic; skeletal hyphae brownish, interwoven to subparallel, occasionally branched, (3.2-)3.8-5.4(-5.8) µm diam (n = 60/3), lumen varying from rather wide to capillary, side branches 2-3.5 µm diam, generative hyphae rare, hyaline, slightly thick-walled, 2-3 µm diam. Trama dimitic; skeletal hyphae dominating, brownish to rusty brown, densely interwoven, occasionally branched, sometimes twisted and irregularly inflated, $(3.0-)3.2-4.8(-5.3) \mu m$ diam (n = 80/4), lumen mostly narrow to capillary, generative hyphae rather rare, thin- to slightly thick-walled, 2-3 µm diam. Subhymenium sometimes distinct, up to 20 µm thick. Skeletocystidia present as swollen (up to 5.5 µm diam), acute or blunt apices of tramal skeletal hyphae, slightly projecting above hymenium. Cystidioles abundant, tapering, often with a long hyphoid neck, 11-20.5 × 3-5 µm. Basidia clavate to long clavate, (11.8-)12.3-20.8(-22.3) × $(4.1-)4.2-5.7(-5.8) \mu m$ (n = 30/3), in senescent hymenium slightly thick-walled and often glued together. Basidiospores thin-walled or with a distinct wall, cylindrical-subfusiform or narrowly ellipsoid, (3.8–)3.9–5.3(–5.8) × (2.0–)2.1–2.9(–3.0) µm (n = 110/4), L = 4.40– 4.91, W = 2.26–2.38, Q = 1.87–2.11.

Specimens examined: Indonesia, Riau, Kampar, Balung, logged over natural forest, dicot, 25 Dec. 2006, *Miettinen* 11290.1 (BO, H); Kampar, Koto Lamo, dicot, 23 Oct. 2016, *Miettinen* 20535* (BO, H); Sumatera Barat, Padang, Limau Manis, primary forest, *Fagaceae*, 10 Jul. 2008, *Miettinen* 12905 (ANDA, H); dicot, 11 Jul. 2008, *Miettinen* 12957.1 (ANDA, H); dicot, 16 Jul. 2008, *Miettinen* 13128.1 (ANDA, H). **Malaysia**, Penang, Pulau Pinang, Pantai Aceh Nat. Park, fallen tree (*Shorea?*), 1 Dec. 2006, *Miettinen* 11154.3 (BORH, H).

Notes: Fomitopsis gilvidula seems to be widely distributed in the tropical zone of Southeast Asia. Morphologically, it is most close to *F. aculeata*, with which it occasionally occurs side by side. Fomitopsis gilvidula differs from *F. aculeata* in having lighter-coloured basidiocarps with larger pores and a smooth or felty surface. Under the microscope, it can be differentiated from the latter species



Fig 22. Basidiospores of Fomitopsis spp. F. gilvidula (Miettinen 12905); F. incana (LE313649); F. lapidosa (holotype); F. leioderma (Vlasák 1908/82); F. lignea (lectotype of Fomes subferreus); F. lignicolor (holotype); F. luzonensis (Miettinen 14311). Scale bar = 5 µm.

in having a well-developed subhymenium and longer hymenial cells. Another similar species from the same geographic area is *F. incana* (see below). Despite their certain morphological similarity, *F. gilvidula*, *F. aculeata* and *F. incana* are not closely related (Suppl. Fig. S2). Two GenBank sequences of an unidentified polypore from East Kalimantan (AJ542523, 542524) belong to *F. gilvidula*.

Fomitopsis glabricystidia (Ipulet & Ryvarden) Miettinen & Ryvarden, *comb. nov.* MycoBank MB 844915.

Basionym: Junghuhnia glabricystidia Ipulet & Ryvarden, Syn. Fung. 20: 93. 2005.

Typus: **Uganda**, Kabarole, Kibali Nat. Park, Ngogo, rotten hardwood log, 6 Jun. 2002, *Ipulet* 378* (**holotype** O!).

Description: Ipulet & Ryvarden (2005, as J. glabrocystidia).

Notes: The species was originally described in *Junghuhnia* due to the presence of abundant thick-walled skeletocystidia (Ipulet & Ryvarden 2005). They are, however, not encrusted as in typical representatives of the latter genus, and the hyphae are broad and show no sign of a cyanophilous reaction. DNA data undoubtedly place this species in *Fomitopsis* as redefined here (Figs 1, 3). See further remarks under *F. tunicata*.

Fomitopsis globispora (Ryvarden & Aime) Spirin, *comb. nov.* MycoBank MB 844916.

Basionym: Trametes globispora Ryvarden & Aime, Syn. Fung. 26: 28. 2009 (as '*globospora*').

Typus: **Belize**, Cayo, Maya Mts., Doyle's Delight, dead hardwood log, 23 Aug. 2007, *Aime* 3413* (**holotype** LSUM).

Description: Ryvarden et al. (2009, as T. globospora).

Note: Using sequence data, Decock *et al.* (2022) confirmed the close relationship of this species with *F. spraguei* (see also Fig. 15).

Fomitopsis hartmannii (Cooke) M.D. Barrett & Spirin, *comb. nov.* MycoBank MB 844917.

Basionym: Polyporus hartmannii Cooke, Grevillea 12: 14. 1883.

Typus: **Australia**, Queensland, Toorvoomba [Toowoomba], [no collection date], *Hartmann* (**lectotype** K(M) 252596!) (selected by Ryvarden 1988b: 50).

Synonyms:

Piptoporus ulmi Bondartsev & Ljub., Bot. Mat. Otd. Spor. Rast. 14: 198. 1961.

Typus: **Russia**, Primorie, Ussuriisk Dist., Ussuri Nat. Res., *Ulmus* sp., 11 Aug. 1945, *Vassiljeva* (**holotype** LE 22548!).

Polyporus sublignosus J.D. Zhao & X.Q. Zhang, Acta Mycol. Sin. 10: 269. 1991.

Typus: **China**, Hainan, Bawangling, 'on the ground', 18 Apr. 1977, *Han* 803 (**holotype** HMAS 54101).

Tyromyces squamosellus Núñez & Ryvarden, Fungal Diversity 3: 117. 1999.



Typus: Japan, Ibaraki, Ogawa, dead hardwood, 11 Aug. 1994, *Núñez* 554* (holotype O!).

Buglossoporus eucalypticola M.L. Han, B.K. Cui & Y.C. Dai, Fungal Diversity 80: 351. 2016.

Typus: **China**, Hainan, Danzhou, *Eucalyptus* sp., 15 Jun. 2014, *Dai* 13660* (**holotype** BJFC 17399).

Description: Núñez & Ryvarden (1995, as Laccocephalum hartmannii).

Specimen examined: Japan, Shikoku, Ehime Pref., Takanawa Mt., 7 Sep. 1994, Okino (coll. number Núñez 679*) (O 11264, H).

Notes: We studied the type material of *P. hartmannii* and could not find substantial morphological differences between it and specimens collected in East Asia. Nevertheless, the identity of *P. hartmannii* sensu typi should be re-established based on sequenced material from the eastern part of Australia.

Fomitopsis hyalina (Spirin, Miettinen & Kotir.) Spirin & Miettinen, *comb. nov.* MycoBank MB 844918.

Basionym: Antrodia hyalina Spirin, Miettinen & Kotir., Mycol. Progr. 12: 56. 2013.

Typus: **Russia**, Nizhny Novgorod Reg., Lukoyanov Dist., Razino, *Populus tremula*, 5 Aug. 2008, *Spirin* 2772* (**holotype** H!).

Description and phylogenetic data: Spirin et al. (2013b, as A. hyalina); see also Figs 1 and 3.

Fomitopsis hypoxantha (Bres.) Spirin & Miettinen, *comb. nov.* MycoBank MB 848358.

Basionym: Polyporus hypoxanthus Bres., Ann. Mycol. 10: 494. 1912.

Typus: Indonesia, Java, Tjibodas, 1907, Höhnel (isotype BPI US021111!).

Description: Basidiocarps annual or short-living perennial, sessile, ungulate, broadly attached, projecting up to 6 cm. Upper surface first cream-coloured to pale ochraceous, azonate, glabrous, later covered by brown to blackish brown crust, smooth, not cracking. Pileal edge normally blunt, concolourous with pore surface, fertile. Pore surface first cream- or pale wood-coloured, then brownish, flat or slightly concave; pores angular, 4-6 per mm, with thin, entire or serrate dissepiments. Section: crust (present in mature basidiocarps) tough, dark brown, matt, up to 1 mm thick, context fibrous to soft corky, cream-coloured, up to 5 mm thick; tubes rather soft, fragile, one-layered or indistinctly stratified, concolourous with hymenial surface, up to 1 cm thick. Hyphal structure dimitic; hyphae clamped. Context dimitic; skeletal hyphae dominating, hyaline or yellowish, interwoven, occasionally branched, (3.3-3.7-5.2(-5.3) µm diam (n = 20/1), lumen mostly capillary to indistinct, generative hyphae rare, hyaline, thin- to slightly thickwalled, 2-4 µm diam. Trama dimitic; skeletal hyphae hyaline to brownish, interwoven, easily crumbling, occasionally branched, (2.7-)2.8-4.2(-4.3) µm diam (n = 40/2), lumen rather wide to capillary or indistinct, side branches 2-3 µm diam, generative hyphae rather abundant, hyaline, thin- to slightly thick-walled, 2-3.5 µm diam, in juvenile tubes producing subhymenial layer up to 20 µm thick. Resinous droplets abundant among tramal and subhymenial tissues of senescent basidiocarps. Cystidioles

rather abundant, tapering, $14-20 \times 3.5-7 \ \mu$ m. *Basidia* clavate, $(13.0-)14.0-18.9(-21.0) \times (5.4-)5.8-8.3(-8.6) \ \mu$ m (n = 20/2), senescent basidia slightly thick-walled. *Basidiospores* thin-walled or with a distinct wall, broadly ellipsoid to ellipsoid, $(4.8-)4.9-6.3(-6.7) \times (3.8-)3.9-5.3(-6.0) \ \mu$ m (n = 80/3), L = 5.27-5.63, W = 4.47-4.56, Q = 1.16-1.27.

Specimens examined: China, Hubei, Lichuan, Xiaohe, *Castanea* sp. (living tree), 27 Sep. 2004, *Dai* 5983* (H). Indonesia, Java, Tjibodas Bot. Gdn, 26 Jan. 1995, *Núñez* 707 (O 10876, H).

Notes: Fomitopsis hypoxantha is reinstated here as the South-East Asian relative of *F. spraguei* (Fig. 15). We failed to find any certain morphological differences between the two species, due to a huge morphological variability of *F. spraguei*. At the moment, *F. hypoxantha* can be separated from *F. spraguei* based on geographic distribution (South-East Asia *vs.* temperate Europe and North America) and genetic distance.

Fomitopsis incana (Lév.) Spirin & V. Malysheva, *comb. nov.* MycoBank MB 844920. Fig 22.

Basionym: Trametes incana Lév., Ann. Sci. Nat., Bot. 3 (2): 196. 1844.

Typus: **Philippines**, Luzon, Manila, 'ad truncos', Nov. 1836, *Gaudichaud* (holotype PC!, isotype BPI US0247025!).

Synonym: Daedalea allantoidea M.L. Han, B.K. Cui & Y.C. Dai, Fungal Diversity 80: 357. 2016.

Typus: **China**, Yunnan, Jinghong, hardwood, 22 Oct. 2013, *Dai* 13612A* (**holotype** BJFC 15075).

Description: Basidiocarps seasonal, effused-reflexed, projecting up to 2 cm. Upper surface first cream-coloured, smooth, even or indistinctly zonate, later pale ochraceous to brownish. Pileal edge sharp, concolourous with hymenial surface, sterile, up to 0.5 mm wide. Pore surface first cream-coloured, then pale ochraceous or greyish, flat or concave; pores roundish to angular, some strongly elongated, (2-)3-4 per mm, with thin, entire or serrate dissepiments. Section: context leathery, almost white to creamcoloured or pale ochraceous, up to 1.5 mm thick; tubes leathery, one-layered, concolourous with hymenial surface, up to 3 mm thick. Hyphal structure dimitic; hyphae clamped. Context dimitic; skeletal hyphae yellowish to brownish, densely interwoven, richly branched, (3.0-)3.1-4.1(-4.3) µm diam (n = 20/1), lumen mostly capillary to indistinct, side branches 2-3 µm diam, generative hyphae rare, hyaline, slightly thick-walled, 3-4 µm diam. Trama dimitic; skeletal hyphae dominating, hyaline to yellowish or brownish, densely interwoven, occasionally branched, sometimes twisted, (3.0-)3.1-5.0(-5.2) μ m diam (n = 40/2), lumen varying from rather wide to indistinct, generative hyphae rather rare, thin- to slightly thickwalled, 2-3 µm diam. Subhymenium indistinct. Skeletocystidia present as blunt or sharp apices of tramal skeletal hyphae, 3-4 µm diam, slightly projecting above hymenium. Cystidioles abundant, tapering, 9-13 × 3-4 µm. Hyphidia present, mostly simple, scattered among basidia, 1.5-2 µm diam at the apex. Basidia clavate, $(10.8-)10.9-15.0(-22.0) \times (4.1-)4.2-5.1(-5.2) \mu m (n = 20/1), in$ senescent hymenium slightly thick-walled. Basidiospores thinwalled or with a distinct wall, cylindrical-subfusiform, sometimes slightly curved, (3.8–)3.9–5.2(–5.7) × (2.0–)2.1–2.8(–2.9) µm (n = 30/1), L = 5.23, W = 2.50, Q = 2.12.

Notes: The identity of T. incana has been interpreted in the literature in two different ways. Hjortstam & Ryvarden (1984) believed it represents the same species as D. dickinsii (= F. dickinsii above) widely distributed in warm-temperate forests of East Asia. On the contrary, Hattori (2005) accepted T. incana as a separate species of Daedalea and stated it is identical with Trametes pseudodochmia (= F. moritziana below). We restudied the type of T. incana and cannot accept either of these opinions. The remaining material in PC and BPI comprises tiny pieces, evidently of a resupinate part of a basidiocarp, glued on the paper and subsequently soaked in mercury. Nevertheless, it is evident these remains belonged to a light-coloured, leathery polypore 2-3 mm thick, with angular pores 3-4 per mm. The basidiocarp consistency and thickness certainly preclude F. dickinsii and F. moritziana, since both are robust and much sturdier species. Although extremely vague, the protologue (Léveillé 1844) describes the whole polypore as white (but the species epithet refers to light grey), and this description does not accord with F. moritziana which has a reddish-brown to almost black cap surface. In turn, F. dickinsii is a temperate species not known in Southeast Asia (Hattori 2005). Microscopically, the type of T. incana is characterized by dimitic hyphal structure with hyaline or brownish, occasionally branched skeletal hyphae (3.2-)3.3-5.0(-5.2) μ m (n = 20/1) diam. Hymenial cells are totally collapsed but a few turgid spores were observed in phase contrast illumination, $5.1-5.2 \times 2.3-2.8 \ \mu m$ (n = 3/1). After comparing the type of T. incana with a newly collected and sequenced specimen from India, we concluded they are identical and conspecific with D. allantoidea recently described from China. Therefore, a new combination, F. incana, is proposed here.

Fomitopsis incana is morphologically similar to *F. gilvidula*, distributed in the same geographic region. The latter species differs from *F. incana* in having slightly larger, in older basidiocarps clearly elongated pores, warmer-coloured basidiocarps and darker, brownish to rusty-brown skeletal hyphae. Another macroscopically similar species, *F. malicola* (= *Antrodia malicola*, see below) has larger basidiospores than *F. incana*, (6.1–)6.2–10.2(–10.6) × (2.6–) 2.7–4.0(–4.1) µm (Spirin *et al.* 2016).

Fomitopsis infirma (Renvall & Niemelä) Miettinen & Niemelä, *comb. nov.* MycoBank MB 844921.

Basionym: Antrodia infirma Renvall & Niemelä, Karstenia 32: 35. 1992.

Typus: **Finland**, Pohjois-Karjala, Lieksa, Patvinsuo, *Pinus sylvestris*, 14 Sep. 1989, *Penttilä* 1235 (**holotype** H!).

Description: Renvall & Niemelä (1992, as A. infirma).

Note: For phylogenetic placement, see Spirin et al. (2013b).

Fomitopsis juniperina (Murrill) Spirin & Vlasák, *comb. nov.* MycoBank MB 844922.

Basionym: Agaricus juniperinus Murrill, Bull. Torrey Bot. Club 32 (2): 85. 1905.

Typus: **USA**, Kansas, Rooks Co., Rockport, *Juniperus* sp., 1894, *Bartholomew* (**holotype** NY 00774779!).

Synonym: Antrodia juniperina (Murrill) Niemelä & Ryvarden, Trans. Br. Mycol. Soc. 65: 427. 1975. Description: Niemelä & Ryvarden (1975, as Antrodia juniperina).

Specimens examined: **Spain**, Madrid, Tamajon, *Juniperus turifera*, 1 Mar. 2011, *E. Larsson* 15-11* (GB, H). **USA**, Arizona, Cochise Co., Coronado Nat. Forest, *Juniperus monosperma*, 23 Aug. 1958, *Lowe* 9090 (H); Coconino Co., Sedona, *Juniperus* sp., Nov. 2017, *Vlasák Jr*. 1711/13-J* (JV, H); Santa Cruz Co., Madera Canyon, *Juniperus deppeana*, 1 Sep. 2012, *Vlasák* 1209/14* (JV); Arkansas, Searcy Co., Harriet, Shepherd of the Ozarks, *Juniperus* sp., 25 Oct. 2013, *Cho* (H7068514*); Georgia, Stephens Co., Toccoa, *Juniperus virginiana*, 18 Aug. 1950, *Lowe* 3969 (H ex SYRF); Pennsylvania, Montgomery Co., Landsdale, *J. virginiana*, Oct. 2003, *Vlasák Jr*. 0310/1-J* (JV, H); South Carolina, Pickens Co., Clemson, *Juniperus* sp., 5 Sep. 1950, *Lowe* 4480 (H ex SYRF); Virginia, Prince William Co., Woodbridge, 21 Sep. 2007, *Vlasák* 0709/154* (JV, H); Shenandoah Co., Edinburg, *J. virginiana*, 15 Sep. 1939, *Hepting* & Roth 68635 (H ex SYRF).

Note: See remarks to F. algumicola and Antrodia uzbekistanica.

Fomitopsis kenyensis Spirin & Ryvarden, *nom. nov.* MycoBank MB 848359.

Basionym: Daedalea africana Ryvarden & I. Johans., A preliminary polypore flora of East Africa: 304. 1980.

Typus: **Kenya**, Kwale, Shimba Hills, Makadara, 14 Feb. 1973, *Ryvarden* 16485 (**holotype** O!).

Etymology: Kenyensis (Lat., adj.) – in reference to Kenya where the holotype of this species was collected.

Notes: Han *et al.* (2016) published sequences of a paratype of *D. africana* (O 15372) and detected that it belongs to *Daedalea* clade (see also Fig. 5). Due to the existence of *F. africana* (see above), a new name for *D. africana* is necessary to place it in *Fomitopsis*.

Fomitopsis kuzyana (Pilát ex Pilát) Spirin & Vlasák, *comb. nov.* MycoBank MB 844923.

Basionym: Trametes kuzyana Pilát ex Pilát, Acta Mus. Nat. Pragae 9 (B), 2 (1): 104. 1953.

Typus: **Ukraine**, Zakarpats'ka Reg., Trebušany (Dilove), Mt. Menchul, *Fagus sylvatica*, Aug. 1934, *Pilát* (**holotype** PRM 108267!).

Synonym: Antrodia submalicola A. David & Dequatre, Cryptog. Mycol. 5 (4): 299 (1985).

Typus: **France**, Gard, La Valbonne, Combe du Ruisseau de l'Arnave, *Populus* sp., 23 Aug. 1983, *Callac* (**holotype** LY AD-4497!).

Description and phylogenetic data: Spirin et al. (2016, as Antrodia kuzyana); see also Figs 1 and 3.

Fomitopsis labyrinthica Bernicchia & Ryvarden, Mycol. Helv. 8 (2): 6. 1996.

Typus: **Italy**, Forlì Cesena: Casentinesi, Sasso Fratino, *Abies alba*, 18 Oct. 1995, *Bernicchia* 6497 (**holotype** HUBO!).

Synonym: Antrodia kmetii Vlasák, Cryptog. Mycol. 34 (3): 206. 2013.

Typus: **Slovakia**, Banská Bystrica: Badín, *Abies alba*, 12 Oct. 1993, *Vlasák* 9310/14* (PRM 861180!, **holotype**).



SPIRIN ET AL.

Description and phylogenetic data: Vlasák et al. (2013, as A. kmetii).

Specimens examined: **Romania**, Braşov, Şinca, *A. alba*, 14 Sep. 2021, Spirin 14932 & 14960 (H). **Slovenia**, Kočevje, Borovec pri Kočevski Reki, Krokar Forest Reserve, *A. alba*, 18 Aug. 2021, *Spirin* 14700 & *Grebenc* (H, LJF).

Fomitopsis lapidosa Miettinen & Spirin, *sp. nov.* MycoBank MB 844924. Figs 21, 22.

Typus: **Indonesia**, Papua Barat, Manokwari, Gunung Meja, -0,84929° 134,07458° (\pm 50 m), secondary forest with abundant *Pometia pinnata*, by the forest road, on a man-made stump (dicot, decay stage 2, 45 cm in diameter), 8 Nov. 2018, *Miettinen* 21981* (**holotype** MAN, **isotypes** H7200141, BO).

Etymology: Lapidosus (Lat., adj.) - stone-hard.

Description: Basidiocarps perennial, sessile, conchate, solitary or partly fusing together, projecting up to 5 cm. Upper surface blackish brown to black, with several distinct annual zones, accidentally longitudinally cracking, growing margin much paler, woodcoloured to pale ochraceous, indistinctly zonate and occasionally radially striate. Pileal edge sharp or rather blunt, concolourous with hymenial surface, first sterile, up to 3 mm wide, then fertile. Pore surface cream-coloured or beige to pale ochraceous, slightly concave; pores roundish, 8-10 per mm, with rather thick, entire dissepiments. Section: crust black, tough, up to 1 mm thick, context corky, cream-coloured to pale ochraceous, up to 3 mm thick; tubes corky, indistinctly stratified, concolourous with hymenial surface, up to 2 mm thick. Hyphal structure dimitic; hyphae clamped. Context dimitic; skeletal hyphae dominating, hyaline to yellowish, densely interwoven, rarely branched, (3.2-)3.3-5.0(-5.1) µm diam (n = 20/1), lumen varying from wide to capillary, generative hyphae hyaline, thin- to slightly thick-walled, 2-3 µm diam. Trama dimitic; skeletal hyphae dominating, hyaline to yellowish, densely interwoven, rarely branched, (2.0-)2.3-3.3(-3.7) µm diam (n = 20/1), lumen mostly capillary to indistinct, generative hyphae rare, thin- to slightly thick-walled, 1.5-2 µm diam. Subhymenium indistinct. Cystidioles rare, tapering, 10-14 × 2.8-3.2 µm. Basidia clavate, $(10.1-)10.2-15.0(-18.7) \times (3.8-)3.9-4.7(-4.8) \mu m$ (n = 20/1), in senescent hymenium partly glued together. Basidiospores thin-walled or with a distinct wall, cylindrical, sometimes slightly curved, rarely narrowly ellipsoid, (2.9-)3.0-3.8(-4.1) × (1.8-)1.9-2.1 µm (n = 30/1), L = 3.22, W = 1.98, Q = 1.63.

Specimen examined: Indonesia, Papua, Jayapura, Waena, fallen log, 2006, anonymous collector (H).

Notes: Fomitopsis lapidosa is introduced here based on two collections from New Guinea, Indonesia. Morphologically, it is most similar to *F. ferrea* and *F. elevata* and differs from them in having more lightweight (although exceptionally tough) basidiocarps and considerably smaller pores. No reliable microscopic traits were detected to separate these three species. Phylogenetically, *F. lapidosa* is the closest relative of the Caribbean *F. lignea* and thus it is very distant from the *F. dochmia* group.

Fomitopsis leioderma (Mont.) Spirin & Vlasak, *comb. nov.* MycoBank MB 844925. Figs 21, 22.

Basionym: Polyporus leiodermus Mont., Ann. Sci. Nat., Bot. 4 (1): 134. 1854.

Typus: **French Guiana**, [no locality indicated], 'ad cortices', [no collection date], *Leprieur* 855 (**syntype** PC!).

Description: Basidiocarps seasonal, sessile, often with a contracted base (fan-shaped), projecting up to 2 cm. Upper surface first cream-coloured, smooth, even or indistinctly zonate, later pale ochraceous to brownish, with a silky lustre. Pileal edge sharp, concolourous with hymenial surface, sterile, up to 1 mm wide. Pore surface first cream-coloured, then pale ochraceous, flat or concave; pores angular or sinuous, 3-4 per mm, with thin, entire or serrate dissepiments. Section: context leathery, cream-coloured to pale ochraceous, up to 1 mm thick; tubes leathery, one-layered, concolourous with hymenial surface, up to 1 mm thick. Hyphal structure dimitic; hyphae clamped. Context dimitic; skeletal hyphae brownish, interwoven, occasionally branched, (3.8–)3.9–5.0(–5.2) μ m diam (n = 20/1), lumen varying from rather wide to capillary, side branches 2-3 µm diam, generative hyphae rare, hyaline, slightly thick-walled, 2-3 µm diam. Trama dimitic; skeletal hyphae dominating, brownish, densely interwoven, occasionally branched, (2.9-)3.0-4.3(-4.8) µm diam (n = 40/2), lumen mostly narrow to indistinct, generative hyphae rather rare, thin- to slightly thickwalled, 2-3 µm diam. Subhymenium indistinct. Skeletocystidia present as swollen (up to 5.5 µm diam) apices of tramal skeletal hyphae, slightly projecting above hymenium. Cystidioles abundant, tapering, 11.5-17 × 3-4.5 µm. Basidia clavate, (10.0-)10.2-16.2(-17.9) × (4.3–)4.4–5.8(–6.1) µm (n = 20/2), occasionally pleural, in senescent hymenium slightly thick-walled. Basidiospores thinwalled or with a distinct wall, cylindrical, sometimes slightly curved, longest spores subfusiform, (4.1-)4.2-6.2(-6.8) × (2.0-)2.1-2.9(-3.0) µm (n = 30/1), L = 5.23, W = 2.50, Q = 2.12.

Specimen examined: **French Guiana**, Roura, Camp Cayman, dead log, 31 Aug. 2019, *Vlasák* 1908/82* (JV, H).

Notes: Montagne (1854) described *P. leiodermus* based on two collections by Leprieur from French Guiana. We were able to locate and study one of them. This specimen is morphologically identical to one recent sequenced collection from the same area, and it certainly represents a good species from the *Daedalea* clade (Fig. 5). Ryvarden (1982) included *P. leiodermus* in the synonymy of *Trametes modesta* (Kuntze ex Fr.) Ryvarden (see below as *F. modesta*). The latter species differs from *P. leiodermus* in having much smaller, more regular pores and shorter basidiospores.

Fomitopsis leucaena (Y.C. Dai & Niemelä) Spirin & Miettinen, *comb. nov.* MycoBank MB 844926.

Basionym: Antrodia leucaena Y.C. Dai & Niemelä, Ann. Bot. Fenn. 39 (4): 259. 2002.

Typus: **China**, Jilin, Antu Co., Changbaishan Nat. Res., *Populus davidiana*, 14 Sep. 1998, *Dai* 2190a & *Niemelä** (**holotype** H!).

Description and phylogenetic data: Spirin *et al.* (2013b, 2017, as *A. leucaena*).

Fomitopsis lignea (Berk.) Ryvarden, Norw. J. Bot. 19: 231. 1972. Fig. 22.

Basionym: Polyporus ligneus Berk., Ann. Mag. Nat. Hist. 3: 387. 1839.

Typus: **St. Vincent and the Grenadines**, St. Vincent, '*Polyporus fasciatus* Swz. Fl.' (**lectotype** K, **isolectotype** BPI US0231445!) (selected by Ryvarden 1976: 95). Synonym: Fomes subferreus Murrill, North American Flora 9 (2): 97. 1908.

Typus: **Cuba**, Pinar del Rio, Herradura, dead wood, 7–12 Mar. 1905, *Earle & Murrill* 184 (**lectotype** NY00780693!) (selected by Ryvarden 1985: 176).

Description: Basidiocarps perennial, sessile, dimidiate, projecting up to 9 cm. Upper surface blackish brown to black, with a few indistinct annual zones, accidentally longitudinally cracking. Pileal edge sharp or rather blunt, concolourous with hymenial surface, first sterile, up to 1 mm wide, then fertile. Pore surface cream-coloured or beige to pale ochraceous, flat or concave; pores roundish to angular, 5-7 per mm, with rather thick, entire or minutely serrate dissepiments. Section: context corky, cream-coloured to brownish, up to 10 mm thick; tubes corky, indistinctly stratified, concolourous with hymenial surface, up to 10 mm thick. *Hyphal structure* dimitic; hyphae clamped. Context dimitic; skeletal hyphae yellowish to brownish, interwoven, occasionally branched, (3.0-)3.2-6.4(-7.0) µm diam (n = 40/2), lumen capillary to indistinct, side branches 2-4 µm diam, generative hyphae rare, hyaline, thin- to slightly thickwalled, 2-3 µm diam. Trama dimitic; skeletal hyphae dominating, yellowish to brownish, densely interwoven, occasionally branched, sometimes twisted, $(2.7-)2.8-4.4(-4.9) \mu m$ diam (n = 40/2), lumen mostly narrow to indistinct, generative hyphae thin- to slightly thick-walled, 1.5-3 µm diam. Subhymenium indistinct. Cystidioles infrequent, tapering, sometimes with a long hyphoid neck, 9.5–14 × 2.5–3.5 µm. Basidia clavate, (8.1–)8.2–13.0(–13.2) × (3.2–)3.7– 4.3(-4.4) μ m (n = 16/2), in senescent hymenium glued together. Basidiospores with a distinct wall, narrowly ellipsoid to broadly cylindrical, $(2.8-)2.9-4.1(-4.3) \times (1.8-)1.9-2.3(-2.4) \mu m (n = 40/2)$, L = 3.34–3.44, W = 2.07–2.08, Q = 1.61–1.66.

Specimens examined: Belize, Cayo, Blue Hole Nat. Park, angiosperm, 18 Nov. 2001, *Ryvarden* 44326 (O 17633); Orange Walk, La Milpa, dead hardwood, 24 Oct. 2002, *Ryvarden* 45153 (O 18199). Cuba, Oriente, Jaguey, fallen log, *Maxon* 4234 (Kryptogamae exsiccatae #1908, H ex W). Jamaica, Trelawny, Crowlands, dead wood, 10 Apr. 1999, *Ryvarden* 41624* (O 10794). Panama, Veraguas, Montijo, Coiba Nat. Park, dead wood, 21 Nov. 1996, *Núñez* 1265 (O 10792).

Notes: Fomitopsis lignea is reinstated here as a species closely related to *F. lapidosa*. It was previously known as *Fomes suferreus* and usually treated as a synonym of *F. dochmia* (Lowe 1957, Carranza-Morse & Gilbertson 1986). Despite their high morphological similarity, these species are not closely related. *Fomitopsis lignea* is distributed in the Caribbean, and all older records of *F. dochmia* from this area are highly likely to belong to this species. See further notes under *F. dochmia* and *F. lapidosa*. Ryvarden (2015) misapplied *F. lignea* to another species, described here as *F. lignicolor*.

Fomitopsis lignicolor Vlasák & Spirin, *sp. nov.* MycoBank MB 848360. Fig 22.

Typus: **Costa Rica**, Puntarenas, Tarcoles, Carara Nat. Park, fallen log, 18 Apr. 2015, *Vlasák* 1504/15* (**holotype** PRM933860, **isotype** H).

Etymology: Lignicolor (Lat., adj.) - wood-coloured.

Description: Basidiocarps annual or short-living perennial, sessile, ungulate, broadly attached, projecting up to 7 cm. Upper surface first ivory to pale ochraceous, azonate, felty, later covered by brown to blackish brown crust, smooth, not cracking. Pileal edge blunt,



concolourous with pore surface, fertile. Pore surface first ivory or pale wood-coloured, then brownish, flat or slightly convex; pores roundish, 3-4 per mm, with thin, entire dissepiments. Section: crust (present in mature basidiocarps) tough, black, matt, up to 1 mm thick, context corky, ochraceous or brownish, up to 15 mm thick, sharply delimited from tubes; tubes tough, one-layered or indistinctly stratified, concolourous with hymenial surface, up to 1 cm thick. Hyphal structure dimitic; hyphae clamped. Context dimitic; skeletal hyphae dominating, brownish, interwoven, occasionally branched, (2.6-)2.7-4.2(-4.4) µm diam (n = 20/1), lumen capillary to indistinct, generative hyphae rare, hyaline, thin-walled, 2.5-4.0 µm diam. Trama dimitic; skeletal hyphae brownish, tightly interwoven, sometimes twisted, rarely branched, (2.3-)2.6-3.4(-3.7) μ m diam (n = 40/2), lumen rather wide to capillary, generative hyphae hyaline, thin-walled, 2.0-3.5 µm diam, often producing distinct subhymenial layer up to 20–30 µm thick. Resinous droplets abundant among tramal and subhymenial tissues of senescent basidiocarps. Cystidioles rare, tapering, 12-16 × 4-5.4 µm. Basidia short-clavate, (9.4–)9.6–13.7(–13.8) × (4.1–)4.3–5.8(–6.3) µm (n = 20/1), senescent basidia slightly thick-walled. Basidiospores thinwalled or with a distinct wall, cylindrical to subfusiform, (4.1-)4.2- $7.1(-7.2) \times (2.0-)2.1-2.9(-3.0) \ \mu m \ (n = 60/2), \ L = 5.05-5.78, \ W =$ 2.41-2.45, Q = 2.12-2.38.

Specimens examined: **Costa Rica**, Puntarenas, Tarcoles, Carara Nat. Park, fallen log, Dec. 2013, *J. Vlasak Jr.* 1312/A-4 (JV). **Panama**, Colón, Barro Colorado, 20 Feb. 1985, *Grimaldi* (O 10814). **Venezuela**, Aragua, Romerito, Henri Pittier Nat. Park, Feb. 2004 *Kout* 0402/M* (H, JV).

Notes: First DNA sequences, as well as coloured photographs of this species were published by Vlasák *et al.* (2016) (as *F. lignea*). According to our data, *F. lignicolor* occupies an isolated position within the genus (Figs 1, 3). Short-lived basidiocarps with rather pale-coloured, not stratified tubes and a pronounced crust make this species easily distinguishable from other representatives of the genus. *Fomitopsis lignicolor* is so far found only in the Caribbean.

Fomitopsis lilacinogilva (Berk.) J.E. Wright & J.R. Deschamps, Rev. Invest. Agropec. INTA, Serie 5, Pat. Veg. 12 (3): 143. 1975. *Basionym: Polyporus lilacinogilvus* Berk., Ann. Mag. Nat. Hist. 3: 324. 1839.

Typus: **Australia**, Tasmania, charred wood, [no collection date indicated], *Gunn* (**lectotype** K, **isolectotype** PC!) (selected by Ryvarden 1976: 95).

Description: Basidiocarps perennial, sessile, often with a contracted base, projecting up to 5 cm. Upper surface greyishochraceous to pinkish brown, first adpressed-hirsute to strigose, indistinctly zonate, then almost smooth, radially furrowed, often with a silky lustre. Pileal edge sharp, concolourous with hymenial surface, usually sterile, up to 2 mm wide. Pore surface pinkish to pinkish brown, usually concave; pores angular, 3-5 per mm, with thin or moderately thickened, entire or serrate dissepiments. Section: context corky, pinkish to pale ochraceous or brownish, up to 7 mm thick; tubes corky, one-layered or indistinctly stratified, concolourous with hymenial surface, up to 7 mm thick. Hyphal structure dimitic; hyphae clamped. Context dimitic; skeletal hyphae brownish to almost hyaline, rather loosely interwoven, occasionally branched, (4.0-)4.1-6.7(-7.2) µm diam (n = 20/1), lumen mostly wide, side branches 2.5–4 µm diam, generative hyphae hyaline, slightly thick-walled, 4–7 µm diam. Trama dimitic; skeletal hyphae dominating, brownish to reddish-brown, interwoven, occasionally branched, (2.8-)3.0-4.6(-5.0) µm diam (n = 60/3), lumen rather wide to capillary, generative hyphae rather rare, thin- to slightly thick-walled, 2–3 µm diam. Subhymenium indistinct. Cystidioles uncommon, tapering, $14-21 \times 3.5-6$ µm. *Basidia* clavate, $(13.1-)13.8-18.2(-20.2) \times (5.1-)5.4-7.0(-7.2)$ µm (n = 20/2), occasionally pleural, in senescent hymenium partly glued together. *Basidiospores* thin-walled or with a distinct wall, cylindrical-subfusiform, $(5.1-)5.2-9.2(-9.4) \times (2.3-)2.6-3.2(-3.3)$ µm (n = 60/2), L = 6.71-6.76, W = 2.92-3.02, Q = 2.24-2.29.

Specimens examined: **Australia**, Queensland, Cairns, Lake Barrine, angiosperm, 19 Aug. 2006, *Schigel* 5193* (H); Victoria, Grampians Nat. Park, Halls Gap, charred wood, 5 Mar. 2003, *Hausknecht* 12/03 (O 19243); Western Australia, Perth, Byford Maryedal Creek, charred wood, 8 Sep. 1964, *Smith* (O 10818).

Notes: Fomitopsis lilacinogilva is a member of the *F. feei* complex distributed in Oceania. It differs from other species of this group from the same region (*F. eucalypti, F. foedata* and *F. marchionica*) in having distinctly larger pores and longer basidiospores, as well as by the roughly hirsute pileal surface of its vigorously growing basidiocarps. The identity of *F. lilacinogilva* from the neotropics deserves further study. The single available ITS sequence from Costa Rica (GenBank DQ491400) shows a 10 bp difference vs. sequences from Australian collections, and therefore it may belong to an undescribed sister species of *F. lilacinogilva*.

Fomitopsis luzonensis (Murrill) Spirin & Miettinen, *comb. nov.* MycoBank MB 844927. Figs 21, 22.

Basionym: Trametes luzonensis Murrill, Bull. Torrey Bot. Club 34: 474. 1907.

Typus: **Philippines**, Luzon, Bataan, Mt. Mariveles, dead sticks, Nov. 1904, *Elmer* 6932 (holotype NY00705039!).

Description: Basidiocarps annual, sessile or effused-reflexed, often fusing together in large imbricate groups, projecting up to 5 cm. Upper surface first cream coloured to pale ochraceous, smooth or scrupose, later greyish ochraceous to mouse grey, sometimes with a brownish tint, azonate. Pileal edge sharp to rather blunt, concolourous with cap surface, usually fertile. Pore surface pale ochraceous to grey, sometimes with brownish stains, as a rule concave; pores roundish to angular, 8-10 per mm, with thin, entire dissepiments. Section: context tough, pale creamcoloured to pale ochraceous, up to 5 mm thick; tubes tough, one-layered, concolourous with hymenial surface, up to 5 mm thick. Hyphal structure dimitic; hyphae clamped. Context dimitic; skeletal hyphae hyaline, densely interwoven or rarely in subparallel bundles, occasionally branched, (2.8-)2.9-6.0(-6.1) µm diam (n = 60/3), lumen narrow to almost invisible, side branches 2–3 um diam, generative hyphae rather abundant to rare, hyaline, thin- or moderately thick-walled, 3-6 µm diam. Trama dimitic; skeletal hyphae hyaline to yellowish, interwoven, some flexuous, occasionally branched, $(2.0-)2.2-4.2(-4.7) \mu m$ diam (n = 100/5), lumen wide to capillary, generative hyphae thin- or slightly thickwalled, 2-3 µm diam, dissepiment edges dimitic, consisting of thinwalled generative hyphae and winding skeletals with a wide lumen. Subhymenium usually indistinct. Cystidioles frequent to rare, distinctly tapering to the apex (mostly bottle-shaped), 9-15 × 3.5-7 µm. Basidia short-clavate, (9.4–)9.8–16.3(–17.2) × (4.3–)4.6–6.4(– 6.7) μ m (n = 34/3), often glued together in a dense palisade layer. Basidiospores thin-walled, cylindrical to fusiform, (5.0-)5.1-8.1(-8.3) × 2.0–3.1(–3.2) μm (n = 120/4), L = 5.94–6.15, W = 2.39–2.89, Q = 2.06–2.56.

Specimens examined: Indonesia, Jawa Barat, Bogor, dicot stump, 8 May 2016, Miettinen 19950 (BO, H); Nusa Tenggara Barat, Lombok Utara, Gili Meno, Casuarina, 6 Jan. 2012, Miettinen 15300 (BO, H); Papua Barat, Manokwari, Cocos nucifera, 1 Feb. 2007, Miettinen 11573* (MAN, H); Aman, Senna, 9 Nov. 2018, Miettinen 21985 (MAN, H); Amberbaken, Wefiani-Wasarak, C. nucifera, 31 Oct. 2010, Miettinen 14261* (MAN, H); Saukorem, dicot, 1 Nov. 2010, Miettinen 14311* (MAN, H); ibid., 4 Nov. 2010, Miettinen 14417* (MAN, H); Riau, Pelalawan, Kampar Peninsula, Serkap, dicot, 16 Dec. 2006, Miettinen 11224* (BO, H); Tasik Besar Wildlife Reserve, 14 Dec. 2006, Miettinen 11184 (BO, H); Pekanbaru, Sukajadi, Filicum decipiens (?) 20 Jul. 2008, Miettinen 13162* (ANDA, H); C. nucifera, 20 Jul. 2008, Miettinen 13163* (ANDA, H); C. nucifera, 30 Nov. 2011, Miettinen 15089 (BO, H); Pometia pinnata, 16 Mar. 2020, Miettinen 23504 (BO, H); Jalan Sudirman, Arecaceae, 6 Jul. 2013, Miettinen 16598 (BO, H); Siak, Tasik Besar Wildlife Reserve, dicot, 10 Apr. 2002, Miettinen 5678* (BO, H); Yogyakarta, Sleman, Pekembinangun, Bambusoidae, 19 Dec. 2011, Miettinen 15222* (BO, H).

Notes: Fomitopsis luzonensis is the correct name for the Southeast Asian species formerly mislabelled as *F. ostreiformis* (Rungjindamai *et al.* 2009, Li *et al.* 2013, Ortiz-Santana *et al.* 2013). It is one of the most common brown rot fungi in insular Southeast Asia. The latter species represents the same taxon as *F. cana* (see *F. osteiformis* below). The two species are morphologically highly similar and they occur in the same habitats. *Fomitopsis luzonensis* has smaller pores and on average longer basidiospores than *F. ostreiformis*. Moreover, its basidiocarps are normally sessile-pileate (in contrast to the usually resupinate or effused-reflexed ones of *F. ostreiformis*), and they are sturdier and heavier than those of *F. ostreiformis*. Small-pored and hard basidiocarps differentiate *F. luzonensis* from the phylogenetically closely related *F. marianii* and *F. nivosella* (see Table 3).

Fomitopsis maculatissima (Lloyd) Spirin, *comb. nov.* MycoBank MB 844928.

Basionym: Polyporus maculatissimus Lloyd, Mycol. Writ. 7 (66): 1113. 1922.

Typus: **Australia**, Tasmania, [no collection date], *Rodway* (**lectotype** BPI 304927) (selected by Ryvarden 1990: 92).

Synonym: Neolentiporus maculatissimus (Lloyd) Rajchenberg, Nordic J. Bot. 15: 106. 1995.

Description: Rajchenberg (1995a, as Neolentiporus maculatissimus).

Notes: For phylogenetic placement, see Fig. 3 and Suppl. Figs S2 and S8.

Fomitopsis maculosa Miettinen & Spirin, *sp. nov.* MycoBank MB 844929. Figs 21, 23.

Typus: **Indonesia**, Bali, Bedugul, Mt. Tapak, Cagar Alam Batu Karu, -8.27669° 115.14604° (± 50 m), natural (primary) forest slope, plenty of *Podocarpus*, on a fallen branch (decay stage 2,5 cm in diameter), 25 Dec. 2007, *Miettinen* 12233.1* (**holotype** BO, **isotype** H7200142).

Etymology: Maculosus (Lat., adj.) - stained, spotted.

Description: Basidiocarps effused, first orbicular, gregarious, then fusing together and up to 3 cm in widest dimension. Margin adnate, compact, first violet, fading to cream-coloured, later ochraceous to brownish, up to 1 mm broad. Hymenial surface even or nodulose, violet, quickly fading to greyish to ochraceous-



Fig 23. Basidiospores of *Fomitopsis* spp. *F. maculosa* (holotype); *F. marchionica* (Miettinen 11454); *F. marianii* (Spirin 10503); *F. meliae* (Dollinger 989); *F. modesta* (Vlasák 1504/52); *F. moritziana* (Miettinen 11662); *F. nivosella* (3 left – O F10833, 3 right – holotype). Scale bar = 5 μm.

brownish; pores angular to lacerate, 3-5 per mm, dissepiments thin, uneven. Section: subiculum compact, cream-coloured, hardly visible, 0.05-0.1 mm thick; tubes soft leathery, concolourous with hymenial surface, 0.5-2 mm thick. Hyphal structure dimitic; hyphae clamped. Subiculum dimitic; skeletal hyphae hyaline to brownish, subparallel, occasionally branched, (3.7-)3.8-5.8(-6.2) µm diam (n = 20/1), lumen narrow to capillary, side branches 2.5-3.5 µm diam, generative hyphae hyaline, slightly thick-walled, 3-5 µm diam. Trama dimitic; skeletal hyphae hyaline, loosely interwoven, brownish, sometimes covered by small needle-like crystals or cemented by brownish amorphous substance, occasionally branched, (3.0-)3.1-5.2(-5.8) µm diam (n = 40/2), lumen rather wide to capillary, side branches 2-3.5 µm diam, generative hyphae abundant, hyaline, slightly thick-walled, 3-5 µm diam. Subhymenium distinct, up to 25 µm thick. Cystidioles abundant, tapering to the apex, 13-19 × 3-5 µm. Basidia clavate, (15.2-)17.2-22.7(-28.0) × (5.8-)6.0-7.2(-7.3) µm (n = 20/2), in older hymenium often covered by amorphous brownish matter. Basidiospores with a distinct wall, broadly cylindrical to subfusiform, (6.2-)6.4-8.6(-8.7) × (2.7–)2.8–3.9(–4.1) µm (n = 60/2), L =7.41–7.49, W = 3.20–3.22, Q = 2.33 - 2.34, often with numerous oil droplets.

Specimen examined: Indonesia, Bali, Bedugul, Mt. Tapak, montain rainforest, fallen branch, 25 Dec. 2007, *Miettinen* 12230* (BO, H).

Notes: Fomitopsis maculosa is the closest relative of Antrodia tropica (= Fomitopsis tropica below) recently described from the southern part of China (Cui 2013). It differs from the latter

in having rather abundant, brownish skeletal hyphae and wider basidiospores. *Fomitopsis maculosa* is so far only known from the type locality in Indonesia.

Fomitopsis madronae (Vlasák & Ryvarden) Vlasák & Ryvarden, *comb. nov.* MycoBank MB 844930.

Basionym: Antrodia madronae Vlasák & Ryvarden, Mycotaxon 119: 220. 2012.

Typus: **USA**, Oregon, Josephine Co., Oregon Caves, *Arbutus menziesii*, 14 Sep. 2007, *Vlasák Jr.* 0709/117-J* (holotype PRM 899296!, isotype H7200207).

Description and phylogenetic placement: Vlasák et al. (2012, as A. madronae); see also Figs 1, 3 and Suppl. Fig. S8.

Fomitopsis maire (G. Cunn.) P.K. Buchanan & Ryvarden, Mycotaxon 31: 15. 1988.

Basionym: Laricifomes maire G. Cunn., Bull. N.Z. Dept. Sci. Industr. Res. 164: 262. 1965.

Typus: New Zealand, Auckland, Waitakere Ranges, Anawhata, *Nestegis cunninghamii*, Aug. 1947, *Dingley* (holotype PDD38093, isotype H7004760!).

Description: Buchanan & Ryvarden (1988).

Notes: Morphologically, F. maire is very similar to F. sulcata from which it differs mainly in having considerably smaller pores (3-4



per mm in the type of *F. maire* vs. 0.3–1 per mm in *F. sulcata*). The phylogenetic position of *F. maire* can be established only after getting sequenced material from the type locality.

Fomitopsis malicola (Berk. & M.A. Curtis) Spirin, *comb. nov.* MycoBank MB 844931.

Basionym: Trametes malicola Berk. & M.A. Curtis, J. Acad. Nat. Sci. Philad. 3: 209. 1856.

Typus: **USA**, Pennsylvania, Bethlehem, *Malus* sp., [no collection date], *Schweinitz* 366 (**lectotype** K(M) 180488!) (selected by Ryvarden 1984: 347).

Synonym: Antrodia malicola (Berk. & M.A. Curtis) Donk, Persoonia 4: 339. 1966.

Description and phylogenetic data: Spirin et al. (2016, as Antrodia malicola).

Fomitopsis marchionica (Mont.) Spirin & Miettinen, *comb. nov.* MycoBank MB 844932. Fig 23.

Basionym: Trametes marchionica Mont., Voyage au Pôle Sud et dans l'Océanie, Botanique 1: 204. 1845.

Typus: Marquesas Islands, Nuku Hiva, 1841, Hombron 1 (holotype PC!).

Description: Basidiocarps perennial, sessile, often with a contracted base (fan-shaped), solitary or imbricate groups, sometimes fusing together, projecting up to 10 cm. Upper surface smooth, pinkish buff to brownish, covered by numerous darker zones. Pileal edge sharp, concolourous with hymenial surface or slightly darker, usually sterile, up to 2 mm wide. Pore surface first pink to pinkish grey, then fading to almost white, in senescent basidiocarps brownish, concave; pores roundish to angular, 5-7 per mm, with moderately thickened, entire dissepiments. Section: context corky, pink or pinkish brownish, in older basidiocarps brownish, up to 5 mm thick; tubes corky, one-layered or indistinctly stratified, concolourous with hymenial surface, up to 3 mm thick. Hyphal structure dimitic; hyphae clamped. Context dimitic; skeletal hyphae yellowish to brownish, densely interwoven, richly branched, (3.3–)3.8–6.0(–6.2) µm diam (n = 40/2), lumen wide to capillary or indistinct, side branches 2–4 µm diam, generative hyphae rare, hyaline, slightly to distinctly thickwalled, 3.5-5 µm diam. Trama dimitic; skeletal hyphae dominating, yellowish to brownish, densely interwoven, occasionally branched, (2.8-)2.9-4.2(-4.3) µm diam (n = 20/2), lumen predominantly narrow to indistinct, generative hyphae rather rare, thin- to slightly thick-walled, 2-3 µm diam. Subhymenium indistinct. Cystidioles infrequent, tapering, 8-11 × 2.5-4 µm. Basidia short-clavate, (8.3-) $8.7-10.8(-12.0) \times (4.2-)4.6-5.4(-5.8) \mu m$ (n = 20/1), in senescent hymenium partly glued together. Basidiospores with a distinct wall, cylindrical-subfusiform to narrowly ellipsoid, occasionally slightly curved, (3.1–)3.2–4.2(–4.3) × (1.8–)1.9–2.2(–2.3) µm (n = 30/1), L = 3.63, W = 2.08, Q = 1.75.

Specimen examined: Indonesia, Papua, Merauke, Wasur NP, dry natural forest, fallen dicot tree, 21 Jan. 2007, *Miettinen* 11454* (MAN, H).

Notes: To date, *T. marchionica* has been treated as a synonym of *F. feei* (Ryvarden 1982). The type material studied by us was compared with a newly collected and sequenced specimen from New Guinea, and no essential differences were detected. We therefore consider them conspecific. It is still possible, however, that the type specimen from Marquesas Islands and our New Guinean specimen belong

to different species. Solving this problem is possible only after getting new material from the *locus classicus*. As defined here, *F. marchionica* differs from the similar-looking members of the *F. feei* complex in having robust but rather thin basidiocarps with a densely zonate upper surface (see also Table 3). Phylogenetically, it is not closely related to the *F. feei* group (Suppl. Fig. S2).

Fomitopsis marianii (Bres.) Spirin, Vlasák & Cartabia, *comb. nov.* MycoBank MB 844933. Figs 21, 23.

Basionym: Polyporus marianii Bres., Nuovo G. Bot. Ital. 7: 313. 1900.

Typus: **Italy**, Lazio, Latina, Terracina, *Quercus cerris*, [no collection date], *Mariani* (**lectotype** S F14590!) (selected by Ryvarden 1988a: 315).

Synonyms:

Poria incarnata Pers., Ann. Bot. 11: 30. 1794.

Typus: No locality indicated (probably Germany), [no collection date and collector], herb. Persoon (**lectotype** designated here L 0115607!, MycoBank MBT 10008290).

Trametes lignea Murrill, North American Flora 9: 44. 1907.

Typus: **Nicaragua**, [no locality indicated], on dead timber, Feb. 1891, *C.L. Smith* (**holotype** NY 00705034!).

Trametes subalutacea Bourdot & Galzin, Bull. Soc. Mycol. France 41: 165. 1925.

Typus: **France**, Aveyron, Saint-Sernin-sur-Rance, *Alnus glutinosa*, 8 Aug. 1905, *Galzin* 1229 (herb. Bourdot 3967) (**lectotype** selected here PC!, MycoBank MBT 10008291).

Leptoporus epileucinus Pilát, Acta Mus. Nat. Pragae 9 (B), 2 (1): 105. 1953.

Typus: **Ukraine**, Zakarpats'ka Reg., Kobylecká Polana, *Fagus sylvatica*, Jul. 1929, *Pilát* (holotype PRM 486790!).

Fomitopsis iberica Melo & Ryvarden, Bolm. Soc. Broteriana 62: 228. 1989.

Typus: **Portugal**, Ribatejo, Chamusca, Chouto, *Quercus suber*, 13 Nov. 1986, *Melo, Correira* & *Cardoso* 3141 (**holotype** LISU, **isotype** H!).

Antrodia bondartsevae Spirin, Mikol. Fitopatol. 36: 33. 2002.

Typus: **Russia**, Nizhny Novgorod Reg., Sharanga Dist., Kilemary, *Tilia cordata*, 24 Aug. 2000, *Spirin** (**holotype** LE 209783!).

Antrodia wangii Y.C. Dai & H.S. Yuan, Mycosystema 25: 372. 2006.

Typus: **China**, Beijing, Xianshan, *Prunus* sp., 25 Jul. 2005, *Dai* 6613* (isotype H!).

Fomitopsis caribensis B.K. Cui & Shun Liu, Mycol. Progr. 18: 1322. 2019.

Typus: **Puerto Rico**, Rio Abajo, hardwood, 16 Jul. 2018, *Cui* 16871* (holotype BJFC).

Fomitopsis ginkgonis B.K. Cui & Shun Liu, Mycol. Progr. 18: 1325. 2019.

Typus: **China**, Hubei, Huanggang, Yiaihu, *Ginkgo biloba*, 20 Oct. 2018, *Cui* 17170* (**holotype** BJFC).

Description: Basidiocarps annual, sessile or effused-reflexed, usually fusing together in large groups, projecting up to 7 cm, rarely totally resupinate, up to 8 cm in widest dimension. Upper surface first cream coloured to pale ochraceous, azonate, finely velutinous, later greyish-ochraceous to brownish, smooth or finely striate, often with a few indistinct brownish zones. Pileal edge sharp, concolourous with cap surface, fertile, sometimes incurving during drying. Pore surface cream-coloured or pale ochraceous, sometimes with brownish stains, as a rule concave; pores angular to lacerate, 4–6 per mm, with thin, serrate or dentate dissepiments. Section: context soft, white to cream-coloured, up to 25 mm thick; tubes soft, easily cut by a razor blade, one-layered, concolourous with hymenial surface, up to 10 mm thick. *Hyphal structure* dimitic; hyphae clamped. Context dimitic; skeletal hyphae hyaline, densely interwoven or in subparallel bundles, richly branched, (3.0-)3.1-7.3(-7.8) µm diam (n = 120/7), lumen narrow to almost invisible, side branches 2-3 µm diam, generative hyphae abundant to rare, hyaline, thin- or moderately thick-walled, 2-4.5 (-5) µm diam. Trama dimitic; skeletal hyphae hyaline, interwoven, some flexuous, occasionally branched, (2.0-)2.2-4.8(-4.9) µm diam (n = 190/9), lumen wide to capillary, generative hyphae thin- or slightly thickwalled, 2-4 µm diam, in some parts dominating and producing distinct subhymenial layer up to 35–50 µm thick, dissepiment edges monomitic. Small angular or rhomboid crystals abundant among tramal tissues, up to 5-7 µm in longest dimension. Cystidioles frequent, tapering, 12-21 × 3-6 µm. Basidia clavate, often with a tapering basal part, (12.0-)12.4-21.3(-25.2) × (4.4-)4.7-7.0(-7.2) μ m (n = 51/5), sometimes pleural. *Basidiospores* thin-walled, cylindrical to fusiform, longest spores sigmoid, (5.0-)5.1-8.7(-9.4) × 2.0–3.2(–3.3) μm (n = 331/11), L = 5.81–7.11, W = 2.32–2.90, Q = 2.31–2.84.

Specimens examined: Croatia, Primorje-Gorski Kotar, Rab, Pinus sp., 23 Sep. 1994, Varjů (MJ4158*). Czech Republic, Brno, Lanžhot, Ranšpurk, Fraxinus angustifolia, 19 Jun. 1999, Vampola (MJ4606*); Zlín, Buchlovice, Holý Kopec, Fagus sylvatica, 2 Aug. 2010, Běták 10/743* (JV). France, Aveyron, St. Sernin, Alnus glutinosa, 12 Aug. 1906, Galzin 1753 (herb. Bourdot 5999) (PC); Salles-la-Source, manufactured wood, 24 Oct. 2016, Rivoire (LY-BR 6563*). Italy, Lombardy, Varese, Via Tasso, Cedrus deodara, 8 Jun. 2019, Cartabia 104* (H); Villa Toeplitz, F. sylvatica, 3 Jul. 2019, Cartabia 129 (H); Villa Mylius, C. deodara, 23 May 2020, Cartabia (H); Inarzo, Betula pendula, 10 Jun. 2019, Cartabia 105 (H); Viggiù, C. deodara, 23 Jun. 2020, Cartabia (H). Russia, Khabarovsk Reg., Khabarovsk Dist., Ilga, Tilia amurensis, 15 Aug. 2012, Spirin 5302* (H); Pravaya Ilga, T. amurensis, 11 Aug. 2012, Spirin 5175* & 5176* (H); Nizhny Novgorod Reg., Bogorodsk Dist., Podvyazie, T. cordata, 30 Jul. 2005, Spirin 2306 (H); Lukoyanov Dist., Panzelka, T. cordata, 9 Aug. 2016, Spirin 10575* (H); Razino, T. cordata, 15 Aug. 2015, Spirin 9267* (H); ibid., 7 Aug. 2016, Spirin 10503* (H); ibid., 29 Jul. 2017, Spirin 11249* (H); B. pendula, 31 Jul. 2017, Spirin 11281 (H). USA, Louisiana, Baton Rouge, Louisiana State University Campus, Ligustrum sp., 6 Jul. 1986, Gilbertson 14757* (O 16323). Slovakia, Trnava, Lakšárska Nová Ves, Pinus sylvestris, 18 Jun. 1994, Kukulka (MJ4157*). Slovenia, Ljubljana, Mala ulica, angiosperm stump, 31 Jul. 2020, Spirin 14034 (H, LJF).

Notes: Fomitopsis marianii is a macroscopically extremely flexible species, with basidiocarps varying from robust pileate to effused-reflexed with thin flabelliform caps or even totally resupinate. This is the reason why the species was described several times in different genera. The oldest available name for it is *Poria incarnata.* Although sterile, the single authentic specimen designated here as

a lectotype of *P. incarnata* is certainly conspecific with *F. marianii*. Ryvarden (1991) selected another specimen as the lectotype of P. incarnata. That one was collected by Lindblad in Sweden and it is conspecific with Steccherinum collabens (= Junghuhnia collabens). However, this solution cannot be accepted for two reasons. First, Lindblad's specimen was evidently collected after Fries compiled his sanctioning treatment. Therefore, it could serve only as a neotype, not as a lectotype. However, neotype selection is precluded if the authentic material suitable for lectotypification is still available (Code Art. 9.13). Second, if accepted, the typification of P. incarnata with Lindblad's gathering will necessitate a name change for S. collabens. This would be highly undesirable because the latter one is an important indicator species of old-growth spruce-dominated forests in Europe, and it is well known not only to professional mycologists but also to amateurs. Nevertheless, P. incarnata cannot be combined in Fomitopsis because of the presence of Fomitopsis incarnatus (see synonymy under F. ussuriensis). Polyporus marianii is next in line and it is combined here in *Fomitopsis*. We also studied the type material of *Fomitopsis* epileucina and F. iberica treated as two independent species by Ryvarden & Gilbertson (1993) and in other subsequent manuals. We concluded they represent the same species and are conspecific with F. marianii.

Fomitopsis marianii is widely distributed in temperate forests of Eurasia, and it seems to be not rare in temperate – subtropical areas of the United States. In North America, it was often mixed up with other similar-looking species, in particular, with F. palustris and F. nivosella (= F. durescens, see below). The first species produces rather small, sessile basidiocarps with somewhat smaller pores, and it is restricted to Pinus spp. in warm temperate - subtropical areas of North America. Moreover, it has on average larger basidia and basidiospores than F. marianii. The only available genome of F. palustris (ATCC 62978) in fact belongs to F. marianii. In turn, F. nivosella can be differentiated from F. marianii due to slightly smaller and more regular pores with mostly entire orifices, as well as more abundant tramal skeletal hyphae reaching dissepiment edges which are monomitic in F. marianii. The name Fomitopsis nivosa was misapplied in North and South America either to F. marianii or to F. nivosella. Liu et al. (2019) introduced two new species, F. caribensis and F. ginkgonis. ITS and partial TEF1 sequences of these species submitted to GenBank show no differences from F. marianii, and no unique morphological traits are mentioned in their protologues. Therefore, we treat them as later synonyms of F. marianii.

Fomitopsis meliae (Underw.) Gilb., Mycotaxon 12 (2): 385. 1981. Fig 23.

Basionym: Polyporus meliae Underw., Bull. Torrey Bot. Club 24: 85. 1897.

Typus: **USA**, Alabama, Auburn, *Melia azedarach*, 10 Oct. 1895, *Underwood* (holotype NY 00730808!).

Synonyms:

Trametes submurina Murrill, North American Flora 9: 43. 1907.

Typus: Jamaica, Kingston, Hope Gardens, on old log, 16 Nov. 1902, *Earle* 483 (holotype NY 00705075!).

Trametes subnivosa Murrill, North American Flora 9: 43. 1907.

Typus: **USA**, Louisiana, [no locality], Jan. 1887, *Langlois* (holotype NY 00705078!).



Description: Basidiocarps annual, sessile or effused-reflexed, often fusing together in large imbricate groups, projecting up to 4 cm, very rarely resupinate. Upper surface first cream-coloured to greyish, azonate, felty, later mouse-grey, occasionally with ochraceous or brownish tints, smooth or indistinctly wrinkled, rarely indistinctly zonate. Pileal edge sharp to rather blunt, concolourous with pore surface, up to 1 mm wide, sterile. Pore surface cream-coloured or pale ochraceous, then greyish, sometimes with brownish flecks, as a rule concave; pores roundish to angular, 4-7 per mm, with thin, entire or serrate dissepiments. Section: context soft corky, creamcoloured to grevish, up to 8 mm thick; tubes rather soft, easily cut by a razor blade, one-layered, concolourous with hymenial surface, up to 6 mm thick. Hyphal structure dimitic; hyphae clamped. Context dimitic; skeletal hyphae hyaline, rarely greyish or brownish, mostly loosely interwoven, occasionally branched, (3.0–)3.3–7.7(–8.2) µm diam (n = 120/6), with a variably pronounced lumen, side branches 1.5–3 µm diam, generative hyphae thin- to moderately thick-walled, 3-5 µm diam. Trama dimitic; skeletal hyphae hyaline or greyish, loosely interwoven, some flexuous, occasionally branched, (2.7-)2.8-4.9(-5.0) µm diam (n = 140/7), swelling in KOH and CB, lumen rather wide to capillary, side branches 1.5-2.5 µm diam, generative hyphae thin- or slightly thick-walled, 2-4 µm diam, sometimes producing distinct subhymenial layer up to 35-40 µm thick. Rhomboid or cubical crystals occasionally present among context and tramal tissue, solitary or in large groups, up to 13 µm in widest dimension. Cystidioles infrequent, tapering, 12-21 × 3.5-6.0 µm. Basidia clavate, often with a tapering basal part, (10.2–)11.1– $17.6(-18.0) \times (4.6-)4.7-6.1(-6.2) \ \mu m \ (n = 40/5). \ Basidiospores$ thin-walled, cylindrical to fusiform, longest spores sigmoid, (4.1-) 4.2-7.2(-7.4) × (2.0-)2.1-2.9(-3.0) µm (n = 180/6), L = 4.87-6.33, W = 2.23–2.55, Q = 2.19–2.50.

Specimens examined: Colombia, Chocó, Turbo, 1 Jul. 1978, Ryvarden 16893 (O 10826). Costa Rica, Puntarenas, Golfito, 20 Apr. 2017, Vlasák 1704/78-J* (JV, TUF); Playa Nicuesa, 19 Apr. 2017, Vlasák 1704/61* (JV, TUF); San José, Cerro Vueltas, 18 Jul. 2001, Ryvarden 43883 (O 18733). French Guiana, Remire-Montjoly, Lac du Rorota, 23 Aug. 2018, Vlasák 1808/33* (JV); Roura, Sentier Molokoï, 26 Aug. 2018, Vlasák 1808/81* & 1808/82* (JV). Martinique, Le Vauclin, Grand Macabou, 25 Dec. 2017, Vlasák 1712/27* (JV). Peru, Alto Amazonas, Yurimaguas, decaying trunk, 30 Jun. 1984, Hormia 2109* (H). Puerto Rico, Luquillo, Luquillo Beach, C. *nucifera*, 12 Jan. 2014, *Miettinen* 18134 (H). USA, Florida, Miami – Dade Co., Miami Beach, 14 Oct. 2016, *Dollinger* 989* & 991* (JV, H); Texas, Austin, Eanes Cree, felled tree, 15 Aug. 2013, *Miettinen* 16679 (H); Victoria Co., Coleto Creek, *Prunus* sp., 26 Sep. 2011, *Vlasák Jr*. 1109/40-J* (JV).

Notes: Rather small, greyish, imbricate or effused-reflexed basidiocarps, often fusing together in large groups help in macroscopic identification of *F. meliae*. The species is widely distributed in the warm-temperate – tropical areas of North America, with a few verified records from the north-eastern part of South America. Microscopically, it is distinguishable from the similarly looking species occurring in the same geographic region (*i.e. F. marianii, F. nivosella* and *F. palustris*) primarily due to greyish skeletal hyphae and rather short basidiospores.

The taxonomic status of *F. meliae* from the neotroics *vs. F.* ostreiformis from the paleotropics deserves further studies. These species did not resolve as two distinct clades in our phylogenetic analyses. The main reason seems to be an unusually high variability of ITS sequences (Fig. 8, and, to a lesser extent, *TEF1* region, Suppl. Fig. S4) in *F. meliae* blurring its differences from *F. ostreiformis*. Nevertheless, we keep them as two separate

species because of their distinct distribution areas and small but constant morphological differences. Although being rather smallsized, F. meliae produces more robust and thicker (up to 1.5 cm thick) basidiocarps than F. ostreiformis, and they are normally pileate. In F. ostreiformis, basidiocarps are thinner (up to 0.6 cm thick but usually less) and they often show a strong tendency to effused growth. Moreover, the grey colouration of basidiocarps (especially tubes) is much more pronounced in F. ostreiformis, often approaching the colours of Bjerkandera adusta. Greyish tints are often present in F. meliae, too, but they are detectable mainly in the pileal surface. Microscopically, the two species are rather similar, although skeletal hyphae in *F. meliae* are hyaline or greyish, in contrast to the normally brownish skeletals of F. ostreiformis. Furthermore, cystidioles of F. meliae have sturdy walls while they are often collapsing at the very apex in F. ostreiformis (this feature is still observable in the type material of the latter species although it is over 150 years old).

Fomitopsis mellita (Niemelä & Penttilä) Niemelä & Miettinen, *comb. nov.* MycoBank MB 844934.

Basionym: Antrodia mellita Niemelä & Penttilä, Ann. Bot. Fenn. 29: 56. 1992.

Typus: **Finland**, Pohjois-Karjala, Lieksa, Patvinsuo Nat. Park, *Populus tremula*, 21 Sep. 1989, *Penttilä* 1350 (**holotype** H!).

Description and phylogenetic placement: Niemelä & Penttilä (1992) and Spirin et al. 2013a (as A. mellita); see also Fig. 3.

Fomitopsis microcarpa (B.K. Cui & Shun Liu) Spirin, *comb. nov.* MycoBank MB 848361.

Basionym: Pseudofomitopsis microcarpa B.K. Cui & Shun Liu, Fungal Diversity 118: 58. 2022.

Typus: **Vietnam**, Dong Nai, Thac Mai, Tan Phu Forest Enterprise, angiosperm, 14 Oct. 2017, *Cui* 16404* (**holotype** BJFC).

Description and phylogenetic placement: Liu et al. (2022, as *P. microcarpa*); see also Fig. 3.

Fomitopsis micropora (B.K. Cui & Shun Liu) Spirin, *comb. nov.* MycoBank MB 848362.

Basionym: Daedalella micropora B.K. Cui & Shun Liu, Fungal Diversity 118: 50. 2022.

Typus: **Malaysia**, Selangor, Taman Botani Negara Shah Alam, angiosperm, 12 Apr. 2018, *Dai* 18509* (**holotype** BJFC).

Description and phylogenetic placement: Liu *et al.* (2022, as *D. micropora*); see also Fig. 3.

Fomitopsis minutispora Rajchenb., Mycotaxon 54: 441. 1995.

Typus: **Argentina**, Neuquén, Lago Queñi, *Nothofagus* sp., 27 Apr. 1994, *Rajchenberg* 10851 (**holotype** BAFC 33360).

Description: Rajchenberg (1995b).

Notes: We used the sequences of Han *et al.* (2016); for phylogenetic placement, see Fig. 3 and Suppl. Fig. S2.

Fomitopsis minutula Spirin, *nom. nov.* MycoBank MB 844935. *Synonym: Antrodia minuta* Spirin, Mycotaxon 101: 150. 2007. *Typus*: **Russia**, Nizhny Novgorod Reg., Lukoyanov Dist., Razino, *Populus tremula*, 24 Sep. 2000, *Spirin* 1725 (**holotype** H!).

Description and phylogenetic data: Spirin et al. (2016, as A. minuta); see also Fig. 3.

Note: The new species epithet is introduced here to avoid homonymy with *Fomitopsis minuta* Aime & Ryvarden (see under Excluded taxa).

Fomitopsis modesta (Kuntze ex Fr.) Vlasák & Spirin, *comb. nov.* MycoBank MB 844936. Figs 23, 24.

Basionym: Polyporus modestus Kuntze ex Fr., Linnaea 5: 519. 1830.

Typus: **Surinam**, [no locality], 'in truncis, Weigelt', [no collection date and collector] (**holotype** UPS F-174971!).

Synonyms:

Polyporus monochrous Mont., Ann. Sci. Nat., Bot. 2 (15): 109. 1841.

Typus: **French Guiana**, [no locality], 1838, *Leprieur* 536 (**lectotype** PC!) (selected by Ryvarden 1982: 79).

Polyporus albocervinus Berk., Hooker's J. Bot. 8: 234. 1856.

Typus: Brazil, Panurè, dead trunks, Spruce 22 (holotype K, isotype PC!).

Daedalea rajchenbergiana Kossmann & Drechsler-Santos, Lilloa 59: 283. 2022.

Typus: **Brazil**, Bahia, Uruçuca, Parque Estadual da Serra do Condurú, 28 Nov. 2012, *Drechsler-Santos* 863* (holotype FLOR 70928).

Description: Basidiocarps short-living perennial, sessile, partly fusing together, often with a contracted base (fan-shaped), projecting up to 6 cm. Upper surface first cream coloured to beige, indistinctly zonate, later pinkish brownish, sometimes with numerous narrow concentric zones. Pileal edge sharp, concolourous with cap surface, first sterile, up to 2 mm wide, then fertile. Pore surface creamcoloured or beige to pale ochraceous, sometimes with a faint pinkish tint or vinaceous-reddish stains, flat or concave; pores roundish to angular, 6-8 per mm, with thin, entire dissepiments. Section: context corky, cream- to wood-coloured, normally less than 2 mm thick; tubes corky, one-layered, concolourous with hymenial surface, up to 2 mm thick. Hyphal structure dimitic; hyphae clamped. Context dimitic; skeletal hyphae hyaline to brownish, densely interwoven or in subparallel bundles, occasionally branched, (3.0–)3.2–5.8(–6.0) μ m diam (n = 20/1), lumen changing from wide to narrow, side branches 2-3 µm diam, generative hyphae infrequent, hyaline, slightly to distinctly thick-walled, 2.5-4 µm diam. Trama dimitic; skeletal hyphae dominating, pale ochraceous to brownish, densely interwoven, occasionally branched, (2.0-)2.1-3.6(-3.8) µm diam (n = 80/4), lumen mostly capillary, generative hyphae rather rare, thin- to slightly thick-walled, 2-3 µm diam. Subhymenium indistinct. Cystidioles abundant to rather rare, tapering, $10-14 \times 3-6 \mu m$. Basidia clavate, (9.8-)10.1-17.3(-17.8) × (4.2-)4.4-5.8(-6.0) µm (n = 38/4), occasionally pleural. Basidiospores with a distinct wall, broadly cylindrical to ellipsoid, longest spores subfusiform, (2.9-) $3.1-5.1(-5.2) \times (2.0-)2.1-3.1(-3.2) \ \mu m \ (n = 120/4), \ L = 3.51-4.36,$ W = 2.23–2.69, Q = 1.57–1.86.

Specimens examined: Brazil, Bahia, Ituberá, hardwood, 2 Mar. 2006, Oinonen 60302003 (H). Costa Rica, Guanacaste, Rincón de la Vieja, hardwood, 28 Jan. 1997, *Lindblad* 2608A (O 19047); Villa La Paz, 21 Apr. 2015, *Vlasák* 1504/52* (JV, TUF); Limón, Lomas Bardubal Park, 30 Jul. 2014, *Vlasák* 1407/90* (JV, H); Puntarenas, Tarcoles, Carara Nat. Park, 18 Apr. 2015, *Vlasák* 1504/21* (JV, TUF). French Guiana, Montsinéry-Tonnegrande, Patawa, 31 Aug. 2018, *Vlasák* 1808/143 (JV, H); Remire-Montjoly: Rorota, wooden bridge, 24 Aug. 2018, *Vlasák* 1808/36 (JV, H); Roura, Amazon Lodge, boardwalk, 25 Aug. 2018, *Vlasák* 1808/58 (JV, H); Sentier Molokoï, Aug. 2018, *Vlasák* 1808/87* (JV, H). Guyana, Potaro-Siparuni, Paramakatoi, fallen log, 24 Feb. 1996, *Ahti* 53384 (H).

Notes: Here we re-introduce the species based on studies of type material and newly collected and sequenced specimens from the area in which it was originally found. *Fomitopsis modesta* is distributed in the eastern and southern parts of the Caribbean, as well as in South America. Northwards, it seems to be replaced by *F. subectypa* (see below). Sequences of *F. modesta* published by Cristaldo *et al.* (2022) indicate that they belong to another, probably yet unnamed neotropical species. See further remarks under *F. atypa*.

Fomitopsis monomitica (Yuan Y. Chen) Spirin & Viner, *comb. nov.* MycoBank MB 844937.

Basionym: Antrodia monomitica Yuan Y. Chen, Mycosphere 8 (7): 882. 2017.

Typus: **China**, Heilongjiang, Harbin, *Morus* sp., 6 Aug. 2016, *Dai* 16894* (holotype BJFC 22529).

Description: Chen & Wu (2017, as A. monomitica).

Specimen examined: Russia, Primorie, Khasan Dist., hardwood log, 25 Jul. 2016, Viner KUN2550* (H).

Note: See remarks to F. oleracea.

Fomitopsis morganii (Lloyd) Spirin & Vlasák, *comb. nov.* MycoBank MB 844938.

Basionym: Trametes morganii Lloyd, Mycol. Writ. 5 (Letter 69): 15. 1919.

Typus: **USA**, Ohio, Preston, [no collection date], *Morgan* (Lloyd Herb. #53852) (**lectotype** BPI 320499!) (selected by Stevenson & Cash 1936: 145).

Description and phylogenetic data: Spirin et al. (2017, as Antrodia morganii).

Fomitopsis moritziana (Lév.) Spirin & Miettinen, *comb. nov.* MycoBank MB 848363. Figs 23, 24.

Basionym: Polyporus moritzianus Lév., Ann. Sci. Nat., Bot. 3 (5): 130. 1846.

Typus: **Indonesia**, Java, 'ad truncos', [no collection date], *Zollinger* 2061 (**syntype** PC!).

Synonyms:

Trametes pseudodochmia Corner, Beih. Nova Hedwigia 97: 138. 1989.

Typus: **Malaysia**, Sabah, Kinabalu, on a living tree, 14 Jun. 1961, *Corner* (**holotype** E00430837).





Fig 24. Basidiocarps of Fomitopsis spp. A. F. modesta (Vlasák 1808/87). B. F. moritziana (Miettinen 11662). C. F. ochracea (Miettinen 18568). D. F. ostreiformis (Miettinen 23532). E. F. perhiemata (holotype). F. F. pinicola (Niemelä 9424). G. F. pseudopetchii (Miettinen 14284). H. F. pulvina (Niemelä 9281).

Trametes fulvirubida Corner, Beih. Nova Hedwigia 97: 104. 1989.

Typus: **Malaysia**, Johore, Guning Panti, 31 Jan. 1930, *Corner* (**holotype** E00218200).

Description: Basidiocarps perennial, sessile, at first conchate, later ungulate, broadly attached, projecting up to 12 cm. Upper surface initially reddish brownish or greyish-brown, smooth, later almost black or fading to brownish grey, with distinct annual zones, occasionally cracking. Pileal edge sharp to rather blunt, concolourous with pore surface, up to 3 mm wide, sterile. Pore surface wood-coloured to brownish-arey. flat or slightly concave: pores angular, (2-)3-4 per mm, with rather thin or thick, entire dissepiments. Section: crust (present in old basidiocarps) exceptionally tough, greyish black, glancing or matt, up to 2 mm thick, context hard corky, brownish to reddish-brown, up to 3 mm thick, sharply delimited from tubes; tubes tough, clearly stratified, wood-coloured, brownish-grey or brown, in total up to 7.5 cm thick, each annual layer 2-6 mm thick, sterile tissue between tube layers absent. Hyphal structure dimitic; hyphae clamped. Context dimitic; skeletal hyphae dominating, brown, tightly interwoven, occasionally branched, (3.1-)3.2-5.9(-6.2) µm diam (n = 40/2), lumen capillary to indistinct, generative hyphae very rare, hyaline, slightly or distinctly thick-walled, 1.5-2.5 µm diam. Trama dimitic; skeletal hyphae brownish to reddish-brown, tightly interwoven, occasionally branched, sometimes twisted, (2.9-)3.1-4.1(-4.2) µm diam (n = 20/1), lumen capillary to indistinct, generative hyphae hyaline, thin-walled, infrequent, 1.5-3 µm diam. Subhymenium indistinct. Skeletocystidia present as sharp or blunt (3-4 µm diam) apices of tramal skeletal hyphae, slightly projecting above hymenium. Cystidioles not seen; hyphidia present, simple or bi-trifurcate, 1.5-2 um diam at the apex. Basidia clavate, pedunculate or occasionally pleural, 12-15 × 5-5.8 µm, rarely observed, scattered among hyphidia and skeletocystidia. Basidiospores with a distinct wall, broadly cylindrical, usually slightly concave at the ventral side, (3.8–)3.9–4.8(–5.0) × 2.0–2.3(–2.4) µm (n = 30/1), L = 4.27, W = 2.15, Q = 1.98.

Specimens examined: Indonesia, Riau, Indragiri Hulu, Bukit Tigapuluh NP, primary rainforest, fallen dicot tree, 22 Mar. 2002, *Miettinen* 4873 (BO, H). **Malaysia**, Penang, Pulau Pinang, Batu Feringgi, rainforest, on a dicot snag, 11 Feb. 2007, *Miettinen* 11662* (BORH, H).

Notes: Fomitopsis moritziana is a robust, perennial polypore developing a dark-coloured crust and having rather large pores. It is distributed in Southeast Asia (Indonesia, Malaysia) and is evidently rare. We were able to generate a single ITS sequence from one collection of *F. moritziana* (*Miettinen 11662*) which shows no close matches in the genus (Suppl. Fig. S2, as *D. pseudodochmia*). Based on morphological and DNA evidence, we concluded the earlier assumed conspecifity of *F. moritziana* (as *T. pseudodochmia*) and *F. incana* cannot be accepted (see notes to *F. incana*). *Trametes fulvirubida* evidently represents a juvenile form of *F. moritziana* and is placed in the synonymy of this species.

Fomitopsis neotropica (D.L. Lindner, Ryvarden & T.J. Baroni) Vlasák, *comb. nov.* MycoBank MB 844939.

Basionym: Daedalea neotropica D.L. Lindner, Ryvarden & T.J. Baroni, North American Fungi 6: 6. 2011.

Typus: **Belize**, Toledo, Cockscomb Ridge, Doyle's Delight, *Quercus* sp., 12 Aug. 2004, *Lindner* 04-74* (**holotype** CFMR).

Description and phylogenetic data: Lindner et al. (2011, as *D. neotropica*); see also Fig. 5.

Fomitopsis nigra (Berk.) Spirin & Miettinen, *comb. nov.* MycoBank MB 844940.

Basionym: Polyporus niger Berk., London J. Bot. 4: 304. 1845.

Typus: **USA**, Ohio, 'March, on rotten trunk', [no collection date], *Lea* 112 (holotype K, isotype PC!).

Synonym: Melanoporia nigra (Berk.) Murrill, North American Flora 9: 15. 1907.

Description: Gilbertson & Ryvarden (1987, as M. nigra).

Specimen examined: **USA**, Pennsylvania, Montgomery Co., Schwenksville, *Quercus* sp., Oct 2014, *Vlasák* 1410/10J* (JV).

Note: This species is the generic type of *Melanoporia* and closely related to other species, *M. castanea* and *M. condensa*, formerly included in that genus (see Figs 1, 3).

Fomitopsis niveomarginata L.W. Zhou & Y.L. Wei, Mycol. Progr. 11: 437. 2012.

Typus: **China**, Jilin, Antu, Changbai, *Tilia* sp., 14 Sep. 2007, *Dai* 9175* (**holotype** IFP 15643).

Description and phylogenetic data: Zhou & Wei (2012); see also Fig. 3 and Suppl. Fig. S2.

Fomitopsis nivosella (Murrill) Spirin & Vlasák, *comb. nov.* MycoBank MB 844941. Fig 23.

Basionym: Tyromyces nivosellus Murrill, North American Flora 9: 32. 1907.

Typus: **Cuba**, Guantánamo, Baracoa, El Yunque, *Roystonea regia*, Mar. 1903, *Underwood & Earle* 1114 (**holotype** NY00776435!).

Synonyms:

Tyromyces palmarum Murrill, North American Flora 9: 32. 1907.

Typus: **Cuba**, Guantánamo: Baracoa, El Yunque, *Roystonea regia*, Mar. 1903, *Underwood & Earle* 1142 (**holotype** NY00776434!).

Polyporus durescens Overh. ex J. Lowe, Mycotaxon 2 (1): 65. 1975.

Typus: **USA**, Ohio, Preble Co., West Elkton, *Fagus* sp., 28 Jul. 1917, *Overholts* 4215* (**holotype** BPI, **isotype** PRM 807350!).

Description: Basidiocarps annual, sessile or effused-reflexed, occasionally fusing together in large groups, projecting up to 7 cm. Upper surface first cream coloured, azonate, smooth, later pale ochraceous, sometimes with greyish tints, smooth or irregularly wrinkled. Pileal edge sharp to rather blunt, concolourous with cap surface, occasionally with brownish stains, fertile, sometimes incurving during drying. Pore surface cream-coloured or pale ochraceous, in older basidiocarps often reddish brownish, as a rule concave; pores roundish to angular, very rarely sinuous, (4–)5–6(–7) per mm, with thin, even or only rarely serrate dissepiments. *Section:* context rather soft, white to cream-coloured, up to 20 mm thick; tubes soft, easily cut by a razor blade, one-layered,



concolourous with hymenial surface, up to 10 mm thick. Hyphal structure dimitic; hyphae clamped. Context dimitic; skeletal hyphae hyaline or pale yellowish, densely interwoven or in subparallel bundles, occasionally branched, (2.6-)2.8-5.4(-6.2) µm diam (n = 100/5), lumen wide to almost invisible, side branches 1.5–3 um diam, generative hyphae abundant to rare, hyaline, thin- or slightly thick-walled, 2-4.5 µm diam. Trama dimitic; skeletal hyphae hyaline, interwoven, occasionally branched, (2.0-)2.2-4.0(-4.2) μ m diam (n = 120/6), lumen rather wide to capillary or indistinct, generative hyphae thin- or slightly thick-walled, 2-3.5 µm diam, in some parts dominating and producing distinct subhymenial layer up to 20-35 µm thick, dissepiment edges dimitic, consisting of thinwalled, flexuose generative hyphae and winding skeletals with a wide lumen. Cystidioles rare, tapering, 9-18 × 4-5 µm. Basidia clavate, often with a tapering basal part, (10.2-)10.9-17.0(-19.8) × (4.1–)4.2–6.8(–7.3) μ m (n = 55/5), sometimes pleural. Basidiospores thin-walled, cylindrical to fusiform, longest spores sigmoid, (4.8-)5.0-8.0(-8.3) × 1.8-3.0(-3.1) µm (n = 160/6), L = 5.89–6.91, W = 1.96–2.65, Q = 2.49–3.02.

Specimens examined: **Brazil**, Amazonas, Manaus, Nov. 1983, *de Jesus** (O F10833, SP 193509); Paraná, Antonina, Cacatu, *Syagrus romanzoffiana*, 12 Oct. 1997, *de Meijer* 3465* (O 16014). **Puerto Rico**, San Juan, Pinetas, palm tree, Jul. 2018, *Kout* 1807/19* (H). **Venezuela**, Aragua, Rancho Grande Res. Station, 14 Apr. 1999, *Ryvarden* 41410* (O 10796).

Notes: Fomitopsis nivosella is distributed in North and South America although it is evidently rarer than its look-alike, *F. marianii*. Morphological differences between the two species are discussed under *F. marianii*.

Fomitopsis oboensis (Decock, Amalfi & Ryvarden) Spirin, *comb. nov.* MycoBank MB 844942.

Basionym: Niveoporofomes oboensis Decock, Amalfi & Ryvarden, Mycol. Progr. 21 (2, no. 29): 7. 2022.

Typus: **São Tomé and Príncipe**, São Tomé, Ôbo de São Tomé National Park, *Olea capensis*, 12 Apr. 2011, *Decock* ST-11-04* (**holotype** O).

Description and phylogenetic data: Decock et al. (2022, as N. oboensis).

Fomitopsis ochracea Ryvarden & Stokland, Syn. Fung. 25: 46. 2008. Fig 24.

Typus: **Canada**, Alberta, Slave Lake, *Populus tremuloides*, 8 Jun. 2005, *Stockland* 223* (**holotype** O).

Description and phylogenetic data: Haight *et al.* (2019); see also Fig. 10 and Suppl. Fig. S5.

Specimens examined: **Canada**, Alberta, Yellowhead Co., William A. Switzer Provincial Park, *P. tremuloides*, 24 Jul. 2015, *Spirin* 8847* (H). **USA**, Idaho, Boundary Co., Upper Priest River, *Tsuga heterophylla*, 16 Oct. 2014, *Miettinen* 18865 (H); Washington, Clallam Co., Willoughby Creek, *Picea sitchensis*, 7 Oct. 2014, *Spirin* 8165* (H); Jefferson Co., Hoh River, *P. sitchensis*, 20 Oct. 2014, *Miettinen* 18984.1 (H).

Notes: This species belongs to the *F. pinicola* complex. Minor genetic differences, mating tests and a few morphological (mainly macroscopic) traits support its recognition as a separate species. See discussion under *F. pinicola* for more details.

Fomitopsis oleracea (R.W. Davidson & Lombard) Spirin & Vlasák, *comb. nov.* MycoBank MB 844943. Fig 16.

Basionym: Poria oleracea R.W. Davidson & Lombard, Mycologia 39: 317. 1947.

Typus: **USA**, Michigan, Detroit, unidentified wood, 15 Jul. 1942, *Hirt** (holotype BPI 241465).

Synonym: Antrodia oleracea (R.W. Davidson & Lombard) Ryvarden, A preliminary polypore flora of East Africa: 252. 1980.

Description: Basidiocarps annual, effused, up to 10 cm in widest dimension. Margin adnate, compact, white to cream-coloured, up to 1 mm wide. Hymenial surface even or somewhat nodulose, cream-coloured to pale-ochraceous or greyish; pores angular, 4-6 per mm, dissepiments uneven to serrate. Section: subiculum compact, white, crumbling, up to 0.5 mm thick; tubes soft, fragile, easily crumbling in dry condition, cream-coloured to greyish or pale ochraceous, 2-5 mm thick. Hyphal structure monomitic; hyphae clamped. Subicular hyphae hyaline, thin- to moderately thickwalled, interwoven to subparallel, $(2.4)2.9-5.1(-5.2) \mu m (n = 20/1)$. Tramal hyphae hyaline, thin-walled, spaced, subparallel, (2.7–)2.8– $4.1(-4.2) \mu m$ (n = 40/2), occasionally anastomosing. Subhymenium distinct, up to 20 µm thick. Cystidioles rather abundant to rare, tapering to hyphoid, $(12.1-)12.2-18.1(-18.3) \times (3.0-)3.3-5.0(-5.2)$ µm (n = 16/2). Basidia clavate, occasionally pleural, (11.4–)13.0– 19.4(-20.1) × (5.0-)5.1-6.8(-7.2) µm (n = 20/2), in senescent hymenium with slightly thickened walls. Basidiospores thin-walled or with a distinct wall, cylindrical-subfusiform, (5.0–)5.1–8.4(–8.8) × $(2.2-)2.3-3.1(-3.2) \mu m (n = 60/2), L = 6.11-6.47, W = 2.79-2.82,$ Q = 2.18–2.32.

Specimens examined: **USA**, Florida, Alachua Co., San Felasco Hammock Preserve, *Quercus* sp., 24 Nov. 2013, *Miettinen* 17902 (H); Gainesville, *Quercus* sp., 11 Aug. 1950, *Lowe* 4335 (H ex SYRF); Pennsylvania, Montgomery Co., Schwenksville, Goshenhoppen Creek, *Quercus* sp., Sep. 2010, *Vlasák* 1009/31* (JV, H).

Notes: Lowe (1966) and Gilbertson & Ryvarden (1986) described *F. oleracea* as dimitic. A culture obtained from the type specimen was sequenced (Vu et al. 2019) and the resulting ITS sequence is identical with that obtained from the specimen we studied (Vlasák 1009/31 from Pennsylvania, USA). This specimen is completely monomitic, as are two other collections from Florida we examined (Miettinen 17902 and Lowe 4335). Gilbertson and Ryvarden clearly used material of some other species when describing A. oleracea, possibly Fomitopsis dollingeri. Fomitopsis oleracea is phylogenetically closely related to F. monomitica from East Asia. Morphological differences between these species are subtle: F. oleracea has on average smaller pores (3-4 per mm in F. monomitica) and slightly wider basidiospores than F. monomitica (according to our measurements, spores in the latter species are $(5.0-)5.1-6.8(-7.1) \times (2.1-)2.2-3.1(-3.2) \mu m (n = 30/1), L = 5.74,$ W = 2.64, Q = 2.19). With so few specimens studied, it is eventually impossible to decide how constant these differences are. The species complex deserves a closer look with much wider specimen sampling.

Fomitopsis ostreiformis (Berk.) T. Hatt., Mycoscience 44 (4): 272. 2003. Figs 24, 25.

Basionym: Polyporus ostreiformis Berk., J. Linn. Soc., Bot. 16: 46. 1877.



Fig 25. Basidiospores of Fomitopsis spp. F. ostreiformis (isolectotype); F. pannucea (holotype); F. perhiemata (holotype); F. pinicola (Kotiranta 26782); F. pseudopetchii (Miettinen 14284); F. psilodermea (Vlasák 1504/34). Scale bar = 5 µm.

Typus: **Philippines**, 'Malamon Ids., 30 Jan.–4 Feb. 1875, *Challenger'* (**lectotype** K, **isolectotype** NY 00730855!) (selected by Ryvarden 1984: 349).

Synonyms:

Polyporus griseodurus Lloyd, Mycol. Writ. 5 (68): 12. 1918.

Typus: Japan, Kyoto, Kasagi, Aug. 1910, *Gono* 6 (holotype BPI US0304291!).

Tyromyces perskeletalis Corner, Beih. Nova Hedwigia 96: 187. 1989.

Typus: **Singapore**, Jurong, 'fallen and burnt trunk', 25 Dec. 1932, *Corner* (**holotype** E00604926).

Fomitopsis cana B.K. Cui, Hai J. Li & M.L. Han, Mycol. Progr. 12: 710. 2013.

Typus: **China**, Hainan, Qiongzhong, Limushan, hardwood, 24 May 2008, *Dai* 9611* (**holotype** BJFC).

Description: Basidiocarps annual, sessile or effused-reflexed, often fusing together in large imbricate groups, projecting up to 2 cm, occasionally totally resupinate and then up to 4 cm in widest dimension. Upper surface felty or smooth, greyish-ochraceous to mouse-grey, occasionally with pinkish or violet hues disappearing in herbarium specimens, sometimes with a darker brownish tint after drying, azonate, occasionally indistinctly striate. Pileal edge sharp, concolourous with cap surface, usually fertile, sometimes incurving during drying, margin of resupinate parts white or cream-coloured, slightly elevated, adnate or partly detaching, sharply delimited. Pore surface pale ochraceous to dark grey, sometimes with brownish stains, as a rule concave; pores roundish to angular, 5–8 per mm, with thin, entire or serrate dissepiments. Section: context rather soft, white, pale cream-coloured or rarely greyish, up to 3 mm thick; tubes tough, one-layered, concolourous with hymenial surface, up to 3 mm



thick. Hyphal structure dimitic; hyphae clamped. Context dimitic; skeletal hyphae almost hyaline to brownish, densely interwoven or rarely in subparallel bundles, occasionally branched, (2.8-)3.0-6.3(-7.3) μ m diam (n = 80/4), lumen varying from wide to narrow, side branches 2–3 µm diam, generative hyphae rather abundant to rare, hyaline, thin- or slightly thick-walled, 3-6 µm diam. Trama dimitic; skeletal hyphae pale ochraceous to brownish, interwoven, some flexuous, occasionally branched, (2.4-)2.8-4.3(-4.7) µm diam (n = 120/6), lumen capillary to invisible, generative hyphae thin- or slightly thick-walled, 2–3 µm diam, in some places forming subhymenial layer up to 10-15 µm thick, dissepiment edges dimitic, consisting of thinwalled generative hyphae and winding skeletals with a wide lumen. Rhomboid crystals occasionally present among tramal tissues, up to 15–20 µm in longest dimension. Cystidioles frequent to rare, gradually tapering to the apex, $10-14.5 \times 4-6 \mu m$, often collapsing at the very top. Basidia clavate, (9.7-)9.8-18.2(-18.4) × (4.3-)4.7-6.1(-6.2) µm (n = 50/5), partly glued together and covered by amorphous grainy substance. Basidiospores thin-walled, cylindrical to fusiform, (4.1-) $4.2-7.3(-7.6) \times (2.0-)2.1-3.0(-3.1) \ \mu m \ (n = 180/6), \ L = 5.43-5.96,$ W = 2.47–2.59, Q = 2.14–2.38.

Specimens examined: Australia, Northern Territory, Buley Rockhole, Lichfield National Park, unidentified wood, 25 Jan. 2014, Barrett F118/14 (MEL 2382710A). China, Yunnan, Xishuangbanna Botanical Garden, Bambusoidae, 7 Aug. 2005, Miettinen 10071* (H). India, Gujarat, Bhavnagar, unidentified wood, 16 Jun. 1989, Yesodharan KY44 (O 12724). Indonesia, Papua Barat, Manokwari, Amban, Azadirachta indica, 5 Feb. 2007, Miettinen 11629* (MAN, H); Riau, Kampar, Balung, 24 Dec. 2006, Miettinen 11279.2 (BO, H); Pekanbaru, Sukajadi, Mangifera indica, 12 Nov. 2018, Miettinen 21986* (BO, H); Rokan Hilir, Sungai Majo, Koompassia malaccensis, 8 Jul. 2004, Miettinen 8854.1* (H); Teluk Nilap, Sapotaceae, 10 Jul. 2004, Miettinen 8879 (BO, H); Siak, Kampar Peninsula, Beruk S, 14 Apr. 2002, Miettinen 5912 (BO, H). Kenya, Western Province, Kakamega, Yala River, 21 Jan. 1970, Ryvarden 5556 (O 18054). Singapore, Windsor Nature Park, Hevea brasiliensis, 22 Mar. 2020, Miettinen 23661 (H); Yishun, Nee Soon pipeline, dicot, 17 Mar. 2020, Miettinen 23532 (SING, H). Sri Lanka, Beruwela, Plumeria obtusa (hanging branch), 15 Feb. 2003, Dämmrich (O 18269, H*).

Notes: Fomitopsis ostreiformis is a South Asian species, reaching East Africa (Kenya) as the westernmost point of its distribution, and northern Australia in the south. Morphologically, it is most similar to *F. luzonensis*; differences are listed under *F. luzonensis*. Basidiocarps of *F. ostreiformis* are macroscopically extremely variable, and pore size varies considerably between pileate and resupinate fruitbodies (6–8 vs. 5–6 pores per mm). See further remarks under *F. meliae*.

Fomitopsis palustris (Berk. & M.A. Curtis) Gilb. & Ryvarden, Mycotaxon 22 (2): 364. 1985.

Basionym: Polyporus palustris Berk. & M.A. Curtis, Hooker's J. Bot. 1: 102. 1849.

Typus: **USA**, South Carolina, Santee River, *Pinus palustris*, [no collection date], *Ravenel* 1566 (**lectotype** K(M) 170428!) (selected by Ryvarden 1977: 223).

Description: Basidiocarps annual, pileate, sessile, often solitary, rarely fusing together in groups of 2-3, projecting up to 5.5 cm. Upper surface first cream coloured to pale ochraceous, azonate, finely velutinous, later greyish-ochraceous to brownish, smooth. Pileal edge sharp, concolourous with cap surface, fertile. Pore surface cream-coloured or pale ochraceous, sometimes with brownish stains, as a rule concave; pores roundish to angular, (4-)5-7(-8) per mm, with thin, entire or servate dissepiments. Section: context soft corky, white to cream-coloured, up to 15 mm thick; tubes rather soft, easily cut by a razor blade, one-layered, concolourous with hymenial surface, up to 5 mm thick. Hyphal structure dimitic; hyphae clamped. Context dimitic; skeletal hyphae hyaline, mostly loosely interwoven, occasionally branched, (3.0-) 3.3-7.2(-8.1) µm diam (n = 60/3), with a variably pronounced lumen, generative hyphae thin- to moderately thick-walled, 3-5 µm diam. Trama dimitic; skeletal hyphae hyaline, loosely interwoven, some flexuous, occasionally branched, (2.7-)2.8-4.8(-5.0) µm diam (n = 80/4), swelling in KOH and CB, lumen usually rather wide, generative hyphae thin- or slightly thick-walled, 2.5-4 µm diam, producing distinct subhymenial layer up to 35-40 µm thick. Rhomboid or cubical crystals occasionally present among context and tramal tissue, solitary or in large groups, up to 8 µm in widest dimension. Cystidioles infrequent, tapering, 14.5–18 × 3.5–6.0 µm. Basidia clavate, often with a tapering basal part, (13.4-)13.8-22.1(-22.2) × (5.6-)5.7-7.2(-7.4) µm (n = 44/4), sometimes pleural. Basidiospores thin-walled, cylindrical to fusiform, longest spores sigmoid, (6.1–)6.2–8.2(–9.2) × (2.3–)2.4–3.7(–3.9) µm (n = 120/4), L = 6.96–7.21, W = 2.80–3.11, Q = 2.34–2.50.

Specimens examined: Belize, Cayo, Douglas d'Silva, Pinus sp., 20 Nov. 2001, Ryvarden 44439* (O 17631); Five Sisters, Pinus caribaea, 2 Nov. 2002, Ryvarden 45413 (O 18279). USA, Florida, Manatee Co., Duette Preserve, Pinus ellitottii, 8 May 2016, Dollinger 782* (JV, H, PRM944378); Polk Co., Arbuckle Creek, Pinus clausa, Apr. 2019, Vlasák Jr. 1904/1-J* (JV, H); Georgia, Laurens Co., Dublin, Pinus sp., 3 Aug. 1950, Lowe 4092* (PRM 559516); Louisiana, Shreveport, Pinus sp., 13 Oct. 1913, Bartholomew (Fungi Columbiani #4449, H).

Notes: Earlier sequences of *F. palustris* from USA and Japan are based on misidentified material and in fact belong to *F. marianii* (see above). Here we re-introduce the species based on type material and newly sequenced specimens. *Fomitopsis palustris* is restricted to warm-temperate or subtropical areas of the eastern part of North America, and it occurs exclusively on wood of *Pinus* spp. (*P. palustris, P. caribaea* and other southern pines). Morphologically,

it is most similar to *F. marianii* and *F. nivosella*, and it differs from them mainly due to host specificity and rather small basidiocarps. Microscopically, long and wide basidia and basidiospores make *F. palustris* distinguishable from the two latter species. The single European record of *F. palustris* (Rivoire 2020) belongs to *F. marianii*.

Fomitopsis pannucea Runnel & Spirin, *sp. nov.* MycoBank MB 844944. Fig 25.

Typus: **French Guiana**, Roura, Patawa, 4.55410° -52.15245°, cut angiosperm log, 14 Nov. 2014, *Runnel* 824* (**holotype** TUF130274).

Etymology: Pannuceus (Lat., adj.) - shabby, frayed.

Description: Basidiocarps annual, sessile, dimidiate, projecting up to 1.5 cm, occasionally fusing together. Upper surface creamcoloured to greyish, smooth or finely pubescent, even. Pileal edge blunt, concolourous with pileal surface, sterile, up to 0.5 mm wide. Pore surface cream-coloured to greyish, flat or slightly concave; pores roundish to angular, 2-3 per mm, with rather thin, entire or serrate dissepiments. Section: context soft leathery, creamcoloured, up to 1 mm thick; tubes soft leathery, one-layered, concolourous with hymenial surface, up to 7 mm thick. Hyphal structure dimitic; hyphae clamped. Context dimitic; skeletal hyphae hyaline to brownish, loosely interwoven, occasionally branched, (3.2-)3.4-4.7(-5.2) µm diam (n = 20/1), lumen narrow to capillary, side branches 2–2.5 µm diam, generative hyphae rather rare, hyaline, slightly thick-walled, 2-3 µm diam. Trama dimitic; skeletal hyphae dominating, hyaline to brownish, loosely interwoven, occasionally branched, $(2.8-)2.9-4.1(-4.2) \mu m$ diam (n = 20/1), lumen mostly narrow to capillary, generative hyphae abundant, thin- to slightly thick-walled, 2-3.5 µm diam. Subhymenium distinct, up to 20 µm thick. Skeletocystidia present as slightly swollen (up to 4 µm diam) apices of tramal skeletal hyphae, slightly projecting above hymenium. Cystidioles abundant, tapering, 11–16 × 3–4 µm. Basidia clavate to long clavate, (13.1-)13.2-20.0(-21.8) × (4.2-) 4.3–5.3(–6.0) μ m (n = 20/1), occasionally pleural, in senescent hymenium slightly thick-walled and encrusted by amorphous grainy matter. Basidiospores with a distinct wall, narrowly ellipsoid, longest spores subfusiform, (4.0–)4.1–5.2(–5.3) × (2.0–)2.1–3.1(–3.2) µm (n = 30/1), L = 4.49, W = 2.49, Q = 2.16.

Notes: Of the South American *Fomitopsis* species, *F. pannucea* is most similar to *F. leioderma*. It differs from the latter species in having slightly paler and softer basidiocarps with somewhat larger pores, rather abundant generative hyphae forming a distinct subhymenial layer, as well as shorter basidiospores. Despite their high outward similarity, these species are not closely related. *Fomitopsis pannucea* is so far known only from the type locality in French Guiana.

Fomitopsis perhiemata Viner & Spirin, *sp. nov.* MycoBank MB 844945. Figs 24, 25.

Typus: **Russia**, Krasnodar Reg., Sochi, Krasnaya Polyana, Melnichnyi, 43.69414° 40.20198°, *Quercus petraea* (base of living tree), 3 May 2021, *Viner* 2021/35* (**holotype** H7200198).

Etymology: Perhiematus (Lat., adj.) - overwintered.

Description: Basidiocarps perennial, effused-reflexed, projecting up to 2.5 cm. Upper surface greyishbrown, occasionally with a light pinkish tint, smooth, growing margin paler, light grey or
pale ochraceous. Pileal edge blunt, concolourous with pileal margin, sterile, up to 2 mm wide. Pore surface grey to greyish brown, slightly concave; pores angular, 5-7 per mm, with rather thick, entire or serrate dissepiments. Section: context soft-corky, pinkish brown to brown, up to 5 mm thick; tubes corky, indistinctly stratified, concolourous with hymenial surface, up to 12 mm thick. Hyphal structure dimitic; hyphae clamped. Context dimitic; skeletal hyphae dominating, reddish-brown to brown, loosely interwoven, occasionally branched, (3.9-)4.0-5.0(-5.2) µm diam (n = 20/1), lumen mostly narrow to indistinct, side branches 2-3 µm diam, generative hyphae rare, hyaline, slightly thick-walled, 2-3.5 µm diam. Trama dimitic; skeletal hyphae dominating, brown, rather loosely interwoven, occasionally branched, (2.4–)2.8–3.8(–3.9) µm diam (n = 20/1), lumen mostly capillary to indistinct, side branches 2-2.5 µm diam, generative hyphae thin- or slightly thick-walled, 2-3 µm diam. Subhymenium indistinct. Cystidioles abundant, distinctly tapering, 12–18 × 3–6 µm. Basidia clavate, (12.1–)12.8–16.1(–16.3) \times (4.3–)5.0–6.3(–6.4) µm (n = 20/1), senescent basidia slightly thick-walled and partly glued together. Basidiospores thin-walled or with a distinct wall, broadly cylindrical to narrowly ellipsoid, longest spores subfusiform, (4.0–)4.1–5.2(–5.3) × (2.0–)2.1–3.0(–3.1) µm (n = 30/1), L = 4.50, W = 2.40, Q = 1.89.

Notes: Fomitopsis perhiemata is introduced here as a member of the *F. rosea* complex (Fig. 12). So far, it was collected once in Caucasus from a living oak tree. Both macroscopically and anatomically, it is similar to the East Asian *F. ussuriensis* which also grows mainly on *Quercus* spp. The latter species differs from *F. perhiemata* in having more regular and slightly smaller pores, 6–7 per mm, and a clearly stratified tube layer (see Table 4).

Fomitopsis philippinensis (Murrill) Spirin & Vlasák, *comb. nov.* MycoBank MB 844946.

Basionym: Fomes philippinensis Murrill, Bull. Torr. Bot. Club 34: 477. 1907.

Typus: **Philippines**, Luzon, Bataan, Mt. Mariveles, dead trunk, 23 Mar. 1904, *Williams* (holotype NY00780679!).

Description: Basidiocarps perennial, sessile, conchate, solitary or in groups, projecting up to 10 cm. Upper surface first greyishbrown, then darkening to almost black, with several distinct annual zones and occasional radial fissures, in old specimens fading to ochraceous-brownish, densely longitudinally cracking, growing margin much paler, beige to pale ochraceous. Pileal edge sharp or rather blunt, concolourous with hymenial surface, first sterile, up to 1 mm wide, then fertile. Pore surface wood-coloured or beige, then ochraceous or brownish, slightly concave; pores roundish, 6-7 per mm, with thick, entire dissepiments. Section: crust dark brown to black, tough, up to 1 mm thick, context corky, pale ochraceous to brownish, up to 8 mm thick; tubes corky, stratified, concolourous with hymenial surface, up to 15 mm thick, sterile tissue often present between annual layers. *Hyphal structure* dimitic; hyphae clamped. Context dimitic; skeletal hyphae dominating, almost hyaline to yellowish or brownish, densely interwoven, richly branched, (3.0-) 3.2-5.1(-5.2) µm diam (n = 40/2), lumen rather wide to indistinct, side branches 2-3 µm diam, generative hyphae rare, hyaline, thickwalled, 2–2.5 µm diam. Trama dimitic; skeletal hyphae dominating, yellowish to brownish, densely interwoven, occasionally branched, (2.2-)2.3-4.4(-5.0) µm diam (n = 60/3), lumen mostly capillary to indistinct, side branches 1.5-2.5 µm diam, generative hyphae rare, thin- or slightly thick-walled, 1.5-3 µm diam. Subhymenium indistinct. Skeletocystidia occasionally present as slightly swollen (up to 5.5 µm diam) apices of tramal skeletal hyphae, embedded or slightly projecting above hymenium. Cystidioles abundant, tapering, 8–12 × 3–4 µm. *Basidia* clavate, (8.0–)8.9–12.8(–13.2) × (3.9–)4.0–5.1(–5.3) µm (n = 20/2), senescent basidia slightly thick-walled and partly glued together. *Basidiospores* thin-walled, cylindrical to broadly cylindrical or narrowly ellipsoid, (3.1–)3.2– $5.0(-5.2) \times (1.9–)2.0-2.3(-2.8)$ µm (n = 48/3), L = 3.87–4.12, W = 2.11–2.15, Q = 1.83–1.92.

Specimens examined: India, Assam, 27 Aug. 1934, Parkinson (O 10853, H). Indonesia, Jambi, Bukit Perekas, 30 May 1995, *Núñez* 822 (O 10854, H). Malaysia, Sabah, Kinabalu, Sep. 1931, *Clemens* (O 10795, H). Thailand, Chiang Mai, Doi Inthanon, fallen log, 20 Feb. 1979, *Ryvarden* 17840* (O, H); Sukhotai, Khiri Mat, Ramkamhaeng, 12 Aug. 2014, *Kout* 1408/K2* (JV, H).

Notes: Fomitopsis philippinensis is a member of the *F. dochmia* complex distributed in Southeast Asia. It differs from *F. elevata*, another species from this group distributed in the same geographic region, in having a darker and clearly stratified tube layer, as well as distinctly rimose pileal surface strongly fading in senescent basidiocarps. Our data confirm the presence of *F. philippinensis* in Indonesia (Sumatra), Malaysian Borneo, Thailand and the easternmost part of India (Assam), in addition to the type locality in Philippines. ITS sequences labelled as *F. dochmia* in GenBank (DQ491401, MG719293) belong to *F. philippinensis*.

Fomitopsis pinicola (Sw.) P. Karst., Meddeland. Soc. Fauna Fl. Fenn. 6: 9. 1881. Figs 24, 25.

Basionym: Boletus pinicola Sw., K. Svenska Vetensk.-Akad. Handl. 2, 31: 88. 1810.

Typus: Plate 953 in Flora Danica 16, 1787 (**iconotype**) (selected by Ryvarden 1991: 149).

Description: Ryvarden et al. (2017).

Specimens examined: China, Jilin, Antu, Huangshongpu, Larix sp., 27 Jul. 1993, Dai 759 (H); Fushong, Shongjianghe, Larix sp., 4 Jun. 1993, Dai 261 (H). Czech Republic, South Bohemia, České Budějovice, Hluboká nad Vltavou, Picea abies, 19 May 2019, Vlasák 1905/1* (H). Finland, Uusimaa, Helsinki, Koskela, Alnus incana, 2 Oct. 2016, Miettinen 20458 (H); *ibid.*, 6 Apr. 2008, Miettinen 12391* (H); Satakunta, Viljakkala, Niemelä, Betula sp., 12 Aug. 2019, Niemelä 9425 (H). Poland, Podlasie, Hajnówka, Białowieża, *T. cordata*, 12 Sep. 2009, Niemelä 8625 (H). Russia, Bashkortostan, Bashkirian Nat. Park, Nugush, Betula sp., 1 Aug. 2012, Kotiranta 25428 (H); Chukotka, Anadyr' Dist., Beringovski, coniferous timber, 30 Aug. 2009, Kotiranta 27183* (H); Khabarovsk Reg., Solnechnyi Dist., Gorin, *L. gmelinii*, 13 Aug. 2011, Spirin 4111* (H); Tuva, Turgen, Larix sibirica, 23 Aug. 2014, Kotiranta 26782* (H). USA, Washington, Clark Co., Gifford Pinchot Nat. Forest, Tsuga heterophylla, 11 Oct. 2014, Spirin 8367* (H).

Notes: Ryvarden & Stokland (2008) were first to address species delimitation in the *F. pinicola* complex. Based on morphological and geographic evidence, they introduced *F. ochracea*, a species with a North American distribution. Haight *et al.* (2016, 2019) significantly expanded sampling in this group for their three-gene analyses. They found several lineages, which allowed them to introduce two more North American species, *F. mounceae* and *F. schrenkii* and exclude *F. pinicola sensu stricto* from the American mycota. Later Liu *et al.* (2021) further expanded sampling by a number of sequences from East Asia, an area which was poorly covered in the previous studies.

Our phylogenetic analyses constantly resolve *F. ochracea* as a separate clade. *Fomitopsis schrenkii* (including the genome strain *FP-58527*) receives decent support only in the three-gene analyses (BI pp = 0.99, ML bs = 96 %; Fig. 10), but is nestled among the rest of *F. pinicola sensu lato* sequences in the ITS+*TEF1* tree (Suppl. Fig. S5). As for all other North American sequences from Haight *et al.* (2016, 2019), our analyses do not resolve *F. mounceae* and the rest of *F. pinicola* as mutually exclusive clades – *F. mounceae* is not supported.

Why this different pattern? The first reason is the difference in genetic datasets. We detected only five parsimony informative sites across the three DNA loci (ITS, *TEF1*, *RPB2*) that distinguish *F. mounceae* unambiguously from European *F. pinicola*. These sites might have yielded support for the separate European *F. pinicola* and the American *F. mounceae* clades in analyses with Haight *et al.* (2016, 2019). However, adding more sequences from a wider geographic area to our analyses led to an attenuation of the phylogenetic signal and lack of support for separate lineages due to an increase in polymorphic sites. Consequently, after adding more sequences, the number of nucleotide positions that separate *F. mounceae* unambiguously from the Eurasian *F. pinicola* drops from five to two positions. Both of these positions are in ITS, and none remained in *RPB2* and *TEF1*. Further sampling would likely reduce this number even more.

The second reason for the differences is that Haight et al. (2016, 2019) draw their conclusions based on a coalescent method. Haight et al. (2016) explained that they preferred this method due to its greater performance in phylogenetic resolution where reciprocal monophyly of the separate DNA loci has not been achieved, which was the case in their three-gene analyses. However, usefulness of coalescent models for the species recognition has been contested, especially for species with allopatric distribution, which is the case for North American and Eurasian populations of the F. pinicola species complex. Addressing this theoretical question, Sukumaran & Knowles (2017) and Leaché et al. (2019) came to the conclusion that such models cannot discern a true speciation event from geographically structured intraspecific variation. The application of coalescent models may still be useful for cases when analysed DNA loci are strongly incongruent due to such phenomena as incomplete lineage sorting or hybridization events (Degnan & Rosenberg 2009). This is not the case for F. pinicola complex, where trees of independent markers do not yield any mutually exclusive clades (Haight et al. 2016, our analysis - data not shown). Though we point out limitations of the coalescent approach, it is not the aim of this paper to judge between different analysis methods. Here we have consistently relied on phylogenetic analyses of concatenated datasets for taxonomic conclusions. Whatever the analysis method, there is no substitute for a high-quality dataset with enough informative characters and geographic coverage.

While the conclusions reached by Haight *et al.* (2016, 2019) may have been supported by their geographically limited dataset, the situation is different for the recently introduced Asian species. We see no obvious genetic pattern, which could justify the description of six more species from the *F. pinicola* complex by Liu *et al.* (2021). Re-running their phylogenetic analyses was not possible as the corresponding alignment was not traceable in TreeBase, but we see that it could suffer from a "gappy" alignment approach. The concatenated alignment assembled by Liu *et al.* contained a lot of missing data. A number of specimens were represented by just two loci while missing the third one; in the case of *F. tianshanensis*, all specimens lack the third DNA locus (*RPB2*). Such pattern of missing data could be problematic for the phylogenetic analysis (Hartmann

& Vision 2008), but Liu *et al.* did not mention any statistical methods compensating for the missing data. Besides that, they excluded a number of Haight *et al.* (2016, 2019) specimens with all three loci sequenced, which could have been integrated in the analyses.

Based on the current genetic evidence, including our phylogenetic analyses, we question whether the *F. pinicola* complex consists of as many species as currently recognized based on our phylogenetic analyses. Our results do not preclude the existence of genetically isolated lineages within the *F. pinicola* group, especially considering the strong internal phylogenetic structure of the complex but the division into eight separate species seems unwarranted.

Previous mating tests between European, North American and East Asian material have identified two intersterility groups in the *F. pinicola* complex (Mounce & Macrae 1938, Högberg *et al.* 1999), with only one group present in Eurasia. Conveniently, Haight *et al.* (2019) used DNA data to connect four old cultures utilized in mating tests by Mounce & Macrae (1938) to four currently recognized species: *F. ochracea, F. mounceae, F. schrenkii*, and *F. pinicola sensu stricto.* They found that *F. ochracea* belongs to a group intersterile with the other three species, which were all compatible. This pattern corresponds well with the phylogenetic position of *F. ochracea* at the deepest split of the *F. pinicola* clade. Positive results of mating tests (*i.e.* interfertility) are not conclusive evidence that significant mating takes place in the natural environment, but clearly the bar for recognizing interfertile populations as species should be high.

Another line of evidence to distinguish species came from morphological data. In our opinion, only the North American F. ochracea can be separated from all the other representatives of the F. pinicola complex with some confidence. However, their morphological differences are not as obvious as presented by Ryvarden & Stockland (2008) and Haight et al. (2019). Inconveniently, most specimens of F. ochracea are sterile or contain juvenile spores only. These spores are often still attached to basidia and clearly thin-walled. We studied and measured two collections of F. ochracea with ripe basidiospores possessing slightly thickened wall (this feature is also characteristic for F. pinicola sensu stricto). They were clearly larger than described in the two aforementioned sources, *i.e.* (4.9–)5.0–6.2(–6.8) × (3.4–)3.6–5.2 µm (n = 60/2), L = 5.49–5.74, W = 3.91–4.13, Q = 1.40–1.41. Their average values are exactly between the East Asian specimens of the F. pinicola complex and the rest of the collections from Europe, North America and Siberia studied by us, severely restricting usability of spore size as a separating character. The easiest way to identify F. ochracea is to carefully check the macroscopic characters: the absence of a resinous substance in the crust (no signs of melting in a flame) and a pale-coloured, almost white growing margin, as well as rather small (5-6 per mm) pores, are the most stable morphological features of this species.

Basidiospore dimensions of the American *F. mounceae* and *F. schrenkii*, as reported by Haight *et al.* (2019) and corroborated by our own limited measurements, fall within the variation range of *F. pinicola* from Europe and Siberia. The Eurasian specimens excluding East Asian collections measure $(5.9-)6.0-9.2(-10.2) \times (3.0-)3.1-5.0(-5.1) \mu m (n = 150/5), L = 6.51-7.64, W = 3.58-4.06, Q = 1.61-2.15$. All of them have a resinous pileal crust melting over a flame, and other morphological traits (pore size, basidiocarp colour, *etc.*) do not separate them either.

As for the East Asian taxa, we do not regard the morphological differences (pore and spore size) reported by Liu *et al.* (2021) as sufficiently strong evidence for maintaining them as separate

species. While the protologues of *F. abieticola* and *F. tianshanensis* describe normal *F. pinicola*, *F. subpinicola* is different in several respects. We studied several (and sequenced two) specimens from temperate to boreal East Asia, which likely represent this taxon. They have smaller pores than *F. pinicola* from Europe and Siberia (5–7 vs. (2–)3–4 per mm) and their basidiospores are also smaller, $(4.0-)4.2-6.1(-6.3) \times (2.8-)3.0-4.1(-4.2) \mu m (n = 120/4), L = 4.97-5.23, W = 3.36-3.44, Q = 1.44-1.54. The same differences from$ *F. pinicola*are intrinsic to the other three species introduced in the same paper,*F. hengduanensis, F. kesiyae*, and*F. massoniana*and, besides them, to*F. subungulata*, described from Philippines over a hundred years ago. Nevertheless, small pore and spore size are characteristic of the East Asian*F. pinicola sensu lato*, regardless of how many lineages are recognized.

The fourth line of reasoning leading to the splitting of the F. pinicola complex into many species (in addition to DNA, mating tests and morphology) is that according to current information they all originate from different areas (except for the F. ochracea / F. mounceae pair separated by other traits). Considered together, the structure of genetic variation and morphological trends point to geographic differentiation within the F. pinicola complex. We argue that this variation is currently best interpreted as intraspecific variation, possibly warranting recognition of some subspecies such as F. schrenkii, rather than accepting ambiguous species of which three are found only in their type localities. Moreover, a proper revision of F. pinicola in East Asia is impossible without re-establishing the identity of Polyporus thomsonii Berk. from northern India and Fomes subungulatus Murrill from Philippines, both currently listed among the synonyms of F. pinicola (Ryvarden 1977, 1985).

In conclusion, current data do not support the division of *F. pinicola* into many species, with the exception of *F. ochracea*. At the same time, the observed pattern of geographic variation does not exclude the possibility of more than two species. Therefore, we treat *F. abieticola*, *F. hengduanensis*, *F. kesiyae*, *F. massoniana*, *F. mounceae*, *F. schrenkii*, *F. subpinicola*, *F. tianshanensis* and *Fomes subungulatus* as insufficiently known taxa. We call for solid evidence in the form of deeper genetic sampling based on a large number of spatially representative specimens and/or mating tests, before any of these names are accepted. Studies on *Heterobasidion* spp., conifer-dwelling polypores, offer an example of how to approach the question (Dai et al. 2003, Chen et al. 2015). Clearly, the *F. pinicola* complex will offer a highly interesting research subject on speciation and population genetics for years to come.

Fomitopsis primaeva (Renvall & Niemelä) Miettinen & Niemelä, *comb. nov.* MycoBank MB 844947.

Basionym: Antrodia primaeva Renvall & Niemelä, Karstenia 32: 30. 1992.

Typus: **Finland**, Sompion Lappi, Savukoski, Urho Kekkonen Nat. Park, *Pinus sylvestris*, 19 Sep. 1988, *Renvall* 1372 (**holotype** H!).

Description: Renvall & Niemelä (1992, as A. primaeva).

Note: For phylogenetic placement, see Spirin et al. (2013b, 2017).

Fomitopsis pseudopetchii (Lloyd) Ryvarden, Norw. J. Bot. 19: 231. 1972. Figs 24, 25.

Basionym: Fomes pseudopetchii Lloyd, Mycol. Writ. 7 (69): 1202. 1923.

Typus: Indonesia, Sumatra, Kisaran Asahan, 1923, *Yates* (lectotype K (M) 264878!) (selected by Ryvarden 1972: 231).

Synonym: Tyromyces singularis Corner, Beih. Nova Hedwigia 96: 194. 1989.

Typus: **Solomon Ids.**, Guadalcanal, Mt. Gallego, 3 Jul. 1965, *Corner* (holotype E00604897).

Description: Basidiocarps perennial, sessile or pendant, ungulate, projecting up to 4 cm. Upper surface first greyish-white to brownishgrey, smooth, matt, then covered by brownish-black or black, sulcate, shining crust. Pileal edge blunt, greyish to brownish, sterile, up to 1 mm wide. Pore surface first greyish-white to creamcoloured, then brownish, concave or flat; pores roundish or angular, 7-10 per mm, with thin, entire disseptiments. Section: crust grey to brownish-black, 0.2-1 mm thick, context soft corky, easily crumbling, cream-coloured to pale ochraceous, up to 5 mm thick; tubes chalk-like, easily crumbling, indistinctly stratified, up to 15 mm thick, concolourous with hymenial surface. Hyphal structure dimitic; hyphae clamped. Context dimitic; skeletal hyphae hyaline to brownish, interwoven, easily crumbling, occasionally branched, (2.0-)2.1-5.0(-5.1) µm diam (n = 40/2), lumen mostly capillary to indistinct, side branches 2-3 µm diam, generative hyphae rare, hyaline, slightly or distinctly thick-walled, 1.5-4 µm diam. Trama dimitic; skeletal hyphae sparse (and then trama seemingly monomitic) to abundant, hyaline to brownish, loosely interwoven, crumbling or sturdy, often covered by small angular crystals or sand-like deposits, occasionally branched, (1.8-)1.9-3.5(-3.8) μ m diam (n = 60/3), lumen varying from rather wide to capillary or indistinct, generative hyphae rather abundant and in some parts dominating, thin- to slightly thick-walled, 2-3.5 µm diam. Subhymenium well-differentiated in younger part of tubes, up to 10 μ m thick. Cystidioles rather frequent, tapering, 9–16 × 3–5 μ m. Basidia clavate, (9.0–)9.4–11.8(–12.7) × (4.0–)4.1–6.2(–6.3) µm (n = 13/2), in senescent hymenium partly glued together and covered by sand-like deposits. Basidiospores with a distinct wall, ellipsoid to narrowly ellipsoid, more rarely broadly cylindrical, (2.6-)2.7-4.0(-4.1) × (1.6-)1.7-2.3(-2.4) µm (n = 71/3), L = 3.23-3.35, W = 1.98–2.16, Q = 1.56–1.60.

Specimens examined: Indonesia, Papua Barat, Manokwari, Amberbaken, Anjii, *Pometia pinnata* (fallen tree), 1 Nov. 2010, *Miettinen* 14284* (H); Minjanbiat, *P. pinnata* (felled tree), 3 Nov. 2010, *Miettinen* 14373.1* (H). Malaysia, Johor, Gunong Panti, 31 Jan. 1930, *Corner* (O 10856, H).

Notes: Perennial basidiocarps with multilayered, pale, soft tubes, spaced, easily crumbling skeletal hyphae and small basidiospores make *F. pseudopetchii* morphologically highly similar to *F. caseosa* and *F. niveomarginata*. In spite of their superficial similarity, these species are not closely related (Fig. 3, Suppl. Fig. S2). Morphological differences of *F. pseudopetchii* from *F. caseosa* are discussed under the latter species. In turn, *F. niveomarginata* possesses robust, often effused-reflexed basidiocarps with larger (5–6 per mm) pores than in *F. pseudopetchii*.

Hattori (2003) re-described *F. singularis* with convincing details as similar to *F. pseudopetchii*. We studied one collection (*Miettinen 14284*) with a rudimentary, pale-coloured pileal crust and almost monomitic tubes, which were considered the main diagnostic features of *F. singularis vs. F. pseudopetchii*. However, ITS sequence obtained from this species showed only 1 bp difference from that one of *F. pseudopetchii*. Therefore, we tentatively treat *F. singularis* as a synonym of *F. pseudopetchii*. As interpreted here, *F.*



pseudopetchii is a rare species distributed in South-East Asia and adjacent areas of Oceania.

Fomitopsis psilodermea (Berk. & Mont.) Spirin & Vlasák, *comb. nov.* MycoBank MB 848364. Figs 25, 26.

Basionym: Polyporus psilodermeus Berk. & Mont., Ann. Sci. Nat., Bot. 3 (11): 239. 1849.

Typus: **Brazil**, Bahia, 'ad truncos', [no collection date], *Blanchet* (**holotype** PC!).

Synonym: Trametes supermodesta Ryvarden & Iturr., Mycologia 95 (6): 1074. 2003.

Typus: **Venezuela**, Bolívar, Las Nieves, hardwood log, 12 Jun. 1995, *Ryvarden* 37779 (**isotype** O!).

Description: Basidiocarps short-living perennial, sessile, dimidiate or with a contracted base (fan-shaped), projecting up to 3 cm. Upper surface first beige to pale ochraceous, smooth, indistinctly zonate, later ochraceous-brownish to dark brown. Pileal edge sharp to rather blunt, concolourous with hymenial surface, first sterile, up to 1 mm wide, then fertile. Pore surface cream-coloured or beige to pale ochraceous, sometimes with pinkish or grevish tint, flat or concave; pores angular to sinuous, occasionally fusing together, 3-4 per mm, with thin or rather thick, entire or serrate dissepiments. Section: context leathery, cream- to wood-coloured, normally less than 2 mm thick; tubes corky, one-layered, concolourous with hymenial surface, up to 2 mm thick. Hyphal structure dimitic; hyphae clamped. Context dimitic; skeletal hyphae brownish, interwoven, occasionally branched, $(2.8-)2.9-4.3(-4.4) \mu m$ diam (n = 40/2), lumen narrow to indistinct, side branches 1.5-2.5 µm diam, generative hyphae infrequent, hyaline, slightly to distinctly thick-walled, 2-3.5 µm diam. Trama dimitic; skeletal hyphae dominating, brownish, interwoven, occasionally branched, (2.7-)2.8-4.1(-4.2) µm diam (n = 60/3), lumen mostly capillary to indistinct, side branches 1.5-2 µm diam, generative hyphae thin- to slightly thick-walled, 2-3.5 µm diam. Subhymenium distinct in some parts, up to 15-20 μ m thick. Cystidioles infrequent, tapering, 12–15 × 3–4 μ m. Skeletocystidia present as slightly swollen (up to 4 µm diam), acute or blunt apices of tramal skeletal hyphae, slightly projecting above hymenium. Basidia clavate, (12.4-)13.2-19.2(-20.0) × $(4.4-)4.8-5.8(-6.0) \mu m$ (n = 20/2). Basidiospores with a distinct wall, broadly cylindrical to narrowly ellipsoid, longest spores subfusiform, $(5.0-)5.1-8.1(-8.2) \times (2.0-)2.1-3.1(-3.2) \mu m$ (n = 60/2), L = 5.55-6.42, W = 2.34-2.74, Q = 2.35-2.39.

Specimens examined: Brazil, Roraima, Alto Alegre, Maraca Res., 13 Mar. 1987, *Edwards* (O 17841 ex K). Costa Rica, Puntarenas, Golfito, Piedras Blancas Nat. Park, *Peltogyne* sp., 20 Apr. 2015, *Vlasák* 1504/34* (JV, TUF).

Notes: Fomitopsis psilodermea is a neotropical species from the Daedalea clade (Fig. 5). Morphologically, it is most similar to *F. leioderma*. It differs from the latter species in having a darker pileal surface and longer basidiospores. Another similar-looking species, *F. subectypa*, has distinctly smaller pores and basidiospores. We studied the types of *P. psilodermeus* and *T. supermodesta*, as well as two recent specimens from the neotropics, and concluded that they seem to be conspecific. However, small differences can be found in spore size, as well as in the shape and colour of basidiocarps. Therefore, we cannot preclude that *F. psilodermea* as

interpreted here may turn out a species complex. More material is needed to solve this problem.

Fomitopsis pulverulenta (Rivoire) Rivoire, *comb. nov.* MycoBank MB 844949.

Basionym: Antrodia pulverulenta Rivoire, Bull. Mens. Soc. Linn. Lyon 79 (7–8): 185. 2010.

Typus: **France**, Savoie, Les Avanchers, Valmorel, *Sorbus aucuparia*, 20 Jul. 2008, *Rivoire* (**holotype** LY BR-3413!).

Description: Rivoire (2010, as A. pulverulenta).

Note: The species is a member of the *Fomitopsis pulvinascens* complex (Spirin *et al.* 2013b).

Fomitopsis pulvina (Pers.) Spirin & Vlasák, *comb. nov.* MycoBank MB 844950. Fig 24. *Basionym: Boletus pulvinus* Pers., Obs. Mycol. 2: 7. 1799.

Typus: **Czech Republic**, Jihočeský kraj, České Budějovice, Hluboká nad Vltavou, *Quercus robur*, 16 Jun. 2014, *Vlasák* 1406/1* (**neotype** PRM 956226) (designated here, MycoBank MBT 10008292).

Synonyms:

Boletus quercinus Schrad., Spic. Fl. Germaniae 1: 157. 1794.

Typus: Plate 5, figs 3–5 in J.V. Krombholz, Naturgetreue Abbildungen und Beschreibungen der Schwämme 1, 1831 (**iconotype**) (selected by Ryvarden 1991: 119).

Buglossoporus quercinus (Schrad.) Kotlaba & Pouzar, Česká Mykol. 20: 82. 1966.

Description: Ryvarden et al. (2017, as Piptoporus quercinus).

Specimens examined: **France**, Seine-et-Marne, Fontainebleau, *Quercus* sp., 15 Sep. 2001, *Rivoire* (LY BR-2030, H). **Poland**, Podlasie, Hajnówka, Białowieża, *Q. robur*, 2 Sep. 2017, *Niemelä* 9281 (H). **USA**, Pennsylvania, Montgomery Co., Norristown, Valley Forge, *Quercus* sp., 28 Jun. 2009, *Vlasák Jr.* 0906/15-J* (JV).

Notes: Donk (1971) argued that *Boletus pulvinus* represents the same species as *Boletus quercinus* (= *Buglossoporus quercinus*). The latter name has priority over *B. pulvinus*. However, it is unavailable as a basionym if *B. quercinus* is being moved to *Fomitopsis*, due to the existence of *Agaricus quercinus* (= *Daedalea quercina*, see *Fomitopsis quercina* below). Therefore, we use Persoon's epithet to recombine this species in *Fomitopsis*. No authentic material of *B. pulvinus* survived, and a neotype for this species is designated above.

Fomitopsis pulvinascens (Pilát ex Pilát) Niemelä & Miettinen, *comb. nov.* MycoBank MB 844951.

Basionym: Poria pulvinascens Pilát ex Pilát, Acta Mus. Nat. Pragae 9 (B), 2 (1): 106. 1953.

Typus: **Sweden**, Upland, Bondkyrka, Vårdsätra, *Salix* sp., 16 Oct. 1936, *Lundell* (**holotype** PRM 756485!).

Description: Niemelä (1978, as Antrodia plicata).

Note: See Figs 1 and 3 for phylogenetic placement.



Fig 26. Basidiocarps of Fomitopsis spp. A. F. quercina (Niemelä 4030). B. F. roseofusca (Vlasák 1909/82). C. F. scalaris (Vlasák 1909/66). D. F. sulcata (Miettinen 11275). E. F. psilodermea (Vlasák 1504/34). F. F. tristis (holotype). G. F. tunicata (holotype). H. F. uralensis (Spirin 10946).

Fomitopsis purpurea Spirin & Ryvarden, *sp. nov.* MycoBank MB 844952. Fig 27.

Typus: **Tanzania**, Arusha, Arusha Nat. Park, Mt. Meru, -3.24° 36.753°, hardwood, 8 Feb. 1973, *Ryvarden* 10118* (**holotype** O F915520).

Etymology: Purpureus (Lat., adj.) - purple.

Description: Basidiocarps perennial, sessile, conchate to ungulate, broadly attached, projecting up to 7 cm. Upper surface blackish brown to totally black, with distinct annual zones, sometimes irregularly cracking. Pileal edge sharp to rather blunt, concolourous with pore surface, up to 2 mm wide, sterile. Pore surface pink to pinkish brown, usually concave; pores roundish, 6-7 per mm, with rather thick, entire dissepiments. Section: crust exceptionally tough, brownish black to black, matt, up to 2 mm thick, context corky, pinkish brown to brown, up to 1 cm thick, more or less clearly delimited from tubes; tubes corky, stratified, pinkish brown to brown, in total up to 2.5 cm thick, each annual layer 1–3 mm thick. Hyphal structure dimitic; hyphae clamped. Context dimitic; skeletal hyphae dominating, brownish to reddish-brown, interwoven, occasionally branched, (3.0-)3.2-4.8(-5.1) µm diam (n = 20/1), lumen capillary to indistinct, generative hyphae rare, hyaline, variably thickwalled, 2–3.5 µm diam. Trama dimitic; skeletal hyphae brownish to reddish-brown, interwoven, occasionally branched, (2.4-)2.7-3.3(-3.7) μ m diam (n = 40/2), lumen wide to capillary, side branches 2-3 µm diam, generative hyphae hyaline, thin-walled, 2-3 µm diam. Subhymenium distinct, up to 20 µm thick. Cystidioles rare, tapering, 9-14 × 3-5 µm. Basidia clavate, (10.1-)10.2-13.1(-14.3) × (4.9-)5.1-6.1(-6.2) µm (n = 20/2). Basidiospores with a distinct wall, long cylindrical to subfusiform, $(4.8-)5.0-6.7(-7.1) \times (1.9-)$ $2.0-2.2(-2.3) \mu m (n = 60/2), L = 5.60-5.98, W = 2.09-2.10, Q =$ 2.68-2.86.

Specimen examined: Tanzania, Arusha, Arusha Nat. Park, Ngurdoto, hardwood, 10 Aug. 1966, Cain et al. (O F915519*).

Notes: This species was treated as *F. carnea* by Ryvarden & Johansen (1980), Carranza-Morse & Gilbertson (1986) and Han *et al.* (2016). We argued above that the epithet *F. carnea* is not applicable to the African species so named and should be reserved for the member of the *F. feei* complex widely distributed in Southeast Asia. Therefore, the African species is formally introduced here as *F. purpurea*. Large, ungulate basidiocarps of *F. purpurea* are reminiscent of those of *F. lilacinogilva*. The latter species is distributed in Australia and differs from *F. purpurea* in having a hirsute pileal surface, larger pores and wider basidiospores (see description above). So far, *F. purpurea* has been recorded twice in Tanzania.

Fomitopsis quercina (L.) Spirin & Miettinen, *comb. nov.* MycoBank MB 844953. Figs 26, 27. *Basionym: Agaricus quercinus* L., Syst. Pl.: 1176. 1753.

Typus: Plate 181 in Sowerby 1799 (**iconotype**) (selected by Ryvarden 1991: 135).

Synonym: Daedalea quercina (L.) Pers., Syn. Meth. Fung. 2: 500. 1801.

Description: Ryvarden et al. (2017, as Daedalea quercina).

Specimens examined: **Czech Republic**, Jihočeský Reg., České Budějovice, Hluboká nad Vltavou, *Quercus robur*, 1979, *Vlasák* 7913/63 (H). **Finland**, Varsinaissuomi, Parainen, Lenholm, *Q. robur*, 2 May 2008, *Miettinen* 12662* (H); Raasepori, Solböle, *Q. robur*, 11 Aug. 1987, *Niemelä* 4030 (H). **USA**, Georgia, Habersham Co., Tallulah, *Quercus* sp., IV.2004, *Vlasák Jr.* 0404/2-J* (JV, H).

Note: See remarks to F. derelicta.



Fig 27. Basidiospores of Fomitopsis spp. F. purpurea (holotype); F. quercina (Miettinen 12662); F. retorrida (holotype); F. roseofusca (Vlasák 1908/83J); F. sagraeana (O 14113); F. scalaris (Vlasák 1909/66). Scale bar = 5 µm.

Fomitopsis ramentacea (Berk. & Broome) Spirin & Vlasák, *comb. nov.* MycoBank MB 844954.

Basionym: Polyporus ramentaceus Berk. & Broome, Ann. Mag. Nat. Hist. 3: 210. 1879.

Typus: **UK**, Scotland, Angus, Glamis, 'on dead sticks' [*Pinus sylvestris*], *Stevenson* 284 (**lectotype** K(M) 192120!) (selected by Ryvarden 1984: 352).

Synonyms:

Polyporus cerebrinus Berk. & Broome, Ann. Mag. Nat. Hist. 3: 210. 1879.

Typus: **UK**, Scotland, Angus, Glamis, 'fir' [*Pinus sylvestris*], *Stevenson* w/n (**lectotype** K, **isolectotype** BPI US0205257!) (selected by Ryvarden 1984: 334).

Trametes subsinuosa Bres., Ann. Mycol. 1: 81. 1903.

Typus: **Italy**, Tyrol, Trento, *Pinus sylvestris*, 1897, *Bresadola* (**lectotype** BPI US0321236!) (selected by Ryvarden 1988a: 324).

Antrodia subramentacea A. David & Dequatre, Cryptog. Mycol. 5 (4): 299. 1985.

Typus: **France**, Var, Le Faron, *Pinus halepensis*, Mar. 1974, *David* 3182* (holotype LY AD-3182!).

Description: Basidiocarps effused-reflexed, often 3-4 cm diam, sometimes fusing together and then up to 7 cm in widest dimension. Reflexed part projecting up to 5 mm, upper surface pubescent or smooth, sometimes indistinctly zonate, almost white to creamcoloured; margin sharp, often incurved. Margin of resupinate part adnate or partly detaching, compact, white to cream-coloured, up to 2 mm wide. Hymenial surface even, white to cream-coloured or pale ochraceous; pores angular, 1-3 per mm, dissepiments uneven to serrate. Section: context soft, white, up to 0.5 mm thick; tubes soft, in older parts partly agglutinated, pale cream-coloured to pale ochraceous, 1-3 mm thick. Hyphal structure monomitic; hyphae clamped. Context hyphae hyaline, moderately thick-walled to subsolid, (3.0-)3.2-5.3(-5.6) µm diam (n = 30/2). Tramal hyphae hyaline, slightly to distinctly thick-walled, (2.6-)2.7-5.2(-5.3) µm diam (n = 180/9), with occasional inflations up to 6 µm diam, often distinctly twisted at dissepiment edges. Cystidioles absent. Basidia clavate, (13.3-)14.8-27.7(-28.4) × (4.2-)4.3-6.1(-6.7) µm (n = 31/3). Basidiospores with a distinct wall, cylindrical, occasionally slightly curved, longest spores subfusiform, (6.0-)6.1-10.3(-11.3) × (2.0–)2.1–3.2(–3.6) µm (n = 450/15), L = 6.70–8.40, W = 2.28– 2.92, Q = 2.52-3.48.

Specimens examined: Czech Republic, South Bohemia, Tábor, Soběslav, Pinus uliginosa, 25 Jul. 1973, Kotlaba, Pouzar & Niemelä (H, TN); Plzeň, Plzeň Sever, Lesni Závod, Pinus sylvestris, Oct. 2001, Kout 1001/1* (H, JV). Finland, Ahvenanmaa, Vårdö, Vargata, P. sylvestris, 20 Nov. 1967, Olofsson (H); Varsinaissuomi, Korppoo, Hjortö, P. sylvestris, 17 Oct. 2010, Kunttu 7419 (H); Länsi-Turunmaa, Nauvo, P. sylvestris, 26 Jul. 2010, Kunttu 6172 (H); Uusimaa, Vantaa, Mustavuori, P. sylvestris, 27 Sep. 1987, Saarenoksa 34987 (H); Etelä-Häme, Hartola, Kirkkola, P. sylvestris, 24 Oct. 1991, Haikonen 13653 (H). Germany, Brandenburg, Triglitz, P. sylvestris, Jaap (H ex Fungi selecti exsiccati #943); Mecklenburg-Vorpommern, Rügen, P. sylvestris, 23 Nov. 1994, Doll (H). Italy, Friuli-Venezia Giulia, Trieste, Pinus nigra, 8 Oct. 1992, Bernicchia 5840 (H ex HUBO). Norway, Rogaland, Forsand, Skiftåsen, P. sylvestris, 18 Jan. 2004, Førland 6* (O F177697). Poland, Warmia-Masuria, Szczytno, P. sylvestris, 8 Jul. 1969, Niemelä & Rykowsky (H). Russia, Nizhny Novgorod Reg., Lukoyanov



Dist., Panzelka, *P. sylvestris*, 15 Aug. 2006, *Spirin* 2552* (H); Razino, *P. sylvestris*, 13 Aug. 2006, *Spirin* 2540* (H).

Notes: Fomitopsis ramentacea is a rare European species occurring on dry branches or just fallen, still corticated logs or hanging branches of *Pinus* spp. It is easily recognizable due to almost white, flexible, effused-reflexed basidiocarps with large, irregular pores and a peculiar host. Two related species distributed in Europe, *i.e. F. renehenticii* and *F. solaris*, are microscopically nearly identical to *F. ramentacea*. Fomitopsis renehenticii has smaller pores than *F. ramentacea*, and it mainly inhabits angiosperm hosts (with a few records on conifers). In turn, *F. solaris* occurs on both coniferous and deciduous trees, and it has somewhat smaller pores than *F. ramentacea* (and larger than in *F. renehenticii*) showing a tendency to radial arrangement in pileate parts. The Asian *F. uralensis* has clearly smaller basidiospores than found in the three aforementioned species.

Fomitopsis renehenticii (Rivoire, Trichies & Vlasák) Rivoire & Vlasák, *comb. nov.* MycoBank MB 844955.

Basionym: Cartilosoma renehenticii Rivoire, Trichies & Vlasák, Bull. Mens. Soc. Linn. Lyon 84: 8. 2015.

Typus: **France**, Ain, Poncin, *Corylus avellana*, 7 Sep. 2011, *Rivoire* (holotype LY BR-4111*!).

Description: Basidiocarps effused-reflexed, often 3-5 cm diam, sometimes fusing together and then up to 10 cm in widest dimension. Reflexed part projecting up to 6 mm, upper surface finely pubescent or smooth, azonate, cream-coloured; margin sharp. Margin of resupinate part adnate or partly detaching, compact, white to cream-coloured, up to 1 mm wide. Hymenial surface even, cream-coloured to pale ochraceous; pores angular, 3-5 per mm, dissepiments uneven to serrate. Section: context soft, white, up to 0.5 mm thick; tubes soft, in older parts partly agglutinated, pale cream-coloured to pale ochraceous, 1-2 mm thick. Hyphal structure monomitic; hyphae clamped. Context hyphae hyaline, moderately thick-walled to subsolid, $(3.4-)3.7-5.4(-5.7) \mu m$ diam (n = 20/1). Tramal hyphae hyaline, slightly to distinctly thick-walled, (2.4–)3.0– 5.1(-5.2) µm diam (n = 40/2), more or less straight at dissepiment edges. Cystidioles absent. Basidia clavate, (18.7-)18.8-28.4(-29.2) × (5.0-)5.3-6.1(-6.3) µm (n = 20/2). Basidiospores with a distinct wall, cylindrical, occasionally slightly curved, longest spores subfusiform, $(5.8-)6.2-9.3(-10.4) \times (2.3-)2.4-3.0(-3.1) \mu m$ (n = 150/5), L = 6.94–7.88, W = 2.69–2.83, Q = 2.52–2.80.

Specimens examined: Fomitopsis renehenticii. Belgium, Namur, Philippeville, Viroinval, Fondry des Chiens, *Corylus avellana*, 11 Oct. 2019, *Spirin* 13498 (H); *Salix caprea*, 11 Oct. 2019, *Spirin* 13511, 13518 (H). France, Aveyron, Creissels, *Rubus* sp., 9 May 2022, *Spirin* 15353 (H); Bouches-du-Rhône: Cary le Rouet, *Pinus halepensis*, 20 Jan. 2007, *Rivoire* (LY-BR 3059*); Moselle, Tressange, *Alnus glutinosa*, 1 Nov. 2007, *Trichies* 07400 (H); Meuse, Ornes, *S. caprea*, 12 Jul. 2008, *Trichies* 08150 (H); Rhône, Orliénas, *Cupressocyparis leylandis*, 18 Dec. 2018, *Rivoire* (LY-BR 7347*); Seine-Maritime, Elbeuf sur Andelle, *Salix* sp., 19 Sep. 2015, *Penz* (LY BR-6274*). Germany, Baden-Württemberg, Hockenheim, *Salix cinerea*, 14 Dec. 1985, *Winterhoff* (H). Slovenia, Cerknica, Goričice, *C. avellana*, 30 Sep. 2023, *Spirin* 16857 (H). *Fomitopsis renehenticiix solaris*. France, Lot, Villesèque, Coumes, *Juniperus communis*, 13 Jan. 2016, *Hannoire* (LY-BR 6356*).

Notes: Fomitopsis renehenticii is a close relative of *F. ramentacea* and *F. solaris*; their differences are listed under the first species. The distribution of *F. renehenticii* is seemingly limited to the western

and central parts of Europe (Belgium, Czech Republic, France, Germany, Italy, Slovenia).

Fomitopsis retorrida Spirin & Kotiranta, *sp. nov.* MycoBank MB 844956. Fig 27.

Typus: **Russia**, Sakhalin, Korsakov Dist., Bolshoe Vavaiskoe Lake, 46.637° 143.192°, *Abies* sp. (fallen corticated log), 23 Aug. 2007, *Kotiranta* 28979* (**holotype** H7200205).

Etymology: Retorridus (Lat., adj.) - burnt-up, sunburnt.

Description: Basidiocarps resupinate, first orbicular, then partly fusing together, up to 5 cm in widest dimension. Margin adnate, compact, white to cream-coloured, up to 2 mm broad. Hymenial surface even, pale ochraceous to bright ochraceous-brownish; pores angular to lacerate, 3-5 per mm, often fusing together, dissepiments uneven to serrate. Section: context soft, white or pale cream-coloured, up to 0.5 mm thick; tubes soft, in older parts partly agglutinated, pale cream-coloured to pale ochraceousbrownish, 0.2-0.5 mm thick. Hyphal structure monomitic; hyphae clamped. Context hyphae hyaline, slightly to distinctly thick-walled, (1.9-)2.0-3.4(-4.2) µm diam (n = 20/1). Tramal hyphae hyaline, thin- to distinctly thick-walled, interwoven, flexuous, partly glued together, (2.6-)2.8-4.2(-4.8) µm diam (n = 20/1), often twisted at dissepiment edges. Cystidioles rare, tapering, 15-20 × 3-4 µm. Basidia long clavate, (15.2–)16.0–25.3(–25.7) × (5.0–)5.1– $6.3(-6.4) \mu m$ (n = 20/1). Basidiospores with a distinct wall, long cylindrical, occasionally slightly curved, longest spores subfusiform, $(5.6-)5.8-7.3(-7.4) \times (2.2-)2.3-3.1(-3.2) \mu m (n = 30/1), L = 6.49,$ W = 2.77, Q = 2.35.

Notes: The monomitic basidiocarps composed of predominantly thick-walled, flexuous generative hyphae with a variable lumen, rather long basidia and cylindrical basidiospores of *F. retorrida* are strongly reminiscent of the *F. ramentacea* complex. However, those taxa are phylogenetically not closely related. According to our data, *F. retorrida* is a sister species of *F. mellita* and *F. pulvinascens* (Figs 1, 3) although the latter ones show no certain morphological similarity to it. The aforementioned anatomical traits, in combination with totally resupinate basidiocarps and brightly coloured hymenial surface differentiate *F. retorrida* from all other *Fomitopsis* spp. treated here. The species is so far known only from the type locality in the Russian Far East.

Fomitopsis rosea (Alb. & Schwein.) P. Karst., Meddeland. Soc. Fauna Fl. Fenn. 6: 9. 1881.

Basionym: Boletus roseus Alb. & Schwein., Conspectus Fungorum in Lusatiae Superioris: 251. 1805.

Typus: **Norway**, Oslo, [no collection date], *Blytt* (herb. Fries) (**lectotype** UPS) (selected by Ryvarden 1991: 218).

Description: Carranza-Morse & Gilbertson (1986).

Notes: This species is the generic type of *Rhodofomes*. For phylogenetic affinity, see Figs 1, 3 and 12.

Fomitopsis roseoalba A.M. Soares, Ryvarden & Gibertoni, Fungal Diversity 83: 210. 2017.

Typus: **Brazil**, Amapá: Porto Grande, hardwood, Feb. 2014, Soares* (holotype URM 86923).

Description and phylogenetic data: Tibpromma et al. (2017).

Fomitopsis roseofusca (Romell) Spirin & Vlasák, *comb. nov.* MycoBank MB 844957. Figs 26, 27.

Basionym: Polyporus roseofuscus Romell, Bih. K. Svenska Vetensk.-Akad. Handl. 26 (16): 32. 1901.

Typus: **Brazil**, Mato Grosso, Serra da Chapada, Buriti, rotten log, 4 Jun. 1894, *Malme* 609 (**holotype** S F14845!).

Synonym: Nigroporus macroporus Ryvarden & Iturr., Mycologia 95 (6): 1070. 2004.

Typus: **Venezuela**, Bolívar, Canaima Nat. Park, 24 Feb. 2000, *Ryvarden* 42363* (**isotype** O!).

Description: Basidiocarps perennial, sessile, at first conchate or more rarely bracket-shaped, solitary, then fusing together in large imbricate groups, broadly attached, projecting up to 8 cm. Upper surface initially brownish black, indistinctly zonate, smooth, later totally black, with distinct annual zones, not cracking. Pileal edge sharp, concolourous with pore surface, up to 1 mm wide, sterile. Pore surface pinkish grey to brownish, flat or slightly concave; pores elongated-angular to sinuous, 1-2 per mm, with thick, entire dissepiments. Section: crust exceptionally tough, black, matt or glossy, up to 1 mm thick, context hard corky, dark brown, up to 2 mm thick, sharply delimited from tubes; tubes tough, clearly stratified, pinkish brown to brown, in total up to 2.5 cm thick, each annual layer 3-7 mm thick, separated from surrounding tube strata by a darker sterile tissue 0.2-0.5 mm thick. Hyphal structure dimitic; hyphae clamped. Context dimitic; skeletal hyphae dominating, dark brown, tightly interwoven, occasionally branched, sometimes encrusted by amorphous blackish matter, (2.8–)3.2–5.5(–5.6) µm diam (n = 20/1), lumen indistinct, generative hyphae brownish, slightly thick-walled, 2.5-3.5 µm diam. Trama dimitic; skeletal hyphae brownish to dark brown, tightly interwoven, occasionally branched, (2.4-)3.1-5.1(-5.2) μ m diam (n = 40/2), lumen capillary to indistinct, generative hyphae hyaline, thin-walled, infrequent, (1.5–)2.0–3.0 µm diam. Skeletocystidia abundant, acute, not encrusted, distinctly thickwalled, 3-5 µm diam at the apex, slightly projecting above hymenium. Cystidioles rarely present in senescent hymenium, tapering, slightly thick-walled, 14.5-18.0 × 4.0-5.0 µm. Basidia clavate, (9.8-)10.7-16.2(-17.1) × (4.0-)4.2-6.0(-6.2) µm (n = 20/1), senescent basidia slightly thick-walled, often densely glued together. Basidiospores with a distinct wall, cylindrical to subfusiform, (4.6-)4.8-6.2(-6.8) × (1.7-)1.8-2.8(-3.0) µm (n = 36/2), L = 5.30–5.52, W = 2.24–2.55, Q = 2.12–2.51.

Specimens examined: Brazil, Amazonas, Yutajé, dead deciduous wood, 12 Jun. 1997, *Ryvarden* 40776 (O 10781). French Guiana, Camp Cayman, old fallen log, 31 Aug. 2019, *Vlasák Jr.* 1908/83-J* (JV, H).

Notes: Fomitopsis roseofusca is a Neotropical species morphologically most similar to *F. cupreorosea* (*F. feei* complex) which is distributed in the same geographic area. It produces thicker, tougher and darker basidiocarps than *F. cupreorosea*. Pores of *F. roseofusca* are on average larger than in *F. cupreorosea*. Microscopically, the species can be separated due to different skeletocystidia, acute in *F. roseofusca* and obtuse in *F. cupreorosea*. Phylogenetically, *F. roseofusca* seems to be isolated from other members of *Fomitopsis* (see Figs 1 and 3, as *N. macroporus*). *Fomitopsis sagraeana* (Mont.) Vlasák & Spirin, *comb. nov.* MycoBank MB 844958. Fig 27.

Basionym: Polyporus sagraeanus Mont., Ann. Sci. Nat., Bot. 2 (17): 127. 1842.

Typus: **Cuba**, Sancti Spíritus, San Marcos, 'ad truncos arborum', [no collection date], *de la Sagra* (**isotype** BPI 248508!).

Description: Basidiocarps perennial, sessile, often with a contracted base (fan-shaped), projecting up to 7.5 cm. Upper surface first pinkish ochraceous to purplish-brownish, velvety, then occasionally fading to light greyish, smooth and indistinctly zonate. Pileal edge sharp to rather blunt, concolourous with hymenial surface, sterile, up to 1 mm wide, then fertile. Pore surface deep pink to pinkishgreyish, flat or concave; pores roundish to angular, 6-8 per mm, with thin or moderately thickened, entire or uneven dissepiments. Section: context corky, deep pink or pinkish brownish, up to 7 mm thick; tubes corky, one-layered or indistinctly stratified, concolourous with hymenial surface, up to 5 mm thick. *Hyphal structure* dimitic; hyphae clamped. Context dimitic; skeletal hyphae almost hyaline to brownish, densely interwoven, occasionally branched, (3.1-)3.2- $5.2(-5.8) \mu m$ diam (n = 40/2), lumen normally wide, side branches 2-3 µm diam, generative hyphae rare, hyaline, thin- to slightly thickwalled, 3–5 µm diam. Trama dimitic; skeletal hyphae dominating, brownish to reddish-brown, densely interwoven to subparallel, occasionally branched, (2.2-)2.3-3.8(-4.0) µm diam (n = 100/5), lumen varying from rather wide to capillary, generative hyphae rare, thin- to slightly thick-walled, 2-4 µm diam. Subhymenium partly distinct, up to 10 µm thick. Cystidioles tapering, 11-28 × 4.0-6.0 µm. Basidia clavate, (11.3–)12.0–20.8(–23.2) × (4.8–)5.0–6.4(–6.8) µm (n = 38/3), occasionally pleural. Basidiospores with a distinct wall, cylindrical-subfusiform, (4.8-)4.9-7.3(-7.4) × (2.4-)2.6-3.9(-4.0) μm (n = 111/4), L = 5.75–5.89, W = 2.87–3.29, Q = 1.76–2.05.

Specimens examined: **Costa Rica**, Alajuela, San Carlos, Arenal, hardwood, 23 Dec. 2015, *Vlasák Jr*. 1512/2J* (JV, TUF); Guanacaste, Lomas Barbudal Park, hardwood, 24 Dec. 2014, *Vlasák Jr*. 1412/5J* (JV, TUF); Puntarenas: Las Tablas, 24 Apr. 2000, *Navarro* 1897 (O 14113, H). **Dominican Republic**, La Vega, Ebano Verde Nat. Res., angiosperm branch, 29 Dec. 2001, *Perdomo* 671 (O 16293, H). **USA**, Florida, Miami-Dade Co., Long Pine Key, hardwood, 19 Apr. 2009, *Vlasák* 0904/39* (JV, H); Monroe Co., Key Largo, John Pennekamp Coral Reef State Park, hardwood, 29 Aug. 2010, *Vlasák Jr*. 1008/76J* (JV, H).

Notes: Fomitopsis sagraeana is a member of the *F. feei* complex. It is distributed in the northern and western parts of the Caribbean. It differs from *F. feei sensu stricto* in having slightly smaller pores and larger basidiospores. As redefined here, *F. feei* occurs in tropical areas of South America (see above). Lowe (1957) accepted *F. feei* and *F. sagraeana* as two different species, but his description of the latter one refers to *F. cupreorosea*.

Fomitopsis sandaliae (Bernicchia & Ryvarden) Bernicchia & Vlasák, *comb. nov.* MycoBank MB 844960.

Basionym: Antrodia sandaliae Bernicchia & Ryvarden, Mycotaxon 79 (1): 58. 2001.

Typus: **Italy**, Sud Sardegna, Foresta Demaniale di Montarbu, *Arbutus unedo*, 4 Dec. 2000, *Bernicchia & Ryvarden* (**holotype** HUBO 7348!).

Description: Bernicchia & Ryvarden (2001), Bernicchia & Gorjón 2020 (as *A. sandaliae*).

Specimen examined: Italy, Sud Sardegna, Foresta Demaniale di Montarbu, A. unedo, 29 Nov. 2003, Bernicchia (HUBO7803*).

Note: This nearly monomitic species belongs to the *Buglossoporus* subclade (Suppl. Fig. S8).

Fomitopsis scalaris (Cooke) Ryvarden, Mycotaxon 20: 354. 1984. Figs 26, 27.

Basonym: Fomes scalaris Cooke, Grevillea 14 (69): 18. 1885.

Typus: **Brazil**, Panurè, dead trunks of trees, Feb. 1853, *Spruce* 62 (**syntype** K); *ibid.*, *Spruce* 199 (**syntype** K, **isosyntype** PC!).

Synonym: Nigroporus rigidus Ryvarden, Mycotaxon 28: 532. 1987.

Typus: **Venezuela**, Amazonas, Cerro de la Neblima, on wood, 21 Apr. 1984, *Samuels* 1478 (**isotype** O 18149!).

Description: Basidiocarps perennial, sessile, at first bracketshaped, later ungulate, broadly attached, projecting up to 5 cm. Upper surface initially brownish, indistinctly zonate, smooth or slightly felty, later blackish brown to totally black, with distinct annual zones, not cracking. Pileal edge sharp, concolourous with pore surface, up to 1 mm wide, sterile. Pore surface pinkish-grey to brownish-grey, flat or slightly concave, finally fading to mousegrey; pores roundish, 6-8 per mm, with rather thin or thick, entire dissepiments. Section: crust (present in old basidiocarps) exceptionally tough, black, matt, up to 0.5 mm thick, context hard corky, brown, up to 1 mm thick, sharply delimited from tubes; tubes tough, clearly stratified, brownish grey to brown, in total up to 30 mm thick, each annual layer 1-3 mm thick, separated from surrounding tube strata by a darker sterile tissue 0.2-1 mm thick. Hyphal structure dimitic; hyphae clamped. Context dimitic; skeletal hyphae dominating, brown, tightly interwoven to subparallel, occasionally branched, (2.8-)3.2-4.3(-4.6) µm diam (n = 20/1), lumen capillary to indistinct, generative hyphae rare, hyaline, slightly thick-walled, 2–4 µm diam. Trama dimitic; skeletal hyphae brownish to dark brown, tightly interwoven, occasionally branched, sometimes covered by amorphous brownish encrustation, (2.1-2.2-3.8(-4.2) µm diam (n = 60/3), lumen wide to capillary, some skeletals with frequent adventive septa, generative hyphae hyaline, thin- or slightly thick-walled, infrequent, (1.0-)1.5-2.5 µm diam. Subhymenium indistinct. Skeletocystidia present as swollen (up to 4.5 µm diam) apices of tramal skeletal hyphae, slightly projecting above hymenium. Cystidioles rare, tapering, $14-15 \times 4-5 \mu m$. Basidia short-clavate, (6.7–)8.4–11.1(–12.8) × (3.8–)3.9–4.9(–5.2) μ m (n = 15/2), quickly collapsing. *Basidiospores* with a distinct wall, cylindrical, longest spores slightly tapering to the distal end, (3.0-) 3.1–5.0(–5.2) × (1.9–)2.0–2.3(–2.5) µm (n = 70/3), L = 3.39–3.90, W = 2.10–2.13, Q = 1.60–1.83, sometimes glued in groups of 3–4.

Specimens examined: **Brazil**, Paragominas, Mina da Hydro, angiosperm snag, 18 Nov. 2014, *Runnel* 1211 (MG211148, O). **French Guiana**, Kourou, Monkey Hill, old fallen log, 6 Sep. 2019, *Vlasák* 1909/66* (JV, H), Roura, Montagne Tresor, fence prop, 24 Aug. 2018, *Vlasák* 1808/50* (JV). **Venezuela**, Bolívar, Canaima, 10 Jan. 1972, *Bresinsky* (O 10869).

Notes: Ungulate basidiocarps with blackish crust and partly pinkish pore surface, as well as brown skeletal hyphae and rather small-sized basidiospores might suggest a close relationships of *F. scalaris* and members of the *F. rosea* or the *F. feei* complexes. Our phylogenetic analyses show that, contrary to morphological indications, it occupies an isolated position within the genus (Figs



SPIRIN ET AL.

1, 3). *Fomitopsis scalaris* is a Neotropical species, with confirmed records from the Amazon basin and adjacent areas. One of the authentic specimens (*Spruce 199*) is in perfect condition, fertile, and it is undoubtedly identical to our newly collected and sequenced material.

Fomitopsis sclerotina (Rodway) M.D. Barrett & Spirin, *comb. nov.* MycoBank MB 844961.

Basionym: Polyporus sclerotinus Rodway, Pap. Proc. R. Soc. Tasm. 1917: 108. 1918.

Typus: **Australia**, Tasmania, Mt. Field, 'on gravelly earth', Nov. 1917, *Rodway* (holotype HO 120637).

Description: Núñez & Ryvarden (1995, as Laccocephalum sclerotinum), Buchanan & Ryvarden (1993, as *P. sclerotinus*).

Specimen examined: Australia, Western Australia, Collis Rd, Walpole-Nornalup National Park, 7 May 2018, *Syme* 2967* (PERTH).

Notes: Fomitopsis sclerotina is an unusual species, with small, stipitate basidiocarps arising from a pebble-sized white sclerotium of the homogenous consistency. Skeletal hyphae are dominant in the stipe, but often almost absent in the pileus (Buchanan & Ryvarden 1993). See remarks under *F. tumulosa* for discussion of *Laccocephalum*.

Fomitopsis serialiformis (Kout & Vlasák) Vlasák, *comb. nov.* MycoBank MB 844962.

Basionym: Antrodia serialiformis Kout & Vlasák, Mycotaxon 108: 331. 2009.

Typus: **USA**, Pennsylvania, Philadelphia, Wissahickon Creek Park, *Quercus* sp., 31 Aug. 2008, *Vlasák* 0808/47* (**isotype** PRM 915459!).

Description and phylogenetic data: Kout & Vlasák (2009, as A. serialiformis); see also Fig. 3.

Fomitopsis serialis (Fr.) Spirin & Runnel, *comb. nov.* MycoBank MB 844963.

Basionym: Polyporus serialis Fr., Syst. Mycol. 1: 370. 1821.

Typus: **Norway**, Telemark, Nome, Mørkvasslia Nat. Res., *Picea abies*, 23 Sep. 2003, *K.H. Larsson* 12010* (**neotype** GB!) (designated by Spirin *et al.* 2017: 227).

Synonym: Antrodia serialis (Fr.) Donk, Persoonia 4: 340. 1966.

Description and phylogenetic data: Spirin et al. (2017, as Antrodia serialis); see also Figs 1 and 3.

Fomitopsis serrata (Vlasák & Spirin) Vlasák & Spirin, *comb. nov.* MycoBank MB 844964.

Basionym: Antrodia serrata Vlasák & Spirin, Mycologia 109: 228. 2017.

Typus: **USA**, New Hampshire, Carroll Co., Slippery Brook, *Picea* sp., Sep. 2008, *Vlasák* 0809/72* (**holotype** H!).

Description and phylogenetic data: Spirin et al. (2017, as A. serrata).

Fomitopsis solaris Rivoire, A.M. Ainsworth & Vlasák, *sp. nov.* MycoBank MB 844965. Fig 28.

Typus: **France**, Val de Marne, Vincennes, Bois de Vincennes, coniferous tree (*Pinus*?), 3 Dec. 2012, *Hentic* (**holotype** LY-BR 4732*, **isotype** H7200196).

Etymology: Solaris (Lat., adj.) – resistant to sunlight; in reference to open habitats where the species can sometimes occur.

Description: Basidiocarps annual or biennial, sessile, effusedreflexed or totally resupinate, often 2-4 cm diam, often not fusing together. Reflexed part projecting up to 10 mm, upper surface finely pubescent or smooth, azonate, uneven and sometimes with low concentric or radial ridges, cream-coloured, in persistent basidiocarps covered by epiphytic algae; margin sharp, incurved, or rather blunt. Margin of resupinate part adnate or partly detaching, compact, white to cream-coloured, up to 1 mm wide. Hymenial surface even, cream-coloured to pale ochraceous; pores angular, 2-3 per mm, in pileate parts showing a tendency to radial arrangement, dissepiments uneven to serrate. Section: context soft, white or pale cream-coloured, up to 1 mm thick; tubes soft, in older parts partly agglutinated, pale cream-coloured to pale ochraceous, 1-3 mm thick. Hyphal structure monomitic; hyphae clamped. Context hyphae hyaline, moderately thick-walled to subsolid, (3.0-) 3.2-5.2(-6.2) µm diam (n = 40/2). Tramal hyphae hyaline, slightly to distinctly thick-walled, $(2.2-)2.3-4.3(-4.7) \mu m \text{ diam } (n = 100/5)$, occasionally twisted at dissepiment edges. Cystidioles absent. Basidia (15.6-)15.7-24.0(-26.0) × (4.8-)5.0-7.1(-7.3) µm (n = 50/4). Basidiospores with a distinct wall, cylindrical, occasionally slightly curved, longest spores subfusiform, $(5.8-)5.9-9.6(-10.4) \times$ (2.0–)2.1–3.4(–3.6) µm (n = 210/7), L = 6.71–8.30, W = 2.35–2.99, Q = 2.78-3.15.

Specimens examined: Canada, Northwest Territories, Inuvik, Picea sp., 20 Sep. 1984, Niemelä 3058* (H); Salix sp., 14 Sep. 1984, Niemelä 2992 (H); Alnus crispa, 20 Sep. 1984, Niemelä 3061* (H). Denmark, Midtjylland, Herning, Stovbæk, Salix sp., 29 Mar. 2013, Boertmann 501446* (C, H); Syddanmark, Assens, Aarup, Salix cinerea, 26 Apr. 2016, Kaballe & Boertmann 737876 (C, H); Vejen, S. cinerea, 29 Dec. 2013 Boertmann 658643 (C, H). Germany, Niedersachsen, Hagenburg, Salix sp., 27 Mar. 1989, Wöldecke (H). Israel, [no collection locality], Cupressus sempervirens, 2008, Zmitrovich (LE, H*). Jersey, St. Martin, Rozel Woods, S. cinerea, 20 Jan. 2014, Legon (K(M) 191007*). Sweden, Skåne, Mörarp, Salix sp., 25 Dec. 1994, Hanson & Gustafsson (H ex S). United Kingdom, England, Berkshire vc22, Bisham Wood, Salix sp., 30 Jan. 2000, Ainsworth & Green (K(M) 85251*); Buckinghamshire vc24, Wraysbury, by Colne Brook, Salix sp., 24 Feb. 2006, Ainsworth (K(M) 137688*); North Hampshire vc12, Cricket Hill, Salix sp., 6 Feb. 2000, Ainsworth & Lucas (K(M) 84579*); South Somerset vc5, Yeovil, Salix sp., 16 Feb. 2011, Legon (K(M) 180117*); Surrey vc17, Langham Pond Salix fragilis, 29 Aug. 2007, Legon (K(M) 153625*); West Kent vc16, Lullingstone Park, Salix sp., 7 Feb. 2011, Pitt (K(M) 169193*).

Notes: Morphological differences between *F. solaris* and its close relatives are discussed under *F. ramentacea*. The species is widely distributed in Eurasia and it occurs in the north-western part of North America, as well as in the southern part of Argentina (reported as *A. ramentacea* by Rajchenberg *et al.* 2011). *Fomitopsis solaris* inhabits both gymnosperm and angiosperm wood. An "uncultured *Antrodia*" sequence (GenBank KT334658) from oak roots from Poland belongs to this species. In the UK, this species has thus far only been found on the wood of *Salix* spp. and, despite the chosen epithet, these have been in predominantly wet woodland habitats.



Fig 28. Basidiospores of *Fomitopsis* spp. *F. solaris* (holotype); *F. subectypa* (holotype); *F. tristis* (holotype); *F. tunicata* (holotype); *F. uralensis* (Spirin 5399); *F. visenda* (holotype). Scale bar = 5 μm.

These British collections were previously referred to *Antrodia* ramentacea and photographs of the sequenced paratype collection K(M) 85251 can be found in Ainsworth (2001).

Fomitopsis spraguei (Berk. & M.A. Curtis) Gilb. & Ryvarden, Mycotaxon 22 (2): 364. 1985.

Basionym: Polyporus spraguei Berk. & M.A. Curtis, Grevillea 1 (4): 50. 1872.

Typus: **USA**, 'New England, Murray', [no collection date and collector] (**lectotype** K) (selected by Ryvarden 1984: 356).

Synonym: Polyporus castaneae Bourdot & Galzin, Bull. Soc. Mycol. France 41: 105 (1925).

Typus: **France**, Aveyron, Combette, *Castanea sativa*, 28 Aug. 1911, *Galzin* 9879 (**lectotype** PC!) (selected here, MycoBank MBT 10008293).

Description: Gilbertson & Ryvarden (1986).

Specimens examined: **USA**, New York, Oswego, Pulaski, *Quercus rubra*, Aug. 2016, *Vlasák* 1608/14* (JV); Tennessee, Great Smoky Mountains NP, dicot, 13 Dec. 2004, *Ryvarden* 46569* (O, H).

Note: See Figs 1, 3 and 15 for phylogenetic placement.

Fomitopsis squamosella (Bernicchia & Ryvarden) Bernicchia & Ryvarden, *comb. nov.* MycoBank MB 844966.

Basionym: Antrodia squamosella Bernicchia & Ryvarden, Cryptog. Mycol. 19 (4): 282. 1998.

Typus: **Italy**, Nuoro, Supramonte di Orgosolo, *Juniperus oxycedrus*, 9 Nov. 1994, *Bernicchia* 6650 & Curreli (**isotype** O 10239!).

Description: Bernicchia & Ryvarden (1998, as A. squamosella).

Specimen examined: **Italy**, Sardinia, Nuoro, Supramonte di Orgosolo, *J. oxycedrus*, 2 Dec. 2003, *Bernicchia* (HUBO 7690*).

Note: See Figs 1, 3 and Suppl. Fig. S8 for phylogenetic placement.

Fomitopsis stereoides (Fr.) Spirin, *comb. nov.* MycoBank MB 844967.

Basionym: Daedalea stereoides Fr., Nova Acta R. Soc. Scient. Upsal. 3, 1: 99. 1851.

Typus: **Costa Rica**, San José, 'ad truncos', [no collection date], Örsted (holotype UPS F-127299!).

Description: Ryvarden (2015, as D. stereoides).

Note: Lindner *et al.* (2011) showed that this species belongs to the *Daedalea* clade (see also Fig. 5).

Fomitopsis subectypa (Murrill) Spirin & Vlasák, *comb. nov.* Fig 25. MycoBank MB 844968. Fig 28.

Basionym: Coriolus subecTypus Murrill, North American Flora 9: 22. 1907.

Typus: **USA**, Florida, [no locality indicated], dead wood, Apr. 1885, *Rau* 254 (**holotype** NY00705010!).

Synonyms: Coriolus hollickii Murrill, Mycologia 2: 187. 1910.

Typus: **Jamaica**, Moneague, Union Hill, on log in woods, 6–7 Apr. 1908, *Britton & Hollick* (holotype NY 00704966!).

Daedalea americana M.L. Han, Vlasák & B.K. Cui, Phytotaxa 204 (4): 280. 2015.



Typus: **USA**, Florida, Miami, Matheson Hammock, hardwood, 19 Apr. 2009, *Vlasák* 0904/20* (**holotype** BJFC 15575!).

Description: Basidiocarps short-living perennial, sessile, dimidiate or with a contracted base (fan-shaped), projecting up to 7 cm. Upper surface first wood-coloured to beige, velutinous, indistinctly zonate, later pale ochraceous to tan, smooth, with numerous narrow concentric zones, usually radially striate. Pileal edge sharp or rather blunt, concolourous with cap surface, first sterile, up to 1 mm wide, then fertile. Pore surface cream-coloured or beige to pale ochraceous, sometimes with a faint pinkish tint or vinaceousreddish stains, flat or concave, later fading to greyish-white; pores roundish to angular, 5-7 per mm, with thin or rather thick, entire dissepiments. Section: context corky, cream- to wood-coloured, up to 7 mm thick; tubes soft corky, one-layered, concolourous with hymenial surface, up to 3 mm thick. Hyphal structure dimitic; hyphae clamped. Context dimitic; skeletal hyphae brownish, interwoven or in subparallel bundles, occasionally branched, (2.6-)2.7-7.3(-7.8) μ m diam (n = 60/3), lumen changing from wide to capillary, side branches 1.5–3 µm diam, generative hyphae infrequent, hyaline, thin- to slightly thick-walled, 2-4 µm diam. Trama dimitic; skeletal hyphae dominating, pale ochraceous to brownish, interwoven, occasionally branched, (2.0-)2.1-5.3(-5.8) µm diam (n = 60/3), in older basidiocarps sometimes inflated up 6-7 µm diam, lumen mostly narrow to capillary, generative hyphae thin- to slightly thick-walled, 2-3.5(-4) µm diam, occasionally forming distinct subhymenial layer up to 10 µm thick. Cystidioles rather rare, tapering, 11-16 × 3-5.5 µm. Skeletocystidia present as swollen (up to 6 µm diam) apices of tramal skeletal hyphae, slightly projecting above hymenium. Basidia clavate, (10.3-)10.8-17.4(-18.1) × (4.2-) 4.3-6.2(-6.4) µm (n = 41/3), occasionally pleural. Basidiospores thin-walled or with a distinct wall, ellipsoid-ovoid, longest spores subfusiform, $(4.0-)4.1-6.0(-6.2) \times (2.1-)2.2-3.2(-3.3) \mu m (n = 90/3)$, L = 4.52–5.02, W = 2.57–2.86, Q = 1.58–1.79.

Specimens examined: Costa Rica, Guanacaste: Rincón de la Vieja, hardwood, 1 Aug. 2014, Vlasák 1407/3* & 1407/23 (JV); Villa La Paz, hardwood, 22 Apr. 2017, Vlasák 1704/107J* (JV). USA, Florida, Miami, Matheson Hammock, Quercus sp., 19 Apr. 2009, Vlasák 0904/17 (JV, H).

Notes: Fomitopsis subectypa is a North and Central American species closely related to *F. modesta* (Fig. 5). It normally produces larger basidiocarps than those of *F. modesta*, and it has slightly wider pores and on average larger basidiospores than in the latter species. *Fomitopsis subectypa* has been found in Costa Rica, Jamaica, and the southern part of Florida (USA) although its distribution might be wider. Distribution areas of *F. modesta* and *F. subectypa* overlap at least in Costa Rica.

Fomitopsis substratosa (Malençon) Spirin & Miettinen, *comb. nov.* MycoBank MB 844970.

Basionym: Ungulina substratosa Malençon, Bull. Soc. Mycol. France 71: 311. 1956.

Typus: **Morocco**, Middle Atlas, *Cedrus atlantica* (burnt log), [no collection date indicated], *Malençon* 1297 (**lectotype** designated hereMPU!, MycoBank MBT 10008294).

Synonym: Fomitopsis subfeei B.K. Cui & M.L. Han, Mycoscience 56: 170. 2015.

Typus: **China**, Sichuan: Dujiangyan, Qingcheng, *Cunninghamia* sp., 13 Sep. 2010, *Cui* 9231* (**holotype** BJFC 8169). Description and phylogenetic data: Han & Cui (2015, as *F. subfeei*); see also Fig. 11.

Specimens examined: China, Guangdong, Shixing, Chebaling Nat. Res., Pinus sp., 14 Sep. 2009, *Cui* 7448 (H); Hunan, Sangzhi, Badagongshan Nat. Res., 23 Sep. 2000, *Härkönen* K805 (H). Morocco, Middle Atlas, *Cedrus atlantica*, [no collection date indicated], Male inçon s/n, 1133, 1139, 1242, 1296, 2979 (MPU).

Notes: We studied the type material of *U. substratosa* from Morocco and found it morphologically indistinguishable from *F. subfeei* which was described as widely distributed in the southern part of China. Therefore, we place the latter species to the synonyms of *F. substratosa*, although sequenced specimens from North Africa are highly desirable for confirming this synonymy.

Fomitopsis sulcata (Berk.) Corner, Beih. Nova Hedwigia 96: 39. 1989. Fig 26.

Basionym: Hexagonia sulcata Berk., London J. Bot. 6: 510. 1847.

Typus: **Sri Lanka**, [no locality, collection date or collector], herb. E. Fries (**lectotype** designated here UPS F-126402!, MycoBank MBT 10008295).

Synonyms:

Favolus resinosus Murrill, Bull. Torrey Bot. Club 35: 398. 1908.

Typus: **Philippines**, Luzon, Rizal, Bosoboso, dead wood, Jul. 1906, *Ramos* 1214 (**holotype** NY00704732!).

Fomitopsis cystidiata B.K. Cui & M.L. Han, Mycol. Progr. 13: 908. 2014.

Typus: **China**, Hainan, Baoting, Qixianling, hardwood, 27 Nov. 2007, *Cui* 5481* (**holotype** BJFC).

Description and phylogenetic data: Han et al. (2014, as F. cystidiata); see also Fig. 3.

Specimens examined: China, Hainan, Guandong, rotten wood, 17 Apr. 1977, Han 701 & Zhao (H ex HMAS 40517). India, Uttarakhand, Dehradun, Lachhiwala Forest Range, *Shorea robusta*, 10 Oct. 1973, *Dhanda* 6844 (H ex O 10548). Indonesia, Riau, Kampar, Balung, 24 Dec. 2006, *Miettinen* 11275 (BO, H). Malaysia, Pahang, 9 Jun. 1931, *Corner* (H ex O 10556). Thailand, Sukhotai, Khiri Mat, hardwood, Aug. 2014, *Kout* 1408/K5* (JV, TUF).

Notes: Ryvarden (1977) stated he could not detect authentic material of *H. sulcata* in European herbaria. However, there is a specimen in Fries's herbarium in Uppsala, evidently a part of the original collection sent to him by Berkeley. Here it is designated as a lectotype of *H. sulcata*. Corner (1989) combined *H. sulcata* in *Fomitopsis* and our data support his solution. The species can be easily identified in the field due to its robust but rather soft basidiocarps with a dark-coloured crust and exceptionally large pores. *Fomitopsis sulcata* seems to be widely distributed in Southeast Asia; here we confirm records from India, Indonesia, Malaysia, Sri Lanka, Thailand and the southern part of China (Hainan).

Fomitopsis tristis Miettinen & Spirin, *sp. nov.* MycoBank MB 844972. Figs 26, 28.

Typus: Indonesia, Papua Barat, Manokwari, Amberbaken, River Anjii/ Wepai, -0.5771° 133.1634° (±300 m), seasonally dry riverbed, a piece of wood (dicot, decay stage 2, 27 cm in diameter), 1 Nov. 2010, *Miettinen* 14263* (holotype MAN, isotypes H7200140, BO).

Etymology: Tristis (Lat., adj.) - gloomy.

Description: Basidiocarps annual, effused-reflexed, solitary or imbricate, projecting up to 0.5 cm, occasionally fusing together in large groups and then up to 5 cm in longest dimension. Upper surface ridged, greyish-brown to almost black, sometimes covered by incomplete pores. Pileal edge sharp to blunt, concolourous with cap surface, often covered by open pores, margin of resupinate parts grevish, compact, adnate, sharply delimited, Pore surface grey to greyish-brown; pores angular to elongated, 5-7 per mm, with thin, entire or uneven dissepiments. Section: context sturdy, dark grey to almost black, up to 0.5 mm thick; tubes sturdy, one-layered, concolourous with hymenial surface, up to 3 mm thick. Hyphal structure dimitic; hyphae clamped. Context dimitic; skeletal hyphae greyish to brownish, interwoven or subparallel, sometimes glued together by amorphous brownish matter, occasionally branched, (2.7-)2.8-3.8(-4.2) µm diam (n = 20/1), lumen varying from narrow to capillary or indistinct, side branches 1.5–2.5 µm diam, generative hyphae hyaline, slightly thick-walled, 2-3 µm diam. Trama dimitic; skeletal hyphae greyish to brownish, rather loosely interwoven, some flexuous, occasionally branched, $(2.8-)2.9-4.0(-4.1) \mu m$ diam (n = 20/1), lumen wide to capillary, generative hyphae thin- or slightly thickwalled, 2-3.5 µm diam. Subhymenium indistinct. Rhomboid or prismatic crystals abundant among tramal hyphae, up to 5 µm in longest dimension. Cystidioles abundant, gradually tapering to the apex, 12-15.5 × 4-6 µm. Basidia clavate, (11.8-)12.9-19.1(-19.7) × (5.1–)5.2–6.4(–6.8) µm (n = 20/1). Basidiospores with a distinct wall, broadly cylindrical to narrowly ellipsoid, sometimes slightly curved, (4.2–)4.4–5.8(–5.9) × (2.7–)2.8–3.1(–3.2) µm (n = 30/1), L = 5.05, W = 2.94, Q = 1.72.

Notes: Annual, small, half-resupinate, mouse-grey basidiocarps occurring in large groups are a unique macroscopic trait of *F. tristis*. Clearly coloured skeletal hyphae, non-encrusted cystidioles and rather small basidiospores of this species are reminiscent of *F. nigra* and its siblings (= *Melanoporia* spp.) but they are not closely related to *F. tristis* phylogenetically (Suppl. Fig. S2). To date, the species has been recorded only at the type locality in New Guinea.

Fomitopsis tropica (B.K. Cui) Spirin, *comb. nov.* MycoBank MB 844973.

Basionym: Antrodia tropica B.K. Cui, Mycol. Progr. 12: 226. 2013.

Typus: **China**, Hainan, Changjiang, Bawangling, *Engelhardtia hainanensis*, 9 May 2009, *Cui* 6471* (**holotype** BJFC).

Description and phylogenetic data: Cui (2013, as *A. tropica*); see also Suppl. Fig. S2.

Fomitopsis tumulosa (Cooke) M.D. Barrett & Spirin, *comb. nov.* MycoBank MB 844974.

Basionym: Polyporus tumulosus Cooke, Grevillea 17: 55. 1889.

Typus: **Australia**, Queensland, Brisbane, 'on the ground', [no collection date], *Bailey* 607 (**lectotype** K) (selected by Cunningham 1965: 78).

Description: Núñez & Ryvarden (1995, as Laccocephalum tumulosum).

Notes: This stipitate species belongs to the Buglossoporus subclade (see Fig. 3 and Suppl. Fig. S8). Fomitopsis tumulosa and F. hartmannii are unique in the genus in having sclerotia composed of sand bound within a mycelial mass, which in F. tumulosa can be very large and weighing up to 20 kg. The genus Laccocephalum was reinstated by Núñez & Ryvarden (1995) and expanded to contain five stipitate species arising from sclerotia, all Australian with L. hartmannii extending to East Asia. Laccocephalum sensu Núñez & Ryvarden (1995) is here considered polyphyletic, with only three of their five species belonging to the Fomitopsidaceae (L. hartmannii, L. sclerotinum and L. tumulosum), and even these do not form a monophyletic lineage, although all belong within the Buglossoporus subclade (Suppl. Fig. S8). The other two Laccocephalum species treated by Núñez & Ryvarden (1995), L. mylittae and the generic type L. basilapidoides, belong outside the Fomitopsidaceae, and will be treated elsewhere.

Fomitopsis tunicata Miettinen & Spirin, *sp. nov.* MycoBank MB 844975. Figs 26, 28.

Typus: **Indonesia**, Riau, Pekanbaru, Rumbai, Caltex Camp, 0.601° 101.442° (±500 m), selectively logged mosaic of freshwater swamp and mineral soil forest, fallen dicot tree, 17 Jun. 2004, *Miettinen* 8579* (**holotype** BO, **isotype** H7200147).

Etymology: Tunicatus (Lat., adj.) - coated, tunicate.

Description: Basidiocarps annual, effused, up to 13 cm in widest dimension. Margin adnate, compact, cream-coloured, up to 1 mm broad. Hymenial surface even, cream-coloured to ivory; pores roundish to angular, 7-9 per mm, dissepiments even. Section: subiculum compact, white to pale cream-coloured, compact, 0.2-0.5 mm thick; tubes leathery, concolourous with pore surface, 0.5-2 mm thick. Hyphal structure dimitic; hyphae clamped. Subiculum dimitic; skeletal hyphae hyaline or yellowish, interwoven to subparallel, occasionally branched, (3.7–)3.8–5.7(–6.3) µm diam (n = 20/1), lumen mostly capillary to indistinct, side branches 2–3 µm diam, generative hyphae rather abundant, hyaline, slightly thick-walled, 2-4 µm diam. Trama dimitic; skeletal hyphae hyaline or yellowish, occasionally branched, (2.8–)2.9–4.1(–4.2) µm diam (n = 20/1), lumen narrow to indistinct, generative hyphae abundant, hyaline, thin- to slightly thick-walled, 2-3.5 µm diam. Subhymenium distinct in some parts, up to 20 µm thick. Cystidioles abundant, tapering, 11-15 × 3-4 µm. Skeletocystidia present as somewhat swollen (up to 4.5 µm diam), blunt apices of tramal skeletal hyphae, slightly projecting above hymenium. Basidia broadly clavate, $(10.8-)11.0-15.1(-16.0) \times (5.2-)5.3-6.4(-7.2) \ \mu m \ (n = 20/1).$ Basidiospores slightly thick-walled, ellipsoid, (3.4-)3.5-4.3(-5.1) × (2.6–)2.7–3.0(–3.1) μm (n = 30/1), L =3.95, W = 2.87, Q = 1.38, slightly cyanophilous, often with a large central oil-drop.

Specimen examined: Indonesia, Sumatera Barat, Padang, Limau Manis, forest edge, fallen dicot branch, 14 Jul. 2008, *Miettinen* 13050* (ANDA, H).

Notes: Phylogenetically, *Fomitopsis tunicata* is most closely related to *F. glabricystidia* (Figs 1, 3). Both species possess slightly thick-walled and weakly cyanophilous basidiospores reminiscent those of *Perenniporia* spp. However, neither their spores nor skeletal hyphae are dextrinoid, and this feature certainly separates the two species from the representatives of *Perenniporia*. *Fomitopsis tunicata* differs from *F. glabricystidia* in having smaller pores (4–6 per mm in *F. glabricystidia*), as well as narrower skeletal hyphae in the tube trama (4–6 µm diam in the latter species).



Moreover, *F. glabricystidiata* bears more pronounced and abundant skeletocystidia, and its basidiospores are slightly larger than *F. tunicata*, $(3.9-)4.0-4.7(-4.9) \times (2.9-)3.0-3.3(-3.4) \mu m$ (n = 30/1), L =4.24, W = 3.13, Q = 1.35. *Fomitopsis tunicata* was found twice in Southeast Asia while *F. glabricystidia* has been so far detected in two localities in Central Africa (Uganda).

Fomitopsis tuvensis (Spirin, Vlasák & Kotir.) Spirin & Vlasák, *comb. nov.* MycoBank MB 844976.

Basionym: Antrodia tuvensis Spirin, Vlasák & Kotir., Mycol. Progr. 15 (51): 10. 2016.

Typus: **Russia**, Tuva, Kaa-Khem Dist., Malyi Yenissei, *Populus* sp., 21 Aug. 2014, *Kotiranta* 26735* (**holotype** H!).

Description and phylogenetic data: Spirin et al. (2016, as A. tuvensis).

Fomitopsis uralensis (Pilát) Spirin & Miettinen, *comb. nov.* MycoBank MB 844977. Figs 26, 28.

Basionym: Leptoporus uralensis Pilát, Bull. Soc. Mycol. France 48: 11. 1932.

Typus: **Russia**, Ural, *Picea obovata*, 13 Sep. 1930, *Chomutsky* 204 (holotype PRM 37776!).

Synonym: Antrodia huangshanensis Y.C. Dai & B.K. Cui, Mycotaxon 116: 16. 2011.

Typus: **China**, Anhui, Huangshan Co., Mt. Huangshan Nat. Park, *Pinus massoniana*, 11 Oct. 2004, *Dai* 6082* (**holotype** BJFC).

Description: Basidiocarps annual, effused-reflexed or totally resupinate, often 1-2 cm diam, sometimes fusing together and then up to 5 cm in widest dimension. Reflexed part projecting up to 7 mm, upper surface finely pubescent or smooth, azonate, cream-coloured; margin sharp, incurved. Margin of resupinate part adnate or partly detaching, compact, white to cream-coloured, up to 0.5 mm wide. Hymenial surface even, cream-coloured to pale ochraceous; pores angular, 2-4 per mm, dissepiments uneven to serrate. Section: context soft, white or pale cream-coloured, up to 0.5 mm thick; tubes soft, in older parts partly agglutinated, pale cream-coloured to pale ochraceous, 0.5-1.5 mm thick. Hyphal structure monomitic; hyphae clamped. Context hyphae hyaline, moderately thick-walled to subsolid, (2.8-)3.0-5.1(-5.2) μ m diam (n = 45/2). Tramal hyphae hyaline, slightly to very thickwalled, (2.8-)2.9-4.9(-5.0) µm diam (n = 40/2), often distinctly twisted at dissepiment edges. Cystidioles absent. Basidia clavate, $(13.4-)16.2-20.7(-21.0) \times (3.8-)4.0-5.3(-5.4) \ \mu m \ (n = 25/2).$ Basidiospores with a distinct wall, cylindrical, occasionally slightly curved, (4.8–)4.9–6.8(–7.0) × (1.8–)1.9–2.3(–2.4) µm (n = 120/4), L = 5.16–6.23, W = 2.02–2.12, Q = 2.56–2.95.

Specimens examined: **Russia**, Khabarovsk Reg., Khabarovsk Dist., Malyi Kukachan, *Picea ajanensis*, 19 Aug. 2012, *Spirin* 5399* (H); Solnechnyi Dist., Igdomi, *P. ajanensis*, 4 Sep. 2016, *Spirin* 10946*, 10966 (H).

Notes: Kotlaba & Pouzar (1990) moved *L. uralensis* to *Skeletocutis* due to a superficial similarity of this species to *S. amorpha*, the type of the latter genus. While doing so, they also pointed out the absence of encrusted hyphal tips at the dissepiment edges, which are so characteristic of *Skeletocutis* spp. We studied the type of *L. uralensis* as well as three recent collections from the

Russian Far East. The species is morphologically highly similar to *F. ramentacea* and its relatives, and it differs from them mainly due to distinctly smaller basidiospores. Like *F. ramentacea, F. uralensis* inhabits exposed, dry branches or recently fallen logs, and it seems to be restricted to spruce (*Picea ajanensis, P. obovata*) and pine (*P. massoniana* – Cui *et al.* 2011, as *A. huangshanensis*) in Asia.

Fomitopsis ussuriensis (Bondartsev & Ljub.) Spirin & Miettinen, *comb. nov.* MycoBank MB 844978.

Basionym: Phellinus ussuriensis Bondartsev & Ljub., Nov. Syst. Plant. non Vasc. 2: 143. 1965.

Typus: **Russia**, Primorie, Shkotovo Dist., Artyomovka, *Kalopanax septemlobus*, 3 Aug. 1946, *Ljubarsky* (**holotype** LE 22526!).

Synonym: Fomitopsis incarnatus K.M. Kim, J.S. Lee & H.S. Jung, Mycologia 99: 835. 2008.

Typus: **Korea**, Kangwon, Chiak, *Fraxinus mandshurica*, 25 Jul. 2005, *Lee* & *Kim* (**holotype** SNU m-05072501*).

Description: Basidiocarps perennial, sessile, at first bracket-shaped, later ungulate, broadly attached, projecting up to 4 cm, occasionally effused-reflexed or totally resupinate (effused part up to 10 cm in longest dimension). Upper surface initially pinkish brown, indistinctly zonate, smooth or slightly felty, later blackish brown to totally black, with distinct annual zones, not cracking. Pileal edge sharp to rather blunt, concolourous with pore surface, up to 2 mm wide, sterile; margin of resupinate parts pinkish-grey, sharply delimited. Pore surface pinkish-grey to brownish-grey, flat or concave, finally fading to mouse-grey; pores roundish to angular, 6-7 per mm, with thin or rather thick, entire dissepiments. Section: crust (present in old basidiocarps) exceptionally tough, black, matt, up to 0.5 mm thick, context hard corky, brown, up to 10 mm thick, clearly delimited from tubes; tubes corky, distinctly stratified, pinkish-grey to reddish-brown, in total up to 20 mm thick, each annual layer 2-3 mm thick, usually separated from surrounding tube strata by a darker sterile tissue 0.1-1 mm thick. Hyphal structure dimitic; hyphae clamped. Context dimitic; skeletal hyphae dominating, brownish to brown, tightly interwoven to subparallel, rarely branched, (1.8-)1.9-3.0(-3.4) µm diam (n = 20/1), lumen capillary to indistinct, side branches 1.8-2.2µm diam, generative hyphae very rare, hyaline to brownish, slightly thick-walled, 1.5–2 µm diam. Trama dimitic; skeletal hyphae brownish to dark brown, tightly interwoven, sparsely branched, (2.2-)2.3-3.2(-3.3) μ m diam (n = 40/2), lumen predominantly capillary to indistinct, side branches 1.8–2.2 μm diam, generative hyphae hyaline, thin- or slightly thick-walled, rare, 2-3 µm diam. Subhymenium indistinct. Cystidioles rather abundant, variably tapering, 9-17 × 3-5 µm. Basidia clavate, (8.6-)8.8-14.2(-14.3) × (3.8-)3.9-5.3(-5.8) µm (n = 20/2), in senescent hymenium partly glued together. Basidiospores thin-walled or with a distinct wall, cylindrical, sometimes slightly curved, (3.6–)3.7–4.7(–5.1) × (1.8–)1.9–2.2(–2.5) µm (n = 60/2), L = 4.04–4.09, W = 2.01–2.03, Q = 2.02.

Specimens examined: China, Hunan, Liuyang Co., Daweishan Nat. Park, angiosperm, 21 Dec. 2000, *Dai* 3269 (H); Sangzhi Co., Badagongshan Nat. Res., unidentified wood, 20 Sep. 2000, *Härkönen* K567 (H); *ibid.*, 22 Sep. 2000, Härkönen K736 (H); *ibid.*, 26–28 Sep. 1999, *Härkönen* K292, K401 (H); *Prunus pseudocerasus*, 26–28 Sep. 1999, *Härkönen* K353, 398 (H); Jilin, Antu Co., Dianzhan, *Quercus* sp., 20 Sep. 1998, *Dai* 3010, 3023* (H); Huadian Co., Dongxing, *Acer* sp., 19 Sep. 1993, *Dai* 1724 (H). Japan, Hokkaido, Takinoshita, hardwood, 25 Sep. 1994, *Núñez* 651 (O 10800, H).

Notes: Because of its dark-coloured basidiocarps, this species was first described as a member of *Phellinus* and then moved to *Nigroporus* (Dai & Niemelä 1995). Our data show, however, that *P. ussuriensis* belongs to the *F. rosea* complex (Fig. 12). Sequences of our specimens are identical to those of *F. incarnata* described from Korea; therefore, the latter species is treated here as a synonym of *F. ussuriensis*.

Fomitopsis variiformis (Peck) Vlasák & Spirin, *comb. nov.* MycoBank MB 844979.

Basionym: Polyporus variiformis Peck, Ann. Rep. N.Y. St. Mus. 42: 122. 1889.

Typus: **USA**, New York, Essex Co., North Elba and Cascadeville, *Picea mariana*, 'July and September' [year not indicated], *Peck* (**syntypes** NYSf3331, 3332).

Synonym: Antrodia variiformis (Peck) Donk, Persoonia 4: 340. 1966.

Description and phylogenetic data: Spirin et al. (2017, as A. variiformis); see also Figs 1 and 2.

Fomitopsis visenda Miettinen & Spirin, *sp. nov.* MycoBank MB 848365. Fig. 28.

Typus: **Indonesia**, Jambi, Sungai Penuh, Sungai Penuh-Muara Sako roadside, -2.059° 101.286° (±5 000 m), lower montane rainforest, on a snag (dicot, decay stage 2, 20 cm in diameter), 25 Apr. 2002, *Miettinen* 6223* (**holotype** BO, **isotype** H7200588).

Etymology: Visendus (Lat., adj.) - distinctive, remarkable.

Description: Basidiocarps perennial, conchate, broadly attached, partly fusing together, projecting up to 4 cm. Upper surface brown, smooth or slightly felty, sulcate, not cracking. Pileal edge sharp, brownish to brown, up to 1 mm wide, sterile. Pore surface light grey, with scattered brownish spots, concave; pores roundish, 8-10 per mm, with rather thin, entire dissepiments. Section: context corky, brown, up to 5 mm thick, sharply delimited from tubes; tubes tough, indistinctly or rather clearly stratified, brownishgrey to brown, in total up to 8 mm thick, each annual layer up to 1-3 mm thick. Hyphal structure dimitic; hyphae clamped. Context dimitic; skeletal hyphae dominating, brownish to brown, tightly interwoven, occasionally branched, (2.7-)2.8-4.0(-4.1) µm diam (n = 20/1), lumen capillary to indistinct, generative hyphae rare, hyaline, thin- or slightly thick-walled, 2-4 µm diam. Trama dimitic; skeletal hyphae dominating, brownish to brown, tightly interwoven, occasionally branched, (2.1-)2.2-3.1(-3.2) µm diam (n = 20/1), lumen mostly narrow to capillary, side branches 1.5-2.2 µm diam, generative hyphae hyaline, thin- or slightly thick-walled, not rare, 1.5-3 µm diam. Subhymenium indistinct. Skeletocystidia present

THE GENUS FOMITOPSIS RECONSIDERED

as swollen (up to 4.5 µm diam) apices of tramal skeletal hyphae, slightly projecting above hymenium. Cystidioles rare, tapering or hyphoid, occasionally bifurcate, 9–13 × 3–4 µm. *Basidia* clavate, (8.2–)8.8–10.2(–10.3) × (4.2–)4.6–6.0(–6.2) µm (n = 10/1), in senescent hymenium slightly thick-walled and partly glued together. *Basidiospores* with a distinct wall, narrowly ellipsoid to cylindrical, longest spores slightly tapering to the distal end, (2.9–)3.0–4.2(–4.3) × (1.8–)1.9–2.3 µm (n = 30/1), L = 3.46, W = 2.07, Q = 1.67.

Notes: Fomitopsis visenda is morphologically similar and phylogenetically close to *F. scalaris* from the neotropics (Fig. 3). It differs from the latter species mainly due to rather thin, conchate basidiocarps with a downcurved margin, and it has no pileal crust so characteristic for *F. scalaris*. So far, *F. visenda* has been found only in the type locality.

Fomitopsis yunnanensis (M.L. Han & Q. An) Spirin, *comb. nov.* MycoBank MB 844980.

Basionym: Antrodia yunnanensis M.L. Han & Q. An, Phytotaxa 460: 6. 2020.

Typus: **China**, Yunnan, Jingdong, Wuliangshan Nat. Res., living angiosperm tree, 6 Oct. 2017, *Han* 1157* (**holotype** LFNC).

Description and phylogenetic data: Han et al. (2020, as A. yunnanensis); see also Suppl. Fig. S2.

Fomitopsis widdringtoniae Masuka & Ryvarden, Mycol. Helv. 5: 144. 1993.

Typus: **Malawi**, Southern Province, Thylo, Mulanje Mts., *Widdringtonia nodiflora*, 25 Jan. 1992, *Ryvarden* 31459 (**holotype** O).

Description: Masuka & Ryvarden (1993).

Notes: The species was discussed by Decock *et al.* (2022) as a relative of *F. oboensis* and *F. spraguei*.

Fomitopsis zuluensis (Wakef.) Ryvarden, Norw. J. Bot. 19: 231. 1972.

Basionym: Fomes zuluensis Wakef., Bothalia 4: 948. 1948.

Typus: **South Africa**, KwaZulu-Natal, King Cetshwayo, Nkandla, 'ad lignum', May 1935, *Rump* 374 (**holotype** K).

Description: Ryvarden & Johansen (1980).

Notes: A re-description of this species in Ryvarden and Johansen (1980) suggests *F. zuluensis* might be a close relative of *F. pinicola*. However, this morphological evidence should, if possible, be confirmed using newly collected and sequenced specimens.

A condensed key for the accepted *Fomitopsis* spp.

- 2. Hyphae predominantly thin-walled, moderately thick-walled hyphae occasionally occurring in subiculum only



SPIRIN ET AL.

(2). Hyphae with variably thickened walls, often distinctly swelling inwards in KOH Asia: F. ramentacea, F. retorrida, F. uralensis; Europe: F. ramentacea, F. renehenticii, F. solaris; North America: F. fissa, F. solaris; South America: F. solaris 3. Basidiocarps stipitate or sessile (then usually with a contacted base), generative hyphae dominating in tubes Asia: F. hartmannii; Europe: F. pulvina, F. squamosella; North America: F. amygdalina, F. pulvina; Oceania: F. hartmannii, F. maculatissima, F. sclerotina, F. tumulosa: South America: E. maculatissima (3). 4. Basidiocarps soft, light-coloured, totally effused, generative hyphae dominating in tube trama Asia: F. maculosa, F. primaeva, F. tropica, F. tuvensis, F. yunnanensis; Europe: F. infirma, F. primaeva, F. pulverulenta, F. sandaliae; North America: F. dollingeri, F. flavimontis, F. madronae (note F. madronae and F. sandaliae occasionally produce effused-reflexed basidiocarps) (4). 5. Basidiocarps compound-imbiricate; hymenophore lamellate Oceania (F. concentrica) (5). 6. (6). 7. Basidiocarps annual, soft to hard leathery Asia: F. juniperina, F. mellita; Europe: F. albidoides, F. algumicola, F. juniperina, F. labyrinthica, F. mellita; North America: F. alaskana, F. cellularis, F. juniperina, F. stereoides; South America: F. stereoides; cf. also F. gilvidula and Antrodia heteromorpha complex (7). Basidiocarps perennial, as a rule corky Europe: F. quercina; North America: F. derelicta, F. guercina; South America: F. roseofusca 8. (8). Basidiocarps lacking distinctive pink or violet colouration 11 9. Pores 2-5 per mm Europe: F. lilacinogilva; North America: F. cupreorosea, F. lilacinogilva, F. neotropica; South America: F. cupreorosea, F. flabellata, F. lilacinogilva; Oceania: F. lilacinogilva Pores smaller, usually more than 5 per mm 10 (9). Upper surface light-coloured, often fading in older individuals, no distinct crust; basidiocarps fan-shaped to effused-reflexed 10. Asia: F. carnea, F. visenda; North America: F. sagraeana; Oceania: F. eucalypti, F. marchionica; South America: F. feei; cf. also F. atypa, F. gilvidula, F. modesta, F. roseoalba and F. subectypa (10). Upper surface pinkish- or grevish-brown to black, often with a crust when old; basidiocarps of most species ungulate Asia: F. africana, F. cajanderi, F. rosea, F. substratosa, F. ussuriensis; Europe: F. cajanderi, F. perhiemata, F. rosea; North America: F. cajanderi, F. cupressicola, F. rosea; Oceania: F. foedata; South America: F. scalaris 12 11 Pores 2-5 per mm regular angular or sinuous

		14
(11).	Pores 5 and more per mm, usually regular	14

12.	Basidiocarps perennial, as a rule sessile, often covered by a crust	
		Africa: F. avellanea, F. zuluensis; Asia: F. pinicola, F. moritziana;
		Europe: F. pinicola;
	ſ	North America: F. Ilgriicolor, F. pinicola; Dceania: F. maire: cf. also F. circularis and Laricifornes officinalis
(12).	Basidiocarps annual or biennial, sessile to totally resupinate, no crus	st on pileal surface
13.	Basidiocarps sessile or effused-reflexed, often large, sappy in fresh richly branched	condition, rather soft when dry, skeletal hyphae hyaline,
		Africa: F. oboensis;
		Asia: F. betulina, F. hypoxantha, F. marianii;
		Europe: F. Detulina, F. marianii, F. spraguei; North Amorica: E. botulina, E. globispora, E. marianii, E. spraguei;
(13).	Basidiocarps sessile, effused-reflexed or resupinate, small or mediu occasionally or rarely branched, in some species brownish	m-sized, leathery, rather though when dry; skeletal hyphae
		Africa: F. malicola;
	Asia: F. acul F. m	leata, F. angusta, F. gilvidula, F. incana, F. kuzyana, F. leucaena, palicola, F. minutula; Europe: F. hyalina, F. kuzyana, F. leucaena, E. minutula, E. pulvinascons, F. sorialis;
	North America: F. calcitrosa, F. malicola, F. m	organii, F. serialiformis, F. serrata, F. psilodermea, F. variiformis; Oceania: F. cyclopis, F. eucalypticola;
	South America: F. aethalodes, F. le	ioderma, F. malicola, F. pannucea, F. roseoalba, F. psilodermea; cf. also F. glabricystidia and F. meliae
14.	Basidiospores ellipsoid, slightly thick-walled and cyanophilous; prom Basidiocarps completely resupinate, light-coloured	ninent blunt non-encrusted skeletocystidia present.
		Africa: F. glabricystidia;
		Asia: F. tunicata
(14).	Basidiospores cylindrical to narrowly ellipsoid, thin-walled or with differentiated. Basidiocarps of totally resupinate species dark-colour	i a distinct wall, acyanophilous; skeletocystidia rather weakly ed
15.	Basidiocarps perennial, sturdy; hymenophore mouse-grey to greyish	n-brown or almost black
	North Amo	rice: E condense, E nigro: of clos E perhiamete and E cooloria
(15).	Basidiocarps annual or perennial; hymenophore light-coloured, if gre	eyish then basidiocarps annual and leathery, not corky
16.	Basidiocarps annual, leathery to corky, tubes one-layered	
	Asia: <i>F. atypa, F. bambusae, F. caesp</i> North Ameri	Africa: F. atypa, F. caespitosa, F. ostreiformis, F. widdringtoniae; itosa, F. luzonensis, F. micropora, F. microcarpa, F. ostreiformis; ca: F. meliae, F. modesta, F. nivosella, F. palustris, F. subectypa; Oceania: F. caespitosa, F. luzonensis, F. ostreiformis, F. tristis;
(16).	Basidiocarps perennial, corky, woody-hard or chalk-like, tubes indist	inctly or clearly stratified 17
17.	Hymenophore clearly stratified, tubes chalky, easily crumbling	
		Asia: F. niveomarginata, F. pseudopetchii;
		North America: F. caseosa;
		Oceania: F. pseudopetchii;
(17)	Hymopophore indictingtly or clearly stratified, types your taugh	South America: F. minutispora
(17).		a: E circularis, E dochmia. E elevata. E ferrea E nhilinninensis:
		North America: <i>F. ochracea, F. lignea</i> ; Oceania: <i>F. lapidosa</i> ; cf. also <i>F. pinicola</i>
Excl	luded and insufficiently known taxa	tes: Antrodia bambusicola was described based on two collections

Antrodia bambusicola Y.C. Dai & B.K. Cui, Mycotaxon 116: 14. 2011.

Typus: **China**, Anhui, Huangshan Co., Mt. Huangshan Nat. Park, *Bambusa* sp., 21 Oct. 2010, *Dai* 11901* (**holotype** BJFC).

Notes: Antrodia bambusicola was described based on two collections from the southern part of China (Cui *et al.* 2011). The presence of cystidioles with several side outgrowths rules out *Fomitopsis* in the current sense; Liu *et al.* (2022) published sequences of this species and re-confirmed its placement in *Antrodia sensu stricto.*

SPIRIN ET AL.

Antrodia conchata D.A. Reid, Bothalia 11: 222. 1974. (as 'A. conchata (Lloyd) D.A. Reid').

Basionym: Polyporus conchatus Lloyd, Mycol. Writ. 5: 700. 1917.

Typus: **South Africa**, Western Cape Province, Klapmuts, *Populus* sp., [Dec. 1916], *van der Bijl* 358 (**lectotype** PRE) (selected by Reid 1974: 222).

Notes: The species was illegitimately introduced as *P. conchatus* by Lloyd (1917) (a later homonym of *P. conchatus* (Pers.) Fr.) and then moved to *Antrodia* by Reid (1974). Combining it in *Antrodia*, Reid in fact correctly introduced it as a new species. *Antrodia conchata* is so far known from the type material only. Newly collected and sequenced specimens are highly desirable to assign it to *Fomitopsis* as outlined here.

Antrodia rupamii Virdi, Int. J. Mycol. Lichenol. 5: 307. 1992.

Typus: India, Arunachal Pradesh, West Kameng, Rupam, angiosperm log, 9 Sep. 1981, *Virdi* 21866 (holotype PAN).

Notes: The species was collected twice in the northeastern part of India (Virdi 1992). *Antrodia rupamii* was described as having large-pored, soft basidiocarps and medium-sized ellipsoid basidiospores. These features, as well as its occurrence on angiosperm hosts suggest it is likely related to the *F. mellita – F. pulvinascens* group. This problem should be addressed to a future DNA-based study of this species.

Antrodia uzbekistanica Yuan Yuan, Gafforov & F. Wu, Phytotaxa 303 (1): 51. 2017.

Typus: **Uzbekistan**, Jizzakh: Zomin Nat. Park, *Juniperus seravschanica*, 8 Sep. 2016, *Dai* 17104* (**holotype** BJFC 22509).

Notes: Antrodia uzbekistanica was described as a sibling species of A. juniperina (= Fomitopsis juniperina above) distributed in the Middle Asia (Yuan et al. 2017). We obtained five new sequences of F. juniperina and compared them with GenBank sequences labelled as A. juniperina. Only ITS sequences of 'A. juniperina' from Macedonia are surely different from the rest of the A. juniperina sequences, and therefore F. algumicola was described above to accommodate them. All other A. juniperina sequences from North America (eastern and western parts of USA), Europe (Spain) and Africa (Ethiopia and Tanzania) form a strongly supported clade including A. uzbekistanica (Suppl. Fig. S7). It is still possible that F. juniperina as accepted here is a collective species. Proving this hypothesis will require the use of non-ribosomal markers.

Buglossoporus americanus D.A. Reid, Mem. N.Y. Bot. Gdn. 28: 179. 1976.

Notes: Buglossoporus americanus was introduced as a relative of *B. quercinus* (= *F. pulvina* above) (Reid 1976). However, its small basidiospores and dimitic tube trama described in the protologue preclude an affinity with *F. pulvina* and satellite taxa. The species is unlikely to be a member of *Fomitopsis* as redefined in the present study.

Buglossoporus matangensis Corner, Beih. Nova Hedwigia 78: 172. 1984.

Typus: **Malaysia**, Sarawak, Gunong Matang, 20 Aug. 1972, *Corner* (**holotype** E00159665).

Notes: No sequenced collections are available for this species. The protologue (Corner 1984) suggests it could be a sister species of *F. hartmannii*. Hattori (2000) concluded it was a small-pored (5–6 per mm) form of *B. malesianus*, another species of an uncertain affiliation.

Coriolus perpusillus Murrill, Bull. Torrey Bot. Club 35: 396. 1908.

Typus: **Philippines**, Mindanao, Lake Lanao, Camp Keithley, dead wood, Jul. 1907, *Clemens* 6f (**holotype** NY 00704981!).

Notes: The species was listed among synonyms of *F. modesta* (Ryvarden 1985). We restudied the type material and concluded it belongs to *Postia*. Crumbling tubes and very thick-walled tramal hyphae are reminiscent of the core *Postia* spp., *i.e. P. lactea* (the generic type), *P. grata* and *P. calcarea*. Unfortunately, the type specimen is almost sterile and no clear conclusions about species identity can be drawn based on a morphological study only. Nevertheless, *C. perpusillus* should be taken into account in future studies of *Postia* spp. in Southeast Asia.

Coriolus substipitatus Murrill, North American Flora 9: 22. 1907.

Typus: Jamaica, Portland, Port Antonio, old log, 24 Jun. [no year indicated], *Earle* 629 (holotype NY00705001!).

Notes: The species was listed among synonyms of *F. modesta* (Ryvarden 1985). The type is completely sterile although the nearly white, leathery basidiocarps and trimitic hyphal structure clearly point to *Trametes* (*Polyporaceae*).

Daedaleopsis candicans (P. Karst.) Spirin, *comb. nov.* MycoBank MB 844981.

Basionym: Daedalea candicans P. Karst., Trudy Troitskogo Otdeleniya Russkogo Imperatorskogo Geograficheskogo Obshchestva 12: 110. 1911.

Typus: **Russia**, Zabaikalie, Chita, Bayan Darga, [1908 or 1909], *Mikhno* (lectotype H 7044541!) (selected by Lowe 1956: 105).

Synonym: Daedalea sinensis Lloyd, Mycol. Writ. 7 (66): 1112. 1922.

Notes: We re-studied the single authentic collection of *D. candicans*. It is richly fertile and undoubtedly represents *Daedaleopsis sinensis* widely distributed in East Asia. Since *D. candicans* has priority over *Daedalea sinensis*, we recombine it in *Daedaleopsis*.

Daedalea hydnoides I. Lindblad & Ryvarden, Mycotaxon 71: 339. 1999.

Typus: **Costa Rica**, Guanacaste, Guanacaste Nat. Park, hardwood, 3 Nov. 1997, *Lindblad* 3679 (**isotype** O 14083).

Notes: We restudied the authentic material of this species and concluded it is identical to *Fuscocerrena portoricensis* (*Polyporaceae*) or represents a closely related taxon. Han *et al.* (2016) claimed they sequenced the type of *D. hydnoides* and their sequences confirmed its placement within *Daedalea*. The ITS sequence of *D. hydnoides* from these authors (GenBank KP171203) is identical to the ITS sequences of *D. sprucei* and *D.* stevensonii that appeared in the same paper, as well as sequences of *D. circularis* published three years earlier (Li & Cui 2013). We consider this to be the result of a lab contamination and exclude *D. hydnoides* from *Fomitopsis* in the current sense.

Daedalea microsticta Cooke, Grevillea 10 (56): 122. 1882.

Typus: **Brazil**, Rio de Janeiro, [no collecting date], *Glaziou* 13381 (**lectotype** K) (selected by Fidalgo & Fidalgo 1967: 848).

Notes: Vlasák et al. (2011) proved this species is a member of *Trametes*. The correct name for the species is *T. ochroflava*.

Daedalea ryvardenica Drechsler-Santos & Robledo, Kurtziana 37: 66. 2012.

Typus: **Brazil**, Mato Grosso, Chapada dos Guimarães, Véu da Noiva, hardwood, 12 Jun. 2011, *Ferreira-Lopes* 001 (**holotype** FLOR 41052).

Notes: *Daedalea ryvardenica* was recently described from Brazil based on morphological evidence (Drechsler-Santos *et al.* 2012). Cristaldo *et al.* (2022) published DNA sequences of *D. ryvardenica* and proved that it belongs to the *Daedalea* clade of *Fomitopsis* (see also Fig. 5). We have not studied material of *D. ryvardenica*. We feel it is premature to combine it in *Fomitopsis* until the Neotropical species of the *Daedalea* clade have properly been revised and a dozen of the older names currently treated as synonyms of *D. aethalodes* and *D. stereoides* are sorted-out.

Daedalea sprucei Berk., Hooker's J. Bot. 8: 236. 1856.

Typus: **Brazil**, Panurè, trunks of trees, Mar. 1853, *Spruce* 41 (**lectotype** K(M) 51997) (selected by Ryvarden 1984: 357)

Specimens examined: **Cuba**, Pinar del Rio, Sierra del Rosario, *Guazuma tomentosa*, 18 Feb. 1976, *Ortiz* (O F-910547). **Taiwan**, Keshun, Kuraru, Jan. 1909, *Kusano* (O F-910546, H7004131).

Notes: Figueroa and Decock (2007) studied this species by DNA methods and confirmed its placement in *Trichaptum* (*Hymenochaetales*). Han *et al.* (2016) sequenced two specimens of *D. sprucei* and accepted it as a member of *Daedalea*. We rechecked these collections (O F-910546, O F-910547) and could confirm they belong to *Trichaptum*. Two available ITS sequences (GenBank KP171211 and KR605794) are identical to those of *D. circularis* (= *F. circularis* above). This is evidently due to a lab contamination. *Daedalea sprucei* clearly does not belong to *Fomitopsis*.

Daedalea stevensonii Petr., Sydowia 13: 139. 1959.

Typus: **Malaysia**, Sabah, Kinabalu, 29 Apr. 1932, *Stevenson* (**isotype** O 10543!).

Notes: The species was described based on a single sterile collection (Petrak 1959). We have studied its isotype, which represents a typical member of *Trametes* although its species affiliation within the genus is vague. The ITS sequence from the type of *D. stevensonii* published by Han *et al.* (2016) is identical to *D. circularis* (= *F. circularis* above), morphologically a widely different species. We discarded it from our phylogenetic analyses as a lab contamination and excluded *D. stevensonii* from *Fomitopsis*.

Fomes subungulatus Murrill, Bull. Torrey Bot. Club 35: 410. 1908.

Typus: **Philippines**, Luzon, Benguet, Bagnio, *Pinus insularis*, Oct.– Nov.1905, *Merrill* 5005 (**lectotype** NY 00780696!) (selected by Ryvarden 1985: 176).

Notes: The species was treated among synonyms of *F. pinicola* (Ryvarden 1985); see notes under that species.

Fomitopsis abieticola B.K. Cui, M.L. Han & Shun Liu, Frontiers in Microbiology 12 (644979): 4. 2021.

Typus: **China**, Yunnan, Shangi-La Co., Pudacuo Nat. Park, *Abies* sp., 24 Sep. 2011, *Cui* 10532* (**holotype** BJFC 011427).

Note: See remarks to F. pinicola.

Fomitopsis hengduanensis B.K. Cui & Shun Liu, Frontiers in Microbiology 12 (644979): 7. 2021.

Typus: **China**, Yunnan, Lanping Co., Tongdian, *Picea* sp., 19 Sep. 2017, *Cui* 16259* (**holotype** BJFC 029558).

Note: See remarks to F. pinicola.

Fomitopsis kesiyae B.K. Cui & Shun Liu, Frontiers in Microbiology 12 (644979): 9. 2021.

Typus: **Vietnam**, Dam Dong, Da Lat, Bidoup Nui Ba Nat. Park, *Pinus kesiya*, 15 Oct. 2017, *Cui* 16437* (**holotype** BJFC 029736).

Note: See remarks to F. pinicola.

Fomitopsis massoniana B.K. Cui, M.L. Han & Shun Liu, Frontiers in Microbiology 12 (644979): 11. 2021.

Typus: **China**, Fujian, Wuping Co., Liangyeshan Nat. Reserve, *Pinus massoniana*, 25 Oct. 2013, *Cui* 11304* (**holotype** BJFC 015420).

Note: See remarks to F. pinicola.

Fomitopsis minuta Aime & Ryvarden, Syn. Fung. 23: 26. 2007.

Typus: **Guyana**, Potaro-Siparuni, Upper Potaro River, decorticated hardwood log, 15 Jun. 2002, *Aime* 2018 (**isotype** O).

Notes: Fomitopsis minuta was described as having trimitic hyphal structure and allantoid basidiospores $4 \times 1 \mu m$ (Aime *et al.* 2007). These characters do not fit to the genus *Fomitopsis* as defined here. The identity and generic affiliation of this species should be reassessed with the use of DNA methods.

Fomitopsis mounceae Haight & Nakasone, Mycologia 111 (2): 344. 2019.

Typus: **Canada**, Alberta, Yellowhead Co., Edson, *Populus tremuloides*, 9 Oct. 2010, *Haight* 78* (**holotype** CFMR).

Note: See remarks to F. pinicola.

Fomitopsis rubida (Berk.) A. Roy & A.B. De, Mycotaxon 60: 317. 1996.

Basionym: Polyporus rubidus Berk., London J. Bot. 6: 500. 1847.



Typus: **Sri Lanka**, Southern Prov., Point de Galle, 'on fallen trees', Dec. 1844, *Gardner* 96 (holotype K(M) 189712!, isotype UPS F-175076!).

Note: See remarks to F. carnea.

Fomitopsis scortea (Corner) T. Hatt., Mycoscience 44: 275. 2003. *Basionym: Tyromyces scorteus* Corner, Beih. Nova Hedwigia 96: 195. 1989.

Typus: **Solomon Islands**, Guadalcanal, Tsuva, 8 Nov. 1965, *Corner* (holotype E00604914).

Notes: Hattori (2003) likened the type specimen to *F. palustris*. However, the unusually large pores are an aberrant character, and Hattori could not determine the type of rot. Its placement in *Fomitopsis* needs confirmation.

Fomitopsis schrenkii Haight & Nakasone, Mycologia 111 (2): 349. 2019.

Typus: **USA**, South Dakota, Custer Co., Black Hills, *Pinus ponderosa*, Jul. 2014, *Haight* 150* (**holotype** CFMR).

Note: See remarks to F. pinicola.

Fomitopsis subpinicola B.K. Cui, M.L. Han & Shun Liu, Frontiers in Microbiology 12 (644979): 12. 2021.

Typus: **China**, Heilongjiang, Yichun, Fenglin Nat. Reserve, *Pinus koraiensis*, 2 Aug. 2011, *Cui* 9836* (**holotype** BJFC 010729).

Note: See remarks to F. pinicola.

Fomitopsis subvinosa (Corner) T. Hatt. & Sotome, Mycoscience 54: 307. 2013.

Basionym: Trametes subvinosa Corner, Beih. Nova Hedwigia 97: 166. 1989.

Typus: Indonesia, Sumatra, Karo, Berastagi, 10 Sep. 1931, *Corner* (holotype E00159614).

Notes: Hattori and Sotome (2013) described this species as similar to *F. scortea*, differing in context colour and possibly spore length. The description leaves it open whether *F. subvinosa* might be a synonym of *F. scortea* and whether it belongs to *Fomitopsis*. Further analysis would be required to confirm its status and position.

Fomitopsis tianshanensis B.K. Cui & Shun Liu, Frontiers in Microbiology 12 (644979): 12. 2021.

Typus: **China**, Xinjiang, Fukang Co., Tianshan Tianchi Nat. Reserve, *Picea schrenkiana*, 4 Jul. 2018, *Cui* 16821* (**holotype** BJFC 030120).

Note: See remarks to F. pinicola.

Laricifomes officinalis (Vill.) Kotl. & Pouzar, Česká Mykol. 11 (3): 158. 1957.

Basionym: Boletus officinalis Vill., Histoire des Plantes du Dauphiné 3: 1041. 1783.

Typus: Plate 61, fig. 1 in Micheli 1727 (**iconotype**) (selected by Ryvarden 1991:171).

Specimens examined: Italy, Piedmont, Verbano-Cusio-Ossolo, Alpe Devero, Larix decidua, 2 Aug. 2019, Cartabia (H). Russia, Yakutia, Yakutsk, Larix cajanderi, 6 Aug. 2016, Kotiranta 27358* (H 7034504).

Notes: Based on ITS and nrLSU sequences, Ortiz-Santana *et al.* (2013) and Justo *et al.* (2017) suggested that *L. officinalis* should be excluded from *Fomitopsis*. Here we support their results (Figs 1, 2) and thus confirm *Lariciformes* as the correct genus for this species.

Megasporoporia eutelea (Har. & Pat.) Spirin & Viner, *comb. nov.* MycoBank MB 848366.

Basionym: Trametes eutelea Har. & Pat., Bull. Soc. Mycol. France 28: 144. 1912.

Typus: **Mauritania**, Adrar, Atar, Bat'a, *Tamarix*, 19 May 1911, *Chudeau* (lectotype FH!, isolectotype PC!) (selected by Ryvarden 1983: 18).

Description: Basidiocarps seasonal, effused, first orbicular, then fusing together and up to 5 cm in widest dimension. Margin adnate, densely floccose to compact, white to cream-coloured, up to 1 mm broad. Hymenial surface even, cream-coloured to pale ochraceous or greyish; pores roundish to angular, 5-7 per mm, dissepiments thin, uneven. Section: subiculum rather soft, white, up to 0.5 mm thick; tubes soft-corky, in older specimens often crumbling, concolourous with hymenial surface, 2-5 mm thick. Hyphal structure dimitic; hyphae clamped, skeletal hyphae moderately to distinctly dextrinoid, slightly or moderately cyanophilous. Subiculum dimitic; skeletal hyphae hyaline to brownish, interwoven or subparallel, occasionally branched, (2.9–)3.0–5.1(–5.2) µm diam (n = 30/2), lumen rather wide to capillary, terminal branches 1–2.5 µm diam, generative hyphae rather abundant, hyaline, thin- to slightly thick-walled, 3-6 µm diam. Trama dimitic; skeletal hyphae hyaline rather loosely interwoven, hyaline or brownish, occasionally dichotomously branched, $(2.3-)2.7-4.4(-5.2) \mu m$ diam (n = 70/4), lumen rather wide to capillary, terminal branches 1-2 µm diam, generative hyphae rather abundant, hyaline, thin-walled, 2-3 µm diam. Subhymenium indistinct. Cystidioles rather rare, tapering to the apex, 11-17 × 4-6.5 µm. Hyphidia rarely present, bi- or trifurcate, often somewhat swollen at the base, apical ougrowths 1.5-2 µm diam. Basidia broadly clavate, (11.2-)12.3-18.3(-19.0) × $(6.0-)6.1-10.2(-11.0) \mu m (n = 36/4)$, in senescent hymenium partly glued together. Basidiospores with a distinct wall, narrowly ellipsoid to cylindrical or subfusiform, (6.0-)6.3-9.2(-9.8) × (2.9-)3.0-4.3(-4.4) µm (n = 111/4), L =7.37–7.69, W = 3.56–3.79, Q = 1.99–2.10, often with a large central oil drop.

Specimens examined: **Oman**, Dhofar, Wadi Darbat, angiosperm, 2 Jan. 2022, *Razmadze* 2202/9* (TUF). **Sudan**, Wadi Halfa, Ashkeit, buried wood (under *Acacia* and *Tamarix*), 9 Oct. 1962, *Ahti* 16255 (H7045438).

Notes: Ryvarden (1983) combined *T. eutelea* in Antrodia. We studied the type material and a few recent collection of *T. eutelea*. The species has dextrinoid and cyanophilous, occasionally dichotomously branched skeletal hyphae and short, wide, barrel-shaped basidia; these traits preclude *Fomitopsidaceae* and point to *Polyporaceae*. DNA data confirm this suggestion and show that *T. eutelea* belongs to *Megasporoporia* (as redefined by Wang *et al.* 2022). *Megasporoporia eutelea* is a sister species of *M. minor* differing from the latter species in 10 bp in ITS region. GenBank sequences MK157424, MW922713 (Egypt), KT153994, KF954704 (India), ON845731 (Saudi Arabia), JN630804 (Iran) and MN909156 (Pakistan) represent *M. eutelea*.

Melanoporia tropica B.K. Cui & Shun Liu, Fungal Diversity 118: 53. 2022.

Typus: **Vietnam**, Dam Dong, Da Lat, Bidoup Nui Ba National Park, living angiosperm tree, 15 Oct. 2017, *Cui* 16444* (**holotype** BJFC).

Notes: The species was described by Liu *et al.* (2022). We had no access to the type material. The name change is necessary for moving *M. tropica* to *Fomitopsis*.

Neofomitella hemitephra (Berk.) M.D. Barrett, *comb. nov.* MycoBank MB 844982.

Basionym: Polyporus hemitephrus Berk. in Hooker, The botany of Antarctic voyage II, Flora Novae Zealandiae 2: 179. 1855.

Typus: **New Zealand**, [no locality and collection date indicated], *Colenso* (**lectotype** K) (selected by Ryvarden 1977: 221).

Synonym: Neofomitella australiensis B.K. Cui & Xing Ji, Mycol. Progr. 18: 598. 2019.

Typus: **Australia**, Victoria, Yarra Ranges National Park, dead tree of *Nothofagus*, 10 May 2018, *Cui* 16571* (**holotype** BJFC; **isotype** stated to be in MEL but no collections annotated with this number exist).

Specimens examined: Australia, New South Wales, Mt. Boss State Forest, NW of Wanchope, 2 Feb. 1985, *Coveny* 3 (O 10806, H); Tasmania, Track to Philosopher Falls, near Waratah, 23 May 2016, S.J.M. McMullan-Fisher 2852 (MEL 2397595A). New Zealand, South Island, Golden Bay Dist., Cobb Valley, Asbestos track, dead wood, 23 Mar. 1996, *Ryvarden* 38462 (O 16449, H).

Notes: This species was described by Berkeley (in Hooker 1855) as having ungulate basidiocarps with a dark upper surface, small pores and stratified tubes. The species was described based on a New Zealand specimen, but it is also common in southeastern Australia. We studied specimens from Australia and New Zealand fitting well to the protologue and the later redescription of Heterobasidion hemitephrum by Cunningham (1965). Trimitic hyphal structure and distinctly coloured, strongly cyanophilous skeletal hyphae rule out Fomitopsis as a generic affiliation for this species and point to Polyporaceae as the correct family. The species has been shuffled between many different genera since its initial publication. Cunningham (1965) in his monograph of New Zealand polypores treated it under Heterobasidion, but earlier Cunningham (1948) had considered it a member of Fomitopsis. Based on culture studies, Rajchenberg (1995a) demonstrated that the species formed a white rot (associated with white heart rot, according to Cunningham 1965) and concluded it was best accommodated in the genus Fomes. More recently, Han et al. (2016) sequenced a single specimen purportedly of P. hemitephrus from New South Wales, and reinstated Cunningham's combination in Fomitopsis. The conclusion of Han et al. (2016) was followed by Zmitrovich (2018) in creating the combination Pilatoporus hemitephrus. However, P. hemitephrus causes a white rot, so it cannot be placed in the exclusively brown-rot genus Fomitopsis.

Recently, a new species *Neofomitella australiensis* was described by Ji *et al.* (2019), for a novel genetic lineage of *Neofomitella*. The protologue of *N. australiensis* clearly matches all diagnostic features of *P. hemitephrus*, including large, tough perennial basidiocarps, a crustose pileus, a distinct orange layer beneath the pileus crust ('tawny' in the protologue of *P. hemitephrus*), variably cream- to dark-brown context, and pore

and spore dimensions. Two sequences of *F. hemitephra* from New Zealand (GenBank MK404665 and MN007024) are identical to those of *Neofomitella australiensis*. However, ITS and *TEF1* sequences of *F. hemitephra* published earlier by Han *et al.* (2016) are identical to those of *F. marianii* (Figs 4, 5). We did not study the specimen (O 10808) which was the source of these sequences, and therefore we cannot decide if the specimen was misidentified or there is a case of lab contamination, but neither case would affect the application of the epithet *P. hemitephrus*. It is likely that Ji *et al.* (2019) were persuaded to exclude *P. hemitephrus* as an earlier name for their *N. australiensis* due to the conclusions of Han *et al.* (2016) that it belonged in *Fomitopsis*. However, a broader reading of the literature for this species leaves no doubt that *Polyporus hemitephrus* is a white-rot species, and that *Neofomitella australiensis* is its later synonym.

Neolentiporus tropicus B.K. Cui & Shun Liu, Fungal Diversity 118: 55. 2022.

Typus: **China**, Hainan, Ledong, Jianfengling National Park, angiosperm, 19 Jun. 2016, *Cui* 13915* (**holotype** BJFC).

Notes: The species was described by Liu *et al.* (2022). We had no access to the type material. Phylogenetically, the species belongs to *Buglossoporus* clade (Fig. 2 and Suppl. Fig. S8). The identity of *N. tropicus vs. Buglossoporus matangensis* and *B. malesianus* should be verified before moving it to *Fomitopsis*.

Pilatoporus maroccanus Kotl. & Pouzar, Cryptog. Mycol. 14: 215. 1993.

Typus: **Morocco**, Middle Atlas, Ifrane, *Cupressus sempervirens*, 17 Apr. 1992, *Kotlaba* (**holotype** PRM 842893!*).

Notes: Kotlaba & Pouzar (1993) introduced this species as a member of *Pilatoporus* (= *F. palustris* complex). Vampola (1996) concluded that *P. maroccanus* is a genuine species of *Trametes* and suggested it could be identical to *T. suaveolens*. We restudied the type material with morphological and DNA methods, and our data confirm *P. maroccanus* is a later synonym of *Trametes junipericola* (*Polyporaceae*).

Polyporus fulvitinctus Berk. & M.A. Curtis, J. Linn. Soc., Bot. 10: 313. 1869.

Typus: **Cuba**, [no locality or collection date indicated], *Wright* 136 (holotype K(M) 264880!).

Notes: Ryvarden (1984) placed *P. fulvitinctus* to the synonyms of *Fomitopsis nivosa* (discussed below as *Polyporus nivosus*). However, this synonymy cannot be maintained because the type specimen represents a polypore with dichotomously branched, brown, strongly cyanophilous skeletal hyphae. These anatomical traits, in combination with sturdy, greyish-brownish, small-pored basidiocarps and rather long, cylindrical-subfusiform basidiospores indicate that *P. fulvitinctus* has affinities with *Datronia* (*Polyporaceae*).

Polyporus nivosus Berk., Hooker's J. Bot. 8: 196. 1856.

Typus: **Brazil**, Panurè, dead trunks of trees, Feb. 1853, *Spruce* 192 (**lectotype** K(M) 257627!, **isolectotype** PC!) (selected by Ryvarden 1984: 348).



Description: Basidiocarps annual or probably short-living perennial, sessile or effused-reflexed, projecting up to 3.5 cm. Upper surface first cream coloured to pale ochraceous, azonate, smooth. Pileal edge sharp, concolourous with cap surface, sterile, up to 0.5 mm wide. Pore surface cream-coloured or pale ochraceous, sometimes with a faint pinkish tint, concave; pores roundish to angular, (5–)6–8(–9) per mm, with thin, entire dissepiments. Section: context corky, cream- to wood-coloured, up to 5 mm thick; tubes sturdy, one-layered or indistinctly stratified, concolourous with hymenial surface, up to 7 mm thick. Hyphal structure dimitic; hyphae clamped. Context dimitic; skeletal hyphae hyaline to pale ochraceous, densely interwoven or in subparallel bundles, occasionally branched, $(3.2-)3.7-5.8(-6.1) \mu m$ diam (n = 40/2), lumen changing from wide to almost invisible, side branches 2-3 µm diam, often subsolid, generative hyphae rare, hyaline, thin- or slightly thick-walled, 3-4 µm diam. Trama dimitic; skeletal hyphae dominating, hyaline to pale ochraceous, interwoven, some flexuous, accidentally branched, (3.0-)3.1-4.7(-4.8) µm diam (n = 40/2), lumen capillary to indistinct, generative hyphae rather rare, thinwalled, quickly collapsing, 2–3 µm diam, dissepiment edges dimitic, consisting of thin-walled, flexuose generative hyphae and winding skeletals with a wide lumen. Subhymenium indistinct. Cystidioles not seen. Basidia short-clavate, (8.2-)8.8-11.6(-12.3) × (4.0-)4.1-5.1(-5.2) µm (n = 14/2), rare; basidioles widely dominating in hymenium, broadly ovoid to subglobose, 6-9 × 5.5-7 µm. Basidiospores thin-walled, cylindrical-fusiform, (6.0-)6.1-8.0(-8.4) × (2.5–)2.6–3.2(–3.3) μ m (n = 60/2), L = 6.91–7.07, W = 2.88–2.95, Q = 2.35 - 2.46, often with one or a few small guttulae.

Specimen examined: **Brazil**, Pernambuco, Paulista, hardwood, Jul. 2002, *Barbosa* 360* (O 17846).

Notes: Due to the light-coloured and seemingly annual basidiocarps, F. nivosa was considered a relative of F. palustris and its sibs (Gilbertson & Ryvarden 1986), and therefore transferred to the genus Pilatoporus (Kotlaba & Pouzar 1993). However, it differs from them in having rather small pores, short basidia and fusiform basidiospores, and it lacks sterile hymenial elements. Only two specimens of F. nivosa are known to us, i.e. the type specimen and a recent collection from Pernambuco (Brazil) which morphologically agrees with the type. From the latter specimen, we were able to generate a low-quality ITS sequence showing Antrodiella aurantilaeta from the residual polyporoid clade of the Polyporales as the closest hit in GenBank. Though the sequence is somewhat ambiguous (and was therefore not submitted to GenBank), it clearly excludes affinity to Fomitopsidaceae. For this reason, we exclude P. nivosus from Fomitopsis and leave the question about its identity and phylogenetic position for future studies.

Polyporus notopus Lév., Ann. Sci. Nat., Bot. 3 (2): 194. 1844.

Typus: **Indonesia**, Java, 'ad truncos', [no collection date and collector indicated] (**holotype** PC!).

Notes: Ryvarden (1981) suggested that *P. notopus* represents a juvenile individual of *F. modesta*. We studied the type of this species. It is a small pileate basidiocarp with resinous, tiny pores (9–12 per mm). It is sterile and infected by moulds. In our opinion, *P. notopus* does not belong to *Fomitopsidaceae* or *Trametes*. It gives the appearance of cottony, dimitic context and monomitic, agglutinated lower trama. Only simple septa were seen and they are not uncommon in the skeletal-like hyphae of context. No thick-

walled or other cystidia could be seen. It reminds of *Flaviporus liebmannii* (*Steccherinaceae*), but the context structure, as well as the lack of cystidia and clamps suggest otherwise. In short, we cannot connect this low-quality specimen with any species or genus known to us.

Polyporus portentosus Berk., London J. Bot. 3: 188. 1844.

Typus: **Australia**, Western Australia, Swan River, [no collection date indicated], *Drummond* 125 (**holotype** K).

Notes: Based on morphological and cultural traits, Rajchenberg (1995) placed *P. portentosus* in *Laetiporus*. Blasting available ITS and LSU sequences of *P. portentosus* shows that it could be a member of *Fomitopsis*. Additional markers (in particular, *RPB1*) are highly desirable to re-establish its generic position.

Pseudoantrodia monomitica B.K. Cui, Y.Y. Chen & Shun Liu, Fungal Diversity 118: 56. 2022.

Typus: **China**, Fujian, Fuzhou, Gushan Forest Park, *Pinus* sp., 29 Nov. 2019, *Dai* 21129* (**holotype** BJFC).

Notes: The species was described by Liu *et al.* (2022). We had no access to the type material. According to the protologue, *P. monomitica* is morphologically very similar to *F. monomitica* and *F. oleracea* but phylogenetically quite distant. The name change is necessary for moving *P. monimitica* to *Fomitopsis*.

Pseudophaeolus soloniensis (Dubois) Spirin & Rivoire, comb. nov. MycoBank MB 844983.

Basionym: Agaricus soloniensis Dubois, Méthode Éprouvée (Orleans): 177. 1803.

Typus: **France**, Tarn, Montirac, *Castanea sativa*, 27 May 2014, *Rivoire* (**neotype** designated here LY BR-5263*, MycoBank MBT 10008296).

Synonym:

Polyporus irpex Schulz. ex E.H.L. Krause, Arch. Freunde Naturgesch. Mecklenb. 1: 129. 1925.

Typus: **Slovenia**, Črny gaj, *Quercus* sp., [no collection date and collector indicated] (**syntypes** W0132391!, W0132392!).

Notes: For a long time, this species was treated as a member of *Piptoporus* (see under *P. soloniensis* in Ryvarden *et al.* 2017). Han *et al.* (2016) discovered that *P. soloniensis* is phylogenetically distant from the generic type of *Piptoporus*, *P. betulinus* (= *F. betulina* above) and placed it in the separate genus, *Piptoporellus*. Based on DNA data, Tibuhwa *et al.* (2020) showed that *Laetiporus baudonii* is closely related to *P. soloniensis* and moved it to *Piptoporellus*. However, they overlooked that *Polyporus baudonii* is the generic type of *Pseudophaeolus*, a monotypic genus which was described 40 years earlier than *Piptoporellus*. Therefore, we recombine *P. soloniensis* in *Pseudophaeolus* and treat *Piptoporellus* as a synonym of the latter genus. Additionally, a neotype for *A. soloniensis* is lacking.

Han *et al.* (2016) introduced two more species, *Piptoporellus hainanensis* and *P. triqueter*, as close relatives of *P. soloniensis*. Unfortunately, they did not pay attention to six species (*Polyporus appendiculatus*, *P. komatsuzakii*, *P. medullae*, *P. sambuceus*, *Tyromyces armeniacus* and *T. imbricatus*) described from the

southern and eastern parts of Asia and currently treated as synonyms of *P. soloniensis*. Therefore, we are unwilling to combine *P. hainanensis* and *P. triqueter* in *Pseudophaeolus* until the identity of these older taxa is fully resolved.

Pseudophaeolus trichrous (Berk. & M.A. Curtis) Vlasák & Spirin, *comb. nov.* MycoBank MB 844984.

Basionym: Polyporus trichrous Berk. & M.A. Curtis, Ann. Mag. Nat. Hist. 2 (12): 434. 1853.

Typus: **USA**, South Carolina, 'old logs', [no collection date indicated], *Curtis* 2844 & *Ravenel* 973 (**syntypes** K).

Specimen examined: **Costa Rica**, Puntarenas, Monteverde, Santa Elena, Quercus sp. (?), Mar. 2022, *Vlasák* 2203/5* (JV, TUF).

Notes: Pseudophaeolus trichrous is the North American relative of *P. soloniensis*. Morphologically, both species are highly similar and they were therefore considered conspecific (Gilbertson & Ryvarden 1987). However, DNA sequences clearly separate them. As redefined here, *P. trichrous* differs from *P. soloniensis* in having smaller pores (4–6 per mm vs. 2–3 per mm) and slightly narrower basidiospores, (4.1–)4.2–5.7(–6.2) × (2.1–)2.2–3.0 µm (n = 30/1), L = 4.88, W = 2.57, Q = 1.91 (vs. (4.1–)4.2–6.1(–6.2) × (2.6–)2.8–3.3(–3.6) µm (n = 30/1), L = 5.03, W = 3.05, Q = 1.65 in *P. soloniensis*).

Trametes fulvidochmia Corner, Beihefte zur Nova Hedwigia 97: 104. 1989.

Typus: **Malaysia**, Terengganu, Kemaman, fallen log, 24 Jun. 1932, *Corner* (**holotype** E00438040).

Notes: Hattori (2005) suggested this species is related to *F. dochmia*. No modern collections of *T. fulvidochmia* are available, and we have not studied the type, why we are uncertain if it is related to the *F. dochmia* complex or any other *Fomitopsis* spp.

DISCUSSION

In this study, we argued for retaining the largest clade of *Fomitopsidaceae* as one genus, *Fomitopsis*, encompassing 111 already existing and 17 newly introduced species. Based on a revision of over 500 herbarium specimens (including 133 types) from four continents and newly produced or already available DNA sequences, we reduced 26 recently described species to synonyms and resurrected 26 older species previously listed among synonyms of other taxa.

Being reassessed for 128 accepted species, *Fomitopsis* becomes one of the largest polypore genera. However, species diversity in the genus is likely much higher than presented in this study. Among newly described taxa, two conspicuous species (*F. algumicola* and *F. perhiemata*) came from Europe and two (*F. cupressicola* and *F. derelicta*) from North America, *i.e.* from areas studied by mycologists for over two centuries. It means that more extensive collecting, especially in tropical areas and the southern hemisphere, will likely result in further taxonomic novelties. To date, *Fomitopsis* is represented by approximately the same number of species in three regions: warm temperate to boreal northern hemisphere (with 29 species from Europe, 24 from Asia and 32 from North America), tropical Asia (32 species) and the Neotropics (31

species). At the same time, 18 species were detected in Oceania (including Australia) and only 13 are known from Africa. This is a clear indication of insufficient sampling in the latter regions. In addition to purely taxonomic and floristic purposes, discovery of new species accompanied by deeper sequencing will certainly facilitate a much better understanding of the inner structure and evolutionary trends in *Fomitopsidaceae*.

Numerous rearrangements of species names and identities highlight the primary challenge in all contemporary studies in fungal taxonomy. It lies in a choice between immediate publication of taxonomic novelties (mainly based on using of the ITS region as a universal barcoding marker; Schoch *et al.* 2012) and undertaking deeper study of a presumed new species, which requires critical reassessment of related taxa (including their type material), broader geographic sampling and the use of additional genetic markers, and exhaustive study of relevant type material. In general, the first alternative has certain advantages because it makes newly obtained data available for a broader audience in a reasonable time. Moreover, fungi are one of the largest groups with hidden and undersampled species diversity, which means that many quickly introduced species names will likely survive in the future. However, the fast way of doing taxonomy does carry several disadvantages.

It is particularly likely in well-studied conspicuous fungi such as polypores, that many potentially new species already have an older name. The only way to diminish the risk of introducing superfluous names is to investigate type material of all taxa, both accepted and considered as synonyms, which appear in phylogenetic analyses as close relatives of a newly detected species. Although it may appear self-evident, this important step is often neglected. This has caused an emergence of new unnecessary names making species delimitation in Fomitopsidaceae even more challenging than it was before the introduction of DNA methods. Alongside agarics, polypores are the most frequently collected basidiomycetes, both in temperate forests and tropical areas. Seventy-five *Fomitopsis* spp. treated above produce pileate, robust and in many cases perennial basidiocarps, which are frequently collected (and described as new). The Fomitopsis palustris complex revised in the present paper exemplifies this situation. Of five species described in this group in the last ten years (in addition to numerous names introduced in the pre-DNA era), only one will probably survive while we place four others to the synonymy of species described over a hundred years ago. The members of the F. palustris complex are primary wooddecomposers inhabiting various (including industrially important) plant species (Rungjindamai et al. 2009, Roccotelli et al. 2014), and therefore the introduction of ill-defined species has not only purely scientific but also practical consequences.

The next challenge facing taxonomists arises from the binomial nature of a species name. According to the Code (Art. 35.1), valid publication of a new species implies the species is going to be described as a member of an already existing or simultaneously introduced genus. Formally, indication of the single feature which, in opinion of the author, distinguishes a newly introduced taxon from other ones is enough for introducing a new species or a new genus (Code Art. 38.2). This, somehow ambiguous, provision in the Code opens a door for describing new genera based on arbitrarily selected traits, without critical evaluation of their constancy and taxonomic significance in a given group. As a consequence, many of these genera turn out to be monotypic (Parmasto 1994). Nowadays, it is not an exceptional situation that DNA data show a newly found species is equally distant from already described and sequenced members of other genera, and thus seemingly requiring its own genus. The next step often taken is using any features differentiating the new species from its phylogenetic neighbours for justifying a new genus for it. This 'microgeneric approach', *i.e.* a tendency to raise each particular clade in the phylogenetic tree to the generic rank, currently dominates fungal taxonomy.

The microgeneric approach to the taxonomy of *Fomitopsis* and allied taxa fits best with the 'nomothetic paradigm' as introduced by Sigwart *et al.* (2018). According to their view, plants and fungi are considered as groups containing large genera that should be further split to fulfil the criteria of monophyly. This conclusion was based on a comparison of genus-size distribution in six large groups of animals with simulated phylogenies constructed under various speciation / extinction rates, and it imposes a law that most genera across all eukaryotic organisms are naturally small or even monotypic, and the number of larger genera should decrease proportionally to their size.

[The term 'nomothetic' was first introduced by the German neo-Kantian philosopher Wilhelm Windelband (Windelband 1904). It refers to one of two possible ways of presenting scientific knowledge, namely in a form of a universal law or rule installed for a given group of objects. Its alternative is the so-called 'idiographic' method oriented to specific, non-repeatable aspects of things or events. While the first way of representing reality is typical for natural sciences, the second one is more characteristic for history and allied disciplines. However, Windelband emphasized these two methods are not mutually exclusive, and the same class of objects or even the single object could be studied by them both. Even more important is that these methods do not define the contents of scientific knowledge (empirical reality) but characterize its treatment or interpretation ("Behandlung") in a given science.]

We argue that, in spite of being entitled nomothetic, the approach by Sigwart et al. (2018) has certain limitations and cannot serve as a theoretical framework for our study, at least at the present level of our knowledge about the target group. The reason is that primary data about species richness of genera used by Sigwart et al. in the generic size distribution analyses came from taxonomic experts in six selected groups of animals. This poses two problems. Firstly, the taxonomic experts are, to some degree, influenced by the ongoing taxonomic fashion. Sigwart et al. explicitly recognize and then reject this possibility: they suggest the analysed groups are so divergent and investigated by so different methods that the taxonomists studying them can hardly sway each other. Secondly, the groups that their analyses rely on are difficult to compare to fungi and plants. These groups (accepted genera of marine invertebrates, odonates, fish, reptiles, birds, and mammals) are much better structured organisms with (as a rule) more complex life cycle than plants and fungi, which possess plenty of morphological traits potentially significant for taxonomists. The situation in plants and especially in fungi is dramatically different: some sister genera or even similar-looking but not closely related genera can be distinguished through very few morphological characters whose relevance is strongly dependent on growing conditions and good preservation of collected samples (cf. Spirin et al. 2019a, 2021).

We exemplified that a single morphological character, however peculiar it is, cannot give a sufficient justification for erecting a new genus, even if this option has been supported by DNA data. In our case, the suprageneric unit we were looking at was the family *Fomitopsidaceae* as redefined in multigene analyses by Justo *et al.* (2017). Denser taxon sampling of *Fomitopsidaceae* initiated by Runnel *et al.* (2019) and continued in the present study revealed three strongly supported lineages none of which, however, could be separated from the others based on a single morphological trait. Nevertheless, they can be distinguished via sets or combinations of characters (see Results) and thus are morphologically definable. Further splitting of these clades is possible based on DNA data although attempts to define them in morphological terms mainly lead to evident overestimation of rather ephemeral features. Validity of these differences becomes vague when more extensive material is involved in the microscopic scrutiny. This conclusion is grounded in our critical study of 124 from 142 species currently accepted in the Fomitopsidaceae, i.e. 87 % of the known species diversity. Our general conclusion is that searching for an appropriate genus for the species in hand should start with a critical reassessment of morphological traits taxonomically significant for a given suprageneric unit (a family or, in a case of a poorly established family division, an order) revealed in multigene phylogenetic analyses. Not the single character but only a stable combination of characters intrinsic to members of a well-supported clade in the family / order-level phylogeny can provide a good reason for (re) establishing it as a genus.

Several recent publications followed the same vein and argued in favour of a more conservative, 'macrogeneric' approach for fungal taxonomy, especially in the species-rich groups (e.g., Spirin et al. 2018, 2019b, 2019c, Kuo et al. 2020, Koukol & Delgado 2021, Meiras-Ottoni et al. 2021, Viner et al. 2023). However, merging smaller genera together is not an end in itself, and it should be undertaken only after thorough estimation of further changes the proposed solution would have for the neighbouring taxa. The present study also exemplified how lumping taxa together meets with a nomenclatural problem of choosing the most appropriate name for the re-established genus. Although the principle of priority is among the cornerstones of nomenclature for plants and fungi, the Code makes a provision for another solution – a conservation, *i.e.* retaining the younger generic name and suppressing the older one. The oldest available name is not always the most desirable, and consequences of possible nomenclatural and taxonomic actions, both for experts and for a broader audience, should be carefully weighed in each case.

ACKNOWLEDGEMENTS

We are deeply indebted to the curators of O, S, PC, K, PRM, TUF, LY, UPS, L, NY, BPI, MICH, FH, W and MCF who sent us types and important specimens. Neil Dollinger, Josef Vlasák Jr. (USA), Jiří Kout (Czech Republic), Heikki Kotiranta, Daria Razmadze (Finland), David Boertmann (Denmark), Evgeniy Dunayev (Russia), Katerina Rusevska and Mitko Karadelev (North Macedonia) provided us with valuable collections used in the present study. Kare Liimatainen (United Kingdom), Beatriz Ortiz-Santana (USA), Ellen Larsson and Elisabeth Sjökvist (Sweden) helped us with sequencing of some important specimens. Vera Malysheva (Russia) generously helped us with completing illustrations and provided us with sequence data of F. incana. The research of JV was financed by the institutional support of the Academy Sciences of the Czech Republic (RVO: 60077344). The research of IV has been supported by Societas pro Fauna et Flora Fennica. The contribution of TG was supported by research project J4-3098 "The unrevealed information on soil biodiversity in leached waters" and the Research Program in Forest Biology, Ecology and Technology (P4-0107), both of the Slovenian Research Agency.

DECLARATION ON CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

REFERENCES

- Aime L, Ryvarden L, Henkel W (2007). Studies in neotropical polypores 22. Additional new and rare species from Guyana. Synopsis Fungorum 23: 15–31.
- Ainsworth AM (2001). Antrodia ramentacea on Salix in S.E. England. Field Mycology 2 (2): 46–49.

Audet S (2017). New genera and new combinations in Antrodia sensu lato. In: Mushrooms nomenclatural novelties nos. 1–9. https:// sergeaudetmyco.com/antrodia/

- Berkeley MJ, Curtis MA (1853). Centuries of North American fungi. *The* Annals and Magazine of Natural History **2**: 417–435.
- Berkeley MJ (1854). Decades of fungi. Decades XLI XLIII. Hooker's Journal of Botany 6: 129–143.
- Bernicchia A (2005). Polyporaceae sensu lato Fungi Europaei 10: 1-808.
- Bernicchia A, Gorjón S (2020) Polypores of the Mediterranean region. Romar, Gessate.
- Bernicchia A, Ryvarden L (1998). Two new brown-rot polypores from Italy. Mycologia Helvetica 8: 3–10.
- Bernicchia A, Ryvarden L (2001). A new Antrodia species (Coriolaceae, Basidiomycetes). Mycotaxon 79: 57–66.
- Blume C, Nees von Esenbeck TFL (1826). Fungi Javanici, editi conjunctis studiis et opera. Nova Acta Physico-Medica Academiae Caesareae Leopoldino-Carolinae Naturae Curiosum 13: 10–22.
- Buchanan PK, Ryvarden L (1988). Type studies in the *Polyporaceae*. 18. Species described by G.H. Cunningham. *Mycotaxon* **31**: 1–38.
- Buchanan PK, Ryvarden L (1993). Type studies in the *Polyporaceae* 24. Species described by Cleland, Rodway and Cheel. *Australian Systematic Botany* 6: 215–235.
- Carranza-Morse J, Gilbertson RL (1986). Taxonomy of the *Fomitopsis* rosea complex. *Mycotaxon* **25**: 469–486.
- Castresana J (2000) Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Molecular Biology and Evolution* **17**: 540–552.
- Chen JJ, Cui BK, Zhou LW, et al. (2015). Phylogeny, divergence time estimation, and biogeography of the genus Heterobasidion (Basidiomycota, Russulales). Fungal Diversity 71: 185–200.
- Chen YY, Wu F (2017). A new species of *Antrodia* (*Basidiomycota*, polypores) from China. *Mycosphere* 8: 878–885.
- Cooke MC (1886). Praecursores ad Monographia Polypororum. *Grevillea* **14**: 77–87.
- Corner EJH (1935). The fruit-body of *Polystictus xanthopus* Fr. *Transactions* of the British Mycological Society **46**: 71–111.
- Corner EJH (1953). The construction of polypores 1. Introduction: Polyporus sulphureus, P. squamosus, P. betulinus and Polystictus microcyclus. Phytomorphology **3**: 152–167.
- Corner EJH (1984). Ad Polyporaceaes II & III. Beihefte zur Nova Hedwigia 78: 1–222.
- Corner EJH (1989). Ad Polyporaceaes VI. *Beihefte zur Nova Hedwigia* 97: 1–197.
- Cristaldo E, Kossmann T, Campi M, et al. (2022). Neotropical Daedalea (Basidiomycota, Fomitopsidaceae) revisited: Daedalea rajchenbergiana sp. nov. from Brazil. Lilloa **59**: 273–289.
- Cui BK (2013). *Antrodia tropica sp. nov.* from southern China inferred from morphological characters and molecular data. *Mycological Progress* **12**: 223–230.
- Cui BK, Li HJ, Dai YC (2011). Wood-rotting fungi in eastern China 6. *Mycotaxon* **116**: 13–20.
- Cunningham GH (1948). New Zealand Polyporaceae. 5. The genus Fomitopsis. Bulletin of the New Zealand Department of Scientific and Industrial Research **76**: 1–8.
- Cunningham GH (1954). Hyphal systems as aids in identification of species and genera of the *Polyporaceae*. *Transactions of the British Mycological Society* **37**: 44–50.
- Cunningham GH (1965). *Polyporaceae* of New Zealand. *Bulletin of the New Zealand Department of Scientific and Industrial Research* **164**: 1–304.
- Dai YC, Niemelä T (1995). Changbai wood-rotting fungi 4. Annales Botanici Fennici **32**: 211–226.



- Darriba D, Posada D, Kozlov AM, *et al.* (2020). ModelTest-NG: A new and scalable tool for the selection of DNA and protein evolutionary models. *Molecular Biology and Evolution* **37**: 291 294.
- David A (1980). Étude du genre Tyromyces sensu lato: répartition dans les genres Leptoporus, Spongiporus et Tyromyces sensu stricto. Bulletin Mensuel de la Société Linnéenne de Lyon 49: 6–56.
- David A, Dequatre B (1985). Deux ultraspecies: Antrodia malicola (Berk. et M.A. Curtis) Donk et A. ramentacea (Berk. et Br.) Donk. Cryptogamie, Mycologie 5: 293–300.
- Decock CA, Ryvarden L, Amalfi M (2022). Niveoporofomes (Basidiomycota, Fomitopsidaceae) in tropical Africa. Mycological Progress **21**: 29.
- Degnan JH, Rosenberg NA (2009). Gene tree discordance, phylogenetic inference and the multispecies coalescent. *Trends in Ecology and Evolution* **24**: 332–340.
- Donk MA (1966). Notes on European polypores I. Persoonia 4: 337-343.
- Donk MA (1971). Notes on European polypores VI (A). Proceedings van de Koninklijke Nederlandse Akademie van Wetenschappen, Section C 74: 1–14.
- Drechsler-Santos ER, Cavalcanti MAQ, Loguercio-Leite C, et al. (2012). On neotropical Daedalea species: Daedalea ryvardenica sp. nov. Kurtziana **37**: 65–72.
- Fidalgo O, Fidalgo MEPK (1967). *Polyporaceae* from Trinidad and Tobago. 2. *Mycologia* **59**: 833–869.
- Figueroa SH, Decock C (2007). On *Trichaptum sprucei* and the genus *Phaeodaedalea* (*Basidiomycota*, polypores). *Cryptogamie*, *Mycologie* **28**: 189–201.
- Garbelotto MM, Lee HK, Slaughter G, *et al.* (1997). Heterokaryosis is not required for virulence of *Heterobasidion annosum*. *Mycologia* **89**: 92–102.
- Gardes M, Bruns TD (1993). ITS primers with enhanced specificity for basidiomycetes application to the identification of mycorrhizae and rusts. *Molecular Ecology* **2**: 113–118.
- Gilbertson RL (1980). Wood-rotting fungi of North America. *Mycologia* **72**: 1–49.
- Gilbertson RL, Ryvarden L (1986). North American polypores. 1. Fungiflora, Oslo.
- Gilbertson RL, Ryvarden L (1987). North American polypores. 2. Fungiflora, Oslo.
- Haight JE, Laursen GA, Glaeser JA, et al. (2016) Phylogeny of Fornitopsis pinicola: a species complex. Mycologia **108**: 925–938.
- Haight JE, Nakasone K, Laursen GA, et al. (2019). Fomitopsis mounceae and F. schrenkii – two new species from North America in the F. pinicola complex. Mycologia 111: 339–357.
- Hallenberg N (1990). Culture studies in the *Corticiaceae* (*Basidiomycetes*). *Windahlia* **18**: 25–30.
- Han ML, Song J, Cui BK (2014). Morphology and molecular phylogeny for two new species of *Fomitopsis* (*Basidiomycota*) from South China. *Mycological Progress* 13: 905–914.
- Han ML, Cui BK (2015). Morphological characters and molecular data reveal a new species of *Fomitopsis* (*Polyporales*) from southern China. *Mycoscience* 56: 168–176.
- Han ML, Chen YY, Shen LL, et al. (2016). Taxonomy and phylogeny of the brown-rot fungi: Fomitopsis and its related genera. Fungal Diversity 80: 343–373.
- Han ML, An Q, Fu WX, *et al.* (2020). Morphological characteristics and phylogenetic analyses reveal *Antrodia yunnanensis sp. nov.* from China. *Phytotaxa* **460**: 1–11.
- Hartmann S, Vision T (2008). Using ESTs for phylogenomics: can one accurately infer a phylogenetic tree from a gappy alignment? *BMC Evolutionary Biology* 8: 95.
- Hattori T (2000). Type studies of the polypores described by E.J.H. Corner from Asia and West Pacific Areas. I. *Mycoscience* **41**: 339–349.
- Hattori T (2003). Type studies of the polypores described by E.J.H. Corner from Asia and West Pacific Areas. V. *Mycoscience* **44**: 265–276.
- Hattori T (2005). Type studies of the polypores described by E.J.H. Corner from Asia and West Pacific Areas. VII. *Mycoscience* **46**: 303–312.

245

SPIRIN ET AL.

- Hattori T, Ryvarden L (1994). Type studies in the *Polyporaceae* 25. Species described from Japan by R. Imazeki and A. Yasuda. *Mycotaxon* **50**: 27–46.
- Hattori T, Sotome K (2013). Type studies of the polypores described by E.J.H. Corner from Asia and West Pacific Areas. VIII. *Mycoscience* **54**: 297–308.
- Hjortstam K, Ryvarden L (1984). Some new and noteworthy *Basidiomycetes* (*Aphyllophorales*) from Nepal. *Mycotaxon* **20**: 133–151.
- Hooker JD (1855). Flora Novae-Zelandiae. Part 2. Flowerless plants. The Botany of the Antarctic Voyage of H.M. Discovery Ships Erebus and Terror, in the years 1839 – 1843. 2: 1–378.
- Högberg N, Holdenreider O, Stenlid J (1999). Population structure of the wood decay fungus *Fomitopsis pinicola*. *Heredity* 83: 354–360.
- Ipulet P, Ryvarden L (2005). New and interesting polypores from Uganda. Synopsis Fungorum 20: 87–99.
- Ji W, Wu DM, Song CG, et al. (2019). Two new Neofomitella species (Polyporaceae, Basidiomycota) based on morphological and molecular evidence. Mycological Progress 18: 593–602.
- Justo A, Miettinen O, Floudas D, *et al.* (2017). A revised family-level classification of the *Polyporales* (*Basidiomycota*). *Fungal Biology* **121**: 798–824.
- Karasiński D, Niemelä T (2016). Anthoporia, a new polypore genus in the Polyporales (Agaricomycetes). Polish Botanical Journal **61**: 7–14.
- Karsten PA (1881a). Enumeratio Boletinearum et Polyporearum Fennicarum, systemate novo dispositarum. *Revue Mycologique Toulouse* **3**: 16–19.
- Karsten PA (1881b). Symbolae ad mycologiam Fennicam. *Meddelanden af Societas pro Fauna et Flora Fennica* 6: 7–13.
- Katoh K, Rozewicki J, Yamada KD (2019). MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. *Briefings in Bioinformatics* **20**: 1160–1166.
- Kim KM, Yoon YG, Jung HS (2005). Evaluation of the monophyly of *Fomitopsis* using parsimony and MCMC methods. *Mycologia* 97: 812–822.
- Kim KM, Lee JS, Jung HS (2008). Fomitopsis incarnatus sp. nov. based on generic evaluation of Fomitopsis and Rhodofomes. Mycologia 99: 833 – 841.
- Kim CS, Jo JW, Kwang YN, et al. (2015). Mushroom flora of Ulleunggun and a newly recorded *Bovista* species in the Republic of Korea. *Mycobiology* **43**: 239–257.
- Kozlov AM, Darriba D, Flouri T, *et al.* (2019). RAxML-NG: a fast, scalable and user-friendly tool for maximum likelihood phylogenetic inference. *Bioinformatics* 35: 4453–4455.
- Kotlaba F, Pouzar Z (1957). Notes on classification of European pore fungi. Česká Mykologie 11: 152–170.
- Kotlaba F, Pouzar Z (1958). Polypori novi vel minus cogniti Cechoslovakiae 3. Česká Mykologie 12: 95–104.
- Kotlaba F, Pouzar Z (1990). Type studies of polypores described by A. Pilát 3. Česká Mykologie 44: 228–237.
- Kotlaba F, Pouzar Z (1993). *Pilatoporus maroccanus sp. nov.*, a new polypore of the *Polyporus palustris* group. *Cryptogamie, Mycologie* **14**: 215–218.
- Kotlaba F, Pouzar Z (1998). Notes on the division of the genus *Fomitopsis* (*Polyporales*). *Folia Cryptogamica Estonica* **33**: 49–52.
- Koukol O, Delgado G (2021). Why morphology matters: the negative consequences of hasty descriptions of putative novelties in asexual ascomycetes. *IMA Fungus* **12**: 26.
- Kout J, Vlasák J (2009). Antrodia serialiformis from the eastern USA, a new and abundant polypore similar to A. serialis. Mycotaxon 108: 329–335.
- Kout J, Vlasák J, Vlasák J Jr (2017). Antrodia multiformis and A. tenerifensis spp. nov. (Fomitopsidaceae, Basidiomycota): new brownrot polypores. Mycological Progress 16: 737–742.
- Kuo M, Ortiz-Santana B (2020). Revision of leccinoid fungi, with emphasis on North American taxa, based on molecular and morphological data. *Mycologia* **112**: 197–211.
- Larsson A (2014). AliView: a fast and lightweight alignment viewer and editor for large datasets. *Bioinformatics* **30**: 3276–3278.
- Leaché AD, Zhu T, Rannala B, Yang Z (2019). The spectre of too many species. *Systematic Biology* **68**: 168–181.

- Léveillé JH (1844). Champignons exotiques. Annales des Sciences Naturelles 3: 167–221.
- Léveillé JH (1846). Descriptions des champignons de l'herbier du Múseum de Paris. Annales des Sciences Naturelles 3: 111–167.
- Li HJ, Cui BK (2013). Two new Daedalea species (Polyporales, Basidiomycota) from South China. Mycoscience 54: 62–68.
- Li HJ, Han ML, Cui BK (2013). Two new *Fomitopsis* species from southern China based on morphological and molecular characters. *Mycological Progress* **12**: 709–718.
- Liimatainen K, Ainsworth AM (2018). Fifteen *Cortinarius* species associated with *Helianthemum* in Great Britain: results of a DNA-based analysis. *Field Mycology* **19**: 119–135.
- Lindblad I, Ryvarden L (1999). Studies in neotropical polypores 3. *Mycotaxon* **71**: 335–359.
- Lindner DL, Ryvarden L, Baroni TJ (2011). A new species of *Daedalea* (*Basidiomycota*) and a synopsis of core species in *Daedalea sensu* stricto. North American Fungi **6**: 1–12.
- Liu S, Song CG, Cui BK (2019). Morphological characters and molecular data reveal three new species of *Fomitopsis* (*Basidiomycota*). *Mycological Progress* 18: 1317–1327.
- Liu S, Han ML, Xu TM, *et al.* (2021). Taxonomy and phylogeny of the *Fomitopsis pinicola* complex with descriptions of six new species from East Asia. *Frontiers in Microbiology* **12**: 644979.
- Liu S, Chen YY, Sun YF, *et al.* (2022). Systematic classification and phylogenetic relationships of the brown-rot fungi within the *Polyporales*. *Fungal Diversity* **118**: 1–94.
- Lloyd CG (1915). Synopsis of the genus *Fomes. Mycological Writings* **4**: 209–288.
- Lloyd CG (1917). Mycological notes 49. Mycological Writings 5: 685–700.
- Lowe JL (1957). Polyporaceae of North America: the genus Formes. Technical Publication of the State University College of Forestry at Syracuse University 80: 1–96.
- Lowe JL (1966). Polyporaceae of North America: the genus Poria. Technical Publication of the State University College of Forestry at Syracuse University 90: 1–183.
- Lowe JL (1975). *Polyporaceae* of North America: the genus *Tyromyces*. *Mycotaxon* **2**: 1–82.
- Lowe JL, Pegler D (1973). *Polyporus amygdalinus* and *P. pseudosulphureus*. *Mycologia* **65**: 208–211.
- Löytynoja A, Goldman N (2010). webPRANK: a phylogeny-aware multiple sequence aligner with interactive alignment browser. BMC Bioinformatics 11: 579.
- Martin KJ, Rygiewicz PT (2005). Fungal-specific PCR primers developed for analysis of the ITS region of environmental DNA extracts. BMC Microbiology 5: 1–11.
- Masuka A, Ryvarden L (1993). Two new polypores from Malawi. *Mycologia Helvetica* **5**: 143–148.
- Matheny PB, Liu YJ, Ammirati JF, Hall BD (2002). Using *RPB1* sequences to improve phylogenetic inference among mushrooms (*Inocybe*, *Agaricales*). *American Journal of Botany* **89**: 688–698.
- Matheny PB, Wang Z, Binder M, *et al.* (2007). Contributions of *RPB2* and *TEF1* to the phylogeny of mushrooms and allies (*Basidiomycota, Fungi*). *Molecular Phylogenetics and Evolution* **43**: 430–451.
- de Meiras-Ottoni A, Larsson KH, Gibertoni TB (2021). Additions to Trechispora and the status of Scytinopogon (Trechisporales, Basidiomycota). Mycological Progress 20: 203–222.
- Miettinen O, Vlasák J, Rivoire B, *et al.* (2018). *Postia caesia* complex (*Polyporales, Basidiomycota*) in temperate Northern Hemisphere. *Fungal Systematics and Evolution* **1**: 101–129.
- Milne I, Lindner D, Bayer M, et al. (2008). TOPALi v2: a rich graphical interface for evolutionary analyses of multiple alignments on HPC clusters and multi-core desktops. *Bioinformatics* **25**: 126–127.
- Miyauchi S, Kiss E, Kuo A, *et al.* (2020). Large-scale genome sequencing of mycorrhizal fungi provides insights into the early evolution of symbiotic traits. *Nature Communications* **11**: 5125.
- Montagne JPFC (1840). Sécond centurie de plantes cellulaires exotiques nouvelles, Décades I et II. Annales des Sciences Naturelles 2: 193–207.
- Montagne JPFC (1854). Cryptogamia Guyanensis. Annales des Sciences Naturelles 4: 91–144.

- Mossebo DC, Ryvarden L (1997). Fomitopsis africana nov. sp. (Polyporaceae, Basidiomycotina). Sydowia 49: 147–149.
- Mounce I, Macrae R (1938). Interfertility phenomena in *Fomes pinicola*. *Canadian Journal of Research* **16**: 354–376.
- Müller J, Müller K, Quandt D (2010). PhyDE Phylogenetic Data Editor, version 0.997. http://phyde.de.
- Nguyen LT, Schmidt HA, von Haeseler A, *et al.* (2015). IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution* **32**: 268–274.
- Niemelä T (1978). On Fennoscandian polypores 6. *Antrodia plicata n. sp. Karstenia* **18**: 43–48.
- Niemelä T (2005). Polypores, lignicolous fungi. Norrlinia 13: 1–320.
- Niemelä T, Penttilä R (1992). *Antrodia mellita (Basidiomycetes)*, a new large-pored polypore species with a continental distribution. *Annales Botanici Fennici* **29**: 55–65.
- Niemelä T, Ryvarden L (1975). Studies in the Aphyllophorales of Africa 4. Antrodia juniperina, new to Africa. Transactions of the British Mycological Society 65: 427–432.
- Nobles MK (1958). Cultural characters as a guide to the taxonomy and the phylogeny of the Polyporaceae. *Canadian Journal of Botany* **36**: 883–926.
- Nobles MK (1971). Cultural characters as a guide to the taxonomy of the *Polyporaceae*. In: *Evolution in the higher basidiomycetes* (Petersen R, ed.). University of Tennessee Press: 169–196.
- Núñez M, Ryvarden L (1995). *Polyporus (Basidiomycotina)* and related genera. *Synopsis Fungorum* **10**: 1–85.
- Núñez M, Ryvarden L (2001). East Asian polypores 2. Synopsis Fungorum 14: 170–522.
- Ortiz-Santana B, Lindner DL, Miettinen O, et al. (2013). A phylogenetic overview of the Antrodia clade (Basidiomycota, Polyporales). Mycologia 105: 391–1411.
- Parmasto E (1994). Limits of splitting (on schizotaxia). *Mycologia Helvetica* **6**: 8–34.
- Persoon CH (1801). Synopsis methodica fungorum. 2. Heinrich Dieterich, Göttingen.
- Petrak F (1959). Über eine neue *Daedalea*-Art aus Borneo. *Sydowia* **13**: 139–142.
- Rajchenberg M (1986). On *Trametes aethalodes* and other species of Daedalea (Polyporaceae). Canadian Journal of Botany 64: 2130– 2135.
- Rajchenberg M (1994). A taxonomic study of the subantarctic *Piptoporus* (*Polyporaceae*, *Basidiomycota*) 12. *Nordic Journal of Botany* 14: 435–449.
- Rajchenberg M (1995a). A taxonomic study of the subantarctic *Piptoporus* (*Polyporaceae*, *Basidiomycota*) 2. *Nordic Journal of Botany* **15**: 105–119.
- Rajchenberg M (1995b). New polypores from the *Nothofagus* forests of Argentina. *Mycotaxon* **54**: 427–453.
- Rajchenberg M, Gorjón SP, Pildain MB (2011). The phylogenetic disposition of Antrodia sensu lato taxa (Polyporales, Basidiomycota) from Patagonia, Argentina. Australian Systematic Botany 24: 111– 120.
- Rambaut A, Drummond AJ, Xie D, et al. (2018). Posterior summarization in Bayesian phylogenetics using Tracer 1.7. Systematic Biology 67: 901–904.
- Reid DA (1974). A reappraisal of type and authentic material of the larger *Basidiomycetes* in the Pretoria herbarium. *Bothalia* **11**: 221–230.
- Reid DA (1976). Notes on polypores 2. Memoirs of the New York Botanical Garden 28: 179–198.
- Renvall P, Niemelä T (1992). Basidiomycetes at the timberline in Lapland 3. *Karstenia* **32**: 29–42.
- Rivoire B (2010). Antrodia pulverulenta (Basidiomycetes, polypore), une espèce nouvelle produisant des amas de mitospores blanches. Bulletin Mensuel de la Société Linnéenne de Lyon **79**: 185–190.
- Rivoire B, Trichies G, Vlasák J (2015). Cartilosoma rene-hentic (Basidiomycota, Polyporales), une espèce nouvelle dans le groupe d'Antrodia ramentacea. Bulletin Mensuel de la Société Linnéenne de Lyon 84: 5–18.

Rivoire B (2020). Polypores de France et d'Europe. Mycopolydev, Orliénas.

www.studiesinmycology.org

- Ronquist F, Teslenko M, Van der Mark P, et al. (2012). MrBayes 32: Efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61: 539–542.
- Rungjindamai N, Pinruan U, Choeyklin R, et al. (2009). Molecular characterization of basidiomycetous endophytes isolated from leaves, rachis and petioles of the oil palm, *Elaeis guineensis*, in Thailand. *Fungal Diversity* **33**: 139–161.
- Runnel K, Spirin V, Miettinen O, et al. (2019). Morphological plasticity in brown-rot fungi: Antrodia is redefined to encompass both poroid and corticioid species. Mycologia 111: 871–883.
- Ryvarden L (1972). A critical checklist of the *Polyporaceae* in tropical east Africa. *Norwegian Journal of Botany* **19**: 229–238.
- Ryvarden L (1976). Type studies in the *Polyporaceae* 7. *Kew Bulletin* **31**: 83–103.
- Ryvarden L (1977). Type studies in the *Polyporaceae* 10. *Norwegian Journal of Botany* **24**: 213–230.
- Ryvarden L (1981). Type studies in the *Polyporaceae* 13. *Mycotaxon* 13: 175–186.
- Ryvarden L (1982). Type studies in the Polyporaceae 11. Nordic Journal of Botany 2: 75–84.
- Ryvarden L (1983). Type studies in the Polyporaceae 14. Occasional Papers of the Farlow Herbarium of Cryptogamic Botany 18: 1–39.
- Ryvarden L (1984). Type studies in the *Polyporaceae* 16. *Mycotaxon* **20**: 329–363.
- Ryvarden L (1985). Type studies in the *Polyporaceae* 17. *Mycotaxon* 23: 169–198.
- Ryvarden L (1988a). Type studies in the *Polyporaceae* 20. *Mycotaxon* 33: 303–327.
- Ryvarden L (1988b). Type studies in the *Polyporaceae* 19. *Mycotaxon* **31**: 45–58.
- Ryvarden L (1990). Type studies in the *Polyporaceae* 22. *Mycotaxon* **38**: 83–102.
- Ryvarden L (1991). Genera of polypores: nomenclature and taxonomy. *Synopsis Fungorum* **5**: 1–363.
- Ryvarden L (2015). Neotropical polypores 2. Synopsis Fungorum 34: 232–443.
- Ryvarden L (2016). Neotropical polypores 3. Synopsis Fungorum 36: 445–613.
- Ryvarden L, Aime MC, Baroni TJ (2009). Studies in neotropical polypores 26. Synopsis Fungorum **26**: 24–26.
- Ryvarden L, Johansen I (1980). A preliminary polypore flora of East Africa. Fungiflora, Oslo.
- Ryvarden L, Gilbertson RL (1993). European polypores 1. Synopsis Fungorum 5: 1–387.
- Ryvarden L, Melo I, Niemelä T (2017). Poroid fungi of Europe. Synopsis Fungorum **37**: 1–431.
- Schoch, CL, Seifert KA, Huhndorf S, et al. (2012). Nuclear ribosomal internal transcribed spacer (ITS) region as a universal DNA barcode marker for Fungi. Proceedings of the National Academy of Sciences of the United States of America109: 6241–6246.
- Sigwart JD, Sutton MD, Bennett KD (2018). How big is a genus? Towards a nomothetic systematics. *Zoological Journal of the Linnean Society* **183**: 237–252.
- Soares AM, Nogueira-Melo G, Plautz L, et al. (2017). A new species, two new combinations and notes on *Fomitopsidaceae* (Agaricomycetes, Polyporales). Phytotaxa 33: 75–83.
- Spirin V, Zmitrovich I (2003). Notes on some rare polypores found in Russia 1. *Karstenia* **43**: 67–82.
- Spirin V, Zmitrovich I, Wasser S (2006). Oligoporus balsameus rare Eurasian species plus notes on some related taxa. Mycotaxon 97: 73–82.
- Spirin V, Vlasák J, Niemelä T, et al. (2013a). What is Antrodia sensu stricto? Mycologia **105**: 1555–1576.
- Spirin V, Miettinen O, Pennanen J, et al. (2013b). Antrodia hyalina, a new polypore from Russia, and A. leucaena, new to Europe. Mycological Progress 12: 53–61.

- Spirin V, Runnel K, Vlasák J, et al. (2015a). Species diversity in the Antrodia crassa group (Polyporales, Basidiomycota). Fungal Diversity 119: 1291–1310.
- Spirin V, Vlasák J, Milakovsky B, et al. (2015b). Searching for indicator species of old-growth spruce forests: studies in the genus Jahnoporus (Polyporales, Basidiomycota). Cryptogamie, Mycologie 36: 1–10.
- Spirin V, Vlasák J, Rivoire B, et al. (2016). Hidden diversity in the Antrodia malicola group (Polyporales, Basidiomycota). Mycological Progress 15: 1–13.
- Spirin V, Vlasák J, Miettinen O (2017). Studies in the Antrodia serialis group (Polyporales, Basidiomycota). Mycologia **109**: 217–230.
- Spirin V, Malysheva V, Trichies G, et al. (2018). A preliminary overview of the corticioid Atractiellomycetes (Pucciniomycotina, Basidiomycota). Fungal Systematics and Evolution 2: 311–340.
- Spirin V, Malysheva V, Haelewaters D, *et al.* (2019a). Studies in the *Stypella vermiformis* group (*Auriculariales, Basidiomycota*). *Antonie van Leeuwenhoek* **112**: 753–764.
- Spirin V, Malysheva V, Roberts P, et al. (2019b). A convolute diversity of the Auriculariales (Agaricomycetes, Basidiomycota) with sphaeropedunculate basidia. Nordic Journal of Botany **37**: e02394.
- Spirin V, Malysheva V, Miettinen O, et al. (2019c). On Protomerulius and Heterochaetella (Auriculariales, Basidiomycota). Mycological Progress 18: 1079–1099.
- Spirin V, Volobuev S, Viner I, et al. (2021). On Sistotremastrum and similarlooking taxa (Trechisporales, Basidiomycota). Mycological Progress 20: 453–476.
- Stevenson JA, Cash EK (1936). The new fungus names proposed by C. G. Lloyd. Bulletin of the Lloyd Library and Museum **35**: 1–209.
- Stiller JW, Hall BD (1997). The origin of red algae: implications for plastid evolution. *Proceedings of the National Academy of Sciences of the United States of America* **94**: 4520–4525.
- Stockland J, Ryvarden L (2008). Fomitopsis ochracea species nova. Synopsis Fungorum **25**: 44–47.
- Sukumaran J, Knowles LL (2017). Multispecies coalescent delimits structure, not species. Proceedings of the National Academy of Sciences of the United States of America 114: 1607–1612.
- Tamm H, Pöldmaa K (2013). Diversity, host associations and phylogeography of temperate aurofusarin-producing *Hypomyces/ Cladobotryum* including causal agents of cobweb disease of cultivated mushrooms. *Fungal Biology* **117**: 348–367.
- Thiers B (2021). Index Herbariorum: a global directory of public herbaria and associated staff New York Botanical Garden's Virtual Herbarium. http://sweetgumnybgorg/ science/ih/
- Tibpromma S, Hyde K, Jeewon R, *et al.* (2017). Fungal diversity notes 491–602: taxonomic and phylogenetic contributions to fungal taxa. *Fungal Diversity* **83**: 1–261.
- Tibuhwa DD, Hussein JM, Ryvarden L, *et al.* (2020). A phylogeny for the plant pathogen *Piptoporellus baudonii* using a multigene data set. *Mycologia* **112**: 1017–1025.
- von Thümen F (1875). Symbolae ad floram mycologicam Australiae. Grevillea 4: 70–76.
- Vampola P (1996). New localities of *Pilatoporus ibericus* in Europe and Asia. *Czech Mycology* **49**: 85–90.
- Vellinga EC, Kuyper TW, Ammirati J, et al. (2015). Six simple guidelines for introducing new genera of fungi. IMA Fungus 6: 65–68.
- Vilgalys R, Hester M (1990). Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. *Journal of Bacteriology* **172**: 4238–4246.
- Viner I, Kokaeva L, Spirin V, *et al.* (2021). Significance of incongruent DNA loci in the taxonomy of wood-decaying *Basidioradulum radula*. *Mycologia* **113**: 995–1008.
- Viner I, Spirin V, Larsson KH, et al. (2023). Systematic placement of Lagarobasidium cymosum and description of two new species. Mycologia 115: 122–134.
- Virdi SS (1992). Two Antrodia species from Arunachal Pradesh (India). International Journal of Mycology and Lichenology 5: 307–311.
- Vlasák J, Kout J, Vlasák J Jr, *et al.* (2011). New records of polypores from southern Florida. *Mycotaxon* **118**: 159–176.

Vlasák J, Vlasák J Jr, Ryvarden L (2012). Four new polypore species from

the western United States. Mycotaxon 119: 217-231.

- Vlasák J, Vlasák J Jr, Cui BK (2013). Antrodia kmetii, a new European polypore similar to Antrodia variiformis. Cryptogamie, Mycologie 34: 203–209.
- Vlasák J, Vlasák J Jr, Ryvarden L (2016). Studies in neotropical polypores 42. Synopsis Fungorum **35**: 9–33.
- Wang YR, Dai YC, Liu HG, et al. (2022). A new contribution to Megasporoporia sensu lato: six new species and three new combinations. Frontiers in Microbiology 13: 1046777.
- White TJ, Bruns TD, Lee S, et al. (1990). Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: PCR protocols: a guide to methods and applications (Innis MA, Gelfand H, Sninsky JS, et al. eds). Academic Press: 315–322.
- Windelband W (1904). Geschichte und Naturwissenschaft. Heitz & Mündel, Straßburg.
- Wu SH, Yu ZH, Dai YC, et al. (2004). Taiwanofungus, a polypore new genus. Fungal Science 19: 109–116.
- Yuan Y, Gafforov Y, Chen YY, et al. (2017). A new species of Antrodia (Basidiomycota, Polyporales) from juniper forest of Uzbekistan. Phytotaxa 303: 47–55.
- Yuan HS, Lu X, Dai YC, et al. (2020). Fungal diversity notes 1277–1386: taxonomic and phylogenetic contributions to fungal taxa. Fungal Diversity 104: 1–266.
- Vu D, Groenewald M, de Vries M, et al. (2019). Large-scale generation and analysis of filamentous fungal DNA barcodes boosts coverage for kingdom fungi and reveals thresholds for fungal species and higher taxon delimitation. *Studies in Mycology* **92**: 135–154.
- Zhou LW, Wei YL (2012). Changbai wood-rotting fungi 16. *Mycological Progress* **11**: 435–441.
- Zhou M, Wang CG, Wu YD, et al. (2021). Two new brown rot polypores from tropical China. *MycoKeys* 82: 173–197.
- Zmitrovich IV (2018). Conspectus systematis Polyporacearum v. 1.0. Folia Cryptogamica Petropolitana 6: 1–145.

Supplementary Material: https://studiesinmycology.org/

Fig. S1. Phylogenetic placement of the *Daedalea – Fomitopsis* clade (box) within *Polyporales* based on Maximum Likelihood of the ITS + LSU + SSU + mtSSU + *RPB1* + *RPB2* + *TEF1* dataset. Numbers on nodes represent bootstrap values > 70 % and Bayesian Inference posterior probabilities > 0.85. The scale bar indicates the number of expected substitutions per site. Two-letter codes in the parentheses denote the country of origin.

Fig. S2. Phylogenetic relationships of species in the *Daedalea* – *Fomitopsis* clade based on Maximum Likelihood of the ITS + LSU dataset. Numbers on nodes represent bootstrap values > 70 % and Bayesian Inference posterior probabilities > 0.85. The species represented with ITS only are marked with an asterisk (*). The scale bar indicates the number of expected substitutions per site. Two-letter codes in the parentheses denote the country of origin.

Fig. S3. Phylogenetic relationships of species in the *Fomitopsis marianii* complex based on Maximum Likelihood of the *TEF1* dataset. Numbers on nodes represent bootstrap values > 70 % and Bayesian Inference posterior probabilities > 0.85. The scale bar indicates the number of expected substitutions per site. Two-letter codes in the parentheses denote the country of origin.

Fig. S4. Phylogenetic relationships of species in the *Fomitopsis meliae* complex based on Maximum Likelihood of the *TEF1* dataset. Numbers on nodes represent bootstrap values > 70 % and Bayesian Inference posterior probabilities > 0.85. The scale bar indicates the number of expected substitutions per site. Two-letter codes in the parentheses denote the country of origin.

Fig. S5. Phylogenetic relationships of species in the *Fomitopsis pinicola* complex based on Maximum Likelihood of the ITS + *TEF1* dataset. Numbers on nodes represent bootstrap values > 70 % and Bayesian Inference posterior probabilities > 0.85. The scale bar indicates the number of expected substitutions per site. Two-letter codes in the parentheses denote the country of origin.

Fig. S6. Phylogenetic relationships of species in the *Fomitopsis* (Antrodia) ramentacea clade based on Maximum Likelihood of the ITS dataset.

Numbers on nodes represent bootstrap values > 70 % and Bayesian Inference posterior probabilities > 0.85. The scale bar indicates the number of expected substitutions per site. Two-letter codes in the parentheses denote the country of origin.

Fig. S7. Phylogenetic relationships of species in the *Fomitopsis* (*Antrodia*) *juniperina* clade based on Maximum Likelihood of the ITS dataset. Numbers on nodes represent bootstrap values > 70 % and Bayesian Inference posterior probabilities > 0.85. The scale bar indicates the number of expected substitutions per site. Two-letter codes in the parentheses denote the country of origin. The tree is midpoint-rooted.

Fig. S8. Phylogenetic relationships of species in the *Buglossoporus* clade based on Maximum Likelihood of the ITS dataset. Numbers on nodes represent bootstrap values > 70 % and Bayesian Inference posterior probabilities > 0.85. The scale bar indicates the number of expected substitutions per site. Two-letter codes in the parentheses denote the country of origin.

Table S1. List of reference species used for comparisons in this study and their accession numbers.

 Table S2.
 Phylogenetic statistics for the different analyses performed in this study.

