Research Article
Morphological and phylogenetic characterization of fungi within Hymenochaetales: introducing two new species from southern China
Xi Luo, Yuxin Chen, Chong-ling Zhao
Nordic Journal of Botany | Early View
First published: 17 November 2021
Abstract

Research Article
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First published: 16 November 2021
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Dhriti.Basu Prasad, Shubha Tapshi, Shishir Jamwal, Neha Yadav, Priyanka Agnihotri
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First published: 19 October 2021
Abstract

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Alexander J. Formling, Nina A. Whit
Nordic Journal of Botany | Volume 38, Issue 11
First published: 19 October 2021
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Chao Zhang, Xian-Feng Lu, Ya-Hong Lin, Zhi-Hua Zhang, Fei Ren, Huan-Kun Zhao
Nordic Journal of Botany | Volume 38, Issue 11
First published: 12 October 2021
Abstract

Research Article
Legacies of historic charcoal production affect the forest flora in a Swedish mining district
Ove Brekke, Linda Söderlind
Nordic Journal of Botany | Volume 38, Issue 11
First published: 13 October 2021
Abstract
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 grandinioid 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).

Corticioid 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 reflected 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 corticioid 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). The specimens studied were deposited at the herbarium of the Kunming Institute of Botany, Chinese Academy of Sciences, 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).

**Material and methods**

**Morphology**

The species 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://lutilab.com/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 45 s and 72°C for 1 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.

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<tr>
<th>Species name</th>
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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 taxon 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-HPC2 through the CIPRES Science Gateway (<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 was 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

### Table 1. Continued.

<table>
<thead>
<tr>
<th>Species name</th>
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<td>LIP GG-MAR12-238</td>
<td>Martinique</td>
<td>MH880207 MH884905</td>
<td>Riebesehl et al. 2019</td>
</tr>
<tr>
<td><em>X. quercinus</em> (Pers.) Gray</td>
<td>B.Nordon 30915</td>
<td>Sweden</td>
<td>DQ873622 DQ873622</td>
<td>Larsson et al. 2006</td>
</tr>
<tr>
<td><em>X. rimosissimus</em> (Peck) Hjortstam &amp; Ryvarden</td>
<td>CBS 333.62</td>
<td>France</td>
<td>DQ873619 DQ869761</td>
<td>Vu et al. 2019</td>
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<tr>
<td></td>
<td>Ryberg 21031</td>
<td>Sweden</td>
<td>DQ873627 DQ873628</td>
<td>Larsson et al. 2006</td>
</tr>
</tbody>
</table>

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- Cooke) Riebesehl & Langer
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- Ryvarden
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- & Spirin
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- & Fr.
- & Hjortstam & Ryvarden
- & Sandgren
- & Gruhn
- & Gruhn
- Donk
- & P. Karst.
- & Hjortstam & Ryvarden
- & Hjortstam & Ryvarden
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- & Hjortstam & Ryvarden
- & K.H. Larss., Viner & Spirin
- & Hjortstam & Ryvarden
- (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-HPC2 through the CIPRES Science Gateway (<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 was 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 (iset nst = 6, rates = inv-gamma; preset 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 ≥ 70%, parsimony bootstrap values ≥ 50% and Bayesian posterior probabilities ≥ 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*.

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 ≥ 70%, parsimony bootstrap values ≥ 50% and Bayesian posterior probabilities ≥ 0.95, respectively. The new species are in bold.
Lyomyces niveus C.L. Zhao, sp. nov. (Fig. 3, 4)

Holotype: China, Yunnan Province: Yuxi, Xinping 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 µm 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 µm in diameter; IKI–, CB–; tissues unchanged in KOH.

Cystidia of two types: 1) capitate cystidia colorless, thin-walled, smooth, 12.5–20.5 × 4.5–5.0 µm; 2) fusiform cystidia colorless, thin-walled, smooth, 12.5–22.0 × 3.0–5.0 µm; cystidioles absent. Basidia barreled, with 4 sterigmata and a basal clamp connection, 9.5–15.0 × 3.5–5.5 µm; 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) × (2.5–)3.0–4.0(–5.0) µm, L = 4.45 µm, W = 3.31 µm, 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 µm thick, cracking. Hymenial surface smooth, greyish white when fresh, turning buff to pale ochreous upon drying. Margin narrow, greyish white.

Hyphal system monomitic; generative hyphae with clamp connections, colorless, thin-walled, frequently branched, interwoven; subicular hyphae richly covered by crystals, 2.0–4.5 µm in diameter; IKI–, CB–; tissues unchanged in KOH.

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

Basidiospores ellipsoid, colorless, thin-walled, smooth, with one or two oil-like globules, 4.0–5.0(–5.5) × 2.5–3.5(–4.0) µm, L = 4.56 µm, W = 3.04 µm, Q = 1.43–1.55 (n = 120/4).

Etymology
Ochraceoalbus (Lat.): referring to the ocherous 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, Xinping County, Mopanshan National Forestry Park, 100°02’E, 23°58’N, 2487 m a.s.l., on fallen angiosperm branch.
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, Kneiffielle 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 μm; Eriksson 1958); *L. vietnamensis* differs by the presence of peg-like hyphal aggregations, longer basidia (17–20 μm) and basidiospores (6.0–6.5 μm; Yurchenko et al. 2013); *L. juniperi* differs by having longer basidia (15–25 μm; Hjortstam and Ryvarden 2009).

*Lyomyces crustosus* differs from *L. ochraceoalbus* by having a fruitbody that is suberaceous when alive, crustaceous when dried, small aculei and longer basidia (20–30 μm; Eriksson 1958); *L. vietnamensis* differs by having a grandinioid hymenophore, presence of peg-like hyphal aggregations...
and slightly longer basidia (17–20 μm) and basidiospores (6.0–6.5 μm; Yurchenko et al. 2013); L. juniperi differs by having smooth to slightly grandinoid 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, 9. sambuci, L. tenuissimus (Yurchenko & Sheng H. Wu) Riebesehl & Langer and L. wulianshanensis 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 5. Basidiomata of Lyomyces ochraceoalbus sp. nov. Bars: (A) = 1 cm, (B) = 1 mm (holotype).

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 μm, (B–D) = 10 μm.
Funding — The research was supported by the Yunnan Fundamental Research Project (grant no. 202001AS0700043) and the Science Research Foundation of Yunnan Provincial Department of Education Project (project no. 2021Y275).

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.2rbnzs7p1> (Luo et al. 2021).

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