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## Research Article

**Morphological and phylogenetic characterization of fungi within Hymenochaetales: introducing two new species from southern China**

Xi Luo, Yu-Hui Chen, Chang-Lin Zhao

Nordic Journal of Botany | Early View

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Abstract

## Research Article

***Conocybe romagnesii* and *Gerranema subclavatum* (Basidiomycota: Agaricales) in the Central Black Sea Region of Turkey**

Meryem Senay Sengul Demirak, Ibrahim Turkekul, Hakan Isik

Nordic Journal of Botany | Early View

First published: 10 November 2021

Abstract

## Research Article

***Hedyotis pubirachis* (Rubiaceae), a new species from Guangdong, China**

Yi-De Xu, Rui-Jiang Wang

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First published: 03 November 2021

Abstract

## Research Article

***Trisetopsis pirpanjalensis* and *Tzeveviochloa yadavii* (Poaceae: Aveninae), two new oat-like perennial grass species from India**

Dileshwar Prasad, Shailja Tripathi, Shubham Jaiswal, Rekha Yadav, Priyanka Agnihotri

Nordic Journal of Botany | Volume 39, Issue 11

First published: 19 October 2021

Abstract

## Research Article

***Lophozia svalbardensis* (Lophoziaaceae) in continental North America, Greenland and Siberia, its identity, variation and differentiation**

Alexey D. Potemkin, Anna A. Vilnet

Nordic Journal of Botany | Volume 39, Issue 11

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Abstract

## Research Article

**Effects of experimental warming on vegetative and reproductive growth of *Polygonum viviparum* in the Qinghai-Tibet Plateau**

Chan Zhang, Xian-Ting Li, Yu-Meng An, Zhong-Hua Zhang, Fei Ren, Hua-Kun Zhou

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Abstract

## Research Article Open Access

**Legacies of historic charcoal production affect the forest flora in a Swedish mining district**

Ove Eriksson, Linnea Glav Lundin

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Abstract

# NORDIC JOURNAL OF BOTANY

## Research

### Morphological and phylogenetic characterization of fungi within Hymenochaetales: introducing two new species from southern China

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Two new wood-inhabiting fungal species, *Lyomyces niveus* and *L. ochraceoalbus* spp. nov. are proposed based on a combination of morphological and molecular evidence. *Lyomyces ochraceoalbus* is characterised by resupinate basidiomata with tuberculate, cracking hymenial surface, clavate basidia with a median constriction, gathering numerous irregular crystals, and thin-walled basidiospores with one or two globules. *Lyomyces niveus* is characterised by resupinate basidiomata, smooth to grandinoid hymenial surface, presence of three kinds of cystidia, and broadly ellipsoid basidiospores. Sequences of the ITS and nLSU gene regions were generated, and phylogenetic analyses were performed with maximum likelihood, maximum parsimony and Bayesian inference methods. The phylogenetic reconstruction of Schizoporaceae based on a concatenated ITS+nLSU dataset showed that the two new species are nested in *Lyomyces*. A second phylogenetic analysis, of the genus *Lyomyces*, demonstrated that multiple isolates of *L. niveus* forms a monophyletic lineage which is sister to a clade comprising *L. crustosus*, *L. juniperi*, *L. ochraceoalbus* and *L. vietnamensis*. Moreover, *L. ochraceoalbus* is closely related to *L. crustosus*.

Keywords: corticioid fungi, *Lyomyces*, molecular systematics, Schizoporaceae, taxonomy, Yunnan Province

#### Introduction

Fungi are the most important organisms in nature, in which the multiple roles of fungi in forest ecosystems are well known. When they live as heterotrophic organisms, their nutrition is pathogenic, symbiotic or saprobic and the mode of nutrition determines their forestry significance. When they live as pathogens, they can cause diseases, sometimes death of the forest trees, or discoloration and heart rot in their trunk. When they live as symbiotic partners on roots of forest trees (mycorrhiza), they improve the nutrition and defense capacity of trees against root pathogens (Szabó 1999). The saprobic activity of fungi decomposing dead wood and leaf litter is very important in the humification process, but they can also cause serious damages by staining and



destroying felled trunks or stored and utilized wood products. Furthermore, the basidiomata of many fungi growing in forest are comestible and represent a not negligible source of human alimentation (Szabó 1999).

Since numerous wood-decay fungi have the capability to degrade the lignin constituent, wood-decay fungi play an essential role in the decomposition of coarse woody debris (CWD) derived from trees and other woody plants that make up the major component of the vegetation in forest ecosystems, (Gora et al. 2018). The decomposition of CWD is an exceedingly critical environmental process since CWD is important in nutrient recycling, represents the primary carbon resource in ecosystems, and exerts a major influence on the development of soils (Hättenschwiler et al. 2005, Kwaśna et al. 2017). Rot fungi (WRF) are well known for their extensive organic compound degradation abilities and display a considerable ability to transform or degrade different environmental contaminants (Zhuo and Fan 2021).

Corticoid fungi are a diverse and heterogeneous group of fungi mainly referred to basidiomycete fungi in which basidiomes are generally resupinate, in which basidiome construction is often simple, and in most cases, only generative hyphae are found, and in more structured basidiomes, those with a reflexed margin or with a pileate surface, more or less sclerified hyphae are usually found (Gorjón 2020). Molecular phylogenetic studies have elucidated the relationships among different taxa of corticoid fungi, which is now known to be a polyphyletic group (Larsson and Larsson 2003, Larsson et al. 2004, Binder et al. 2005, 2010, Larsson 2007, Sulistyo et al. 2021).

*Lyomyces* P. Karst. (Hymenochaetales, Basidiomycota) is a small corticoid genus, typified by *L. sambuci* (Pers.) P. Karst. The genus is characterized by resupinate to effused basidiomata with smooth to granular or odontoid hymenophore, a monomitic hyphal system bearing clamp connections, strongly encrusted generative hyphae, the presence of several types of cystidia, clavate to suburniform basidia, and smooth, thin- to slightly thick-walled and cyanophilous basidiospores (Karsten 1881, Bernicchia and Gorjón 2010). Species of *Lyomyces* are found on dead, still-attached or fallen branches of angiosperms, on dead wooden or herbaceous stems, or occasionally on gymnosperm wood (Yurchenko et al. 2017). Worldwide, thirty-eight *Lyomyces* species are currently known (Karsten 1881, 1882, 1884, 1889, Bourdot and Galzin 1991, Cunningham 1959, 1963, Wu 1990, Hjortstam and Ryvarden 2009, Xiong et al. 2009, Yurchenko and Wu 2013, Yurchenko et al. 2013, 2017, 2020, Gafforov et al. 2017, Riebesehl and Langer 2017, Chen and Zhao 2020).

Riebesehl and Langer (2017) concluded that *Hyphodontia* s.l. should be divided into several genera, viz. *Hastodontia*, *Hyphodontia*, *Kneiffella*, *Lagarobasidium*, *Lyomyces* and *Xylodon* and thus proposed 35 new combinations, including fourteen *Lyomyces* species. Yurchenko et al. (2017) clarified *Lyomyces sambuci* as a species complex based on sequences of the internal transcribed spacer (ITS) and the nuclear large subunit (nLSU) ribosomal DNA gene and described four new species. Viner et al. (2018) studied the taxonomy of *Lagarobasidium* and *Xylodon* and showed that twelve species

clustered into the *Lyomyces* clade and then grouped with *Xylodon* clade. Riebesehl et al. (2019) emended the generic concept of *Lyomyces* and presented an identification key to all 22 species, and their phylogenetic reconstruction showed that *L. sambuci* was sister to *L. crustosus* (Pers.) P. Karst. which formed a single lineage with a high support. Based on sequences of ITS and nLSU, Yurchenko et al. (2020) revealed that *Fasciodontia*, *Hastodontia*, *Hyphodontia*, *Lyomyces*, *Tubulicrinis* and *Xylodon* grouped together and seven species clustered into *Lyomyces*. A taxonomic study of *Lyomyces* by Chen and Zhao (2020) plotted macro- and micromorphological characteristics onto an ITS-based phylogeny and found that none of them are phylogenetically informative.

During investigations on wood-inhabiting fungi in southern China, the authors found two species of *Lyomyces* that could not be assigned to any of the described species. These species are here described as *L. niveus* and *L. ochraceoalbus* based on morphological study and molecular phylogenetic analyses.

## Material and methods

### Morphology

The specimens studied were deposited at the herbarium of Southwest Forestry University (SWFC), Kunming, Yunnan Province, China. The macromorphological descriptions presented here are based on field notes and photos captured in the field and lab. Colour terminology follow Petersen (1996). Micromorphological data were obtained from dried specimens, which were observed under a light microscope following Dai (2012) and Cui et al. (2019). The following abbreviations were used: KOH = 5% potassium hydroxide water solution, CB = Cotton Blue, CB- = acyanophilous, IKI = Melzer's reagent, IKI- = both inamyloid and indextrinoid, L = mean spore length (arithmetic average for all spores), W = mean spore width (arithmetic average for all spores), 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

CTAB rapid plant genome extraction kit-DN14 (Aidlab Biotechnologies Co., Ltd., Beijing) was used to obtain genomic DNA from dried specimens, according to the manufacturer's instructions. The ITS region was amplified with the primer pair ITS5 and ITS4 (White et al. 1990). The nuclear nLSU region was amplified with the primer pair LR0R and LR7 (<<http://lutzonilab.org/primer-sequences/>>; 4 June 2021). The PCR cycling 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 LSU 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 followed Shen et al. (2019). The PCR products were purified and directly sequenced at

Table 1. Name, specimen number, country and corresponding GenBank accession numbers of the sequences used in this study.

Species name	Specimen no.	Country	GenBank accession no.		References
			ITS	nLSU	
<i>Fasciodontia brasiliensis</i> Yurchenko & Riebesehl	MSK-F 7245a	Brazil	MK575201	MK598734	Yurchenko et al. 2020
<i>F. bugellensis</i> (Ces.) Yurchenko, Riebesehl & Langer	KAS-FD 10705a	Greece	MK575203	MK598735	Yurchenko et al. 2020
<i>Hastodontia hastata</i> (Litsch.) Hjortstam & Ryvarde	KHL 14646	Norway	MH638232	MH638232	Viner et al. 2018
<i>Hyphodontia borbonica</i> Riebesehl, Langer & Barniske	FR-0219441	La Réunion	KR349240	MH884915	Riebesehl et al. 2015
<i>Kneiffiella barba-jovis</i> (Bull.) P. Karst.	KHL 11730	Sweden	DQ873609	DQ873610	Larsson et al. 2006
<i>K. palmae</i> Rick ex Hjortstam & Ryvarde	KAS-GEL 3456	China	DQ340333	DQ340369	Yurchenko et al. 2020
<i>Lyomyces allantosporus</i> Riebesehl, Yurchenko & E. Langer	KAS-GEL 4933	La Réunion	KY800401	—	Yurchenko et al. 2017
<i>L. allantosporus</i>	FR 0249548	La Réunion	KY800397	KY795963	Yurchenko et al. 2017
<i>L. bambusinus</i> C.L. Zhao	CLZhao 4808	China	MN945970	—	Chen and Zhao 2020
<i>L. bambusinus</i>	CLZhao 4831	China	MN945968	MW264919	Chen and Zhao 2020
<i>L. cremeus</i> C.L. Zhao	CLZhao 4138	China	MN945974	MW264922	Chen and Zhao 2020
<i>L. cremeus</i>	CLZhao 8295	China	MN945972	—	Chen and Zhao 2020
<i>L. crustosus</i> (Pers.) P. Karst.	YG-G 39	Uzbekistan	MF382993	—	Gafforov et al. 2017
<i>L. crustosus</i>	UC 2022841	USA	KP814310	—	Rosenthal et al. 2017
<i>L. crustosus</i>	KHL 11731	Finland	DQ873614	DQ873614	Larsson et al. 2006
<i>L. erastii</i> (Saaren. & Kotir.) Hjortstam & Ryvarde	MA-Fungi 34336	Spain	JX857800	—	unpubl.
<i>L. erastii</i>	YG 022	Uzbekistan	MF382992	—	Gafforov et al. 2017
<i>L. fimbriatus</i> (Sheng H. Wu) Riebesehl & Yurchenko	Wu 910620-7	China	MK575209	—	Yurchenko et al. 2020
<i>L. fimbriatus</i>	Wu 911204-4	China	MK575210	MK598740	Yurchenko et al. 2020
<i>L. fissuratus</i> C.L. Zhao	CLZhao 4291	China	MW713738	MW713730	unpubl.
<i>L. fissuratus</i>	CLZhao 4352	China	MW713742	—	unpubl.
<i>L. fumosus</i> C.L. Zhao	CLZhao 8188	China	MW713744	MW713736	unpubl.
<i>L. griseliniae</i> (G. Cunn.) Riebesehl & E. Langer	KHL 12971	Costa Rica	DQ873651	DQ873651	Larsson et al. 2006
<i>L. juniperi</i> (Bourdote & Galzin) Riebesehl & E. Langer	KAS-GEL 4940	La Réunion	DQ340316	—	unpubl.
<i>L. juniperi</i>	FR-0261086	La Réunion	KY081799	—	Riebesehl and Langer 2017
<i>L. macrosporus</i> C.L. Zhao	CLZhao 4516	China	MN945977	MW264920	Chen and Zhao 2020
<i>L. macrosporus</i>	CLZhao 8605	China	MN945975	—	Chen and Zhao 2020
<i>L. mascarensis</i> Riebesehl, Yurchenko & E. Lange	KAS-GEL 4833	La Réunion	KY800399	KY795964	Yurchenko et al. 2020
<i>L. mascarensis</i>	KAS-GEL 4908	La Réunion	KY800400	—	Yurchenko et al. 2017
<i>L. microfasciculatus</i> C.L. Zhao	CLZhao 5109	China	MN954311	MW264921	Chen and Zhao 2020
<i>L. niveus</i> C.L. Zhao	CLZhao 2458	China	MZ262540	—	this study
<i>L. niveus</i>	CLZhao 6431	China	MZ262541	MZ262526	this study
<i>L. niveus</i>	CLZhao 6442	China	MZ262542	MZ262527	this study
<i>L. niveus</i>	CLZhao 6474	China	MZ262543	MZ262528	this study
<i>L. niveus</i>	CLZhao 6483	China	MZ262544	MZ262529	this study
<i>L. niveus</i>	CLZhao 6496	China	MZ262545	MZ262530	this study
<i>L. niveus</i>	CLZhao 6565	China	MZ262546	MZ262531	this study
<i>L. ochraceoalbus</i> C.L. Zhao	CLZhao 4385	China	MZ262535	MZ262521	this study
<i>L. ochraceoalbus</i>	CLZhao 4725	China	MZ262536	MZ262522	this study
<i>L. ochraceoalbus</i>	CLZhao 6224	China	MZ262537	MZ262523	this study
<i>L. ochraceoalbus</i>	CLZhao 9819	China	MZ262538	MZ262524	this study
<i>L. ochraceoalbus</i>	CLZhao 10474	China	MZ262539	MZ262525	this study
<i>L. organensis</i> Yurchenko & Riebesehl	MSK-F 7247	Brazil	KY800403	KY795967	Yurchenko et al. 2017
<i>L. orientalis</i> Riebesehl, Yurchenko & E. Langer	KAS-GEL 3376	China	DQ340325	DQ340351	Yurchenko et al. 2017
<i>L. orientalis</i>	KAS-GEL 3400	China	DQ340326	—	Yurchenko et al. 2017
<i>L. pruni</i> (Lasch) Riebesehl & E. Langer	Ryberg 21018	Sweden	DQ873624	DQ873625	Larsson et al. 2006
<i>L. pruni</i>	KAS-GEL 2327	Germany	DQ340312	—	Yurchenko et al. 2020

(Continued)

Table 1. Continued.

Species name	Specimen no.	Country	GenBank accession no.		References
			ITS	nLSU	
<i>L. sambuci</i> (Pers.) P. Karst.	80 SAMHYP	Sweden	JX857721	—	Yurchenko et al. 2017
<i>L. sambuci</i>	83 SAMHYP	USA	JX857720	—	Yurchenko et al. 2017
<i>L. sambuci</i>	KAS-JR 7	Germany	KY800402	KY795966	Yurchenko et al. 2017
<i>L. vietnamensis</i> (Yurchenko & Sheng H. Wu) Riebesehl & E. Langer	Wu 9807-88 /TNM F9073	Vietnam	JX175044	KX857814	Yurchenko et al. 2013
<i>L. vietnamensis</i>	He 3260	China	MW507086	—	unpubl.
<i>L. wuliangshanensis</i> C.L. Zhao	CLZhao 4167	China	MN945979	—	Chen and Zhao 2020
<i>L. wuliangshanensis</i>	CLZhao 4108	China	MN945980	—	Chen and Zhao 2020
<i>Oxyporus populinus</i> (Schumach.) Donk	CBS 218.39	USA	MH855986	MH867486	Vu et al. 2019
<i>Palifer verecundus</i> (G. Cunn.) Stalpers & P.K. Buchanan	KHL 12261	USA	DQ873642	—	Larsson et al. 2006
<i>Xylodon asperus</i> (Fr.) Hjortstam & Ryvarden	UC 2023169	USA	KP814365	—	unpubl.
<i>X. detriticus</i> (Bourdot) K.H. Larss., Viner & Spirin	Zibarová 26.05.17	Czech Republic	MH320794	MH638264	Viner et al. 2018
<i>X. exiliss</i> Yurchenko, Riebesehl & Langer	TUB-FO 42565	China	MH880198	MH884898	Riebesehl et al. 2019
<i>X. flaviporus</i> (Berk. & M.A.Curtis ex Cooke) Riebesehl & Langer	MA-Fungi 79440	Germany	MH260071	MH260066	Fernández-López et al. 2018
<i>X. hyphodotinuss</i> (Hjortstam & Ryvarden) Riebesehl, Yurchenko & G.Gruhn	LIP GG-MAR12-238	Martinique	MH880207	MH884905	Riebesehl et al. 2019
<i>X. nespori</i> (Bres.) Hjortstam & Ryvarden	B.Nordon 30915	Sweden	DQ873622	DQ873622	Larsson et al. 2006
<i>X. quercinus</i> (Pers.) Gray	CBS 333.62	France	MH858169	MH869761	Vu et al. 2019
<i>X. rimosissimus</i> (Peck) Hjortstam & Ryvarden	Ryberg 21031	Sweden	DQ873627	DQ873628	Larsson et al. 2006

Kunming Tsingke Biological Technology Limited Company, Kunming, Yunnan Province, China. All newly generated sequences were deposited in NCBI GenBank (Table 1).

Sequences were aligned in MAFFT 7 (<<https://mafft.cbrc.jp/alignment/server/>>) using G-INS-i strategy for ITS+nLSU combined dataset, and manually adjusted in BioEdit (Hall 1999). The aligned dataset was deposited in TreeBASE (submission ID 28334). Two datasets were compiled with Mesquite. The first one, consisting of ITS+nLSU sequences, was used to position the new species among genera related to *Lyomyces* in Schizoporaceae. The second, ITS-only dataset was used to place the new taxa among previously described species of *Lyomyces*. Outgroups were *Oxyporus populinus* (Schumach.) Donk for the ITS+nLSU dataset, and *Palifer verecundus* (G. Cunn.) Stalpers & P.K. Buchanan and *Xylodon asperus* (Fr.) Hjortstam & Ryvarden for ITS, following previous studies (Yurchenko et al. 2017, 2020).

Maximum parsimony (MP), maximum likelihood (ML) and Bayesian inference (BI) analyses were applied to the combined two datasets. Its approaches followed a previous study (Zhao and Wu 2017), and the tree construction procedure was performed in PAUP\* ver. 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 bootstrap (BT) analysis with 1000 replicates (Felsenstein 1985). Descriptive tree statistics: tree length (TL), consistency index (CI), retention index (RI), rescaled

consistency index (RC) and homoplasy index (HI) were calculated for each maximally parsimonious tree generated. The datamatrix was also analyzed using a maximum likelihood (ML) approach with RAxML-HP2 through the CIPRES Science Gateway (<[www.phylo.org](http://www.phylo.org)>; Miller et al. 2009). Branch support (BS) for ML analysis was determined by 1000 bootstrap replicates and evaluated under the gamma model.

MrModeltest ver. 2.3 (Nylander 2004) was used to determine the best-fit evolution model for each data set for Bayesian inference (BI), which was performed using MrBayes ver. 3.1.2 with a GTR+I+G model of DNA substitution and a gamma distribution rate variation across sites (Ronquist and Huelsenbeck 2003). Four Markov chains were used in each of two runs from random starting trees for 350 000 generations (Fig. 1) and 650 000 generations (Fig. 2), with trees and parameters sampled every 100 generations. The first quarter of generations were discarded as burn-in. A majority rule consensus tree of all remaining trees and posterior probabilities were calculated. Branches were considered as significantly supported if they received a maximum likelihood bootstrap value (BS) > 70%, maximum parsimony bootstrap value (BT) > 70% or Bayesian posterior probabilities (BPP) > 0.95.

## Results

### Molecular phylogeny

The ITS+nLSU dataset (Fig. 1) included sequences from 41 fungal specimens representing 32 species. The dataset had

an aligned length of 2207 characters, of which 1321 characters were constant and 513 parsimony-informative. The MP analysis yielded 2 equally parsimonious trees (TL=2772, CI=0.4852, HI=0.5148, RI=0.6233, RC=0.3024). The best-fit model for the ITS+nLSU alignment estimated and applied in the BI was GTR+I+G (lset nst=6, rates=invgamma; prset statefreqpr=dirichlet (1,1,1,1)). At the end of the BI runs, the average standard deviation of split frequencies was 0.009966 (BI), and the effective sample size (ESS) across the two runs is the double of the average ESS (avg

ESS)=205. The tree topology obtained by BI was similar to the one from MP and ML. The phylogenetic reconstruction (Fig. 1) of Schizoporaceae showed that the two new species nested into *Lyomyces* and formed a well-supported lineage.

The ITS-alone dataset (Fig. 2) included sequences from 49 fungal specimens representing 23 species of *Lyomyces*. The dataset had an aligned length of 636 characters, of which 283 characters were constant and 285 parsimony-informative. The MP analysis yielded 8 equally parsimonious trees (TL=1211, CI=0.4707, HI=0.5293, RI=0.7779,

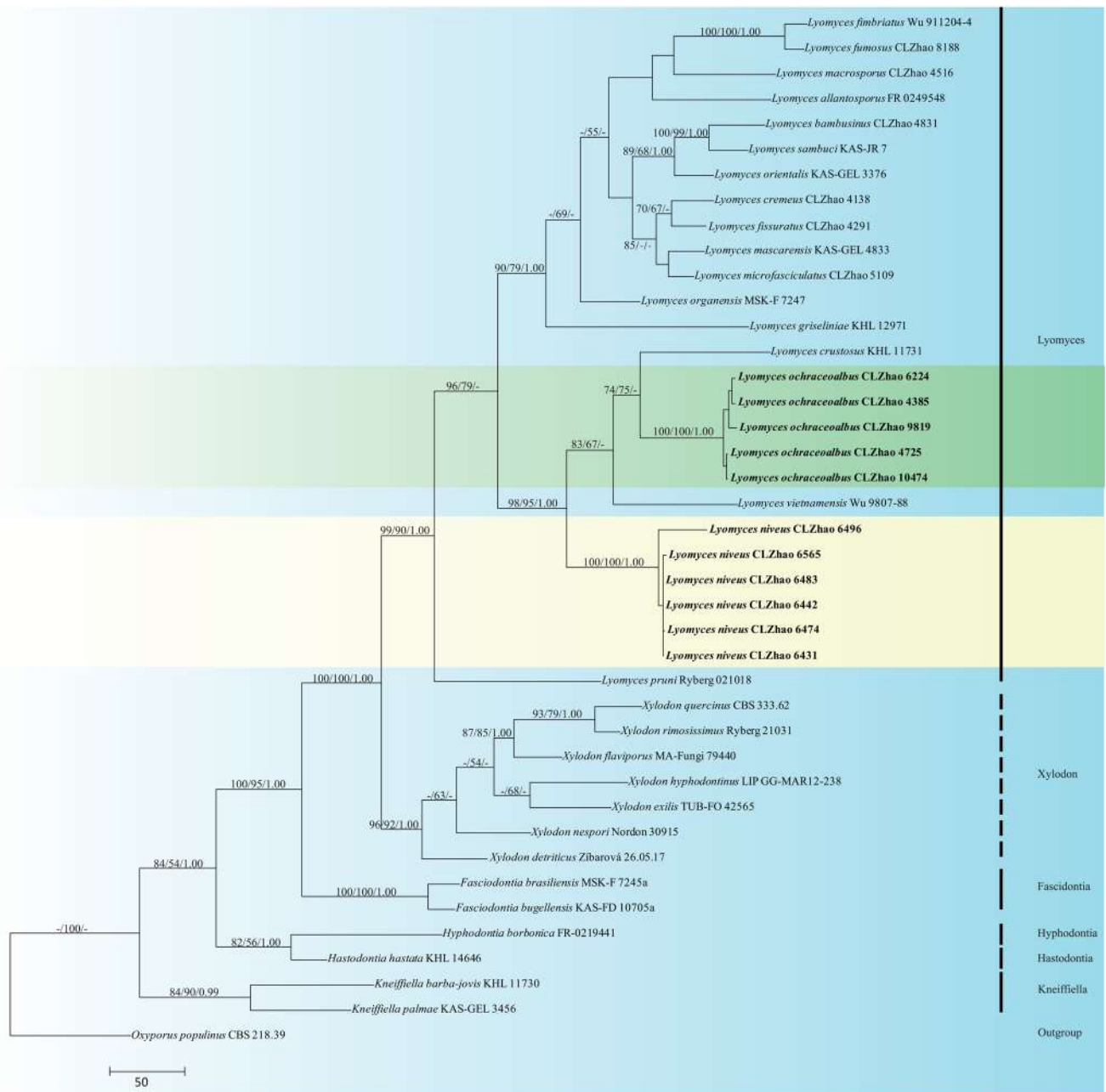


Figure 1. Maximum parsimony strict consensus tree illustrating the phylogeny of two new *Lyomyces* species and related genera in Schizoporaceae based on ITS+nLSU sequences. Branches are labelled with maximum likelihood bootstrap values  $\geq 70\%$ , parsimony bootstrap values  $\geq 50\%$  and Bayesian posterior probabilities  $\geq 0.95$ , respectively. The new species are in bold.

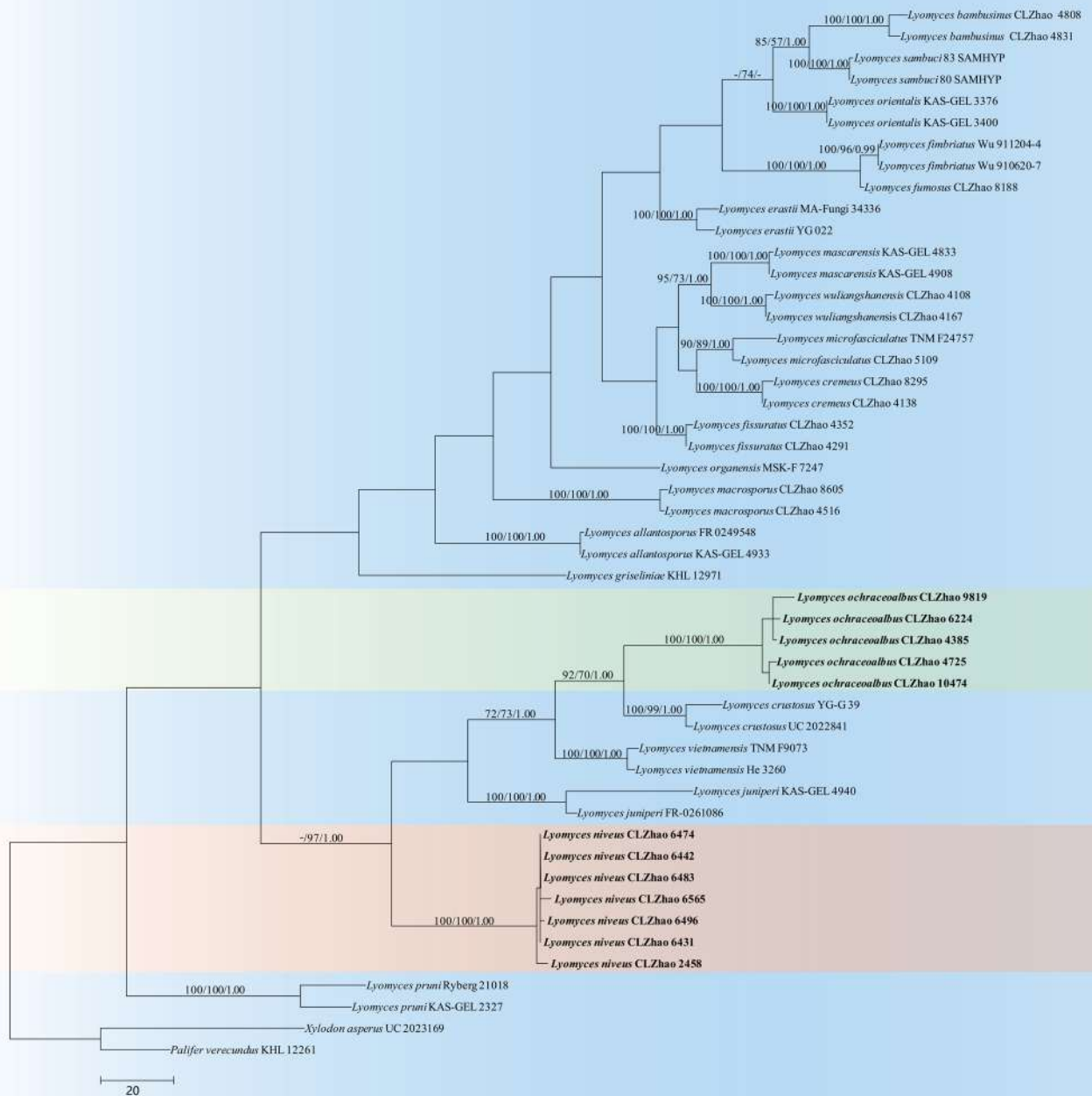


Figure 2. Maximum parsimony strict consensus tree illustrating the phylogeny of two new species and related species in *Lyomyces* based on ITS sequences. Branches are labelled with maximum likelihood bootstrap values  $\geq 70\%$ , parsimony bootstrap values  $\geq 50\%$  and Bayesian posterior probabilities  $\geq 0.95$ , respectively. The new species are in bold.

RC = 0.3661). The best-fit model for the ITS alignment estimated and applied in the BI was GTR+I+G. At the end of the BI runs, the average standard deviation of split frequencies was 0.009981 (BI), and the effective sample size (ESS) across the two runs is the double of the average ESS (avg ESS) = 197. The tree topology obtained by BI was similar to the one from MP and ML. The phylogenetic reconstruction

of the ITS-alone dataset (Fig. 2) demonstrated that *L. niveus* sp. nov. formed a monophyletic lineage and then grouped with a clade comprising *L. juniperi* (Bourdot & Galzin) Riebesehl & Langer, *L. vietnamensis* (Yurchenko & Sheng H. Wu) Riebesehl & Langer and *L. crustosus* (Pers.) P. Karst., while *L. ochraceoalbus* sp. nov. was resolved as the sister species of *L. crustosus*.



## Taxonomy

### *Lyomyces niveus* C.L. Zhao, sp. nov. (Fig. 3, 4)

**Holotype:** China, Yunnan Province: Yuxi, Xiping County, Mopanshan National Forestry Park, 101°57'E, 23°57'N, 2185 m a.s.l., on the trunk of *Pinus armandii*, leg. C.L. Zhao, 19 Jan 2018, CLZhao 6496 (SWFC, HKAS).

MB 841134

Basidiomata annual, resupinate, subcoriaceous when fresh, becoming pruinose upon drying, up to 20 cm long and 3.5 cm wide, 50–130  $\mu\text{m}$  thick. Hymenial surface smooth, white when fresh, turning white to pale buff upon drying. Margin indistinct, white.

Hyphal system monomitic; generative hyphae with clamp connections, colorless, thin-walled, frequently branched; subhymenium with moderately encrusted crystals, 1.5–4.0  $\mu\text{m}$  in diameter; IKI–, CB–; tissues unchanged in KOH.

Cystidia of two types: 1) capitate cystidia colorless, thin-walled, smooth, 12.5–20.5  $\times$  4.5–5.0  $\mu\text{m}$ ; 2) fusiform cystidia colorless, thin-walled, smooth, 12.5–22.0  $\times$  3.0–5.0  $\mu\text{m}$ ; cystidioles absent. Basidia barreled, with 4 sterigmata and a basal clamp connection, 9.5–15.0  $\times$  3.5–5.5  $\mu\text{m}$ ; basidioles abundant, in shape similar to basidia, but slightly smaller.

Basidiospores broadly ellipsoid, colorless, thin-walled, smooth, IKI–, cyanophilous, with a single oil-like globule, (3.0–)3.5–5.0(–6.5)  $\times$  (2.5–)3.0–4.0(–5.0)  $\mu\text{m}$ , L=4.45  $\mu\text{m}$ , W=3.31  $\mu\text{m}$ , Q=1.28–1.46 (n=150/5).

#### **Etymology**

*Niveus* (Lat.): referring to the white hymenial surface.

#### **Ecology and distribution**

The species is known from Yunnan Province of China in subtropical inland plateau climate area. It grows in semi-wet evergreen broad-leaved primary and secondary primary forest, and provokes white rot.

#### **Additional specimens examined (paratypes)**

China, The same locality as holotype, on fallen angiosperm branch, leg. C.L. Zhao, 19 Aug 2017, CLZhao 2458; 19 Jan 2018, CLZhao 6442, CLZhao 6474, CLZhao 6483, CLZhao 6565; on the trunk of *Pinus armandii*, leg. C.L. Zhao, 19 Jan 2018, CLZhao 6431 (SWFC, HKAS).

### *Lyomyces ochraceoalbus* C.L. Zhao, sp. nov. (Fig. 5, 6)

**Holotype:** China, Yunnan Province, Puer, Jingdong County, Wuliangshan National Nature Reserve, 100°24'E, 23°52'N, 2594 m a.s.l., on fallen angiosperm branch, leg. C.L. Zhao, 7 Jan 2019, CLZhao 9819 (SWFC, HKAS).

MB 841135

Basidiomata annual, resupinate, adnate, coriaceous when fresh, becoming membranaceous upon drying, up to 10 cm long and 2.5 cm wide, 50–100  $\mu\text{m}$  thick, cracking. Hymenial surface smooth, greyish white when fresh, turning buff to pale ochraceous upon drying. Margin narrow, greyish white.

Hyphal system monomitic; generative hyphae with clamp connections, colorless, thin-walled, frequently branched,

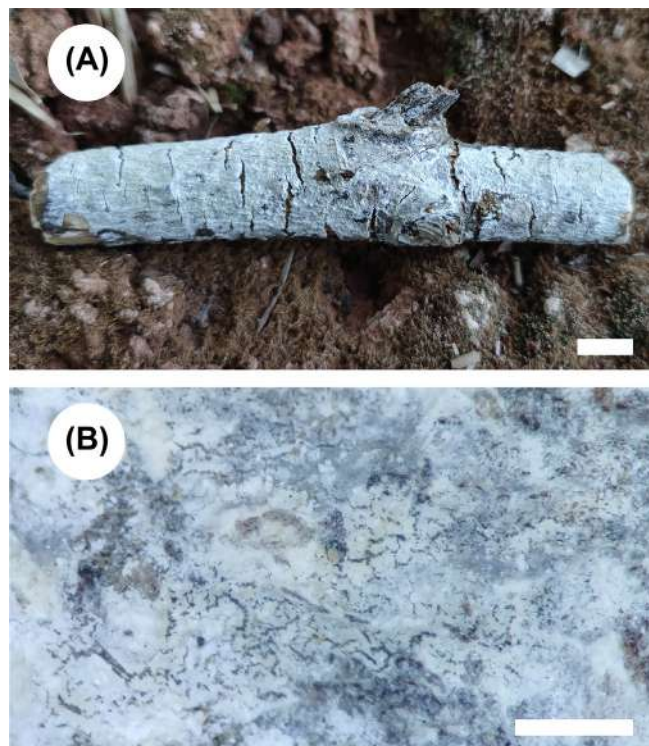


Figure 3. Basidiomata of *Lyomyces niveus* sp. nov. Bars: (A) = 1 cm; (B) = 1 mm (holotype).

interwoven; subicular hyphae richly covered by crystals, 2.0–4.5  $\mu\text{m}$  in diameter; IKI–, CB–; tissues unchanged in KOH.

Cystidia absent, cystidioles colorless, thin-walled, smooth, 10.0–15.0  $\times$  3.0–4.5  $\mu\text{m}$ . Basidia clavate with a median constriction, with 4 sterigmata and a basal clamp connection, 11.0–16.5  $\times$  3.5–5.0  $\mu\text{m}$ ; basidioles abundant, in shape similar to basidia, but slightly smaller.

Basidiospores ellipsoid, colorless, thin-walled, smooth, with one or two oil-like globules, IKI–, cyanophilous, (3.5–)4.0–5.0(–5.5)  $\times$  2.5–3.5(–4.0)  $\mu\text{m}$ , L=4.56  $\mu\text{m}$ , W=3.04  $\mu\text{m}$ , Q=1.43–1.55 (n=120/4).

#### **Etymology**

*Ochraceoalbus* (Lat.): referring to the ochreous and white hymenial surface.

#### **Ecology and distribution**

The species is known from southern China, growing in subtropical and middle-mountain moist evergreen broad-leaved forest, and provokes white rot.

#### **Additional specimens examined (paratypes)**

China, Yunnan Province, Puer, Jingdong County, Wuliangshan National Nature Reserve, 100°24'E, 23°52'N, 2594 m a.s.l., on fallen angiosperm branch, leg. C.L. Zhao, 6 Jan 2017, CLZhao 4385; on dead bamboo, CLZhao 4725; Yuxi, Xiping County, Mopanshan National Forestry Park, 100°02'E, 23°58'N, 2487 m a.s.l., on fallen angiosperm

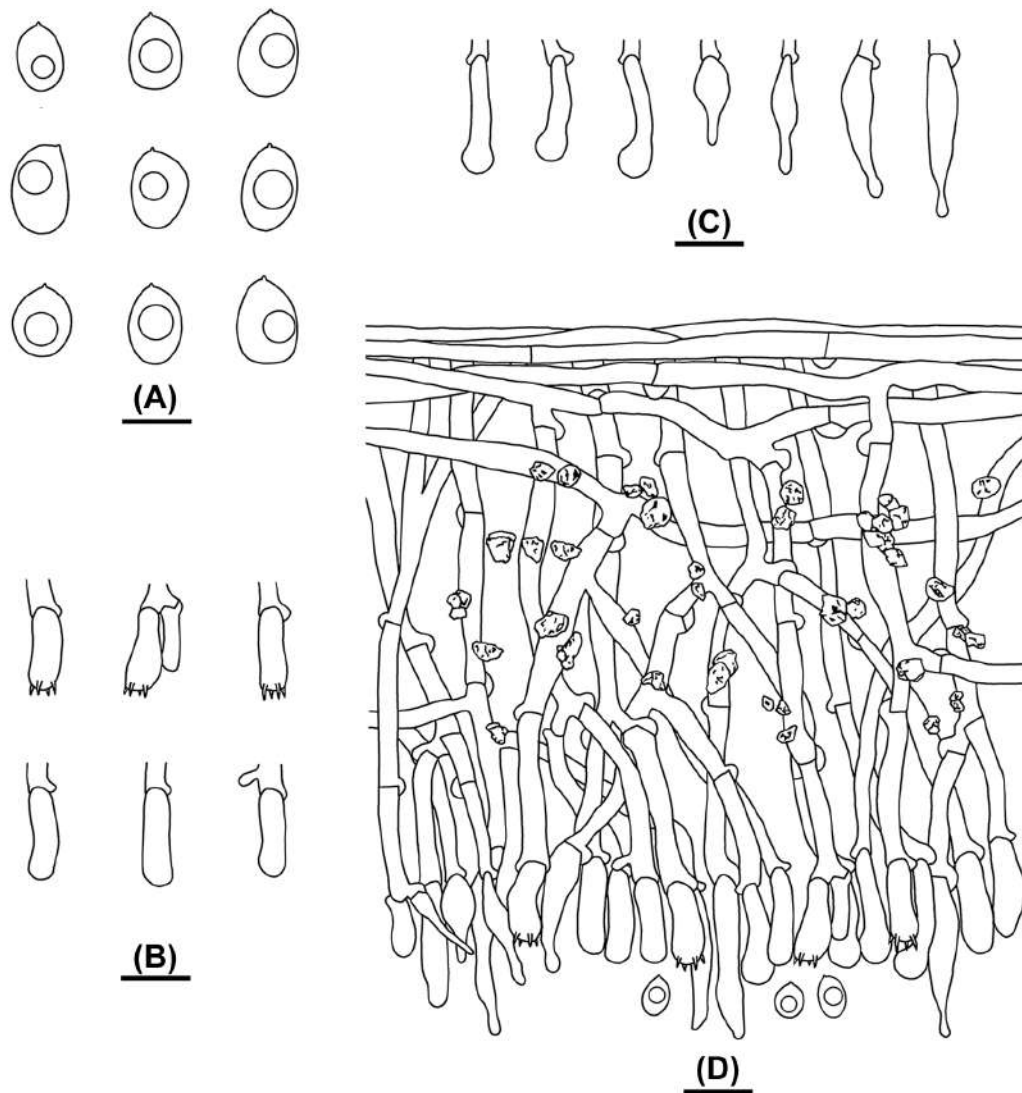


Figure 4. Microscopic structures of *Lyomyces niveus* (drawn from the holotype). (A) basidiospores, (B) basidia and basidioles, (C) cystidia, (D) a section of hymenium. Bars: (A) = 5  $\mu$ m, (B–D) = 10  $\mu$ m.

branch, leg. C.L. Zhao, 18 Jan 2018, CLZhao 6224; Dali, Nanjian County, Lingbaoshan National Forestry Park, 100°30'E, 24°46'N, 2351 m a.s.l., on fallen angiosperm branch, leg. C.L. Zhao, 10 Jan 2019, CLZhao 10474 (SWFC, HKAS).

## Discussion

The phylogenetic reconstruction of ITS+nLSU dataset by Yurchenko et al. (2020) revealed that *Fasciodontia*, *Hastodontia*, *Hyphodontia*, *Lyomyces*, *Tubulicrinis* and *Xylodon* grouped together, with *Lyomyces* and *Xylodon* as sister genera. In the present study, based on ITS and nLSU (Fig. 1) we found that *Lyomyces* grouped with *Fasciodontia*, *Hastodontia*, *Hyphodontia*, *Kneiffiella* and *Xylodon*, and the two new species were nested within *Lyomyces*. Based on ITS topology (Fig. 2),

*L. niveus* formed a monophyletic lineage with strong support (100% BS, 100% BP, 1.00 BPP), sister to a clade comprised of *L. juniperi*, *L. vietnamensis*, *L. crustosus* and *L. ochraceoalbus*. *Lyomyces ochraceoalbus* was resolved as closely related to *L. crustosus*.

Morphologically, *Lyomyces crustosus* differs from *L. niveus* by having small aculei and longer basidia (20–30  $\mu$ m; Eriksson 1958); *L. vietnamensis* differs by the presence of peg-like hyphal aggregations, longer basidia (17–20  $\mu$ m) and basidiospores (6.0–6.5  $\mu$ m; Yurchenko et al. 2013); *L. juniperi* differs by having longer basidia (15–25  $\mu$ m; Hjortstam and Ryvarden 2009).

*Lyomyces crustosus* differs from *L. ochraceoalbus* by having a fruitbody that is subcrustaceous when alive, crustaceous when dried, small aculei and longer basidia (20–30  $\mu$ m; Eriksson 1958); *L. vietnamensis* differs by having a grandinioid hymenophore, presence of peg-like hyphal aggregations

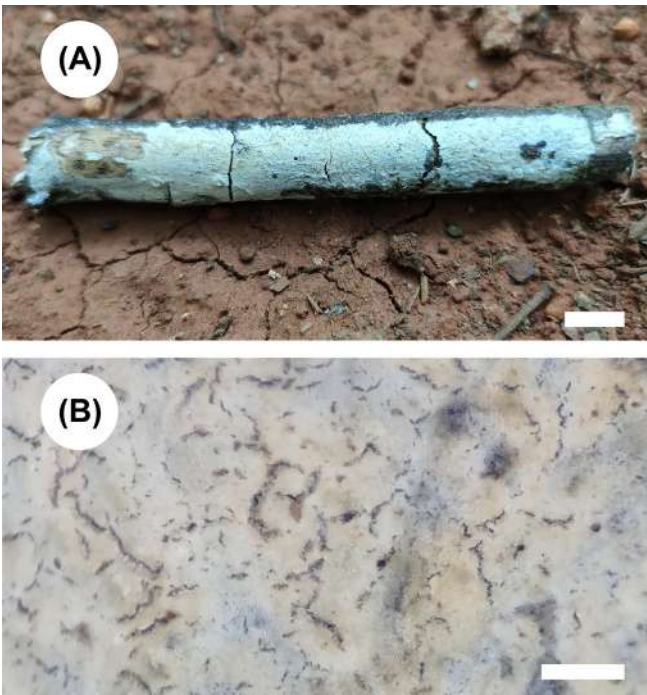


Figure 5. Basidiomata of *Lyomyces ochraceoalbus* sp. nov. Bars: (A) = 1 cm, (B) = 1 mm (holotype).

and slightly longer basidia (17–20  $\mu\text{m}$ ) and basidiospores (6.0–6.5  $\mu\text{m}$ ; Yurchenko et al. 2013); *L. juniperi* differs by having smooth to slightly grandinioid hymenophore (Langer 1994). *Lyomyces niveus* is similar to *L. ochraceoalbus* but have more visible cystidia.

Eleven *Lyomyces* species were reported from China prior to this study. These are *Lyomyces albus* (Sheng H. Wu) Riebesehl & Langer, *L. bambusinus* C.L. Zhao, *L. capitatocystidiatus* (H.X. Xiong, Y.C. Dai & Sheng H. Wu) Riebesehl & Langer, *L. cremeus* C.L. Zhao, *L. fissuratus* C.L. Zhao, *L. fumosus* C.L. Zhao, *L. macrosporus* C.L. Zhao, *L. microfasciculatus* (Yurchenko & Sheng H. Wu) Riebesehl & Langer, *L. sambuci*, *L. tenuissimus* (Yurchenko & Sheng H. Wu) Riebesehl & Langer and *L. wuliangshanensis* C.L. Zhao (Xiong et al. 2009, Yurchenko and Wu 2013, Yurchenko et al. 2013, Riebesehl and Langer 2017, Chen and Zhao 2020). Based on our morphology and phylogeny studies, all of these can be separated from the two new species (Fig. 1, 2).

The family Schizoporaceae is an extensively studied group of Hymenochaetales (Dai 2012, Zhao et al. 2014, Viner et al. 2018, Cui et al. 2019, Riebesehl et al. 2019, Shi et al. 2019, He et al. 2020, Xu et al. 2020), but the Chinese species diversity is still not well known, especially in subtropical and tropical areas. The two new *Lyomyces* species here described are from the subtropics. It is likely that more new taxa will be found after further fieldwork and molecular analyses.

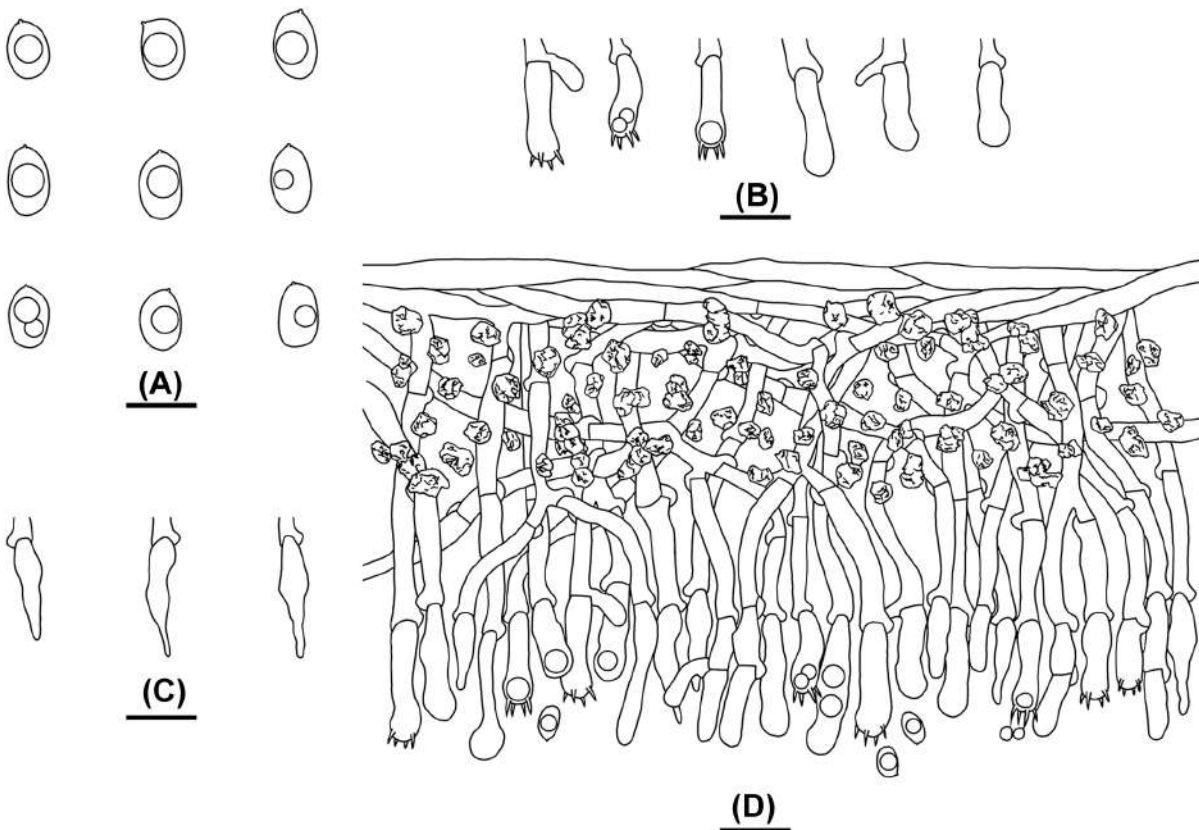


Figure 6. Microscopic structures of *Lyomyces ochraceoalbus* (drawn from the holotype). (A) basidiospores, (B) basidia and basidioles, (C) cystidioles, (D) A section of hymenium. Bars: (A) = 5  $\mu\text{m}$ , (B–D) = 10  $\mu\text{m}$ .

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## Author contributions

**Xi Luo:** Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Software (equal); Validation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Yuhui Chen:** Data curation (equal); Project administration (equal); Writing – original draft (equal); Writing – review and editing (equal). **Changlin Zhao:** Conceptualization (lead); Data curation (lead); Formal analysis (lead); Funding acquisition (lead); Investigation (lead); Methodology (lead); Project administration (lead); Resources (lead); Software (lead); Supervision (lead); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead).

## Data availability statement

Data are available from the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.2rbnz7p1>> (Luo et al. 2021).

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