



Fasciodontia gen. nov. (Hymenochaetales, Basidiomycota) and the taxonomic status of *Deviodontia*

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Abstract

A new genus *Fasciodontia* is described to classify *Xylodon bugellensis*, known mostly from Europe, and one new species, *F. brasiliensis*, collected in Atlantic rainforests of Brazil. A new combination *F. bugellensis* is proposed and the lectotype for this taxon was selected. The genus is characterized by fascicles of skeletal-like hyphae in aculeal trama and thick-walled basidiospores. The generic concept was supported by Bayesian and Maximum Likelihood molecular phylogenetic reconstructions based on the ITS region and D1/D2 domains of 28S rRNA gene. The morphological distinctions between *Lyomyces pruni* and *F. bugellensis* (earlier considered as conspecific) and their phylogenetic independence are described and illustrated. Additionally, *Deviodontia pilaecystidiata* is put into the genus *Kneiffiella*; *Hyphodontia mongolica* is referred to synonyms of *K. pilaecystidiata*. The phylogenetic position of *Hastodontia halonata*, *Kneiffiella alienata*, and *Lyomyces fimbriatus* are discussed for the first time, and the new combination *Lyomyces fimbriatus* is introduced.

Keywords Agaricomycetes · Corticioid fungi · New genus · New species · Skeletal-like hyphae · Taxonomy

Introduction

The basidiomycetous genus *Hyphodontia* J. Erikss. was described by John Eriksson (1958), based on the generic type *H. pallidula* (Bres.) J. Erikss. A first phylogenetic tree, which included DNA sequences of *Hyphodontia* s.l. species (Larsson et al. 2006), showed that the genus is polyphyletic. Hjortstam and Ryvarde (2002, 2009) divided the genus into 14 segregate genera on the basis of

morphological features. Later, Riebesehl and Langer (2017) revised the system and reduced the number of genera to seven, considering phylogenetic results. Subsequently, the genera *Lagarobasidium* Jülich and *Palifer* Stalpers & P.K. Buchanan were synonymized with *Xylodon* by Viner et al. (2018) and Riebesehl et al. (2019). Today, five genera are distinguished in *Hyphodontia* s.l.: *Hastodontia* (Parmasto) Hjortstam & Ryvarde, *Hyphodontia* s.s., *Kneiffiella* P. Karst., *Lyomyces* P. Karst., and *Xylodon* (Pers.) Gray.

This study dealt with the species complex of *Lyomyces pruni* (Lasch) Riebesehl & Langer and *Xylodon bugellensis* (Ces.) Hjortstam & Ryvarde. Phylogenetic analyses demonstrate two different taxa for this complex, not belonging to sister groups. The new genus *Fasciodontia* is introduced to represent *X. bugellensis* and related taxa. One new species is described and illustrated: *Fasciodontia brasiliensis*. In addition, DNA sequences of *Kneiffiella pilaecystidiata* (S. Lundell) Jülich & Stalpers, *Hastodontia halonata* (J. Erikss. & Hjortstam) Hjortstam & Ryvarde, and *Lyomyces fimbriatus* (Sheng H. Wu) Hjortstam & Ryvarde were obtained for the first time and resulted in two new combinations and in the synonymization of one species and one genus.

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Materials and methods

Morphological study

The morphology was studied on dried specimens, deposited in collections CFMR, GB, HAL, KAS, MSK, TFC (acronyms follow *Index Herbariorum*, <http://sweetgum.nybg.org/science/ih>) as main specimens or duplicates (dup.). Microscopic characters were studied and measurements were done in 3% KOH solution (abbreviated below as KOH); additionally, spores and crystals were examined in Melzer's reagent and spore cyanophily was checked in lactophenol-cotton blue solution. For the determination of average spore length (L) and width (W), 30 spores randomly selected in squash preparations were measured. Spore quotient (Q) was calculated as length/width ratio for individual spores.

Molecular study

Pieces of dried basidiomata, about 2–3 mm², were used for DNA extractions with the E.Z.N.A.® Fungal DNA Mini Kit (Omega Bio-Tek, VWR, USA). Two ribosomal DNA markers were chosen for amplifications: the internal transcribed spacer (ITS), including ITS1, 2, and 5.8S gene, and the D1/D2 domains of 28S. Different combinations of the following primers were used for ITS: ITS1-F (Gardes and Bruns 1993), ITS1, ITS2, ITS3, ITS4, ITS5 (White et al. 1990), and ALR0 (Collopy et al. 2001); and for 28S: NL1, NL4 (O'Donnell 1993), LR0R (Bunyard et al. 1996), and LR5 (Vilgalys and Hester 1990). The primer ALR0 was modified in one position (Riebesehl and Langer 2017). PCR products were purified with innuPREP PCRpure Kit (Analytik Jena, Berlin, Germany) and the DNA sequencing was implemented by Eurofins Genomics (Ebersberg, Germany).

Newly generated sequences were edited with MEGA7 (Kumar et al. 2016) and deposited in NCBI GenBank (Benson et al. 2018; Tab. 1) after a quality check following the five guidelines by Nilsson et al. (2012). NCBI GenBank served also as the source for other DNA sequences used in this study. One or two representatives from the genera most related to *Hyphodontia* s.l. (Larsson et al. 2006; Larsson 2007) were selected for combined ITS+28S dataset, with *Oxyporus populinus* as an outgroup. *Skeletocutis odora* (Polyporales) was selected as the outgroup for rooting phylograms based on ITS sequences. The alignments were done with MAFFT v.7 online (Kato and Standley 2013), using L-INS-i strategy for ITS dataset, G-INS-i for 28S, and E-INS-i for ITS sequences within the combined dataset. Both datasets were used for analysis with Bayesian inference (BI) and maximum likelihood (ML) methods. The BI phylograms were computed with MrBayes v.3.2.1 and v.3.2.6 (Ronquist and Huelsenbeck 2003), using DNA substitution models estimated by MrModeltest v.2.3 and v.2.4 (Nylander 2004). Akaike

information criterion was used to select the best model for ITS+28S dataset, and Bayesian information criterion—for ITS dataset. For combined ITS+28S dataset, the settings were ngen = 500,000, samplefreq = 500, nchans = 4, and other parameters as default. For ITS dataset, the settings were ngen = 10,000,000, samplefreq = 1000, and other parameters as default. Partitioned analyses were applied to ITS alignments with independent nucleotide substitution models and likelihood values for ITS1, ITS2, and 5.8S. The best-fitting models for ML phylograms were calculated with MEGA7, including 1000 bootstrap (BS) replicates, the partial deletion of gapped positions with 95% site coverage cut-off, and other settings as default. MEGA7, FigTree v.1.3.1 and v.1.4.2 (Rambaut 2012) were used for processing the phylograms. The ready phylograms were prepared in CorelDRAW v.9 (Corel Corp., Ottawa, Canada, 1999). Sequence alignments and trees are deposited in TreeBASE (<http://purl.org/phylo/treebase/phylo/study/TB2:S24117>).

Results

Phylogeny

The aligned combined ITS+28S datamatrix comprised of 41 taxa and 1512 positions. It was partitioned as follows: ITS1 = positions 1–473, 5.8S rRNA gene = 474–631, ITS2 = 632–986, and 28S = 987–1512. The aligned ITS datamatrix consisted of 86 taxa and 926 positions. It was partitioned as follows: ITS1 = positions 1–399, 5.8S rRNA gene = 400–561, and ITS2 = 562–926. The used positions from ITS matrix amounted 453 in the ML analysis. The best models suggested by MrModeltest were GTR + I + G for ITS1, ITS2, 28S, and SYM + I for 5.8S.

The high degree of accordance between BI and ML phylograms was observed for ITS+28S dataset, and moderate degree of accordance between BI and ML phylograms for ITS dataset. Bayesian topologies with integrated posterior probability (PP) values and BS values from ML analyses are presented in Figs. 1 and 2.

The phylogram based on combined ITS+28S dataset (Fig. 1) includes 31 sequences of *Hyphodontia* s.l. specimens and strains, of which seven were generated in this study. Sequences of the new genus, introduced herein, are clustered together in a strongly supported clade (PP = 1, BS = 100). The most related genera to it are *Xylodon* and *Lyomyces*, and the all three genera are clustered in a common clade (PP = 1, BS = 91).

The phylogram based on ITS dataset (Fig. 2) includes 85 sequences of *Hyphodontia* s.l. specimens and strains, of which 11 were generated in this study. Sequences of the new genus belong to a distinct clade (PP = 1, BS = 91), having a significant distance to all other sequences of the genera *Hastodontia*, *Hyphodontia* s. str., *Kneiffiella*, *Lyomyces*, and *Xylodon*. A

Table 1 Specimens used in the phylogenetic study^a

Species	Specimen voucher or isolate code	GenBank accession number		Reference	Country
		ITS	28S		
<i>Basidioradulum radula</i> (Fr.) Nobles	KAS-GEL 2493, AFTOL-ID 451	DQ234537	AY700184	Unpublished	Germany
<i>Coltricia perennis</i> (L.) Murrill	J. Kinnunen 2033, H 6049336	MF319058	MF318910	Unpublished	Finland
<i>Coltriciella dependens</i> (Berk. & M.A. Curtis) Murrill	CBS 247.50	MH856606	MH868112	Yu et al. 2019	Argentina
<i>Fasciodontia brasiliensis</i> Yurchenko & Riebesehl	MSK-F 7245a, holotype	MKS598734	MKS598734	This study	Brazil
<i>F. bugellensis</i> (Ces.) Yurchenko, Riebesehl & Langer	KAS-FD 7504	MKS575202	MKS575202	This study	Greece
	KAS-FD 10705a	MKS575203	MKS598735	This study	France
	MSK-F 5548	MKS575204	MKS598736	This study	Belarus
	MSK-F 7353	MKS575205	MKS598737	This study	Belarus
	TFC-Mic 3217	MKS575206		This study	Canary Islands
<i>Fasciodontia</i> sp.	KUC 20121109-15	KJ668516	KJ668368	Jang et al. 2016	South Korea
<i>Fibricium rade</i> (P. Karst.) Jülich	CBS 339.66	MH858815	MH870454	Vu et al. 2019	France
<i>Hastodontia halonata</i> (J. Erikss. & Hjortstam) Hjortstam & Ryvarden	HHB-17058 (CFMR)	MKS575207	MKS598738	This study	Mexico
<i>Hastodontia hastata</i> (Litseh.) Hjortstam & Ryvarden	KHL 14646 (GB)	MH638232	MH638232	Viner et al. 2018	Norway
<i>Hymenochaete cinnamomea</i> (Pers.) Bres.	He 2074	KU975460	KU975500	Unpublished	USA
<i>Hyphodontia alutaria</i> (Burt) J. Erikss.	KHL 11978 (GB)	EU118631	EU118631	Larsson 2007	Norway
<i>H. arguta</i> (Fr.) J. Erikss.	FR-0219451	KR349243		Riebesehl et al. 2015	Réunion
<i>H. borbonica</i> Riebesehl, Langer & Barmiske	FR-0219441, holotype	KR349240		Riebesehl et al. 2015	Réunion
<i>H. mongolica</i> Min Wang, Yuan Y. Chen & B.K. Cui	Cui 13239, holotype		MH884915	Riebesehl et al. 2019	China
<i>H. pallidula</i> (Bres.) J. Erikss.	Cui 13240	KY290984		Wang and Chen 2017	China
<i>H. subdetrítica</i> S.S. Rattan	UC2022820	KY290985		Wang and Chen 2017	USA
<i>H. zhixiangii</i> L.W. Zhou & Gafforov	FR-0261085	KP814340		Rosenthal et al. 2017	USA
<i>Kneiffella abieticola</i> (Bourdot & Galzin) Jülich & Stalpers	LWZ 20160909-4, holotype	KY081793		Riebesehl and Langer 2017	Réunion
<i>K. alienata</i> (S. Lundell) Jülich & Stalpers	KHL 12498 (GB)	KY440396		Kan et al. 2017	Uzbekistan
<i>K. alutacea</i> (Fr.) Jülich & Stalpers	CBS 127219	DQ873601		Larsson et al. 2006	Sweden
<i>K. barba-jovis</i> (Bull.) P. Karst.	KAS-GEL 2284	MH864327	MH875772	Vu et al. 2019	USA
<i>K. cineracea</i> (Bourdot & Galzin) Jülich & Stalpers	KAS-GEL 2937	DQ340340		This study	Germany
K. decoricans (Gresl. & Rajchenb.) Hjortstam & Ryvarden	KHL 11730 (GB)	DQ340338	DQ340365	This study	Germany
K. efbulata (J. Erikss. & Hjortstam) Jülich & Stalpers	KAS-GEL 4958	DQ873609	DQ873610	Larsson et al. 2006	Sweden
<i>K. floccosa</i> (Bourdot & Galzin) Jülich & Stalpers	SP 415980	DQ340336		This study	Réunion
<i>K. palmae</i> Riek ex Hjortstam & Ryvarden	GB 151167, holotype	KY081795		Riebesehl and Langer 2017	Argentina
	UC2022902	KY081796		Riebesehl and Langer 2017	Sweden
	FR7	KP814441		Rosenthal et al. 2017	USA
	KAS-GEL 3456	KP689185		Wang et al. 2016	China
K. pileocystidiata (S. Lundell) Jülich & Stalpers	MSK-F 4723	DQ340333	DQ340369	This study	Taiwan
<i>K. stercicola</i> (Bres.) Nakasone	Blackwell 2141	MKS575208	MKS598739	This study	Belarus
<i>K. subulatata</i> (P. Karst.) Jülich & Stalpers	KAS-GEL 2196	KY081797		Riebesehl and Langer 2017	USA
<i>K. subglobulata</i> (Jia J. Chen & L.W. Zhou) Riebesehl & E. Langer	Dai 10803	DQ340341	DQ340362	This study	Norway
<i>K. subglobosa</i> (Sheng H. Wu) Hjortstam	Wu 890805-2, holotype	KY081798		Chen et al. 2016	China
<i>Lyomyces allantosporus</i> Riebesehl, Yurchenko & E. Langer	FR-0249548, holotype	KY800397		Riebesehl and Langer 2017	Taiwan
				Yurchenko et al. 2017	Réunion

Table 1 (continued)

Species	Specimen voucher or isolate code	GenBank accession number	Reference	Country
<i>L. crustosus</i> (Pers.) P. Karst.	KHL 11731 (GB)	DQ873614	Larsson et al. 2006	Finland
<i>L. erasii</i> (Saaren. & Kotir.) Hjortstam & Ryvarden	MA-Fungi 34336	JX857800	Unpublished	Spain
<i>L. fimbriatus</i> (Sheng H. Wu) Riebesehl & Yurchenko	Wu 910620-7	MK575209	This study	Taiwan
	Wu 911204-4	MK575210	This study	Taiwan
<i>L. griseolinae</i> (G. Cunn.) Riebesehl & E. Langer	KHL 12971 (GB)	DQ873651	Larsson et al. 2006	Costa Rica
<i>L. juniperi</i> (Bourd. & Galzin) Riebesehl & E. Langer	FR-0261086	KY081799	Riebesehl and Langer 2017	Réunion
<i>L. mascarenensis</i> Riebesehl, Yurchenko & E. Langer	KAS-GEL 4833, holotype	KY800399	Yurchenko et al. 2017	Réunion
<i>L. microfasciculatus</i> (Yurchenko & Sheng H. Wu) Riebesehl & E. Langer	TNM F24757, holotype	JN129976	Yurchenko and Wu 2014	Taiwan
<i>L. organensis</i> Yurchenko & Riebesehl	MSK-F 7247, holotype	KY800403	Yurchenko et al. 2017	Brazil
<i>L. orientalis</i> Riebesehl, Yurchenko & E. Langer	KAS-GEL 3400	DQ340326	Yurchenko et al. 2017	Taiwan
<i>L. pruni</i> (Lasch) Riebesehl & Langer	GB 90287	MK575211	This study	Sweden
	KAS-GEL 2327	DQ340312	This study	Germany
	Ryberg 21018 (GB)	DQ873624	Larsson et al. 2006	Sweden
	KAS-JR 7	KY800402	Yurchenko et al. 2017	Germany
<i>L. sambuci</i> (Pers.) P. Karst.	TNM F9073	JX175044	Yurchenko and Wu 2014	Vietnam
<i>L. vietnamensis</i> (Yurchenko & Sheng H. Wu) Riebesehl & E. Langer	CBS 218.39	MH855986	Vu et al. 2019	USA
<i>Oxyporus populinus</i> (Schumacher) Donk	JV 1408/40-J	KY000006	Dai et al. 2017	Czechia
<i>Porodaedalea chrysoloma</i> (Fr.) Fiasson & Niemelä		MH152355	Unpublished	Czechia
<i>Sketlocutis odora</i> (Peck ex Sacc.) Gimms	KAS-MMS 7223	MK575212	This study	Czechia
<i>Trichaptium abietinum</i> (Pers. ex J.F. Gmel.) Ryvarden	UBCF 20347	KC581332	Unpublished	Canada
<i>Tubulicrinis globisporus</i> K.H. Larss. & Hjortstam	KHL 12133 (GB)	DQ873655	Larsson et al. 2006	Sweden
<i>T. hirtellus</i> (Bourd. & Galzin) J. Erikss.	KHL 11717 (GB)	DQ873657	Larsson et al. 2006	Finland
<i>Xylodon apacheriensis</i> (Gilb. & Canf.) Hjortstam & Ryvarden	Canfield 180, holotype	KY081800	Riebesehl and Langer 2017	USA
<i>X. asperus</i> (Fr.) Hjortstam & Ryvarden	UC2023169	KP814365	Rosenthal et al. 2017	USA
<i>X. astrocystidiatus</i> (Yurchenko & Sheng H. Wu) Riebesehl, Yurchenko & Langer	Wu 9211-71	JN129972	Yurchenko and Wu 2014	Taiwan
<i>X. attenuatus</i> Spirin & Viner	Spirin 8775, holotype	MH324476	Viner et al. 2018	USA
<i>X. borealis</i> (Kotir. & Saaren.) Hjortstam & Ryvarden	UC2022850	KP814307	Rosenthal et al. 2017	USA
<i>X. crystalliger</i> Viner	KUN 2312, holotype	MH324477	Viner et al. 2018	Russia
<i>X. cystidiatus</i> (A. David & Rajchenb.) Riebesehl & Langer	FR-0249200	MH880195	Riebesehl et al. 2019	Réunion
<i>X. detriticus</i> (Bourd.) K.H. Larss., Viner & Spirin	Zibarová 26.05.17	MH320794	Viner et al. 2018	Czechia
<i>X. exilis</i> Yurchenko, Riebesehl & Langer	TUB-FO 42565, holotype	MH880198	Riebesehl et al. 2019	Taiwan
<i>X. filicinus</i> Yurchenko & Riebesehl	MSK-F 12869, holotype	MH880199	Riebesehl et al. 2019	Taiwan
<i>X. flaviporus</i> (Berk. & M.A. Curtis ex Cooke) Riebesehl & Langer	FR-0249797	MH880201	Riebesehl et al. 2019	Réunion
<i>X. hastifer</i> (Hjortstam & Ryvarden) Hjortstam & Ryvarden	MA-Fungi 79440	MH260071	Fernández-López et al. 2018	Germany
<i>X. heterocystidiatus</i> (H.X. Xiong, Y.C. Dai & Sheng H. Wu) Riebesehl, Yurchenko & Langer	Ryvarden 19767, holotype	KY081801	Riebesehl and Langer 2017	Argentina
	Wu 9209-27	JX175045	Yurchenko and Wu 2014	Taiwan
<i>X. hypodontinus</i> (Hjortstam & Ryvarden) Riebesehl, Yurchenko & G. Grulh	LIP GG-MAR12-238	MH880207	Riebesehl et al. 2019	Martinique
<i>X. lenis</i> Hjortstam & Ryvarden	Wu 890714-3, holotype	KY081802	Riebesehl and Langer 2017	Taiwan
<i>X. mollissimus</i> (L.-W. Zhou) C.C. Chen & Sheng H. Wu	LWZ 20160318-3	KY007517	Kan et al. 2017	China
<i>X. nespori</i> (Bres.) Hjortstam & Ryvarden	KAS-JR 14	MH880210	Riebesehl et al. 2019	Germany

Table 1 (continued)

Species	Specimen voucher or isolate code	GenBank accession number	Reference	Country
<i>X. niemelaei</i> (Sheng H. Wu) Hjortstam & Ryvarden	B. Nordon 30915 (GB)	DQ873622	Larsson et al. 2006	Sweden
<i>X. nongravis</i> (Lloyd) C.C. Chen & Sheng H. Wu	GC 1508-146	KX857798	Chen et al. 2017	Taiwan
<i>X. nothofagi</i> (G. Cunn) Hjortstam & Ryvarden	GC 1412-22	KX857801	Chen et al. 2017	Taiwan
<i>X. ovisporus</i> (Cormer) Riebesehl & Langer	PDD 91630	GQ411524	Fukami et al. 2010	New Zealand
<i>X. paradoxus</i> (Schrad.) Chevall.	KAS-GEL 3493	EU583421	This study	Taiwan
<i>X. pruinosis</i> (Bres.) Spirin & Viner	FCUG 2425	AF145571	Paulus et al. 2000	Russia
<i>X. pseudolanatus</i> Nakasone, Yurchenko & Riebesehl	Spirin 2877	MH332700	Viner et al. 2018	Russia
<i>X. pseudotropicus</i> (C.L. Zhao, B.K. Cui & Y.C. Dai) Riebesehl, Yurchenko & Langer	FP-150922 (CFMR), holotype Dai 10768	MH880220 KF917543	Riebesehl et al. 2019 Zhao et al. 2014	Belize China
<i>X. quercinus</i> (Pers.) Gray	Miettinen 15050.1 (H 6013352)	KT361632	Ariyawansa et al. 2015	Finland
<i>X. radulooides</i> (Pers.) Riebesehl & Langer	CBS 333.62	MH858169	Vu et al. 2019	France
<i>X. ramicida</i> Spirin & Miettinen	ICMP 13833	AF145580	Paulus et al. 2000	Australia
<i>X. reticulatus</i> (C.C. Chen & Sheng H. Wu) C.C. Chen & Sheng H. Wu	Spirin 7664 (H), holotype	KT361634	Ariyawansa et al. 2015	Russia
<i>X. rhizomorpha</i> (C.L. Zhao, B.K. Cui & Y.C. Dai) Riebesehl, Yurchenko & Langer	Wu 1109-178, holotype Dai 12354	KX857805 KF917544	Chen et al. 2017 Zhao et al. 2014	Taiwan China
<i>X. rimosissimus</i> (Peck) Hjortstam & Ryvarden	Ryberg 21031 (GB)	DQ873627	Larsson et al. 2006	Sweden
<i>X. serpentiformis</i> (Langer) Hjortstam & Ryvarden	KAS-GEL 3668	MH880227	Riebesehl et al. 2019	Taiwan
<i>X. spathulatus</i> (Schrad.) Kuntze	KHL 7085 (GB)	KY081804	Riebesehl and Langer 2017	Sweden
<i>X. subclavatus</i> (Yurchenko, H.X. Xiong & Sheng H. Wu) Riebesehl, Yurchenko & Langer	TUB-FO 42167	MH880232	Riebesehl et al. 2019	Taiwan
<i>X. subflaviporus</i> C.C. Chen & Sheng H. Wu	Wu 0809-76	KX857803	Chen et al. 2017 (as <i>Hyphodontia ovispora</i>); Chen et al. 2018	China
<i>X. subtropicus</i> (C.C. Chen & Sheng H. Wu) C.C. Chen & Sheng H. Wu	Wu 9806-105, holotype	KX857807	Chen et al. 2017	Vietnam
<i>X. ussuriensis</i> Viner	KUN 1989, holotype	MH324468	Viner et al. 2018	Russia
<i>X. verecundus</i> (G. Cunn.) Yurchenko & Riebesehl	KHL 12261 (GB)	DQ873642	Larsson et al. 2006	USA

^a Newly generated sequences are shown in bold; earlier unpublished sequences with updated records are marked “this study” in regular font

basic local alignment search tool (BLAST) search of the newly generated *Fasciodontia bugellensis* ITS sequences revealed that they have 94% identity to a sequence from South Korea identified as *Hyphodontia* sp. 2 (KUC 20121109-15). This sequence was added to our phylograms as *Fasciodontia* sp. (Figs. 1 and 2). The distance to sequences of *F. brasiliensis* and *F. bugellensis* indicates that this sequence belongs to different new *Fasciodontia* species, but a further study is needed with a special emphasis on the morphology of this specimen. As a result, three lineages are distinguished within the *Fasciodontia* clade: *F. bugellensis*, the newly described species *F. brasiliensis*, and *Fasciodontia* sp. from South Korea.

The phylogram based on combined dataset shows the placement of *Deviodontia pilaecystidiata* among species of *Kneiffiella* (Fig. 1). After the analysis of ITS sequences, no significant distance between *Kneiffiella pilaecystidiata* and *Hyphodontia mongolica* was observed; both taxa comprise a branch with PP = 1 and BS = 99 (Fig. 2); only 3 positions (0.6%) are different on comparable 531 nucleotides between

the ITS sequences of MSK-F 4723 (*K. pilaecystidiata*) and Cui 13239 (*H. mongolica* holotype). Two sequences of *Hyphodontia mongolica* show no independent cluster in ML phylogram. These data indicate that the taxa should be considered as conspecific.

The newly generated ITS and 28S sequences of *Hastodontia halonata* demonstrate that this taxon belongs to one clade with *H. hastata* and *Hyphodontia* s. str. on ITS+28S phylogram (PP = 0.99) and ITS phylogram (PP = 0.77). However, no high support values were obtained to consider *H. halonata* and *H. hastata* as the members of one genus in phylogenetical sense. The position of *Xylodon fimbriatus* is apparently located in the genus *Lyomyces* (Figs. 1 and 2). ITS and 28S sequences of *Kneiffiella alienata* (obtained from NCBI GenBank) confirm its classification in the genus *Kneiffiella* (Figs. 1 and 2). *Kneiffiella alienata* occurred to be most phylogenetically close to *K. cineracea* and *K. pilaecystidiata* (PP = 1, Figs. 1 and 2).

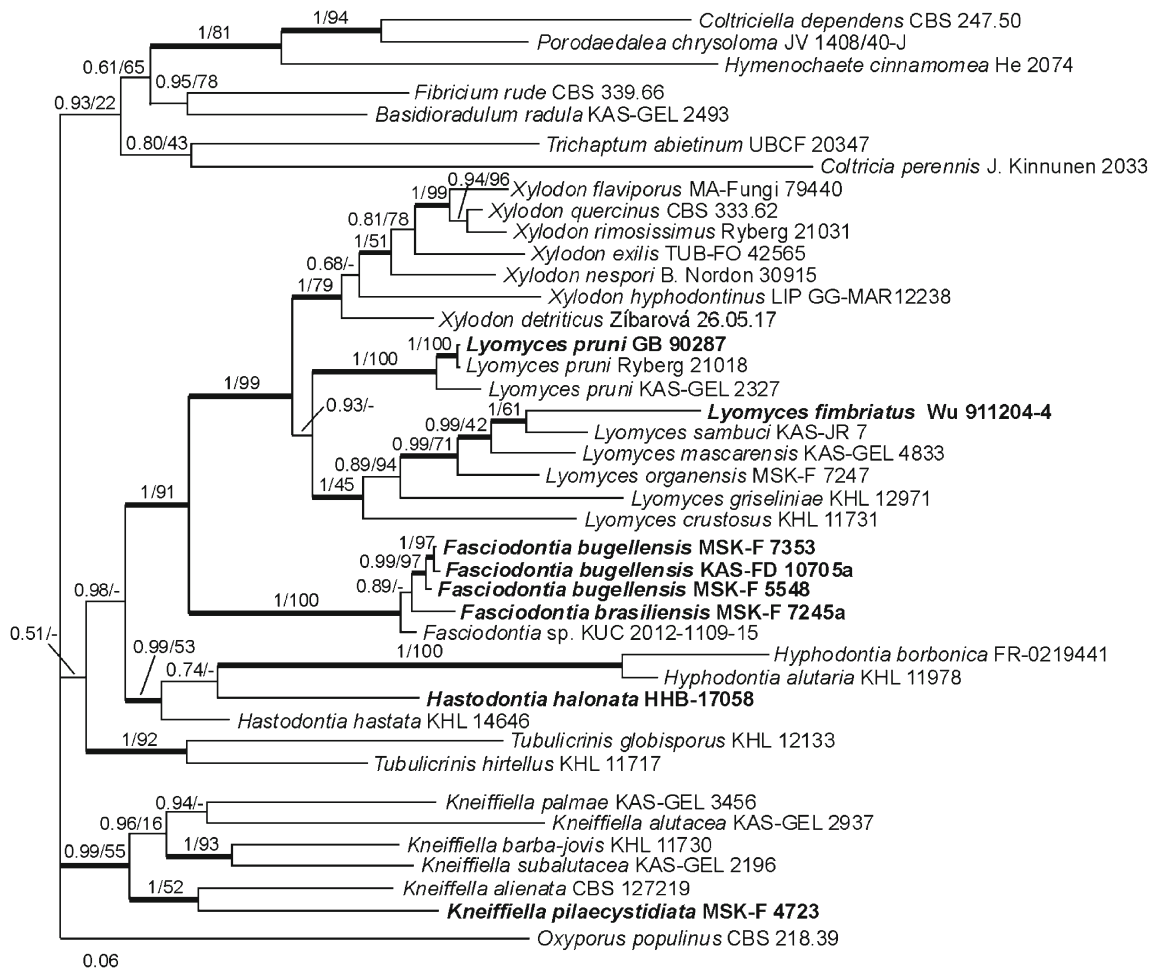


Fig. 1 Bayesian phylogram for *Fasciodontia* and related fungi based on combined dataset of ITS and 28S sequences. Numbers above branches indicate Bayesian posterior probability/bootstraps support (from Maximum Likelihood tree) values. Thick branches have PP \geq 0.99.

Scale bar: number of substitutions per nucleotide position. Names of specimens for which sequences were obtained in this study are given in bold



Fig. 2 Bayesian phylogram for *Fasciodontia* and related fungi based on ITS sequences. Conventions as for Fig. 1

Morphology

Fasciodontia Yurchenko & Riebesehl, gen. nov.

Mycobank no.: MB829454

Type species: Fasciodontia bugellensis (Ces.) Yurchenko, Riebesehl & Langer, comb. nov. (MB 829456). Basionym: *Odontia bugellensis* Ces. in Rabenhorst, Klotzschii Herb. Viv. Mycol. no. 1915, 1855. Typus: Italy, Piemonte, ‘in ligno durissimo Castaneae vetustae reperi Bugellae ao 1850’, leg. V. Cesati [Rabenh., Klotzschii Herb. Viv. Mycol., Cent. 20: no. 1915 (HAL, s.n.)], **lectotype** (Mycobank no.: MBT390118), see a remark below]

Etymology. ‘Fascio’ (Lat.) refers to fasciculate arrangement of hyphae in aculei, ‘dontia’ stresses the derivative origin from *Hyphodontia* s.l.

Description. Basidioma effused, membranaceous, cracking with age; margin thinning out, rarely abrupt. Hymenial surface minutely odontoid, whitish or cream-colored; aculei sterile except bases and consisting of projecting hyphae. Hyphal system pseudodimitic; hyphae clamped at all primary septa, colorless in water, slightly yellowish in mass in KOH, moderately cyanophilous, negative in Melzer’s reagent; skeletal-like thick-walled hyphae present in basal subhymenium and in aculeal trama; skeletal-like hyphae in aculei loosely encrusted, apically thin-walled, partly agglutinated with age. Cystidia from cylindrical to slightly moniliform and capitate. Basidia utriform to subcylindrical, with two slight constrictions, thin-walled or slightly thick-walled in lower 1/2–2/3, with four sterigmata. Spores ellipsoid, smooth, with thickened or thick wall (about 0.2–0.3 μm thick), colorless, negative in Melzer’s reagent, slightly to moderately cyanophilous.

Distribution and ecology. The species of the genus are known from Europe, Canary Islands, Africa (Hjortstam and Ryvarden 2007a), East Asia, South America, and grow on dead wood.

Remarks. The main diagnostic features of the genus are minutely odontoid hymenophore, presence of thick-walled skeletal-like hyphae, associated with aculeal trama, submoniliform cystidia, which are from seldom to numerous, confined mostly to the base of aculei, and thick-walled basidiospores. *Xylodon* is the closest genus to *Fasciodontia* in both morphological and molecular aspects. However, the species of *Xylodon* with thick-walled spores [*X. brevisetus*, *X. capitatus* (G. Cunn.) Hjortstam & Ryvarden, *X. detriticus*, *X. rickii* (Hjortstam & Ryvarden) Riebesehl & Langer, and *X. septocystidiatus* (H.X. Xiong, Y.C. Dai & Sheng H. Wu) Riebesehl & Langer] lacked the combination of characters listed above. *Xylodon crassisporus* (Greslebin & Rajchenberg) Hjortstam & Ryvarden has spores, basidia, cystidia, and pseudoskeletal hyphae in teeth similar with *Fasciodontia*. However, this species possesses capitate cystidia with yellowish resinous caps (Greslebin and Rajchenberg 2000). *Hyphodontia sinensis* H.X. Xiong, Y.C. Dai & Sheng H. Wu has hyphae, structure of aculeal trama, and basidiospores somewhat

similar with *Fasciodontia*. In the same time, *H. sinensis* has long-cylindrical, thin-walled embedded cystidia (Xiong et al. 2010), which are not peculiar to *Fasciodontia*. The exact taxonomic position of *X. crassisporus* and *H. sinensis* will be stated only after their DNA sequences will be available.

Publication of the new species *Odontia bugellensis* was based on exsiccata “Herbarium Vivum Mycologicum” distributed and stored in several herbaria, with no indication of a solitary holotype. In this study, we have selected and designated as lectotype an exsiccatum stored in HAL (see Braun 2018). Microscopic examination of this material showed the main diagnostic features of *F. bugellensis*: cracking odontoid basidioma, constricted cystidia, and thick-walled spores; L = 6.07 μm , W = 4.12 μm , and Q = 1.48.

Fasciodontia brasiliensis Yurchenko & Riebesehl, sp. nov. Figs. 3 and 4.

Mycobank no.: MB829457

Etymology. ‘Brasiliensis’ refers to Brazil, the country where this species was found.

Holotype. Brazil, Rio de Janeiro State, Serra dos Órgãos Mt. Range, E slopes of Mt. Pico do Tinguá, Tinguá village vicinity, 22°36.5' S, 43°27.5' W, ca 1000 m asl., tropical rainforest, on fallen angiosperm branch, leg. E. Yurchenko, 23 Aug 2009 (MSK-F 7245a; isotypes in CFMR and KAS).

Description. Basidioma effused, ca 0.5–5 cm long, cream-colored, odontoid with conical aculei 50–125 μm long and 20–60 μm in diameter at base, 7–10 aculei/mm; the part between aculei loose, minutely porulose, 40–70 μm thick. Margin diffuse or felty and then about 0.25 mm wide. Hyphal system pseudodimitic, hyphae colorless, smooth or poorly encrusted, clamped at all primary septa. Subicular hyphae moderately branched, 2–3 μm wide, thin- to thick-walled (walls up to 0.8 μm thick), smooth, with rare simple (secondary) septa. Subhymenial hyphae moderately to richly branched, 1.5–3 μm wide, thin-walled. Aculei sterile, consisting of densely arranged, parallel projecting hyphae, originating in subiculum. Projecting hyphae flexuous, 45–75 \times 2.5–3.5 μm , from thin- to usually thick-walled (walls ca 1 μm thick in lower 2/3) and then skeletal-like, with simple septa and slight constrictions, loosely encrusted by crystals 2–3 μm across, apically blunt, subacute, seldom subcapitate. Hymenial elements thin-walled. Cystidia arranged mostly at bases of aculei, subcylindrical, clavate or capitate, sometimes slightly moniliform, smooth or barely encrusted, 15–25(45) \times 3–5 μm . Elements of intermediate morphology between cystidia and basidioles present. Basidioles clavate to utriform, smooth or slightly encrusted, 10–20 \times 3.5–4.5 μm . Basidia utriform with 2 constrictions, 19–21 \times 4–5 μm , with four sterigmata 4.5–5 \times 0.5–0.7 μm . Basidiospores ellipsoid, 4.5–5(5.5) \times 3–3.5(3.8) μm (for holotype L = 4.89 μm , W = 3.41 μm , Q = 1.44), smooth, slightly thick-walled, negative in Melzer’s reagent, slightly cyanophilous, with short and blunt apiculus, contents often somewhat granular and with a large central drop (Table 1).

Fig. 3 Hymenial surface view of *Fasciodontia bugellensis* (KAS-FD 10705a, left) and *F. brasiliensis* (MSK-F 7245a, holotype, right). Scale bars = 1 mm

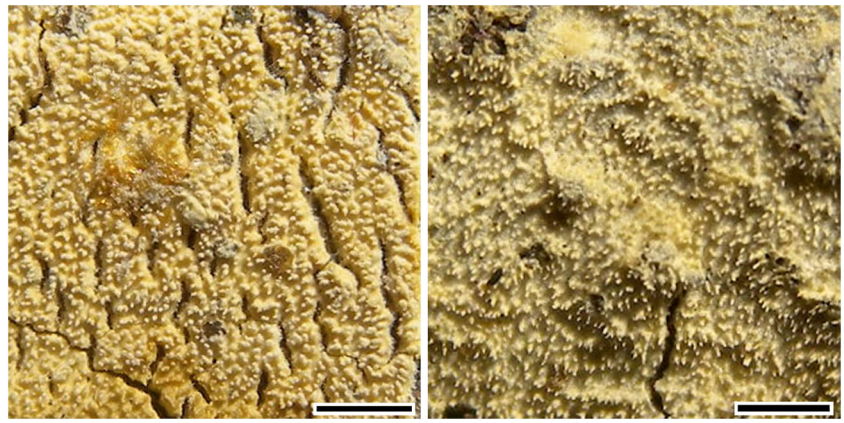


Fig. 4 Micromorphology of *Fasciodontia brasiliensis* (MSK-F 7245a, holotype): **a** Vertical section of basidioma. **b** Subicular hyphae. **c** Hyphae at base of aculeal trama. **d** Projecting hyphae in aculeus. **e** Separate projecting hyphae. **f** Encrusted apices of projecting hyphae. **g** Cystidia at base of aculeus. **h** Portion of hymenium and subhymenium. **i** Cystidia. **j** Basidia. **k** Basidiospores. Scale bars: **a** = 20 μ m; **b–j** = 10; **k** = 5 μ m

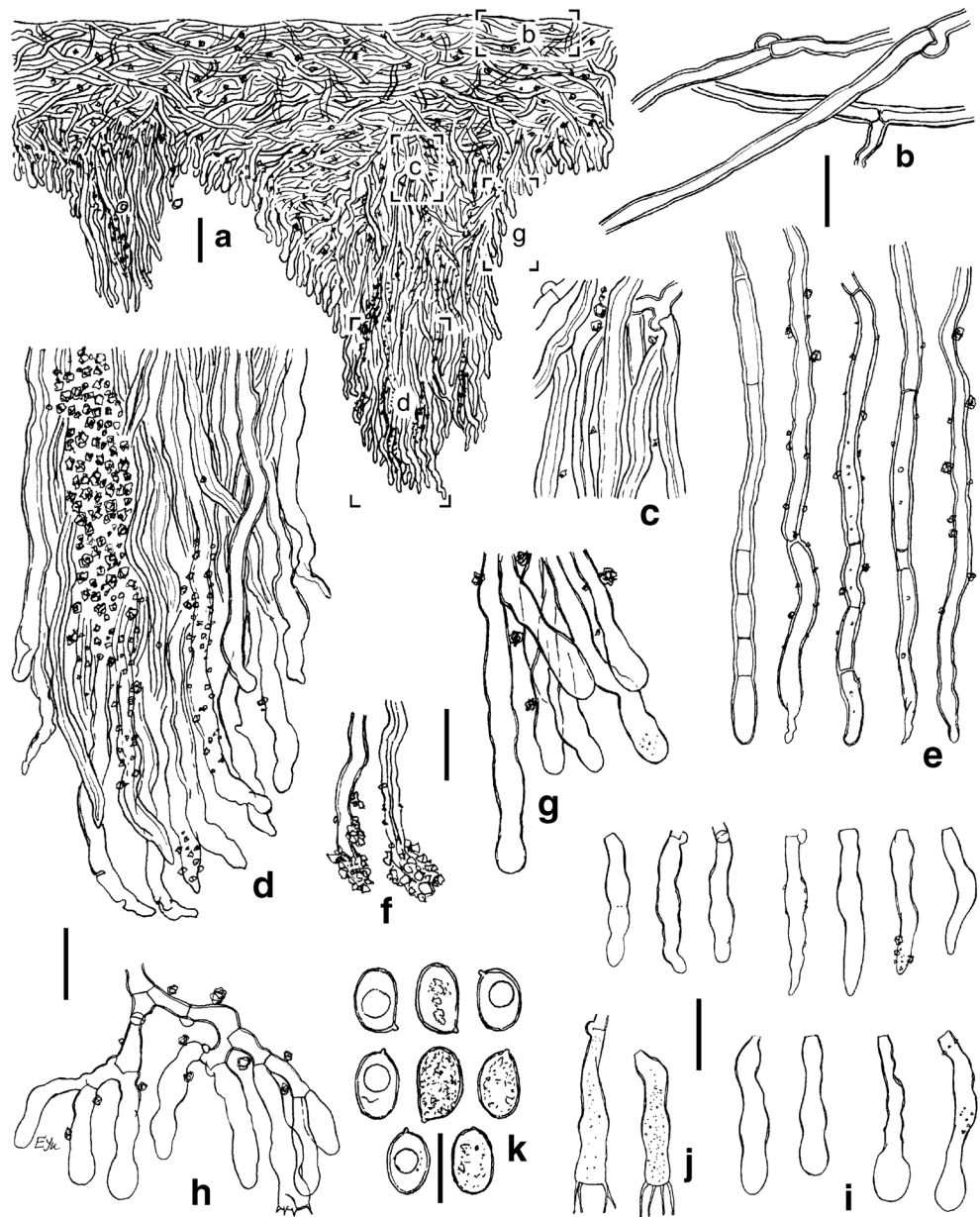


Table 2 Morphological differences between *Fasciodontia* species

	<i>F. bugellensis</i>	<i>F. brasiliensis</i>
Basidioma consistency	Membranaceous to almost cretaceous	Membranaceous
Crystals in subiculum and subhymenium	Usually abundant	In most parts un abundant or poor
Subhymenium thickness, μm	100–250	15–40
Subhymenium texture	Dense due to agglutinated hyphae	Slightly open (in thin vertical sections)
Skeletal-like hyphae arrangement	Present mostly in basal subhymenium	Often penetrate the whole volume of basidioma from subiculum to aculeal apices
Submoniliform cystidia occurrence	Scattered to common	Scattered or rare
Walls of cystidia	Often slightly thick-walled towards the base	Mostly thin-walled or almost so
Basidia size, μm	(18)22–30 \times 4–4.5	19–21 \times 4–5
Basidiospores size, μm	5.3–6.3 \times 3.7–4(4.5)	4.5–5(5.5) \times 3–3.5(3.8)

Fig. 5 Micromorphology of *Fasciodontia bugellensis*. KAS-FD 10705: **a** Vertical section of basidioma. **b** Subicular hyphae. **c** Hyphae in basal subhymenium. **d** Separate skeletal-like hyphae from basal subhymenium. **e** Hyphae in middle subhymenium. **f, g** Projecting hyphae in aculei. **h** Cystidia. **i** Basidioles. **j** Basidia. **k** Basidiospores. MSK-F 7353: **m** Subcapitate cystidia. Scale bars: **a** = 100 μm ; **b–j, m** = 10 μm ; **k** = 5 μm

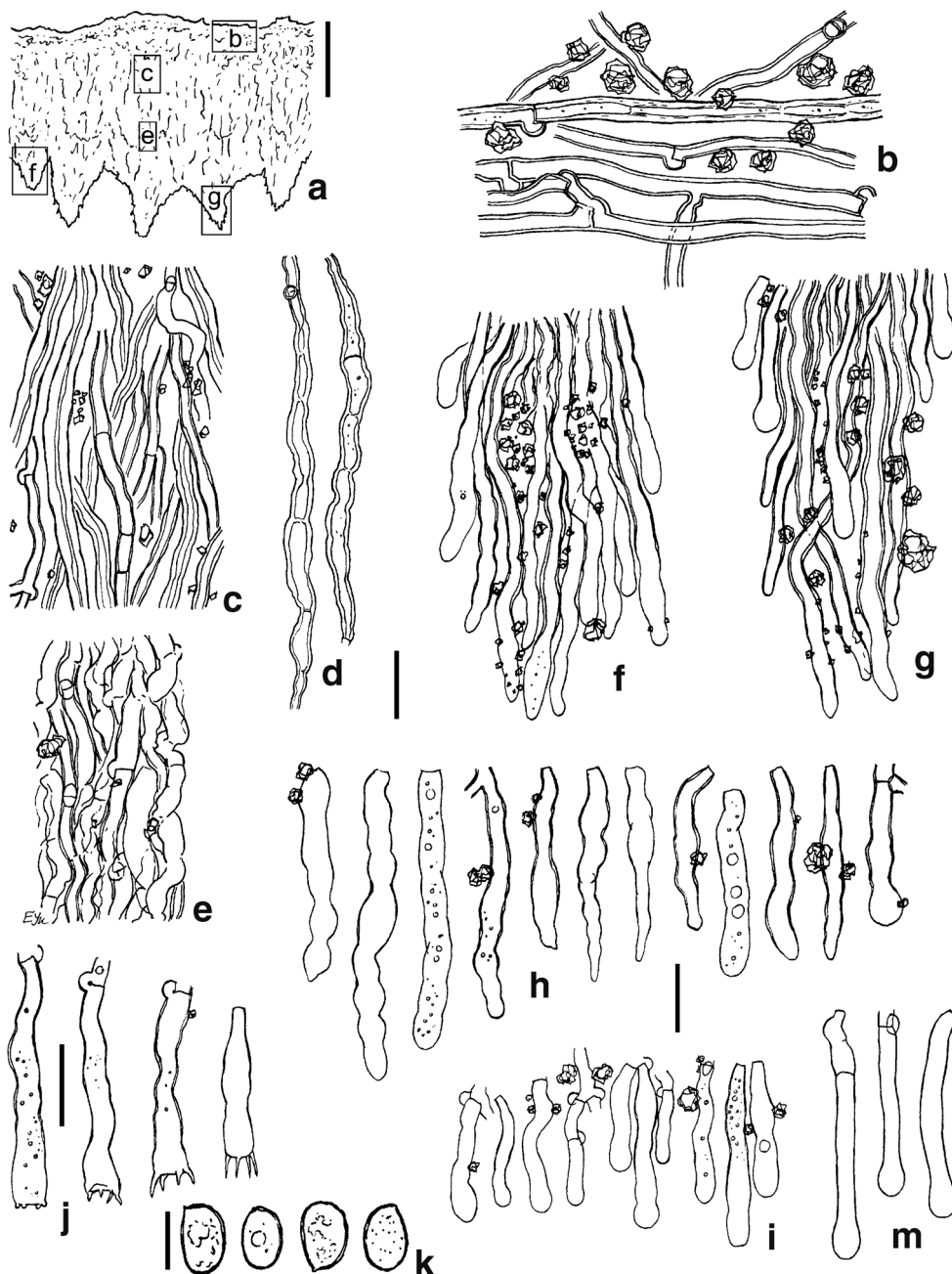
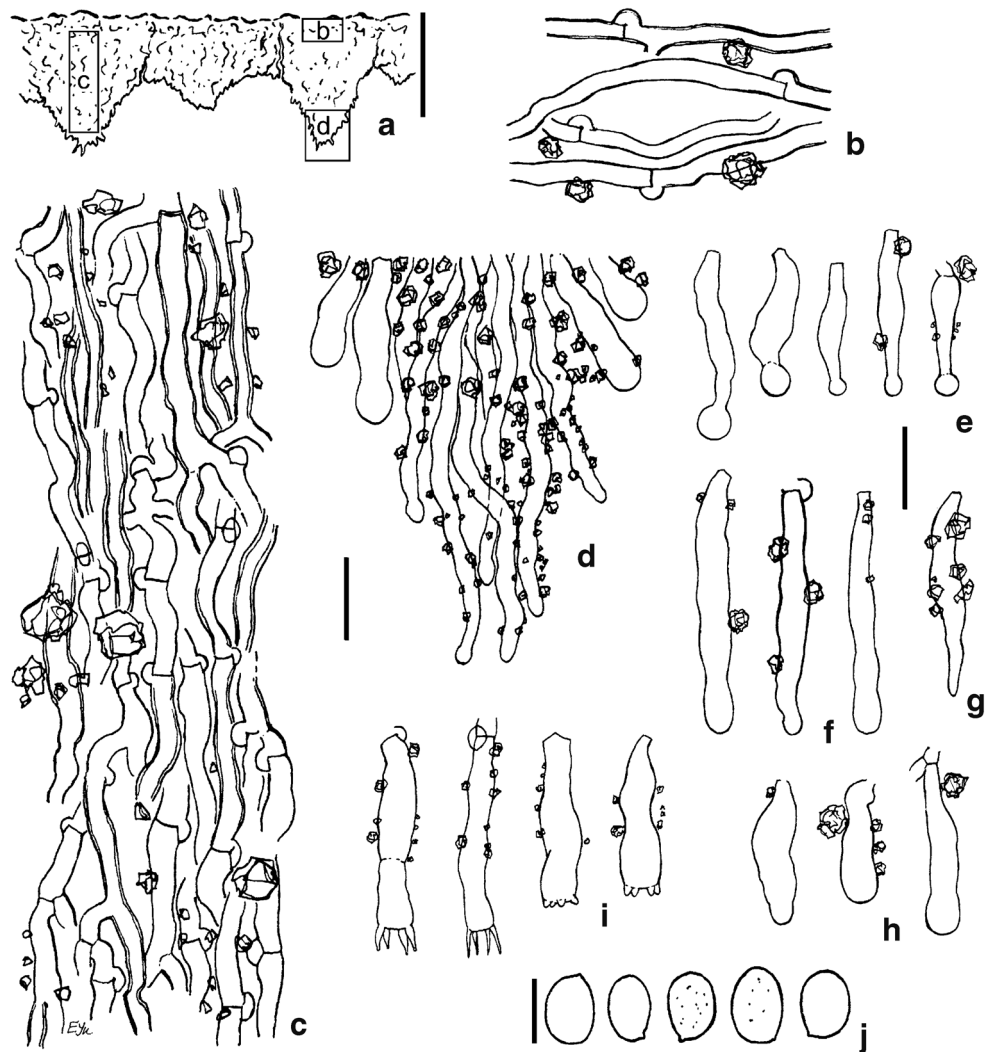


Fig. 6 Micromorphology of *Lyomyces pruni* (GB 90287). **a** Vertical section of basidioma. **b** Subicular hyphae near substratum. **c** Subicular (medullary) and subhymenial hyphae. **d** Aculeal apex. **e** Capitate cystidia. **f** Cylindrical cystidia. **g** Subulate cystidium. **h** Basidioles. **i** Basidia. **j** Basidiospores. Scale bars: **a** = 100 μ m; **b–i** = 10 μ m; **j** = 5 μ m



Additional specimens examined. Brazil: the same locality as holotype, on fallen angiosperm twigs, leg. E. Yurchenko, 23 Aug 2009 (MSK-F 7245b, 7245c, 7255).

Distribution and ecology. The species is so far known from southeastern Brazil, in the natural region of Atlantic rainforests. It inhabits small-sized corticated dead wood.

Remark. The differences between *F. brasiliensis* and *F. bugellensis* are shown in Table 2.

Kneiffiella pilaecystidiata (S. Lundell) Jülich & Stalpers

Syn.: *Hyphodontia mongolica* Min Wang, Yuan Y. Chen & B.K. Cui, in Wang & Chen, Phytotaxa 309 (1): 50, 2017; *H. pilaecystidiata* (S. Lundell) J. Erikss.; *Deviodontia pilaecystidiata* (S. Lundell) Hjortstam & Ryvarden

After analysis of the original description of *Hyphodontia mongolica* (Wang and Chen 2017), we found that this taxon fits in most features to the specimen of *H. pilaecystidiata* from Belarus (Yurchenko and Kotiranta 2007) and description of *H. pilaecystidiata* in Eriksson and Ryvarden (1976). The substratum of Chinese collections (*Populus*) is also in agreement with the

preference of *H. pilaecystidiata* to Salicaceae. The specimen of *H. pilaecystidiata* from Belarus was compared by us with a specimen from Sweden, identified by J. Eriksson under the same name, and we found that their morphology was identical. The description of *H. mongolica* shows larger cystidia and shorter basidia than we have seen in specimens from Belarus and Sweden. However, taking into account ITS sequence and ITS phylogeny data (see above), *H. mongolica* should be synonymized with *Kneiffiella pilaecystidiata*. Consequently, the genus *Deviodontia*, proposed with a single species *D. pilaecystidiata* (Hjortstam and Ryvarden 2009), is a synonym of *Kneiffiella*. For description and illustration of *K. pilaecystidiata*, we refer to Yurchenko and Kotiranta (2007). The description of *H. pilaecystidiata* by Eriksson and Ryvarden (1976) notes thin-walled hyphae in basidioma; the picture from the same source shows heterogeneous contents of cystidia. However, our data, together with the data of Wang and Chen (2017), demonstrated thin- to thick-walled hyphae and homogeneous contents of cystidia.

Specimens examined. Belarus: Lepel' distr., Byarezinski Biosphere Reserve, near Domzharytsy village, on dead, erect trunk

Table 3 Morphological differences between *Fasciodontia bugellensis* and *Lyomyces pruni*

	<i>F. bugellensis</i>	<i>L. pruni</i>
Basidioma consistency	Hard-membranaceous to almost cretaceous	Soft-membranaceous, fragile in dry state
Basidioma thickness between aculei, μm	75–400	40–200
Aculei height \times width (at base), μm	40–125 \times 40–100	25–90 \times 25–75
Aculei fertility	Lacked fertile hymenium or with inabundant hymenial elements at base	Fertile except the apical part
Walls of subicular hyphae	Thickened to thick	Thin
Skeletal-like hyphae	Present	Absent
Constricted cystidia	Present	Absent
Bowl-pin-shaped cystidia	Absent	Present
Cystidial elements and basidia walls	Often slightly thick-walled in lower 2/3	Thin-walled
Shape of the ends of projecting hyphae at aculeal tips	Obtuse or tapering	Obtuse or capitulate
Basidioles shape	Subcylindrical	Mostly clavate
Basidia width, μm	4–4.5	4.5–5
Basidia contents	More or less guttulate	Homogeneous
Spore wall	More or less thick-walled	Thin-walled

of *Salix pentandra* L., leg. E. Yurchenko, 2 Jun 1999 (MSK-F 4723); Sweden: Norrbotten, Nedertorneå Co., Säivisnäs, on decayed wood of cf. *Salix*, leg. J. Eriksson, 25 Aug 1960 (GB 94365).

***Lyomyces fimbriatus* (Sheng H. Wu) Riebesehl & Yurchenko, comb. nov.**

Mycobank no.: MB830811

Basionym: *Hyphodontia fimbriata* Sheng H. Wu, Acta Botanica Fennica 142: 90 (1990)

Syn.: *Xylodon fimbriatus* (Sheng H. Wu) Hjortstam & Ryvarde, Synopsis Fungorum 26: 43 (2009), nom. illeg.

Typus: Taiwan, Nantou, Yushan National Park, 2200 m asl., on fallen twig of angiosperm, leg. S.H. Wu, 29 Jul 1988 (Wu 880729-13, holotype in H, isotype in TNM)

In respect to morphology, *L. fimbriatus* has white or whitish basidiomata, loose hyphal texture, rich crystalline material in subhymenium and subiculum, thin-walled capitulate cystidia, and guttulate basidiospores (Wu 1990; Langer 1994), like the taxa of *Lyomyces sambuci* complex.

The name *Xylodon fimbriatus* (Sheng H. Wu) Hjortstam & Ryvarde must be considered as illegitimate according to Art. 53.1 (Turland et al. 2018) because of existence of the name *X. fimbriatus* (Pers.) Chevall., published in 1826, and today belonged to synonyms of *Steccherinum fimbriatum* (Pers.) J. Erikss. (Species Fungorum 2019).

Discussion

Fasciodontia bugellensis and *Lyomyces pruni*

Our morphology and molecular phylogeny studies showed clear differences between *Fasciodontia bugellensis* (Figs. 3

and 5) and *Lyomyces pruni* (Fig. 6). Earlier *Hyphodontia bugellensis* and *H. pruni* were treated as conspecific by the authors of “The Corticiaceae of North Europe” (Eriksson and Ryvarde 1976). They grounded this conclusion on the analysis of type material, stored in S herbarium, done by Kurt Hjortstam. Later, Hjortstam (1991) reintroduced the name *H. bugellensis*. In subsequent works, *H. bugellensis* (combined also as *Xylodon bugellensis*) was treated as an independent species (Melo and Tellería 1997; Hjortstam and Ryvarde 2007a, b; Bernicchia and Gorjón 2010; Martini 2016). The main distinctive feature for *X. bugellensis* was described as spores “distinctly thick-walled” (Hjortstam 1991; Bernicchia and Gorjón 2010) or “when mature with a slight wall thickening” (Hjortstam and Ryvarde 2007b). In the same time, *H. pruni* and *H. bugellensis* were treated as conspecific by Langer (1994). The differences between these species are described in Table 3.

Along with these features, spore and crystalline material size and shape are identical in both species. Besides, both taxa have cylindrical cystidia and the tendency to form aculei in parallel rows. The descriptions of *Hyphodontia bugellensis* were published by Melo and Tellería (1997), Bernicchia and Gorjón (2010), and Martini (2016). In the description of *H. bugellensis* specimens from Venezuela (Hjortstam and Ryvarde 2007b), the authors note tibiiform and lecythiform cystidia which we did not observe in the European material.

We emend the species concept of *Fasciodontia bugellensis* by thick-walled, skeletal-like hyphae, confined to the aculei and situated also beneath them. Such hyphae, or hyphal segments, are observed in the core of aculei and partly on the border between subiculum and subhymenium, whereas in middle subhymenium they are evidently masked by hyphae with thinner walls, or absent.

Specimens examined. *Fasciodontia bugellensis*-Belarus: Mar'ina Horka town vicinity, on dead attached branches of *Malus* sp., leg. E. Yurchenko, 15 Nov 1992 (MSK-F 5548); Zhytkavichy distr., Khlupinskaya Buda, on branch of dead erect *Malus sylvestris* Mill., leg. E. Yurchenko, 20 May 2010 (MSK-F 7353); France: Îles d'Hyères, Porquerolles, on fallen branch of *Pinus halepensis* Mill., leg. F. Dämmrich, 13 Nov 2013 (KAS-FD 10705a, dup. in private herbarium of Frank Dämmrich); Greece: Rhodos, on deciduous wood, leg. F. Dämmrich, 20 Oct 2004 (KAS-FD 7504, dup. in private herbarium of Frank Dämmrich); Spain: Canary Islands, El Hierro, Fayal-Brezal forest, on dead wood of *Myrica faya* Ait., leg. E. Beltrán, L. Rodríguez, 10 Sep 1988 (TFC-Mic 3217, dup. in KAS); Canary Islands, La Gomera, on dead wood, leg. L. Ryvarden, 16 Jan 1974 (KAS-LR 12558). *Lyomyces pruni*-Sweden: Västergötland, Medelplana, Råbäck, on decayed trunk of *Ulmus* sp., leg. K. Hjortstam, 9 Oct 1970 (GB-Hjm 5257; dup. in KAS and MSK); *ibid.*, on wood of cf. *Corylus*, leg. K. Hjortstam, 17 Oct 2007 (GB 90287; dup. in KAS and MSK).

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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