



Taxonomic studies of crust fungi with spines in *Radulomyces*, *Sarcodontia*, and the new genus *Noblesia*

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Abstract

Species of *Radulomyces* (*Radulomycetaceae*, *Agaricales*) with spines were studied by morphological and molecular methods. Phylogenetic analyses and morphological studies show that *Radulomyces paumanokensis* is a later synonym of *Radulomyces copelandii* and that *Radulomyces licentii* is a distinct taxon. Based on morphologic and molecular data, the new genus *Noblesia* (*Meruliaceae*, *Polyporales*) is proposed to accommodate *Sistotrema croceum* and *Peniophora fensjoeensis*. *Sarcodontia* is emended and restricted to three species with 13 taxa excluded from the genus. For many years, *Sarcodontia crocea* was based on an erroneous concept of *Sistotrema croceum*. The correct name for the taxon with striking yellow spines found on *Malus* and *Pyrus* in Europe is *Sarcodontia setosa*; its North American sister species is *Sarcodontia amplissima* comb. nov. *Hydnum sulphureum* is a synonym of *Sarcodontia uda*, and *Acia flava* is a later synonym of *Xylodon quercinus*. Species excluded from *Sarcodontia* are discussed, and the new combination *Hyalodon sibirica* is proposed.

Keywords Basidiomycota, Crust fungi · New genus · 4 new combinations · 2 new typifications

Introduction

Radulomyces M.P. Christ. (*Radulomycetaceae*, *Agaricales*) was established in 1960, with *Thelephora confluens* Fr. as type, for taxa with effused to effused-reflexed, waxy basidiomes, smooth, tuberculate to spinose hymenophores, clavate or pleural basidia, and large, globose to ellipsoid basidiospores. Christiansen (1960) included two taxa with spines: *R. pachydon* (Pers.) M.P. Christ. and *Radulomyces molaris* (Chaillet ex Fr.) M.P. Christ. Currently, there are five additional species of *Radulomyces* with spines, namely, *Radulomyces arborifer* Malysheva & Zmitr., *Radulomyces copelandii* (Pat.) Hjortstam & Spooner, *Radulomyces licentii* (Pilát) Parmasto, *Radulomyces paumanokensis* J. Horman, Nakasone & B. Ortiz, and *Radulomyces pseudomucidus*

(Petch) Jülich. Conflicting results from recently obtained ITS sequences of *R. copelandii* from eastern United States and China prompted a thorough re-examination of *Radulomyces* collections with spines, including type specimens. Phylogenetic studies show that *Radulomyces* forms a distinct clade in the *Radulomycetaceae* Leal-Dutra, Dentiger & G.W. Griff. and are closely related to *Radulotubus* Y.C. Dai, S.H. He & C.L. Zhao and *Aphanobasidium* Jülich (Zhao et al. 2016; Wang et al. 2018; Leal-Dutra et al. 2020; Olariaga et al. 2020).

During our study, we discovered that *Radulomyces* specimens with spines in North America were occasionally misidentified as *Sarcodontia crocea* (Schwein.) Pouzar, triggering a re-examination of this taxon. This striking, robust species, also known as *Sarcodontia setosa* (Pers.) Donk, has long, bright yellow spines, a strong odor, and is typically associated with dead branches and trunks of living apple trees in eastern North America and Europe (Banker 1906; Miller and Boyle 1943; Kotlaba 1953). The type of *Sistotrema croceum* Schwein. was presumably lost or destroyed (Banker 1906: 122; Lloyd 1914), and a literature search revealed conflicting interpretations of this taxon. Apart from Nikolajeva (1961) and Spirin (2001), the genus *Sarcodontia* Schulzer is considered monotypic by most researchers. Phylogenetic studies show that *Sarcodontia crocea* is in a

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lineage with *Phlebia uda* (Fr.) Nakasone and *Crustodontia chrysocreas* (Berk. & M.A. Curtis) Hjortstam & Ryvar den in the *Meruliaceae* (*Polyporales*) (Tomšovský 2016; Justo et al. 2017).

We used phylogenetic analyses and morphological studies, including types whenever possible, to resolve several taxonomic problems of crust fungi with teeth or spines classified in the *Radulomycetaceae* (*Agaricales*) and *Meruliaceae* (*Polyporales*). *Radulomyces copelandii* and *R. licentii* are re-described and illustrated, and we determine that *R. paumanokensis* is conspecific with *R. copelandii*. The new genus *Noblesia* is introduced for *Sistotrema croceum* which is an earlier name for *Phlebia hydnoidea* Schwein. We determine that the correct name for the taxa widely known in Europe as *Sarcodontia crocea* is *S. setosa*, and its North American counterpart is *Hydnum amplissimum* Berk. & M.A. Curtis. Taxa excluded from *Sarcodontia* are discussed. Neotypes for *Hydnum setosum* Pers. and *Hydnum sulphureum* Schwein. are designated herein.

Materials and methods

Morphological studies

Specimens were borrowed from ARIZ, BPI, BRNM, F, FH, ISC, K, LE, LSU, NCU, NY, PH, PRM, UT, and VT. Herbarium code designations follow Index Herbariorum (Thiers 2021). Thin, freehand sections or scrapings from basidiomes were mounted in 2% (w/v) aqueous potassium hydroxide (KOH), 1% (w/v) aqueous phloxine, or Melzer's reagent. Cyanophily of hyphal and basidiospore walls was observed in 1% (weight/volume) cotton blue in 60% (w/v) lactic acid. Basidiospores in side-view were measured in KOH and phloxine mounts under oil immersion with a $\times 100$ objective; number of spores/number of specimens are noted in parenthesis. Q values were calculated from mean spore length divided by mean spore width of at least 30 spores unless noted otherwise. Color codes and names follow Kornerup and Wanscher (1978). Mycobank (mycobank.org, Robert et al. 2013), Index Fungorum (indexfungorum.org), and MyCoPortal (mycoportal.org) websites were visited many times throughout this study.

DNA sequencing and phylogenetic analyses

DNA extraction and amplification were performed from cultures or fruiting bodies at the Center for Forest Mycology Research (CFMR) following a standard CTAB protocol (Mercado and Ortiz-Santana 2018) or at Beijing Forestry University following procedures described in Zhao et al. (2021). Sequencing was conducted at the University of Wisconsin Biotechnology Center (UWBC) in

Madison, WI, or at Beijing Genomics Institute. The internal transcribed spacer region (ITS), including ITS1, 5.8S, and ITS2, was amplified with primer pairs ITS1F/ITS4 or ITS5/ITS4 (Gardes and Bruns 1993; White et al. 1990). The 5' end of the 28S large subunit of the nuclear ribosomal RNA (nrLSU) was amplified with primers LR0R (Cubeta et al. 1991) and LR5 or LR7 (Vilgalys and Hester 1990). Newly generated sequences were edited with Sequencher 4.8 (Gene Codes Corp., Ann Arbor, MI). For this study, seven new ITS and nine nrLSU sequences were generated; GenBank accession numbers are given in Table 1.

Taxa selection for phylogenetic analyses, based on a combination of BLAST® searches and previous phylogenetic studies, is discussed below for the three fungal groups. Two phylogenetic analyses, Bayesian inference (BI) and maximum likelihood (ML), were executed on three datasets—*Radulomycetaceae* ITS + nrLSU, *Noblesia* ITS + nrLSU, and *Sarcodontia* ITS + nrLSU. DNA sequences were aligned using Clustal W2.1 through CIPRES Science Gateway (Miller et al. 2010). The alignments were manually adjusted with AliView 1.18 (Larsson 2014). The final alignments were submitted to TREEBASE (submission#: 28338, 28339, 28341). The loci were concatenated using Sea View 4 (Gouy et al. 2010), and the nexus files were converted into phylip files then run through jModelTest 2 (Guindon and Gascuel 2003; Darriba et al. 2012) in CIPRES to estimate the best substitution model for the analyses. The best-fit model estimated for the *Radulomyces* ITS + nrLSU dataset was TIM2 + G (MrBayes parameters $nst = 6$, rates = gamma), for *Noblesia* ITS + nrLSU was TIM2ef + I + G (MrBayes parameters $nst = 6$, rates = invgamma), and for *Sarcodontia* ITS + nrLSU was TIM + I + G (MrBayes parameters $nst = 6$, rates = invgamma). Bayesian inference analyses were conducted using MrBayes 3.2.2 (Ronquist et al. 2012) on XSEDE through CIPRES. The parameters mentioned above were used for each dataset for 1,000,000 generations in two runs and four chains with trees sampled every 100 generations. The burn-in period was set to 0.25. Maximum likelihood analyses were performed using RAXML-HPC2 on XSEDE through CIPRES under the GTR model with GAMMA distributed rate heterogeneity and 1000 rapid bootstrap replicates; other parameters were kept at their default settings. Phylogenetic trees were visualized and edited in FigTree 1.4.4 (Rambaut 2016), and final trees were edited in Adobe Illustrator CC 2018 (San José, CA). Strong support values of clades are $> 90\%$ in ML and > 0.95 posterior probabilities (PPs) in BI analyses, whereas moderate support values are $> 70\%$ and > 0.90 , respectively. The bootstrap frequencies ($> 50\%$) and posterior probabilities (> 0.80) are shown on branches.

Table 1 List of samples with GenBank accession numbers of sequences used in the phylogenetic analyses. Taxa are segregated into three sections that correspond to the *Radulomycetaceae*, *Noblesia*, and *Sarcodontia* groups. New sequences are in boldface

Accepted name	Original name	Voucher specimen	Country	GenBank accession numbers		Reference
				nrITS	nrLSU	
<i>Aphanobasidium pseudotsugae</i>	<i>A. pseudotsugae</i>	HHB 822	USA: Maryland	GU187509	GU187567	Binder et al. 2010
<i>A. pseudotsugae</i>	<i>A. pseudotsugae</i>	K(M)180787	UK: Scotland	MK953244	—	Leal-Dutra et al. 2020
<i>A. pseudotsugae</i>	<i>Phlebiella pseudotsugae</i>	NH10396	Denmark	—	AY586696	Larsson et al. 2004
<i>Radulomyces confluens</i>	<i>R. confluens</i>	CBS 108.71	Germany	MH860025	MH871809	Vu et al. 2019
<i>R. confluens</i>	<i>R. confluens</i>	CBS 212.52	France	MH857007	MH868527	Vu et al. 2019
<i>R. confluens</i>	<i>R. confluens</i>	K(M)181613	UK: England	MK953390	MK953401	Leal-Dutra et al. 2020
<i>Radulomyces cope-landii</i>	<i>R. copelandii</i>	CFMR 276	USA: New Hampshire	MZ322824	MZ322832	This study
<i>R. copelandii</i>	<i>R. copelandii</i>	CFMR-311	USA: New York	MZ322825	MZ322833	This study
<i>R. copelandii</i>	<i>R. copelandii</i>	CFMR-312	USA: New York	MZ322826	MZ322834	This study
<i>R. copelandii</i>	<i>Radulomyces paumanokensis</i>	CLZhao 8329	China: Yunnan	MK404496	—	Direct submission, Zhao 2019
<i>R. copelandii</i>	<i>R. paumanokensis</i>	CLZhao 8704	China: Yunnan	MK404498	—	Direct submission, Zhao 2019
<i>R. copelandii</i>	<i>R. copelandii</i>	He 1619	China: Yunnan	—	MZ322835	This study
<i>R. copelandii</i>	<i>R. copelandii</i>	He 1650	China: Yunnan	MZ322827	MZ322836	This study
<i>R. copelandii</i>	<i>R. copelandii</i>	He 20120923–21	China: Sichuan	—	MZ322837	This study
<i>R. copelandii</i>	<i>R. paumanokensis</i>	IMG 5985–16	USA: New York	MG050100	MG050110	Wang et al. 2018
<i>R. copelandii</i>	<i>R. copelandii</i>	K(M) 173275	USA: Massachusetts	MK953391	MK953465	Leal-Dutra et al. 2020
<i>R. copelandii</i>	<i>R. copelandii</i>	LE–BIN 3899	Georgia	MG722738	—	Direct submission, Psurtseva et al. 2017
<i>Radulomyces licentii</i>	<i>R. copelandii</i>	Dai 15061	China: Guizhou	KU535664	KU535672	Zhao et al. 2016
<i>R. licentii</i>	<i>R. copelandii</i>	Wu 9606–5	China: Taiwan	KU535663	KU535671	Zhao et al. 2016
<i>Radulomyces molaris</i>	<i>Radulomyces molaris</i>	G1144	Hungary	—	MK278542	Varga et al. 2019
<i>R. molaris</i>	<i>R. molaris</i>	ML0499	Sweden	—	AY586705	Larsson et al. 2004
<i>Radulomyces rickii</i>	<i>Radulomyces rickii</i>	G1066	Poland	—	MK278543	Varga et al. 2019
<i>R. rickii</i>	<i>R. rickii</i>	JK951007	Switzerland	—	AY586706	Larsson et al. 2004
<i>Radulomyces sp.</i>	<i>Radulomyces confluens</i>	Cui 5977	China	KU535661	KU535669	Zhao et al. 2016
<i>Radulomyces sp.</i>	<i>R. confluens</i>	He 2224	USA: Wisconsin	KU535662	KU535670	Zhao et al. 2016
<i>Radulotubus resupinatus</i>	<i>Radulotubus resupinatus</i>	Cui 8383	China: Yunnan	KU535660	KU535668	Zhao et al. 2016
<i>R. resupinatus</i>	<i>R. resupinatus</i>	Dai 15315	China: Guangxi	KU535658	KU535666	Zhao et al. 2016
<i>Stephanospora caroticolor</i>	<i>Stephanospora caroticolor</i>	Tle1408	UK: England	KM086827	KM086921	Lebel et al. 2015
<i>Aurantipileus mayanensis</i>	<i>Aurantipileus mayanensis</i>	TJB 10228	Belize	HM772140	HM772139	GINNS et al. 2010
<i>Aurantiporus croceus</i>	<i>Hapalopilus croceus</i>	Miettinen 16483	Malaysia	KY948745	KY948901	Justo et al. 2017
<i>Ceriporiopsis gilvescens</i>	<i>Ceriporiopsis gilvescens</i>	L3519	USA: New York	KY948761	—	Justo et al. 2017
<i>Merulius tremellosus</i>	<i>Phlebia tremellosa</i>	CBS 46572	Netherlands	MH860534	—	Vu et al. 2019
<i>M. tremellosus</i>	<i>P. tremellosa</i>	DLL2011 289	USA: Wisconsin	KJ140765	—	Brazeo et al. 2014
<i>Mycocacia fuscoatra</i>	<i>Phlebia fuscoatra</i>	HHB 10782	USA: Wisconsin	KP135365	KP135265	Floudas and Hibbett 2015
<i>Mycocacia nothofagi</i>	<i>Phlebia nothofagi</i>	HHB 4273	USA: Tennessee	KP135369	KP135266	Floudas and Hibbett 2015

Table 1 (continued)

Accepted name	Original name	Voucher specimen	Country	GenBank accession numbers		Reference
				nrITS	nrLSU	
<i>Noblesia crocea</i>	<i>Phlebia</i> cf. <i>hydroidea</i>	HHB 1993	USA: Georgia	KY948778	KY948853	Justo et al. 2017
<i>Pappia fissilis</i>	<i>T. fissilis</i>	BRNM 699803	Czech Republic	HQ728292	HQ729002	Tomsovsky 2012
<i>P. fissilis</i>	<i>T. fissilis</i>	HHB 9530	USA: Florida	KY948774	—	Justo et al. 2017
<i>Phlebia acerina</i>	<i>Phlebia acerina</i>	FD 301	USA: Massachusetts	KP135378	KP135260	Floudas and Hibbett 2015
<i>Phlebia fuscotuberculata</i>	<i>Phlebia fuscotuberculata</i>	CLZhao 10227	China: Yunnan	MT020759	MT020737	Huang and Zhao 2020
<i>P. fuscotuberculata</i>	<i>P. fuscotuberculata</i>	CLZhao 10239	China: Yunnan	MT020760	MT020738	Huang and Zhao 2020
<i>Phlebia lindtneri</i>	<i>Phlebia lindtneri</i>	GB501	Norway	KY948772	KY948847	Justo et al. 2017
<i>Lilaceophlebia livida</i>	<i>Phlebia livida</i>	FP 135046	USA: Montana	KY948758	KY948850	Justo et al. 2017
<i>Phlebia nantahalensis</i>	<i>Phlebia nantahalensis</i>	HHB 2816	USA: North Carolina	KY948777	KY948852	Justo et al. 2017
<i>Phlebia radiata</i>	<i>Phlebia radiata</i>	FD 85	USA	KP135377	—	Floudas and Hibbett 2015
<i>Phlebia rufa</i>	<i>Phlebia rufa</i>	HHB-14924	USA: Washington	KP135374	—	Floudas and Hibbett 2015
<i>Phlebia serialis</i>	<i>Phlebia serialis</i>	FCUG2868	USA: Georgia	HQ153429	—	Ghobad-Nejhad and Hallenberg 2012
<i>Phlebia setulosa</i>	<i>Phlebia setulosa</i>	HHB-6891	USA: Florida	KP135382	KP135267	Floudas and Hibbett 2015
<i>Phlebia tomentopileata</i>	<i>Phlebia tomentopileata</i>	CLZhao 9509	China: Yunnan	MT020762	MT020740	Huang and Zhao 2020
<i>P. tomentopileata</i>	<i>P. tomentopileata</i>	CLZhao 9563	China: Yunnan	MT020765	NG075330	Huang and Zhao 2020
<i>Phlebia</i> sp.	<i>Phlebia</i> sp.	UC2023146	USA: Virginia	KP814195	—	Rosenthal et al. 2017
<i>Sarcodontia amplissima</i>	<i>Sarcodontia crocea</i>	OMC1488	USA: Arkansas	KY948798	KY948903	Justo et al. 2017
<i>Crustodontia chrysocreas</i>	<i>Phlebia chrysocreas</i>	HHB 3946	USA: Tennessee	KP135357	—	Floudas and Hibbett 2015
<i>C. chrysocreas</i>	<i>P. chrysocreas</i>	HHB 6333	USA: Wisconsin	KP135358	KP135263	Floudas and Hibbett 2015
<i>Luteoporia albomarginata</i>	<i>Luteoporia albomarginata</i>	Dai 15229	China: Hainan	KU598873	NG_060338	Wu et al. 2016
<i>L. albomarginata</i>	<i>L. albomarginata</i>	Dai 15240	China: Hainan	KU598874	KU598879	Wu et al. 2016
<i>Luteoporia citriniporia</i>	<i>Luteoporia citriniporia</i>	Dai 19507	Sri Lanka	MT872218	MT872216	Liu and Yuan 2020
<i>L. citriniporia</i>	<i>L. citriniporia</i>	Dai 19622	Sri Lanka	MT872219	MT872217	Liu and Yuan 2020
<i>Odoria alborubescens</i>	<i>Odoria alborubescens</i>	BP 106943	Hungary	MG097864	MG097867	Papp and Dima 2018
<i>O. alborubescens</i>	<i>O. alborubescens</i>	PC 0706595	France	MG097863	—	Papp and Dima 2018
<i>Phlebia nigrodentea</i>	<i>Phlebia</i> sp.	CLZhao 2445	China: Yunnan	MT896821	MT896818	Huang et al. 2020
<i>P. nigrodentea</i>	<i>Phlebia</i> sp.	CLZhao 2729	China: Yunnan	MT896823	MT896819	Huang et al. 2020
<i>Phlebia tongxiniana</i>	<i>Phlebia tongxiniana</i>	CLZhao 2255	China: Yunnan	MT020773	MT020751	Huang and Zhao 2020
<i>P. tongxiniana</i>	<i>P. tongxiniana</i>	CLZhao 2719	China: Yunnan	MT020776	MT020754	Huang and Zhao 2020
<i>Phlebiporia bubalina</i>	<i>Phlebiporia bubalina</i>	Dai 15183	China: Hainan	KU598875	KU598880	Wu et al. 2016
<i>P. bubalina</i>	<i>P. bubalina</i>	Dai 15239	China: Hainan	KU598877	KU598882	Wu et al. 2016
<i>Sarcodontia amplissima</i>	<i>Sarcodontia amplissima</i>	FP 101997	USA: Wisconsin	MZ322828	MZ322838	This study
<i>S. amplissima</i>	<i>S. amplissima</i>	FP 104176	USA: Maryland	MZ322829	MZ322839	This study
<i>S. amplissima</i>	<i>S. amplissima</i>	He 2120	USA: Minnesota	MZ322830	MZ322840	This study
<i>S. amplissima</i>	<i>Sarcodontia crocea</i>	OMC 1488	USA: Arkansas	KY948798	KY948903	Justo et al. 2017
<i>Sarcodontia setosa</i>	<i>S. crocea</i>	BRNM 721609	Czech Republic	KX831470	KX831472	Tomsovsky 2016

Table 1 (continued)

Accepted name	Original name	Voucher specimen	Country	GenBank accession numbers		Reference
				nrITS	nrLSU	
<i>S. setosa</i>	<i>S. crocea</i>	BRNM 761841	Czech Republic	KX831471	KX831473	Tomsovsky 2016
<i>Sarcodontia uda</i>	<i>Phlebia uda</i>	FP 101544	USA: Wisconsin	KP135361	KP135232	Floudas and Hibbett 2015
<i>S. uda</i>	<i>Mycoacia uda</i>	Kropp 1	USA: Oregon	KY948764	—	Justo et al. 2017
<i>Scopuloides hydnooides</i>	<i>Scopuloides hydnooides</i>	KHL 11916	Sweden	EU118665	EU118665	Larsson 2007
<i>Scopuloides rimosa</i>	<i>Scopuloides rimosa</i>	HHB 7042	USA: Florida	KP135350	KP135282	Floudas and Hibbett 2015

Results

Phylogenetic and taxonomic studies in *Radulomyces* (*Radulomycetaceae*, *Agaricales*)

Based on previous studies and BLAST® searches, the *Radulomycetaceae* ITS + nrLSU dataset includes 22 samples of *Radulomyces* distributed among seven taxa, with an emphasis on species with spines, two samples of *Radulotubus resupinatus* Y.C. Dai, S.H. He & C.L. Zhao, and three of *Aphanobasidium pseudotsuga* (Burt) Boidin & Gilles (see Table 1; Zhao et al. 2016; Wang et al. 2018). Following Leal-Dutra et al. (2020) and Olariaga et al. (2020), *Stephanospora caroticolor* (Berk.) Pat. (*Stephanosporaceae*) was selected as the outgroup taxon. This dataset had an aligned length of 1517 characters, 635 for ITS and 882 for nrLSU. The Bayesian consensus tree of the ITS + nrLSU dataset is shown in Fig. 1 with *Radulomyces*, *Radulotubus*, and *Aphanobasidium* forming strongly supported monophyletic lineages. The ML analysis produced a tree with similar topology except the *R. molaris* clade dissolved with sample G1144 placed basally among all *Radulomyces* species. Within *Radulomyces*, there were seven well-supported lineages corresponding to three species with spines, namely, *R. copelandii*, *R. licentii*, and *R. molaris*, and four taxa with smooth or tuberculate hymenophores, *R. confluens*, *R. rickii* (Bres.) M.P. Christ., and two unnamed samples from the USA (He2224) and China (Cui5977). Included among the *R. copelandii* samples was the paratype of *R. paumanokensis* (IMG 5985–16). *Radulomyces licentii* was represented by Dai 15061 and Wu 96096–5, samples from China originally identified as *R. copelandii*. Four species of *Radulomyces* with spines are described below; because of the morphological similarity of *R. copelandii* and *R. licentii*, they are described in full.

Radulomyces copelandii (Pat.) Hjortstam & Spooner, Kew Bulletin 45(2): 314. 1990. [MycoBank# 132794] Figs. 2 a–b.

≡ *Hydnum copelandii* Pat., Leaflets Philippine Botany 6 (no. 104): 2251. 1914. [MycoBank# 228209].

≡ *Oxydontia copelandii* (Pat.) S. Ito, Mycological flora Japan. Basidiomycetes 2(4): 189. 1955. [MycoBank# 335503].

≡ *Sarcodontia copelandii* (Pat.) Imazeki, Coloured illustrations of fungi of Japan, Vol. 2: 127. 1965. [MycoBank# 338813].

≡ *Mycoacia copelandii* (Pat.) Aoshima & H. Furuk., Transactions Mycological Society Japan 7(2–3): 136. 1966. [MycoBank# 334660].

≡ *Radulodon copelandii* (Pat.) N. Maek., Reports Tottori Mycological Institute 31: 93. 1993. [MycoBank# 362733].

≡ *Hydnum pseudomucidum* Petch, Annals Royal Botanic Gardens Peradeniya 6(2): 156. 1916. [MycoBank# 222205].

≡ *Radulomyces pseudomucidus* (Petch) Jülich, Persoonia 10(3): 334. 1979. [MycoBank# 322222].

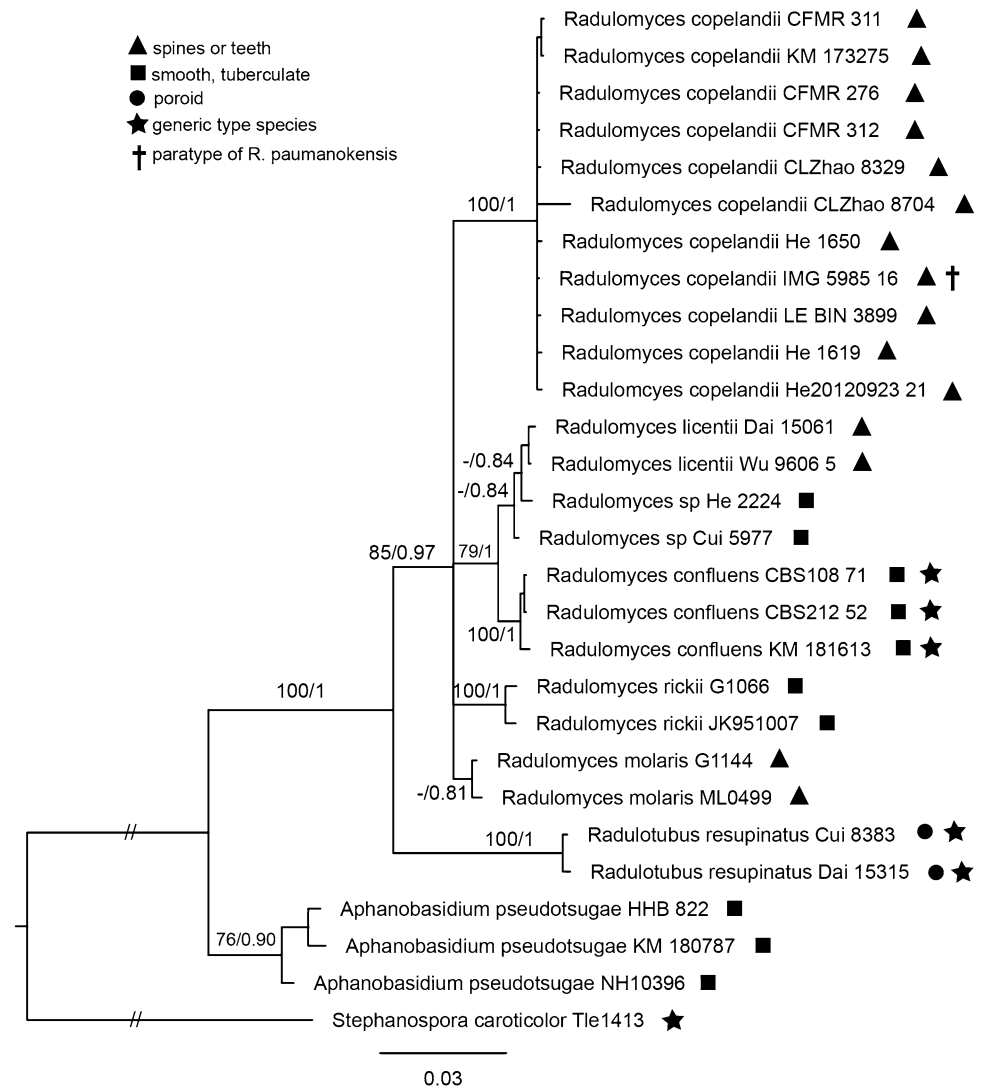
≡ *Cerocorticium pseudomucidum* (Petch) Jülich, Persoonia 11(4): 427. 1982. [MycoBank# 110536].

≡ *Radulodon pseudomucidus* (Petch) Stalpers, Folia Cryptogamica Estonica 33: 137. 1998. [MycoBank# 445312].

= *Radulomyces paumanokensis* J. Horman, B. Ortiz & Nakasone, Cryptogamie Mycologie 39(2): 237. 2018. [MycoBank# 825443].

Basidiomes resupinate, at first compact, hemispherical to ovoid clusters of radiating, branching, pendant spines then becoming widely effused, spreading up to 30 cm, 1–3 mm thick, ceraceous to firm membranous, hydneous, in well-developed specimens curved, pendant spines form from projecting tubercular nodules, yellowish white (4A2), pale yellow (4A3), grayish yellow [4B(3–4)], orange white (5A2), pale orange (5A3), light orange (5A4), or grayish orange (5B3). Context dense, fibrous, ceraceous, white to yellowish brown. Spines crowded, 1–3 per mm, 3–10(20) × 0.5–1 mm, terete to compressed, sometimes branched, single but often fused at base, straight then slightly sinuous when dried, gradually narrowing to a fine, entire, acute tip, sometimes branched or flattened at apex, surface smooth to finely

Fig. 1 Phylogeny of the *Radulomycetaceae* group inferred from BI analysis of ITS and nrLSU sequences. Support values along branches are from ML Bootstrap ($\geq 50\%$) and Bayesian posterior probabilities ($PP \geq 0.80$), respectively

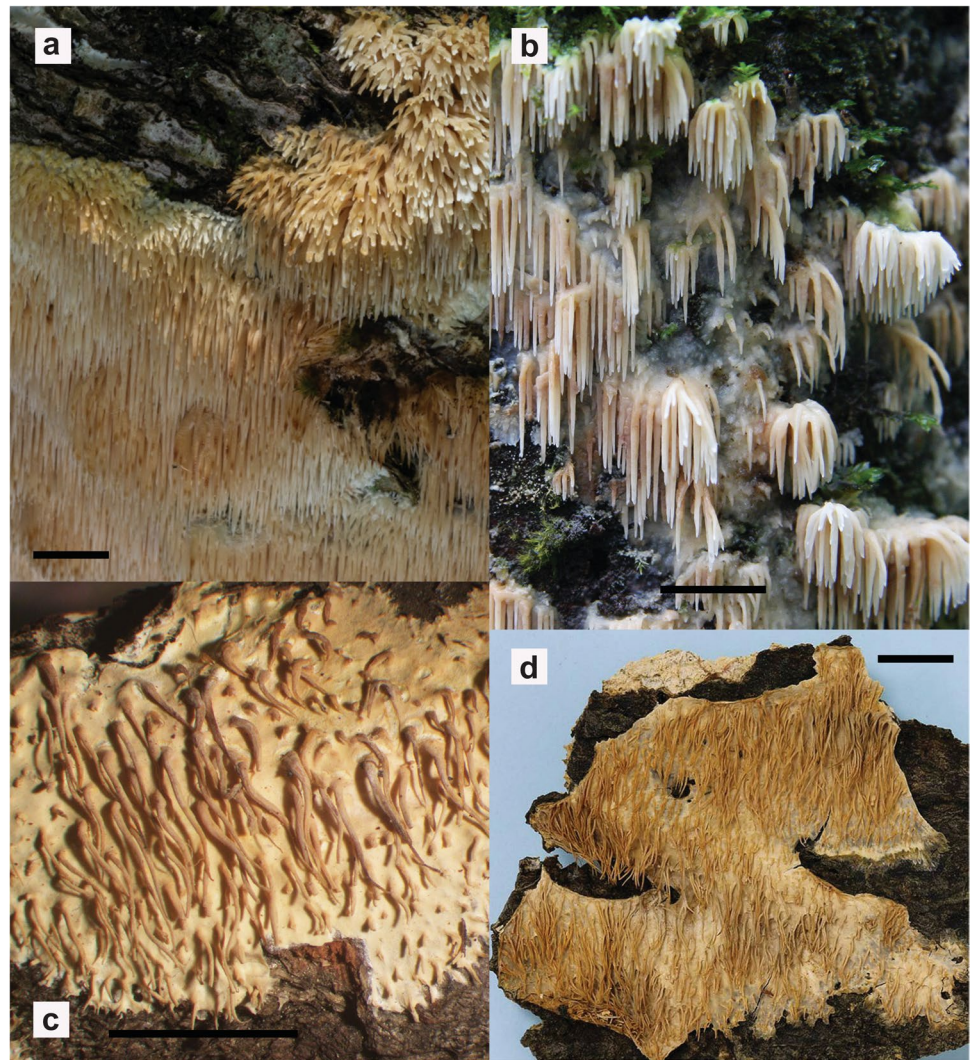


farinaceous, white, orange white to pale orange [5A(2–3)] at first then pale orange (5A3), grayish orange (5B3), orange gray (6B2), brownish orange (5C4, 6C5), or light brown (6D6), often apices drying darker, brittle and often breaking to reveal a dark yellow to pale brown trama, when bruised or over-mature then hygrophanous, darkening to yellowish brown; odor absent. Margin adnate or detached, smooth or with developing spines, white, appressed, 0.5–2 mm wide; edges finely fimbriate.

Hyphal system monomitic with clamp connections. Spines composed of a dense core of distinct non-agglutinated hyphae arranged in parallel, terminal hyphae at apex mostly undifferentiated but occasionally slightly capitate; tramal hyphae 2–3.5 μm diameter, clamped, sparsely branched, walls distinct, hyaline, thin to slightly thickened, smooth, often weakly to distinctly cyanophilous. Subiculum up to 700 μm thick, a moderately dense tissue of non-agglutinated, distinct hyphae arranged parallel to substrate; subicular hyphae 2–4.5 μm diam., clamped, moderately

branched, walls hyaline, thin to slightly thick, smooth, weakly cyanophilous. Subhymenium up to 100 μm thick, a densely interwoven tissue of non-agglutinated hyphae; subhymenial hyphae 3–3.5 μm diam., clamped, short-celled, frequently branched, walls hyaline, thin, smooth, acyanophilous. Hymenium up to 50 μm thick, a dense palisade of hyphidia, cystidia, and basidia. Hyphidia scarce to abundant, filiform, often sinuous, simple, 20–45(60) \times 2–4 μm , clamped at base, walls hyaline, thin, smooth. Cystidia absent or scarce, embedded, clavate, subulate or subfusiform, 16–50 \times 4–7 μm , clamped at base, walls hyaline, thin, smooth. Basidia clavate, often with a distinct stalk, rarely pleural, 30–50(65) \times 6–8.5 μm , clamped at base, 4-sterigmate, often containing oil-like droplets, walls hyaline, thin, smooth. Basidiospores globose to subglobose, often partially collapsed, adaxial side often distinctly flattened, (5.7)6–7.2(7.5) \times (5)5.5–6.5(7) μm , average (438/13) 6–7 \times 5.4–6.4 μm , $Q = 1.1$ –1.2, often containing oil-like droplets, walls hyaline, thin to slightly thickened, smooth

Fig. 2 *Radulomyces copelandii* basidiomes in situ. **a** LE–BIN–3899 from Georgia. **b** He20120923–21 from China; *R. licentii* dried basidiomes. **c** SNU 9108160–56 from South Korea. **d** Dai 18173 from China. Scale bars in **a**, **b**, and **d** = 10 mm, **c** = 5 mm



or occasionally ornamented with one or more, tiny, hyaline papillae, weakly to strongly cyanophilous, not reacting to Melzer's reagent.

Ecology and distribution. Associated with a white rot decay; saprobic on bark and wood of hardwoods, esp. *Quercus* and *Acer*. Reported from China, northern India, Nepal, Philippines, Sri Lanka, eastern Russia (Zmitrovich et al. 2017), Georgia, and north eastern U.S.A.

Type specimens examined. PHILIPPINES. *E.B. Copeland*, *C.G. Lloyd* 36682 (isotype of *H. copelandii* BPI 0324650). SRI LANKA (Ceylon). Hakgala, Apr 1919, *Petch* 5962 (neotype of *H. pseudomucidum* K: K(M)56913). USA. NEW YORK: Nassau County, Glen Cove, Welwyn Preserve County Park, on bark of rotten hardwood, 19 Nov 2016, *A. Norarevian* (holotype of *R. paumanokensis* CFMR: CFMR–300).

Other specimens examined. CHINA. CHANSI (Shanxi): Yao Chan, (on bark of branch), 31 Aug 1935, *E. Licent* 4595 (PRM 169,104, as *Acia licentii*); CHONGQING: Nanchuan

District, Jinfoshan Nature Reserve, on fallen angiosperm branch, 9 Jul 2018, *S.H. He* 5495 (CFMR). GUIZHOU: Jiangkou County, Fanjingshan Nature Reserve, on fallen angiosperm trunk, 11 Jul 2018, *S.H. He* 5566 (CFMR); HEBEI: Xinglong County, Wulingshan Nature Reserve, 2 Sep 2017, *S.H. He* 4958 (BJFC 024477, CFMR); SICHUAN: Qionglai County, Tiantaishan Forest Park, on angiosperm stump, 23 Sep 2012, *S.H. He* 20120923–21 (CFMR); YUNNAN: Jingdong County, Ailaoshan Nature Reserve, on dead angiosperm tree, 13 Jul 2013, *S.H. He* 1619 (CFMR); Nanhua County, Dazhongshan Nature Reserve, on fallen angiosperm trunk, 15 Jul 2013, *S.H. He* 1650 (CFMR). GEORGIA. WESTERN CAUCASUS: Abkhazia, on fallen branch of *Quercus hartwissiana*, 12 Jul 2016, *A. Kiyashko*, LE–BIN 3899 (LE 329476). INDIA. JAMMU: Jammu and Kashmir, Sanasar, on angiospermic log, 10 Aug 1966, *H.S. Khara* 4144 (UT 38845, BPI 285991). NEPAL. Kathmandu, Sundrijal, on angiospermic forest tree bark, 8 Sep 1969, *H.S. Khara* 4303 (UT 38913, BPI 259625); Daman, Simbhanjyang,

on decaying stump, 13 Sep 1969, *H.S. Khara 4305* (BPI 259624). USA. MASSACHUSETTS: Essex County, Ipswich, Bradley Palmer State Park, on bark of *Acer rubrum* log, 13 Nov 2009, *L. Millman, Ginns 11837* (BPI 882466); Middlesex County, Concord, Walden Pond, on bark of *Fagus*, 7 Mar 2010, *L. Millman* (HUH 01146405), on *Quercus*, Dec 2009, *L. Millman* (BPI 882467); Norfolk County, Sharon, Eastabrook Woods, on *A. rubrum*, 16 Oct 2010, *L. Millman* (HUH 00822870); NEW HAMPSHIRE: Grafton County, Groton, on deciduous log, 1 Oct 2016, *L. Millman* (CFMR: CFMR–276); NEW YORK: Suffolk County, Wildwood State Park, 25 Aug 2019, *J. Horman* (CFMR: CFMR–311); Nassau County, East Norwich, Muttontown Preserve, 21 Sep 2018, *J. Horman* (CFMR: CFMR–312), on rotten hardwood log, 2 Oct 2016, *J. Horman* (paratype of *R. paumanokensis* CFMR: CFMR–301); VIRGINIA: Shenandoah, George Washington National Forest, Elizabeth Furnace Recreation Area, on *Quercus* log, 10 Sep 2016, *C. Foor, C0296175* (F: NAMA–2016–331, as *Sarcodontia setosa*).

Descriptions and illustrations. Ginns and Millman (2011), Hjortstam et al. (1990: 314–315), Wang et al. (2018: 237–239, as *R. paumanokensis*), Zmitrovich et al. (2017).

Remarks. *Radulomyces copelandii* is characterized by pale yellow to brown basidiomes bearing long spines, clamped hyphae, and subglobose basidiospores with weakly cyanophilous walls. The basidiomes are quite variable from small, cushion-shaped, widely effused, or projecting outwards from knobby tubercles with decurrent spines that are single or fused at base, terete or compressed, and sometimes branched. There are some excellent photographs of *R. copelandii* in Gary Emberger's Fungi Growing on Wood website (www.messiah.edu/Oakes/fungi_on_wood/index.htm). Inconspicuous, hyaline papillae, or spines on the basidiospore walls are described in *R. copelandii* for the first time and were present in most specimens examined. Similar minutely spiny or warted basidiospores in *R. rickii* were reported by Boidin et al. (1988) and Ghobad-Nejhad and Kotiranta (2007).

Radulomyces copelandii is nearly identical to *R. licentii* with respect to micromorphology except that basidia in the former are consistently longer than in the latter, 30–50(60) μm and 20–35 μm long, respectively. Overall, basidiomes of *R. copelandii* are more robust and thicker, 1–3 mm thick, compared to those in *R. licentii* that are more delicate and much thinner, up to 0.5 mm thick. Differences in spine morphology and density were observed also. For example, spines in *R. copelandii* are more robust, often compressed, fused, and in well-developed specimens, developing small, knobby, tubercular nodules (Fig. 2b) with decurrent, pendant spines. In contrast, spines in *R. licentii* are fragile, terete, rarely fused at the base, developing directly from the effused subiculum, and less densely arranged with distinct, smooth

areas between them. Young, hemispherical to cushion-like basidiomes of *R. copelandii* have branched spines that are not found in *R. licentii*. In addition, the slender, gracile spines in *R. licentii* are typically more sinuous when dried than in *R. copelandii*. Finally, *R. copelandii* has a wide distribution in tropical and temperate Asia and north eastern USA whereas *R. licentii* appears to be restricted to temperate East Asia. Phylogenetically, the two species are congeneric but in distinct lineages based on ITS + nrLSU sequences (Fig. 1); their ITS sequences are 92% identical as reported in BLAST® searches.

Hjortstam et al. (1990: 316) placed *H. pseudomucidum* in synonymy with *R. copelandii*, and we concur. The neotype of *H. pseudomucidum* at K is poorly preserved and contaminated with a hyphomycete, but it is typical of *R. copelandii* with long spines, up to 11 \times 2–4 mm, nodose-septate hyphae, and numerous globose to subglobose basidiospores, 6–7.5 \times 5.5–6.5 μm . Although E. Licent 4595 was one of three collections cited when *A. licentii* was described (Pilát 1940), it is different from the other two collections by having distinctly compressed spines that are typical of *R. copelandii*. This specimen is colonized by an anamorphic species with two-celled conidiospores. *Radulomyces paumanokensis* was based on young, cushion-like basidiomes that are quite different from the widely effused, mature forms of *R. copelandii*; see LE–BIN 3899 in Fig. 2a that shows both cushion and effused basidiome configurations. Additionally, the paratype of *R. paumanokensis*, IMG 5985–16, is shown to be conspecific with *R. copelandii* by phylogenetic analyses (Fig. 1); its ITS sequence is 99% identical to other strains of *R. copelandii* as calculated from BLAST® searches (data not shown). We conclude that *R. paumanokensis* is a later synonym of *R. copelandii*.

Radulomyces licentii (Pilát) Parmasto, *Conspectus systematis Corticiacearum* p. 111. 1968. [MycoBank# 338150] Figs. 2 c–d.

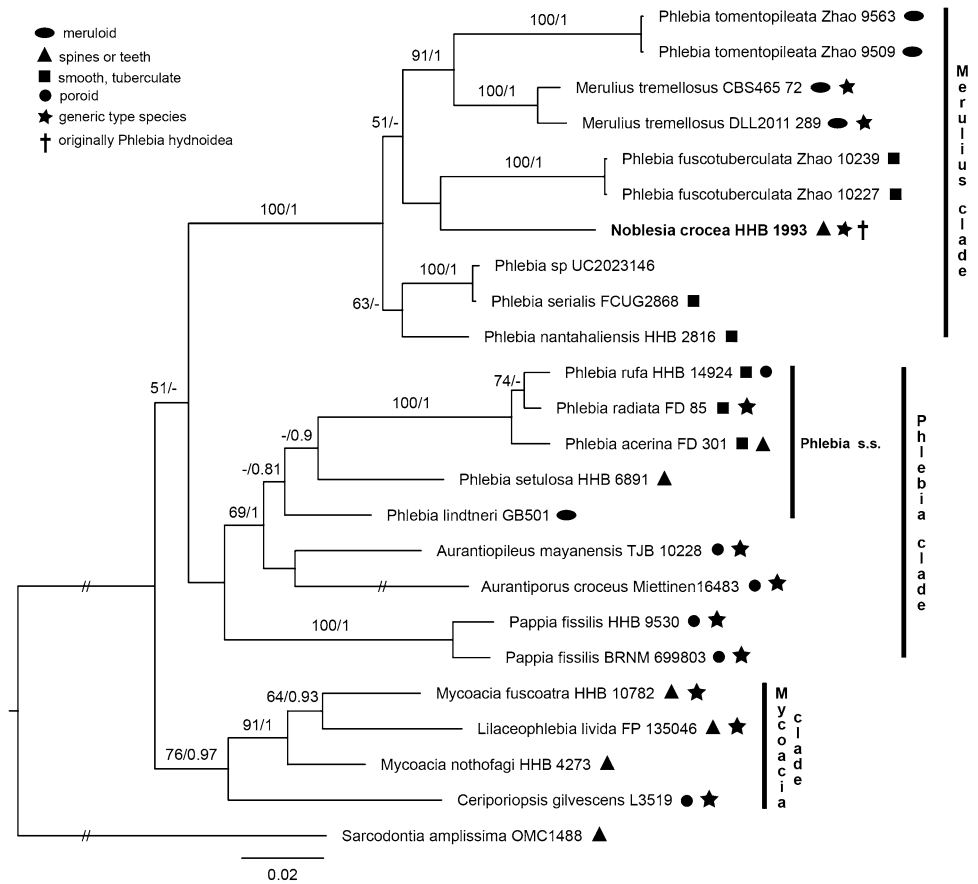
≡ *Acia licentii* Pilát, *Annales Mycologici* 38(1): 66. 1940. [MycoBank# 283867].

≡ *Radulum licentii* (Pilát) Nikol., *Flora plantarum cryptogamarum URSS* 6(2): 98. 1961. [MycoBank# 338165].

≡ *Radulodon licentii* (Pilát) Ryvar den, *Česká Mykologie* 30(1): 40. 1976. [MycoBank# 322220].

Basidiomes resupinate, widely effused, adnate to loosely adnate, thin to moderately thick, 200–500 μm thick, subceraceous, spinose with distinct smooth areas between erect or pendant spines, orange white (5A2) to pale orange (5A3); context fibrous, white. Context cream-colored, fibrous. Spines brittle, cylindrical, 0–4 per mm, 2–5(6) \times 0.15–0.4 mm, terete, single, rarely fused at base, gradually tapering to an acute apex, sinuous when dried, grayish orange (5B3), brownish orange (5C4), light brown (6D5), or brown [6(D–E)7]. Margin adnate, thinning out, edges smooth or spinose, fimbriate. (Fig. 2c)

Fig. 3 Phylogeny of the *Noblesia* group inferred from BI analysis of ITS and nrLSU sequences. Support values along branches are from ML Bootstrap ($\geq 50\%$) and Bayesian posterior probabilities ($PP \geq 0.80$), respectively



Hyphal system monomitic with clamp connections. Spines composed of non-agglutinated hyphae arranged in parallel, at apex hyphae undifferentiated; tramal hyphae 2–4.5 μm diam., clamped, long-celled, sparsely branched, walls distinct, hyaline, thin to 0.7 μm thick, smooth, acyanophilous. Subiculum 150–300 μm thick, a non-agglutinated tissue of hyphae arranged more or less parallel to substrate; subicular hyphae 2–5.5 μm diam., clamped, rarely branched, walls hyaline, thin to 1.5 μm thick, smooth, sometimes weakly cyanophilous. Subhymenium indistinct, up to 25 μm thick, a compact, dense tissue of short-celled, partially agglutinated hyphae; subhymenial hyphae 1.5–3 μm diam., clamped, frequently branched, walls hyaline, thin, smooth, acyanophilous. Hymenium up to 50 μm thick, a dense palisade of hyphidia, cystidia, and basidia. Hyphidia scarce to numerous, filiform but sometimes enlarged at base, often strangulated, rarely branched 18–38 \times 2.5–5 μm , clamped at base, walls hyaline, thin, smooth. Cystidia absent or scarce, embedded, subfusiform with an obtuse or subacute apex, 13–30 \times 5–7 μm , clamped at base, walls hyaline, thin, smooth. Basidia clavate to subcylindric, sometimes with a distinct stalk, 25–30 \times 6–7.5 μm , clamped at base, 4-sterigmate, walls hyaline, thin, smooth. Basidiospores abundant, globose to subglobose, often partially collapsed, adaxial side often distinctly flattened, with a prominent apiculus, 5.8–7.2(7.5) \times (5.2)5.5–6.5 μm , average

(68/2) 6.7–7 \times 5.9–6.2 μm , $Q = 1.1$, often containing refractive, oil-like droplets, walls hyaline, thin to slightly thickened, smooth, rarely with one or more, tiny, hyaline papillae, weakly to strongly cyanophilous, not reacting to Melzer’s reagent.

Ecology and distribution. Associated with a white rot decay; saprobic on bark and wood of various hardwoods, rarely on conifers. Reported from eastern Russia, China (Yunnan, Shanxi, Taiwan), Korea, and probably Japan.

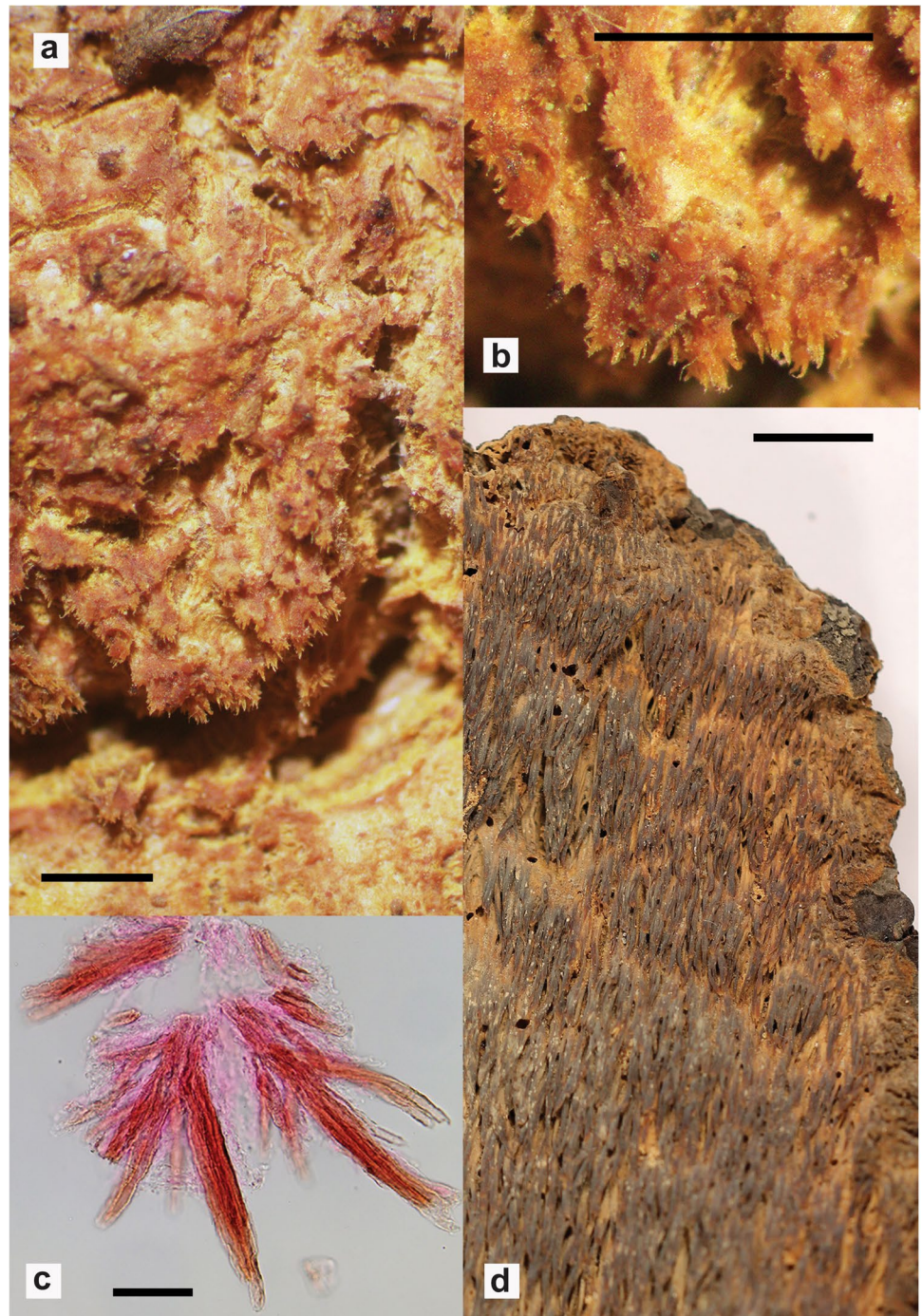
Type specimen examined. CHINA. Chansi (Shanxi): Yao Chan, (on bark of branch), 31 Aug 1935, *E. Licent* 4390 (lectotype PRM 169105).

Other specimens examined. CHINA. Chansi: loc. cit., *E. Licent* 4150 (PRM 501122); TAIWAN: Chiayi, Tatchia, Paiyun Villa, alt. 2600 m, on branch of *Coriaria japonica* ssp. *intermedia*, 12 Jun 1996, *S.H. Wu* 9606–5 (CFMR). KOREA. GYUNGSANGNAM-DO: Gaya Mountains, between Haeinsa Temple and Maebul, on (bark of) *Prunus* branch, 16 Aug 1991, *H.S. Jung* 910816–56 (CFMR).

Descriptions and illustrations. Pilát (1940, plate I, fig. 4, plate II, fig. 3), Nikolajeva (1961: 98–100, plate IX), Ryvarden (1976).

Remarks. *Radulomyces licentii* is characterized by thin, effused basidiomes with well-spaced spines, clamped hyphae,

Fig. 4 *Noblesia crocea*. **a** HHB–10759 dried basidiome. **b** Close-up of aculei in HHB–10759. **b** Fascicles of hyphae in aculei of PH00062606; *Hydnum amplissimum*. **d** Isolectotype, Sprague 297, UVMVT302881. Scale bars in **a** and **b** = 1 mm, **c** = 50 μ m, **d** = 10 mm



short basidia (up to 35 μ m long), and subglobose basidiospores with weakly cyanophilous walls. Inconspicuous, hyaline papillae on the basidiospore walls were only occasionally observed. For further discussion of differences between *R. licentii* and the morphologically similar *R. copelandii*, see comments above. Although information on the distribution of *R. licentii* is scarce, it appears to be sympatric with *R. copelandii* in some parts of China. It is likely that *R. licentii* also occurs in Japan as described and illustrated in Maekawa (1993: 93) and Furukawa

(1974, plate 9, E–F). Although Stalpers (1998) and Nakasone (2001) considered *R. licentii* to be a synonym of *R. copelandii*, phylogenetic analyses show that the taxa are distinct, appearing in different lineages (Fig. 1) and with only 92% sequence identity of the ITS region (data not shown).

When describing *R. indicus* Jyoti & Dhingra (Jyoti and Dhingra 2014), the authors commented on its similarity to *R. pseudomucidus* except for its temperate habit and well-spaced conical spines. The type of *R. indicus* was not available for

study but may be a young, developing basidiome because of the rather short spines, up to 1 mm long. If shown to be synonymous with *R. licentii*, then the range of *R. licentii* expands further westward into central Asia.

Radulomyces molaris (Chaillat ex Fr.) M.P. Christ., Dansk Botanisk Arkiv 19 (2): 232. 1960. [MycBank# 338151].

≡ *Radulum molare* Chaillat ex Fr., Elenchus Fungorum (Greifswald) 1: 151. 1828. [MycBank# 176952].

Specimens examined. SLOVAKIA. Banskobystricky kraj, Prencow, Bohojo vrsok., in ramo Carpini bet., 21 Nov 1892, A. Kmet (ARIZ: AN035074). SWEDEN. Halland, Släp, Särö, unweit Kungsbacka, on *Quercus*, 29 Sep 1914, L. Romell 5019 (ARIZ: AN035071). UKRAINE. KHARKIV OBLAST: Homilshanski Lisy National Nature Park, near Haidary, Zmieiev view, 21 Jul 2002, A. Akulov (CFMR: MYC-1701).

Descriptions and illustrations. Bernicchia and Gorjón (2010: 568, 911–912), Eriksson et al. (1981: 1240–1243), Martini (2016).

Remarks. This species is well characterized by thick, coarse spines, up to 5 mm long, and large ellipsoid basidiospores, 8–12 × 6–7.5 μm, with smooth, slightly thickened walls. It is widely distributed in Europe on hardwoods, especially oak, but also reported from the Himalayas on *Pinus* and *Cedrus* (Prasher 2015: 134–135) and southern India (Natarajan and Kolandavelu 1997). Phylogenetically, *R. molaris* is distinct from both *R. copelandii* and *R. licentii* that also develop spiny hymenophores (Fig. 1).

Radulomyces arborifer Malysheva & Zmitr., Karstenia 46: 25. 2006. [MycBank# 521668].

Type specimen examined. RUSSIA. Samara Region, Zhiguli Nature Reserve, on fallen log of *Tilia cordata*, 24 Aug 2003, V. Malysheva and I. Zmitrovich (holotype LE: 2147063).

Remarks. *Radulomyces arborifer* is known only from the type. Its basidiospores, 9.3–11(11.5) × (5.5)5.8–6.5 μm, average (31/1) 10 ± 0.8 × 6 ± 0.3 μm, Q = 1.7 ± 0.1, are similar in shape and size to *R. molaris*, but *R. arborifer* differs in developing a cream-colored basidiomes with flattened aculei with short branches. The cystidia and ampullate pseudocystidia in the aculei as described in the original description (Malysheva 2006) could be interpreted as immature, developing basidia and terminal, clavate hyphal end cells, respectively. Additional specimens and sequence data are necessary to determine if *R. arborifer* is a distinct species or an aberrant form of *R. molaris*.

Phylogenetic and taxonomic studies in the new genus *Noblesia* (Meruliaceae, Polyporales)

Previous phylogenetic studies placed *Phlebia hydnoidea* (a later synonym of *Sistotrema croceum*, see below) in a

clade with *Phlebia nantahaliensis* Nakasone & Burds. and *Merulius tremellosus* Schrad. (Justo et al. 2017, fig. 5; Chen et al. 2018; Huang and Zhao 2020). Included in this clade, called the *Merulius* clade herein, were two samples of *Phlebia* retrieved from BLAST® searches in GenBank and two newly described species of *Phlebia* from China, *P. fuscotuberculata* C.L. Zhao and *P. tomentopileata* C.L. Zhao (Huang and Zhao 2020). The sister clade, designated the *Phlebia* clade, includes taxa in *Phlebia* s.s., such as *P. radiata* Fr., generic type of *Phlebia*, and *P. acerina* Peck as well as *Aurantipileus mayaensis* Ginns, D.L. Lindner & T.J. Baroni, generic type of *Aurantipileus* Ginns, D.L. Lindner & T.J. Baroni, *Aurantiporus croceus* (Pers.) Murrill, generic type of *Aurantiporus* Murrill, and *Pappia fissilis* Berk. & M.A. Curtis Zmitr., generic type of *Pappia* Zmitr. (Justo et al. 2017, fig. 5). The *Mycoacia* clade is closely related to the two clades mentioned above; taxa in this clade include *Lilaceophlebia livida* (Pers.) Spirin & Zmitr., generic type of *Lilaceophlebia* (Parmasto) Spirin & Zmitr., *Mycoacia fuscoatra* (Fr.) Donk, generic type of *Mycoacia* Donk, and *Ceriporiopsis gilvescens* (Bres.) Domański, generic type of *Ceriporiopsis* Domański (Justo et al. 2017, fig. 5; Chen et al. 2018). An ITS + nrLSU dataset was compiled of the *Noblesia* group, composed of taxa in the three clades mentioned above (see Table 1 for a complete list), and phylogenetically analyzed with *Sarcodontia amplissima* as the outgroup taxon. This dataset had an aligned length of 1604 characters, 687 for ITS and 917 for nrLSU. The BI and ML analyses resulted in phylogenetic trees of identical topology with one minor exception that is described below. In the BI consensus tree of the *Noblesia* group shown in Fig. 3, there are three major lineages—the *Merulius*, *Phlebia*, and *Mycoacia* clades. These clades were also recovered in three and five loci phylogenetic analyses by Justo et al. (2017) and Chen et al. (2018), respectively. In Fig. 3, *P. hydnoidea* (as *Noblesia crocea*) is nested in the *Merulius* clade that is sister to the *Phlebia* clade. The ML tree (not shown) differed from Fig. 3 by the dissolution of the weakly supported clade composed of *P. hydnoidea* and *P. fuscotuberculata*. A nucleotide BLAST® query showed that the ITS sequence of *P. hydnoidea* HHB-1993 was distantly related to the other taxa in the *Merulius* clade, with only 85–88% sequence identity (data not shown). Based on phylogenetic and morphologic data, the new genus *Noblesia* is proposed below for *P. hydnoidea*.

Noblesia Nakasone, *gen. nov.*

MycBank# 839627.

Basidiomes widely effused, up to 10 mm thick, soft ceraceous when fresh, drying crustaceous, hymenophore tuberculate, odontoid to hydneous, light yellow, bright orange-yellow or brown, turning red to black in 2% KOH solution,

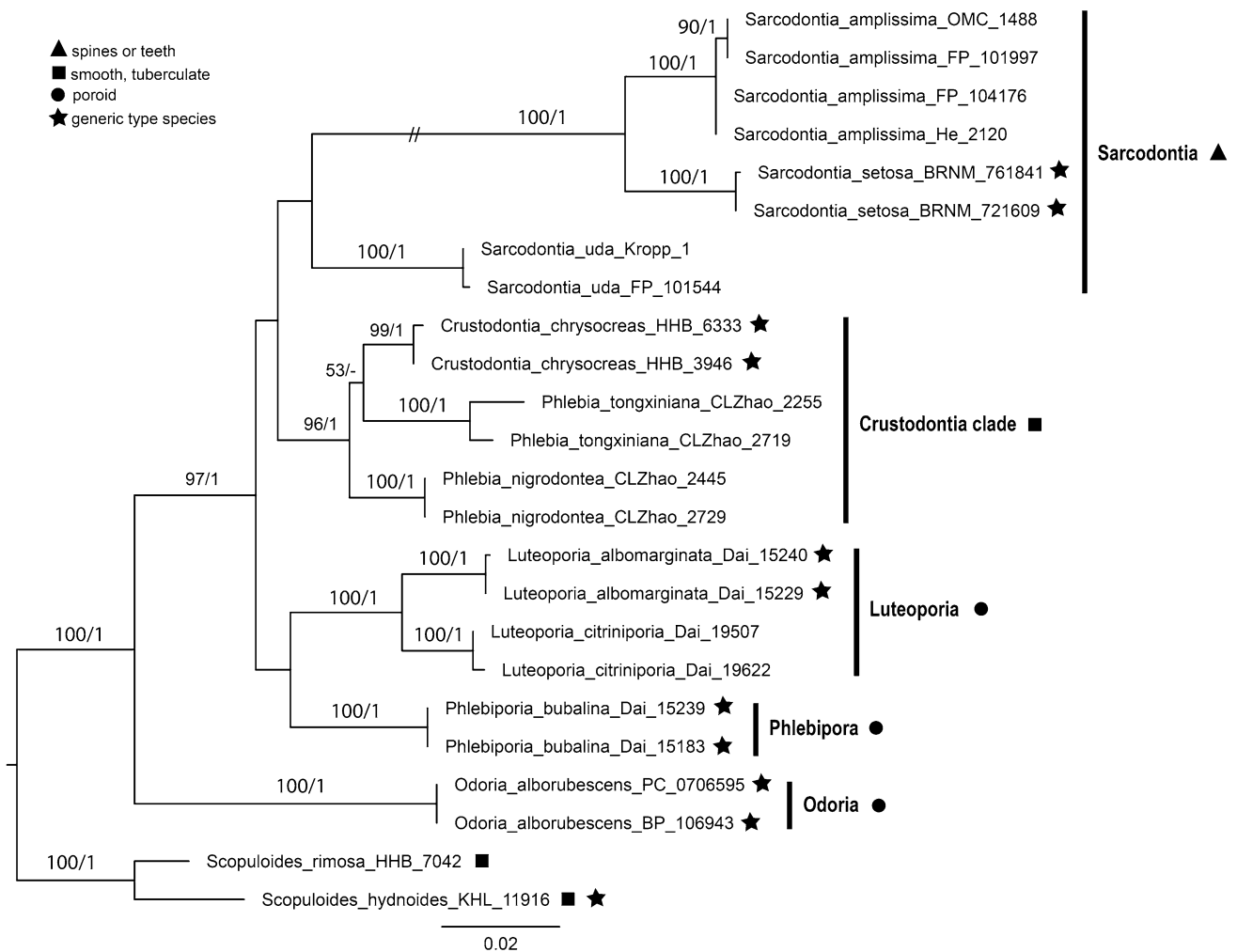


Fig. 5 Phylogeny of the *Sarcodontia* group inferred from ML analysis of ITS and nrLSU sequences. Support values along branches are from ML Bootstrap ($\geq 50\%$) and Bayesian posterior probabilities ($PP \geq 0.80$), respectively

often developing deep cracks when dried, with or without hyphal cords; aculei or teeth single or fused at base, with reddish brown bristles emerging from sides and apices; hyphal system monomitic with nodose-septate generative hyphae, agglutinated; single or fascicles of fusiform to cylindrical terminal hyphae covered with yellowish brown, mucilaginous matter or adherent crystalline material, projecting through hymenium and at aculeal apices (Fig. 4c); basidia narrowly clavate, basally clamped, 4-sterigmate; basidiospores ellipsoid to cylindrical, walls hyaline, slightly thickened, distinct, smooth, acyanophilous, not reacting in Mezler's reagent.

Generic type: *Noblesia crocea* (Schwein.) Nakasone.

Etymology: For Mildred K. Nobles (1903–1993), Canadian mycologist who developed the “Species code” for the characterization and identification of wood-decay fungi in culture.

Remarks. *Noblesia* is a small genus characterized by yellow, orange, or brown basidiomes with a ceraceous texture

that darken in KOH, fascicles of hyphae encased in yellowish brown mucilaginous material, narrowly clavate basidia, and small, ellipsoid basidiospores with hyaline, slightly thickened, smooth walls. Two species, with limited distribution and restricted host preferences, are accepted in the genus. Although *P. fuscotuberculata* was paired with *P. hydnoidea* (= *N. crocea*) in phylogenetic analyses by Huang and Zhao (2020, fig. 2), they are not considered congeneric since the former taxon lacks the brightly colored basidiomes and fasciculate hyphae encased by mucilaginous materials characteristic of both *Noblesia* species. Additionally, ITS sequences of *P. fuscotuberculata* are only 85% identical to *P. hydnoidea* (= *N. crocea*) as calculated from a BLAST® query (data not shown).

Morphologically, *Noblesia* and *Phlebia* s.s. share ceraceous basidiomes, clamped generative hyphae, agglutinated subicular tissue, and clavate basidia. In contrast, cultures of *N. crocea* (as *P. hydnoidea*) grew very slowly on malt

extract agar and gallic and tannic acid agars compared to the rapid growth by *Phlebia* s.s. (Nakasone 1990). Phylogenetic analyses place *Noblesia* in the *Merulius* clade, composed of morphologically diverse and distantly related taxa, that is distinct from the *Phlebia* clade (Fig. 3) and the *Sarcodontia-Crustodontia* lineage (Justo et al. 2017, fig. 5; Chen et al. 2018; Shen et al. 2018, fig. 2). Although Zmitrovich (2018) transferred *P. hydnoidea* to *Merulius* Fr., there is scant evidence that they are congeneric with respect to morphology and phylogeny. For example, effused to effused-reflexed, imbricate basidiomes with tomentose to hirsute abhymenial surface and pitted hymenophore of *M. tremellosus*, the generic type of *Merulius*, are unlike the effused, tuberculate to hydneous basidiomes in *Noblesia*. In addition, *M. tremellosus* lacks fasciculate hyphae (Fig. 4c) found in *Noblesia*, although they share monomitic hyphal systems with clamped generative hyphae that are coated with mucilaginous material, narrowly clavate basidia, and small, cylindrical to ellipsoid basidiospores. Finally, ITS sequences of *M. tremellosus* and *P. hydnoidea* are only 87% identical by BLAST® query, suggesting that they are not congeneric (data not shown).

The generic status and placement of the other *Phlebia* species in the *Merulius* clade in Fig. 3 are unresolved and beyond the scope of our study. Justo et al. (2017, figs. 4–5) showed that species of *Phlebia* are distributed throughout the *Meruliaceae* based on phylogenetic analyses of three loci. Future phylogenetic studies must include more taxa and sequence data from additional loci to determine if *Phlebia* should be restricted to *P. radiata* and closely related species or expanded to encompass *Aurantiopileus*, *Aurantiporus*, *Pappia*, and other poroid taxa that are in the *Phlebia* clade.

Noblesia crocea (Schwein.) Nakasone, *comb. nov.* Figs. 4 a–c.

Mycobank# 839628.

≡ *Sistotrema croceum* Schwein., *Schriften der Naturforschenden Gesellschaft Leipzig* 1: 102. 1822. [basionym Mycobank# 202956].

≡ *Hydnum croceum* (Schwein.) Fr., *Elenchus Fungorum* (Greifswald) 1: 137. 1828. [Mycobank# 232212].

≡ *Hericium croceum* (Schwein.) Banker, *Memoirs Torrey Botanical Club* 12(2): 121. 1906. [Mycobank# 439922].

≡ *Odontia crocea* (Schwein.) Lloyd, *Mycological Writings* 4, Letter 53, p. 11. 1914. [Mycobank# 356899].

≡ *Sarcodontia crocea* (Schwein.) Kotl., *Česká Mykologie* 7(3): 117. 1953. [Mycobank# 305493].

= *Phlebia hydnoidea* Schwein., *Transactions American Philosophical Society* 4(2): 165. 1832. [Mycobank# 207657].

≡ *Gloeoradulum hydnoideum* (Schwein.) Lloyd, *Mycological Writings* 5. The genus *Radulum* p. 9. 1917. [Mycobank# 439895].

≡ *Radulum hydnoideum* (Schwein.) Lloyd, *Mycological Writings*. The genus *Radulum* 5: 9. 1917. [Mycobank# 440399]. nomen illegit., non *R. hydnoideum* (Pers.) P. Karsten 1882. [Mycobank# 440398].

≡ *Merulius hydnoideus* (Schwein.) Zmitr., *Folia Cryptogamica Petropolitana* 6: 101. 2018. [Mycobank# 827513].

= *Odontia lateritia* Berk. & M.A. Curtis, *Grevillea* 1(10): 147. 1873. [Mycobank# 232263].

Ecology and distribution. Saprobic on hardwood, especially *Castanea dentata*, occasionally on *Quercus* and *Pinus*. Reported throughout eastern U.S.A., as far west as Wisconsin.

Type specimens examined. U.S.A. ALABAMA: on *Quercus deject.*, Peter, Curtis 6084 (holotype of *O. lateritia* K(M) 255185). PENNSYLVANIA: Bethlehem, on rotten trunk, Schweinitz (holotype of *P. hydnoidea* PH 00064989; isotypes PH 00064988, BPI-Michener Collection).

Other specimens examined. U.S.A. GEORGIA: Rabun County, Chattahoochee National Forest, Warwoman Dell, on *Castanea dentata*, 8 Jul 1969, H.H. Burdsall, Jr., 1993 (CFMR). PENNSYLVANIA: Bethlehem, Schweinitz s.n. (PH 00062606, as *Hydnum croceum* #571).

Descriptions and illustrations. Lloyd (1917, fig. 978, as *Radulum hydnoideum*), Gilbertson (1965: 857, as *O. lateritia*), Ginns (1970: 242, as *P. hydnoidea*), Burdsall (1975: 83, as *P. hydnoidea*), Nakasone and Burdsall (1995: 345, as *P. hydnoidea*).

Remarks. Widely known in the literature as *P. hydnoidea*, *N. crocea* is characterized by teeth or spines composed of reddish-brown fascicles of terminal hyphae encased in mucilaginous material and small, ellipsoid basidiospores. It occurs almost exclusively on American chestnut in eastern United States. See the discussion below for a summary of the misapplication of the name *Sistotrema croceum* for *Sarcodontia setosa*. *Sarcodontia setosa* is the correct name for the well-known and striking species in Europe with long yellow spines and slightly thick-walled, broadly ellipsoid basidiospores that occurs typically on *Malus* and *Pyrus*.

For clarity, a complete nomenclatural history and taxonomic synonyms of *N. crocea* are presented above. The mistaken identity of *Sistotrema croceum* may have begun with Banker (1906: 121) who transferred it to *Hericium* and included *Hydnum schiedermayeri* Heufl. as a synonym, which in turn is a later synonym of *H. setosum* Pers. Because *S. croceum* has priority over *H. setosum*, Banker's synonymy was generally accepted. Kotlaba (1953) proposed the combination *Sarcodontia crocea*, and this name was used widely by most European and North American authors, e.g., Nikolajeva (1961: 176), Eriksson et al. (1981: 1275), Ginns and Lefebvre (1993: 138), Legon and Henrici (2005: 267), and Bernicchia and Gorjón (2010: 581). A few authors, however, such as Bourdot and Galzin (1928: 418), Cejpa (1928: 61–62), Donk (1931: 152), Miller (1933:

364), Miller and Boyle (1943: 40–41), Jülich and Stalpers (1980: 202), and Breitenbach and Kränzlin (1986: 168) used Persoon's name, *H. setosum*, for this taxon. Notably, Donk (1931), Miller (1933), and Miller and Boyle (1943) recognized that Banker's interpretation of *Hericium croceum* was synonymous with *H. setosum* but not *Sistotrema croceum*. Uniquely, Lloyd's (1914) concept of *S. croceum* is that of *Hydnophlebia chrysorhiza* (Eaton) Parmasto (Miller 1933: 364; Martin and Rogers 1958: 308; Burdsall 1985: 61).

The holotype of *S. croceum* from North Carolina in Schweinitz's herbarium is presumably lost or destroyed as reported by Banker (1906: 122) and Lloyd (1914). In 1824, Schweinitz possibly sent material of *S. croceum* to Fries (Shear and Stevens 1917: 202); the specimen at UPS, F-175321, is accepted as the holotype. Because the holotype cannot be borrowed, photographs of this specimen were sent by Dr. Åsa Kruys and show a basidiome that is similar that of *Hydnum croceum* #571 (PH00062606) from Bethlehem in Schweinitz's herbarium. The PH specimen is in fair condition with a degraded hymenium, although the characteristic fasciculate terminal hyphae in the spines are abundant and a few ellipsoid spores, 4×2 – $2.4 \mu\text{m}$, were observed. Banker (1912: 278) also examined this specimen and reported that it was conspecific with *Phlebia hydnoidea* [sic], which is a typographical error since he clearly meant *Phlebia hydnoidea*. A specimen of *Hydnum croceum* #571 was also examined by Berkeley and Curtis (1856: 217) who commented that it is “A well-marked species.”

Berkeley (1873: 147), Cooke (1891: 3), Cooke (1956: 401), Gilbertson (1965: 858), and Ginns (1970) among others proposed that *O. lateritia* and *P. hydnoidea* were conspecific. This was confirmed by Burdsall (1975: 285) and Nakasone and Burdsall (1995: 347) who examined isotypes and holotypes of both species, respectively. We confirm that *O. lateritia* and *P. hydnoidea* are conspecific with and later synonymys of *N. crocea*.

Noblesia femsjoensis (Litsch. & S. Lundell) Nakasone, *comb. nov.*

Mycobank# 839629.

≡ *Peniophora femsjoensis* Litsch. et S. Lundell, *Svensk Botanisk Tidskrift* 32: 290. 1938, as ‘*femsioensis*’ [basionym MycoBank# 374021].

≡ *Phlebia femsjoensis* (Litsch. et S. Lundell) J. Erikss. & Ryvarden, *Corticiaceae* North Europe 6: 1113. 1981, as ‘*femsioensis*’. [MycoBank# 116005].

Ecology and distribution. Saprobic on conifers. Rare, reported from Norway, Sweden, Finland, Estonia, France, Ukraine.

Specimen examined. FRANCE. MEURTHE-ET-MOSELLE: Neufmaison, forêt domaniale des Reclos, sur *Picea* ou *Abies*, 30 juin 2002, *G. Trichies* 02075 (CFMR).

Descriptions and illustrations. Eriksson et al. (1981: 1113–1114), Duhem and Trichies (2009), Kunttu et al. (2018, fig. 15).

Remarks. The transfer of *P. femsjoensis* to *Noblesia* is based solely on morphological criteria. This striking and rare species is characterized by a tuberculate hymenophore and a strigose margin with hyphal strands or cords. The fascicles of hyphae (or cystidia) in *N. femsjoensis* are encased in a yellowish-brown mucilaginous material as in *N. crocea*. Basidiomes of *N. femsjoensis* look somewhat like *P. radiata*, but they are easily distinguished when examined microscopically.

Phylogenetic and taxonomic studies in *Sarcodontia* (Meruliaceae, Polyporales)

Sequences from six samples of *Sarcodontia* from the USA and two from the Czech Republic are included in the *Sarcodontia* ITS + nrLSU dataset as well as seven taxa shown in previous studies to be in the same lineage (see Table 1, Chen and Cui 2014; Tomšovský 2016; Wu et al. 2016; Justo et al. 2017; Papp and Dima 2018; Huang and Zhou 2020; Huang et al. 2020; Liu and Yuan 2020). The outgroup taxa, *Scopuloides* spp., are in a sister clade to *Sarcodontia* (Floudas and Hibbett 2015). This dataset of the *Sarcodontia* group had an aligned length of 1615 characters, 685 for ITS and 930 for nrLSU. In the ML tree shown in Fig. 5, *Sarcodontia* was a weakly supported monophyletic clade that included three distinct taxa; however, in the BI analyses (tree not shown), *S. uda* was not included in this clade. Figure 5 shows that *Sarcodontia amplissima* from the USA and *S. setosa* from the Czech Republic are closely related sister species. There are three genera with poroid hymenophores in the *Sarcodontia* group—*Luteoporia* F. Wu, Jia J. Chen & S.H. He, *Phlebiporia* Kia J. Chen, B.K. Cui & Y.C. Dai, and *Odoria* V. Papp & Dima, with the latter occupying an ancestral or basal position.

The ML tree based on ITS + nrLSU sequences (Fig. 5) is consistent with previous phylogenetic studies utilizing three or more gene regions that place *Sarcodontia* within a clade that includes *Crustodontia chrysocreas*, *Phlebia* (*Sarcodontia*) *uda*, *Odoria alborubescens* (Bourdot & Galzin) V. Papp & Dima, and *Phlebiporia bubalina* Jia J. Chen, B.K. Cui & Y.C. Dai (Justo et al. 2017; Chen et al. 2018; Papp and Dima 2018).

The *Sarcodontia* group shown in Fig. 5 is a morphologically heterogeneous assemblage of taxa with ceraceous, yellow to brownish yellow (except vinaceous brown to black in *Phlebia nigrodontea* C.L. Zhao & R.X. Huang) basidiomes with diverse, hymenophores—poroid (*Phlebiporia*, *Luteoporia*, and *Odoria*), spinose (*Sarcodontia*), or smooth to odontoid (*Crustodontia*, *P. nigrodontea*, and

P. tongxiniana C.L. Zhao) that often turn red or darken in KOH. Most taxa in the *Sarcodontia* group have small basidia (< 25 µm long, except some *Sarcodontia* species) and, correspondingly, small basidiospores with thin, hyaline, and smooth walls (but distinctly thickened in some *Sarcodontia*). Primarily monomitic with clamped generative hyphae (but simple-septate in *P. bubalina*), some taxa also develop microbinding or quasi-binding hyphae, and cystidia are small, fusoid or capitate, < 25 µm long (but longer in *Sarcodontia*). Based on phylogenetic and morphologic data, the generic concept of *Sarcodontia* is restricted and emended to include three species. Comments on taxa excluded from *Sarcodontia* follow.

Sarcodontia Schulzer, Verhandlungen Zoologisch-Botanischen Gesellschaft Wien 16: 41. 1866. [MycBank# 18502], emended.

= *Oxydontia* L.W. Miller, Mycologia 25 (4): 294. 1933. [MycBank# 18168].

Basidiomes widely effused, ceraceous, yellow at first, sometimes darkening to brown or nearly black, often turning red or darkening in KOH; hymenophore denticulate to spinose, aculei up to 20 mm long, on vertical surfaces also developing from nodules. Hyphal system monomitic with clamped generative hyphae, dark yellow mucilaginous material found throughout context. Spine trama composed of parallel, thin- or thick-walled hyphae; tramal cystidia capped with mucilaginous matter. Hymenial cystidia abundant to scarce, fusiform. Basidia clavate, 4-sterigmate. Basidiospores cylindrical to broadly ellipsoid, up to 6 × 4 µm, walls hyaline, thin to slightly thickened, smooth, acyanophilous, negative in Melzer's reagent. Associated with a white-rot decay of hardwoods, sometimes on dead limbs of living trees.

Generic type: *Sarcodontia setosa* (Pers.) Donk [MycBank# 305495].

Remarks. *Sarcodontia* as defined here is a small genus of three taxa, *S. setosa*, the generic type, *S. amplissima*, and *S. uda*, based on morphologic and phylogenetic data. In contrast, Nikolajeva (1961), Spirin (2001), and Zmitrovich et al. (2006) took a broad approach to *Sarcodontia* and included taxa currently classified in *Mycoacia*, *Irpiciporus*, and *Spongipellis*; see discussion of taxa excluded from *Sarcodontia* below. Maintaining *S. uda* in *Phlebia* or *Mycoacia* is not upheld by phylogenetic analyses, whereas its placement in *Sarcodontia* is supported by multiple gene sequence analyses (see Justo et al. 2017, fig. 5; Chen et al. 2018) and weakly supported herein (Fig. 5), but not with ITS sequences alone (Tomšovský 2016). Significant morphological features shared by all three *Sarcodontia* species include basidiomes with ceraceous, yellow or brown spines, a monomitic hyphal system with clamped hyphae, dark yellow mucilaginous material throughout the context, and terminal hyphae

(tramal cystidia) in the spines or subhymenium that are apically capped with mucilaginous material. Species accepted in *Sarcodontia* are discussed below followed by 13 taxa excluded from the genus.

Sarcodontia amplissima (Berk. & M.A. Curtis) Nakasone, *comb. nov.* Fig. 4d.

MycBank# 839630.

= *Hydnum amplissimum* Berk. & M.A. Curtis, Grevillea 1(7): 98. 1873. [basionym MycoBank# 144179].

= *Hydnum subvelutinum* Berk. & M.A. Curtis, Grevillea 1(7): 98. 1873. [MycBank# 209185].

= *Hydnum earleanum* Sumst., Torreya 4: 59. 1904. [MycBank# 249273].

Basidiomes resupinate, adnate, becoming widely effused, up to 100 × 15 cm wide, up to 3 mm thick between spines, membranous to ceraceous, spinose, rarely red in KOH, with a pungent odor; hymenophore composed of pendent spines 4–11 mm long, up to 0.5 mm diam., 2–3 per mm, often developed from tubercular nodules 2–10 mm thick, 0.5–2 cm wide, at first single, terete, slender, narrowly conical, often slightly enlarged at pubescent base, later partially or fully fused along length, apices often free, entire to fimbriate, acute, often brittle and breaking off when dried, cream-colored, golden yellow, pale orange (5A3), or light orange (5A4) at first, darkening on drying to brownish orange (6C5), brown [6E(6–7)], light brown [(6D(4–6), (7D5)], often with a glaucous cast, typically a lighter brown at apices, cross-section reveals a dark brown central core surrounded by light-colored outer rim; margin distinct, adnate, even, abrupt, thin, smooth to odontoid, up to 2 mm wide, grayish orange (6B5) to brownish orange (6C7), edges appressed, fimbriate; context fibrous, pale orange (5A3).

Hyphal system monomitic with clamped, generative hyphae. Spines composed of a core of parallel, somewhat agglutinated hyphae and tramal cystidia (appearing as slightly inflated terminal end-cells) and encased in brownish yellow mucilaginous material, then surrounded by subhymenial and hymenial layers, at apex hyphae undifferentiated; tramal hyphae 3–5 µm diam., clamped, rarely branched, walls hyaline, thin to 2 µm thick, smooth or lightly to heavily coated with brownish yellow mucilaginous material; tramal cystidia embedded, sometimes curving into hymenium, cylindrical to slightly inflated with a mucilaginous cap, 7–11 µm diam. including cap. Subiculum up to 3 mm thick, a non-agglutinated tissue of hyphae arranged parallel to substrate; subicular hyphae 3.5–9 µm diam., clamped, sparsely branched, sometimes with H-connections, long-celled, walls hyaline, thick-walled, up to 3.5 µm thick, smooth, occasionally roughened. Subhymenium in spines thickening, up to 100 µm thick, a dense tissue of partially agglutinated, short-celled, indistinct hyphae and embedded tramal cystidia; subhymenial hyphae 3–5 µm diam., clamped, much branched,

walls hyaline, thin; tramal cystidia as described above. Hymenium composed of cystidia and basidia. Cystidia of two types: (a) inconspicuous, cylindrical to subfusiform, $18\text{--}30 \times 4.5\text{--}5.5 \mu\text{m}$, clamped at base, embedded but occasionally protruding up to $15 \mu\text{m}$, walls hyaline, thin, smooth, sometimes absent; (b) cylindrical to clavate and capped with brownish yellow, mucilaginous material, $15\text{--}55 \times 6\text{--}9 \mu\text{m}$ without cap, $9\text{--}13 \mu\text{m}$ wide with cap, clamped at base, walls hyaline, thin, smooth. Basidia clavate, $25\text{--}42 \times 5.5\text{--}6.5(7) \mu\text{m}$, clamped at base, 4-sterigmate, walls hyaline, thin, smooth. Basidiospores broadly ellipsoid, often slightly tapering to apiculus, $(4.2)4.5\text{--}5.5(5.8) \times (3)3.2\text{--}3.8(4) \mu\text{m}$, average $(127/4) 4.9\text{--}5.2 \times 3.4\text{--}3.6 \mu\text{m}$, $Q = 1.4$, often with a single, large oil-like droplet, walls hyaline, thin to distinctly thickened, smooth, acyanophilous, not reacting in Melzer's reagent.

Ecology and distribution. Associated with a white rot; saprobic on various hardwoods, rarely on conifers. Reported from midwestern and eastern North America.

Descriptions and illustrations. Banker (1906: 121, as *Hericium croceum*), Miller (1933: 366, as *Oxydontia setosa*), Miller and Boyle (1943: 40–41, as *Mycoacia setosa*); Sumstine (1904, as *Hydnum earleanum*).

Type specimens examined. USA. MASSACHUSETTS: [on dying sour cherry (*Cerasus*) tree], Sprague 297, Curtis 5323 (lectotype of *H. amplissimum* K: K(M)264476, isolectotypes FH: HUH 00547930, UVMVT 302881); PENNS[YLVA]NIA, [Curtis] 6010 (holotype of *H. subvelutinum* K(M)264758); Armstrong County, Mud Lick Hollow, on decorticated log (*Ostrya virginiana*?), July 1903, D.R. Sumstine (isotypes of *H. earleanum* NCU-F-0012287, LSU: LSU 00135467).

Other specimens examined. USA. ILLINOIS: Winnebago County, SW of Rockford, Severson Dells Environmental Education Center, on branch of *Acer* sp., 9 Sep 1990, T. Volk (CFMR: FP-102436); INDIANA: Brown County State Park, Bloomington, on *Quercus* log, 23 Aug 1958, R.W. Davidson (CFMR: FP-105238); MARYLAND: Prince George's County, Beltsville, BPI cabin woods, downed hardwood, 2 Nov 1955, H.H. McKay (CFMR: FP-104176); MINNESOTA: Anoka/Isanti County, East Bethel, University Minnesota Cedar Creek Ecosystem Science Reserve, on decorticated *Quercus* sp., 20 Sep 2014, S.H. He 2120 (CFMR); NEW YORK: Ulster County, Ashokan, on hardwood, 10 Sep 1972, J.L. Lowe 15223 (CFMR); VERMONT: Windsor County, Norwich, on hemlock, 1 Dec 1977, H.E. Bigelow (CFMR: FP-101677); WISCONSIN: Dane County, Black Earth, 9350 Union Valley Road, on *Malus* sp., 24 Sep 1989, H.H. Burdsall, Jr. 12886 (CFMR); Columbia County, Leeds Township, Arlington Experimental Farm, on *Malus sylvestris*, 17 Sep 1984, K.K. Nakasone (CFMR: FP-101997).

Remarks. *Sarcodontia amplissima* is a striking species developing long, robust, golden yellow spines on hardwoods throughout eastern and central North America. It is like its European sister, *S. setosa*, in most morphological aspects except for the development of mucilaginous capped tramal cystidia and absence of thick-walled hyphae (sclerocysts). Persistent, brownish yellow, mucilaginous material were observed embedded throughout the spine trama, subiculum, and subhymenium. Phylogenetically, *S. amplissima* and *S. setosa* are paired on a long branch (Fig. 5), and their ITS sequences are 93% similar.

In North America, *S. amplissima* was typically reported as *H. setosum*, *M. setosa*, *H. schiedermayeri*, or *Sarcodontia crocea*. Miller (1933: 366) and Miller and Boyle (1943: 41) placed *H. earleanum* in synonymy with *H. setosum sens. auct. plur.* Later, Gilbertson (1965) examined types of *H. amplissimum* and *H. subvelutinum* and reported that they were synonymous with *H. setosum sens. auct. plur.* We examined type specimens of *H. earleanum*, *H. amplissimum*, and *H. subvelutinum* and confirm that they are conspecific. *Hydnum amplissimum* and *H. subvelutinum* were published on the same page, and the former is chosen to represent the species because lectotype materials are in excellent condition and readily available from several herbaria whereas type material of the latter is sparse and fragmentary. Gilbertson (1965: 865) noted that the collection number No. 6012 for *H. subvelutinum* given in the protologue is wrong, for on the type packets at K and FH the number is 6010.

Sarcodontia setosa (Pers.) Donk, Mycologia 44 (2): 262. 1952. [MycoBank# 305495].

= *Hydnum setosum* Pers., Mycologia Europaea 2: 213. 1825. [MycoBank# 224654].

= *Hydnum luteocarneum* Secr., Mycographie Suisse 2: 528. 1833. nomen invalid. [MycoBank# 201704].

= *Sarcodontia mali* Schulzer, Verhandlungen Zoologisch-Botanischen Gesellschaft Wien 16: 41. 1866. [MycoBank# 432092].

= *Hydnum schiedermayeri* Heufler, Oesterreichische Botanische Zeitschrift 20(2): 33. 1870. [MycoBank# 216321].

= *Kneiffia setigera* var. *pomicola* Schulzer, Verhandlungen Zoologisch-Botanischen Gesellschaft Wien 24: 293. 1874. [MycoBank# 494005].

= *Hydnum foetidum* Velen., České Houby 4–5: 744. 1922. nom. illegit. [MycoBank# 265163] non *H. foetidum* Rabenh. 1844. [MycoBank# 473486].

Misapplied name: *Mycoacia squalina* sensu M.P. Christiansen, Dansk botanisk Arkiv 19(2): 177. 1960.

Basidiomes similar to *S. amplissima* except as follows: (1) context light yellow (4A4) to grayish yellow (4B4) with a distinct light green tint and a granular appearance

with a waxy texture; (2) subiculum with sclerified hyphae 3–6(12) μm diam., moderately branched, walls up to 3 μm thick, acyanophilous; (4) subiculum from tubercular structures supporting spines with light colored areas composed of densely packed, irregularly inflated sclerocysts, up to 40 μm diam., walls hyaline, up to 10 μm thick; (4) tramal cystidia absent; (5) hymenial cystidia absent. Basidiospores ellipsoid to broadly ellipsoid, slightly tapering to apiculus, (4.5)5–5.5(6) \times 3.5–4.5 μm , Q range = (1.1)1.3–1.5, average (92/3) 5–5.3 \times 3.6–4 μm , Q = 1.3–1.4, often with a single, large oil-like droplet, walls hyaline, thin to distinctly thickened, smooth, acyanophilous, not reacting in Melzer's reagent.

Ecology and distribution. Associated with a white-rot decay. Rare, on trunks and dead branches of old, living apple trees, also *Pyrus*, *Quercus* and other hardwoods throughout Europe.

Type specimens examined. FRANCE. In Gallia, prope Rouen, inventum in trunco pomaceo a Behéré, (neotype of *H. setosum* from Herb. Persoon L0111101, No. 910.263–896 designated herein, isoneotype L0111100, No. 910.263–891).

Other specimens examined. CZECH REPUBLIC. SOUTH MORAVIA. Brno, Líšeň, N 49°12' E 16°41', on *Malus*, 25 Jul 2009, A. Vágnor (BRNM 721609); Hodonin, Nechvalin, N 49°03' E 17°04', on *Malus*, 26 Jul 2012, R. Maňák (BRNM 768410). FRANCE. Gallia (from Herb. Persoon L 0111168 910.262–633). GERMANY. SAXONY: Lohmen Rathewalde, on living stem of *Fagus sylvatica*, 28 Sep 2016, *H. Wawrok* (Herb. Dämmrich: Beleg-Nr 11274, CFMR); Zwickau Muldeufer, on *Malus* stem on ground, 15 Sep 2002, *F. Fischer* (Herb. Dämmrich: Beleg-Nr 6460, CFMR); Thuringia, Münchenbernsdorf, on living stem of *Malus* sp., 13 Aug 1994, A. Vesper (Herb. Dämmrich Beleg-Nr 7326, CFMR). LIECHTENSTEIN. Vaduz, on *Malus* sp., 5 Oct 1995, *F. Kotlaba* (Herb. E. Martini 4044, CFMR).

Descriptions and illustrations (as *S. crocea* except as noted). Kotlaba (1953), Nikolajeva (1961: 176–178), Jossierand (1969, as *S. setosa*), Eriksson et al. (1981: 1272, 1274–1276), Breitenbach and Kränzlin (1986: 168, as *S. setosa*), Kotiranta and Saarenoksa (2000: 39–41), Læssøe (2004), Szczepkowski (2010).

Remarks. *Sarcodontia setosa* is readily identified in the field on old apple trees because of its striking, bright yellow basidiomes with long, straight spines and strong odor. The irregularly inflated, thick-walled hyphae in the subiculum are characteristic for this species but is not always included in descriptions; Jossierand (1969) introduced the term sclerocysts for these unique structures. In specimens with well-developed tubercular swellings supporting spines, the sclerocysts sometimes form dense aggregates of light-colored nodules that are embedded in the subiculum and easily observed with a $\times 10$ lens. *Sarcodontia setosa* is included

in the Red List of Threatened Species of some European countries; see Szczepkowski (2010) for a summary. He also reported many new locations of *S. setosa* in Poland, studied its decay capability in the laboratory, and included a comprehensive literature review (Szczepkowski 2010).

In the literature, this taxon is often reported as *Sarcodontia crocea* because of a mistaken identity of *Sistotrema croceum*; see discussion of *Noblesia crocea* above. The synonymy above is compiled from Bresadola (1897: 94), Cejp (1928: 61–62), Donk (1952), and Kotlaba (1953). Hansen and Knudsen (1997: 174) reported that Christianesen's (1960: 177) concept of *M. squalina* is that of *S. setosa*. For a complete synonymy of *S. setosa*, see MycoBank and Index Fungorum.

There are three specimens of *H. setosum* from France in Persoon's Herbarium at L that are possible neotypes. Specimen L0111101, the designated neotype, is probably the best preserved, for although contaminated by a conidial species with echinulate spores, it has some yellow-pigmented areas that darken in KOH, and numerous, typical, ellipsoid basidiospores, (10/1) 5.4 \pm 0.3 \times 4 \pm 0.3 μm , Q = 1.4 \pm 0.1. The hymenium is degraded; no basidia were seen, but clamped hyphae in the spine trama were observed.

Sarcodontia uda (Fr.) Nikol., Flora plantarum cryptogamarum URSS. Fungi. Familia Hydnaceae 6(2): 182. 1961. [MycoBank# 283257].

\equiv *Hydnum udum* Fr., Systema Mycologicum 1: 422. 1821. [MycoBank# 169941].

\equiv *Mycoacia uda* (Fr.) Donk, Mededelingen van de Nederlandse Mycologische Vereeniging 18–20: 151. 1931. [MycoBank# 255241].

\equiv *Phlebia uda* (Fr.) Nakasone, Sydowia 49: 72. 1997. [MycoBank# 437329].

\equiv *Hydnum sulphureum* Schwein., Schriften der Naturforschenden Gesellschaft zu Leipzig 1: 104. 1822. [MycoBank# 205370].

\equiv *Odontia sulphurea* (Schwein.) Rea, British Basidiomycetae p. 649. 1922. [MycoBank# 279543].

Ecology and distribution. Associated with a white-rot decay; saprobic on hardwoods, rarely on conifers. Reported from North America, Europe, central Asia, and northern Africa.

Type specimen examined. USA, [North Carolina], Salem (PH: PH00062650, designated neotype of *H. sulphureum* herein).

Descriptions and illustrations (as *Mycoacia* or *Phlebia uda*). Bernicchia and Gorjón (2010: 538), Breitenbach and Kränzlin (1986: 169), Eriksson and Ryvarden (1976: 884), Nakasone (1997).

Remarks. *Sarcodontia uda* differs from the other taxa in the genus by its much shorter spines, up to 3 mm long that turn red in KOH, and ellipsoid, thin-walled basidiospores. Although

better known in the literature as *Phlebia uda* or *Mycoacia uda*, *S. uda* belongs to a separate lineage from both *Phlebia radiata* and *Mycoacia fuscoatra*, types of *Phlebia* and *Mycoacia*, respectively (Justo et al. 2017, fig. 5; Chen et al. 2018).

The holotype of *Hydnum sulphureum* is probably lost or destroyed, but there is a specimen in Schweinitz's herbarium at PH labeled "Salem, Syn. # 555." This specimen is designated neotype and was likely seen by Schweinitz (1832: 162). The neotype is typical of *S. uda* with a light brown, subceraceous basidiome with a few ellipsoid basidiospores, $5.5 \times 2.5\text{--}3 \mu\text{m}$, although basidia and cystidia were not observed. The spines were mostly broken, but in protected areas, slender spines with acute apices, $400 \times 160 \mu\text{m}$, 4–5 per mm, were observed.

Taxa excluded from *Sarcodontia* — accepted names are in boldface.

Sarcodontia bulliardii Nikol., Flora plantarum cryptogamarum URSS. Fungi. Familia *Hydnaceae* 6(2): 181. 1961. Nomen superfluum, nomen invalid. [MycoBank# 338812].

Remarks. From Nikolajeva's description, the basidiome is reminiscent of *Kneiffiella barba-jovis* (Bull.) P. Karst. whereas the basidiospores are similar to *Mycoacia aurea* (Fr.) J. Erikss. & Ryvarde. Jülich and Stalpers (1980) placed *S. bulliardii* in synonymy under *M. aurea*. Nomenclaturally, *S. bulliardii* is considered a superfluous name for *Hydnum barba-jovis* Fries 1821 (Burdshall and Larsen 1983) and invalidly published for lack of a Latin diagnosis, (Index Fungorum, accessed 10 Aug 2020).

Sarcodontia copelandii (Pat.) Imazeki, Coloured Illustrations fungi Japan II: 127. 1965. [MycoBank# 338813].

≡ *Radulomyces copelandii* (Pat.) Hjortstam & Spooner [MycoBank# 132794].

Sarcodontia delectans (Peck) Spirin, Mycena 1(1): 68. 2001. [MycoBank# 510515].

Remarks. This taxon is better known as *Spongipellis delectans* (Peck) Murrill. Phylogenetic studies by Tomšovský (2012, 2016) and Westphalen et al. (2016), however, show that *S. delectans*, *Spongipellis unicolor* (Fr.) Murrill, and *Spongipellis litschaueri* Lohwag form a clade in the *Cerrenaceae* (*Polyporales*) that is distantly related to *Sarcodontia* in the *Meruliaceae* and *Spongipellis spumeus* (Sowerby) Pat, the type of *Spongipellis*.

Sarcodontia denticulata (Pers.) Nikol., Flora plantarum cryptogamarum URSS. Fungi. Familia *Hydnaceae* 6(2): 185. 1961 (sensu Bourdot and Galzin 1914). [MycoBank# 338814].

≡ *Acia uda* subsp. *denticulata* (Pers.) Bourdot & Galzin, Bulletin Société Mycologique France 30(2): 255. 1914. [MycoBank# 439647].

= *Resinicium bisporum* Stalpers, Persoonia 9(1): 145. 1976. [MycoBank# 322402].

≡ *Mycoaciella bispora* (Stalpers) J. Erikss. & Ryvarde. [MycoBank# 318043].

Remarks. The type of *Hydnum denticulatum* Pers. is *Steccherinum ochraceum* (Pers. ex J.F. Gmel.) Gray (Maas Geesteranus 1974: 531). However, Bourdot and Galzin's subspecies *denticulata* (1914: 255, 1928: 415) is a different species as explained by Stalpers (1976) and Eriksson et al. (1978: 900–903). Some authors, such as Cejp (1928: 60), Pilát (1926), and Nikolajeva (1961), followed Bourdot and Galzin's interpretation, and Stalpers (1976) named this taxon *R. bisporum*. Although phylogenetic analyses place *M. bispora* in the *Meruliaceae*, its relationship to *Sarcodontia* sensu stricto, *Mycoacia nothofagi* (G. Cunn.) Ryvarde, and *M. aurea* remains unsettled (Larsson et al. 2004; Moreno et al. 2011). Morphologically, *M. bispora* is easily distinguished from *Sarcodontia* because it has a dimitic hyphal system with skeletal hyphae in the aculei and lacks dark yellow mucilaginous material in the context and capping the tramal cystidia.

Sarcodontia flava (Cejp) Nikol., Flora plantarum cryptogamarum URSS. Fungi. Familia *Hydnaceae* 6(2): 189. 1961. [MycoBank# 338815].

≡ *Acia flava* Cejp, Fauna Flora Cechoslov. II *Hydnaceae*: 50. 1928. [MycoBank# 264995].

= *Xylodon quercinus* (Pers.) Gray [MycoBank# 505180].

Remarks. The holotype of *A. flava* from PRC (PRC 3985, [Czech Republic], Roblín, ad truncus *Carpinus betulinus*, IV 1927, legit Cejp) was examined and identified as *X. quercinus*. It has spines 1–2 mm long, subulate or subcapitate cystidia apically capped with a golden yellow exudate, and cylindrical basidiospores, average $(33/1) 6.7 \pm 0.5 \times 2.9 \pm 0.1 \mu\text{m}$, $Q = 2.3 \pm 0.2$. The basidia observed were 16–17 μm long and much shorter than reported by Eriksson and Ryvarde (1976: 669) and Langer (1994: 193). Jülich and Stalpers (1980: 157) suggested that *A. flava* was a possible synonym of *Mycoacia uda*. A label in the type packet left by E. Parmasto, dated 5 Mar 1981, identified this specimen as *Hyphodontia nesporii* (Bres.) J. Erikss. & Hjortstam. This species, however, has short aculei up to 0.5 mm long, lacks subulate cystidia, and has smaller basidiospores, $4.5\text{--}6 \times 2\text{--}2.5(3) \mu\text{m}$ (Eriksson and Ryvarde 1976: 653; Langer 1994: 156).

Sarcodontia fragilissima (Berk. & M.A. Curtis) Nikol., Flora plantarum cryptogamarum URSS. Fungi. Familia *Hydnaceae* 6(2): 184. 1961. [MycoBank# 338816].

≡ *Hydnum fragilissimum* Berk. & M.A. Curtis, Grevillea 1(7): 100. 1873. [MycoBank# 176884].

= *Hydnophlebia chrysorhiza* (Eaton) Parmasto [MycoBank# 3321800].

Remarks. *Hydnum fragilissimum* is accepted as a later synonym of *H. chrysorhiza* (Martin and Rogers 1958; Burdall 1985: 57); see MycoBank and Index Fungorum for other heterotypic synonyms of *H. chrysorhiza*. Phylogenetically, *Hydnophlebia* and *Sarcodontia* are in the same family, the *Meruliaceae*, but distantly related (Justo et al. 2017; Chen et al. 2018; Liu et al. 2020).

Sarcodontia isidioides (Berk.) D.A. Reid, Kew Bulletin 10(4): 641. 1956. [1955]. [MycoBank# 305494].

≡ *Hydnum isidioides* Berk., London Journal Botany 4: 58. 1845. [MycoBank# 195851].

= *Dentipellicula leptodon* (Mont.) Y.C. Dai & L.W. Zhou [MycoBank# 564154].

Remarks. Reid (1956) and Stalpers (1976) described gloeocystidia and small, amyloid basidiospores in *H. isidioides*. After examining type specimens, Ginns (1986) placed *H. isidioides*, from Australia, in synonymy with *H. leptodon*, from Chile.

Sarcodontia pachyodon (Pers.) Spirin, Mycena 1: 68. 2001. [MycoBank# 510516].

≡ *Irpiciporus pachyodon* (Pers.) Kotl. & Pouzar [MycoBank# 299102].

Sarcodontia sibirica (Pilát) Nikol., Flora plantarum cryptogamarum URSS. Fungi. Familia *Hydnaceae* 6(2): 178. 1961. [MycoBank# 338817].

≡ *Acia sibirica* Pilát, Bulletin Société Mycologique France 51(3–4): 396. 1936 [basionym MycoBank# 254697].

≡ *Hyalodon sibirica* (Pilát) Nakasone, *comb. nov.* [MycoBank# 839645].

Remarks. When describing the type of *A. sibirica*, Ryvar den (1976) observed a resupinate basidiome with an odontoid hymenophore and a loose, finely floccose subiculum 0.5 mm thick, longitudinally septate basidia, and globose to subglobose basidiospores, 3–5 µm diam. He placed it in synonymy with *Protodontia piceicola* (Kühner ex Bourdot) G.W. Martin (≡ *Hyalodon piceicola* (Kühner ex Bourdot) Malysheva & Spirin). Although this synonymy was accepted by Roberts (1998: 245), we disagree because *H. piceicola* has a very thin subiculum that is nearly invisible when dried and ellipsoid basidiospores, 4–6 × 3.5–4.5 µm (Bourdot 1932; Breitenbach and Kränzlin 1986: 60–61). The other species in *Hyalodon*, *H. antui* Spirin & V. Malysheva, from Jilin Province, China, on *Abies*, has a well-developed subiculum and broadly ellipsoid to ellipsoid basidiospores, 5.4–6.9 × 4.2–5.2 µm (Malysheva et al. 2018). We propose that *A. sibirica* is congeneric with *H. piceicola* and *H. antui* but easily distinguished by its smaller, globose to subglobose basidiospores and thick, well-developed subiculum. Recently, Zmitrovich et al. (2017) included *A. sibirica* as a synonym of *Radulomyces copelandii*, but this is clearly incorrect.

Sarcodontia spumea (Sowerby) Spirin, Mycena 1: 68. 2001. [MycoBank# 510518].

≡ *Boletus spumeus* Sowerby, Coloured Figures English Fungi or Mushrooms 2: 89, pl. 211. 1799. [MycoBank# 221111].

≡ *Spongipellis spumeus* (Sowerby) Pat. [MycoBank# 414488].

Remarks. *Boletus spumeus*, the generic type of *Spongipellis*, has been placed in eight different genera by various authors; see MycoBank and Index Fungorum. As discussed above, molecular phylogenetic analyses place this taxon basally in the *Meripliaceae* (Kotiranta et al. 2017) and distant from *S. unicolor*, *S. delectans*, and *S. litschaueri* that cluster together in the *Cerrenaceae* (Tomšovský 2012; Justo et al. 2017).

Sarcodontia stenodon (Pers.) Nikol., Flora plantarum cryptogamarum URSS. Fungi. Familia *Hydnaceae* 6(2): 178. 1961. [MycoBank# 338818].

≡ *Hydnum membranaceum* **stenodon* Pers., Mycologia Europaea 2: 188. 1825. [MycoBank# 439960].

= *Mycoacia aurea* (Fr.) J. Erikss. & Ryvar den [MycoBank# 318040].

Remarks. Eriksson and Ryvar den (1976: 877–878) and Nakasone (1997) placed Persoon's taxon in synonymy under *M. aurea*. In the *Meruliaceae*, *M. aurea* and *M. fuscoatra* Donk, type of *Mycoacia*, cluster together in a clade that is distinct from a related lineage containing *Sarcodontia* s.s. and *C. chrysocreas* (Justo et al. 2017, fig. 5).

Sarcodontia subochracea (Alb. & Schwein.) Nikol., Flora plantarum cryptogamarum URSS. Fungi. Familia *Hydnaceae* 6(2): 187. 1961. [MycoBank# 338819].

≡ *Grandinia subochracea* Bres., Hedwigia 33: 206. 1894. [MycoBank# 449591].

≡ *Phlebia subochracea* (Bres.) J. Erikss. & Ryvar den, *Corticaceae* North Europe 4: 873 1976. [MycoBank# 319881].

Remarks. In the phylogenetic analyses of Justo et al. (2017, fig. 5), *P. subochracea* is in a clade with *Phlebia ludoviciana* (Burt) Nakasone & Burds. and distantly related to species in the *Sarcodontia* s.s. and the *Phlebia* s.s. clades. Currently placed in *Phlebia*, the final generic placement of *P. subochracea* is yet to be determined.

Sarcodontia unicolor (Fr.) Zmitr. & Spirin, Mycena 6: 25. 2006. [MycoBank# 504919].

≡ *Spongipellis unicolor* (Fr.) Murrill, North American Flora 9 (1): 37. 1907 [MycoBank# 446081].

Remarks. This taxon is better known as *Spongipellis unicolor*; see discussion under *Sarcodontia delectans* above.

Discussion

In this paper, we demonstrate how taxonomy of fungi benefits from combination of phylogenetic analyses and careful morphological studies. Specifically, ITS and nrLSU sequences were used to distinguish species in *Radulomyces* and *Sarcodontia* then confirmed by morphology. We show the importance of studying mature basidiomes even with crust fungi. In this example, *R. paumanokensis* is revealed to be a young, developing basidiome of *R. copelandii* by ITS sequence analyses. Phylogenetic analyses confirm that *R. copelandii* is widely distributed from East Asia to eastern USA and is distinct from the morphologically similar *R. licentii* from temperate East Asia. ITS sequences readily distinguished between *Sarcodontia setosa* and *S. amplissima* that are separated by geography but similar in overall basidiome morphology and microscopic features except that sclerocysts are found only in the former. Finally, the erroneous interpretation of *Sistotrema croceum* for over 100 years illustrates the importance of examination and verification of type specimens.

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Author contribution Karen Nakasone is responsible for the initial concept, manuscript draft, and specimen examinations. Beatriz Ortiz-Santana provided sequences, performed the phylogenetic analyses, prepared the figures, and made significant contributions to the manuscript. Shuang-Hui He contributed essential sequences, specimens, and photographs. The findings and conclusions in this paper are those of the authors and should not be construed to represent any official USDA or US Government determination or policy.

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Data Availability Datasets created and analyzed in this study were submitted to TREEBASE (Submission ID:28,338, 28,339, 28,341). Sequence data used herein were deposited in GenBank. Phylogenetic and morphologic results obtained for this study are included in this article. Specimens examined in this study were borrowed from institutional herbaria or fungaria and noted in the text.

Declarations

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

Conflict of interest The authors declare no competing interests.

References

- Banker HJ (1906) A contribution to a revision of the North American *Hydnaceae*. Mem Torrey Bot Club 12:99–194
- Banker HJ (1912) Type studies in the *Hydnaceae* — I. The Genus *Manina* Mycologia 4:271–278
- Berkeley MJ (1873) Notices of North American Fungi Grevillea 1:145–150
- Berkeley MJ, Curtis MA (1856) A commentary on the Synopsis Fungorum in America Boreali media degentium by L. D. de Schweinitz. J Acad Nat Sci Phila 3:205–224
- Bernicchia A, Gorjón SP (2010) *Corticaceae* s.l. Fungi Europaei no. 12. Alassio: Edizioni Candusso.
- Binder M, Larsson K-H, Matheny PB, Hibbett DS (2010) *Amylocorticiales* ord. nov. and *Jaapiales* ord. nov.: early diverging clades of *Agaricomycetidae* dominated by corticioid forms. Mycologia 102:865–880
- Boidin J, Gilles G, Huguenev R (1988) Réhabilitation du *Corticium rickii* Bres. (Basidiomycotina). Cryptogam Mycol 9:43–46
- Bourdot H (1932) Hyménomycètes nouveau ou peu connus. Bull Trimest Soc Mycol Fr 48:204–232
- Bourdot H, Galzin A (1914) Hyménomycètes de France (V. — Hydneés). Bull Trimest Soc Mycol Fr 30:243–280
- Bourdot H, Galzin A (1928) Hyménomycètes de France. Sceaux: Marcel Bry
- Brazee NJ, Lindner DL, D'Amato AW, Fraver FJA, Mladenoff DJ (2014) Disturbance and diversity of wood-inhabiting fungi: effects of canopy gaps and downed woody debris. Biodivers Conserv 23:2155–2172. <https://doi.org/10.1007/s10531-014-0710-x>
- Breitenbach J, Kränzlin F (1986) Fungi of Switzerland. Vol. 2. Non-gilled fungi. Lucerne: Verlag Mykologia
- Bresadola G (1897) Hymenomycetes Hungarici Kmetiani. Atti Dell'imperiale Regia Accademia Roveretana, Serie 3(3):66–120
- Burdsall Jr HH (1975) Taxonomic and distributional notes on *Corticaceae* (Homobasidiomycetes, *Aphyllorphorales*) of the Southern Appalachians. In: Parker BC, Roane MK, eds. Distributional History of the Biota of the Southern Appalachians. Part IV. Algae and fungi. Biogeography, Systematics, and Ecology. University Press of Virginia, Charlottesville. pp 265–286
- Burdsall HH Jr (1985) A contribution to the taxonomy of the genus *Phanerochaete* (*Corticaceae*, *Aphyllorphorales*). Mycol Mem 10:1–165
- Burdsall HH Jr, Larsen MJ (1983) On the recent proposal to conserve *Hyphodontia*. J Erikss against Kneiffiella Karst Mycotaxon 17:513–516
- Cejp K (1928) Monografie Hydnacei Republiky Československé. Fauna et Flora Čechoslovenica. 107 p. + 2 pl. (reprint)
- Chen J-J, Cui B-K (2014) *Phlebioporia bubalina* gen. et. sp. nov. (*Meruliaceae*, *Polyporales*) from southwest China with a preliminary phylogeny based on rDNA sequences. Mycol Prog 13:563–573. <https://doi.org/10.1007/s11557-013-0940-4>
- Chen C-C, Wu S-H, Chen CY (2018) *Hydnophanerochaete* and *Odonotofibula*, two new genera of phanerochaetoid fungi (*Polyporales*, *Basidiomycota*) from East Asia. MycoKeys 39:75–96. <https://doi.org/10.3897/mycokeys.39.28010>

- Christiansen MP (1960) Danish Resupinate Fungi. Part II Homobasidiomycetes Dansk Botanisk Arkiv 19:57–388
- Cooke MC (1891) Species of Hydnei. Additamenta to Saccardo's Sylloge Grevillea 20(93):1–4
- Cooke WB (1956) The genus *Phlebia*. Mycologia 48:386–405
- Cubeta MA, Echandi E, Abernethy T, Vilgalys R (1991) Characterization of anastomosis groups of binucleate *Rhizoctonia* species using restriction analysis of an amplified ribosomal RNA gene. Mol Plant Pathol 81:1395–1400
- Darriba D, Taboada GL, Doallo R, Posada D (2012) jModelTest 2: more models, new heuristics and parallel computing. Nat Methods 9:772. <https://doi.org/10.1038/nmeth.2109>
- Donk MA (1931) Revisie van de Nederlandse Heterobasidiomycetae en Homobasidiomycetae-Aphylllophoraceae. Mededeelingen Nederlandsche Mycologische Vereeniging 18–20:67–200
- Donk MA (1952) The status of the generic name *Oxydonia* L.W. Miller (“*Hydnaceae*”). Mycologia 44:262–263
- Duhem B, Trichies G (2009) *Phlebia femsioensis* un spectaculaire corticié découvert en France. Bull Trimest Soc Mycol Fr 125:183–195
- Eriksson J, Ryvarden L (1976) The *Corticiaceae* of North. Europe 4:547–886
- Eriksson J, Hjortstam K, Ryvarden L (1978) The *Corticiaceae* of North. Europe 5:887–1047
- Eriksson J, Hjortstam K, Ryvarden L (1981) The *Corticiaceae* of North. Europe 6:1048–1276
- Floudas D, Hibbett D (2015) Revisiting the taxonomy of *Phanerochaete* (*Polyporales*, *Basidiomycota*) using a four gene dataset and extensive ITS sampling. Fungal Biol 119:679–719. <https://doi.org/10.1016/j.funbio.2015.04.003>
- Furukawa H (1974) Taxonomic studies of the genus *Odontia* and its allied genera in Japan. Bulletin Government Forest Experiment Station 261:1–87 + 12 pl.
- Gardes M, Bruns TD (1993) ITS primers with enhanced specificity for basidiomycetes application to the identification of mycorrhizae and rusts. Mol Ecol 2:113–118
- Ghobad-Nejhad M, Hallenberg N (2012) Multiple evidence for recognition of *Phlebia tuberculata*, a more widespread segregate of *Phlebia livida* (*Polyporales*, *Basidiomycota*). Mycol Prog 11:27–35. <https://doi.org/10.1007/s11557-010-0722-1>
- Ghobad-Nejhad M, Kotiranta H (2007) Re-evaluation of *Radulomyces rickii* and notes on *Radulomyces* and *Phlebiella* (*Basidiomycota*). Mycotaxon 102:101–111
- Gilbertson RL (1965) Resupinate hydneous fungi of North America V. Type studies of species described by Berkeley and Curtis. Mycologia 57:845–871
- Ginns J (1970) The genus *Merulius* III. Species of *Merulius* and *Phlebia* proposed by Schweinitz and Peck. Mycologia 62:238–255
- Ginns J (1986) The genus *Dentipellis* (*Hericiaceae*). Windahlia 16:35–45
- Ginns J, Lefebvre MNL (1993) Lignicolous corticioid fungi (*Basidiomycota*) of North America. Mycol Mem 19:1–247
- Ginns J, Millman L (2011) Mysterious Asian beauty conquers eastern Massachusetts. Fungi 4:61–63
- Ginns J, Lindner DL, Baroni TJ, Ryvarden L (2010) *Aurantiopileus mayanensis* a new genus and species of polypore (*Polyporales*, *Basidiomycota*) from Belize with connections to existing Asian species. N Am Fungi 5:1–10. <https://doi.org/10.2509/naf2010.005.004>
- Gouy M, Guindon S, Gascuel O (2010) SeaView Version 4: a multiplatform graphical user interface for sequence alignment and phylogenetic tree building. Mol Biol Evol 27:221–224. <https://doi.org/10.1093/molbev/msp259>
- Guindon S, Gascuel O (2003) A simple, fast and accurate method to estimate large phylogenies by maximum-likelihood. Syst Biol 52:696–704. <https://doi.org/10.1080/10635150390235520>
- Hansen L, Knudsen H (1997) Nordic Macromycetes. Vol. 3. Heterobasidioid, aphyllloporoid and gasteromycetoid Basidiomycetes. Copenhagen: Nordsvamp
- Hjortstam K, Spooner BM, Oldridge SG (1990) Some *Aphyllloporales* and Heterobasidiomycetes from Sabah, Malaysia. Kew Bull 45:303–322
- Huang R-X, Zhao C-L (2020) Three new species of *Phlebia* (*Polyporales*, *Basidiomycota*) based on evidence from morphology and DNA sequence data. Mycol Prog 19:753–767. <https://doi.org/10.1007/s11557-020-01591-7>
- Huang R-X, Luo K-Y, Zhao CL (2020) *Phlebia nigrodontea* sp. nov. in *Meruliaceae* (*Polyporales*) with a black hymenial surface. Phytotaxa 458:195–206. <https://doi.org/10.11646/phytotaxa.458.3.2>
- Josserand M (1969) *Sarcodontia setosa* (Pers.) Donk, hydneacée à sclérocystes. Bull Mens Soc Linn Lyon 38:202–209
- Jülich W, Stalpers JA (1980) The resupinate non-poroid *Aphyllloporales* of the temperate northern hemisphere. Verhandelingen Koninklijke Nederlandse Akademie Van Wetenschappen, Afdeling Natuurkunde, Sectie 2(74):1–335
- Justo A, Miettinen O, Floudas D, Ortiz-Santana B, Sjökvist E, Lindner DL, Nakasone KK, Niemelä T, Larsson K-H, Ryvarden L, Hibbett DS (2017) A revised family-level classification of the *Polyporales* (*Basidiomycota*). Fungal Biol 121:798–824. <https://doi.org/10.1016/j.funbio.2017.05.010>
- Jyoti DGS (2014) *Radulodon indicus* sp. nov. (Agaricomycetes) from India. Synopsis Fungorum 32:38–40
- Kornerup A, Wanscher JH (1978) Methuen Handbook of Colour. Eyre Methuen, London
- Kotiranta H, Saarenoksa R (2000) Corticioid fungi (*Aphyllloporales*, *Basidiomycetes*) in Finland. Acta Bot Fenn 168:1–55
- Kotiranta H, Kulju M, Miettinen O (2017) *Caudicicola gracilis* (*Polyporales*, *Basidiomycota*), a new polypore species and genus from Finland. Ann Bot Fenn 54:159–167
- Kotlaba F (1953) Nebezpečný parazit jabloní — *Sarcodontia crocea* Schweinitz c. n. Česká Mykol 7:117–123
- Kunttu P, Juutilainen K, Helo T, Kulju M, Kekki T, Kotiranta H (2018) Updates to Finnish aphyllloporoid funga (*Basidiomycota*): new species and range extensions. Mycosphere 9:519–564. <https://doi.org/10.5943/mycosphere/9/3/7>
- Læssøe T (2004) Æblepig (*Sarcodontia crocea*) — nu fundet i Danmark. Svampe 49:40–42
- Langer E (1994) Die Gattung *Hyphodontia* John Eriksson. Bibl Mycol 154:1–298
- Larsson A (2014) AliView: a fast and lightweight alignment viewer and editor for large datasets. Bioinformatics 30:3276–3278. <https://doi.org/10.1093/bioinformatics/btu531>
- Larsson K-H, Larsson E, Kõljalg U (2004) High phylogenetic diversity among corticioid homobasidiomycetes. Mycol Res 108:983–1002
- Leal-Dutra CA, Griffith GW, Neves MA, McLaughlin DJ, McLaughlin EG, Clasen LA, Dentinger BTM (2020) Reclassification of *Pterulaceae* Corner (*Basidiomycota*: *Agaricales*) introducing the ant-associated genus *Myrmecopterula* gen. nov., *Phaeopterula* Henn. and the corticioid *Radulomycetaceae* fam. nov. IMA Fungus 11(2):1–24. <https://doi.org/10.1186/s43008-019-0022-6>
- Lebel T, Castellano MA, Beever RE (2015) Cryptic diversity in the sequestrate genus *Stephanospora* (*Stephanosporaceae*: *Agaricales*) in Australasia. Fungal Biol 119:201–228. <https://doi.org/10.1016/j.funbio.2014.12.007>
- Legon NW, Henrici A (2005) Checklist of the British and Irish Basidiomycota. Kew: Royal Botanic Gardens
- Liu Z-B, Yuan Y (2020) *Luteoportia citriniporia* sp. nov. (*Polyporales*, *Basidiomycota*), evidenced by morphological characters and phylogenetic analysis. Phytotaxa 461:31–39. <https://doi.org/10.11646/phytotaxa.461.1.4>

- Liu D-M, Xu Y-L, Yue, Li, Liu W-H, Ma, H-X, Huang M-R, He S-H (2020) Two new species of *Hydnophlebia* (Meruliaceae, Polyporales) from China based on morphological and molecular evidence. *Phytotaxa* 477:35–46. <https://doi.org/10.11646/phytotaxa.477.1.2>
- Lloyd CG (1914) Mycological notes of the Lloyd Library and Museum. Volume 4, Letter No. 53
- Lloyd GC (1917) Mycological notes of the Lloyd Library and Museum. Volume 5, The genus *Radulum*
- Maas Geesteranus RA (1974) Studies in the genera *Irpex* and *Steccherinum*. *Persoonia* 7:443–581
- Maekawa N (1993) Taxonomic study of Japanese *Corticaceae* (Aphyllophorales) I. *Rep Tottori Mycol Inst* 31:1–149
- Malysheva VF (2006) Notes on rare species of aphylloporoid fungi found in Zhiguli Nature Reserve (Samara Region, European Russia). *Karstenia* 46:25–33
- Malysheva V, Spirin V, Miettinen O, Motato-Vásquez V, Hernawati SJSS, Larsson KH (2018) Revision of *Protohydnum* (Auriculariales, Basidiomycota). *Mycol Prog* 17:805–814. <https://doi.org/10.1007/s11557-018-1393-6>
- Martin GW, Rogers DP (1958) On *Hydnum chrysothizum* Torrey. *Mycologia* 50:306–308
- Martini E (2016) *Radulomyces molaris*. Excerpts from Crusts and Jells no. 41:1–8. <https://www.aphyllo.net/home.php#excerpts>
- Mercado EM, Ortiz-Santana B (2018) Mountain pine beetle mutualist *Leptographium longiclavatum* presence in the southern Rocky Mountains during a record warm period. *Sydowia* 70:1–10. <https://doi.org/10.12905/0380.sydowia70-2018-0001>
- Miller LW (1933) The *Hydnaceae* of Iowa. I. The Genera *Grandinia* and *Oxydonta* *Mycologia* 25:356–368
- Miller LW, Boyle JS (1943) The *Hydnaceae* of Iowa. *Univ Iowa Stud Nat Hist* 18:1–92
- Moreno G, Blanco M-N, Checa J, Platas G, Peláez F (2011) Taxonomic and phylogenetic revision of three rare irpicoid species within the *Meruliaceae*. *Mycol Prog* 10:481–491. <https://doi.org/10.1007/s11557-010-0717-y>
- Nakasone KK (1990) Cultural studies and identification of wood-inhabiting Corticiaceae and selected Hymenomycetes from North America. *Mycologia Memoirs* 15:1–412
- Nakasone KK (1997) Studies in *Phlebia* — six species with teeth. *Sydowia* 49:49–79
- Nakasone KK (2001) Taxonomy of the genus *Radulodon*. *Harv Pap Bot* 6:163–177
- Nakasone KK, Burdals HH Jr (1995) *Phlebia* species from eastern and southeastern United States. *Mycotaxon* 54:335–359
- Natarajan K, Kolandavelu K (1997) The distribution of resupinate *Aphyllophorales* in Tamil Nadu, South India. In: Janardhanan KK, Rajendran C, Natarajan K, Hawksworth DL (eds) *Tropical Mycology*. Science Publishers Inc, Enfield, New Hampshire, pp 107–113
- Nikolajeva TL (1961) Flora plantarum cryptogamarum URSS. Familia *Hydnaceae*. Vol. VI, Fungi 2
- Oliariaga I, Huhtinen S, Læssøe T, Petersen JH, Hansen K (2020) Phylogenetic origins and family classification of typhuloid fungi, with emphasis on *Ceratellopsis*, *Macrotiophula* and *Typhula* (Basidiomycota). *Stud Mycol* 96:155–184. <https://doi.org/10.1016/j.simyco.2020.05.003>
- Papp V, Dima B (2018) New systematic position of *Aurantiporus alborubescens* (Meruliaceae, Basidiomycota), a threatened old-growth forest polypore. *Mycol Prog* 17:319–332. <https://doi.org/10.1007/s11557-017-1356-3>
- Pilát A (1926) Les *Agaricales* et *Aphyllophorales* des Carpathes Centrales. *Bull Trimest Soc Mycol Fr* 42:81–120
- Pilát A (1940) Basidiomycetes chinenses a cel. Emilio Licentio in itinere per Chinam septentrionalem annis 1914–1936 susceptis, lecti. *Ann Mycol* 38:61–82 + 4 pl.
- Prasher IB (2015) *Wood-rotting non-gilled Agaricomycetes of Himalayas*. Springer, New York
- Rambaut A (2016) FigTree v1.4.4. Institute of Evolutionary Biology, University of Edinburgh. [cited 2019 Oct 18]. <http://tree.bio.ed.ac.uk/software/figtree>
- Reid DA (1956) [1955] New or interesting records of Australasian basidiomycetes. *Kew Bull* 10:631–648
- Robert V, Vu D, Amor ABH, van de Wiele N, Brouwer C, Jabas B, Szoke S, Dridi A, Triki M, Ben Daoud S, Chouchen O, Vaas L, de Cock A, Stalpers JA, Stalpers S, Verkley GJM, Groenewald M, dos Santos FB, Stegehuis G, Li W, Wu L, Zhang R, Ma J, Zhou M, Gorjón SP, Eurwilaichitr L, Ingsriswang S, Hansen K, Schoch C, Robbertse B, Irinyi L, Meyer W, Cardinali G, Hawksworth DL, Taylor JW, Crous PW (2013) MycoBank gearing up for new horizons. *IMA Fungus* 4:371–379. <https://doi.org/10.5598/imafungus.2013.04.02.16>
- Roberts P (1998) A revision of the genera *Heterochaetella*, *Myxarium*, *Protodontia*, and *Stypella* (Heterobasidiomycetes). *Mycotaxon* 69:209–248
- Ronquist F, Teslenko M, Van Der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Syst Biol* 61(3):539–542. <https://doi.org/10.1093/sysbio/sys029>
- Rosenthal LM, Larsson K-H, Branco S, Chung JA, Glassman SI, Liao H-L, Peay KG, Smith DP, Talbot JM, Taylor JW, Vellinga EC, Vilgalys R, Bruns TD (2017) Survey of corticioid fungi in North American pinaceous forests reveals hyperdiversity, underpopulated sequence databases, and species that are potentially ectomycorrhizal. *Mycologia* 109:115–127. <https://doi.org/10.1080/00275514.2017.1281677>
- Ryvarden L (1976) On the identity of *Acia sibirica* Pil. and *A. licentii* Pil. *Česká Mykol* 30:38–40
- Schweinitz LD 1832 [1834]. Synopsis fungorum in America boreali media degentium. *Trans Am Philos Soc, series 2*, 4:141–316
- Shear CL, Stevens NE (1917) Studies of the Schweinitz collections of fungi — I. *Mycologia* 9:191–204
- Shen S, Ma X, Xu T-M, Zhao CL (2018) *Phlebia ailaoshanensis* sp. nov. (Polyporales, Basidiomycota) evidenced by morphological characters and phylogenetic analyses. *Phytotaxa* 373:184–196. <https://doi.org/10.11646/phytotaxa.373.3.2>
- Spirin WA (2001) *Tyromyces* P. Karst and Related Genera *Mycena* 1:64–71
- Stalpers JA (1976) Notes on *Mycoacia* — I. *Persoonia* 9:145–148
- Stalpers JA (1998) On the genera *Sarcodontia*, *Radulodon* and *Pseudolagarobasidium*. *Folia Cryptog Estonica* 33:133–138
- Sumstine DR (1904) A new *Hydnum*. *Torreya* 4:59
- Szczepkowski A (2010) *Sarcodontia crocea* (Polyporales, Basidiomycota) in Poland – distribution and decay ability in laboratory conditions. *Pol Bot J* 55:489–498
- Thiers B (2021, continuously updated). Index herbariorum: a global directory of public herbaria and associated staff. <http://sweetgum.nybg.org/science/ih/>
- Tomšovský M (2012) Delimitation of an almost forgotten species *Spongipellis litschaueri* (Polyporales, Basidiomycota) and its taxonomic position within the genus. *Mycol Prog* 11:415–424. <https://doi.org/10.1007/s11557-011-0756-z>
- Tomšovský M (2016) *Sarcodontia crocea* (Basidiomycota, Polyporales) is unrelated to *Spongipellis*. *Phytotaxa* 288:197–200. <https://doi.org/10.1007/s11557-011-0756-z>
- Varga T, Krizsán K, Földi C, Dima B, Sánchez-García M, Sánchez-Ramírez S, Szöllösi GJ, Szarkándi JG, Papp V, Albert L, Andreopoulos W, Angelini C, Antonín V, Barry KW, Bougher NL, Buchanan P, Buyck B, Bense V, Catcheside P, Chovatia M, Cooper J, Dämon W, Desjardin D, Finy P, Geml J, Haridas S, Hughes K, Justo A, Karasiński D, Kautmanova I, Kiss B,

- Kocsubé S, Kotiranta H, LaButti KM, Lechner BE, Liimatainen K, Lipzen A, Lukács Z, Mihaltcheva S, Morgado LN, Niskanen T, Noordeloos ME, Ohm RA, Ortiz-Santana B, Ovrebo C, Rácz N, Riley R, Savchenko A, Shiryaev A, Soop K, Spirin V, Szabenyi C, Tomšovský M, Tulloss RE, Uehling J, Grigoriev IV, Vágvölgyi C, Papp T, Martin FM, Miettinen O, Hibbett DS, Nagy LG (2019) Megaphylogeny resolves global patterns of mushroom evolution. *Nat Ecol Evol* 3:668–678. <https://doi.org/10.1038/s41559-019-0834-1>
- Vilgalys R, Hester M (1990) Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. *J Bacteriol* 172:4238–4246
- Vu T, Groenewald M, Vries M, Gehrmann T, Stielow B, Eberhardt U, Al-Hatmi A, Groenewald JZ, Cardinali G, Houbraken J, Boekhout T, Crous PW, Robert V, Verkley GJM (2019) Large-scale generation and analysis of filamentous fungal DNA barcodes boosts coverage for kingdom Fungi and reveals thresholds for fungal species and higher taxon delimitation. *Stud Mycol* 92:135–154. <https://doi.org/10.1016/j.simyco.2018.05.001>
- Wang X-H, Das K, Horman J, Antonin V, Baghela A, Chakraborty D, Hembrom DE, Nakasone KK, Ortiz-Santana B, Vizzini A, Hofstetter V, Buyck B (2018) Fungal biodiversity profiles 51–60. *Cryptogam Mycol* 39:211–257. <https://doi.org/10.7872/crym/v39.iss2.2018.211>
- Westphalen MC, Rajchenberg M, Tomšovský M, Gugliotta AM (2016) Extensive characterization of the new genus *Rickiopora* (Polyporales). *Fungal Biol* 120:1002–1009. <https://doi.org/10.1016/j.funbio.2016.05.001>
- White TJ, Bruns T, Lee SS, Taylor J (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ (eds) *PCR protocols: A guide to methods and applications*. Academic Press, New York, pp 315–322
- Wu F, Yuan Y, Chen J-J, He S-H (2016) *Luteoporia albomarginata* gen. et sp. nov. (*Meruliaceae*, *Basidiomycota*) from tropical China. *Phytotaxa* 263:31–41. <https://doi.org/10.11646/phytotaxa.263.1.3>
- Zhao CL, Chen H, He S-H, Dai Y-C (2016) *Radulotubus resupinatus* gen. et sp. nov. with a poroid hymenophore in *Pterulaceae* (*Agaricales*, *Basidiomycota*). *Nova Hedwigia* 103:265–278. https://doi.org/10.1127/nova_hedwigia/2016/0350
- Zhao YN, He S-H, Nakasone KK, Wasantha Kumara KL, Chen C-C, Liu S-L, Ma H-X, Huang MR (2021) Global phylogeny and taxonomy of the wood-decaying fungal genus *Phlebiopsis* (*Polyporales*, *Basidiomycota*). *Front Microbiol* 12:214. <https://doi.org/10.3389/fmicb.2021.622460>
- Zmitrovich IV (2018) *Conspectus systematis Polyporacearum v. 1.0*. *Folia Cryptogamica Petropolitana* 6:1–145
- Zmitrovich IV, Malysheva VF, Spirin WA (2006) A new morphological arrangement of the *Polyporales*. I *Phanerochaetinae* *Mycena* 6:4–56
- Zmitrovich IV, Bondartseva MA, Bolshakov SY, Volobuev SV, Kalinovskaya NI, Myasnikov AG (2017) Records revision of *Radulomyces erikssonii* and *Radulomyces copelandii* in Leningrad Region and St. Petersburg *Mikol Fitopatol* 51:117–122

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