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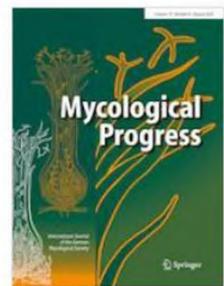
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Three new species of *Phlebia* (Polyporales, Basidiomycota) based on the evidence from morphology and DNA sequence data

Ruo-Xia Huang^{1,2} · Chang-Lin Zhao^{1,2,3}

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Abstract

Three new *Phlebia* species, *Ph. fuscotuberculata*, *Ph. tomentopileata* and *Ph. tongxiniana*, are proposed based on a combination of morphological features and molecular evidence. *Phlebia fuscotuberculata* is characterized by brown, tuberculate hymenial surface, fusiform cystidia and ellipsoid basidiospores. *Phlebia tomentopileata* is distinguished by effused or semi-pileate basidiomata with tomentose upper pileus surface and meruliod hymenophore and allantoid basidiospores ($3.5\text{--}4.5 \times 1\text{--}1.4 \mu\text{m}$). *Phlebia tongxiniana* differs in its effused basidiomata with smooth, buff to cinnamon-buff hymenophore, monomitic hyphal system with clamped hyphae and ellipsoid basidiospores. Sequences of ITS and 28S gene regions of the studied specimens were generated, and phylogenetic analyses were performed with maximum likelihood, maximum parsimony and Bayesian inference methods. The phylogenetic analyses based on combined ITS+28S dataset showed that the three new *Phlebia* species fell into the phlebioid clade. Further study focused on a more representative set of *Phlebia* species based on ITS+28S sequences demonstrated that *Ph. fuscotuberculata* was grouped with *Ph. hydnoides* and *Ph. nantahaliensis*, *Ph. tomentopileata* was closely related to *Ph. tremellosa* and *Ph. tongxiniana* was grouped with *Ph. chrysocreas*.

Keywords China · Meruliaceae · Phylogeny · Taxonomy · Wood-inhabiting fungi

Introduction

The genus *Phlebia* Fr. (Meruliaceae, Polyporales) was erected by Fries (1821) and typified with *Ph. radiata* Fr. It is a large, cosmopolitan genus characterized by

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effused or partly pileate basidiocarps with subceraceous to subgelatinous consistency when fresh, membranaceous to coriaceous when dry, hymenophore smooth, tuberculate, phlebioid, odontoid, meruliod or poroid, a monomitic (rarely dimitic) hyphal structure generally with clamped hyphae, narrowly clavate basidia, and colourless, thin-walled, smooth, allantoid to ellipsoid basidiospores which are acyanophilous, inamyloid and nondextrinoid (Bernicchia and Gorjón 2010). So far, about 100 species have been accepted in the genus worldwide (Indexfungorum, <http://www.indexfungorum.org/names/Names.asp>; MycoBank, <http://www.mycobank.org/Biolomics.aspx?Table=Mycobank>) and 14 species occurred in China (Hjortstam and Ryvarden 1988; Dai et al. 2004; Dai 2011; Shen et al. 2018). Previous studies showed the synonym of *Merulius* Fr., *Mycoacia* Donk and *Mycoaciella* J. Erikss. & Ryvarden with *Phlebia* (Nakasone and Burdsall 1984; Nakasone 1997, 2002). In addition, some species in the genus have potential application in both biomedical engineering and biodegradation (Hofrichter et al. 2001; Wu et al. 2019).

Larsson et al. (2004) studied the high phylogenetic diversity among corticioid homobasidiomycetes and suggested that *Phlebia* clustered into the phlebioid clade and grouped with *Ceriporia* Donk and *Gloeoporus* Mont. and the same conclusion was made by Wu et al. (2017). Larsson (2007) revealed the classification of corticioid fungi, including *Phlebia*, which suggested that *Phlebia* was nested into the Meruliaceae. Tomšovský et al. (2010) aimed the phylogenetic study of European *Ceriporiopsis* Domański taxa and revealed that *Phlebia radiata* and *C. gilvescens* (Bres.) Domański were grouped together on the base of the combined data of the large subunit nuclear ribosomal RNA gene (nLSU) sequences and mitochondrial small subunit rRNA (mtSSU) gene sequences. Kuuskeri et al. (2015) introduced molecular systematics and phylogeny grouping in *Phlebia* and confirmed the polyphyletic nature of the genus *Phlebia*. Justo et al. (2017) revised family-level classification of the Polyporales using multi-gene datasets; the result showed that *Phlebia radiata* belonged to the family Meruliaceae and grouped with *Aurantiporus* Murrill and *C. gilvescens*. Runnel et al. (2019) revealed that *Phlebia griseoflavescens* (Litsch.) J. Erikss. & Hjortstam belonged to *Antrodia* s. str. and *Phlebia* was a polyphyletic group.

During the studies on wood-inhabiting fungi in southern China, three species of phlebioid fungi could not be assigned to any known species. The authors examine taxonomy and phylogeny of these three new species within *Phlebia*, based on the internal transcribed spacer (ITS) regions and 28S sequences.

Materials and methods

Morphology

The specimens studied are deposited at the herbarium of Southwest Forestry University, Yunnan Province, People's Republic of China (SWFC). Macromorphological descriptions are based on field notes. Colour terms follow Petersen (1996). Micromorphological data were obtained from the dried specimens and observed under a light microscope following Dai (2010). The following abbreviations were used: KOH = 5% water solution of potassium hydroxide, CB = Cotton Blue, CB- = acyanophilous, IKI = Melzer's reagent, IKI- = both inamyloid and nondextrinoid, L = mean spore length (arithmetic average), W = mean spore width (arithmetic average), Q = variation in the L/W ratios between the specimens studied, n (a/b) = number of spores (a) measured from given number (b) of specimens.

Molecular phylogeny

The E.Z.N.A. HP Fungal DNA Kit (Omega Biotechnologies Co., Ltd., Kunming) was used to obtain PCR products from dried specimens, according to the manufacturer's instructions with some modifications. ITS region was amplified with primer pair ITS5/ITS4 (White et al. 1990). 28S region was amplified with primer pair LR0R/LR7 (<http://www.biology.duke.edu/fungi/mycolab/primers.htm>). The PCR procedure for ITS was as follows: initial denaturation at 95 °C for 3 min, followed by 35 cycles at 94 °C for 40 s, 58 °C for 45 s and 72 °C for 1 min, and a final extension of 72 °C for 10 min. The PCR procedure for 28S was as follows: initial denaturation at 94 °C for 1 min, followed by 35 cycles at 94 °C for 30 s, 48 °C for 1 min and 72 °C for 1.5 min, and a final extension of 72 °C for 10 min. The PCR products were purified and directly sequenced at Kunming Tsingke Biological Technology Limited Company, Yunnan Province, People's Republic of China. All newly generated sequences were deposited at GenBank (Table 1).

Sequencher 4.6 (GeneCodes, Ann Arbor, MI, USA) was used to edit the DNA sequence chromatograms. Sequences were aligned in MAFFT 7 (<https://mafft.cbrc.jp/alignment/server/>) using the "G-INS-i" strategy and adjusted manually in BioEdit (Hall 1999). The sequence alignments were deposited in TreeBASE (ID 25143). *Heterobasidion annosum* and *Stereum hirsutum* were assigned as the outgroup to root trees in the ITS+28S analysis following Binder et al. (2013); *Hydnophlebia chrysorhiza* was used as the outgroup to root trees in the second analysis following Floudas and Hibbett (2015).

Maximum parsimony analysis was applied to the combined dataset and followed Zhao and Wu (2017); the tree construction procedure was performed in PAUP* version 4.0b10 (Swofford 2002). All characters were equally weighted, and gaps were treated as missing data. Trees were inferred using the heuristic search option with TBR branch swapping and 1000 random sequence additions. Max-trees were set to 5000, branches of zero length were collapsed, and all parsimonious trees were saved. Clade robustness was assessed using a bootstrap (BT) analysis with 1000 replicates (Felsenstein 1985). Descriptive tree statistics tree length (TL), consistency index (CI), homoplasy index (HI), retention index (RI) and rescaled consistency index (RC) were calculated for each maximum parsimonious tree (MPT) generated. Ready datasets were also analysed using maximum likelihood (ML) with RAxML-HPC2 software through the CIPRES Science Gateway (www.phylo.org; Miller et al. 2009). Branch support (BS) for ML analysis was determined by 1000 bootstrap replicate.

Table 1 List of species, specimens and GenBank accession numbers for sequences used in this study

Species name	Sample no.	Host	Country	GenBank accession no.		References
				ITS	28S	
<i>Aboritporus biennis</i> (Bull.) Singer	EL65-03	Angiosperm	Sweden	JN649325	JN649325	Sjökvist et al. 2012
<i>Antrodia albidia</i> (Fr.) Donk	CBS 308.82	Angiosperm	USA	DQ491414	DQ491414	Kim et al. 2007
<i>A. heteromorpha</i> (Fr.) Donk	CBS 200.91	<i>Abies balsamea</i>	Canada	DQ491415	DQ491415	Kim et al. 2007
<i>Antrodiella americana</i> Ryvarden & Gilb.	Gothenburg 3161	<i>Prunus padus</i> ; <i>Fagus</i>	Finland; USA	JN710509	JN710509	Binder et al. 2013
<i>A. semisapina</i> (Berk. & M.A. Curtis) Ryvarden	FCUG 960	Dead hardwood of Angiosperm	New England	EU232182	EU232182	Binder et al. 2005
<i>Ceriporia lacerata</i> N. Maek., Suhara & R. Kondo	Dai 10734	<i>Quercus acutissima</i> decayed wood	Japan	JX623916	JX623916	Jia et al. 2014
<i>Ceriporiopsis gilvescens</i> (Bres.) Dománski	BRNM 710166	<i>Fagus</i>	France	FJ496684	FJ496684	Tonšovský et al. 2010
<i>Climacocystis borealis</i> (Fr.) Kotl. & Pouzar	KH 13318	Gymnosperm	France	JQ031126	JQ031126	Binder et al. 2013
<i>Coriolopsis caperata</i> (Berk.) Murrill	LE(BIN)-0677	On deciduous wood	Mauritius	AB158316	AB158316	Tonšovský et al. 2010
<i>Daedalea quercina</i> (L.) Pers.	Miettinen 12662	On deciduous wood	Finland	JX109855	JX109855	Binder et al. 2013
<i>Earliella scabrosa</i> (Pers.) Gilb. & Ryvarden	PR 1209	On deciduous wood	China	JN165009	JN165009	Binder et al. 2005
<i>Fomitopsis pinicola</i> (Sw.) P. Karst.	CCBAS 536	Gymnosperm	Norway; USA	FI608588	—	Hornokla et al. 2010
<i>F. rosea</i> (Alb. & Schwein.) P. Karst.	ATCC 76767	<i>Picea orientalis</i>	Sweden	DQ491410	DQ491410	Kim et al. 2007
<i>Fragiliporia fragilis</i> Y.C. Dai, B.K. Cui & C.L. Zhao	Dai 13080	<i>Athus</i>	China	KJ734260	KJ734260	Zhao et al. 2015
<i>F. fragilis</i>	Dai 13559	Angiosperm	China	KJ734261	KJ734261	Zhao et al. 2015
<i>Ganoderma lingzhi</i> Sheng H. Wu, Y. Cao & Y.C. Dai	Dai 13561	Angiosperm	China	KJ734262	KJ734262	Zhao et al. 2015
<i>Gelatoporia subvernispora</i> (Pilat) Niemelä	Wu 1006-38	<i>Quercus</i>	China	JQ718158	—	Zhao et al. 2015
<i>Gloeoporus pannocinctus</i> (Romell) J. Erikss.	BRNU 592909	<i>Picea</i> ; <i>Acer</i> ; <i>Populus</i> ; <i>Quercus</i>	USA	FJ496694	FJ496694	Tonšovský et al. 2010
<i>G. dichrous</i> (Fr.) Bres.	BRNM 709972	Angiosperm	Canada	EU546099	EU546099	Tonšovský et al. 2010
<i>Grammothelopsis subtropica</i> B.K. Cui & C.L. Zhao	KHL 111173	<i>Betula</i>	Sweden	EU118627	EU118627	Binder et al. 2005
<i>Heterobasidion annosum</i> (Fr.) Bref.	Cui 9035	Angiosperm	China	JQ845094	JQ845094	Zhao et al. 2015
<i>Hornodermoporus maritimus</i> (Berk.) Teixeira	PFC 5252	Gymnosperm	Sweden	KC492906	KC492906	Binder et al. 2013
<i>Hydnophlebia chrysorhiza</i> (Eaton) Parmasto	MUCL 41677	On deciduous dead wood	Brazil	FJ411092	FJ411092	Robledo et al. 2009
<i>Hypochnicium lydoniae</i> (D.A. Reid) Hjortstam	FD 282	On dead cotton stems	USA	KP135338	KP135338	Floudas and Hibbett 2015
<i>O. valdiviana</i> (Rajchenb.) Miettinen & Rajchenb.	NL 041031	<i>Salix</i>	Australia	JX124704	JX124704	Binder et al. 2013
<i>Junghuhnia nitida</i> (Pers.) Ryvarden	KHL 11903	Angiosperm	Norway	EU118638	EU118638	Binder et al. 2005
<i>Obba rivulosa</i> (Berk. & M.A. Curtis) Miettinen & Rajchenb.	KCTC 6892	Gymnosperm	Cuba	FJ496693	FJ496693	Miettinen and Rajchenberg 2012
<i>Perenniporia medulla-pannis</i> (Jacq.) Donk	FF 503	<i>Nothofagus dombeyi</i>	Argentina	HQ659235	HQ659235	Miettinen and Rajchenberg 2012
<i>Perenniporia medulla-pannis</i> (Jacq.) Donk	MUCL 43250	<i>Quercus</i>	Britain	FJ411087	FJ411087	Robledo et al. 2009

Table 1 (continued)

Species name	Sample no.	Host	Country	GenBank accession no.		References
				ITS	28S	
<i>P. ochroleuca</i> (Berk.) Ryvarden	MUCL 39726	Angiosperm	Australia	FJ411098	FJ411098	Rohledo et al. 2009
<i>Phanerochate chrysosporium</i> Burds.	HHB 6251	<i>Platanus wrightii</i>	USA	KP135094	KP135094	Justo et al. 2017
<i>Phlebia acanthocystis</i> Gilb. & Nakasone	FP 150571	<i>Psidium cattleyanum</i>	Canada	KY948767	KY948844	Floudas and Hibbett 2015
<i>P. acerina</i> Peck	FD 301	<i>Acer saccharinum</i>	Canada	KP135378	KP135378	Justo et al. 2017
<i>P. acerina</i>	HHB 11146	<i>Acer saccharinum</i>	Canada	KP135372	—	Floudas and Hibbett 2015
<i>P. acerina</i>	FP 135252	<i>Acer saccharinum</i>	Russia	KP135371	—	Floudas and Hibbett 2015
<i>P. ailaooshanensis</i> C.L. Zhao	CLZhao 3996	Angiosperm	China	MH784926	MH784926	Shen et al. 2018
<i>P. ailaooshanensis</i>	CLZhao 4036	Angiosperm	China	MH784927	MH784927	Shen et al. 2018
<i>P. aurea</i> (Fr.) Nakasone	DLL 2011100	<i>Quercus; Abies alba</i>	Poland	KJ140614	—	Binder et al. 2013
<i>P. aurea</i>	DLL 2011263	<i>Pinus laricio</i>	Estonia	KJ140747	KJ140747	Binder et al. 2013
<i>P. aurea</i>	FCUG 2767	<i>Abies alba</i>	USA	HQ153409	HQ153409	Binder et al. 2013
<i>P. brevispora</i> Nakasone	HHB 7030	Slash pine	Norway	KP135387	—	Floudas and Hibbett 2015
<i>P. fuscothberculata</i> C.L. Zhao	CLZhao 10227	Angiosperm	China	MT020759	MT020759	Present study
<i>P. fuscothberculata</i>	CLZhao 10239	Angiosperm	China	MT020760	MT020738	Present study
<i>P. fuscothberculata</i>	HHB 9239	<i>Abies excelsa</i>	Russia	KP135380	KP135380	Floudas and Hibbett 2015
<i>P. fuscothberculata</i>	L 15541	<i>Abies excelsa</i>	Russia	KP135381	—	Floudas and Hibbett 2015
<i>P. fuscothberculata</i>	GB 1013	<i>Abies excelsa</i>	Russia	KP135379	—	Floudas and Hibbett 2015
<i>P. centrifuga</i> P. Karst.	HHB 6333	<i>Pinus</i>	USA	KP135358	KP135358	Floudas and Hibbett 2015
<i>P. centrifuga</i>	HBB 3946	<i>Pinus</i>	USA	KP135357	KP135357	Floudas and Hibbett 2015
<i>P. centrifuga</i>	FP 102161	<i>Pinus</i>	USA	AY219367	—	Binder et al. 2005
<i>P. chrysocreas</i> (Berk. & M.A. Curtis) Burds.	KUC 2012112324	<i>Pinus</i>	USA	KJ668482	KJ668482	Floudas and Hibbett 2015
<i>P. chrysocreas</i>	HHB 9905	<i>Carpinus; Quercus</i>	USA	KP135383	KP135383	Justo et al. 2017
<i>P. floridensis</i> Nakasone & Burds.	HHB 6466	<i>Ostrya; Magnolia</i>	USA	KP135385	KP135385	Floudas and Hibbett 2015
<i>P. floridensis</i>	HHB 7175	<i>Carpinus; Quercus</i>	USA	KP135384	KP135384	Floudas and Hibbett 2015
<i>P. floridensis</i>	FP 102562T	<i>Ostrya; Magnolia</i>	USA	KP135386	KP135386	Floudas and Hibbett 2015
<i>P. fuscoatra</i> (Fr.) Nakasone	HHB 10782	<i>Quercus</i>	Austria	KP135364	KP135364	Floudas and Hibbett 2015
<i>P. fuscoatra</i>	HBB 15354	<i>Fagus sylvatica</i>	Finland	KP135367	KP135367	Floudas and Hibbett 2015
<i>P. fuscoatra</i>	HHB 18642	<i>Quercus</i>	Estonia	KP135366	—	Floudas and Hibbett 2015
<i>P. fuscoatra</i>	FP 102173	<i>Fagus sylvatica</i>	France	KP135364	—	Floudas and Hibbett 2015
<i>P. fuscoatra</i>	KHL 13275	<i>Quercus</i>	Sweden	JN649352	JN649352	Tomšovský et al. 2010
<i>P. hydnoides</i> Schwein.	HHB 1993	<i>Castanea dentata</i>	France	KY948778	KY948778	Justo et al. 2017
<i>P. lindneri</i> (Pilát) Parmasto	GB 501	Angiosperm and gymnosperm	Russia	KY948772	KY948772	Justo et al. 2017
<i>P. lividia</i> (Pers.) Bres.	FCUG 2189	<i>Picea</i>	Estonia	AF141624	AF141624	Tomšovský et al. 2010

Table 1 (continued)

Species name	Sample no.	Host	Country	GenBank accession no.		References
				ITS	28S	
<i>P. ludoviciana</i> (Burt) Nakasone & Burds.	FD 427	Angiosperm and gymnosperm	USA	KP135342	—	Floudas and Hibbett 2015
	HHB 2816	<i>Pinus strobus</i>	USA	KY948777	KY948777	Justo et al. 2017
<i>P. namatahensis</i> Nakasone & Burds.	HHB 4273	<i>Nothofagus menziesii</i>	Australia	KP135369	KP135369	Floudas and Hibbett 2015
<i>P. nothofagi</i> (G. Cunn.) Nakasone	HHB 6906	<i>Nothofagus menziesii</i>	New Zealand	KP135368	—	Floudas and Hibbett 2015
<i>P. nothofagi</i>	HHB 12067	<i>Nothofagus menziesii</i>	France	KP135370	—	Floudas and Hibbett 2015
<i>P. nothofagi</i>	KHL 13750	<i>Nothofagus menziesii</i>	Austria	GU480000	GU480000	Tomšovský et al. 2010
<i>P. radiata</i> Fr.	UBCF 1926	On deciduous dead wood	Russia	HQ604797	HQ604797	Binder et al. 2013
<i>P. radiata</i>	AFTOL 484	On deciduous dead wood	Russia	AY854087	AY854087	Binder et al. 2005
<i>P. radiata</i>	FD 85	On deciduous dead wood	Russia	KP135377	KP135377	Justo et al. 2017
<i>P. radiata</i>	FCUG 2423	On deciduous dead wood	Russia	AF141627	AF141627	Parmasto and Hallenberg 2000
<i>P. rufa</i>	HBB 14924	Angiosperm	Britain	KP135374	KP135374	Floudas and Hibbett 2015
<i>P. setulosa</i> (Pers.) M.P. Christ.	HHB 6891	Angiosperm	USA	KP135382	KP135382	Justo et al. 2017
<i>P. setulosa</i>	AH 31879	Angiosperm	USA	GQ259417	GQ259417	Binder et al. 2005
<i>P. setulosa</i>	PH 11749	Angiosperm	USA	GU461312	—	Binder et al. 2005
<i>P. subochracea</i> (Alb. & Schwein.) J. Erikss. & Ryvarden	HHB 8715	<i>Salix</i>	Norway	KY948846	KY948846	Floudas and Hibbett 2015
<i>P. subserialis</i> (Bourdot & Galzin) Donk	FCUG 1434	<i>Pinus</i>	Denmark	AF141631	AF141631	Tomšovský et al. 2010
<i>P. subserialis</i> (Bourdot & Galzin) Donk	CLZhao 5833	Angiosperm	China	MT020761	MT020739	Present study
<i>P. tomentopileata</i> C.L. Zhao	CLZhao 9509	Angiosperm	China	MT020762	MT020740	Present study
<i>P. tomentopileata</i>	CLZhao 9511	Angiosperm	China	MT020763	MT020741	Present study
<i>P. tomentopileata</i>	CLZhao 9515	Angiosperm	China	MT020764	MT020742	Present study
<i>P. tomentopileata</i>	CLZhao 9563	Angiosperm	China	MT020765	MT020743	Present study
<i>P. tomentopileata</i>	CLZhao 9566	Angiosperm	China	MT020766	MT020744	Present study
<i>P. tomentopileata</i>	CLZhao 10158	Angiosperm	China	MT020767	MT020745	Present study
<i>P. tomentopileata</i>	CLZhao 10187	Angiosperm	China	MT020768	MT020746	Present study
<i>P. tomentopileata</i>	CLZhao 10192	Angiosperm	China	MT020769	MT020747	Present study
<i>P. tomentopileata</i>	CLZhao 10209	Angiosperm	China	MT020770	MT020748	Present study
<i>P. tomentopileata</i>	CLZhao 10274	Angiosperm	China	MT020771	MT020749	Present study
<i>P. tomentopileata</i>	CLZhao 10399	Angiosperm	China	MT020772	MT020750	Present study
<i>P. tomentopileata</i>	CLZhao 2255	<i>Quercus</i>	China	MT020773	MT020751	Present study
<i>P. tongxiniana</i> C.L. Zhao	CLZhao 2316	<i>Quercus</i>	China	MT020774	MT020752	Present study
<i>P. tongxiniana</i>	CLZhao 2707	Angiosperm	China	MT020775	MT020753	Present study
<i>P. tongxiniana</i>	CLZhao 2719	Angiosperm	China	MT020776	MT020754	Present study

Table 1 (continued)

Species name	Sample no.	Host	Country	GenBank accession no.		References
				ITS	28S	
<i>P. tongxiniana</i>	CLZhao 3915	<i>Rhododendron</i>	China	MT020777	MT020755	Present study
<i>P. tongxiniana</i>	CLZhao 5217	Angiosperm	China	MT020778	MT020756	Present study
<i>P. tongxiniana</i>	CLZhao 5228	Angiosperm	China	MT020779	MT020757	Present study
<i>P. tongxiniana</i>	CLZhao 5781	Angiosperm	China	MT020780	MT020758	Present study
<i>P. tremellosa</i> (Schrad.) Nakasone & Burds.	ES 20082	Angiosperm	France	JX109859	JX109859	Binder et al. 2013
<i>P. uda</i> (Fr.) Nakasone	FP 101544	<i>Fraxinus; Quercus</i>	Russia	KP135361	KP135361	Floudas and Hibbett 2015
<i>P. uda</i>	FCUG 2452	<i>Fraxinus; Quercus</i>	Russia	AF141614	—	Parmasto and Hallenberg 2000
<i>Piloporia sepianensis</i> (Parmasto) Niemelä	Mannine 2733a	<i>Pinus; Abies; Larix</i>	Sweden	HQ659239	HQ659239	Tonšovský et al. 2010
<i>Podoscypha venustula</i> (Speg.) D.A. Reid	LR 40821	On dead wood	New Zealand	JX109851	JX109851	Binder et al. 2013
<i>Polyporus tuberaster</i> (Jacq. ex Pers.) Fr.	CulTENN 10197	Angiosperm	Australia	AF516596	AF516596	Binder et al. 2013
<i>Sebipora aquosa</i> Miettinen	Miettinen 8680	Angiosperm	Indonesia	HQ659240	HQ659240	Miettinen and Rajchenberg 2012
<i>Skeletocutis amorpha</i> (Fr.) Kotl. & Pouzar	Miettinen 11038	Pinaceae	Norway	FN907913	FN907913	Tonšovský et al. 2010
<i>S. jellicii</i> Tortić & A. David	H 6002113	<i>Abies alba</i>	Yugoslavia	FJ496690	FJ496690	Tonšovský et al. 2010
<i>S. portcrosensis</i> A. David	LY 3493	<i>Pinus</i>	France	FJ496689	FJ496689	Tonšovský et al. 2010
<i>S. subsphaerospora</i> A. David	Rivoire 1048	<i>Cedrus</i>	France	FJ496688	FJ496688	Tonšovský et al. 2010
<i>Stecherinum fimbriatum</i> (Pers.) J. Erikss.	KHL 11905	Angiosperm	France	EU118668	EU118668	Tonšovský et al. 2010
<i>S. ochraceum</i> (Pers. ex J.F. Gmel.) Gray	KHL 11902	<i>Juniperus oxycedrus</i>	Canada; USA	JQ031130	JQ031130	Tonšovský et al. 2010
<i>Stereum hirsutum</i> (Willd.) Pers.	NBRC 6520	Angiosperm	Canada; USA	AB733150	AB733150	Tonšovský et al. 2010
<i>Tyromyces chioneus</i> (Fr.) P. Karst.	Cui 10,225	Angiosperm	Norway	KF698745	KF698745	Zhao et al. 2015
<i>Xanthoporus syringae</i> (Parmasto) Audet	Gothenburg 1488	Angiosperm	Italy; Norway	JN710607	JN710607	Tonšovský et al. 2010

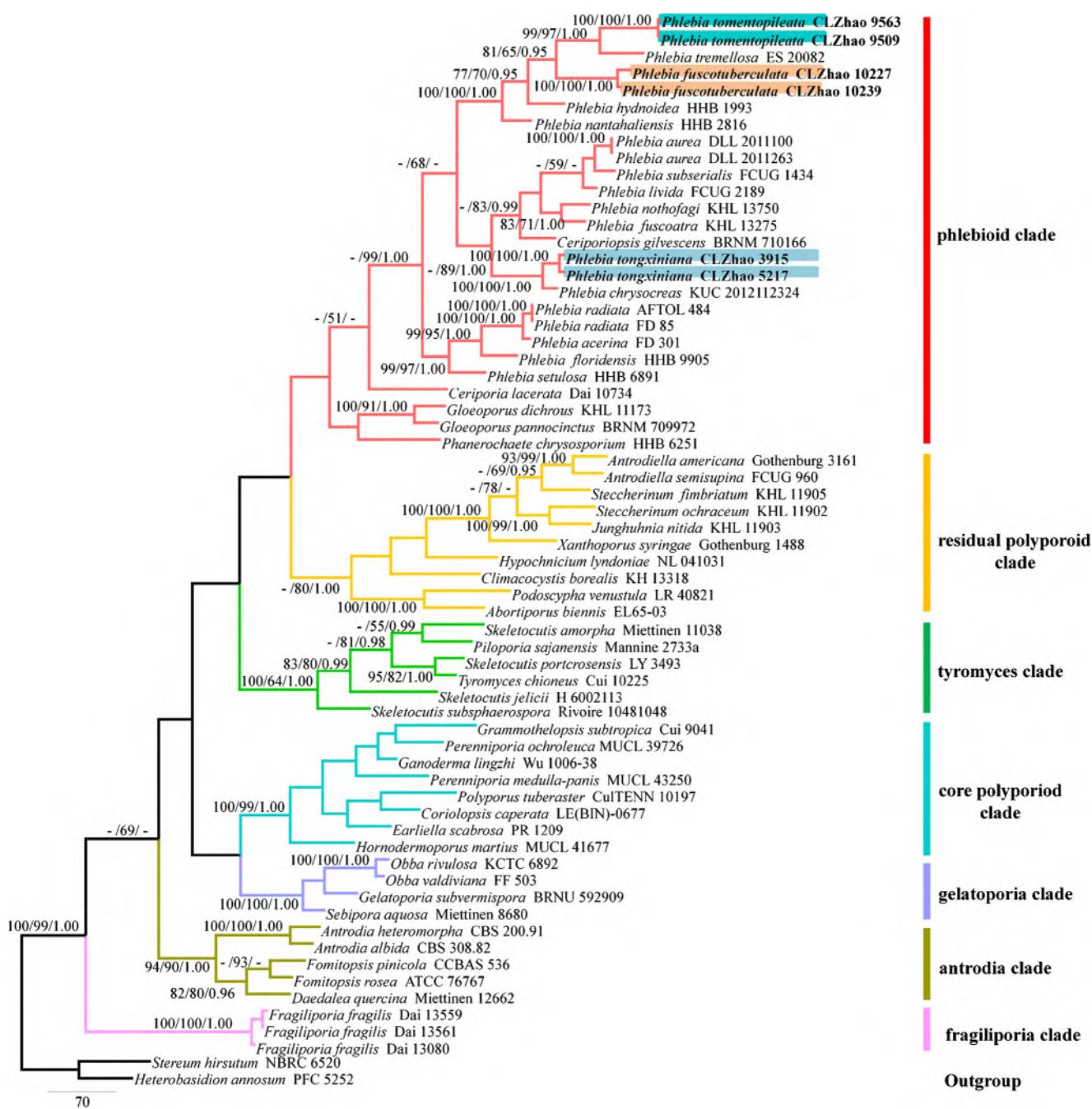


Fig. 1 Maximum parsimony strict consensus tree illustrating the phylogeny of three new *Phlebia* species and related species in Polyporales based on ITS+28S sequences. Branches are labelled with BS > 70%, BT > 50% and PP > 0.95, respectively. Clade names follow Binder et al. (2013)

MrModeltest 2.3 (Nylander 2004) was used to determine the best-fit evolution model for each dataset for Bayesian inference (BI) of the phylogeny. Bayesian inference was calculated with MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003). Four Markov chains were run for 2 runs from random starting trees for 1 million generations for the first dataset, for 2 million generations for the second

dataset and trees were sampled every 100 generations; the first one-fourth of generations were discarded as burn-in. A majority rule consensus tree of all remaining trees was calculated. Branches were considered significantly supported if they received maximum likelihood bootstrap (ML) > 70%, maximum parsimony bootstrap (MP) > 50% or Bayesian posterior probabilities (PP) > 0.95.

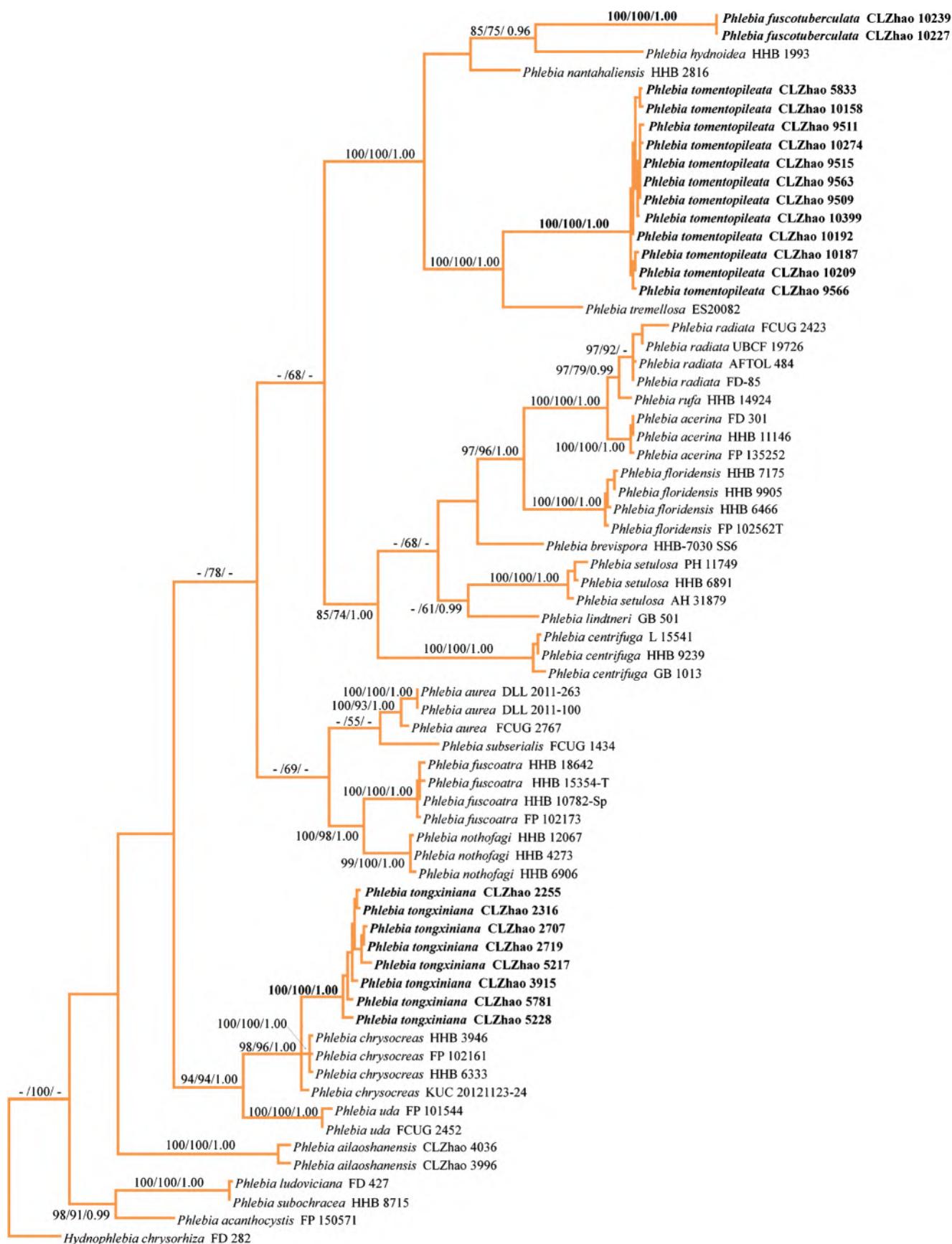


Fig. 2 Maximum parsimony strict consensus tree illustrating the phylogeny of three new *Phlebia* species and related species in *Phlebia* based on ITS+28S sequences. Branches are labelled with BS > 70%, BT > 50% and PP > 0.95, respectively

Results

The first combined ITS+28S dataset comprises sequences from 64 specimens and 57 species. The dataset had an aligned length of 2239 characters, of which 1283 characters were constant, 256 were variable and parsimony-uninformative and 700 were parsimony-informative. Maximum parsimony analysis yielded one equally parsimonious trees (TL = 520, CI = 0.308, HI = 0.692, RI = 0.545, RC = 0.168). Best model suggested by MrModeltest and applied in BI was GTR+I+G. Bayesian analysis and ML analysis resulted in a similar topology as MP analysis; BI had the average standard deviation of split frequencies = 0.009957.

The phylogenetic tree inferred from ITS+28S sequences (Fig. 1) demonstrated seven major clades for 57 sampled species of the Polyporales. The three new *Phlebia* species fell into the phlebioid clade. *Phlebia fuscotuberculata* sp. nov. grouped with *Ph. hydnoides* Schwein.; *Ph. tomentopileata* sp. nov. was closely related to *Ph. tremellosa* (Schrad.) Nakasone & Burds.; *Ph. tongxiniana* sp. nov. grouped with *Ph. chrysocreas* (Berk. & M.A. Curtis) Burds.

The second dataset comprises sequences from 68 specimens and 25 species. The dataset had an aligned length of 2052 characters, of which 1487 characters were constant, 137 were variable and parsimony-uninformative and 428 were parsimony-informative. Maximum parsimony analysis yielded 100 equally parsimonious trees (TL = 1510, CI = 0.534, HI = 0.466, RI = 0.855, RC = 0.456). Best model for the ITS+28S dataset estimated and applied in the Bayesian analysis was GTR+I+G. Bayesian analysis and ML analysis resulted in a similar topology as MP analysis; BI had the average standard deviation of split frequencies = 0.009972.

The phylogeny reconstruction based on the second dataset (Fig. 2) demonstrated that each of three new species formed its own monophyletic lineage with a high 100% BS, 100% BP and 1.00 BPP; *Ph. fuscotuberculata* grouped with *Ph. hydnoides* and *Ph. nantahaliensis* Nakasone & Burds.; *Ph. tomentopileata* was closely related to *Ph. Tremellosa*; *Ph. tongxiniana* grouped with *Ph. chrysocreas*.

Taxonomy

Phlebia fuscotuberculata C.L. Zhao, sp. nov. (Figs. 3 and 4)

MycoBank no.: MB 834289

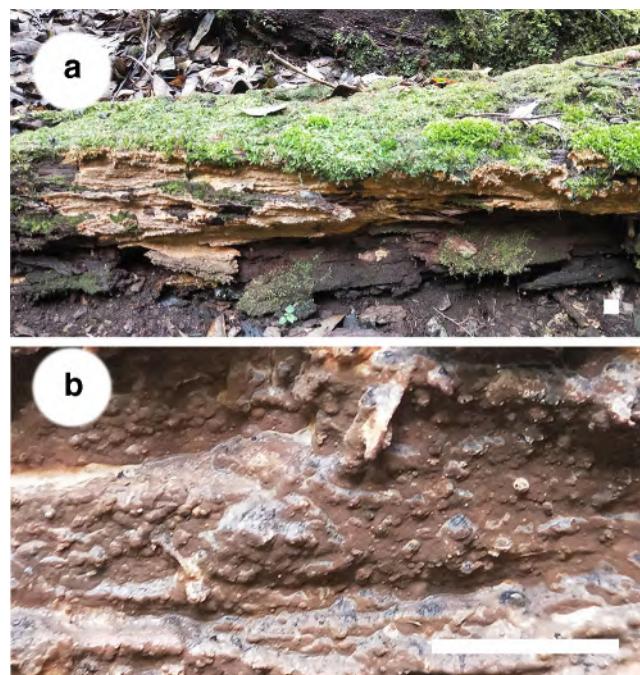


Fig. 3 Basidioma of *Phlebia fuscotuberculata* (holotype). Scale bars = 1 cm

Holotype. China. Yunnan Province, Dali, Nanjian County, Lingbaoshan National Forest Park, E 100°06', N 24°39', alt. 2500 m, on fallen angiosperm trunk, leg. C.L. Zhao, 9 Jan 2019, CLZhao 10239 (SWFC).

Etymology. *fuscotuberculata*: refers to the brown, tuberculate (Lat. *tuber*culatus) hymenial surface.

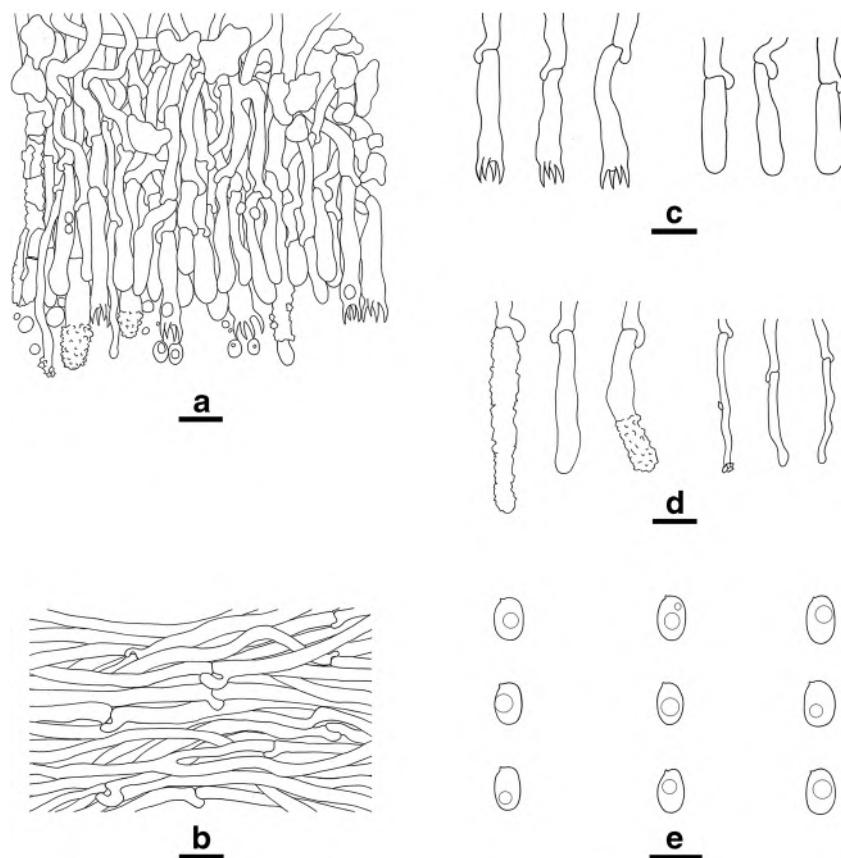
Fruiting body. Basidiomata annual, effused, easily detachable, subceraceous to subgelatinous, without odour or taste when fresh, becoming coriaceous upon drying, up to 25 cm long, 600–900 µm thick. Hymenial surface tuberculate, greyish brown to brown when fresh, brown upon drying. Sterile margin narrow, brown.

Hyphal structure. Monomitic; generative hyphae clamped at all primary septa, colourless, thin-walled, IKI-, CB-; tissues unchanged in KOH. Subicular hyphae infrequently branched, 2.5–4.5 µm in diam.; subhymenial hyphae infrequently branched, 2–4 µm in diam.

Hymenium. Cystidia fusiform, numerous, thin-walled, apically encrusted with large crystals, 23.5–37 × 5.5–6.5 µm; cylindrical cystidioles present, colourless, thin-walled, 11–15.5 × 1.5–4.5 µm; basidia clavate, with four sterigmata and a basal clamp connection, 20–28 × 3.5–5.5 µm. Basidiospores ellipsoid, colourless, thin-walled, smooth, often with 1–2 oildrops, IKI-, CB-, 3.5–4.5 × 2–3.2 µm, L = 3.98 µm, W = 2.76 µm, Q = 1.41–1.47 (n = 60/2); in holotype 3.8–4.5 × 2.3–3.2 µm, L = 4.2 µm, W = 2.86 µm, Q = 1.47 (n = 30/1).

Distribution and ecology. The species is known from Yunnan Province of China in temperate forest area. It grows

Fig. 4 Microscopic structures of *Phlebia fuscotuberculata* (drawn from the holotype). **a** A section of basidioma. **b** Hyphae from subcicum. **c** Basidia and basidioles. **d** Cystidia and cystidioles. **e** Basidiospores. Scale bars: a–d = 10 µm; e = 5 µm



on small-sized and broad-leaved forest trees and provokes white rot.

Additional specimen examined: CHINA. Yunnan Province, Dali, Nanjian County, Lingbaoshan National Forest Park, on angiosperm stump, leg. C.L. Zhao, 9 Jan 2019, CLZhao 10227 (SWFC).

***Phlebia tomentopileata* C.L. Zhao, sp. nov. (Figs. 5 and 6)**
MycoBank no.: MB 834290

Holotype. China. Yunnan Province, Puer, Jingdong County, Wuliangshan National Nature Reserve, E 100°25', N 24°09', alt. 2490 m, on fallen angiosperm trunk, leg. C.L. Zhao, 5 Jan 2019, CLZhao 9563 (SWFC).

Etymology. *tomentopileata* (Lat.): referring to the tomentose pileal surface of the type specimen.

Fruiting body. Basidiomata annual, effused to effused-reflexed, subceraceous to subgelatinous, without odour or taste when fresh, becoming crustaceous upon drying. Pilei flabelliform, projecting up to 2 cm wide, 1.5 mm thick at centre. Pileal surface tomentose, white to cream when fresh and grey upon drying. Hymenophore meruliod, straw-yellow when fresh, turning to buff and orange-yellow or fawn upon drying. Sterile margin distinct, white, fimbriate.

Hyphal structure. Monomitic; hyphae clamped, colourless, thin-walled, sparsely branched, IKI-, CB-; tissues unchanged in KOH. Contextual hyphae subparallel, 2.5–4 µm in diam.; subhymenial hyphae infrequently branched, 2–3.5 µm in diam.

Hymenium. Cystidia absent; fusoid cystidioles present, colourless, thin-walled, 13–20 × 1.5–2.5 µm; basidia clavate, with four sterigmata and a basal clamp connection, 14–20 × 2.5–4.5 µm. Basidiospores allantoid, colourless, thin-walled, smooth, often with 2–3 oildrops, IKI-, CB-, 3.5–4.5 × 1–1.4 µm, L = 4.01 µm, W = 1.18 µm, Q = 3.01–3.51 (n = 360/12); in holotype 3.5–4.2 × 1–1.3 µm, L = 3.93 µm, W = 1.16 µm, Q = 3.39 (n = 30/1).

Distribution and ecology. The species is known from southern China, growing in subtropical evergreen broad-leaved forests and has white rot.

Additional specimens examined: China. Yunnan Province, Puer, Jingdong County, Ailaoshan National Nature Reserve, on fallen angiosperm trunk, leg. C.L. Zhao, 15 Jan 2018, CLZhao 5833 (SWFC); Wuliangshan National Nature Reserve, on fallen angiosperm trunk, leg. C.L. Zhao, 5 Jan 2019, CLZhao 9509, CLZhao 9511, CLZhao 9515, CLZhao 9566 (SWFC); Dali, Nanjian County, Lingbaoshan National Forest

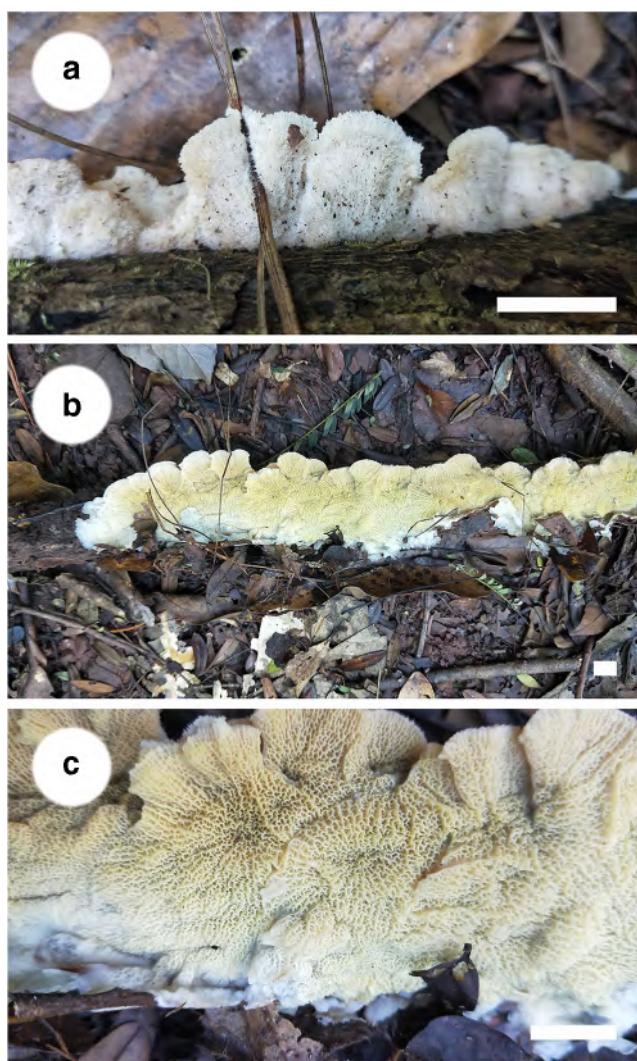


Fig. 5 Basidioma of *Phlebia tomentopileata* (holotype). Scale bars = 1 cm

Park, on fallen angiosperm trunk, leg. C.L. Zhao, 9 Jan 2019, CLZhao 10158, CLZhao 10187, CLZhao 10192, CLZhao 10209, CLZhao 10274 (SWFC), on fallen angiosperm trunk, leg. C.L. Zhao, 10 Jan 2019, CLZhao 10399 (SWFC).

Phlebia tongxiniana C.L. Zhao, sp. nov. (Figs. 7 and 8)
MycoBank no.: MB 834292

Holotype. China. Yunnan Province, Yuxi, Xinping County, Mopanshan National Forest Park, E 101°31', N 23°42', alt. 2650 m, on decayed trunk of *Quercus*, leg. C.L. Zhao, 19 Aug 2017, CLZhao 2255 (SWFC).

Etymology. *tongxiniana* (Lat.): in honour of the Chinese mycologist Prof. Tongxin Zhou.

Fruiting body. Basidiomata annual, effused, ceraceous, without odour or taste when fresh, becoming

membranaceous upon drying, up to 15 cm long, 100–200 µm thick. Hymenophore smooth, buff when fresh, buff to cinnamon-buff upon drying. Sterile margin narrow, buff.

Hyphal structure. Monomitic; hyphae clamped, colourless, thin-walled, IKI-, CB-; tissues unchanged in KOH. Subicular hyphae richly branched, 3–5.5 µm in diam.; subhymenial hyphae barely branched, 2–4 µm in diam.

Hymenium. Cystidia absent; fusoid cystidioles present, colourless, thin-walled, 13–18.5 × 1.5–2.8 µm; basidia clavate, with four sterigmata and a basal clamp connection, 9.5–18.5 × 3.5–5.5 µm. Basidiospores ellipsoid, colourless, thin-walled, smooth, often with 1–3 oildrops, IKI-, CB-, (4)–4.5–5(–5.5) × 2.8–3.5 µm, L = 4.77 µm, W = 3.19 µm, Q = 1.47–1.55 ($n = 300/10$); in holotype 4.22–5.08 × 2.57–3.38 µm, L = 4.76 µm, W = 3.07 µm, Q = 1.55 ($n = 30/1$).

Distribution and ecology. The species is known from Yunnan Province, China, in subtropical evergreen broad-leaved forest. It grows on moderately decayed angiosperm wood and causes white rot.

Additional specimens examined: China. Yunnan Province, Yuxi, Xinping County, Mopanshan National Forest Park, on decayed trunk of *Quercus*, leg. C.L. Zhao, 19 Aug 2017, CLZhao 2252, CLZhao 2316 (SWFC); Shimenxia Forestry Park, on fallen angiosperm trunk, leg. C.L. Zhao, 21 Aug 2017, CLZhao 2707, CLZhao 2719 (SWFC); Puer, Jingdong County, Ailaoshan National Nature Reserve, on decayed trunk of *Rhododendron*, leg. C.L. Zhao, 4 Oct 2017, CLZhao 3915 (SWFC); Yuxi, Xinping County, the Ancient Tea Horse Road, on fallen angiosperm trunk, leg. C.L. Zhao, 13 Jan 2018, CLZhao 5217, CLZhao 5228 (SWFC); on fallen angiosperm trunk, leg. C.L. Zhao, 15 Jan 2018, CLZhao 5781 (SWFC).

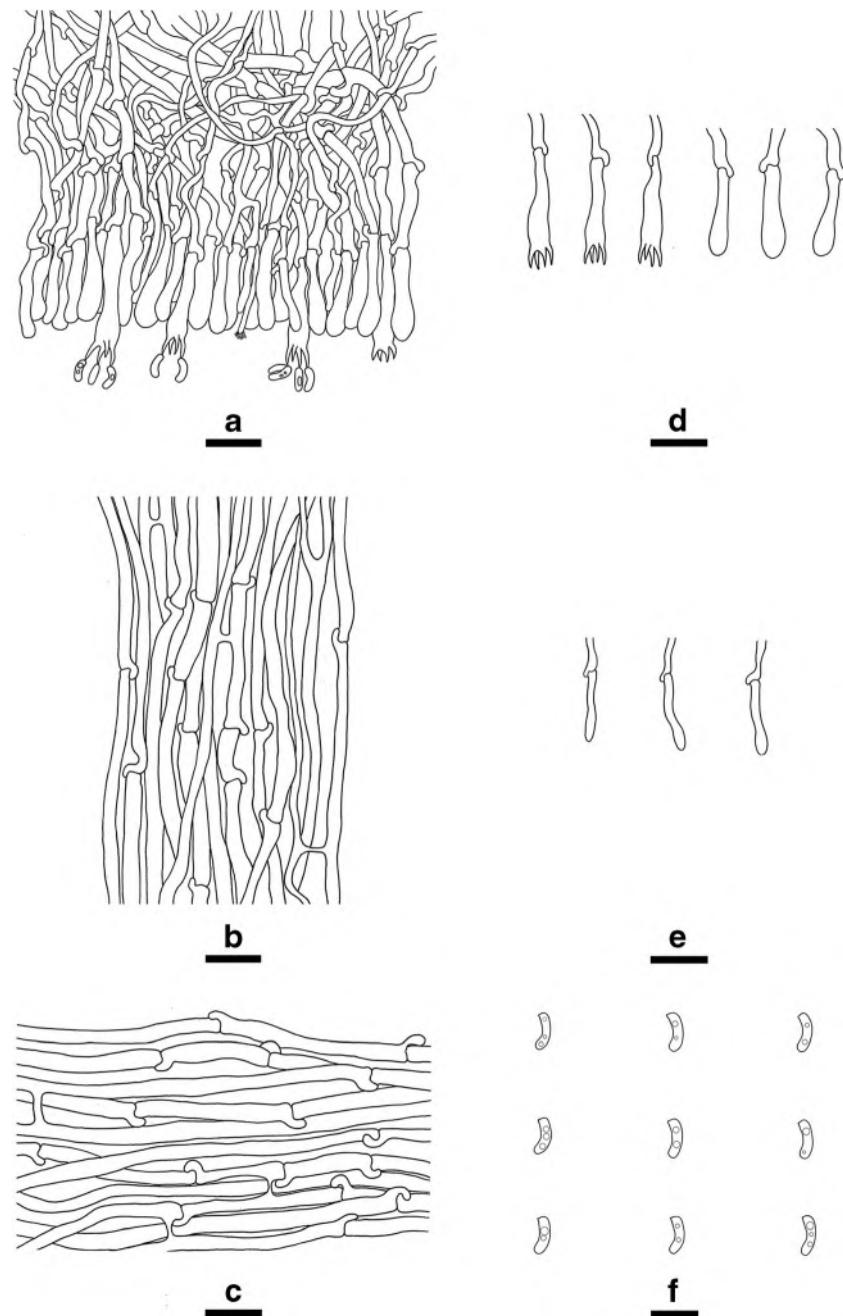
Discussions

In the present study, *Phlebia fuscotuberculata*, *Ph. tomentopileata* and *Ph. tongxiniana* are described as new species based on phylogenetic analyses and morphological characters.

Phylogenetically, Binder et al. (2013) revealed that seven clades were found in the Polyporales: antrodia clade, core polyporoid clade, fragiliporia clade, gelatoporia clade, phlebioid clade, residual polyporoid clade and tyromyces clade. According to our results based on the combined ITS+28S sequence data (Fig. 1), three species are nested into the phlebioid clade with strong support (100% BS, 100% BP, 1.00 BPP).

Phlebia fuscotuberculata occurred to be closely related to *Ph. hydnoidea* and *Ph. nantahaliensis* in the rDNA based on the phylogeny (Fig. 2). But morphologically

Fig. 6 Microscopic structures of *Phlebia tomentopileata* (drawn from the holotype). **a** A section of basidioma. **b** Hyphae from trama. **c** Hyphae from subiculum. **d** Basidia and basidioles. **e** Cystidioles. **f** Basidiospores. Scale bars: a–e = 10 μm ; f = 5 μm



Ph. hydnoides has effused-reflexed basidiomata with grandinioid to hydnaceous hymenial surface and larger cystidia ($35–100 \times 3.5–9 \mu\text{m}$; Schweinitz 1832; Nakasone and Burdsall 1995). *Phlebia nantahaliensis* differs from *Ph. fuscotuberculata* by having the greyish

yellow hymenial surface and allantoid basidiospores ($4.5–5.5 \times 1.8–2 \mu\text{m}$; Nakasone and Burdsall 1995).

Phlebia tomentopileata grouped with *Ph. tremellosa* based on the combined ITS+28S sequence data. However, *Ph. tremellosa* differs in having slightly thick-walled

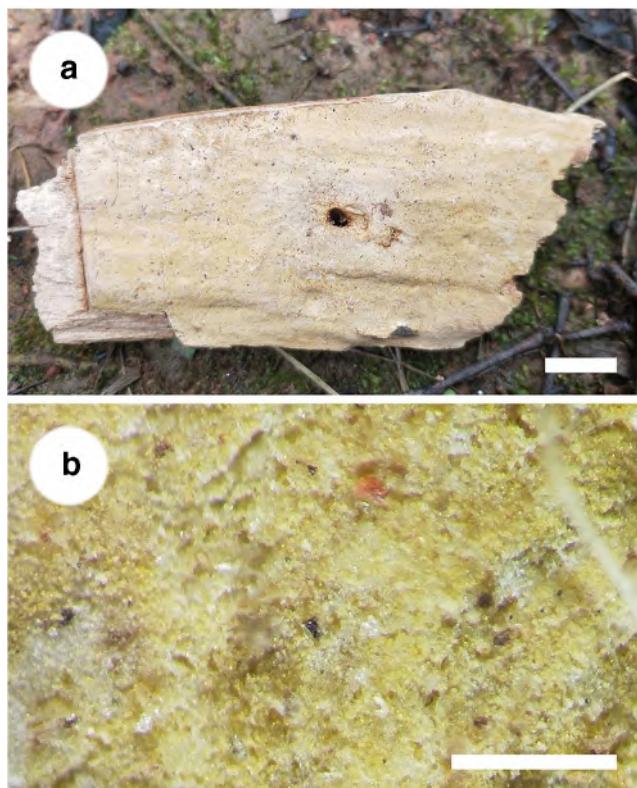


Fig. 7 Basidioma of *Phlebia tongxiniana* (holotype). Scale bars: a = 1 cm; b = 10 cm

generative hyphae and larger basidia ($20\text{--}25 \times 4\text{--}5 \mu\text{m}$; Bernicchia and Gorjón 2010).

Phlebia tongxiniana grouped with *Ph. chrysocreas* based on phylogenetic analyses, but *Ph. chrysocreas* is separated from *Ph. tongxiniana* by smooth to slightly warted, ochraceous-buff to yellow ochre hymenial surface and cylindrical to ellipsoid basidiospores ($4\text{--}5.5 \times 2\text{--}2.5 \mu\text{m}$); in addition, presence of cystidia (Lombard et al. 1975).

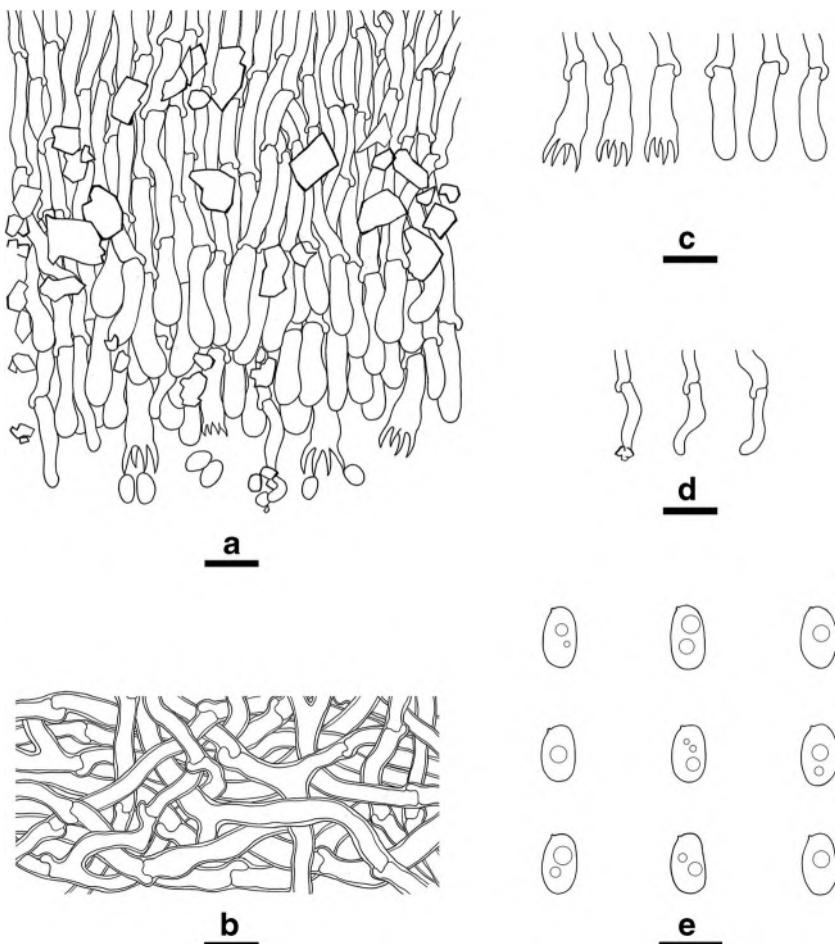
Morphologically, *Phlebia fuscotuberculata* is similar to *Ph. albida* Fr., *Ph. centrifuga* P. Karst., *Ph. chrysocreas* (Berk. & M.A. Curtis) Burds., *Ph. deflectens* (P. Karst.) Ryvarden, *Ph. lilascens* (Bourdot) J. Erikss. & Hjortstam and *Ph. livida* (Pers.) Bres. inferred from the characters by tuberculate hymenophore. However, *Ph. albida* differs from *Ph. fuscotuberculata* by having fimbriate margin and larger basidiospores ($6\text{--}7.5 \times 2.5\text{--}3.5 \mu\text{m}$; Fries 1863). *Phlebia centrifuga* differs in its white to grey hymenial surface, encrusted generative hyphae and larger basidiospores ($6\text{--}9 \times 2.5\text{--}3.5 \mu\text{m}$;

Bernicchia and Gorjón 2010). *Phlebia chrysocreas* is separated from *Ph. fuscotuberculata* by ochraceous-buff to yellow ochre hymenial surface, presence of encrusted generative hyphae and cylindrical to ventricose-rostrate cystidia (Lombard et al. 1975). *Phlebia deflectens* differs in its ochraceous to pale brown hymenial surface and simple generative hyphae (Bernicchia and Gorjón 2010). *Phlebia lilascens* differs from *Ph. fuscotuberculata* by having effuse-reflexed basidiomata with yellowish to pale ochraceous and brown hymenial surface (Bernicchia and Gorjón 2010). *Phlebia livida* is separated from *Ph. fuscotuberculata* by its larger cystidia ($40\text{--}50 \times 3\text{--}4 \mu\text{m}$) and basidiospores ($5\text{--}6 \times 2\text{--}2.5 \mu\text{m}$; Bresadola 1897).

Phlebia tomentopileata is similar to *Ph. rufa* (Pers.) M.P. Christ. and *Ph. tremellosa* on the basis of meruliod hymenophore, but *Ph. rufa* is separated from *Ph. tomentopileata* by pale yellowish, reddish or brownish hymenial surface, presence of cystidia and larger basidiospores ($4.5\text{--}6.5 \times 2\text{--}2.5 \mu\text{m}$; Bernicchia and Gorjón 2010).

Phlebia tongxiniana is similar to *Ph. bresadolae* Parmasto, *Ph. lacteola* (Bourdot) M.P. Christ., *Ph. lilascens* (Bourdot) J. Erikss. & Hjortstam, *Ph. nitidula* (P. Karst.) Ryvarden, *Ph. ochraceofulva* (Bourdot & Galzin) Donk, *Ph. segregata* (Bourdot & Galzin) Parmasto, *Ph. subceracea* (Wakef.) Nakasone, *Ph. subserialis* (Bourdot & Galzin) Donk and *Ph. subulata* J. Erikss. & Hjortstam in smooth hymenophore. However, *Ph. bresadolae* differs in its ochraceous to brownish hymenial surface, slightly thick-walled generative hyphae and larger basidiospores ($6\text{--}7.5 \times 3\text{--}3.5 \mu\text{m}$; Parmasto 1967). *Ph. lacteola* differs in its white hymenial surface with cracked hymenophore (Bernicchia and Gorjón 2010). *Ph. lilascens* differs from *Ph. tongxiniana* by presence of pale ochraceous to brown or violaceous tints in basidiomata and narrower basidiospores ($4\text{--}4.5 \times 2\text{--}2.5 \mu\text{m}$; Bernicchia and Gorjón 2010). *Phlebia nitidula* differs from *Ph. tongxiniana* by the white to yellowish and brownish hymenial surface and larger basidiospores ($6\text{--}8 \times 2.5\text{--}3.5 \mu\text{m}$; Bernicchia and Gorjón 2010). *Ph. ochraceofulva* differs from *Ph. tongxiniana* by dense and conglutinated tissue and the numerous cystida with some secondary septa (Donk 1957). *Phlebia segregata* differs in its white hymenial surface, presence of cystidia and larger basidiospores ($6\text{--}7 \times 2\text{--}2.5 \mu\text{m}$; Parmasto 1967). *Phlebia subceracea* differs from *Ph. tongxiniana* by the white hymenial

Fig. 8 Microscopic structures of *Phlebia tongxiniana* (drawn from the holotype). **a** A section of basidioma. **b** Hyphae from subcicum. **c** Basidia and basidioles. **d** Cystidioles. **e** Basidiospores. Scale bars: a–d = 10 µm; e = 5 µm



surface and allantoid basidiospores ($6\text{--}7 \times 1.5\text{--}2 \mu\text{m}$; Bernicchia and Gorjón 2010). *Phlebia subserialis* differs in its effused-reflexed basidiomata and larger basidiospores ($6\text{--}7 \times 2\text{--}2.5 \mu\text{m}$; Donk 1957; Bernicchia and Gorjón 2010). *Ph. subulata* differs in its subulate cystidia (Eriksson et al. 1981).

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